Pesticides and Bees: ecological-economic modelling of bee populations on farmland.

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Abstract

Production of insect-pollinated crops typically relies on both pesticide use and pollination, leading to a potential conflict between these two inputs. In this paper we combine ecological modelling with economic analysis to investigate the effects of pesticide use on wild and commercial bees, whilst allowing farmers to partly offset the negative effects of pesticides on bee populations by creating more on-farm bee habitat. Farmers have incentives to invest in creating wild bee habitat to increase pollination inputs. However, the optimal allocation of on-farm habitat strongly depends on the negative effects of pesticides, with a threshold-like behaviour at a critical level of the impairment. When this threshold is crossed, the population of wild bees becomes locally extinct and their availability to pollinate breaks down. We also show that availability of commercial bees masks the decrease in pollination services which would otherwise incentivise farmers to conserve the wild pollinator population. If commercial bees are available, optimum profit may be achieved by providing no habitat for wild bees and allowing them to go extinct.. The paper demonstrates the importance of combining ecological modelling with economics to study sustainability in the provision of ecosystem services in agro-ecosystems.

Keywords: pollination, pesticides, wild bees, commercial bees, ecological-economic modelling.

1. Introduction

Globally, around three-quarters of food crops are at least partly dependent on insect pollination [1], and this share has been rising over the past 50 years [2]. Although the data in Aizen and Harder [2] relates to animal pollination in general, not insect pollination specifically, they note that the demand for pollination in agriculture has risen about 6 times more than the population of honey bees over the least 50 years. Ensuring sufficient pollination of these crops will be challenging in the future, due to adverse pressures on the supply of pollination services. Wild insect pollinator populations are threatened by both habitat loss, declines in foraging resources [3,4] and agricultural intensification [5,6], leading to population declines [6,7]. Honeybees are used to supplement or substitute wild pollinators, along with other commercial pollinators such as factory-reared bumblebees [8], although the majority of insect pollination for most crops is currently delivered by wild pollinators [9,10].

Commercial pollinators can be adequate substitutes for wild pollinators for many crops, [11,12], but the use of commercial pollinators is not without risk. Honeybees have suffered losses in recent years due to the abandonment of hives (Colony Collapse Disorder), the impacts of the *Varroa* mite and associated diseases [13] and falling numbers of bee keepers in some countries [14]. If losses of honeybees occur over a wide area, there can be an impact on the supply of these insects for pollination services, which can lead to cost increases to farmers; for example, prices for honeybee hire for use on almond farms doubled between 2006 and 2008 in the US [15]. Given the risks associated with reliance on commercial pollination sources, maintaining viable wild pollinator populations is likely to be crucial for sustaining the production of insect-pollinated crops into the future [10,16].

One of the factors implicated in the decline of insect pollinators is the use of pesticides. There is growing evidence of negative effects of commonly used insecticides on population- determining traits such as foraging rates and navigation in bees, on the overall growth and performance of colonies, and on the pollination services that they provide [17–24]. Awareness of this evidence has led to the temporary banning of the use on flowering crops of a widely used group of insecticides – neonicotinoids – within the European Union, but other insecticides are still widely used.

Farmers of insect pollinated crops therefore face a dilemma, as one input (pesticides) is potentially dangerous to another (pollinators). One option, not investigated here, is to switch production to organic principles, and use zero pesticides. However, in the majority of global agricultural systems, abstaining from the use of all pesticides is not usually possible without sacrificing yields. Farmers must either attempt to reduce the impact of pesticides on wild pollinators, or increase the use of commercial pollinators, as these can in some cases be replenished year after year. Wild pollinators require habitat either off-farm or within the farm area. Although pollinating insects can forage over large distances, in intensive agricultural landscapes there is a decay in visitation of flowers by pollinators with increasing distance from the nearest habitat patch [25,26]. To offset this, farmers can encourage wild bees to nest within foraging distance of crops by providing nesting habitat and providing alternative foraging resources on the farm for when the crop is not in flower [3]. The effect of such interventions has been found to be strongest in intensively farmed areas [27] but depends also on the spatial location of bee-friendly habitat [28,29]. Hence, local or field-scale management practices may offset the negative impacts of intensive monoculture agriculture on pollination services to some extent [30].

In this paper, we develop an ecological-economic model to investigate the relations between two agricultural inputs, pollination and pesticides, and two sources of pollinators with different characteristics; commercial pollinators, which can be replaced at a cost, and wild pollinators, which rely on a population being sustained within the farm area. Dedicating some of the farm area to sustain wild pollinators (eg by cultivating wild flower strips) is assumed to be costly [31]. The model is parameterised using farm management data for strawberries, a relatively well-studied crop on which both wild and commercial bees are used. The neonicotinoid pesticide thiacloprid is also commonly used in strawberry farming to protect the crop from destructive pests such as capsid bugs. Our modelling framework is, however, generalizable to other cropping systems where conflict occurs between pesticides, crop area and wild bee persistence, such as almonds. Our model differs from previous modelling attempts which have looked at either habitat considerations [28,29] or pesticide impacts [32] in isolation. In contrast, we combine these factors co-determining pollinator populations in a realistically-parameterised model which includes both economic and ecological behaviours.

2. Methods: the ecological economic model.

The model has three main linked components: the dynamics of the wild bee population; the production function which links bee populations and pesticide use to output, and farmers' decisions over which inputs to employ via a profit function. We assume a farm that produces a single crop; parameters are chosen to represent a typical soft-fruit production system [33,34]. The farm has an area A which is divided into a wild bee habitat conservation area, vA, and a cropping area $(1-v)A$, where v is the proportion assigned to the wild bee habitat (for modelling purpose we vary this between 0% and 70%). Honeybees and commercially reared bumblebees are both used in fruit production. For simplicity we consider all commercial (non-wild) pollinators to have the characteristics of commercially reared bumblebees in terms of nest size and pollinating efficiency, and generate results for both a scenario where all pollinators are affected by pesticides, and a scenario where wild bees are affected but commercial bees are not. These choices correspond to extreme situations; in reality it is possible that commercial pollinators are affected, but to a slightly lesser extent than wild bees; efforts can be made to minimise chemical exposure to commercial nests such as shutting the bees inside the boxes before spraying, or only spraying before the placement of nest boxes. Wild nests, on the other hand, may be exposed to multiple sprays of insecticides and though both wild and commercial bumblebee nests are vulnerable to disease, wild nests are more likely to have infestations of parasites at the time spraying occurs (commercial bee boxes *should* arrive at the farms free from disease and therefore only pick up infections and parasites from that point onwards) putting wild bees at increased risk of any interactive effects between parasites and pesticides [35]

For simplicity we are assuming that the farm is a closed system with regard to wild or commercial bees, so that bees are not coming in from surrounding non-farmed habitat or leaving the farm. In reality bees do move between farms, which may buffer some of the more extreme effects predicted by our models (such as local extinction), and also means that bee populations supported by the actions of one farmer may benefit their neighbours. We also assume no transfer of pesticides from outside the farm.

