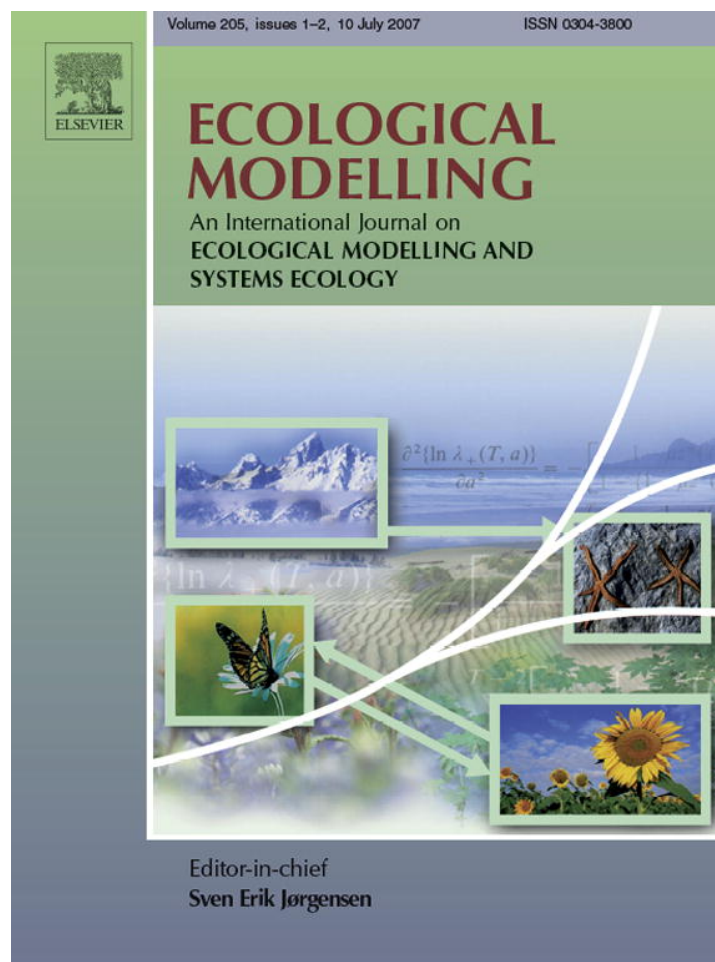


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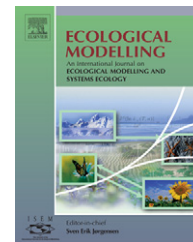
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## Conservation of butterfly populations in dynamic landscapes: The role of farming practices and landscape mosaic

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### ABSTRACT

In a dynamic landscape the rate of change in landscape structure can be even more important than the degree of patch isolation in determining population survival and abundance. If the changes in landscape structure occur at an “extremely” high rate (as in some anthropogenic changes), dispersal may not be able to keep up with the high rates of local extinction. Understanding impacts of such changes is thus crucial for determination of the driving factors for species survival in agricultural landscapes and for elaboration of conservation plans. Here we studied the effects of landscape dynamics under local farming practices on movements and population dynamics of a diurnal butterfly *Maniola jurtina* L. (Satyridae), specifically the impacts of regular yearly mowing on butterfly movements, distribution and abundance over many years. We used an existing simulation model, extended it by the effect of the intensity of disturbance (amount of mown habitat) and timing of disturbance within the reproductive season on the butterfly population dynamics, and validated on our data from a field experiment using a mark-release method. Increase in the amount of disturbed habitats in the landscape led to an increasing isolation of the remnant habitat patches for butterflies. This resulted in decreasing movements between habitat patches and ultimately to population decline, especially in less accessible patches. In the past, influence of landscape dynamics on species survival was usually considered at the long-term scale. Our results demonstrate that the short time scale landscape dynamics induced by farming practices should not be neglected. The novelty of this paper stems in the combination of inclusion of landscape dynamics, of realistic dispersal strategies of individuals, and of considering real landscapes. The effect of man-induced landscape changes on population persistence of a real species in a real landscape has not been possible to be studied by any of the previously developed models.

