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Ecological-economic modelling of interactions between wild and commercial bees and pesticide use

Adam Kleczkowski
Ciaran Ellis
Dave Goulson
Frans P. de Vries
Nick Hanley

University of Stirling

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Ecological-economic modelling of interactions between wild and commercial bees and pesticide use *

Adam Kleczkowski†
Computing Science and Mathematics, School of Natural Sciences, University of Stirling, UK

Ciaran Ellis
Biological and Environmental Studies, School of Natural Sciences, University of Stirling, UK

Dave Goulson
School of Life Sciences, University of Sussex, UK

Frans P. de Vries and Nick Hanley
Economics, Management School, University of Stirling, UK

The decline in extent of wild pollinators in recent years has been partly associated with changing farm practices and in particular with increase of pesticide use. In this paper we combine ecological modelling with economic analysis of a single farm output under the assumption that both pollination and pest control are essential inputs. We show that the drive to increase farm output can lead to a local decline in the wild bee population. Commercial bees are often considered an alternative to wild pollinators, but we show that their introduction can lead to further decline and finally local extinction of wild bees. The transitions between different outcomes are characterised by threshold behaviour and are potentially difficult to predict and detect in advance. Small changes in economic (input prices) and ecological (wild bees carrying capacity and effect of pesticides on bees) can move the economic-ecological system beyond the extinction threshold. We also show that increasing the pesticide price or decreasing the commercial bee price might lead to re-establishment of wild bees following their local extinction. Thus, we demonstrate the importance of combining ecological modelling with economics to study the provision of ecosystem services and to inform sustainable management of ecosystem service providers.

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I. INTRODUCTION

Globally, 35% of food crops are at least partly dependent on insect pollination (Klein *et al.*, 2007). Ensuring sufficient pollination of these crops will be challenging in the future; the fraction of agriculture made up by insect-pollinated crops is increasing (Aizen & Harder, 2009), while wild pollinator populations are threatened by both habitat loss (Winfree *et al.*, 2009) and agricultural intensification, which are thought to be the main causes of reported declines in diversity in the EU and in the USA (Biesmeijer *et al.*, 2006; Cameron *et al.*, 2011).

Honeybees are used to supplement or substitute wild pollinators, along with other commercial pollinators such as laboratory breed bumblebees (Velthuis & van Doorn, 2006). While commercial pollinators are often assumed to be adequate substitutes for wild pollinators (though see (Brittain *et al.*, 2013; Hoehn *et al.*, 2008)), the use of commercial pollinators is itself not without risk. Honeybees have suffered losses in recent years due to the abandonment of hives (Colony Collapse Disorder) and the *Varroa* mite (Cox-Foster *et al.*, 2007). Relying on commercial pollinators such as honeybees puts farmers at risk from shocks of this kind, with consequent implications for farm profits over time.

Given the risks around the supply of pollination services from commercial bees, maintaining viable wild pollinator populations is likely to be crucial to sustaining the production of insect-pollinated crops into the future (Winfree *et al.*, 2007). The potential costs of the loss of local pollination services is illustrated by the need for pollination using farm workers in Sichuan, China, following the loss of local insect pollinator populations (Partap *et al.*, 2001). Whilst this was a viable option when wages were cheap, a 10–fold rise in wages over the last 10 years has led to the abandonment of apple production (Partap & Tang, 2012). One of the factors implicated in this local extinction and in declines elsewhere, is the use of pesticides, or specifically, insecticides.

†Electronic address: ak@maths.stir.ac.uk

There is growing evidence of negative effects of realistic levels of commonly used insecticides on population determining traits such as reproductive rates, foraging rates and navigation in bees (Goulson, 2013; Henry *et al.*, 2012; Mommaerts *et al.*, 2010; Whitehorn *et al.*, 2012). Awareness of this evidence has led to the temporary banning of a very widely used group of insecticides – neonicotinoids – within the European Union.

Farmers who grow insect-pollination dependent crops face a trade-off in their use of pesticides, since whilst this reduces crop damages, it also has potential negative effects on the local supply of pollination services from both wild and commercial pollinators. This is the issue that we study in this paper. To investigate the links between commercial pollinator use, pesticide use and wild pollinator populations we present an ecological-economic model which links crop yields to pollinator numbers and pesticide use and study how the optimal strategy depends on the level of farm output and other parameters.

There are a number of key results in this paper: Firstly, by introducing commercial bees the farmer can achieve higher target output values than by relying on wild pollinators alone, while keeping the costs at minimum. Thus, it is rational to substitute commercial for wild bees and to increase the use of insecticides. Secondly, the resulting increase in pesticide use buffered by usage of commercial bees may lead to a severe reduction in wild pollinator population, even without direct competition between different bee populations. Thirdly, under certain economic conditions, the system becomes unstable and small changes in prices or environmental conditions can result in the local extinction of wild pollinators. As in this paper we are modelling a single farm only, all references to extinction mean that *locally* the wild bee population will tend to zero.

Finally, we discuss a number of options that are available to restore a wild bee population even if it is currently *locally* extinct. These include increase in the pesticide price (or application of a pesticide tax), increase in the carrying capacity characterising the wild bee populations, or a change in the type of insecticides used on the farm. Perhaps surprising, decrease in the price of commercial bees can under some conditions help the wild bee population indirectly by allowing farmers to reduce their reliance on pesticides.

II. MODELLING FRAMEWORK

The model is based on two components, an ecological model describing the bee population and a farmer decision model which decides expenditure on pesticides and commercial bees. The sys-

tem describes a single farm and its surrounding ecosystem supporting wild bees. A single-period optimisation problem forms the general framework we use here. Although we start by describing dynamic changes in wild bee populations as they interact with pesticide and commercial bees, the assumption that within-season dynamic is fast allows us to assume instantaneous response of the wild bees to pesticide levels. Thus, we can consider long-term (equilibrium) population densities found by static optimisation as a substitute for time-dependent values.

A. Ecological model

The wild population of bees, described by their density, y, provides pollination services. The growth of y satisfies a logistic equation

$$\frac{dy}{dt} = ry\left(1 - \frac{y}{\kappa} - g\,\frac{x_1}{\kappa}\right), \tag{1}$$

where r is the intrinsic growth rate (in units per year) and κ is the carrying capacity. The last term in Eqn. (1) summarises the effect of pesticides, x_1, on the population of wild bees, with the constant g quantifying the effect of pesticides on the wild bee population. Commercial bees, which are present at the farm at density x_2, are assumed not to compete directly with the wild bees in terms of foraging.[1]

The dynamics of the wild bee population is assumed to be fast, so that given the levels of pesticides and commercial bees, the population reaches equilibrium instantaneously. Thus for the wild bees, y is either 0 or

$$y = \kappa - gx_1. \tag{2}$$

B. Economic model

Farmer returns consist of two components, output (yield) and costs. Output is assumed to follow a Cobb-Douglas production function with two inputs: pollination services and pest control. However, ecological interactions between bees and pesticides provide a key modification to the standard Cobb-Douglas model by including interactions between inputs. The Cobb-Douglas production function was selected because it represents the need for both pesticides and pollination in agricultural production; the output is zero if *either* of the inputs is zero. Thus, both pollination

[1] There is mixed evidence on this relationship in the scientific literature (Garibaldi *et al.*, 2011).

(from commercial or wild bees) and pest control are assumed to be essential. For simplicity we use a linear production function (Gravelle & Rees, 2004) for the pollination term, reflecting the fact that pollination is assumed to be performed equally well by both commercial and wild bees (and so they are perfect substitutes).[2] Thus,

$$q\left(x_1, x_2\right) = A(y + x_2)^{\alpha} x_1^{1-\alpha}, \tag{3}$$

where α is the output elasticity of pollination services and $1 - \alpha$ is the output elasticity of pest control, i.e., the production function features constant returns to scale. Further, A represents total factor productivity, and without loss of generality we assume $A = 1$.

Wild pollination services come free, whereas other costs are assumed to be linear in output. The cost of pesticides is w_1 per unit and the cost of commercial bees is w_2 per unit. We assume that the farmer minimises the cost function

$$c\left(x_1, x_2\right) = w_1 x_1 + w_2 x_2. \tag{4}$$

The minimisation is subject to satisfying a total output constraint

$$q\left(x_1, x_2\right) = \bar{q}, \tag{5}$$

where $\bar{q}$ is the exogenous target output. Given $\bar{q}$, the levels of pesticides, x_1, and commercial bees, x_2, are chosen by the farmer based upon cost minimisation, $c\left(x_1, x_2\right)$. The wild bee population simply responds to the choice of x_1 through equation (2), so there are only two independent decision variables, x_1 and x_2. If $y = \kappa - g x_1 > 0$, then the total output constraint is

$$q\left(x_1, x_2\right) = (\kappa - g x_1 + x_2)^{\alpha} x_1^{1-\alpha} = \bar{q}\,, \tag{6}$$

whereas for $y = 0$,

$$q\left(x_1, x_2\right) = x_2^{\alpha} x_1^{1-\alpha} = \bar{q}. \tag{7}$$

The farmer's decision problem can therefore be written as

[2] Note that this substitution parameter will vary by crop in reality.

$$\min_{\substack{x_1\geq 0,\, x_2\geq 0,\\ q(x_1,x_2)=\bar{q}}} \; \min_{y=\kappa-gx_1\geq 0} c\left(x_1, x_2\right), \tag{8}$$

For simplicity we assume that there are no limits to the number of commercial bees that can be introduced onto the farm and there are no limits to pesticide use.