Wild bee population

The dynamics of the wild bee population is described in terms of $N_{[t]}$ – a number of nests in a given year, t. This changes according to equation (1):

$$N_{[t]} = \min\left(R\left(N_{[t-1]} - D_{[t-1]}\right), K\right) \qquad (1)$$

where $N_{[t-1]}$ is the number of nests at the beginning of year t-1, $D_{[t-1]}$ represents the number of nests that die during year t-1. $N_{[t-1]}-D_{[t-1]}$ represents the number of live nests at the end of year t-1 that will reproduce in the following year. R is the reproduction rate, i.e. the number of new nests that each reproducing nest produces in the following year. The carrying capacity, K, is calculated from the likely on-farm nesting densities of wild bumblebees, wN, under the assumption that wild bees nest in the conservation area only, $K= wN\ v\ A$.

Not all bumblebee nests will produce queens in a given year, and the likelihood of reproduction will depend in part on nest size. Pesticides can indirectly impact the likelihood of a nest reproducing by impairing the performance of foragers or increasing worker mortality and thus decreasing a nests' ability to gather and process resources. These impacts can lead to increased colony failure, either through early colony death or by limiting the number of new queens produced [19,20,23]. Bryden et al. [32] suggested a model in which the probability of nest death was inversely proportional to the number of foragers adjusted for pesticide impairments. Here we use an equivalent deterministic model in which a proportion *dN* of nests dies in year t-1 so that:

$$D_{[t-1]} = dN \times N_{[t-1]} . \qquad (2)$$

We also consider a stochastic equivalent of model (1), with nest deaths given by a random variable binomially distributed (with the maximum number of $N_{[t]}$ and probability given by *dN*): results are qualitatively similar to the ones presented here for the deterministic model.

Although in principle *dN* can depend on time, in this model we assume the constant probability of nest death following [32],

$$dN = \frac{\mu}{\phi + wBN} \qquad (3)$$

where *wBN* is an effective number of foraging wild bees per nest, *wBN*=*wF* (1-*wI*) with *wF* being an average number of foragers per nest and *wI* the impairment factor due to pesticides. If no pesticides are used, or if pesticides are used but do not affect bees, *wI*=0; otherwise *wI*>0, reflecting for example, the effects on the navigational ability of honeybees which reduces the number of foragers which successfully return to the nest [18,19]. μ and ϕ are parameters determining the response of bumblebee population to pesticide (see Table 1).

Equation (1) can thus be rewritten

$$N_{[t]} = \begin{cases} R \times \left(1 - \dfrac{m}{j + wF \times (1 - wI)}\right) N_{[t-1]} & \text{if smaller than } K, \\ K & \text{otherwise.} \end{cases} \qquad (4)$$

The initial condition is assumed to be $N_{[0]}=K$ for t=0. Under this assumption $N_{[t]}$ will stay constant for t>0, as long as:

$$R \times \left(1 - \frac{m}{j + wF \times (1 - wI)}\right) \geq 1 \qquad (5)$$

and will decline exponentially to zero otherwise. In the following we assume such parameter values that condition (5) is always satisfied if if wI=0, i.e. if there is no impairment due to pesticides.

Pollination and yield.

The single crop is pollinated by foragers originating from both wild and commercial nests. The total effective number of foraging wild bees is given by $wB_{[t]} = wF\ (1\text{-}wI)\ N_{[t]}$, whereas for commercial bees the effective number of foragers is assumed to be constant through time but proportional to the crop area, $cB=cF\ (1\text{-}cI)\ cN\ (1\text{-}v)\ A$. Here, cF is the average number of foragers per commercial nest, cI is the impairment of commercial bees due to pesticide use, cN is the number of commercial nests per ha, and $(1\text{-}v)\ A$ is the area under the crop (here we assume that commercial nests will only be placed where the crop is located, not in the area set aside as on-farm wild bee habitat). As for wild bees, if no pesticides are used or are used but have no effect on commercial bees, then cI=0.

Both wild and commercial bees are assumed to forage across the whole farm, over both crop land and the conservation area. The resulting effective density of foraging pollinators is then given by:

$$B_{[t]} = \frac{wB_{[t]} + cB}{A} = \frac{wF\left(1 - wI\right) N_{[t]} + cF\left(1 - cI\right) cN\left(1 - v\right)A}{A} \quad (6)$$

Production.

The total farm production of a given crop in year *t* is given by $Y_{[t]} \times \left(1 - v\right)A$ where $Y_{[t]}$ is the current yield (in tonnes per ha) which is assumed to be a step-wise linear function of $B_{[t]}$. We assume that without pollinators there is a set but low proportion, αY_{max}, of a maximum yield (Y_{max}) that can be achieved. When pollination is fully supplied, the maximum yield is given by γY_{max} with γ being a maximum proportion of high quality crop [36]. For intermediate values of $B_{[t]}$ the yield per area in year *t* is given by:

$$Y_{[t]} = Y_{max} \times \min\left(\gamma, \alpha + \beta B_{[t]}\right) \quad (7)$$

where γ is the maximum proportion of good quality, α is the proportion of good quality fruits without bees and β is the incremental effect of bee visitation. The maximum attainable yield, Y_{max}, depends on pesticide use and efficiency; we choose a higher value of Y_{max}, $Y_{max.p}$, if pesticides are used, and a lower value, $Y_{max.nop}$, if they are not.

Farm economics.

There are two components to the profit function, the income from the sale of the crop and various costs, thus:

$$\text{Profit} = \text{Income} - \text{Constant costs} - \text{Cost of commercial bees} - \text{Pesticide costs}.$$

The crop is sold at price p and with commission cm so that the income is given by:

$$\text{Income} = p \times (1 - cm) \times Y_{[t]} \times (1 - v) A . \qquad (8)$$

Note that this implicitly accounts for opportunity costs associated with the crop considered here, as it includes 'lost' income due to diminished area under crop.

Total costs for each year are the sum of variable (yield dependent) costs and other costs which include the costs of wild flower seeds, pesticides and commercial bees. Harvesting and packaging costs are assumed to be variable and calculated per tonne. We divide the costs into three components, the first one which does not directly depend on the usage of commercial bees or pesticides, given by:

$$\text{Constant cost} = Cpt \times Y_{[t]} \times (1 - v) A + Cpa \times (1 - v) A + Capa \times A + Cseed \times vA \qquad (9)$$

where Cpt is the cost per tonne (harvesting and packaging), Cpa is the cost per crop area (planting, structures, fieldwork), $Capa$ is the total cost per area regardless of whether it is cropped on not (e.g. land lease costs), and $Cseed$ is the cost of maintaining the conservation area (mainly providing seed and opportunity costs other than growing the crop considered here). If commercial bees are used, there is an additional cost of buying commercial nests which is proportional to the number of commercial nests per ha and the area under crop,

$$\text{Cost of commercial bees} = bC \times cN \times (1 - v) A . \qquad (10)$$

In strawberry production, the main commercial bees used are bumblebees, which are purchased as disposable nests (sometimes called colonies) which last for up to 8 weeks. In other systems, farmers may rent honeybee hives for the duration of crop flowering.

