# 4a

## Biological limits on agricultural intensification: an example from resistance management[1]

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### Abstract

Agricultural intensification could reduce pressures on natural habitats, but biological constraints may mitigate the long-term benefits of improved agricultural technologies. We consider one such constraint: that imposed by resistance to pesticides. The application of pesticides places selective evolutionary pressure on pest populations. Those organisms that survive show resistance. Resistance can be managed by planting 'refuge areas' in which susceptible pests breed. We use a simple model to characterize the optimal refuge strategy when a social planner values both agricultural output and natural habitat. We also examine land use consequences. The amount of land devoted to agriculture is an increasing function of the discount rate. A related finding is that more land would be devoted to agriculture when pest resistance must be managed than would be with a hypothetical 'neutral' technology affording the same yield-per-hectare as in the steady state, but not requiring the management of any biological stocks.

**Keywords:** pest resistance; biotechnology; land use; pesticides; sustainability; optimization

### Introduction

Progress in agricultural technology has resulted in spectacular increases in yields over the last century. Yields of some major food crops in the US have tripled (USDA 1936; 1998), while in many developing countries, the 'green revolution' has transformed agriculture through the use of inputs such as pesticides, herbicides, fertilizers and hybrid seeds. Biotechnology now represents the cutting edge of efforts to increase agricultural yields even more.

Agricultural intensification may be the only way of mitigating the threat posed by the increasing food needs of growing and more prosperous human populations to the natural habitats on which much of the world's biological diversity depends. Many authors have argued that growing more food on the same area of land can reduce the pressure on natural habitats (Southgate 1997; Pagiola et al. 1998; Leisinger 1999). However, others have pointed out that while the intensification of agriculture may increase short-term yields, long-term prospects may be compromised by the absence of sustainable management practices (Perrings and Walker 1995; Pimentel et al. 1995; Krautkraemer 1994; Naylor and Ehrlich 1997; Albers and Goldbach 2000). New agricultural technologies may deplete soils, poison surrounding areas and organisms, or, as in the case we investigate here, induce genetic resistance among pests.

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Sustainable long-term outcomes can only be achieved if deterioration and regeneration are balanced.

It is not always easy to predict how that balance will be struck, however. In this paper we construct a model of land use choice when pest resistance to pesticides must be managed. The application of any pesticide will exert evolutionary pressure in favor of organisms resistant to its toxin. An effective pesticide is one that kills the great majority of the pests it targets. In almost any large population, though, some organisms will be blessed with a fortuitous combination of genetic attributes that enable them to survive the effect of pesticides. Subsequent reproduction will then result in a greater frequency of genetically resistant pests and, consequently, reduced effectiveness of the pesticide.

In this paper we consider one option for managing resistance, the maintenance of 'refuge areas'. A refuge area is a portion of agricultural land planted with the same crop the pests attack, but not treated with a pesticide. Refuge areas promote the reproduction of pests that remain susceptible to the pesticide to which others evolve resistance. Susceptible and resistant pests interbreed, and the proportion of the latter in the population is limited.

The details of the model we develop are laid out below, but briefly, we consider a situation in which a social planner cares about two things: the production of food and the preservation of natural habitat. We abstract from other components of social welfare as well as from many real-world aspects of agricultural production. We suppose that land is the *only* costly input employed in growing a single crop[2]. We also suppose – again somewhat unrealistically, but in the interest of presenting clear results – that the conversion of land from natural habitat to agricultural use and back is costless.

Three interesting insights emerge from our simple model. The first is simply that we can compare and contrast our results with those arising from models that describe the management of other renewable resources over time, such as models of fisheries. We find in our model that maintaining 'maximum sustainable resistance' analogous to 'maximum sustainable yield' in fisheries models is typically not optimal. We also find that it can be optimal to 'exhaust' pesticide effectiveness when discount rates are high enough, a result that is also analogous to findings in the fisheries literature (Clark 1990).

The second insight concerns the allocation of land. We find that higher discount rates result in less environmentally friendly outcomes: more land is devoted to agriculture, at the expense of habitat retained for biodiversity. However, the underlying explanation is different here from that in other biological resource models. In models of fisheries, higher discount rates imply that the stock of fish – the biological resource of interest in that context – is deemed less valuable, and thus lower stocks will be maintained. Higher discount rates also motivate less conservation in our model, but in our context habitat supporting biological diversity is an argument of the period-by-period objective function (the model is similar to Hartman (1976), in this respect).