C. Optimisation

We assume that the farmer wants to achieve the target level of output, $\bar{q}$, and hence the constraint becomes $q\left(x_1, x_2\right) = \bar{q}$. A pair $(\hat{x}_1, \hat{x}_2)$ represents a management strategy that she can choose to achieve this. The minimisation process can be represented on the (x_1, x_2) plane, with the isoquants $q\left(x_1, x_2\right) = \bar{q}$ representing the output constraint, Fig. 1. In the simple case when there is no interaction between pesticides and commercial bees, Eqn. (4), the cost function is represented by a straight line with a negative slope, $-w_1/w_2$ and the intercept c/w_2, see Fig. 1 with c representing the cost. The procedure for optimizing, Eqn. (8), can then be interpreted as finding a minimal value of c such that the straight line still crosses the isoquant line corresponding to the given value of $\bar{q}$, see Fig. 1. The optimum value of c corresponds to the straight line that is tangent to the isoquant line; if more than one such line exists (representing local minima), the one with the smallest value of C is chosen. Fig. 1 gives three examples of such lines for different values of $\bar{q}$.

As the cost is linear in x_1 and x_2, following standard microeconomic theory (Gravelle & Rees, 2004), this procedure can be recast in terms of the following two conditions that can be used to find the conditional factor demands $\hat{x}_1$ and $\hat{x}_2$ that minimise the costs of producing $\bar{q}$ units of output:

$$\frac{\frac{\partial q(x_1,x_2)}{\partial x_1}}{\frac{\partial q(x_1,x_2)}{\partial x_2}} = \frac{w_1}{w_2}, \tag{9a}$$

$$q(x_1, x_2) = \bar{q}. \tag{9b}$$

The former optimality condition simply states that, in the optimum, the marginal rate of technical substitution is exactly equal to the ratio of the factor prices of using x_1 and x_2; the latter is just the constraint. Note that although the output function is continuous, due to the interaction between the two inputs it is non-monotonic and defined differently in different regions of the (x_1, x_2) plane – see Fig. 1b. In particular, three regions can be distinguished. Firstly, $x_1 < \kappa/g$ and wild bees are present; secondly, $x_1 \geq \kappa/g$ and wild bees are locally extinct. Finally, in a special case

when $x_2 = 0$, pollination relies exclusively on wild bees. These three regions are characterised by different optimisation criteria and we first discuss each one separately. We subsequently compare the results to identify the strategy associated with the minimum of c.

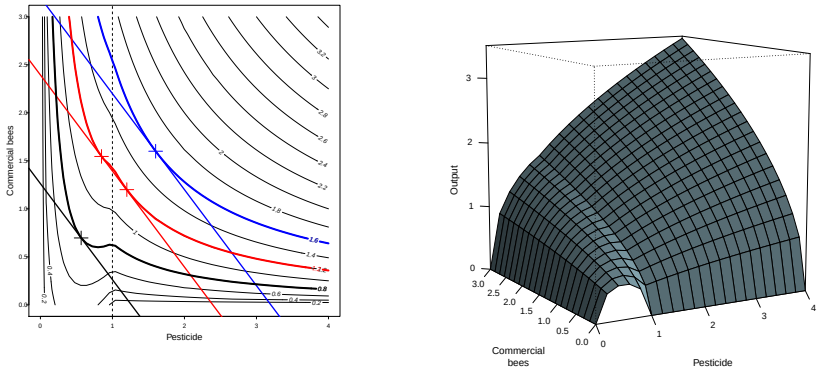

FIG. 1 Farm output as a function of x_1 and x_2, with values on contour lines giving $q(x_1, x_2)$. Straight lines correspond to $w_1 x_1 + w_2 x_2 =$ const. Isoquant lines and the corresponding minimum cost lines are shown for $\bar{q} = 0.8$ (black), $\bar{q} = 1.2$ (red) and $\bar{q} = 1.6$ (blue). Vertical line corresponds to $y = \kappa - g x_1 = 0$ and wild bees are extinct to the right of it. On the right, output is shown in a perspective plot. Other parameters: $\kappa = 1$, $g = 1$, $w_1 = 1$, $w_2 = 1$ and $\alpha = 1/2$.

a. Wild and commercial bees For $x_1 > 0$ and $x_2 > 0$ the equations (9a) and (9b) can be solved to obtain

$$\begin{aligned} \hat{x}_1 &= \Delta_1^\alpha \, \bar{q} \\ \hat{x}_2 &= \Delta_1^\alpha \, \frac{\alpha w_1 + w_2 g}{(1-\alpha) w_2} \, \bar{q} - \kappa \\ \hat{y} &= \kappa - g \Delta_1^\alpha \bar{q} \, . \end{aligned} \tag{10}$$

where $\nu = (1-\alpha)/\alpha$ and

$$\Delta_1 = \frac{\nu w_2}{w_1 + w_2 g} \, . \tag{11}$$

The optimal values of both the pesticide use, $\hat{x}_1$, and the commercial bees use, $\hat{x}_2$, are both linear functions of the target output, $\bar{q}$. Note that $\hat{x}_2 > 0$ if

$$\bar{q} > \bar{q}_c = \frac{k\Delta_1^{1-\alpha}}{1+g\Delta_1}\,. \tag{12}$$

b. Commercial bees only By assuming that $y = \kappa - gx_1 = 0$ we can eliminate x_2 from the output equation and obtain the cost equation in terms of x_1 only,

$$c(x_1) = w_1 x_1 + w_2 \bar{q}^{1/\alpha} x_1^{-\nu}\,. \tag{13}$$

Denote

$$\Delta_2 = \frac{\nu w_2}{w_1}\,. \tag{14}$$

Then,

$$\begin{aligned} \hat{x}_1 &= \Delta_2^{\alpha}\bar{q} \\ \hat{x}_2 &= \Delta_2^{1-\alpha}\,\bar{q} \\ \hat{y} &= 0\,. \end{aligned} \tag{15}$$

Again, the optimal values $\hat{x}_1$ and $\hat{x}_2$ are linear functions of $\bar{q}$.[3]

c. No commercial bees If $x_2 = 0$ then the output equation becomes

$$q(x_1, 0) = (\kappa - gx_1)^{\alpha}\, x_1^{1-\alpha}, \tag{16}$$

which can be solved to find the corresponding value of x_1. However, we can only perform an optimisation if this equation has more than one solution, otherwise the value of x_1 is completely determined by the output level, $\bar{q}$. Unfortunately, no analytical solution can be found in a general case, but for $\alpha = 1/2$ the equation is quadratic and has two solutions if $\bar{q} < \bar{q}_m$, one solution if $\bar{q} = \bar{q}_m$, and no solutions if $\bar{q} > \bar{q}_m$. If equation (16) has two solutions, they are

$$x_1^{\pm} = \frac{\kappa}{2g} \pm \frac{\sqrt{\kappa^2 - 4g\bar{q}^2}}{2g}, \tag{17}$$

[3] Note that, unlike in the previous section, $\hat{x}_2 > 0$ regardless of $\bar{q}$.

both of which are positive. As the cost in this case is $c(x_1, 0) = w_1 x_1$, the smaller one of these solutions, x_1^- is optimal, hence

$$\begin{aligned} \hat{x}_1 &= \frac{\kappa}{2g} - \frac{\sqrt{\kappa^2 - 4g\bar{q}^2}}{2g} \\ \hat{x}_2 &= 0 \\ \hat{y} &= \frac{\kappa}{2} + \frac{\sqrt{\kappa^2 - 4g\bar{q}^2}}{2}\,. \end{aligned} \tag{18}$$

III. RESULTS

In this section we explore how the optimal management options change as the target output $\bar{q}$ increases. We show that there are three critical levels of $\bar{q}$ at which the behaviour changes: $\bar{q}_c$ is a level at which commercial bees become economically viable, $\bar{q}_m \geq \bar{q}_c$ is the maximum output achievable without the commercial bees, and $\bar{q}_e \geq \bar{q}_m \geq \bar{q}_c$ is the output level at which the optimal use of pesticides leads to local extinction of wild bees. We subsequently discuss how these threshold levels depend on pesticide and commercial bee prices, w_1 and w_2, and on the carrying capacity, κ. We also discuss potential strategies that a social planner can use to shift the system from a state in which wild bees are locally extinct to the state in which they can survive. Finally, we discuss extensions to the model.

