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Modelling land use strategies to optimise crop production and protection of ecologically important weed species

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Abstract

There is a need to develop farming systems that enable both a satisfactory level of crop production and good living conditions for natural species. Wildlife-friendly cropping techniques, such as a reduced amount of applied herbicide or a lower crop density, might be adopted in order to maintain populations of weed species of biological interest. An alternative might be to adopt an intensive cropping system in a part of the field and spare the other part as set-aside or field margins, available for the development of natural plant species. The objective of this paper is to present a method to compare two strategies for maintaining a desirable level of abundance of a given species of interest in agricultural areas, specifically (1) a strategy based on a wildlife-friendly cropping system in a large cultivated area and (2) a strategy based on a more intensive cropping system in a reduced area of cultivation. The principle is to calculate the ratio of crop production obtained with strategy (1) to the production obtained with strategy (2) for a given target density of natural species. We show that the value of this ratio, and thus the relative performance of the two strategies, depends on the density of the weed species that can be maintained in an uncultivated ecological area. The method is applied in two case studies to compare the relative performance of wildlife-friendly cropping system and land sparing for maintaining a desirable level of abundance of two plant species with contrasting ecology and preservation goals.

Keywords: *Adonis aestivalis*, biodiversity, cropping system, land use, *Poa annua L.*

Introduction

The intensive use of inputs in crops has caused a decline in biodiversity in European arable ecosystems (Stoate *et al*., 2001; van Wenum *et al*., 2004). Such a decline has been well documented for birds (Chamberlain *et al*., 2000), invertebrates, and plants (e.g. Andreasen *et al*., 1996; Sutcliffe & Kay, 2000 ; Green *et al*., 2005). Concerns about the impact of intensive agriculture on ecosystems are arising both among the European population and policy-makers (Stoate *et al*., 2001; van Wenum *et al*., 2004). Gerowitt *et al.* (2003) have recently proposed that weeds should be considered as ecological goods. Some weed species, e.g. *Poa annua* L., are important components of ecosystems because their biomass constitutes a nutrient resource for birds or other vertebrates (Marshall *et al*., 2003). Other species, such as *Adonis* species, have drastically declined in abundance in Western Europe (Aymonin, 1976) and agronomists are now trying to define precise land use strategies to preserve these species, among others, from extinction.

However, weeds growing in arable land compete with crops for nutrients, light and water, and are therefore likely to reduce crop yields and the cropping system profitability. There is a need to develop systems leading to satisfactory levels of crop production and maintaining appropriate conditions to support populations of natural species. Several solutions have been proposed such as a reduction of pesticide input (Stoate *et al*., 2001), the use of arable field margins (Marshall & Moonen, 2002), or the use of permanent or rotating set-aside (van Wenum *et al*., 2004), but little is known about the relative efficiency of these solutions.

Wildlife-friendly cropping techniques, like a reduced amount of applied herbicide (de Snoo, 1997), a lower crop density and/or restricted fertiliser inputs (Kleijn & van der Voort, 1997) might be adopted in order to maintain populations of weed species of biological interest (target species). But the adoption of such techniques is likely to induce a yield loss due to the development of a large weed community. An alternative might be to adopt a land-sparing strategy of using an intensive cropping system in a part of the field and sparing the other part as set-aside or field margins, available for the development of natural plant species. Using this strategy, a high yield would be obtained in the cultivated part of the field, but the absence of crop on the remaining part results in a loss of production for the farmer. According to Green *et al.* (2005), the optimal choice between a land-sparing strategy and the use of wildlife-friendly cropping techniques depends on the density-yield relationship between population density of a target species growing in a crop and the crop yield. If a small reduction in the farm inputs is likely to trigger a significant increase in the wildlife while resulting in only a small reduction in crop production, then the best strategy to optimize the balance between economy and ecology would be to use all the area for crop production with wildlife-friendly management. However, if any increase in the wildlife may be obtained only through a strong reduction in farm inputs, then the best strategy would be to partition the land area with areas allocated to intensive crop production and areas allocated to wildlife conservation.

The impacts of wildlife-friendly techniques and land sparing on crop production and on weed populations depend on many factors, such as the characteristics of the weed species growing in the field, the weed densities, and the crop yield values. Choosing the best land use strategy is not straightforward. In this paper, we present a method to compare two strategies for maintaining a desirable level of abundance of a given species of interest in the landscape, specifically (1) a strategy based on a wildlife-friendly cropping system in a large cultivated area and (2) a strategy based on a more intensive cropping system in a reduced cultivated area. The proposed method can be used to determine, for each strategy, the area that must remain uncultivated in order to obtain the targeted density of plants. This method can also be used to compare the crop production obtained with the two strategies, either for a given environment or for a series of environments corresponding to different levels of abundance of the plant species.

There is a close relationship between the model of Green *et al.* (2005) and our work. Both aim at comparing crop production and population densities of target species resulting from different land use strategies. But the two approaches differ in the method used to estimate crop production and population densities. Green *et al.* (2005) assessed the relative performance of the wildlife-friendly and intensive land use strategies using the shape of the population density-yield function and, more specifically, the convexity or concavity of this function. Our method is not based on the shape of the density-yield function; the performances of the two land use strategies are compared from measured or estimated values of plant densities and crop yields.

The value of our approach is illustrated through two case studies, namely (i) *Poa annua*, a common grass weed producing many seeds important in the diet of birds and other animal species, and (ii) *Adonis* spp. as an example of a rare weed species.