The final insight concerns a comparison between steady state with resistance management and a hypothetical alternative. In the steady state of the model, yield per hectare planted is, of course, invariant. We might regard the combination of pesticide use and resistance management as an agricultural 'technology' that affords a certain yield per hectare. In steady state, *more* land would be devoted to agriculture using this 'technology' than would be under a hypothetical one that afforded the same yield per hectare but did not involve the management of any biological stock.

This may seem counterintuitive. One consequence of devoting more land to agriculture is that a larger population of pests will be supported. The hypothetical alternative abstracts from such concerns. It might seem, then, that agricultural land use would be lower when there is a shadow price attached to its long-term biological consequences. Here, the biological conditions are crucial. If the pest-management regime is effective, the pest population is constrained by the efficacy of the pesticide rather than the availability of the crop on which it feeds. Surviving pests can be satiated in the short term. The hypothetical technology affords the same constant yield-per-hectare as in the steady-state of the pest-management regime. In the latter, however, the short-term marginal product of agricultural land is greater than the long-term average product. For the functional forms we have employed, at least, this 'marginal product' effect dominates the 'shadow price' effect, leading to our result.

The result is subtle, so we should clarify what we are *not* saying. The model is, by construction, one in which social welfare is maximized. Thus, we are not saying that an externality generates sub-optimal performance. We are also not saying that the improvements afforded by the intelligent combination of technology and resistance management are a bad thing. The point is simply that enthusiasm for these improvements should be tempered. Biotechnological improvements could improve welfare and may well be land-saving. However, the amount of land saved may be less than one might initially suppose.

In the section that follows we discuss resistance-management strategies in somewhat more detail. We introduce our model in the third section. We derive its steady state and summarize its implications in the fourth section. The fifth section summarizes and concludes.

## Resistance management

We have chosen resistance management as a particularly interesting instance of a biological constraint on productivity, but have abstracted from a number of real-world considerations in order to achieve tractable results. In short, our intention is more illustrative than descriptive. Having offered that caveat, however, it may be useful to describe in somewhat more detail the principles underlying resistance management, mention some of the different ways it may be accomplished, and discuss some policy developments.

Resistance can be managed by maintaining refuge areas. It may seem strange to set aside an area of crops for the express purpose of feeding the pests one is trying to eliminate. The argument for doing so is that a population of 'susceptible' organisms from the refuge areas will interbreed with organisms that are genetically resistant to the pesticide. Resistance is often a recessive genetic trait, meaning that it will only occur in the offspring of parents that are both resistant[3]. Refuges assure that the proportion of resistant individuals in the population will remain small, and thus that it will be unlikely that two resistant individuals will mate.

A crucial consideration is that resistance typically comes with an evolutionary 'fitness cost' (Anderson and May 1991). In the absence of the pesticide, mortality is higher, or reproductive success lower, among resistant than among susceptible pest organisms. There are numerous examples of the reduced fitness of resistant strains to natural or synthetic insecticides (Ferrari and Georghiou 1981; Georghiou 1981; Beeman and Nanis 1986; Groeters et al. 1993; Alyokhin and Ferro 1999). Thus refuge areas may renew a population's susceptibility to pesticides.

Earlier studies have considered the economics of resistance management. Hueth and Regev (1974) consider the timing of pesticide applications during the growing season and its effect on resistance (see also Regev, Shalit and Gutierrez 1983). Laxminarayan and Brown (2001) and Goeschl and Swanson (2000) consider analogous issues in the management of antibiotic resistance.

Recent developments in biotechnology have spurred a renewed interest in resistance management. A gene from the bacterium *Bacillus thuringiensis* (frequently abbreviated as *Bt*) has been inserted in crops such as cotton, tobacco and corn. This gene codes for the production of a protein that is highly toxic to many insect pests. In 1990, no genetically modified organisms (GMOs) were under commercial cultivation in the United States. By 1999, nearly 100 million acres – close to a third of all land under cultivation in the US – were planted with GMOs.