A. Comparative statics

In the previous section we have shown that the optimal strategy $(\hat{x}_1, \hat{x}_2)$ is different under different assumptions about the values of y and x_2. In particular, we have identified three regions: (i) *Region 1:* $x_2 = 0$, (ii) *Region 2:* $x_2 > 0$ and $y > 0$, and (iii) *Region 3:* $x_2 > 0$ and $y = 0$ – see Fig. 2. As we, *a priori*, do not know in which of the three regions the optimal solution would lie for a given value of the target output, $\bar{q}$, we first calculate the cost at the optimum, $c(\hat{x}_1, \hat{x}_2)$, using formulas for *all* three regions. As $\hat{x}_2$ can be eliminated using equation (9b), the value of $\hat{x}_1$ that corresponds to the lowest cost is selected as an optimal value; the corresponding pair of the conditional factor demands, $(\hat{x}_1, \hat{x}_2)$, describes the optimal management strategy. Let us now systematically discuss the various interactions in the three different regions.

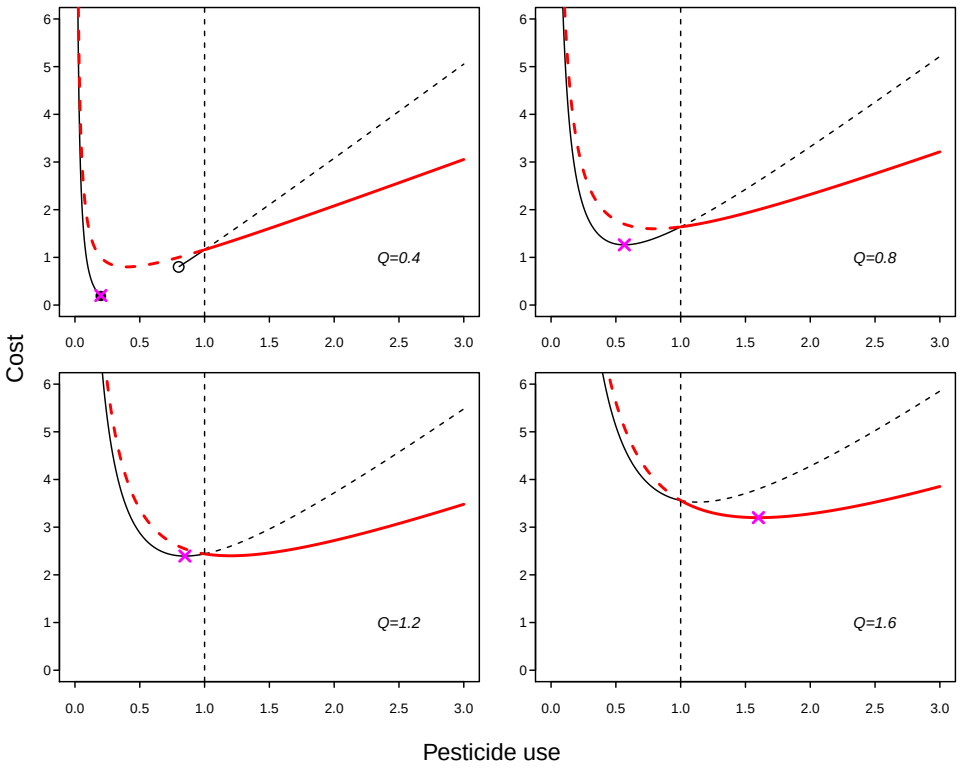

FIG. 2 Cost, $c(x_1, x_2)$ as a function of the pesticide use, x_1, with x_2 eliminated through the constraint equation, $q(x_1, x_2) = \bar{q}$. Graphs correspond to different values of the target output, $\bar{q}$=0.4 (a), 0.8 (b), 1.2 (c) and 1.6 (d) (see also Fig. 1). Thin (black) line represents the case with wild bees and the thick (red) line represents the case without wild bees (lines are extended beyond the validity intervals to illustrate the behaviour; the extensions are marked as broken lines). Vertical line corresponds to $y = \kappa - gx_1 = 0$ and wild bees are extinct to the right of it. Cross represents the location of the optimal solution; solid and empty circles represent solutions of Eqn. (16), i.e. for $x_2 = 0$. Other parameters: $\kappa = 1$, $g = 1$, $w_1 = 1$, $w_2 = 1$ and $\alpha = 1/2$.

1. Region 1: Wild bees only

We first note that for $x_2 = 0$ the optimisation problem has no real solutions if $\bar{q} > \bar{q}_m = \sqrt{\kappa^2/(2g)}$ (we assume here $\alpha = 1/2$). Thus, $\bar{q}_m$ has an interpretation of a maximum target output that can be achieved by using wild bees only. Note that this threshold value depends on ecological

parameters only and not on any economic factors. We can now state:

Proposition 1 *If pollination is provided by wild bees only, there is a maximum output that can be achieved. This output level is determined by ecology of wild bees and their interaction with pesticides.*

The mechanism for this behaviour is related to the balance between pesticide use and pollinator population. If the farmer wants to increase the level of output, she needs to increase the level of pesticide use, which in turn affects the wild bee population. For small values of $\bar{q}$, and therefore for small values of $\hat{x}_1$, this effect is small and so the output can be increased. However, for large values of $\hat{x}_1$, the pollinator population is reduced to such an extent that output starts to decline. Eventually, when $\hat{x}_1 = k/g$, the wild bee population becomes locally extinct which makes agricultural production impossible (as we assume that pollination is an essential input and it is performed here by wild bees only).

For low values of $\bar{q}$, $x_1 = x_1^-$ [*cf.* equation (17)] and $x_2 = 0$ is the optimal choice (see Fig. 1a). In this case, an increase in the target output, $\bar{q}$, is possible by increasing the pesticide use (see Fig. 3a), which results in a gradual decrease in the wild bees population (see Fig. 3c and the resulting pollination services, Fig. 3d). Equation (19) below shows the long run marginal cost (LMC), which increases non-linearly with the target output, $\bar{q}$ (see Fig. 4). That is, the farmer will find it increasingly more costly to increase the output by one unit as $\bar{q}$ approaches $\bar{q}_c < \bar{q}_m$.[4]

$$\frac{\partial c}{\partial \bar{q}} = \frac{2\delta_1 g\bar{q}}{g\sqrt{\kappa^2 - 4g\bar{q}^2}} \tag{19}$$

The assumption that $\hat{x}_2 = 0$ is valid as long as $\bar{q} < \bar{q}_c$. When $\bar{q} > \bar{q}_c$, then $\hat{x}_2 > 0$, see Fig. 2b, so there is a sharp transition at $\bar{q} = \bar{q}_c$. As $\bar{q}_c < \bar{q}_m$, the transition occurs before the maximum possible output level achievable by using wild bees only is reached (see Fig. 3). Thus, $\bar{q}_m$ is not a good guideline for a prediction of changes in the behaviour of the combined bioeconomic system.

The results can be summarised as the following proposition:

Proposition 2 *As the target output level, $\bar{q}$, approaches $\bar{q}_c$, it is increasingly more difficult to increase the output by relying on wild bees only. Thus, commercial bees become an economically attractive option, even though the wild bees still provide sufficient pollination levels. When $\bar{q} = \bar{q}_c < \bar{q}_m$ is reached, introduction of commercial bees become economically optimal.*

[4] Note that the LMC becomes infinite at $\bar{q} = \bar{q}_m$.