If pesticides are used, there is additional cost associated with their purchase, assumed to be proportional to the area under crop,

$$\text{Cost of pesticides} = pC \times (1 - v)A \ . \qquad (11)$$

We assume that the primary decision is over the proportion of on-farm wild bee habitat, *v*, and this is driven by profit maximisation over a decision horizon of one year. We analyse how the optimal choice of *v* and the resulting profit vary as pesticides are used or not, whether they affect wild or commercial bees, and whether the farmer decides to use commercial bees.

Parameters.

Although the model is generic for permanent cropping system, we calibrated it to soft fruit production in the UK [33,34]. The numerical values for parameters used are listed in Table 1. *K* is calculated from the likely on-farm nesting densities of wild bumblebees. Nest densities will depend on the landscape type; around 11 to 15 nests per ha were found in non-linear countryside in a large scale survey in UK habitats, with higher densities in gardens and around linear features [37]. While actual densities will vary between locations, we assume that densities of 15 nests per ha can be found in on-farm habitat and assume that no nesting can occur within the cropped area. We follow Bryden et al. [32] in describing the effect of pesticide impairments on the dynamics of wild nests (Table 1). Costs of seeds, pesticides and bumblebee boxes are taken from a farm survey of 25 soft-fruit farms in Scotland [34]. Other production costs and prices per ha are taken from farm management data from the Farm Management Pocketbook 2016 eds., corresponding to raised-bed June-bearing strawberries see p. 35 of [33].

3. Results

We first analyse the optimal levels of conservation area provision in the absence of pesticide use and commercial bees. The effect of pesticide on wild bees in considered next and then provision of commercial bees is considered, without and with the impact of pesticides on their ability to pollinate.

RESULT 1: When no commercial bees or pesticides are used, profits are negative without on-farm wild bee habitat, and peak at low-moderate levels of its provision. Allowing for pesticide use shifts the yield and therefore the profit upwards, but the peak remains in the same position if pesticides have no adverse impact on wild bees.

We first consider a case when pollination is provided by wild bees only. If pesticides are not used, or if they are used but do not impair pollination ability of wild bees (so that the wild bee impairment wI=0), the profits and the population of wild bees are stable over time (assuming that the initial number of nests is $N_{[0]} = K$). Profits peak when on-farm habitat proportion is between 10% and 20% (Fig. 1a) as they depend on revenues made from the crop area balanced against the loss through providing habitat rather than growing crops on the remaining area. At low levels of on-farm habitat provision, yield is limited by pollination, Fig. 1b, as

$$\alpha + \beta B_{[t]} < \gamma \Rightarrow Y_{[t]} = Y_{\max} \times \left(\alpha + \beta wF \left(1 - wI\right) wN\, v\right) \qquad (12)$$

(where we used the fact that $B_{[t]} = \frac{wF\left(1 - wI\right) N_{[t]}}{A} = wF\left(1 - wI\right) wN\, v$ with $N_{[t]} = K = wN\, vA$; see Fig. 1c). Combining equations (6), (8) and (9) we see that for low values of the proportion of farm area under the crop, v, the leading term in the profit function is of the form $v(1-v)$, see the left hand side of Fig. 1a. When v reaches the critical level

$$v = \frac{\gamma - \alpha}{\beta wF\left(1 - wI\right) wN} \qquad (13)$$

(i.e. when $\alpha + \beta B_{[t]} = \gamma$) then yield becomes independent on the wild bee population, but total production and therefore profit decreases as the area under cropping decreases with increasing v, as in figures 1a and 1b.

Profits can be negative when there is no area of the farm used for wild bee habitat and yields are low due to pesticides not being used, Fig. 1a. When pesticides are used (still under assumption of no adverse effect on wild bees), the profit function is shifted upwards (thick line in Fig. 1a), but this does not change the dynamics of wild bee population over time (Fig. 1c) or the optimal allocation of on-farm habitat. We note that if the initial density of the wild bumblebee nests, $N_{[0]}$ is lower than *K*, the time projection of $N_{[t]}$ will increase towards *K*. Profits in this case will also increase but in the long term the behaviour is the same as that discussed above.

RESULT 2: When no commercial bees are used and wild bees are impacted by pesticides ($wI > 0$), *profits are lower and peak profits occur at higher level of on-farm bee habitat.*

If the pesticide-induced impairment in pollination by wild bees is relatively small (eg. *wI*=0.3), the wild bee population stays constant over time (assuming $N_{[0]} = K$, or increases until $N_{[t]} \simeq K$ if $N_{[0]} < K$), Fig. 2a. As a result, the yield is also constant, as in figure 2c. The corresponding profits are lower and require a higher proportion of on-farm habitat to peak, see equation (13) and Fig. 3a, as more nests (and therefore more habitat) are required to make up for the impairment of foragers. These results are summarised in Fig. 4. Thus, with an increasing impact of pesticides on wild bees, there is a gradual increase in the optimal value of *v*, as shown in figure 4a (compared to figure 3a). This is associated with the gradual decrease in the corresponding maximum profit, as shown in figures. 3a and 4b.

Wild bee numbers respond gradually to changes in the impairment as long as:

$$wI \leq 1 - \frac{1}{wF}\left[\frac{mR}{R-1} - j\right]; \qquad (14)$$

When (14) is not satisfied, the behaviour of the population of wild bees switches from sustainability over long periods of time, $N_{[t]} = K$, to decline over time, $N_{[t]} \to 0$ with $t \to \infty$, Fig. 2b. As a result, there is not enough pollination potential and production declines; in our parameterisation this occurs for $wI > 2/3 = 0.666...$, see figure 4. We choose *wI*=0.67 to illustrate this behaviour in Fig. 2b and d. The resulting profits are significantly lower than for *wI*<0.666… (Figs. 2d and 4b). The optimal percentage of on-farm habitat changes in time and is initially ca. 50%, higher than when there is no impact of pesticides on wild bees.

The qualitative change in the long-term dynamics of wild pollinators results in a threshold-like behaviour for optimal proportion of on-farm habitat, *v*, Fig. 4a, and the associated maximum profit, Fig. 4b, both of which drop rapidly at the transition point, cf. equation (14). This points to very high sensitivity of the results to the effects of pesticides on wild bee population as the threshold of *wI*=0.666… is approached.

RESULT 3: The speed at which wild bumblebees decline depends on the balance of nest death relative to nest reproduction.

When wild bees are used as the sole pollination input, the likelihood of wild bee decline depends on the relationship between the impairment of foragers (and hence nest survival) and the reproductive capacity of the surviving nests each year (Fig. 2b). If the impairment is high enough, the density of nests declines exponentially in time as

$$N_{[t]} = N_{[0]} \times \exp(-rt) \quad \text{with } r = -\ln\left[R \times \left(1 - \frac{m}{j + wF \times (1 - wI)}\right)\right]. \qquad (15)$$

Thus, the characteristic time for the decline is given by r^{-1} and sharply decreases when *wI* increases, Fig. 5, independently of *v*.