In Canada, the regulation of *Bt* corn and *Bt* potato is carried out under the Seeds Act and Part V of the Seeds Regulations administered by the Canadian Food Inspection Agency (CFIA). As of 1998, the CFIA has mandated an industry-wide standard for pest-resistance management that requires growers to plant a minimum of 20% non-*Bt* corn not sprayed with insecticides on their planted acreage each year. These regulations also require that non-*Bt* corn be planted within ¼ mile of the farthest *Bt* corn in a field to provide a refuge where *Bt*-susceptible pests may exist[4]. Similar resistance-management plans have been mandated for *Bt* potato as well. Several economic analyses have now been conducted of these refuge policies (Hurley, Babcock and Hellmich 1997; Hyde et al. 1999; Livingston, Carlson and Fackler 2000).

Refuge areas are not the only option for resistance management. Pesticide applications can be timed in such a way as to allow susceptible individuals to interbreed with resistant ones (Hueth and Regev 1974; Regev, Shalit and Gutierrez 1983). Chemical and/or crop rotation may accomplish similar ends. The intensity of pesticide use may also influence the development of resistance. Invention of new pesticides may also be an option.

There are reasons for which refuge areas may be the preferred option, however. With advances in biotechnology, pesticides are increasingly bred *into* as opposed to applied *onto* crop plants, obviating timing and, to some extent, dosage and rotation, as management strategies. It may not be reasonable to suppose that better pesticides can always be developed. Pests that have developed resistance to existing pesticides may display ‘cross-resistance’ to newly developed toxins.

The effects of refuges may be analogous to other resistance-management options. Refuges call for sacrificing some portion of current production in order to maintain long-term productivity. Rotations among crops or using lower pesticide dosages also represent strategies for achieving a similar trade-off. Thus our results may well constitute an allegory for similar findings in somewhat broader contexts.

## The model

We develop a simple model of the evolution of pest resistance. The setting is a large area in which a single crop is planted. The pest population is assumed to be local; both in-migration and out-migration are ruled out. Other conditions implicit in deriving the Hardy–Weinberg principle, such as random mating between resistant and susceptible pests, negligible mutation, non-overlapping pest generations and sexual reproduction of pests, are all assumed to hold[5]. These assumptions imply a high degree of mobility among pests. Each surviving organism is assumed to be equally likely to mate with every surviving organism of the opposite sex[6].

The pest population is denoted by $D$. The proportion of susceptible pests in the population is denoted by a fraction *w*. Susceptible pests are those that have not developed resistance to the toxin. Put in another way, *w* may be thought of as the stock of effectiveness of the pesticide; it is the proportion of the pest population to which the toxin is lethal.

The pest population is assumed to grow logistically with an intrinsic growth rate of *g* and a carrying capacity of *K* per unit of land planted in the crop. Total land is assumed to be fixed and is normalized to 1. The fraction of total available land area devoted to agriculture is denoted by *Q*. The total number of new pest organisms hatched (presuming they are the offspring of egg-bearing insects) in every period, then, is $gD(1 - D/KQ)$. From this gross increase, we must subtract mortality among both susceptible and non-susceptible pests.

A refuge strategy calls for planting a fraction *q* of the total land devoted to agriculture, *Q*, in a crop to which pesticide is applied (or in the case of GMOs, implanted). Hence, a fraction $1 - q$ of agricultural land is not treated with pesticide. Recall that a fraction *w* of all pests is susceptible. We suppose that all susceptible pests that feed on crops treated with pesticide die after exposure to the toxin. A fraction *r* of non-susceptible pests die, regardless of whether they are exposed to the pesticide[7]. The analysis can be extended to suppose that some susceptible pests survive exposure to the pesticide, but no significant generality is gained as a result.

We assume that pests distribute themselves evenly over the area planted with crops. A fraction *q* of the pest population *D* will feed on the area treated with pesticide. Of these, the fraction *w* that are susceptible will die. A fraction *r* of the fraction $1 - w$ of resistant pests will also die. Note that *r* may be interpreted as the 'excess mortality' among resistant pests relative to susceptible pests, with the 'baseline' mortality of susceptible pests in the absence of the pesticide subsumed in the parameters of the logistic function.

Combining our assumptions, the growth of the pest population can be modelled as

$$(1) \qquad \dot{D} = gD\left(1 - \frac{D}{KQ}\right) - wqD - (1 - w)rD .$$

It can be shown that the proportion of resistant pests in the population also follows a logistic equation, with the growth parameter equal to the difference in relative mortality rates between genotypes (Bonhoeffer, Lipsitch and Levin 1997). Thus

$$(2) \qquad \dot{w} = (q - r)w(w - 1).$$

Because $w < 1$, the larger the fraction of crop land treated with pesticide, the greater the decline in the effectiveness of the pesticide.