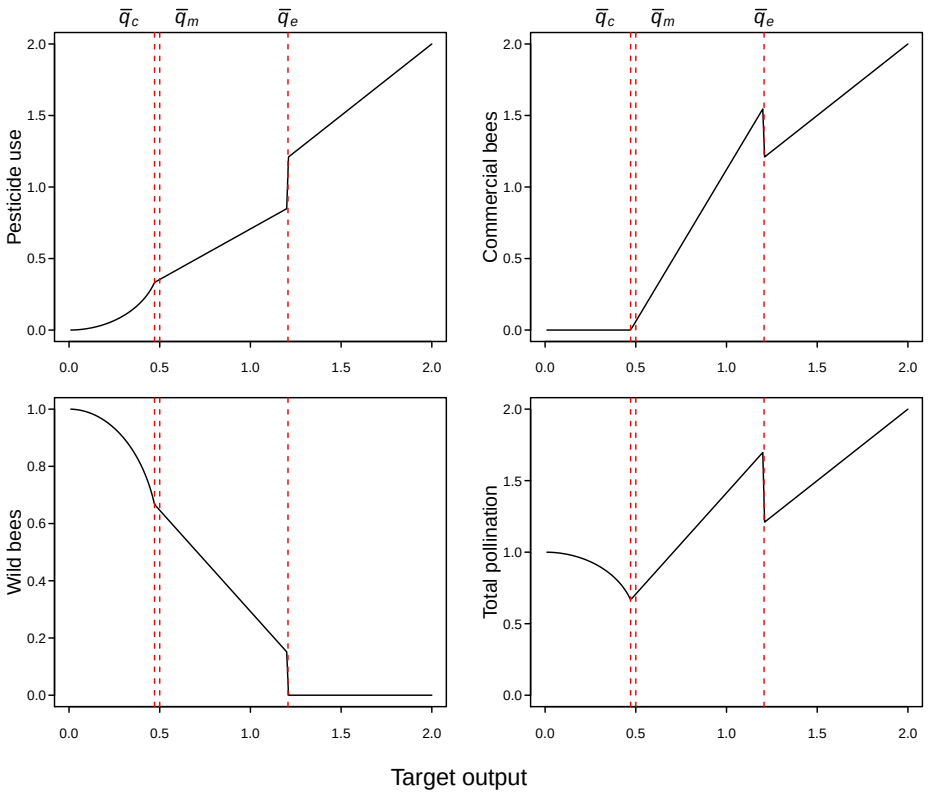

FIG. 3 Optimum values of (a) pesticide use, x_1, (b) commercial bees population, x_2, (c) wild bees population, y, and (d) total pollination services, $y + x_2$, as functions of the target output, $\bar{q}$. Vertical lines correspond to the threshold values of $\bar{q}_c = 0.4714045$, $\bar{q}_m = 0.5$ and $\bar{q}_e = 1.207107$, respectively. Other parameters: $\kappa = 1$, $g = 1$, $w_1 = 1$, $w_2 = 1$ and $\alpha = 1/2$.

2. Region 2: Wild and commercial bees

When $\bar{q} > \bar{q}_c$, the wild and commercial bees coexist, see Fig. 2b and Fig. 3. The pesticide use and the commercial bee usage increase linearly with $\bar{q}$, while the wild bee population decreases linearly – see Fig. 3a and 3b, respectively. The LMC in this case does not depend on $\bar{q}$ (see Fig. 4):

$$\frac{\partial c}{\partial \bar{q}} = \Delta_1^{\alpha} \frac{w_1 + w_2 g}{(1-\alpha) w_2} \tag{20}$$

A desired increase in the target output, $\bar{q}$, is achieved by an increase in the use of pesticides and the corresponding increase in the total pollination services (see Fig. 3d). The increase is made

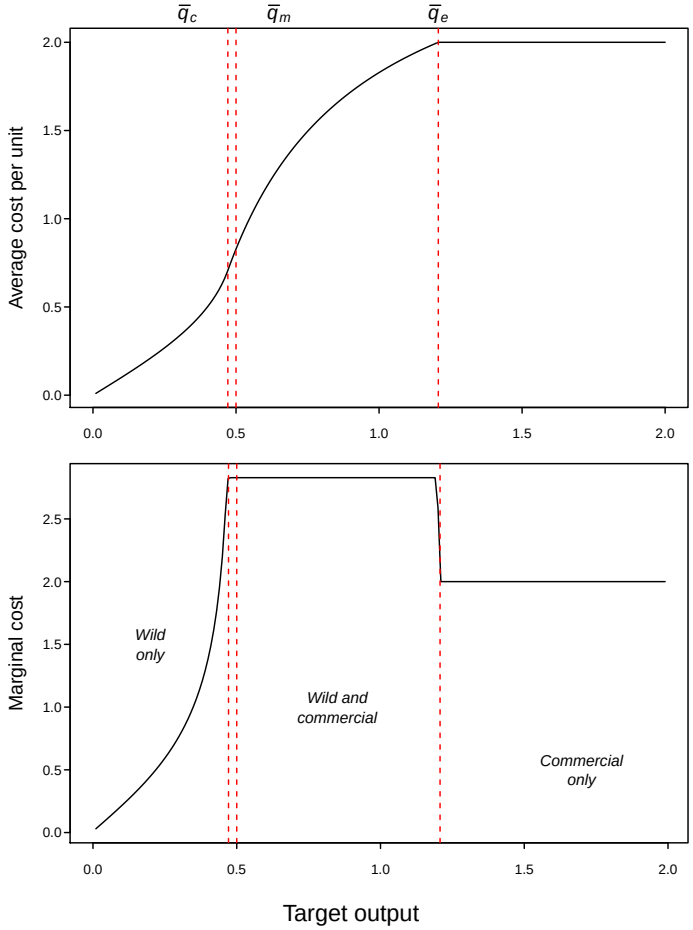

FIG. 4 The average cost of producing a unit output (a) and the LMC, $\partial C/\partial \bar{q}$ (b), as functions of the target output, $\bar{q}$. Vertical lines correspond to the threshold values of $\bar{q}_c = 0.4714045$, $\bar{q}_m = 0.5$ and $\bar{q}_e = 1.207107$, respectively. Other parameters: $\kappa = 1$, $g = 1$, $w_1 = 1$, $w_2 = 1$ and $\alpha = 1/2$.

possible by the usage of commercial bees; the total pollination levels increase, Fig. 3d, although the wild bee population decreases (see Fig. 3c).

3. Region 3: Commercial bees only

For values of $\bar{q}$ corresponding to Region 2, the optimal costs calculated by equations (10) and (15) are similar, but $c(x_1)$ reaches lower values if $y > 0$ (Region 2) – see Fig. 2b. As $\bar{q}$ increases, both curves shift upwards, but at different rates (*cf.* Fig. 2b with Figs. 2c and 2d). At $\bar{q} = \bar{q}_e$ the minimum costs using equations (10) and (15) are the same. Thus, for $\bar{q} = \bar{q}_e$ the solution of the optimality problem is not unique; selection of two different combinations of $(\hat{x}_1, \hat{x}_2)$ (both of

which satisfy $q(\hat{x}_1, \hat{x}_2) = \bar{q}$) results in identical cost values. This transition can be also seen in Fig. 1, where the straight line corresponding to the cost function touches the isoquant line at two places. The threshold value can be found by equating the optimal costs calculated from (10) and (15):

$$\bar{q}_e = \frac{\kappa w_2^2 (1-\alpha)}{(w_1 + w_2 g)\Delta_1^{\alpha} - (1-\alpha) w_2 \left(w_1 \Delta_2^{\alpha} + w_2 \Delta_2^{1-\alpha}\right)} . \tag{21}$$

For $\bar{q} > \bar{q}_e$, the optimum given by (15) is lower. This solution corresponds to $\hat{x}_1 > \kappa/g$ and so to $y = 0$, resulting in the local extinction of wild bees. To understand this transition, we need to look at output levels which depend on both pesticide use and pollination services. At $\bar{q} = \bar{q}_e$ the management strategy undergoes a substantial shift. Instead of relying largely on the increase in the pollination services (see Fig. 3d), the farmer switches to a high use of pesticides (see Fig. 2a) and a lower use of commercial bees (see Fig. 2b). Note that the further increase in the target output will be achieved by increasing the pesticide use more than by increasing the commercial bee population; compare the slopes in Figs. 3a and 3b for $\bar{q} < \bar{q}_e$ and for $\bar{q} > \bar{q}_e$.[5]

The shift in the management strategy causes the wild bees population to collapse (see Fig. 2c). The total pollination services go down at $\bar{q} = \bar{q}_e$, but continue to increase afterwards. Again, the LMC does not depend on $\bar{q}$ and for the parameters used here is lower than in Region 2:

$$\frac{\partial c}{\partial \bar{q}} = w_1 \Delta_2^{\alpha} + w_2 \Delta_2^{1-\alpha}. \tag{22}$$

This adds another incentive for farmers to switch to the new management strategy – leading to extinction of wild bees – as this will not only allow to increase their output, but also to lower its marginal costs.

Proposition 3 *A high target output and a lower LMC can be achieved by increasing the reliance on pesticide use rather than pollination, leading to the local extinction of wild bees.*

B. Sensitivity analysis

1. Sensitivity to changes in factor prices

In this section we explore how sensitive the obtained results are to changes in the price of pesticides and commercial bee prices. The threshold output values $\bar{q}_c$ and $\bar{q}_e$ depend on the pesticide

[5] This can also be shown by noting that $\Delta_1 < \Delta_2$, hence the slope of x_1 as a function of $\bar{q}$ is larger in Region 3 than in Region 2.

price, w_1, (see Fig. 5) and on the price of commercial bees price, w_2, (see Fig. 6). As w_1 increases, Region 2 (coexistence of commercial and wild bees) widens. The introduction of commercial bees becomes increasingly attractive as the price of pesticides, w_1, increases (red line in Fig. 5), as it allows the farmer to lower the usage of pesticides and rely more on pollination to reach the target output $\bar{q}$, even if $\bar{q}$ is substantially lower than $\bar{q}_m$. As expected, the option of switching to increased pesticide usage becomes less attractive as w_1 increases (see black line in Fig. 5).