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## 1. Introduction

During the last decades, evaluating consequences of landscape dynamics under human pressure on ecological processes that may lead to species extinctions became a central issue in landscape ecology and conservation biology. In agricultural landscapes, intensification of production and newly introduced practices led to drastic changes of landscapes in many areas of Western Europe (Agger and Brandt, 1988) and elsewhere, which caused a major loss of biodiversity (McLaughlin and Mineau, 1995; Sotherton, 1998; Wilson et al., 1999; Kitahara and Sei, 2001; Benton et al., 2003). It is not only because of habitat fragmentation and destruction, which have been recognized as two of the major threats to the viability of threatened species (Soulé, 1986; Wiens, 1996), but also because of the rapid temporal landscape spatial structure changes due to various agricultural practices.

The higher the rate of landscape change, the lower the probability of regional population survival (Fahrig and Merriam, 1994). In a dynamic landscape the rate of change in landscape structure can be even more important than the degree of patch isolation in determining population survival and abundance (Fahrig, 1992). If the changes in landscape structure occur at an “unnaturally” high rate (as in some anthropogenic changes), dispersal may not be able to keep up with the high rates of local extinction (Fahrig and Merriam, 1994). Understanding impacts of such changes is thus crucial for determination of the driving factors for species survival in agricultural landscapes and for elaboration of conservation plans (Baker, 1989; Meeus, 1995). Land-use successions between years plus crop growth and farming practices within a year cause rapid changes of the landscape mosaic. However, to our knowledge, only one study investigating interactions between species movement and landscape structure in agricultural landscapes has explicitly considered the effects of farming activities (Baudry et al., 2003). In this paper, we focused on the consequences of landscape dynamics under different farming practices on species movement and distribution, using butterflies as a reference group.

In agricultural landscapes, most butterfly species are restricted to uncultivated herbaceous elements, such as field margins and hedgerows (Dover, 1994), or grasslands (Oates, 1995). Types and regimes of management of these herbaceous areas, i.e., spraying with herbicides or fertilizers, grazing or mowing are critical for butterfly survival, as they drastically modify habitat quality for butterflies by suppressing the availability of nectar-offering plants providing food for adults, of plants suitable for butterfly oviposition and of tall vegetation that can be used as refuges (Oates, 1995). Impacts of farming practices on butterfly survival are dependent on timing of the disturbance within the period of butterfly activity (Oates, 1995). Badly timed practices can produce inappropriate conditions for adults or larvae, and cause populations to collapse (Oates, 1995; Feber and Smith, 1995). Farming practices cause changes in the distribution of resource patches, in spatial heterogeneity and in connectivity at the landscape level. Such changes are expected to influence butterfly abundance (Thomas,

1991) and survival at the long term (Kuussaari et al., 1996).