## Optimal refuge areas and steady-state results

We now characterize the optimal refuge strategy. The proportion of agricultural land set aside as refuge area in each period determines the crop yield net of losses to pests in that period as well as the effectiveness of the pesticide in succeeding periods. There is, then, an intertemporal trade-off between increasing refuge size (and consequently losing more agricultural yield to pests today) and more rapidly eroding pest susceptibility to the toxin.

Suppose that each surviving pest eats an amount $\alpha$. Normalize gross output per unit area planted to 1. If a fraction $q$ of the area $Q$ devoted to agriculture is treated with pesticide, then gross production in this area will be $qQ$. A fraction $q$ of the pest population $D$ will feed on the area exposed to the toxin. Of these, the fraction $1 - w$ that are resistant will survive. Each of these surviving organisms will consume $\alpha$ units. Thus, the net yield from the area exposed to the pesticide is given by $qQ - (1-w)qD\alpha$. Similarly, the gross yield from the area without toxin exposure is $(1 - q)Q$. A fraction $1 - q$ of pests will feed on the unexposed area, where they will consume $(1 - q)D\alpha$ units of the crop[8]. Net yield in the unexposed area is, then, $(1-q)Q - (1-q)D\alpha$. Net yield from agriculture, $Y$, is given by the sum of net yields from the area treated with pesticide and the refuge area:

$$(3) \qquad Y(q, Q, D, w) = qQ - (1-w)qD\alpha + (1-q)Q - (1-q)D\alpha = Q - (1-wq)D\alpha .$$

Expression (3) postulates that net yield has an ‘additive’ form. Net yield is equal to gross yield, $Q$, less the total amount of the crop consumed by pests. The latter quantity depends on the number of pests, *but not on the amount of food available to them*. This is both a special assumption and a crucial one for the results that follow. In ecological terms, it means that the pest population is constrained by the analogue to ‘predation’ imposed by the pesticide (for a discussion of predator–prey relationships, their implications for population constraints, and circumstances under which populations are regulated ‘from above’ by predation as opposed to ‘from below’ by resources Estes, Crooks and Holt 2001). Each *surviving* pest eats until it is satiated. Put in another way, our ‘additive’ assumption is consistent with a successful pest-control regime. The optimal management programme never adopts the trivial solution of ‘managing’ pest numbers by simply allowing them to expand until they are limited by the food planted for their consumption (although if pest numbers were limited by natural predators, our ‘additive’ assumption could continue to hold even if pest populations were not managed by pesticides).

Expression (3) is rarely *literally* true. To the extent that there is always some competition among pests, the amount they consume may be a function not only of their numbers, but also of the amount of food available to them. In situations in which pest populations are controlled at numbers significantly below the carrying capacity of their environment, though, expression (3) is a valid and reasonably accurate first approximation.

It is also worth emphasizing that expression (3) describes the net yield from agriculture at a point in time *during which the pest population is given*. Net yield is equal to gross yield less the amount the current generation of pests consumes. A choice to expand the area planted in crops will, of course, result in a larger pest population. The effects of population growth will not begin to be felt until later, however[9].

For the purposes of our very simple example, we suppose that social welfare depends on two goods: the net yield from agriculture, $Y$ from equation (3), and the total quantity of land conserved as natural habitat, $1 - Q$. To facilitate the derivation of tractable results, we suppose that preferences are of the Cobb–Douglas form[10] $U(Y, 1 - Q) = Y^{\beta}(1 - Q)^{1-\beta}$. Let the discount rate be $\rho$. Then, a social planner would choose $q$ and $Q$ so as to maximize

$$(4) \qquad \int_0^\infty (Q - [1-wq]D\alpha)^\beta (1-Q)^{1-\beta} e^{-\rho t} dt,$$

subject to equations (1) and (2) for the evolution of pest populations and resistance.