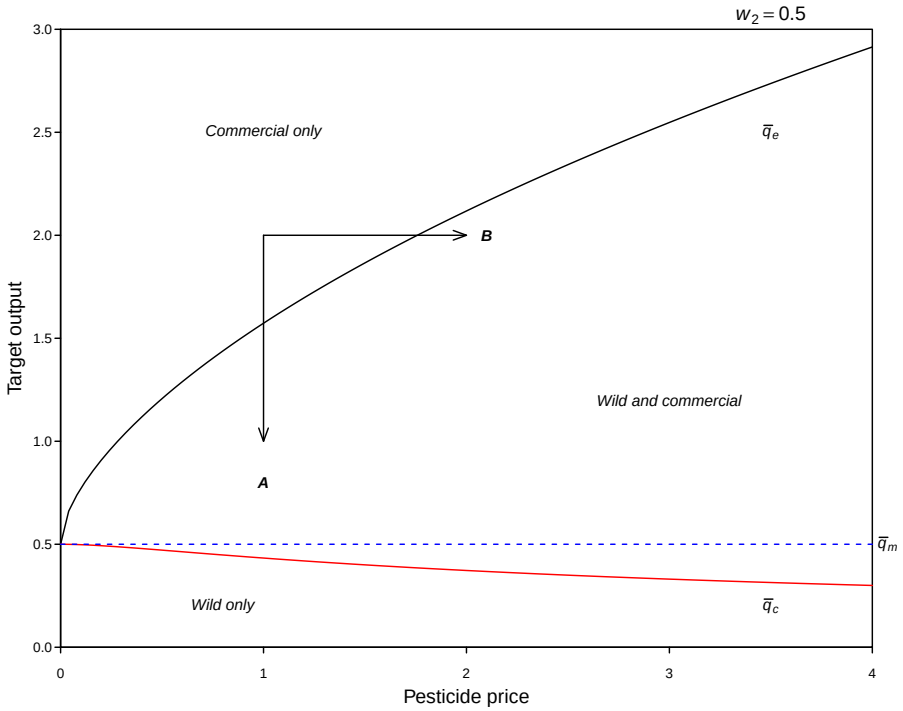

FIG. 5 Ecological outcome under the optimal management strategy as a function of the pesticide cost, w_1, and the target output, $\bar{q}$; $w_2 = 0.5$. Lines represent the threshold budget values, $\bar{q}_c$, $\bar{q}_m$ and $\bar{q}_e$. Other parameters: $\kappa = 1$, $g = 1$ and $\alpha = 1/2$. Arrows and letters denote potential management options to restore wild bees; for details see main text.

If the commercial bees price, w_2, increases, Regions 1 and 3 expand and Region 2 contracts (see Fig. 6). For instance, it becomes less attractive for farmers to employ more commercial bees for low $\bar{q}$ values (red line in Fig. 6), but it also becomes more likely that farmers intensify pesticide

usage (black line in Fig. 6).

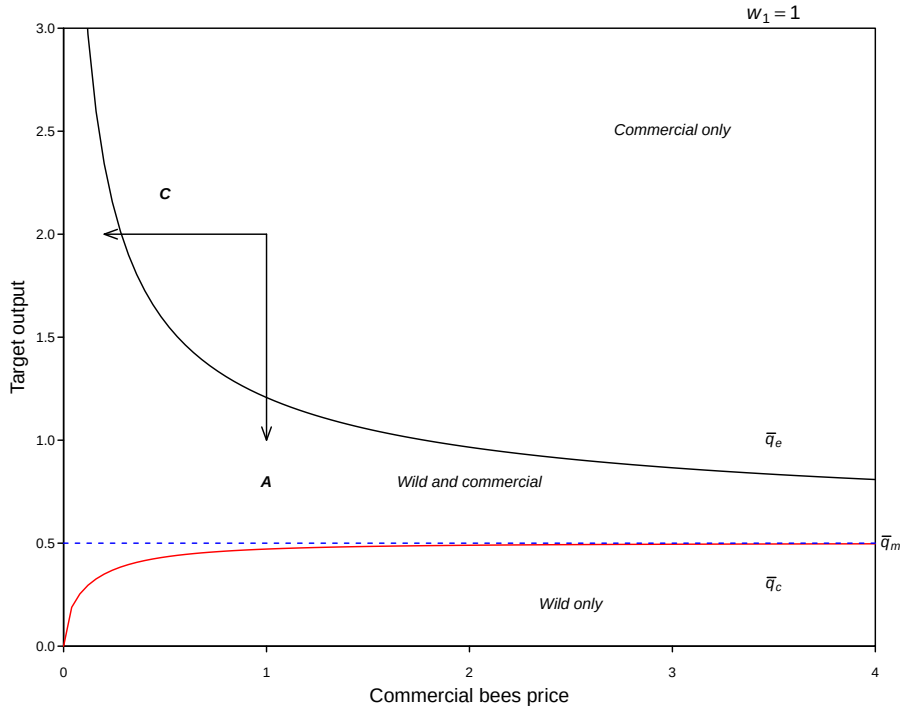

FIG. 6 Ecological outcome under the optimal management strategy as a function of the commercial bees cost, w_2, and the target output, $\bar{q}$; $w_1 = 1$. Lines represent the threshold output values, $\bar{q}_c$, $\bar{q}_m$ and $\bar{q}_e$. Other parameters: $\kappa = 1$, $g = 1$ and $\alpha = 1/2$. Arrows and letters denote potential management options to restore wild bees; for details see main text.

2. Sensitivity to changes in ecological parameters

There are two relevant ecological parameters in the model: carrying capacity, κ, and the effect of pesticide on wild bees, g, as bees are assumed to respond instantaneously to the management options (i.e., r is very large). The threshold output values, $\bar{q}_c$ and $\bar{q}_e$, depend linearly on κ (see Fig. 7). As the carrying capacity increases, wild bees are able to provide most of the pollination services. As a result, both Region 1 (wild bees only) and Region 2 (coexistence of commercial

and wild bees) widens and Region 3 (commercial bees only) narrows.

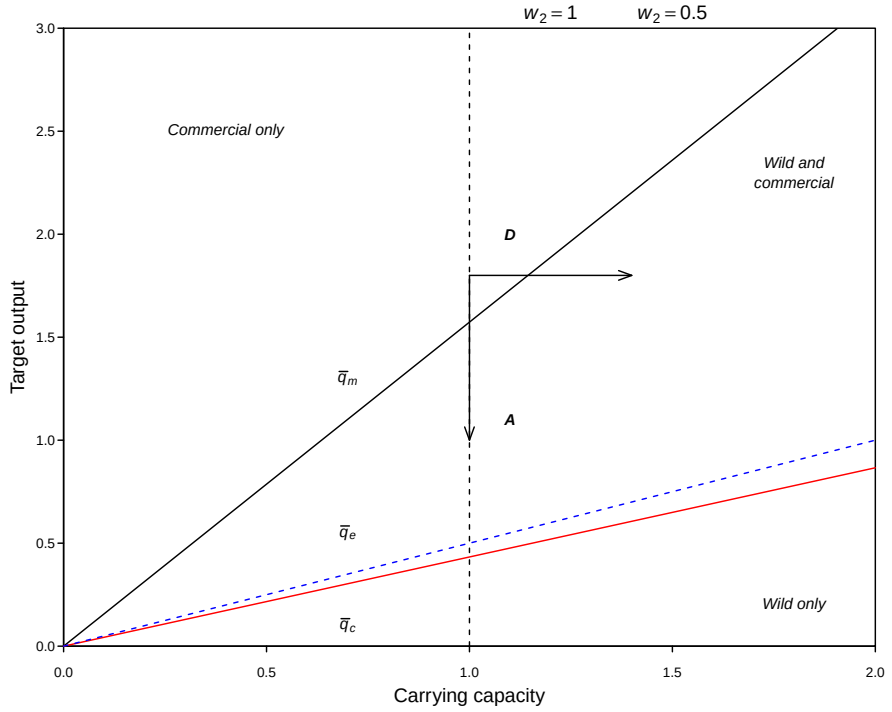

FIG. 7 Ecological outcome under the optimal management strategy as a function of the wild bees carrying capacity, κ and the target output, $\bar{q}$. Lines represent the threshold output values, $\bar{q}_c$, $\bar{q}_m$ and $\bar{q}_e$. Other parameters: $w_1 = 1$, $w_2 = 0.5$, $g = 1$, and $\alpha = 1/2$. Arrows and letters denote potential management options to restore wild bees; for details see text.