However, the resulting decline in the profit can initially be slow (see an example in Fig. 6), effectively masking the decline in nest density (to illustrate this effect better, *wN* is increased by a factor of 5 so that the resulting *K* is higher in Fig. 6 than in other figures). With higher levels of on-farm habitat, there are more wild bees per area of crop, and so there is a period where farms are over supplied with pollinators (this may have negative consequences in some crops as it could lead to too many fruits produced, see e.g. [36]). This continues until the wild bee population drops to a level at which pollination services become limited, at which point profits begin to drop (Fig. 6). Thus, the farmer might not have an incentive to change the pesticide use until populations are too low to be effective.

RESULT 4: When commercial bees are used (and unaffected by pesticides), profits remain stable despite declines in wild bees, and are highest when on-farm habitat is low

When commercial bees are used at the same time as wild bees, Fig. 3b and 4b, the highest profit corresponds to no on-farm habitat, i.e. *v*=0. The resulting optimal profit is higher than when pollination relies on wild bees only. The slight drop in the profit at higher values of *v* in Fig. 3b is due to the cost of buying in commercial bees.

Profits remain stable throughout the projection period regardless of whether wild bee nests decline or not, Figs. 3b, 4b and 7a, with highest yields when no farm area is set aside for habitat. Thus, when farmers can buy-in pollinators which are unaffected by pesticides, and where such commercial bees can provide a perfect substitute for wild bees in terms of their pollination delivery, this acts as a severe disincentive to conserving wild bees or to reduce pesticide use.

RESULT 5: When commercial bees are used and both these and wild bees are affected by pesticides, the optimal strategy is either to rely completely on commercial bees, or to provide a mixture of commercial bees and on-farm habitat for wild bees, depending on the level of impairment.

When both commercial and wild bees are impaired by pesticides, profits generally change little if the impairment is low and equation (14) is satisfied, as shown in figure 4. The optimal area of on-farm habitat is zero, so all pollination is provided by commercial bees. If the impairment is increased (but (14) is still satisfied) it becomes profitable to invest in a mixture of wild and commercial bees, as shown by the dash-dot line in Fig. 3b and the intermediate range of wI and cI in Fig. 4a (here we assume $wI=cI$). This is also associated with a drop in optimal profit as compared to the case when commercial bees are unaffected by pesticides, Fig. 4b. The wild bee population remains steady for low impairment levels (if (14) is satisfied) and starts to decline when impairment becomes too high, resulting in the return to pollination based on commercial bees only, see the drop in Fig. 4a. Profits continue to decline with increasing impairment, as the reduced number of commercial bee foragers cannot provide the entire pollination service, leaving crops vulnerable to pollinator decline (we assume that farmer does not change the provision of commercial bees over time: clearly, this assumption can be relaxed). However, the decline in profits at this point is smaller than if the commercial bees are not used, Fig. 4b, as the commercial bees still manage to moderate the adverse impacts of pesticides.

When the impairment is high and both commercial and wild bees are affected, profit declines over time unless v=0, Fig. 7b. Initially, when there is still sufficient number of wild bee nests, the optimal strategy is to invest in a mixture of wild and commercial bees, Fig. 7b. As wild bee nests die due to pesticide impairment, the farmer starts to rely on commercial bees only, even though they are also affected by pesticides.

Discussion and Conclusions.

Pollination inputs are valued by farmers as they increase the quality and quantity of a range of important crops [38]. However, commercial bee use can effectively mask declines in wild bees (assuming equal efficiency), reducing the private value of wild bee conservation on farms. Moreover, there may be lags in the response of insect pollinators to pesticide use meaning that the market signal to farmers to change their management practice arrives “too late” to stop a permanent decline in pollinators. Since wild pollinators also generate ecosystem benefits for a wide range of wild plants beyond the farm from which society derives value [39], these three factors can all drive the supply of wild bees below the social optimum.

In the modelling presented above, we consider the pollination services provided by a mix of wild and commercial bees which are inputs to a commercial crop. Farmers can “produce” more wild bees by allocating land to bee habitat, but this comes at an opportunity cost in terms of foregone profits from land allocated to cropping. Use of a third input, pesticides, contributes positively to profits through its effect on output, but negatively through any effects on bees. Farmers thus face a trade-off in the costs and benefits of pesticide use, where these costs go beyond the price paid for pesticides.

If commercial bees are unaffected by pesticides, their small cost relative to other inputs means that profits are highest when commercial bees are used and little farm area is converted to on-farm habitat for wild bees. If wild bee numbers decline under pesticide pressure, profits can remain positive, as commercial bee numbers can deliver the required pollination level for maximum yields. This is in contrast to the situation when wild bees alone are used for pollination and there is no option to use commercial bees (this is equivalent to the situation where commercial bees can substitute for wild bees). In this case there is an optimal percentage of land converted to wild bee habitat, a results which is in accordance with other studies [28,29]. How big this area of land allocated to bee habitat is will depend on crop prices and the productivity of land, both for wild bees and for crops.

The outcome changes when commercial bees are impaired by pesticides along with wild bees. In this case, agricultural yields can be stable and high for a number of years and then fall suddenly, as wild pollinators decline past a particular point. High yields are maintained when there is an "over-supply" of pollinators, but fall after wild pollinators numbers decline to a level where overall pollinator numbers limit yields.

In practice, the relative impact of pesticides on commercial and wild bees will depend on farm practices used. Farmers can reduce the impact on commercial bees by shutting the hives or nest boxes when spraying takes place, though systemic pesticides, by design, are likely to persist within the plant for weeks after application so bees will still be equally exposed through the ingestion and transport of contaminated nectar and pollen [7]. Wild pollinators cannot be shut inside nests while spraying takes place and so are potentially left more vulnerable, though some action can still be taken to avoid direct impact on wild pollinators such as spraying when wild bees are not active.

If declines in wild pollinators are irreversible (e.g. as species become extinct), and if there is uncertainty over whether wild pollinators will be more beneficial in the future (e.g. as new varieties, more dependent on pollinators, are bred), then there is an option value to maintaining this natural capital for future use [40,41]. This option value is an additional economic rationale for conserving wild pollinators, even when there are commercial pollinators present. This value, however, will depend on the time-horizon and risk-aversion of the farmer, as farm profits may be stable for years before declines are evident. If farmers are present-bias, then there may be little private benefit to conserving wild pollinators for crop production, implying that government interventions may be required given the wide range of economic and ecological benefits which wild pollinators deliver [39,42].

The wild bee population modelled here will often in practice be made up of multiple populations of bee and non-bee pollinators such as hover-flies, wasps and beetles [11]. The presence of multiple pollinator groups can buffer the system from extinction [43,44], and we have not modelled this buffering capacity here. While different pollinators groups may respond in different ways to external pressure such as pesticide use, the effects are likely to be negative on all groups, and may be stronger on solitary bees and non-bee pollinators as these are often smaller in size and they are not buffered by living in a social colony with numerous expendable workers [21,45]. There is a benefit from maintaining multiple groups of ecosystem service providers as insurance against a fluctuating environmental conditions [46], implying a role for commercial bees in providing "financial insurance" against wild bee declines. On the other hand, commercial bees may contribute to wild bee decline, e.g. by introducing or spreading disease .