The current-value Hamiltonian for our problem is

$$(5) \qquad \begin{aligned} H = (Q - [1-wq]D\alpha)^\beta (1-Q)^{1-\beta} + \lambda_1 D\left[g\left(1 - \frac{D}{KQ}\right) - wq - r(1-w)\right] \\ + \lambda_2 (q-r)w(w-1) \end{aligned},$$

where $\lambda_1$ and $\lambda_2$ are the co-state variables associated with the stock of pests, $D$, and the proportion of susceptible pests, $w$, respectively. Necessary conditions for an optimum are given by equations (5.1) through (5.4)[11]:

$$(5.1) \qquad \beta \frac{U}{Y} wD\alpha - \lambda_1 wD - \lambda_2 w(1-w) \begin{pmatrix} < \\ = \\ > \end{pmatrix} 0 \ as \ q \begin{pmatrix} =0 \\ \in (0,1) \\ =1 \end{pmatrix};$$

$$(5.2) \qquad \beta \frac{U}{Y} - (1-\beta)\frac{U}{1-Q} + \lambda_1 g \frac{D^2}{KQ^2} = 0;$$

$$(5.3) \qquad \rho\lambda_1 - \dot{\lambda}_1 = \beta \frac{U}{Y}(wq-1)\alpha + \lambda_1 \left[g\left(1 - \frac{2D}{KQ}\right) - qw - r(1-w)\right];$$

$$(5.4) \qquad \rho\lambda_2 - \dot{\lambda}_2 = \beta \frac{U}{Y} qD\alpha + \lambda_1 (r - q)D + \lambda_2 (r - q)(1-2w).$$

Let us consider results in a steady state. We will denote steady-state variable values with a superscript '*SS*'. It is obvious from equation (2) that, if (5.1) holds in the steady state (i.e., if $0 < q < 1$), then $q^{SS} = r$. If $r$ were zero, there would be no fitness cost of resistance, resistant organisms must eventually come to dominate the population, and refuge areas would serve no purpose in the long run. In such circumstances the optimal refuge strategy would involve the management of an inevitably exhaustible resource of pesticide susceptibility.

If $D \neq 0$, then from equations (1), (2), (5.3) and (5.4), we have

$$(6) \qquad D^{SS} = \frac{g - r}{g} KQ^{SS},$$

$$(7.1) \qquad \lambda_1^{SS} = \beta \frac{U}{Y} \frac{(w^{SS} r - 1)\alpha}{\rho + g - r},$$

and

$$(7.2) \qquad \lambda_2^{SS} = \beta \frac{U}{Y} \frac{rD^{SS}\alpha}{\rho}.$$

Equation (6) requires that $g > r$ if the pest population is to be positive in steady state. If this were not the case, then it would be optimal to eradicate the pest population.

In equation (7.1), we note that $w^{SS} r - 1$ is non-positive because both $w^{SS}$ and $r$ are fractions. It follows that $\lambda_1^{SS} < 0$; $\lambda_1^{SS}$ represents the shadow price of a 'bad', the pest population. Similarly, from equation (7.2), $\lambda_2^{SS} > 0$, because it is the shadow price of a 'good' stock, susceptibility to the pesticide. Substituting for $\lambda_1^{SS}$ and $\lambda_2^{SS}$ from equations (7.1) and (7.2) and for $D^{SS}$ from equation (6), $w^{SS}$ can be derived from equation (5.1):

$$(8) \qquad w^{SS} = \frac{(r-\rho)(\rho+g-r)-\rho}{r(g-r)}.$$

Our results echo findings from other renewable-resource contexts. Current thinking in the management of genetically modified crops, at least, seems to be that refuge areas should be established to manage resistance (EPA 1998). Equation (8) demonstrates that such a strategy is not always optimal, however. If the discount rate, ρ, is large enough – a sufficient condition is that it be greater than the fitness cost of resistance, $r$ – it is optimal to exhaust the stock of effectiveness at steady state[12]. This conclusion is analogous to a finding from the fisheries literature: it may be 'optimal' (ignoring possible ethical and ecological considerations) to harvest a species to extinction if its growth rate is less than the discount rate (Clark 1990).

In the limit as $\rho$ approaches zero, $w^{SS}$ approaches one. With a vanishing discount rate, resistant pests would be eradicated. So long as there remain any resistant alleles in the population, welfare in the indefinitely long run would be increased by eradicating those alleles[13]. This would not be an optimal strategy under a positive discount rate, of course. The reasoning recalls Tjalling Koopmans's (1960) argument that discount rates *should* be positive: it is unreasonable to sacrifice welfare in all foreseeable periods in anticipation of some date in the indefinite future at which things would be better (Koopmans 1960).