The dependence of the threshold values on the parameter describing the effect of pesticides on wild bees, g, is more complicated. As g increases, Region 3 expands and Regions 1 and 2 contract (see Fig. 8). Thus, choosing pesticides that impact more on wild pollinator dynamics will make the option of reliance on pesticides only more attractive. Interestingly, the discrepancy between $\bar{q}_c$ and $\bar{q}_m$ increases as g becomes smaller. Thus, the switch to Region 2 where commercial bees are economically viable occurs for relatively small values of $\bar{q}$, which in turn are associated with relatively small levels of pesticides and therefore small effect on wild bees. As a result, farmers might opt for the introduction of commercial bees, even though wild bees are still capable of

providing pollination levels.

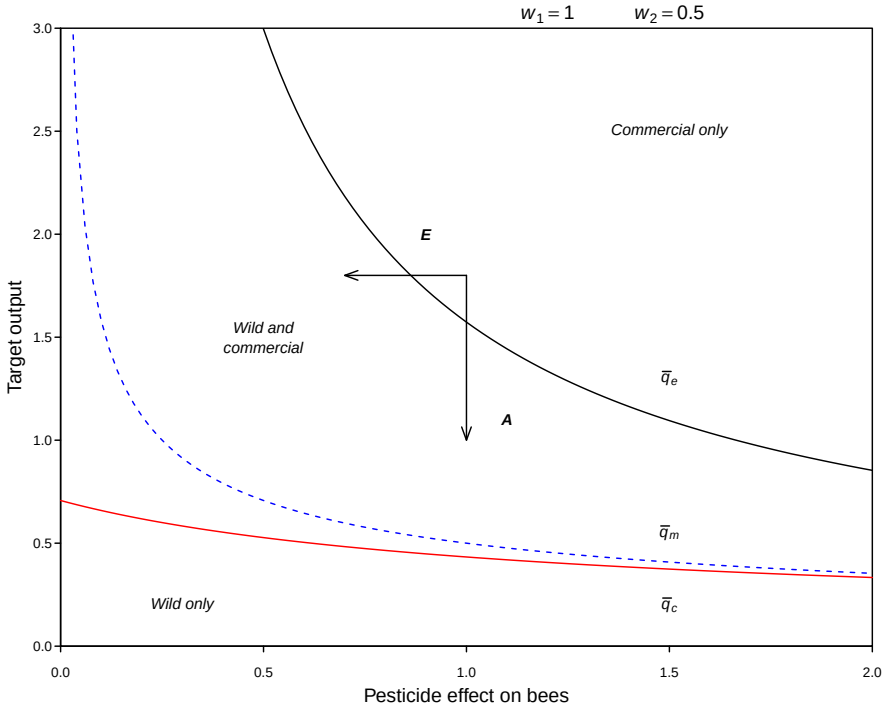

FIG. 8 Ecological outcome under the optimal management strategy as a function of the effect of pesticides on wild bees, g, and the target output, $\bar{q}$. Lines represent the threshold output values, $\bar{q}_c$, $\bar{q}_m$ and $\bar{q}_e$. Other parameters: $w_1 = 1$, $w_2 = 0.5$, $\kappa = 1$, and $\alpha = 1/2$. Arrows and letters denote potential management options to restore wild bees; for details see text.

C. Strategies for conservation and restoration of wild bees

Our results identify a number of strategies that a social planner can use to prevent the extinction of wild bees or to restore the wild bees population. The most obvious strategy is to lower the target output, $\bar{q}$ (see strategy A in Figs. 5, 6, 7 and 8). As shown in Fig. 3, lowering $\bar{q}$ makes the "ecologically safe" strategies economically more attractive (by this we mean such a combination of $(\hat{x}_1, \hat{x}_2)$ for which wild bees can exist or co-exist with commercial bees). As an alternative to

lowering $\bar{q}$, the social planner can increase the pesticide price, w_1, (strategy B in Fig. 5) or decrease the commercial bee price, w_2, (strategy C in Fig. 6), as this might lead to re-establishment of wild bees.

Alternatively, farmers can change the carrying capacity for the wild bee population by expanding field margins or by providing refugia for wild bees, for instance. We do not model explicitly any costs associated with such practices; instead we provide evidence that increasing the wild bees carrying capacity, κ, can shift the system from Region 3 (wild bees extinct) to Region 2 (coexistence of wild and commercial bees) – see strategy D in Fig. 7). In this way, increased capacity of the wild bee population to provide pollination services implies less use of pesticides and less commercial bees, hence leading to the reduction of total cost.[6]

Finally, use of pesticides that are less damaging to wild bees provides an alternative strategy that can lead to a re-introduction of these bees, if used in conjunction with commercial bees (strategy E in Fig. 8). Interestingly, the effect is most pronounced for high target outputs, when even small changes in the parameter describing the effect of pesticides on wild bee population, g, can lead to a shift in the selection of management practices from Region 3 to Region 2.

These results can be summarised as:

Proposition 4 *In addition to an obvious strategy of reducing $\bar{q}$, increasing the pesticide price, w_1, decreasing the commercial bee price, w_2, increasing the wild bees carrying capacity, κ, or switching to less damaging pesticides (reducing g) might be helpful in shifting the management practices from Region 3 to Region 2 to allow recovery of wild bees.*

D. Model extension: Nonlinear functional forms

In the model considered above, based upon a mixture of Cobb-Douglas and linear production functions, farm output is an increasing function of the pollinator population size (both wild and commercial), with a gradient declining to zero, but without an asymptote (see Fig. 9). Thus, by increasing the commercial bee density one can make output to be arbitrarily large. In reality, the functional relationship between pollinator population size and the delivery of pollination services is likely to be an asymptotic type of function, so that output cannot increase unlimitedly. Similar features characterises pesticide use. Adding nonlinear functional forms for y, x_1 and x_2 signifi-

[6] Note that we do not directly model the costs to the farmer of increasing this carrying capacity.

cantly complicates the model and, therefore, we only consider Region 2 which corresponds to a high level of pesticide use and a high commercial bees density (and to $y = 0$). This is the range where the saturation effect is most likely to occur; this assumption will be relaxed in future work. For simplicity we also assume $\alpha = 1/2$.

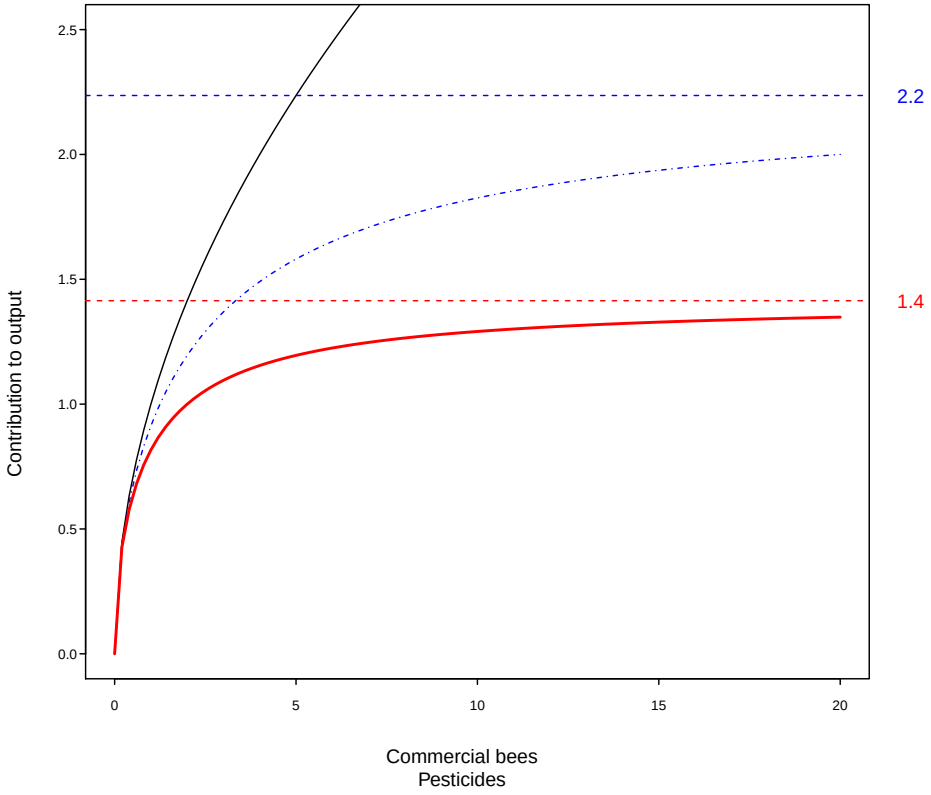

FIG. 9 Functional forms for the output dependence on pollination (here on commercial bees only), for the standard Cobb-Douglas function, Eqn. (5) with $\eta = 0$ (thin line), and for the nonlinear form with $\eta = 0.1$ (dotted line), and with $eta = 0.5$ (thick line). The graphs are the same for pesticide use ($\rho = 0$, $\rho = 0.1$, $\rho = 0.5$, respectively). Horizontal lines show the respective asymptotes when applicable, also indicated in the margin. $\alpha = 1/2$.

