Boundaries of sustainability in simple and elaborate models of agricultural pest control with a pesticide and a non-toxic refuge

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In two models of pest control using a pesticidal crop along with a non-pesticidal refuge to prevent the development of resistance, we numerically compute the bifurcations that bound the region in parameter space where control is sustainable indefinitely. An exact formula for one of the bifurcation surfaces in one of the models is also found. One model is conceptual and as simple as possible. The other is realistic and very detailed. Despite the great differences in the models, we find the same distinctive bifurcation structure. We focus on the parameters that determine: (i) the restriction of pest exchange between the crop and the refuge, which we call 'screening' the refuge, and (ii) the recessiveness of the resistance trait. The screened refuge technique is seen to work in the models up to quite high values of fitness of resistant heterozygotes, that is, even when resistance is not strongly recessive.

Keywords: sustainable; pest control; pesticide resistance; screened refuge; non-recessive resistance

AMS Subject Classification: 92D15, 92D40, 37G10

1. Introduction

Genetically engineered crop plants that produce insecticidal toxins from the bacterium Bacillus thuringiensis (Bt) [28] were introduced in 1996 and have seen significant and increasing adoption in the intervening 15 years. Tens of millions of hectares of Bt maize and cotton were planted in 2009, and future increases are expected [21]. The use of such transgenic plants has the potential to reduce the need for sprayed pesticides [14], which run off into the environment and pose dangers for farm workers [11].

However, the intense and sustained exposure of pest populations to Bt toxins resulting from the use of the transgenic plants creates strong selection pressure for resistance, and the transgenic strains could rapidly cease to be useful if deployed without care. In the USA, the Environmental Protection Agency (EPA) therefore mandates the co-planting of refuges of non-toxic plants [13,15], or the preservation of natural ones, in order to reduce the selection pressure, and
thus delay the development of resistance in the pest populations [3,17]. Combined with the very high toxin concentrations produced by commercial Bt varieties, this constitutes the so-called high-dose/refuge (HDR) technique of pest management. A ‘high’ dose is the one that is high enough to make resistance ‘functionally recessive’ [17,23], that is, to kill essentially all ‘RS’ individuals that are heterozygous for a resistance allele, R, as well as all susceptible homozygous (‘SS’) individuals. The presence of a refuge whose pest population mixes well with the population in the toxic crop reduces the effective overall toxicity (almost equally for all genotypes), which renders resistant homozygotes negligible in the short and medium term. Together, the high dose and the refuge in this way almost equalize the fitnesses of the R and S alleles so that the R fraction increases only slowly. Mathematical modelling [3,34] has indicated the HDR idea as a good one, and experiments have confirmed that it can work in delaying resistance development [29].

However, recent evidence indicates that the toxin doses achieved are not always high enough: Tabashnik et al. [34] cite observations of non-recessive resistance to Bt toxins in Helicoverpa zea. In light of this, alternatives to the current HDR technique, or modifications of it, may be required.

On the basis of a simple deterministic population genetics model, which, in this paper, we refer to as the ‘little’ model, Ringland and George [27] have suggested that physically restricting the flow of pests between the toxic crop and the refuge can restore the effectiveness of the refuge when resistance is not recessive. The model suggests, moreover, that with such ‘screening’ of the refuge, the pest can in fact be controlled indefinitely: the protection afforded by the screening allows the refuge to serve as the kind of source of susceptible individuals that has long been recognized to be able to suppress resistance development forever [2,8,9,12,16,18,22,35,36]. Bantle et al. [6] have corroborated the predictions of the little model using a much more detailed and realistic model which, in this paper, we refer to as the ‘big’ model. This model is essentially the one developed by Sisterson et al. [32] for pink bollworm (Pectinophora gossypiella) on Bt cotton.

The simplicity of the little model allowed Ringland and George [27] to obtain analytical formulas for the important equilibria in the limit of small pest exchange rates between the toxic crop and the refuge, small fitness costs of resistance in the refuge and small mutation rates. While that analysis is useful in establishing and understanding the potential of sustainable pest control with a screened refuge, it does not provide the boundaries in parameter space of the region where the technique is effective. Numerical simulations with the big model in [6] do give some indication of how effectiveness of the screened refuge technique breaks down as the restriction of pest movement is relaxed, but direct dynamical simulation is not an efficient means of locating and characterizing bifurcations. For this paper, we use numerical continuation methods [1] to compute stable and unstable equilibria and their bifurcations in the little and big models. This amounts to stepping along the equilibrium curve (in the state space plus one parameter) or the bifurcation curve (in the state space plus two parameters), using Newton’s method to obtain each new point, starting from an initial guess that is obtained by extrapolating along an approximation to the curve tangent derived either from the previous points on the curve or the null space of the augmented Jacobian at the most recently obtained point. In this way, equilibrium curves can be traced regardless of their dynamical stability, and so can bifurcation loci. We are not aware of any previous bifurcation analysis of this kind in a pest control model as complex as the big one. We also obtain an analytical formula for one of the bifurcation surfaces in the little model. We focus our attention on (i) how severely the movement of pests between the refuge and the crop needs to be restricted in order for the screened refuge technique to work, and (ii) how high the survival rate of heterozygotes can be before the technique fails.