Methods

Cultivated area for a target number of plants

Consider an agricultural area with a surface equal to S and two cropping systems, an intensive one and a wildlife-friendly one, leading to a density of a plant species of ecological interest (e.g. *Poa annua*) equal to d_I and d_{WF} respectively (plants per unit area). Assume that the density is equal to d_U if the field remains uncultivated such as $d_I < d_{WF} < d_U$. d_U is an indicator of the natural abundance of the species in the environment.

If the intensive cropping system is adopted by the farmer, the number of plants in the field, Z, is related to d_I and d_U by

$$Z = d_I s_I + \left(S - s_I\right) d_U \qquad (1)$$

where s_I is the surface of the cultivated area, $d_I s_I$ is the number of plants obtained in the cultivated part, and $\left(S - s_I\right) d_U$ is the number of plants obtained in the uncultivated part (set-aside or field margins).

By dividing the two sides of Eqn (1) by S, we obtain

$$D = d_I f_I + \left(1 - f_I\right) d_U \qquad (2)$$

where D is the number of plants of ecological interest per unit area at the field level and f_I is the cultivated area divided by the total field area. As $0 \le f_I \le 1$, we have $d_I \le D \le d_U$.

We express the fraction of the field that is cultivated (f_I) as a function of the number of plants D. Eqn (2) shows that f_I is related to D by

$$\begin{aligned} f_I &= 1 && \text{if } D = d_I \\ f_I &= \frac{d_U - D}{d_U - d_I} && \text{if } d_I < D < d_U \\ f_I &= 0 && \text{if } D = d_U \end{aligned} \qquad (3)$$

A similar equation can be obtained if the wildlife-friendly cropping system is adopted by the farmer:

$$\begin{aligned} f_{WF} &= 1 && \text{if } D = d_{WF} \\ f_{WF} &= \frac{d_U - D}{d_U - d_{WF}} && \text{if } d_{WF} < D < d_U \\ f_{WF} &= 0 && \text{if } D = d_U \end{aligned} \qquad (4)$$

where f_{WF} is the cultivated area divided by the total area when the wildlife-friendly cropping system is adopted. As $d_{WF} \geq d_I$, we have $f_{WF} \geq f_I$.

The two functions defined by Eqs (3) and (4) can be used to compute the area that can be cultivated by the farmer as a function of a target value D of number of plants per unit area. These two functions are graphically compared in Figure 1. The wildlife-friendly cropping system allows the farmer to cultivate a larger fraction of his field for a given target value D. The drawback of this cropping system is that it may lead to a lower total yield than an intensive cropping system. It is thus necessary to compare the crop production and/or the income obtained with two cropping systems to make the final choice.

Crop production assessment

Let y_I and y_{WF} denote the yield values obtained in the cultivated part with the intensive and wildlife-friendly cropping systems respectively. The crop production per unit area obtained with the two strategies for a given target number of plants D are noted P_I and P_{WF}, and are expressed as:

$$P_I = y_I \times f_I = y_I \frac{d_U - D}{d_U - d_I} \qquad (5)$$

$$P_{WF} = y_{WF} \times f_{WF} = y_{WF} \frac{d_U - D}{d_U - d_{WF}} \qquad (6)$$

Eqs (5) and (6) can be used to compute the crop production obtained with the two strategies. Also, these equations show that the ratio $\frac{P_{WF}}{P_I}$ is defined by

$$R = \frac{P_{WF}}{P_I} = \frac{y_{WF} \times \left[d_U - d_I\right]}{y_I \times \left[d_U - d_{WF}\right]} \qquad (7)$$

The ratio (7) depends on the yields and plant densities obtained with the two cropping systems, and on the plant density obtained in the uncultivated part of the field, but does not depend on the target value *D*.

The partial derivatives of *R* were computed in order to study the sensitivity of *R* to crop yields and weed densities. The signs of the derivatives show that *R* increases as a function of y_{WF} and d_{WF}, but decreases as a function of y_I, d_I, and d_U (Table 1).

The crop production ratio *R* can be used in two ways. Firstly, it is possible to compute a single *R* value for a given environment, characterised by a given value of d_U. This approach is useful in order to compare the crop production obtained with two cropping systems in a specific environment. Secondly, it is possible to compute *R* for a series of environments characterised by different values of d_U. This second approach allows one to study the sensitivity of *R* to the natural abundance of the plant species. It is interesting to calculate the threshold value of d_U corresponding to *R*=1. According to Eqn (7), this value is

$$d_{uT} = \frac{y_I \times d_{WF} - y_{WF} \times d_I}{y_I - y_{WF}} \qquad (8)$$

When d_U is equal to d_{uT}, the production obtained with the two cropping systems is the same. When d_U is higher than d_{uT}, the crop production is higher with the intensive cropping system than with the wildlife-friendly cropping system.

In some applications, it may be useful to replace y_I and y_{WF} in Eqs (7) and (8) by the corresponding gross margins associated with the two cropping systems. This is useful when the prices and the costs associated with the two cropping systems must be taken into account.