Given this setting, let us consider the minimization of the cost $c(x_1, x_2) = w_1 x_1 + w_2 x_2$ subject to the following constraint:

$$q(x_1, x_2) = (f(x_2))^{1/2} g(x_1)^{1/2} = \bar{q}, \tag{23}$$

where it is assumed that $y = 0$. Firstly, assume that the pesticide functional form is linear, $g(x_1) = x_1$, but the pollination production function tends asymptotically to a limit according to:

$$f(x_2) = \frac{x_2}{1 + \eta x_2}, \tag{24}$$

where $1/\eta$ is the asymptotic value for the pollination service (see Fig. 9). The optimal values read as:

$$\begin{aligned} \hat{x}_1 &= \sqrt{\frac{w_2}{w_1}}\,\bar{q} + \eta\bar{q}^2 \\ \hat{x}_2 &= \sqrt{\frac{w_1}{w_2}}\,\bar{q} \\ c(\hat{x}_1, \hat{x}_2) &= 2\sqrt{w_1 w_2}\,\bar{q} + \eta w_1 \bar{q}^2\,. \end{aligned} \tag{25}$$

Note that given $\alpha = 1/2$, v becomes equal to 1 and Δ_2 is simplified to w_2/w_1 (*cf.* Eqn. (14)) so the above result is compatible with equation (15) if $\eta = 0$. Thus, $\hat{x}_2$ is unaffected by the nonlinearity in the pollination production function. However, the pesticide use, $\hat{x}_1$ must increase to offset the relative inefficiency of pollination. Consequently, the LMC now increases as a function of the target output $\bar{q}$:

$$\frac{\partial c}{\partial \bar{q}} = 2\sqrt{w_1 w_2} + 2\eta w_1 \bar{q}\,. \tag{26}$$

Secondly, assume that the pollination production function is not limited, so $f(x_2) = x_2$, but that the pesticide efficiency is an asymptotic function of x_1:

$$g(x_1) = \frac{x_1}{1 + \rho x_1}, \tag{27}$$

where $1/\rho$ is the asymptotic value for the pesticide efficiency (see Fig. 9). The optimal values are then:

$$\begin{aligned} \hat{x}_1 &= \sqrt{\frac{w_2}{w_1}}\,\bar{q} \\ \hat{x}_2 &= \sqrt{\frac{w_1}{w_2}}\,\bar{q} + \rho\bar{q}^2 \\ c(\hat{x}_1, \hat{x}_2) &= 2\sqrt{w_1 w_2}\bar{q} + \rho w_2 \bar{q}^2\,. \end{aligned} \tag{28}$$

As before, equation (28) is compatible with equation (15) if $\rho = 0$. The solution mirrors the previous case in that the optimal use of pesticides is unaffected but that the commercial bee population must increase to offset the inefficiency in pest control. The cost, again, increases and the additional term is a quadratic function of $\bar{q}^2$; the LMC increases with $\bar{q}$:

$$\frac{\partial c}{\partial \bar{q}} = 2\sqrt{w_1 w_2} + 2\rho w_2 \bar{q}\,. \tag{29}$$

Finally, if both pollination and pesticide production functions are limited, i.e. $\eta > 0$ and $\rho > 0$, then:

$$\begin{aligned} \hat{x}_1 &= \frac{\bar{q}}{1-\eta\rho\bar{q}^2}\left(\sqrt{\frac{w_2}{w_1}}+\eta\bar{q}\right) \\ \hat{x}_2 &= \frac{\bar{q}}{1-\eta\rho\bar{q}^2}\left(\sqrt{\frac{w_1}{w_2}}+\rho\bar{q}\right) \\ c(\hat{x}_1,\hat{x}_2) &= \frac{\bar{q}}{1-\eta\rho\bar{q}^2}\left(2\sqrt{w_1w_2}+(w_1\eta+w_2\rho)\bar{q}\right) . \end{aligned} \tag{30}$$

In this case it is not possible to satisfy an arbitrarily increasing target output and the maximum possible $\bar{q}$ is given by $1/\sqrt{\eta\rho}$. This is due to the fact that one cannot offset a saturation in one factor (say, x_1) by increasing the other (say, x_2). Both x_1 and x_2 need to be set very high, resulting in a disproportional cost increase.[7] This leads us to contend:

Proposition 5 *Introducing of saturating functional forms for x_1 or x_2 does not change the results qualitatively for Region 2, but increases the cost and makes LMC a nonlinear function of $\bar{q}$. If the contribution of both pesticide use and pollination services is of an asymptotic form, there is a maximum output that can be achieved.*

We cannot obtain the thresholds $\bar{q}_c$ and $\bar{q}_e$ analytically in this case, but one can draw some general conclusions by observing that higher levels of x_1 (and x_2) are needed to produce the same output level, if $\rho > 0$ ($\eta > 0$). This will cause wild bees to become extinct at lower levels of the target output, $\bar{q}$, as compared to the standard Cobb-Douglas equation. We therefore expect the threshold values $\bar{q}_c$ and $\bar{q}_e$ to be lower in this case.

IV. DISCUSSION

In the paper we studied the dependence of cost-minimising management strategies on the target farm output, $\bar{q}$. Thus, given the target, the farmer will chose a certain strategy, minimising the private costs of output. We have shown that depending on the $\bar{q}$, different strategies emerge, in which it is more profitable for the farmer to either refrain from using commercial bees when $\bar{q} < \bar{q}_c$, or to use them if $\bar{q} \geq \bar{q}_c$. Use of commercial bees allows the farmer to move beyond yield levels that can be achieved by natural pollination ($\bar{q} > \bar{q}_m$). This is achieved by increasing both pesticide use (Fig. 3a) and the total pollination levels (Fig. 3d).

[7] We do not explicitly state the LMC in this case, but it tends to infinity as $\bar{q} \to 1/\sqrt{\eta\rho}$.

Interestingly, we also show that there are two competing strategies that the farmers can use to achieve an output exceeding $\bar{q}_e$: a low-pesticide, high-pollination strategy or a high-pesticide, low-pollination strategy (*cf.* Fig. 3a and Fig. 3d). There are good reasons to move to the latter management strategy, as it leads to a lower long run average cost (LAC) of producing a unit output (see Fig. 4a) and a lower long run marginal cost (LMC) if $\bar{q} \geq \bar{q}_e$ (see Fig. 4b). However, this strategy also leads to local extinction of wild bees if $\bar{q} \geq \bar{q}_e$ holds.

Local extinction occurs because the link between the wild bee population and pesticide use is broken, and the farmers do not get a signal that the wild bees are declining. This is caused by the availability of commercial bees. However, we show that the ecological effect of introduction of commercial bees depends on the intensity of production. In the low-intensity production situation, the introduction of commercial bees leads to an increase in the use of pesticides and therefore to a decrease in the wild bees populations (see Fig. 3). However, Fig. 6 shows that a low commercial bee price (as we observe nowadays) can be associated with a more ecologically desirable outcome, as it discourages farmers from over-reliance on pesticide use in the production system. This surprising and perhaps non-intuitive result originates from our assumption that pollination and pesticides are substitutes; both this assumption and the results of our model can be tested experimentally.

We also note that the transition at $\bar{q} = \bar{q}_e$ is an abrupt one. The wild bees population might be relatively low but healthy (ca. 20% of the carrying capacity for parameters used in this paper – Fig. 3c) for $\bar{q}$ smaller but close to $\bar{q}_e$. However, for $\bar{q} > \bar{q}_e$, farmers are likely to switch to a high-pesticide strategy and the population of wild bees will then likely become extinct. Thus, a small change in the target output, caused for example by a surge in soft fruit prices, can make the high-pesticide use strategy economically attractive, leading to a dramatic decline in the wild bees population.

The threshold output $\bar{q}_e$ is therefore very important from a policy perspective. The social planner faced with a system in which wild bees are locally extinct, might want to formulate policies leading to their re-establishment. The simplest policy is to encourage farmers to lower their target output, $\bar{q}$ below the threshold value, $\bar{q}_e$. Alternatively, the social planner might want to increase the threshold value, $\bar{q}_e$. This can be achieved by: increasing the price of pesticides (increasing w_1)[8], encouraging farmers to stimulate wild bee population (increasing κ), switching to alterna-

[8] This could be done by imposing a tax on pesticide use, for instance.

tive pesticides (decreasing g), and/or decreasing the price of commercial bees (decreasing w_2). Although the formula for $\bar{q}_e$ is known [see equation (21)], and it depends on both ecological (κ, g) and economic (w_1, w_2, α) factors, it is not clear whether it can reliably be estimated in practice. This means that the threshold might be difficult to predict in advance and the transition between management strategies might be difficult to detect (Taylor, 2009).