Several simplifications made in the modelling procedure should be noted. We have assumed that all factors are deterministic. In reality key processes like pollination or be reproduction and death will be stochastic. We assumed that all nests which reproduce produce a set number of queens which survive until the next year, since this simplifies the actual process which will rely on perhaps a larger number of queens being produced by successful colonies, who then may or may not mate, survive until the next year and establish a nest themselves. Overall success is likely to depend on other factors such as weather conditions and the level of disturbance, so the failure rate will vary substantially between years [32]. There is evidence that pesticides can interact synergistically with diseases, poor nutrition and other chemicals, but this is not modelled either [22,35,47]. Moreover, if commercial bee keepers find that their bees are being adversely affected by pesticides, then supply may decline, leading to a future rise in the prices charged for commercial pollinator services.

Our model describes a static permanent crop system which is grown every year with no change to agricultural practices and response of the manager over time. While this might be suitable for crops like strawberries which are grown every year, in many arable systems rotation will affect the year-to-year demands for services and resources available for pollinators. We also ignore feedbacks between the changes to yield and therefore profit and farm management strategies. In reality, farmers will respond to the decrease in availability of pollination services by changing the density of commercial nest or lowering the use of pesticides. We also assume that prices and costs are constant over time and do not depend on the overall level of production.

We consider the bee population on the farm in isolation. Migration from outside will affect the rate at which the population change over time; for example queens of wild bees are mobile so that farms with low or zero bee populations are likely to receive net immigration of nesting queens in spring. This may fill gaps in the resident population and protecting against local extinction, though the farm would then be acting as a sink, reducing the bee population on the surrounding farms. Similarly, foraging bees may fly several kilometres from their nest, spilling out from farms which have taken measures to provide habitat for them, and pollinating crops on neighbouring farms which have deployed no such measures. Discouraging such freeloading may require financial incentives.

Our model also considers only two species, wild and commercial bees; the wild bee model is only suitable for a single species. In practice, different species will have different life patterns, different pollination ability, and will differ in their response to pesticides. The model presented here can be extended to multiple species, but will be even more difficult to parameterise.

We have based model parameters on a specific crop, strawberries. As Keitt [28] concluded, the actual form of the production relationship between pollinators and profits is likely to vary across and within crops, depending on the yield response to both pesticides and bees, and the landscape in which the farmers are working. However, our model is applicable for a range of crops with similar or higher dependency on bees which also benefit from applications of pesticides, and which are grown within intensive agricultural environments, including other soft-fruits and almonds.

We show that pesticide use is not only an externality, affecting wild bees in the vicinity of the farm, but part of an internal trade-off decision for farmers of insect pollination-dependent crops. In the presence of commercial bees, farmers have little incentive to support wild bees around their farms; while bees might be important to crop yields, the availability of cheap substitutes means that high profits can be maintained in the short-term. This is despite a longer term risk of declining profits which can threaten the ability of farmers to maintain production. Safeguarding farmland pollinators may therefore require monetary incentives to encourage the creation of on-farm habitat so that future pollination options are not reduced.

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618 Table 1: Key parameters in the model (modelled after soft fruit production).

Parameter	Interpretation	Value	Source/comments
v	Proportion in conservation area	0-0.7	Key variable
A	Farm area	100ha	Assumed
R	Nest reproduction ratio	4	Incorporates the relatively small chance of queens mating and overwintering
wN	Wild bees nesting density	15	[37]
cN	Commercial bees nesting density	4	[20] gives estimates of 0.32-8.75 imported boxes per ha per year
μ	Nest death parameter	55	[32]
ϕ	Nest death parameter	40	[32]
wF	Avg. number of wild foragers per nest	100	[34]
cF	Avg. number of commercial foragers per nest	100	Same as wF
wI	Impairment due to pesticides, wild bees	0 if no impairment; variable	Key variable
cI	Impairment due to pesticides, commercial bees	0 if no impairment; variable	Key variable
$Y_{max.nop}$	Maximum attainable yield when pesticides are not used	11.5 tonne per ha	Estimated from [33] as 50% of max yield
$Y_{max.p}$	Maximum attainable yield when pesticides are used	23 tonne per ha	Max yield in [33]

γ	maximum proportion of good quality fruits	0.9	[34]
α	proportion of good quality fruits without bees	0.35	[34]
β	incremental effect of bee visitation	0.0024	Combined visitation and efficiency in [34]
p	Price per tonne	3445	[33]
cm	Commission	0.09	[33]
Cpt	Cost per tonne (harvesting and packaging)	£1650 per tonne	[33]
Cpa	Cost per crop area (planting structures, fieldwork)	£18700 per ha	[33]
Capa	Total cost per area (land lease)	£150 per ha	[33]
Cseed	Cost of maintaining the conservation area (mainly seed)	£100 per ha	[33]
bC	Cost of commercial nests, per nest	£60 per nest	[33]
pC	Cost of pesticide use, per ha of crop area	£10 per ha	[33]