Next, consider the steady-state level of agricultural land use. To reduce clutter, we will suppress superscripts, but all variables are assumed to take their steady-state values in the expressions leading up to and including (13) below. This analysis may be conducted most easily by deriving an implicit expression for land in agriculture, $Q$. To do this, we start from expression (5.2). Recall that its three terms equate the marginal utility afforded by more immediate consumption to the marginal utility lost by habitat reduction and the shadow price of the increment in the pest population induced by devoting more land to agriculture. Restate expression (5.2) by adding and subtracting $\beta U/Q$,

$$\beta\frac{U}{Q} + \beta\frac{U}{Y} - \beta\frac{U}{Q} - (1-\beta)\frac{U}{1-Q} + \lambda_1 g\frac{D^2}{KQ^2} = 0,$$

and rearrange it as:

$$(9) \qquad \frac{Q-\beta}{1-Q}U = \beta\frac{(Q-Y)U}{Y} + \lambda_1 g\frac{D^2}{KQ}.$$

In a somewhat more heuristic notation, we could rewrite (9) as

$$(9.1) \qquad \frac{Q-\beta}{1-\beta}U_H = (Q-Y)U_Y + \lambda_1 g\frac{D^2}{KQ},$$

where $U_H$ is the marginal utility afforded by natural habitat and $U_Y$ the marginal utility afforded by agricultural consumption. The final term in (9.1) is the shadow price of the larger pest population induced by more land in agriculture times land used in agriculture. Total crop losses to pests are gross production, $Q$, less net production, $Y$. The first term on the right-hand side of (9.1) is, then, the value of agricultural production lost to pests, calculated at its marginal utility shadow price.

Our results below concerning the discount rate and land devoted to agriculture, $Q$, relate the relative importance of present and future losses to pests. Heuristically, as the discount rate declines, the two terms on the right-hand side of (9.1) will converge. In the limit as the discount rate approaches zero, the optimal policy calls for exactly offsetting the cost of present crop losses with that of future losses. For higher discount rates, present losses will be weighted more heavily than future[14]. The consequence is that more land will be devoted to agricultural production.

Return now to expression (9). Note that

$$(10)\quad Q - Y = (1 - wr)\alpha K \frac{(g-r)}{g} Q,$$

and

$$(11)\quad Y = \left[1 - (1 - wr)\alpha K \frac{(g-r)}{g}\right] Q.$$

From expression (8),

$$(12)\quad 1 - wr = \frac{(1 + \rho - r)(\rho + g - r)}{g - r}.$$

Using expressions (6) and (7.1) above to substitute for $\lambda_1$ and $D$, we can restate (9) as

$$(13)\quad \frac{Q-\beta}{1-Q} = \frac{\beta\rho(1 + \rho - r)\alpha K}{[g - (1 + \rho - r)(\rho + g - r)\alpha K]}.$$

Using (11) and (12), the denominator of (13) is positive, since $Y > 0$. Thus, the right-hand side is positive, and $Q > \beta$.

We could differentiate (9) with respect to $\rho$ and solve for $\partial Q/\partial\rho$, but it is clear on inspection that its left-hand side is increasing in $Q$ and its right-hand side is increasing in $\rho$. Thus $\partial Q/\partial\rho > 0$. The greater is the discount rate, the greater is the quantity of land devoted to agriculture in the steady state – if indeed a non-trivial steady state obtains.

Expression (13) has an interesting interpretation. Suppose that production took place under a hypothetical technology such that net yield, $Y$, were a constant fraction $\theta$ of total area planted regardless of pests and other factors, $Q$: $Y = \theta Q$. If we set the fraction $\theta$ equal to $1 - (1 - wr)\alpha K \frac{(g-r)}{g}$, the hypothetical technology would provide the same net yield per hectare as does the optimally managed pesticide programme (see expression [11]).

It is easily shown, though, that if one were to maximize the Cobb-Douglas objective function

$$(14)\quad U = (\theta Q)^{\beta}(1-Q)^{1-\beta},$$

the solution would be to set $Q = \beta$. Heuristically, expression (14) is formally identical to maximizing utility from food and habitat subject to the fixed 'budget constraint' that agricultural land plus habitat equals 1. Using land as a *numeraire*, the 'price' of food is the inverse of yield-per-hectare, $1/\theta$. As is well known, the solution to such a problem is to set the share of expenditure on food equal to its exponent in the utility function, $\beta$. But the share of expenditure when land is the *numeraire* is simply the share of land devoted to agriculture, $Q$.