We find the same quite distinctive bifurcation structure in the two models, despite the huge difference in the models themselves. In both cases, the boundary of effective population control is composed of two kinds of bifurcation surface. One is a saddle-node bifurcation where the equilibrium that corresponds to stable control of the population is annihilated by collision with a saddle. The other is a transcritical bifurcation associated with collapse of the population in the
refuge. It is the fortunate fact that the transcritical bifurcation occurs at zero population that allows us to obtain an exact analytical formula for the bifurcation surface in the little model. In the big model, we find that the saddle node corresponds to a critical RS fitness in the crop that is almost independent of the exchange rate, whereas the transcritical bifurcation corresponds to a critical exchange rate that is almost independent of the RS fitness. A sensitivity analysis with respect to all the other parameters of the models, along with the similarity of the two-parameter pictures in the two very different models, suggests that the features we describe are quite robust.

2. The models

Both models explored here are deterministic discrete-time population models of a pest with a single genetic locus for resistance to the toxin produced by the crop, with resistant (R) and susceptible (S) alleles. Both models represent the spatial environment as composed of two compartments: the toxic crop and the refuge. Within each compartment, complete homogenization of the pests is assumed, and exchange between the compartments is controlled. Beyond that, the models differ greatly. The little model is spelled out in Appendix 1 and is the one described in [27]. It effectively assumes one synchronized generation per year, and that year comprises just five discrete processes: random mating and reproduction, density-dependent attrition, density-independent selection, exchange between crop and refuge, and mutation. The big model is described in Appendix 2 and is identical to the deterministic version of the model of Bantle et al. [6], which is very close to the model of Sisterson et al. [32], and is in the same class as the models of Peck et al. [26], Caprio [7] and Storer et al. [33]. Following Sisterson, its many parameters are tuned to represent pink bollworm (Pectinophora gossypiella) on Bt cotton in Maricopa, Arizona. It resolves time at the level of the day, and the population is stage-structured (eggs, larvae, pupae, adults, diapaused larvae), and each stage is age-structured. It incorporates such environmental features as climate and host crop planting and development over the course of the year. A fuller description can be found in [6]. Lists of the parameters of the models, as well as the values used in the present paper, are given in Tables 1 and 2. When comparing results between the two models, the reader should bear in mind that parameters such as the RS survival rate on the toxic crop, and the exchange rates between the refuge and the crop, do not directly correspond: they are daily rates in the big model and lifetime rates in the little model.

3. Results

As mentioned above, our attention in this paper is focused on two of the parameters of the models. One is the rate of exchange of the pests between the crop and the refuge, which we quantify as the effective size of the ‘aperture’ through which pests move between crop and refuge. This is because the central idea of the screened refuge technique is restricting the pest movement. The other primary parameter is the survival rate for heterozygotes on the crop. This is because a ‘selling point’ of the screened refuge technique is that it may work even when the toxin dose is not high enough to kill most heterozygotes.

For a large range of parameter values in the little model [27], there are at least four equilibria (fixed points): namely (i) the extinction state (no pests at all in either crop or refuge), (ii) a control-failure state, with a large, mainly resistant, population in the crop, (iii) a ‘control’ state, with a small population in the crop, getting to which is the agricultural goal, and (iv) a ‘separator’ state, a saddle whose stable manifold separates the basins of attraction of the control state and the control-failure state. We know the location of (i) by definition. The precise location of (ii) is not of primary interest because it is always there and has not been observed to participate in any
Table 1. Parameters of the little model, the values used and the sensitivity of the bifurcation locations to each of them.

| Parameter description                        | Parameter name | Values in Figures | Sensitivity of $W_{RR}^{crop}$ at SN to this parameter | Sensitivity of $b/B$ at TC to this parameter |
|----------------------------------------------|----------------|------------------|-------------------------------------------------------|---------------------------------------------|
| RR survival fraction on toxic plants         | $W_{RR}^{crop}$| 0.95             | -0.03%                                                | 0.00%                                       |
| RS survival fraction on toxic plants         | $W_{RS}^{crop}$| 0.2 in Figure 1, varied in Figures 4 and 6 | N/A                                                   | 0.00%                                       |
| SS survival fraction on toxic plants         | $W_{SS}^{crop}$| 0                | +0.15% (for change to 0.01)                           | +0.03% (for change to 0.01)                 |
| RR fitness cost on refuge plants            | $1 - W_{RR}^{ref}$| 0.05             | -0.01%                                                | 0.00%                                       |
| RS fitness cost on refuge plants            | $1 - W_{RS}^{ref}$| 0.005            | -0.24%                                                | 0.00%                                       |
| SS survival fraction on refuge plants       | $W_{SS}^{ref}$| 1                | Not varied                                            | Not varied                                  |
| Pest fecundity                              | $F$            | 1.5              | -1.0%                                                 | +1.98%                                      |
| Crop area                                   | $A$            | 1                | Not varied                                            | Not varied                                  |
| Screened refuge area                        | $B$            | 0.05             | +0.29%                                                | 0.00%                                       |
| Effective aperture size crop into refuge    | $a$            | $= b$ always     | N/A                                                   | N/A                                         |
| Effective aperture size out of refuge into crop | $b$ | 0.0083 in Figure 4, varied in Figures 1 and 6 | -0.53%                                                | N/A                                         |
| Mutation rate R to S                        | $\mu_{RS}$     | $5 \times 10^{-6}$ | 0.00%                                                | 0.00%                                       |
| Mutation rate S to R                        | $\mu_{SR}$     | $5 \times 10^{-6}$ | -0.01%                                                | 0.00%                                       |
| Survivors of density-dependent juvenile attrition | $g(N)$ | $1 - e^{-N}$     | N/A                                                   | N/A                                         |

Notes: The fourth column shows the % change in the value of $W_{RS}^{crop}$ at the saddle node on the path of Figure 4 caused by a 1% change in the corresponding parameter. The fifth column shows the analogous changes in the node–transcritical location on the path of Figure 1.

bifurcations. The locations of (iii) and (iv) and their bifurcations are of the greatest interest, and we have computed them numerically. In the next two subsections, we display their dependence on the two primary parameters.