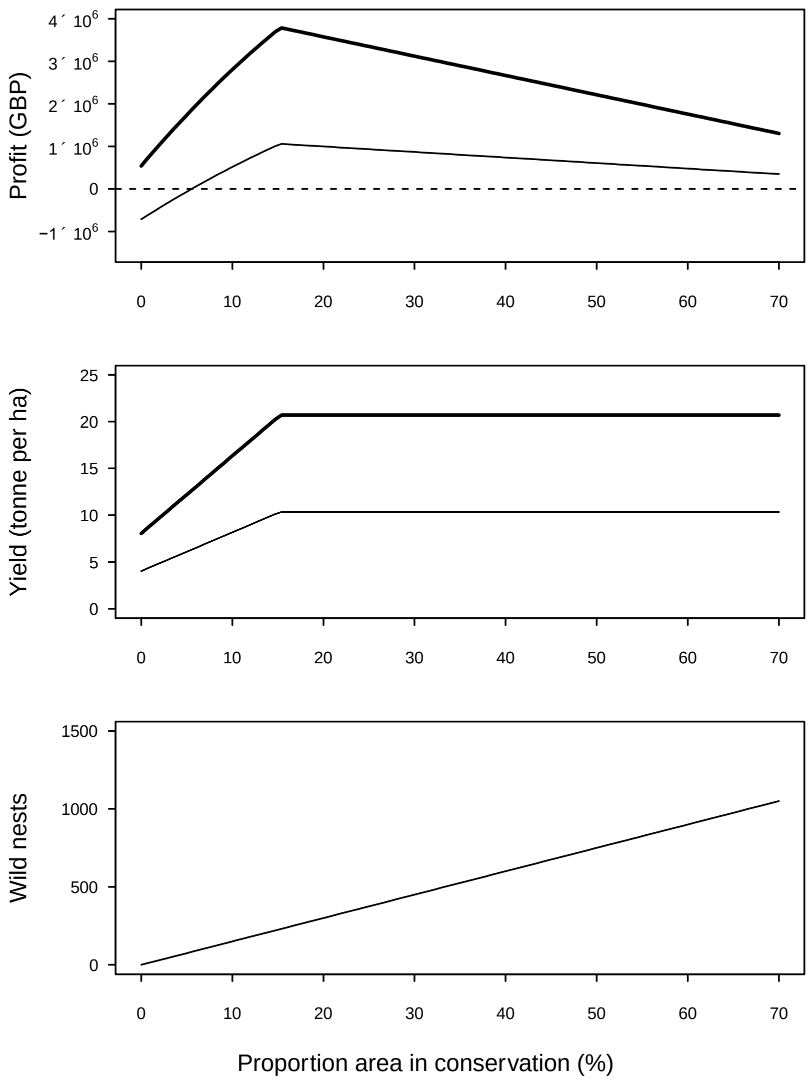

Figure 1: Total profit (a), yield (b), and the number of wild bee nests, $N_{[t]}$ as functions of the proportion of on-farm habitat proportion, *v*. Thin line: no pesticides; thick line: with pesticides. No commercial bees are used and when pesticides are used, they do not affect wild bees. Parameters as in Table 1.

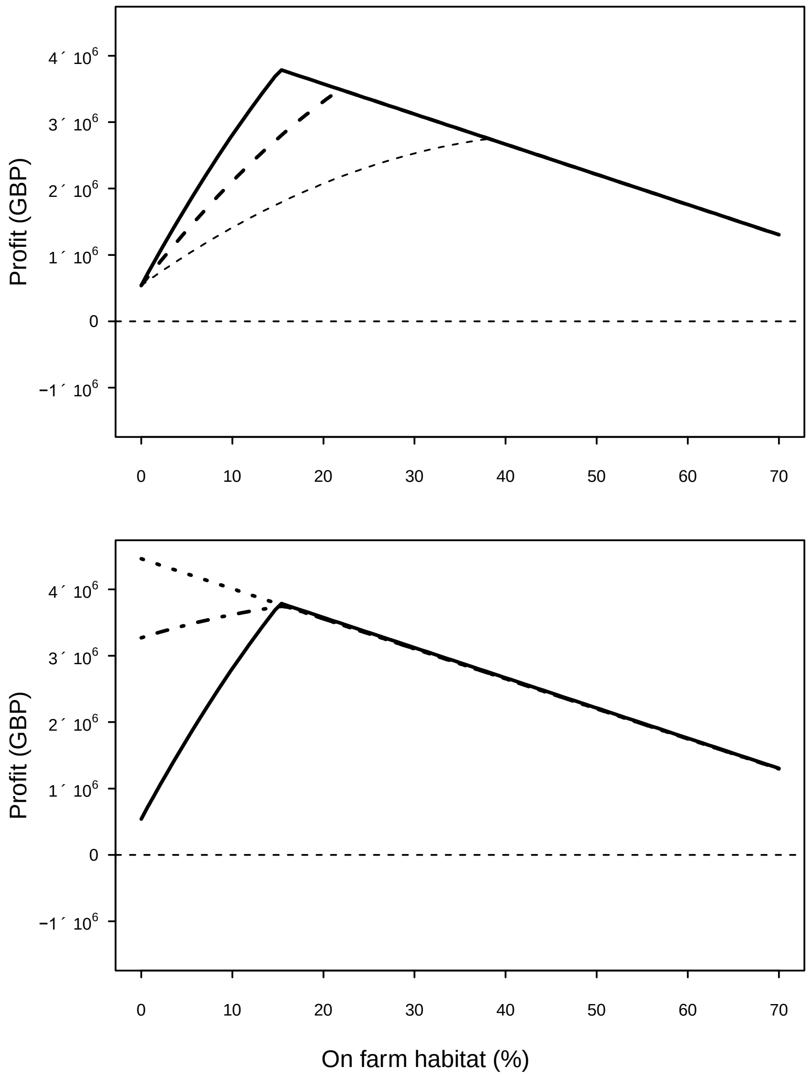

Fig. 2: Total profit as a function of the on-farm habitat proportion, *v*, for (a) no commercial bees, (b) with commercial bees but with small impact of pesticides, and (c) with commercial bees but with large impact of pesticides. Horizontal line represents zero profit. In (a), solid line corresponds to *wI*=1, dashed line to *wI*=0.3 and dotted line to *wI*=0.6. In (b) dotted line corresponds to no impact of pesticides on wild or commercial bees (*wI*=*cI*=0), and dash-dot line corresponds to *wI*=*cI*=0.6 (solid line from (a) is redrawn for comparison). All other parameters as in Table 1.

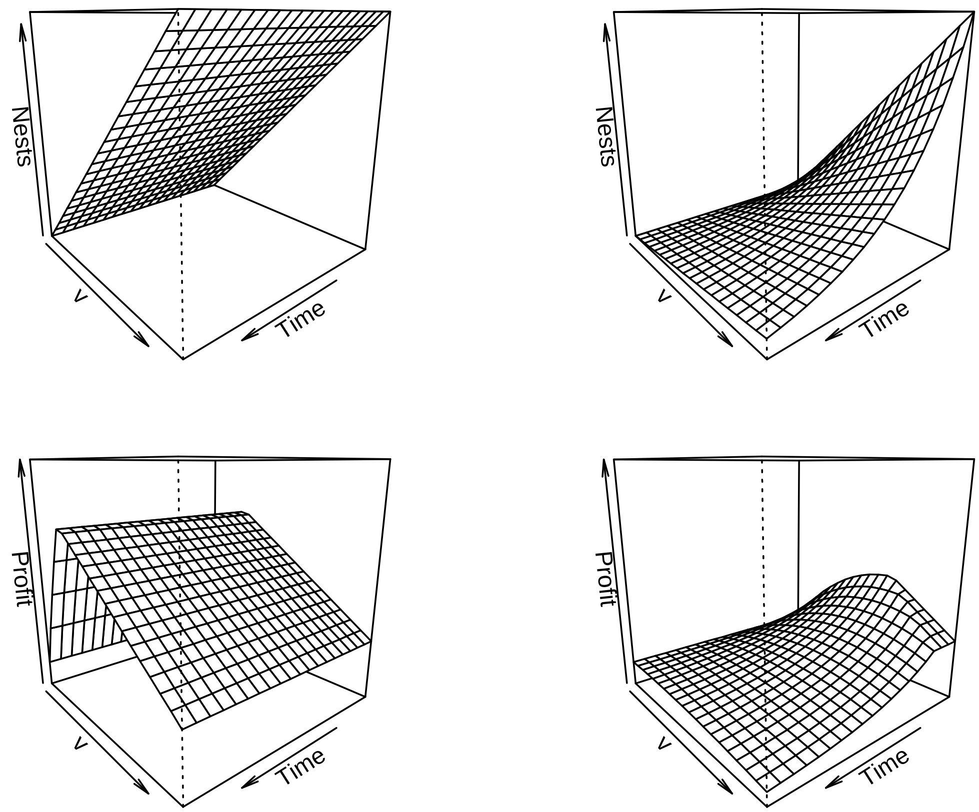

Fig. 3: Dependence of (a) and (b): the number of wild bee nests $N_{[t]}$, and (c) and (d): total profit, on the on-farm habitat proportion, *v* and time (between 0 and 200 years), when pesticides are used but commercial bees are not. In (a) and (c), there is no effect of pesticides on wild bees, *wI*=0, and in (b) and (d), *wI*=0.67. Other parameters as in Table 1.