While we have focused on pesticide use, the switch can also be caused by other factors. For example, if the carrying capacity of wild bees, κ, decreases due to a reduction in the size or quality of habitat, the threshold values $\bar{q}_c$ and $\bar{q}_e$ will decrease (see equations (12) and (21)). If the farmer still wants to attain the same target output, she will need to change the strategy, depending on the combination of the target output and the pesticide and commercial bees prices. If the target output is low, under current conditions ($\kappa = 1$), the farmer does not need to use commercial bees (see strategy X in Fig. 10).

A decrease in the carrying capacity, for example triggered by bad weather conditions or changes in land use causing a reduction in foraging or nesting areas for wild bees, leads to a shift in the optimal farm strategy (see Fig. 10) – point X now lies in Region 2 demarcated by the broken lines. Thus, the farmer might feel that the change in environmental conditions forces her to introduce commercial bees.

If the level of output is high and the farmer already uses commercial bees – strategy Y in Fig. 10 – the reduction in the carrying capacity means switching to a high-pesticide use (as point Y now lies in Region 3) with an associated local extinction in the wild bee population.

As noted above, the change in the wild bee population as the system moves from Region 2 to Region 3 is very abrupt. For instance, we might be dealing with what looks like a farm with a healthy population of wild bees (although smaller than their carrying capacity) for one set of environmental conditions κ. A small change in the environmental conditions results in a limited loss in their ability to pollinate which in turns leads to the farmer modifying her management practices to keep up with demand for agricultural produce. This modification results in a rapid local extinction of wild bees as the threshold, $\bar{q}_e$ is crossed. The importance of maintenance of a conducive environment for wild bees has also been emphasised by Keitt (2009), who also concluded that bee populations would decline abruptly if environmental conditions (in this case, habitat) deteriorated below a certain threshold. The results of this paper support this conclusion, as increasing the carrying capacity of the surrounding area would allow higher outputs without exceeding the threshold leading to population extinction.

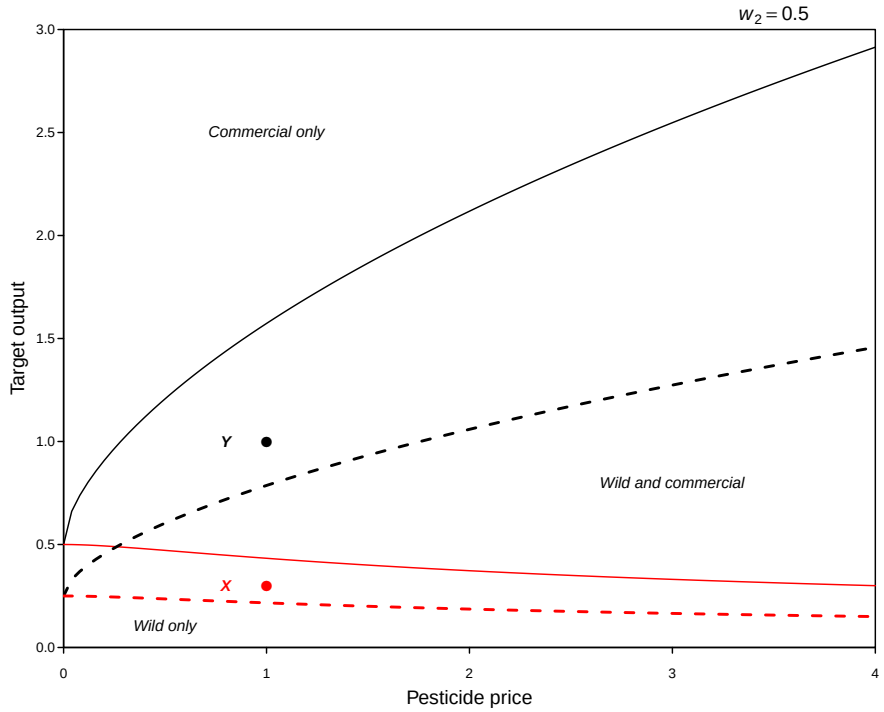

FIG. 10 The effect of changing κ on the ecological outcome under the optimal management strategy as a function of the marginal pesticide cost, w_1 and the target output, $\bar{q}$; $\kappa = 1$ (solid lines) is reduced to $\kappa = 0.5$ (broken lines). Lines represent the threshold budget values, $\bar{q}_c$ (black line) and $\bar{q}_e$ (red line). Other parameters: $g = 1$ and $\alpha = 1/2$; $w_2 = 0.5$.

We have looked at a number of management strategies allowing a shift from Region 3 to Region 2 and thus the re-establishment of wild bees. Shifting from Region 2 to Region 1 (thus removing the need to introduce commercial bees) is much more difficult and can only be done for less intense systems with $\bar{q} < \bar{q}_m$. Although commercial bees create instability by masking the decline in wild pollinators, they are indispensable if the farmer wants to move beyond $\bar{q}_m$. Moreover, in some cases the commercial bees can facilitate the re-introduction of wild bees (see management strategy C in Fig. 6) by reducing the reliance of pesticides to achieve given target output.

The particular functional forms are chosen in this paper for their general applicability to a wide range of agri-ecological problems as well as for their simplicity; this applies to both the Lotka-

Volterra form for the dynamics of wild bees and to the Cobb-Douglas production function. The latter has been chosen over alternative forms to model pollination services because it reflects a complete reliance of the production system on wild or commercial bees. This assumption will be accurate for many crops with a high dependence on pollinators, such as many berries and orchard fruits. In particular, if y and x_2 are both zero, the output is zero, independently of x_1. Although in our paper x_1 represents the use of pesticides, it can also be interpreted as any agricultural practice that (i) is essential for the output generation, and (ii) affects wild bee populations; these include monoculture, selection of crops, and destruction of field margins. This generalisation strengthens the case for the particular functional form. Finally, we assume that commercial bees are not affected by pesticides. This assumption can be relaxed although then no analytical solutions can be found. Preliminary numerical results show that the cost is increased as more commercial bees need to brought onto the farms to compensate for the loss of population, but the overall results and in particular the threshold behaviour are not changed.

In our model the changes are fully reversible (the wild bees population reacts immediately to changes in x_1), but in reality such shifts are likely to be irreversible. This will be problematic if the strategy taken then becomes uneconomic, for example due to an increase in the price of pesticides, or commercial bees. Such a switch has already occurred in the apple growing region of Sichuan, China, where human pollinators were used as substitutes, allowing a high pesticide, low habitat strategy to continue. When human pollination became too expensive, the only option for farmers was to leave the market altogether, and discontinue apple production. When declines in wild capital such as wild pollinators are irreversible, and there is uncertainty over which source of capital will be most beneficial in the future, there is a value to maintaining the natural capital for future use (Arrow & Fisher, 1974; Kassar & Lasserre, 2004). This "option" value is an incentive for conserving wild pollinators, and will be positive even if there are no immediate advantages of supporting wild pollinators.

The wild bee population modelled here will often be made up of multiple populations of bee and non-bee pollinators (such as hover flies). The presence of multiple pollinator groups could buffer the system to extinction; the relative tolerance of pollinator networks to extinction has been shown by Kaiser-Bunbury *et al.* (2010); Memmott *et al.* (2004). However these studies do not assume that threats to the different populations are correlated. While different pollinators groups may respond in slightly different ways to external pressure such as pesticide use, the effects are likely to be negative on all groups, and may be stronger on non-bee pollinators as these are

smaller (Goulson, 2013). The model discussed in this paper is unique in its inclusion of a chronic threat to pollinators (pesticide use), which is likely to affect all pollinator groups. The benefit of maintaining multiple groups of ecosystem service providers as insurance against a fluctuating environmental was discussed by Baumgartner (2007). The problem considered here differs as we consider a threat which is likely to be detrimental on the whole pollinator community, means that holding diverse pollinators will not be beneficial, however maintaining both commercial and wild bees will be valuable as options for pollination provision in the future.

In our model farmers act myopically and only optimise the output given their budget. We also assume that wild bees respond instantaneously to the changes in the management. In effect, the model demonstrates behaviour that would be observed if the farmer can make planning decisions once and see the impact of those in the future without the chance of adaptation. This may well be realistic, as farmers are unlikely to be able to detect small changes in wild bee populations from year to year, but will notice dramatic decreases in pollination services over longer periods of time. However, the model, and in particular its agent-based extension, can be generalised to include different planning horizons for farmers (aside from the current, myopic case) as well as the long-term dynamics of bees, for example in the form of a dynamic model of Khoury *et al.* (2011).

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