We have just shown, then, that more land is used in the steady state of our model than would be used were a technology available that provided the same yield-per-hectare as does the optimally managed pesticide programme, but that did not involve the management of pest populations.

This may seem paradoxical, as pest control introduces an intertemporal consideration. More land in agriculture now implies more pests in the future. One might, then, suspect that a shadow price associated with the current use of land would induce the decision-maker to use less, rather than more, land in agriculture. If $Y$ were equal to $\theta Q$, the analogue to expression (5.2) above would be

$$\beta\theta\frac{U}{\theta Q} - (1-\beta)\frac{U}{1-Q} + \lambda_1 g\frac{D^2}{KQ^2} = 0\,;$$

note that the $\theta$'s cancel from the first term. The analogue to our expression (9) would then be

$$(15)\qquad (Q-\beta)\frac{U}{Q(1-Q)} = \lambda_1 g\frac{D^2}{KQ^2}\,.$$

Since $\lambda_1$ denotes the shadow price of a 'bad' – the pest population – one would reach the opposite of the conclusion implied by (13). In (15), $Q < \beta$.

The reason for this difference is to be found in expression (3) above, in which we presume net yield takes an 'additive' form. This implies that the marginal product of land in agriculture is always one, while the alternative 'multiplicative' specification $Y = \theta Q$ would imply that the marginal product of land is $\theta < 1$. Since the opportunity cost of devoting land to habitat rather than agriculture is always higher under the 'additive' than the 'multiplicative' specification, less land is devoted to habitat.

The assumption that pests can be satiated in the short run is crucial to our results, but for the reasons we have discussed above, it is reasonable. Multiplicative forms have been suggested in the agricultural economics literature (see e.g. Lichtenberg and Zilberman 1986). However, our specification of an additive relationship *in the short run* in expression (3) is not inconsistent with a multiplicative *long-run* relationship in expression (11). In fact, the message of Lichtenberg and Zilberman is that one must model biological relationships carefully, considering and distinguishing short- and long-term effects.

A supplementary question that is easily explored using our current model relates to the impact of pest-resistance management practices on habitat conservation. Foregoing resistance management results in greater losses to pests. Consequently, agricultural output is smaller in this situation and the marginal utility of food is greater than if we were to manage for pest resistance. Needless to add, foregoing resistance management is not an optimal solution from a societal standpoint, but as is demonstrated below, it does have the effect of helping conserve habitat.

The steady-state allocation of land to agriculture can be calculated by solving the optimal control problem where $q$ is invariant and set equal to one. The expression below for this problem that is analogous to equation (13) is

$$(16)\qquad \frac{(Q-\beta)}{(1-Q)} = \beta\frac{\alpha(g-r)K}{g-\alpha(g-r)K}\left[\frac{\rho}{\rho+g-r}\right].$$

By contrasting this expression (16) with equation (13), we can show that the amount of land devoted to agriculture is greater than when we choose to manage for resistance[15].

Cobb-Douglas preferences are a conspicuous and restrictive assumption in our modelling. We have demonstrated in an earlier version of this work (Laxminarayan and Simpson 2000) that the same basic results obtain under a constant elasticity of substitution specification, of which the Cobb-Douglas is a special case. It seems reasonable to suppose that they generalize at least somewhat.

Conventional wisdom holds that demand for food is inelastic, suggesting a low elasticity of substitution at low levels of consumption. Moreover, environmental amenities are likely to be luxury goods. Thus a homothetic representation of preferences is probably unrealistic, and it is not immediately clear how alternatives would affect specific results. It is, then, not constructive to argue too forcefully or concretely on the basis of so simple a model. There is, however, a general principle at work. The fact that short-term yields can be increased to the detriment of long-term prospects implies not only that short-term results may not be sustainable, but also that steady-state prospects may be less optimistic than they might first appear.

## Conclusion

We have employed a simple and analytically tractable model to demonstrate some implications of pesticide use and resistance for land use. It is probably unnecessary to caution readers that the model is intended to be illustrative rather than realistic. Despite these concessions to practicality, we believe that the model develops some useful insights.

Perhaps the most important of these is that biological constraints limit the intensification of agriculture in ways that are not always transparent. Whereas other examples of this phenomenon have been developed, we find the case of pesticide resistance particularly interesting in that the interactions are complicated and the implications subtle. Our results do not hinge on externalities, nor do they suggest that technological advances are not desirable. They only point to the wisdom of measured expectations concerning the potential of agricultural intensification to solve the problem of habitat and biodiversity loss.