3.1. Effect of crop–refuge pest exchange rate

We believe from [27] that when the rate of exchange of pests between crop and refuge is low, a small population of largely susceptible pests in the crop can be controlled indefinitely by the influence of the refuge – at the ‘control’ equilibrium just described above. We also believe from [27] and references therein that at the other extreme, when there is complete mixing of the pests between the crop and the refuge, and resistance is not fully recessive, resistance in the population will develop rapidly. Somewhere in between these two extremes lies a transition, and here we discover and analyse the nature of that transition. In both models, we find it to be a transcritical bifurcation at zero population, as we illustrate below.

For our illustrations, the census point in the little model is just prior to reproduction. At this point, the state is characterized by four variables: the R and S allele densities in each region (crop and refuge). In the big model, the census point is the beginning of the year. At this point, the state is characterized by six variables: the numbers of overwintering larvae of each genotype in each region. In Figures 1 and 2, we plot the logarithms of these measures of the population at the control equilibrium (solid curves) and the separator equilibrium (dashed curves) as a function of the pest exchange rate in the little and big models, respectively. (The choice of the census point, or Poincaré section location, is arbitrary, and in the big model, the point of overwintering
Table 2. Parameters of the big model: names, values, sources and sensitivity of bifurcation locations to their values.

| Name                                      | Value     | Source for value | SN sensitivity | TC sensitivity |
|-------------------------------------------|-----------|------------------|----------------|----------------|
| Toxic field carrying capacity             | 10^7      |                  | +0.00%         | −0.01%         |
| Refuge carrying capacity                  | 10^5      |                  | +0.00%         | +0.01%         |
| Refuge–crop ‘aperture’ size               | Varied    |                  | −0.03%         | N/A            |
| Eggs laid per female daily                | 10        | [32]             | −0.06          | +1.9%          |
| Mutation rate per allele                  | 5 × 10^-5 | [32]             | 0.00%          | 0.00%          |

| Development times (Celsius degree days (CDD)) |
|-----------------------------------------------|
| Egg to larva                                  | 58.8      | [19,32]          | +0.03%         | −0.82%         |
| Larva to pupa and minimum for diapause        | 192.44    | [19,32]          | −0.04%         | −0.00%         |
| Pupa to adult                                 | 181.75    | [19,32]          | +0.05%         | −1.7%          |

| Diapause and emergence                        |
|-----------------------------------------------|
| Day diapausing starts                         | 240       | [32]             | +0.00%         | +0.15%         |
| Day 100% diapause                            | 307       | [32]             | +0.02%         | −0.48%         |
| Overwintering survival rate                   | 0.05      | [32]             | −0.02%         | +0.52%         |
| CDD for complete emergence                   | 1222.22   | [32]             | +0.00%         | +0.02%         |

| Toxic field daily larval survival rates       |
|-----------------------------------------------|
| RR                                           | 0.99      |                  | −0.04%         | −0.00%         |
| RS                                           | Varied    |                  | −0.02%         | −0.00%         |
| SS                                           | 0.1       |                  | +0.00%         | +0.00%         |

| Refuge field daily larval death rates (fitness costs) |
|------------------------------------------------------|
| RR                                                   | 0.005     |                  | 0.00%          | 0.00%          |
| RS                                                   | 0.001     |                  | −0.02%         | 0.00%          |
| SS                                                   | 0         | Not varied       | Not varied     |

| Predation daily survival rates                  |
|-----------------------------------------------|
| Eggs                                          | 1         | [32]             | −0.06%         | +1.9%          |
| Larvae                                        | 0.208     | [32]             | −0.06%         | +1.9%          |
| Pupae                                         | 1         | [32]             | −0.05%         | +1.4%          |
| Adults                                        | 0.9       | [32]             | −0.46%         | +8.9%          |

| Maximum life stage ages (days)                 |
|-----------------------------------------------|
| Maximum age of adults                          | 25        |                  | −0.04%         | +0.17%         |
| Maximum age of pupae                           | 20        |                  | 0              | 0              |
| Maximum age of larvae                          | 30        |                  | −0.02%         | +0.67%         |
| Maximum age of eggs                            | 10        |                  | 0              | 0              |

| Planting times in CDD                          |
|-----------------------------------------------|
| Minimum CDD for planting                      | 277.78    | [25,30,31]       | +0.04%         | −1.28%         |
| Range from first to last planting             | 166.66    | [25,30,31]       | +0.02%         | −0.64%         |
| CDD to squares beginning to form              | 500       | [25,30,31]       | −0.10%         | −3.2%          |
| CDD to squares completion                     | 345       | [32]             | +0.07%         | −1.96%         |