Estimation

The calculation of f_I and f_{WF} requires a knowledge of the plant densities d_I, d_{WF}, and d_U. In addition, the calculation of R requires a knowledge of the yield values y_I and y_{WF}. These can be estimated from yield and plant density measurements performed in cropping system experiments. The experiments must include treatments corresponding to different cropping systems. Yield and natural plant species density must be recorded for each treatment. It is also useful to a have a ‘set-aside’ treatment in the same field, in which the plant density is recorded. If this treatment is present it is possible to estimate d_U. If not, it is possible to compute f_I, f_{WF}, and R for different d_U taken within a reasonable range of values as shown below.

Case studies

Two case studies are presented here for two species with contrasting ecology and preservation goals. The first example is of an *Adonis* species with very low abundance, at risk of population extinction. In this case the main objective is to preserve low densities of the species to avoid its complete disappearance, but fortunately the target densities are low enough to avoid any crop yield loss. The second example regards a common species (*Poa annua*), which is controlled at very low densities in intensive cropping systems, while it is recognised for its ecological function if significant population densities are maintained.

Maintaining the population of an *Adonis* species

The populations of *Adonis* species have steadily decreased in Western Europe for several decades. Fifty years ago three species of *Adonis* (*A. aestivalis*, *A. flammea*, *A. annua*) were still common in wheat fields in France. These species became endangered (less then 1 plant km^{-2}) in the 1970s (Aymonin, 1976) and are no longer found in intensive crops. In this case study, we compare two land use strategies for increasing the population of this species in a given arable area cropped with winter wheat. The first strategy consists in using an intensive cropping system characterised by y_I=8 t ha^{-1} and d_I=0. These values are commonly observed in France when the crop is cultivated using conventional practices. The second strategy consists in using a wildlife-friendly cropping system characterised by y_{WF}=6 t ha^{-1} and by a plant density d_{WF} in the range 0.005-0.01 plants m^{-2}. These values may be obtained in winter wheat fields with low herbicide use, low sowing densities, late sowing dates associated with a stale seed bed, and low fertiliser inputs. However, the density increase of such a rare species induced by wildlife-friendly practices is highly unpredictable. In Sweden, Rydberg & Milberg (2000) found rare weed species in organic arable fields, but on a smaller scale in a cropping system experiment in Germany, none of the species recorded on fields with organic systems were considered rare (Gruber *et al.*, 2000). According to Squire *et al.* (2000), the reduction in herbicide use can result in an increase in the number of weed species, but the commonest species are likely to increase the most, while rarer species are less favoured.

The proportion of the area cultivated (*f*) and the crop production (*P*) depend on *D* (Eqs 3-6) and this dependence is illustrated in Figures 2 (a, b) and 3 (a, b) where two values are considered for *D*, 0.006 and 0.009 plants m^{-2}. The higher the value of *D*, the lower is the cultivated area and crop production. The cultivated area is always larger with the wildlife-friendly cropping system than with the intensive cropping system (Figure 2 a, b).

Figures 2 (a, b) and 3 (a, b) show that the cultivated area and the crop production depend highly on the plant density in the uncultivated land. When the density d_U is low, the cultivated area (and therefore crop production) must be significantly reduced to reach the target number of plants D. For example, when d_U =0.01 plants m^{-2}, it is necessary to keep more than 80% of the area uncultivated to reach the target number of plants D=0.009 plants m^{-2} (Figure 2b).

The values of d_{uT} and R do not depend on the target number of plants D (Eqs 7 and 8). If we assume d_I =0, y_{WF} =6 t ha^{-1}, and y_I =8 t ha^{-1}, the plant density threshold d_{uT} is equal to $4 \times d_{WF}$ (Eqn 8). For example, if the plant density obtained with the wildlife-friendly cropping system is equal to 0.005 plants m^{-2}, the threshold value is equal to d_{uT} =0.02 plants m^{-2}. In this case, the highest winter wheat production is obtained with the intensive cropping system if the plant density in the uncultivated part of the field (d_U) is above 0.02 plants m^{-2}. Alternatively, if the plant density in the uncultivated part of the field is below 0.02 plants m^{-2}, the highest crop production is obtained with the wildlife-friendly cropping system. This is illustrated in Figure 4a where the values of the crop production ratio R (Eqn 7) are reported for a series of values of d_U. The value of R is more than 1 when the density d_U is less than 0.02 plants m^{-2}. This threshold value seems rather low. But the densities of *Adonis* spp. observed in set-aside in France are generally less than 0.02 plants m^{-2} (Chauvel, personnal communication). Thus, the strategy based on the wildlife-friendly cropping system will give the highest crop production in most of the environments.

The derivatives presented in Table 1 were used to study the sensitivity of R to crop yield and plant densities. The derivative values were computed for d_U =0.02 plants m^{-2}, and d_{WF} =0.005 or d_{WF} =0.01 plants m^{-2}. The results show that R is much more sensitive to the plant densities d_I, d_{WF}, and d_U than to the crop yield values y_{WF} and y_I (Table 2). For example, when d_{WF} =0.005, $\frac{\partial R}{\partial d_{WF}}$ is equal to 66.67 but $\frac{\partial R}{\partial y_{WF}}$ is only equal to 0.17. This is due to the low density values of the *Adonis* spp. in both cultivated and uncultivated areas. A small increase in d_{WF} leads to a much larger cultivated area and crop production being obtained with the wildlife-friendly cropping system and thus to a much higher value of *R*. Table 2 also shows that *R* is very sensitive to d_U, especially when $d_{WF}=0.01$. A small increase of d_U leads to a much lower value of *R*. This result is consistent with the response curves shown in Figure 4.