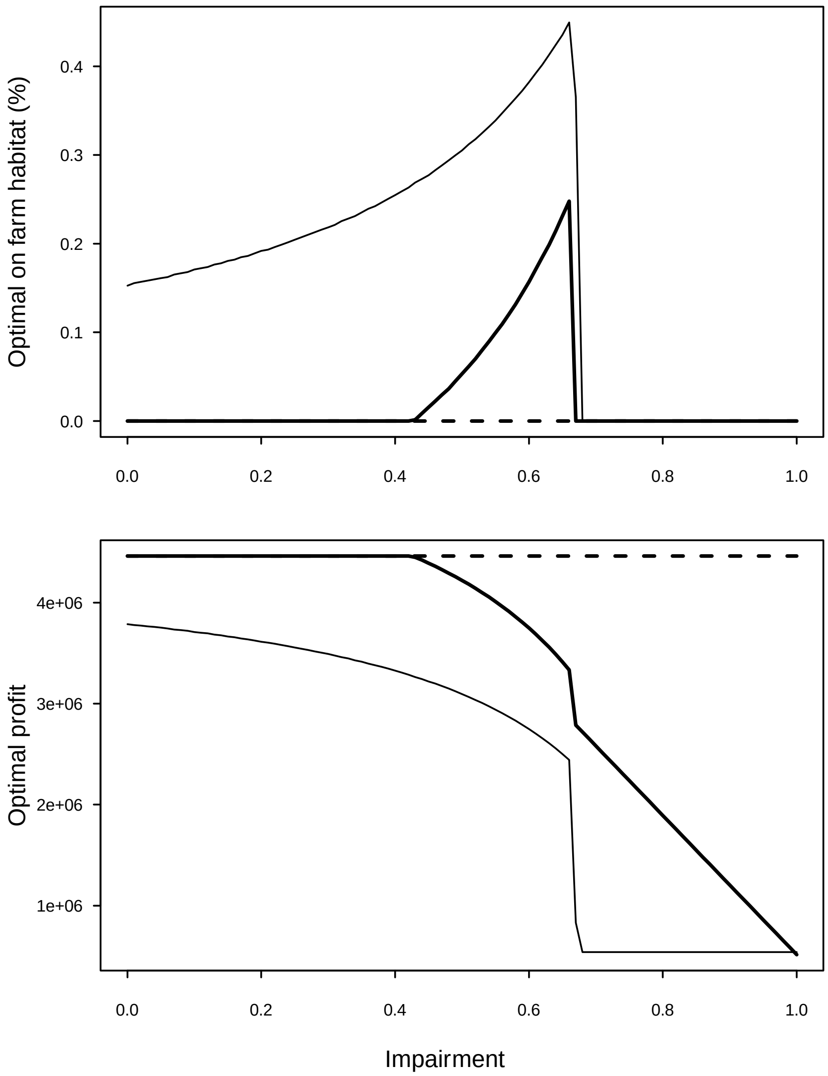

Fig. 4: Dependence of the optimal on-farm habitat proportion (a) and the corresponding total profit (b) on the wild and commercial bee impairment due to pesticides. Thin solid line corresponds to the case without commercial bees; dashed line corresponds to the case with commercial bees, but with no impairment of their performance, *cI*=0. For the thick solid line, commercial bees are used and affected by pesticides in the same way as wild bees, *cI*=*wI*. Other parameters as in Table 1.

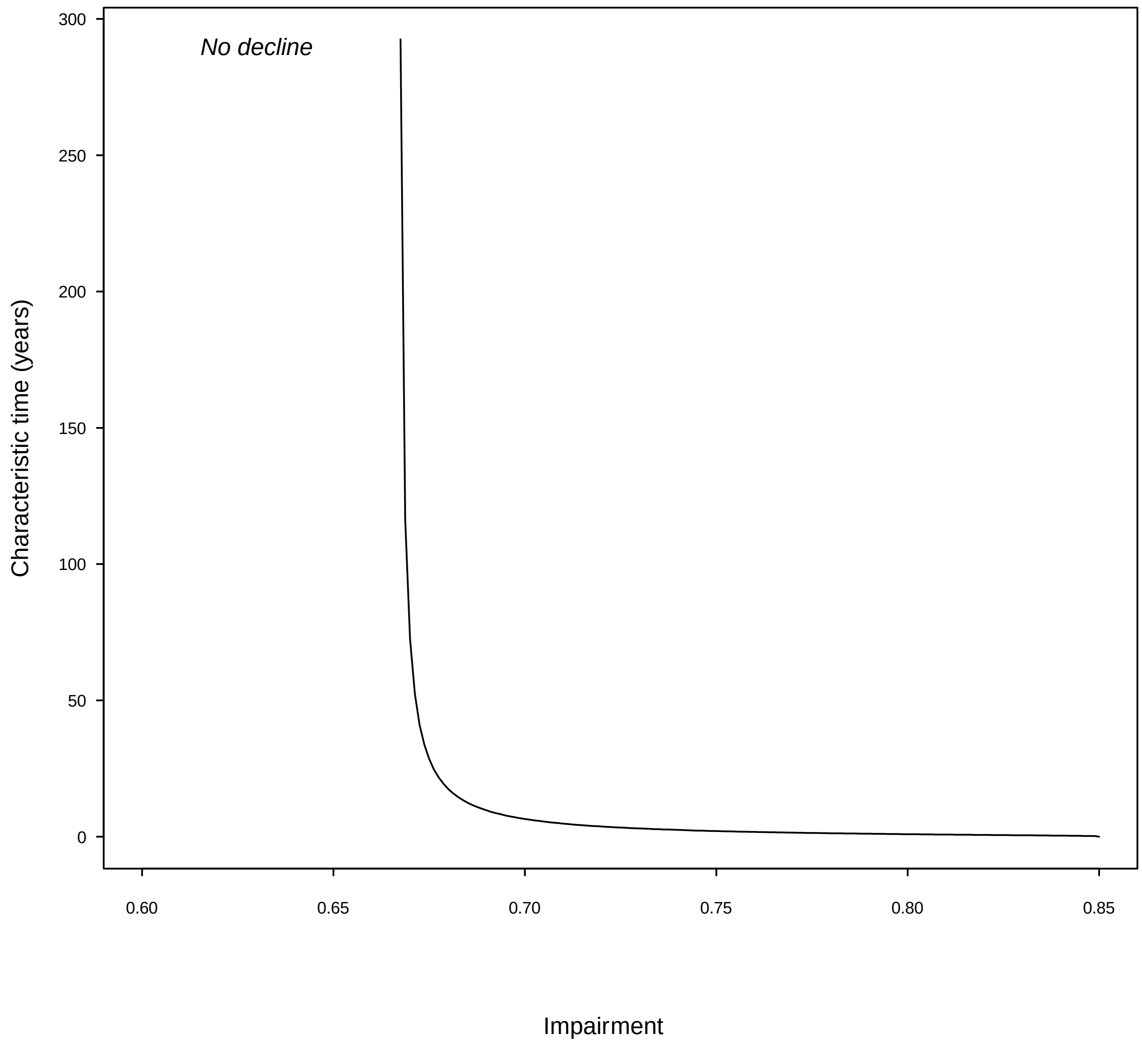

Fig. 5: Dependence of the characteristic time of decay for the wild bee nests, r^{-1}, in response to the impairment, *wI*.