In the deterministic version of the model analysed here, values of the carrying capacities are only relevant relative to each other and to the exchange rates. The refuge fraction was chosen to be impressively small (1%) compared with conventional refuges. RR pests are essentially immune to the pesticide, and SS pests are extremely susceptible (90% chance of dying each day). Small fitness costs of resistance in the refuge were included and made large enough that mutation–selection balance in the non-toxic habitat corresponds to a low R-allele fraction. Maximum ages in life stages were chosen large enough that all or almost all individuals die or move on before reaching the maximum. The fourth and fifth columns are discussed in Section 3.5. The fourth column gives the change in \( W_{\text{crop}} \) at the saddle node in the vertical slice of Figure 5 caused by a 1% change in the parameter. The fifth column gives the change in \( b/B \) at the node–transcritical bifurcation in the horizontal slice of Figure 2 caused by a 1% change in the parameter. For a few parameters, a change of 1% was not appropriate: see text.

is particularly convenient because at any other point of the year 560 variables are used to specify the state. The choice does not, in any way, affect the existence of fixed points, nor the nature, or the parameter-space locations, of the computed bifurcations of the system.)

Exchange of pests is viewed as occurring through some apertures in a physical barrier, or screen, that impedes pest movement between the crop and the refuge. The effective aperture size for movement from the crop to the refuge, \( a \), is taken to be the same as that for movement from the refuge to the crop, \( b \). In Figures 1 and 2, the exchange rate is expressed in relation to the size of the refuge, \( B \), that is, as \( b/B \). The quotient \( b/B \) can be interpreted as the fraction of (adult)
Figure 1. Little model: numerically computed ‘control’ fixed point (solid curves) and ‘separator’ fixed point (dashed curves) as a function of rate of exchange of pests between refuge and toxic crop. As the exchange rate is increased through values corresponding to about 33% of the refuge population leaving, the two fixed points plunge to zero population in rapid succession, each in a transcritical bifurcation: (a) the whole picture, (b) expanded view of the transcritical bifurcations. ($B$ is held fixed in this scan.)

Figure 2. As Figure 1, but in the big model. As in the little model, the fixed points plunge to zero population in transcritical bifurcations as the exchange rate pass through critical values. (a) The whole picture and (b) expanded view of the transcritical bifurcations. The populations sizes are the numbers of overwintering larvae at the beginning of the year (which are substantially lower than the carrying capacities of the crop ($A$) and of the refuge ($B$) which pertain to emerged larvae feeding on the plants).
pests in the refuge that move from the refuge to the crop: in their lifetime in the little model, and daily in the big model.

In accord with the asymptotic results obtained in [27], we see in Figures 1 and 2 that as the pest exchange is shut off \((b/B \to 0)\), the equilibrium pest densities in the crop, in both the control state (solid curves) and the separator state (dashed curves), go to 0. This means that the control state becomes increasingly precarious as the exchange rate is reduced to 0.

At the other end of the exchange rate scale, we see that the control and separator state populations, in the refuge as well as in the crop, plunge to zero as a critical value of \(b/B\) is approached: around 33% (generationally) in the little model and about 10% (daily) in the big model, for the parameters chosen. Parts (b) of Figures 1 and 2 show expanded views of the bifurcation region, and we find that in a very narrow range of the exchange rate parameter, first the separator (saddle) state and then the control (stable node) state intersect transversally with the extinction state. We have plotted the populations logarithmically so that disparate quantities can be seen simultaneously. Above the second transcritical bifurcation, both the separator state and the control state lie outside the biologically meaningful region of non-negative population densities (not plotted). For such high values of the exchange rate, numerical simulations suggest that the control-failure state attracts all trajectories except the extinction state itself: the refuge population collapses, allowing the development of resistance and population explosion in the crop.

The similarity between Figures 1 and 2 is striking and appears to validate the simplifications that lead to the little model.

The state-space scenario as the exchange rate is increased is illustrated schematically in Figure 3. For sufficiently small exchange rates (Figure 3(a)), the control state (\(\star\) in Figure 3, solid curves in Figures 1 and 2) is present and its basin of attraction (shaded) is bounded by the stable manifold of the separator state (saddle \(\bullet\) in Figure 3, dashed curves in Figures 1 and 2). At the first transcritical bifurcation, the saddle passes through the extinction state (\(\bullet\)), disappearing from the biologically meaningful region of non-negative populations. In this collision, the stable manifold of the extinction state gains a dimension, and then bounds the basin of the control state (Figure 3(b)). After another very small increase in the exchange rate, the control state itself collides with the extinction state in the second transcritical bifurcation and disappears from the region of non-negative populations, leaving only the unstable extinction state and the control-failure state (\(\blacksquare\) in Figure 3, not shown in Figures 1 and 2) which is then almost globally attracting (Figure 3(c)).

### 3.2. Effect of resilience of the heterozygotes

Intuitively, we expect resistance development to be unpreventable if the heterozygote (RS) pests, as well as the resistant homozygotes (RR), are sufficiently fit in the toxic crop, that is, for sufficiently

![Figure 3](image-url)
Figure 4. Little model: the control and separator equilibria annihilate each other as the survival rate for RS pests in the crop is raised to high values.