Maintaining the population of *Poa annua*

Poa annua is a grass weed species with a short life cycle and an extended period of emergence in crops, so this species may provide a regular supply of seeds to feed birds and other vertebrates without competing strongly with the infested crop. In addition, the populations of *Poa annua* host a large number of insect species. It is therefore an important component of the ecosystem (Marshall *et al*., 2003). In this case study, we compare two land use strategies for increasing the population of this weed species in a winter wheat crop. The first strategy consists of using an intensive cropping system characterised by $y_I=8$ t ha^{-1} and $d_I=0$ because of the systematic use of herbicides efficient against this species. The second strategy is to use a wildlife-friendly cropping system characterised by $y_{WF}=6$ t ha^{-1} and by a plant density d_{WF} in the range 20-80 plants m^{-2}. These values may be observed in winter wheat fields in diversified crop rotations with Integrated Weed Management, avoiding among other things the use of urea herbicides, and in organic farming (Mortensen *et al*., 2000).

The cultivated area and the crop production values (Eqs 3-6) are shown in Figures 2 (c, d) and 3 (c, d) for $d_{WF}=20$ and for two values of *D*, 50 and 80 plants m^{-2}. These target density values are high enough to ensure a good accessibility of the weed resources to other trophic groups (birds, carabids etc.). Here also, the cultivated area is invariably larger with the wildlife-friendly cropping system than with the intensive cropping system (Figure 2). Figure 3 (c, d) shows that the crop production obtained with the intensive cropping system is higher than that obtained with the wildlife-friendly cropping system for all the tested values of d_U when d_{WF}=20. Figures 2 (c, d) and 3 (c, d) also show that when the density d_U is low, it is necessary to greatly reduce the cultivated area (and hence the crop production) to reach the target number of plants *D*. For example, when d_{WF}=20 and d_U=100 plants m^{-2}, almost all the land must be kept uncultivated to reach the target number of plants *D*=80 plants m^{-2} (Figure 3d).

Here also, the plant density threshold d_{uT} (Eqn 8) is equal to $4\times d_{WF}$. For example, if the plant density obtained with the wildlife-friendly cropping system is 20 plants m^{-2}, the threshold value is d_{uT}=80 plants m^{-2}. In this case, the highest winter wheat production is obtained with the intensive cropping system if the plant density in the uncultivated part of the field (d_U) is higher than 80 plants m^{-2}.

Figure 4 (c, d) shows the values of the crop production ratio *R* (Eqn 7) for a series of values of d_U (100-400 plant.m^{-2}) and for two contrasting values of d_{WF}, 20 and 80 plants m^{-2}. When d_{WF}=20, the value of *R* is lower than 1 for all the tested values of d_U (Figure 4c). This is because, in this case, d_{uT}=80 plants m^{-2} and all the tested values of d_U are above this threshold. Conversely, when d_{WF}=80, *R* is more than 1 for most of the tested values of d_U (Figure 4d). *R* values of less than 1 are obtained only when d_U exceeds 320 plants m^{-2}.

The derivatives of *R* were computed for d_U=200 plants m^{-2} and d_{WF}=20 or d_{WF}=80 plants m^{-2} (Table 2). The results show that *R* is less sensitive to the plant densities d_I, d_{WF}, and d_U than to the crop yield values y_{WF} and y_I. This is because the plant densities d_{WF} and

d_U are high and because the difference between these densities is large. A small increase or decrease in plant density does not significantly affect the crop production ratio.

Discussion

The theoretical analysis of two strategies of management of agricultural areas presented in this paper is an attempt to study the trade-off between wildlife conservation and crop production, adapted to the particular case of plant species referred to as ‘weeds’, because their typical environment is cultivated fields and their surroundings. Green *et al.* (2005) considered a similar problem at the regional level, comparing two options, namely (a) wildlife-friendly farming on the whole area and (b) land sparing, with a proportion of land devoted to wildlife conservation and the remainder devoted to crop production. These authors showed that the optimal choice between these options depends on the shape of the relationship between wildlife density and crop production. In our approach, the best land use strategy is not determined from the shape of yield-density relationship but from values of crop yield and weed densities. The validity of our model and of the numerical results is discussed below.

Estimation of the model parameters

Crop yields and weed densities can be estimated from experiments or farmers’ field surveys. Due to the widespread use of herbicides, weed densities are often very low, for most species. Indeed, only a few species, which are not very sensitive to the herbicides, can develop dense populations (e.g. Colbach *et al.*, 2000). *Adonis* species have almost completely disappeared from areas with intensive agriculture (Pichot, 1991), either because they are sensitive to herbicide or because populations of these species need particular environmental conditions to grow (e.g light availability throughout the plant life cycle) that are not met in current intensive dense crop canopies boosted by high nitrogen fertiliser inputs (Kleijn & van der Voort, 1997). In contrast, *Poa annua* is a very widespread species that was found in 11 to 100% of the fields in different European regions on a North-South transect from Sweden to Italy (Radics *et al*., 2000), and ranked the second most frequently occurring weed species for the frequency of presence in a large field survey conducted in winter cereals in the UK in 1988 (Whitehead & Wright, 1989). However, it is well controlled by herbicide programmes in wheat crops in most regions with intensive cropping systems. It is therefore reasonable to choose a density of zero for both species in intensive cropping systems in the simulation analysis.