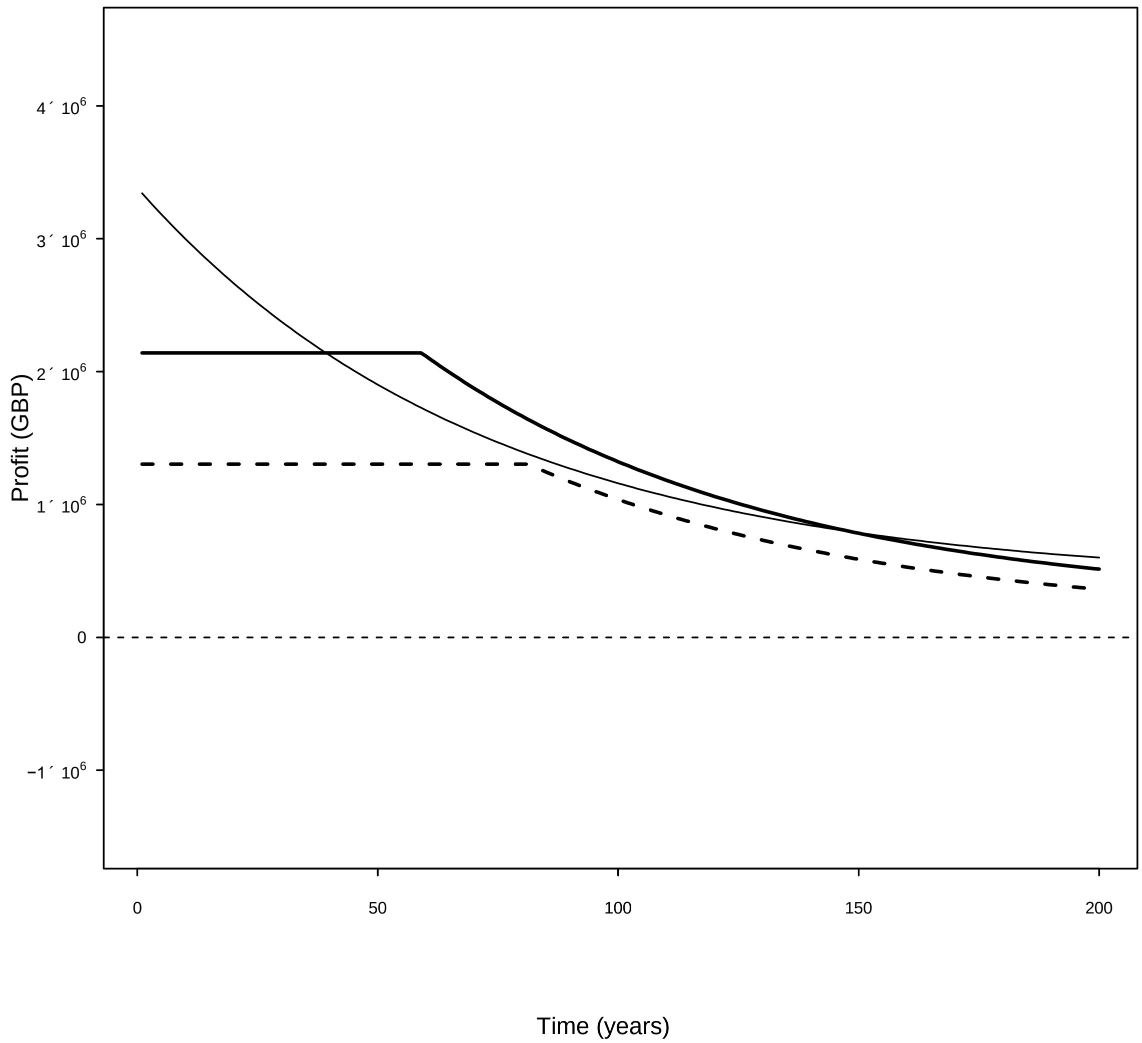

Fig. 6: Examples of time projections for profit over 200 years. Pesticides are used, but no commercial bees; high impact of pesticides on wild bees (*wI*=0.67). For illustration, the carrying capacity for wild bees is doubled so that the effect of overpollination is more pronounced. Solid line: *v*=0.22 (optimal), thick line: *v*=0.52, dashed line: *v*=0.7. Other parameters as in Table 1.

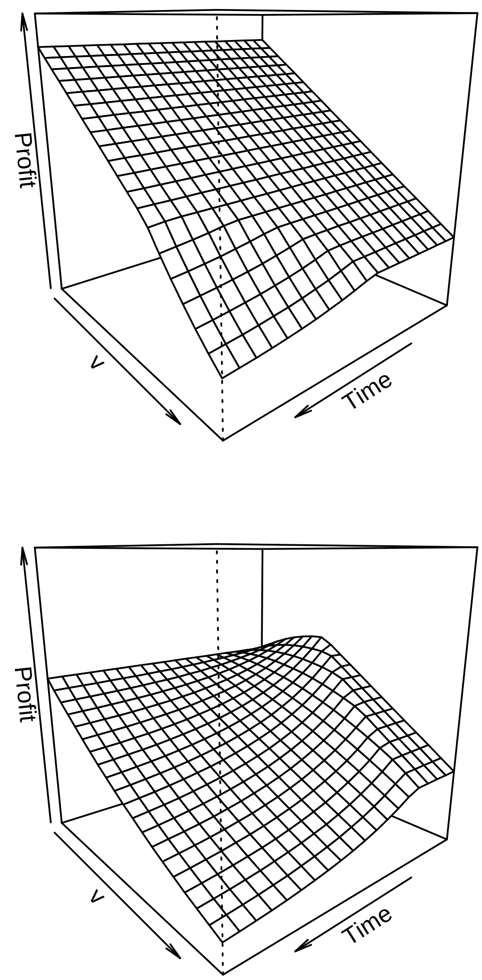

Fig. 7: Comparison of dependence of the profit on time and on-farm habitat proportion for the case when pesticides and commercial bees are used and pesticides strongly affect (a) wild bees only (wI=0.67, cI=0) and (b) both wild and commercial bees (wI=cI=0.67). Other parameters as in Table 1.