Figure 5. Big model: the control and separator equilibria annihilate each other as resistance approaches dominance. The vertical axes are the logs of the absolute population sizes. Here, the refuge is 1/100 the size of the crop, so to compare population densities subtract two orders of magnitude from the crop values.

high values of the survival fraction $W_{RS}^{crop}$. In this section, we show how the control state is lost by colliding with its protective separator state as $W_{RS}^{crop}$ is increased. Again, the two models agree qualitatively, as illustrated in Figures 4 and 5.
From Figure 4, we see that in the little model, there is not much movement of the control state as $W_{\text{crop}}^{\text{RS}}$ is increased. It is primarily the separator state that moves and eventually collides with the control state. Since the separation of the separator and the control state determines the robustness of the control state, we can say that the main effect of increasing $W_{\text{crop}}^{\text{RS}}$ is to make the control state progressively more fragile – in the sense that control of the pest is increasingly susceptible to perturbations, or less able to occur for initial conditions with substantially large populations or substantially resistant ones. Finally, it is lost entirely. For the parameter values illustrated in Figures 4 and 5, the annihilation occurs at $W_{\text{crop}}^{\text{RS}} \approx 0.5$ in the little model, and at $W_{\text{crop}}^{\text{RS}} \approx 0.976$ in the big model. Recalling that these are lifetime and daily values, respectively, the 0.976 value is not quite as high relative to the 0.5 as it might at first seem. If a typical larva lives 7 days before pupating, then roughly speaking $W_{\text{crop}}^{\text{RS}} \approx 0.976$ in the big model would correspond to $W_{\text{crop}}^{\text{RS}} \approx 0.976 \times 7 \approx 0.84$ to get to the pupal stage. For values of $W_{\text{crop}}^{\text{RS}}$ above the bifurcation, numerical simulation suggests the control-failure state attracts all trajectories starting with non-zero population.

### 3.3. The two-parameter picture

The previous two subsections showed the fixed points on a pair of one-parameter paths. In this section, we show the picture in the parameter plane that contains those two paths.

In both the little and big models, we find that the critical value of the crop–refuge pest exchange rate is essentially independent of the fitness of the heterozygotes in the crop, as reflected in the transcritical loci appearing as straight vertical line segments in Figures 6 and 7. An explanation of this is given in the next subsection, where we find an analytical formula for the parameter dependencies of the node–transcritical locus.

Turning to the saddle-node locus, we find that in the little model, the maximum heterozygote fitness for which the control state exists decreases significantly as the exchange rate is increased. We do not currently have an explanation for this, and indeed the effect is much less pronounced in the big model – the saddle-node locus is almost horizontal in Figure 7. (To draw a true quantitative

![Figure 6](image_url)

Figure 6. Two-parameter diagram for the little model. The two transcritical curves are extremely close to each other and are not resolved in this figure (Figure 1(b)). In the unshaded region, the pest population in the crop is controlled at a low level indefinitely. In the shaded region, the population in the crop develops resistance and explodes.
Figure 7. Two-parameter diagram for the big model. The shaded region is where resistance develops in the pest population and pest control fails. (a) The whole picture and (b) expanded view of the transcritical loci.

Comparison between Figures 6 and 7, we should raise the value of $W^{\text{crop}}_{RS}$ in the big model to a power – perhaps 7 or so – that corresponds to the duration in days of the larval stage. This will make the saddle-node locus slant significantly more, but still not enough to match Figure 6.

In both the models, the pictures suggest that there are two essentially independent conditions for successful control of the pest population: the saddle-node and transcritical loci come together almost at a sharp corner – at a singularity where three fixed points (extinction, control and separator) are coincident.

3.4. Analytical formula for the critical pest exchange rate

Finding an exact formula for a fixed-point bifurcation locus in a model as complicated as even the little model of this paper is usually impossible. But the fact that the transcritical bifurcations in this model occur at zero population is a great simplification that prompts us to look for formulas in this case. On the other hand, there are difficulties, because the dynamical map is not differentiable at the origin. It can be seen, for example, that the second component of the dynamical map, namely

$$
\text{typ}_{RS} \left( \begin{bmatrix} N_R \\ N_S \end{bmatrix} \right) = \frac{2N_R N_S}{(N_R + N_S)},
$$

(continuously extended to $N_R = N_S = 0$) is clearly not differentiable at $N_R = N_S = 0$. Nevertheless, the Jacobian matrix of partial derivatives of the dynamical map is defined at $N_R^{\text{crop}} = N_S^{\text{crop}} = N_R^{\text{ref}} = N_S^{\text{ref}} = 0$, and it is tempting to see if there is a signature of the transcritical bifurcations in its eigenvalues. The condition that the Jacobian matrix at zero population has a unit eigenvalue turns out to be quadratic in the aperture size, $b$, and so can be solved in the general case, though the solutions take up many pages, and we do not present them here. We find the following:

(i) The extremely precise coincidence of the higher $b$ solution of the (quadratic) eigenvalue-1 condition with the numerically computed value where the stable node (the control state) transversally passes through the origin leads us to make the following:

Conjecture 1: The higher $b$ solution of the eigenvalue-1 condition corresponds to a transcritical bifurcation involving a stable node and the extinction state.

The coincidence is so precise that we proceed in this paper assuming the conjecture is true, though eventually we would wish to supply a proof.
(ii) The lower of these roots does *not* correspond to any bifurcation we have observed numerically. It is possible that there is a third transcritical bifurcation involving another unstable fixed-point branch that we have not detected by dynamical iteration or fixed-point continuation.

(iii) There is no signature in the eigenvalues of the Jacobian of the numerically observed saddle–transcritical bifurcation. This is not completely perplexing, because the two first-order partial derivatives of Equation (1) certainly do not capture its local behaviour. Consider, in particular, that the directional derivatives along $[\frac{1}{0}]$ and $[\frac{0}{1}]$ are both 0, while the derivative along $[\frac{1}{1}]$ is 1. Fortunately, it is the node–transcritical bifurcation – the one the Jacobians eigenvalues *do* register according to Conjecture 1 – that is the boundary of existence of the stable fixed point we are interested in.