The density of weeds of ecological interest in more wildlife-friendly cropping systems may be derived either from old surveys of weed flora performed before the increase in herbicide and nitrogen use, from recent surveys of organic farming (Hyvönen *et al*., 2003; Rydberg & Milberg, 2000), or from long-term experiments aimed at testing the feasibility of cropping systems based on the principles of Integrated Pest Management. However, there may be large differences in plant density for a given species between different fields, from different soil and climatic conditions and conducted with different "low-input" cropping systems (e.g. Marshall & Arnold, 1994), so the plant density to be expected in a wildlife-friendly cropping system is highly unpredictable.

In uncultivated areas, even less information is available regarding the density of "weed" species although, as shown in this paper, the choice of the strategy that supports best biological diversity depends on this information.

Crop yield and weed values are always variable and imperfectly estimated. It is thus necessary to deal with this uncertainty using, for example, the expression of the derivatives of R given in this paper. In all cases, we advise to perform a sensitivity analyse of the ratio R to crop yield and weed density values. Note that, in some practical applications, it may be useful to use gross margins instead of crop yields in order to account for fertiliser and pesticide prices.

Validity of the model equations

The equations presented in this paper are based on the hypothesis that the density of weed species would be higher in uncultivated areas than in low-input cropping systems. This hypothesis is debatable: indeed some weed species grow preferentially in cultivated fields, where they can find an environment favourable to their life history (for example: short life cycle, seed dormancy, seed persistence in the soil, seasonal emergence, high level of seed production).

It has never been demonstrated that *Adonis* species would develop stable populations in uncultivated areas. In long-term set-aside, the overall soil seed bank is likely to increase dramatically if various annual species produce seeds. However, the growing environment would become strongly competitive after a few years, which is probably not favourable for *Adonis* spp.. If annual species are not allowed to produce seeds, for example through repeated mowing, then the proportion of perennials is likely to change more rapidly, which would also provide a very competitive environment for young *Adonis* seedlings. *Poa annua* is a very short-stemmed species, which would also have difficulty developing stable populations in long term set-aside with a dense competitive canopy.

Short-term set-aside, rotating each year in the landscape, are likely to provide more open canopies that would be much more favourable for weakly competitive species such as *Adonis* spp. and *P. annua.* However, in rotational set-aside, the presence of a species is strongly related to the presence of a significant number of seeds in the seed bank, and this is unlikely for a species that has been very rarely observed in a given landscape for many years, such as *Adonis* spp..

Relative performance of the land use strategies

The first case study presented above showed that, for the *Adonis* spp., the value of the crop production ratio R (Eqn 7) is highly sensitive to density in the wildlife-friendly cropping system (d_{WF}) and to the density in uncultivated areas (d_U). If d_{WF} is set at 0.005 plants m^{-2} (Figure 4a), the ratio R shifts from highly favourable to the wildlife-friendly cropping system when $d_U = 0.01$ plants m^{-2} to more favourable to the intensive system when $d_U = 0.04$ plants m^{-2}. The fourfold increase in weed density is not dramatic compared with the wide range of densities observed in cultivated fields. If the *Adonis* spp. density is low both in cultivated areas with low inputs and in uncultivated areas, then the objective of maintaining a significant population in the landscape will be reached only with a severe decline in the proportion of the area cultivated (Figure 2b), and therefore a proportional decline in the crop production, which is likely to be unacceptable for social reasons.

For *P. annua*, the ratio R is less sensitive to plant density, but the conclusions are different depending on whether a high or a low value is assumed for d_{WF}. If d_{WF} is about 20 plants m^{-2}, the land-sparing option with intensive cropping is more favourable for all the explored values of density in uncultivated areas. However, if the density d_{WF} is about 80 plants m^{-2}, which is only four times higher, then the wildlife-friendly cropping system is more profitable for most of the explored values of density in uncultivated areas.

The results of the calculations should be considered with caution because of the uncertainty regarding the contribution of target species in uncultivated areas. However, we can still make an attempt to identify some trends for land use recommendation as far as weed species conservation is concerned. For rare species such as *Adonis* spp., it is likely that plant density in uncultivated areas devoted to wildlife conservation would be only slightly higher than in low-input wildlife-friendly cropping systems. This corresponds to the left-hand part of Figures 4a and 4b, where the ratio R indicates higher overall crop production with the low-input wildlife-friendly cropping system. For common species with low competitive ability such as *P. annua*, a density of 80 plants m^{-2} seems likely to be reached and maintained in a low-input cropping system, and the density in uncultivated areas would be only slightly higher. These hypotheses correspond to the left-hand part of the Figure 4d, which is again more favourable to the low-input wildlife-friendly cropping system.

Conclusion

The model presented in this paper can be used to compare the relative performance of wildlife-friendly cropping system and land sparing for maintaining a desirable level of abundance of a given species of interest in agricultural areas. We showed that the relative performance of the two strategies depends on the plant densities in cultivated fields and uncultivated areas, but does not depend on the desired level of abundance of the species of interest. This result emphasises the need for more comprehensive knowledge about the effects of management options on weed species of ecological value in both uncultivated areas and low-input cropping systems.

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Table 1. Expressions and signs of the derivatives of $R = \frac{y_{WF} \times (d_U - d_I)}{y_I \times (d_U - d_{WF})}$. It is assumed that $d_U > d_{WF} > d_I$.