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[1] Address correspondence to ramanan@rff.org. We are grateful to seminar participants at Resources for the Future; University of Minnesota; Delhi School of Economics; American Economic Association Annual Meetings (New Orleans) and the IPGRI Workshop on Biotechnology, Environmental Policy and Agriculture in Rome for useful comments. Finally, we are grateful to Sarah Cline for research assistance. Any remaining errors are our responsibility.

[2] This may not be as unrealistic as it seems. When a toxin is expressed in a genetically modified plant, we might suppose that the social planner is deciding how much use to make of a resource that can be acquired at low marginal cost: genetically modified seed. More generally, expenditures on pesticides may be modest compared to other expenses.

[3] 'Heterozygous' individuals (those having one 'resistant' and one 'susceptible' allele) may show some resistance, but typically not as much as those with two resistant alleles.

[4] Similar regulations have been enacted in the United States by the Environmental Protection Agency (EPA), which has mandated that refuge areas be grown in conjunction with certain transgenic crops, such as *Bt* cotton and corn (EPA 1998). In fact, EPA regulations regarding GMOs are the first from any agency in the US that treat pest susceptibility as a public good (Livingston, Carlson and Fackler 2000), even though resistance issues arose with more traditional pesticides as well.

[5] A *genotype* is a particular genetic configuration. An *allele* is any one of the two or more forms that may compose a gene; for example, alleles for blue or brown eyes are common in many human populations. The Hardy–Weinberg principle of quantitative genetics holds that, for a population satisfying the assumptions we have stated and in which expected mortality is the same across different genotypes, the expected proportion of alleles and of genotypes remains constant from generation to generation.

[6] Assumptions concerning pest are important in forming refuge-regulation policy (Secchi and Babcock 2002)

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[7] The continued survival of ‘unfit’ genes in the absence of pesticide use is problematic but might be explained by rare mutations or the infrequent occurrence of random events that temporarily favor otherwise ‘unfit’ organisms.

[8] Implicit in our assumptions are the notions that susceptible pests die so quickly on exposure to the pesticide as to consume only a negligible amount of the crop before expiring and that mortality to other causes occurs after consumption. Alternatively, we could have supposed that pests eat a constant amount of the crop at each instant they are alive and treated lifespan as a random variable drawn from different distributions depending on whether the pest is ‘resistant’ or ‘susceptible’ to the pesticide and whether it feeds in a ‘treated’ or a ‘refuge’ area. We could then replace losses to pests with expected losses. This does not lead to qualitatively different results, however, so we have maintained the simplifying assumptions. Both assumptions could be relaxed, but neither is important for establishing our general results.

[9] The assertion that land devoted to agriculture affects population growth rather than the amount consumed by any individual pest might be best justified by noting that a pest’s mortality risk increases with the effort required to discover an area in which it can consume the crop without competing with another pest to do so.

[10] Our basic results also obtain under a CES utility function of the form $U = \left(\beta Y^{\eta} + (1-\beta)(1-Q)^{\eta}\right)^{1/\eta}$; see Laxminarayan and Simpson (2000).

[11] It can also be shown that these conditions are also sufficient for an optimal solution. A rather laborious process shows that the problem satisfies Arrow’s conditions for an optimum (Kamien and Schwartz 1991, p. 222).

[12] Laxminarayan and Simpson (2002) also show that it may not be optimal to establish refuges when the proportion of resistant pests is very low. Resistance does not yet constitute a sufficient threat as to justify foregoing yield.

[13] This extreme result is an artifact of a specification of the evolution of resistance (see equation (2)) in which resistant alleles can be reduced to arbitrarily small proportions without ever being entirely eliminated. The fundamentally discrete character of alleles and the possibilities of mutation preclude interpreting the model literally. It is, nonetheless, a useful way of thinking about these issues.

[14] This interpretation of losses as ‘totals’ evaluated at prices determined by marginal utility or shadow price would appear to be an artifact of the Cobb-Douglas specification, and hence not necessarily generalizable.

[15] This holds true when $(1 + \rho - r)(\rho + g - r) > g - r$, a condition that is satisfied for all relevant parameter values where the optimal strategy is not to exhaust pesticide effectiveness anyway (see equation 8 of the paper in this regard.)