If Conjecture 1 is true, it allows quite a lot to be said about the location of the bifurcation. The verticality of the transcritical locus in Figure 7, for example, is explained by the fact that the Jacobian at the origin, and hence the eigenvalue condition, do not involve $W_{RS}$ at all. In order to be more specific, it is helpful to consider a special case and make some approximation, because as we have said, the formula for the bifurcation locus in the general case is enormous. If we ignore mutation (i.e. set the mutation rates, typically $\sim 10^{-6}$, to zero), and set the effective aperture sizes to be the same for crop-to-refuge movement as for refuge-to-crop, i.e. $a = b$), the two solutions of the eigenvalue condition are relatively very simple (the discriminant of the quadratic is a square):

$$
\left(\frac{b}{B}\right)_{\text{crit}} = \begin{cases} 
\frac{A(F_W^{\text{crop}} - 1)(F_W^{\text{ref}} - 1)}{F[A W_{\text{ref}}^{\text{crop}}(F_W^{\text{crop}} - 1) + F W_{\text{ref}}^{\text{ref}}(F_W^{\text{ref}} - 1)]}, & \text{(i)} \\
\frac{A(F_W^{\text{crop}} - 1)(F_W^{\text{ref}} - 1)}{F[A W_{\text{SS}}^{\text{SS}}(F_W^{\text{crop}} - 1) + B W_{\text{SS}}^{\text{SS}}(F_W^{\text{ref}} - 1)]}, & \text{(ii)}
\end{cases}
$$

with our interest focusing on (ii) which is the larger one, for the reasons given above. With $W_{SS}^{\text{ref}} = 1$, and considering the ideal case of complete mortality of homozygous susceptibles in the crop, that is, $W_{SS}^{\text{crop}} = 0$, Equation (2) (ii) simplifies even further to

$$
\left(\frac{b}{B}\right)_{\text{crit}} = \frac{F - 1}{F}.
$$

We observe that this is the value of the exchange rate where migration out of the refuge exactly balances the reproductive growth in the refuge (when the population is small so that there is negligible density-dependent attrition), that is, $\#\text{offspring} - \#\text{emigrating offspring} = \#\text{parents}$:

$$
FN - \frac{b}{B}FN = N,
$$

with $N$ denoting the population density. For pest exchange rates $b/B$ lower than $(b/B)_{\text{crit}}$, the refuge population can grow, while for higher exchange rates, it will collapse. Equation (3), which ignores mutation, still provides an excellent approximation of the bifurcation location in Figure 1:

$$
\frac{F - 1}{F} = \frac{1.5 - 1}{1.5} = \frac{1}{3} = 0.333333\ldots
$$

(see part (b) of the figure).

We note that if moderate restriction of pest flow is easier and cheaper to accomplish than severe restriction, then Equation (3) means a pest population that can grow rapidly ($F$ large) is easier to control than a slower reproducing one, in that a larger pest flow between the crop and the refuge can be tolerated.
3.5. Sensitivity to other parameters

The two rightmost columns of Tables 1 and 2 show the sensitivity of the saddle-node and transcritical bifurcation loci to all the other parameters of the models. Specifically, we give the percentage change in the values of RS fitness in the crop at the saddle node and aperture size at the transcritical bifurcations resulting from a 1% change in the parameter in the respective rows of the tables. For a few of the parameters of the big model, an exact 1% change either was not possible (e.g., the integer-valued day when diapausing starts) or was insufficient to cause any change at all (because the parameter determines whether something either does or does not happen on a certain day). In these cases, we chose some other small change and scaled the response appropriately.

In the little model, no strong sensitivities are found. The largest changes come from varying the pest fecundity: a 1% increase in fecundity resulted in a 1% reduction in the maximum tolerable value of $W_{RS}^{crop}$, and a 1.98% increase in the maximum tolerable crop–refuge exchange rate. A 1.98% change is precisely what is predicted in this case by Equation (3).

In the big model, there are no extreme sensitivities either, except seemingly for the 8.9% shift in the transcritical bifurcation for a 1% change in the adult predation survival rate. But recalling that 0.9 is the daily survival rate, summing the corresponding geometric series predicts a 9% change in average adult days alive (and laying eggs). Thus, the 8.9% change in the bifurcation location in the table is not an extreme change either.

4. Discussion

The sensitivity analysis of Section 3.5 leads us to believe that the two-parameter bifurcation structure described in Section 3 is a locally robust feature of each of the models. The great similarity of the structures in the greatly differing little and big models – which, respectively, are among the simplest and the most elaborate of models in the literature on this topic – suggests that the structure is generic among models of the refuge technique of pest control, and perhaps for actual agricultural implementations of the technique. This suggestion is strengthened by the fact that we did not make any effort to harmonize the parameter values used in the two models. For example, the reproductive growth rate was 1.5 in the little model and about 7 in the big model, and the refuge size was 5% of the crop size in the little model and 1% of the crop size in the big model.