Derivative	Sign
$\frac{\partial R}{\partial y_{WF}} = \frac{d_U - d_I}{y_I \times (d_U - d_{WF})}$	+
$\frac{\partial R}{\partial y_I} = \frac{-y_{WF} \times (d_U - d_I)}{y_I^2 \times (d_U - d_{WF})}$	-
$\frac{\partial R}{\partial d_{WF}} = \frac{y_{WF} \times (d_U - d_I)}{y_I \times (d_U - d_{WF})^2}$	+
$\frac{\partial R}{\partial d_I} = \frac{-y_{WF}}{y_I \times (d_U - d_{WF})}$	-
$\frac{\partial R}{\partial d_U} = \frac{y_{WF} \times (d_I - d_{WF})}{y_I \times (d_U - d_{WF})^2}$	-

Table 2. Values of the derivatives of R for y_I=8 t.ha^{-1}, y_{WF}=6 t.ha^{-1}, d_I=0, and for low and high densities d_{WF} of *Adonis sp.* and *Poa annua*.

d_{WF} (plants m^{-2})	d_U (plants m^{-2})	R	Values of the derivatives of R				
			$\frac{\partial R}{\partial y_{WF}}$	$\frac{\partial R}{\partial y_I}$	$\frac{\partial R}{\partial d_{WF}}$	$\frac{\partial R}{\partial d_I}$	$\frac{\partial R}{\partial d_U}$
Adonis sp.							
0.005	0.02	1	0.17	-0.125	66.67	-50	-16.17
0.01	0.02	1.5	0.25	-0.19	150	-75	-75
Poa annua							
20	200	0.83	0.14	-0.104	0.004	-0.0042	-0.00046
80	200	1.25	0.21	-0.156	0.01	-0.0063	-0.0042

Figure captions

Figure 1. Relationship between the target number of plants per unit area (D) and the fraction of the field area that can be cultivated (f) with an intensive cropping system (continuous line) and with a wildlife-friendly cropping system (dashed line).

Figure 2. Ratio of the cultivated area to the total area obtained with the wildlife-friendly cropping system (bold line) and with the intensive cropping system (thin line) for *Adonis* (a, b) and *Poa annua* (c, d). For *Adonis*, the calculations were performed with d_{WF} =0.005 plants m^{-2}, and D=0.006 plants m^{-2} (a) or D=0.009 plants m^{-2} (b), and the value of d_U was in the range 0.01-0.1 plants m^{-2}. For *Poa annua*, the calculations were performed with d_{WF} =20 plants m^{-2}, and D=50 plants m^{-2} (c) or D=80 plants m^{-2} (d), and the value of d_U was in the range 100-400 plants m^{-2}.

Figure 3. Crop production obtained with the wildlife-friendly cropping system (bold line) and with the intensive cropping system (thin line) for *Adonis* (a, b) and *Poa annua* (c, d). For *Adonis*, the calculations were performed with d_{WF} =0.005 plants m^{-2}, and D=0.006 plants m^{-2} (a) or D=0.009 plants m^{-2} (b), and the value of d_U was in the range 0.01-0.1 plants m^{-2}. For *Poa annua*, the calculations were performed with d_{WF} =20 plants m^{-2}, and D=50 plants m^{-2} (c) or D=80 plants m^{-2} (d), and the value of d_U was in the range 100-400 plants m^{-2}.

Figure 4. Ratio (*R*) of the crop production obtained with the wildlife-friendly cropping system to the crop production obtained with the intensive cropping system for *Adonis* (a, b) and *Poa annua* (c, d). For *Adonis*, the calculations were performed with d_{WF} =0.005 plants m^{-2} (a) and d_{WF} =0.01 plants m^{-2} (b), and the value of d_U was in the range 0.01-0.1 plants m^{-2}. For *Poa annua*, the calculations were performed with d_{WF} =20 plants m^{-2} (c) and d_{WF} =80 plants m^{-2} (d), and the value of d_U was in the range 100-400 plants m^{-2}.