If the idea is supported by further analysis, some of the agronomic practices cited elsewhere as necessary or beneficial, for example, in [10], namely the use of larger refuges and the manipulation of Bt cultivars to reduce heterozygotes fitness, may not actually be needed. Our results appear to suggest that conventional open refuges are wasteful and that they have to be made large primarily to prevent collapse of the susceptible pest population. With an appropriate amount of screening (Equation (3)), which prevents the refuge population from decimating itself on the toxic crop, much smaller refuges (1% of crop size, and perhaps even smaller) should work as well if not better than larger open refuges. Screened refuges could therefore provide a significant increase in crop yield compared with current practices (the 15–20% mandated by the US EPA). Secondly, we have shown how a screened refuge can work even when resistance is not recessive.

Our modelling of the actual movement of pests between refuge and crop seems reasonable for a first effort, but leaves room for improvement. We have treated pest movement like the flow of an ideal gas between two containers. This is conventional but ignores pest interaction (e.g., via sight and pheromones), which may be particularly important in contexts such as the one we describe where large density differences exist locally, and we would like to do better. Mathematically, tasks remaining to be done include: a rigorous analysis of the transcritical bifurcations in the little model. In particular, we would like to obtain a proof of Conjecture 1, a characterization of
the saddle–transcritical bifurcation and a normal form for the codimension-2 coincidence of the saddle-node and transcritical loci.

Screened refuges would undoubtedly be more difficult to implement in practice than in conventional open ones. Nevertheless, we believe the results on their potential benefits presented here, along with those in [6,27], demonstrate that the idea has merits that make it worth further investigation.

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Appendix 1. The ‘little’ model

For the reader’s convenience, we specify here the ‘little’ model analysed in this paper. It is the one developed in [27], where additional details and background can be found.

We denote the resistant (R) and susceptible (S) allele densities by \( N_R \) and \( N_S \), respectively. The average number of offspring per individual is \( F \). For random mating, this simply scales the allele densities in each region by \( F \):

\[
\text{rep} \left( \begin{bmatrix} N_R \\ N_S \end{bmatrix} \right) = \begin{bmatrix} FN_R \\ FN_S \end{bmatrix}.
\]

Population size is limited by a density-dependent process \( att \), viewed as occurring at early juvenile stages, which is genotype-neutral, that is, the densities of all genotypes change by the same proportion and the change depends only on the total number of individuals:

\[
\text{att} \left( \begin{bmatrix} N_R \\ N_S \end{bmatrix} \right) = \frac{g(N_R + N_S)}{N_R + N_S} \begin{bmatrix} N_R \\ N_S \end{bmatrix}
\]

and \( \text{att}([0, 0]^T) = [0, 0]^T \), with \( g(N) = 1 - \exp(-N) \) [24].

Genotype densities are obtained from the allele densities using the Hardy–Weinberg formulas for random mating [20]:

\[
\begin{bmatrix}
N_{RR} \\
N_{RS} \\
N_{SS}
\end{bmatrix} = \text{typ} \left( \begin{bmatrix} N_R \\ N_S \end{bmatrix} \right) = \begin{bmatrix}
\frac{N_R^2}{N_R + N_S} \\
\frac{2N_R N_S}{N_R + N_S} \\
\frac{N_S^2}{N_R + N_S}
\end{bmatrix},
\]

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and then the survival rates specific to each genotype and region are applied,

$$\text{sel}_{\text{crop}} \left( \begin{bmatrix} N_{RR} \\ N_{RS} \\ N_{SS} \end{bmatrix} \right) = \left[ \begin{bmatrix} W_{RR}^{\text{crop}} \\ W_{RS}^{\text{crop}} \\ W_{SS}^{\text{crop}} \end{bmatrix} \right], \quad \text{sel}_{\text{ref}} \left( \begin{bmatrix} N_{RR} \\ N_{RS} \\ N_{SS} \end{bmatrix} \right) = \left[ \begin{bmatrix} W_{RR}^{\text{ref}} \\ W_{RS}^{\text{ref}} \\ W_{SS}^{\text{ref}} \end{bmatrix} \right].$$  (A4)

At this point, the allele densities are

$$\begin{bmatrix} N_R \\ N_S \end{bmatrix} = \text{all} \left( \begin{bmatrix} N_{RR} \\ N_{RS} \\ N_{SS} \end{bmatrix} \right) \equiv \begin{bmatrix} N_{RR} + \frac{1}{2} N_{RS} \\ N_{SS} + \frac{1}{2} N_{RS} \end{bmatrix}.$$  (A5)

In Figure A1, the last three steps are represented by the compositions, $\text{poi}_{\text{crop}}$ and $\text{poi}_{\text{ref}}$:

$$\text{poi}_{\text{crop,ref}} \left( \begin{bmatrix} N_R \\ N_S \end{bmatrix} \right) \equiv \text{all} \circ \text{sel}_{\text{crop,ref}} \circ \text{typ} \circ \left( \begin{bmatrix} N_R \\ N_S \end{bmatrix} \right).$$  (A6)

Next, mutation is applied using

$$\text{mut} \left( \begin{bmatrix} N_R \\ N_S \end{bmatrix} \right) = \left[ \begin{array}{cc} 1 - \mu_{RS} & \mu_{SR} \\ \mu_{RS} & 1 - \mu_{SR} \end{array} \right] \begin{bmatrix} N_R \\ N_S \end{bmatrix},$$  (A7)

where $\mu_{RS}$ and $\mu_{SR}$ are the mutation rates from R to S and from S to R, respectively.