Figure 1

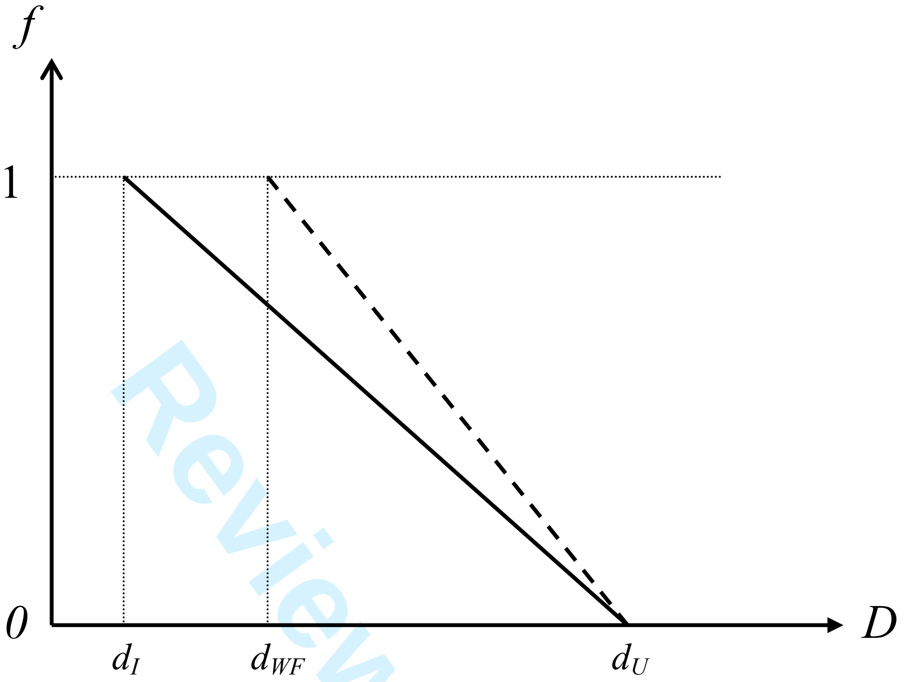
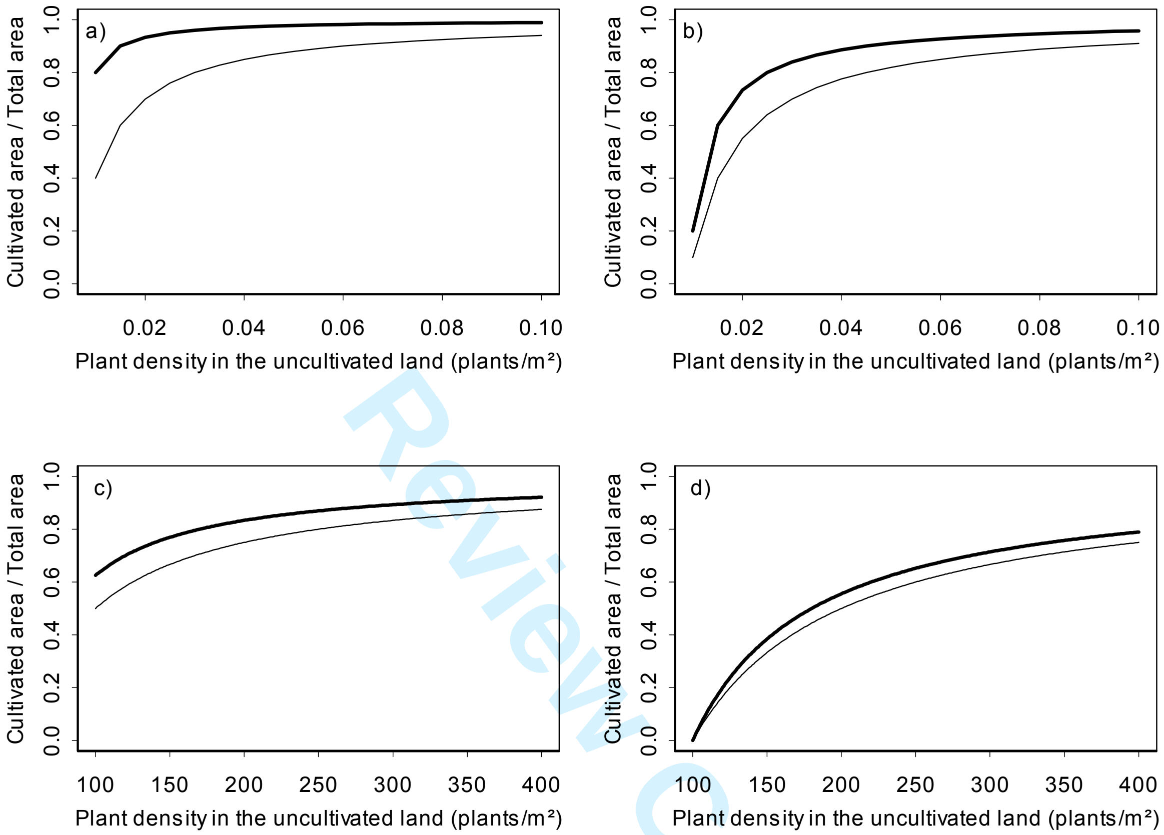


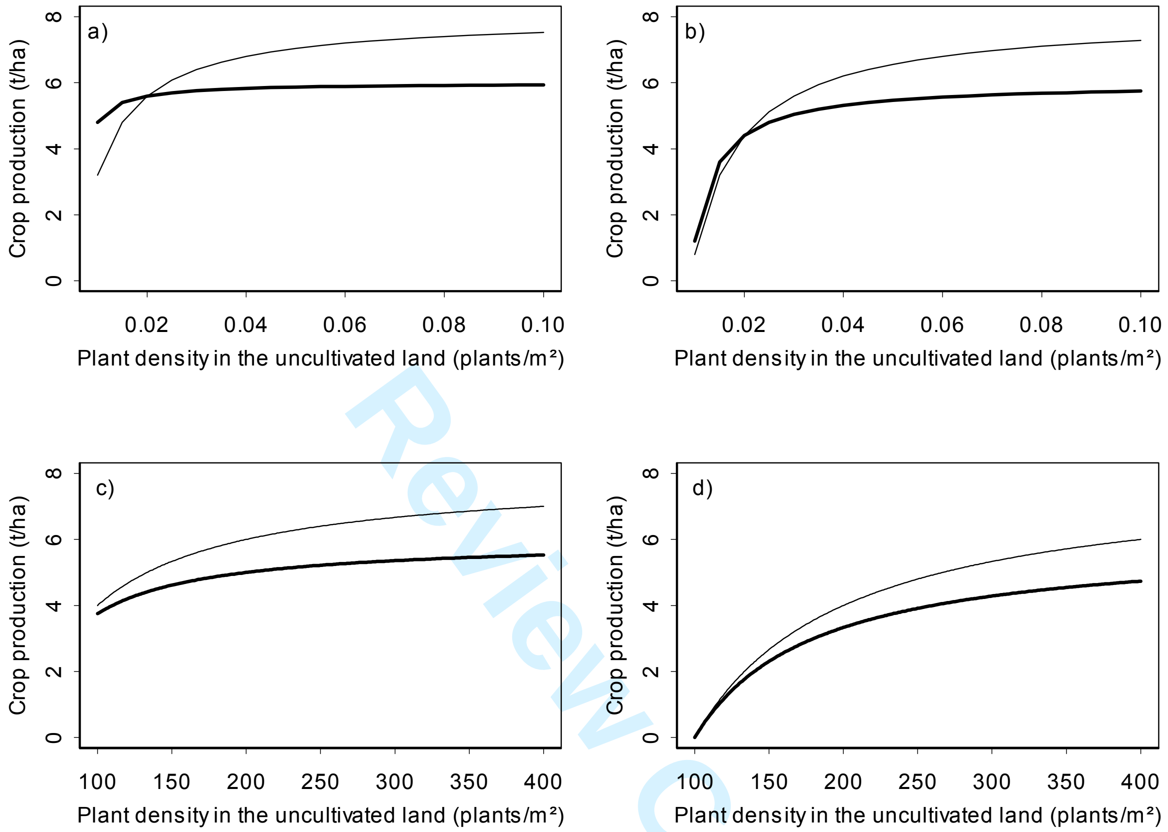
Figure 2


a)
b)
c)
d)
Cultivated area / Total area
0.0
0.2
0.4
0.6
0.8
1.0
0.02
0.04
0.06
0.08
0.10
100
150
200
250
300
350
400
Plant density in the uncultivated land (plants/m²)

Revised version 3

1 Figure 3

2



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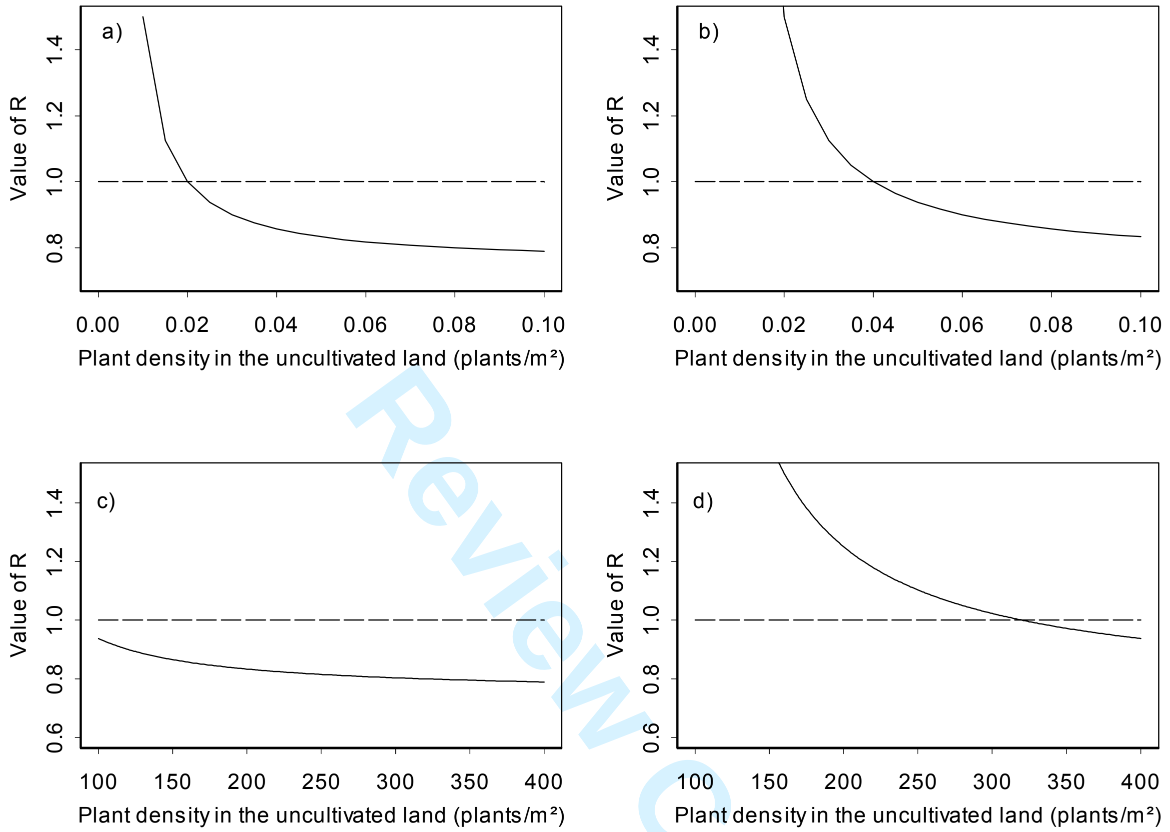
4

Figure 4


a)
b)
c)
d)
Value of R
0.6
0.8
1.0
1.2
1.4
0.00
0.02
0.04
0.06
0.08
0.10
100
150
200
250
300
350
400
Plant density in the uncultivated land (plants/m²)