Finally, exchange of adults between the crop and the refuge is accounted for. As specified in Table 1, $a$ and $b$ are the effective outgoing ‘aperture’ sizes for crop and refuge, respectively, and $A$ and $B$ are the sizes of the crop and refuge regions themselves, respectively. Recalling that the $N$’s are densities, the exchange map is

$$\text{Exc} \left( \begin{bmatrix} N_R^{\text{crop}} \\ N_S^{\text{crop}} \\ N_R^{\text{ref}} \\ N_S^{\text{ref}} \end{bmatrix} \right) = \left[ \begin{array}{cccc} 1 - a/A & 0 & b/A & 0 \\ 0 & 1 - a/A & 0 & b/A \\ a/B & 0 & 1 - b/B & 0 \\ 0 & a/B & 0 & 1 - b/B \end{array} \right] \begin{bmatrix} N_R^{\text{crop}} \\ N_S^{\text{crop}} \\ N_R^{\text{ref}} \\ N_S^{\text{ref}} \end{bmatrix}. \quad (A8)$$

The allele densities after one full generation are thus given by the following composition of the maps described above:

$$\text{Dyn} \left( \begin{bmatrix} N_R^{\text{crop}} \\ N_S^{\text{crop}} \\ N_R^{\text{ref}} \\ N_S^{\text{ref}} \end{bmatrix} \right) = \text{Exc} \circ \text{mut} \circ \text{all} \circ \text{sel}_{\text{crop}} \circ \text{typ} \circ \text{att} \circ \text{rep} \left( \begin{bmatrix} N_R^{\text{crop}} \\ N_S^{\text{crop}} \\ N_R^{\text{ref}} \\ N_S^{\text{ref}} \end{bmatrix} \right). \quad (A9)$$

**Appendix 2. The ‘big’ model**

We give a brief specification of the model below, and refer the reader to [32] for further explanation and details. The model has many parameters, making it adaptable to many pests, crops and climates, but for this study we have used values that
are specific to pink bollworm (Pectinophora gossypiella) on Bt cotton in Maricopa, Arizona. These values are given in Table 1, along with the literature sources for the choices. The model of [32] is stochastic, but we have coded ours in such a way that it can be switched between stochastic and deterministic modes by swapping a small header file and recompiling. In the stochastic mode, the population sizes are integer-valued, and processes are random; for example, the number of a certain type surviving a daily attrition process is a binomially distributed pseudo-random number. In the deterministic mode, the population sizes are real-valued (double precision floating point), and in the analogous attrition process, the number of survivors is obtained simply by multiplying by the survival probability. For the results of the present paper, the model was used in the deterministic mode only.

The dynamical state at the beginning of a day is characterized by the current numbers of pests of each sex of each genotype of each age-class (days) in each life stage (eggs, larvae, pupae, adults, diapaused larvae) in each of the two spatial regions (toxic crop and refuge), as well as the number of heat units that have been accumulated by those of each age, and the number of host plant locations available. For the numbers of classes we have used (Table 1), this corresponds to about 560 numbers to represent the instantaneous state. The corresponding numbers at the beginning of the next day are obtained by (i) advancing each group into the next age-class or moving them into the youngest age-class of the next life stage if sufficient heat units have been accumulated (or, in the case of larvae late in the year, moving some of them into the diapaused state), (ii) removing larvae according to the unavailability of host plants (cotton ‘squares’), the genotype-specific poisoning rate for the region they are in (the same rate for all age-classes) and according to a density-dependent attrition process discussed below, (iii) removing some from all classes, independent of genotype, age or density, as a representation of predation and other fatal processes, (iv) moving some adults between the two spatial regions, (v) mating the newly emerged female adults with available males and (vi) adding the day’s heat units to the heat units accumulated by each age-class. Individuals that leave the oldest age-class without accumulating sufficient heat units to move to the next life stage are assumed to have died. For adults, the only next ‘life stage’ is death. By the end of the year, all pests except diapaused larvae have died, and so at the beginning of 1 January, the dynamical state is characterized by just six numbers – the numbers overwintering of each sex of each genotype. Overwintering survival rate is another parameter.

Historical temperature data were used, and heat units were calculated using the single-sine method with lower and upper thresholds of 12.8°C and 30.0°C [5]. Emergence of overwintering larvae was based on data extracted from weekly Cotton Development Advisories [4]. For the diapausing fraction as a function of day of the year, the work of Sisterson et al. [32] was followed.

In this way, our model follows [32] closely, but it does differ in several respects. (i) Population regulation in our version is not achieved by simulated spraying in the refuge when the population there hits a threshold, but rather by an assumed intrinsic density dependence in which the expected number of survivors from \( n \) competitors is \( k (1 - \exp(-n/k)) \), where \( k \) is a carrying capacity. Thus, almost all survive when \( n \ll k \), and the expected number of survivors increases monotonically with the number of competitors, with a ceiling of \( k \). We have assumed that a monotonic mechanism can be realized because a non-monotonic process such as threshold-triggered spraying can cause oscillatory and possibly chaotic dynamics that is not conducive to our goal, which is predictable control of the pest population. (ii) Springtime emergence of overwintering diapaused larvae [37–40] is based on a tanh curve fit to data in AZMET weekly Cotton Development Advisories [4]. (iii) The values for a few of the parameters are somewhat different based on other literature that is cited in Table 1. (iv) For the present study, spatial resolution is limited to the two spatial compartments representing the toxic crop and the refuge. Panmixia is assumed within each of these compartments separately. The rate of adult pest exchange between the two spatial compartments is one of two primary parameters for this paper. Other differences from [32] pertain only to the stochastic version of the model and are therefore not relevant to the present paper. The source code may be obtained from the authors by request.