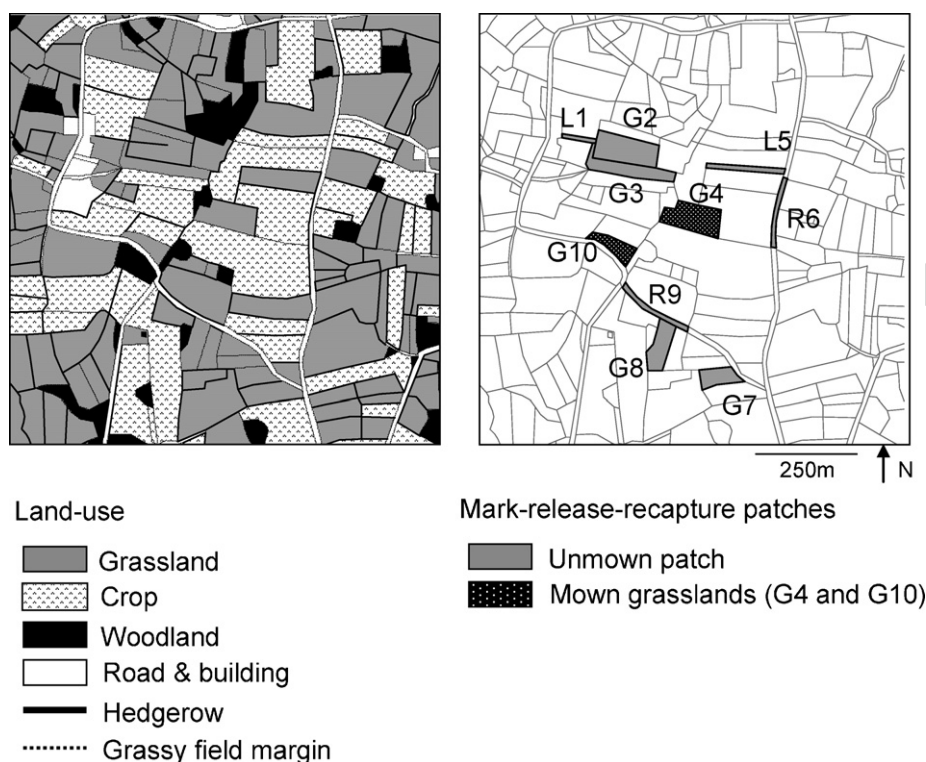
Numerous models have been developed to investigate population dynamics of butterflies or other insects in response to area, quality and isolation of habitats (e.g., Hanski and Thomas, 1994; Hanski et al., 1998; Roland et al., 2000; Hilker et al., 2006). These approaches are, however, often limited to static landscapes and do not consider dynamic landscapes, i.e., temporal variation in habitat quality and distribution. The effect of temporal changes of landscapes on population persistence of butterflies has not been studied before, even if its significance is widely acknowledged (Hanski, 1999; Fleishman et al., 2002). To fill in this gap in our knowledge, we used here a modelling approach to study, how landscape dynamics induced by mowing of grasslands can influence the distribution and abundance of butterflies over years. Models of species movements often simply assume random movement of organisms (Hanski, 1998) and generate colonization patterns for patches depending mainly on patch size and isolation (Matter, 2003). However, a truly realistic model of organism movement should consider both the heterogeneity of the landscape (Gaucherel et al., 2006; Parry et al., 2006), the requirements of individuals (Larson et al., 2004) and their dispersal distance (Vos et al., 2001). Therefore, we used here a model that we had developed previously, which includes all these three aspects (Kindlmann et al., 2004). Thus, the novelty of this paper stems in inclusion of landscape dynamics, of realistic dispersal strategies of individuals, and of considering real landscapes. The effect of man-induced landscape changes on population persistence of a real species in a real landscape has not been possible to be studied by any of the previously developed models.

We simulated the evolution of butterfly distribution and abundance in agricultural landscapes depending on different scenarios of disturbance. We used existing field data on the effect of mowing on butterfly movement to validate the model predictions. We studied, whether repeated mowing over years would lead to a decline of butterfly populations, as a consequence of the progressive isolation of remnant resource patches, whether this decline depends on the amount of disturbed habitats and/or on the timing of mowing within the period of butterfly activity.

## 2. Methods

### 2.1. Study area

The study was conducted in a 1 km<sup>2</sup> landscape unit in Western France (Northern Brittany) (Fig. 1), representing fine-grained hedgerow network landscape (“bocage”). Agriculture in this landscape unit is oriented toward milk production; maize, wheat, and grasslands cover the majority of land. It is characterised by a large proportion of arable land devoted to grasslands (53% of the land) and only few cropped areas of maize and other cereals (33% of the land). It also has a high density of hedgerows and grassy field margins (322 m/ha), and fine grain size (average field size: 0.55 ± 0.53 ha). Grasslands are used both as pastures for animals and mown by farmers for forage.



**Fig. 1** – Study area and mark-release-recapture experimental patches in 2000. G: grassland, L: lane, R: road verge.

## 2.2. Butterfly movement sampling

The studied species, the meadow brown (*Maniola jurtina* L., Satyridae), is a common species with limited dispersal ability as many agricultural endangered species. Sampling of *M. jurtina* movements was conducted in 2000 using mark-release-recapture methods at 10 herbaceous patches: six grasslands (indicated by G2, G3, G4, G7, G8 and G10 further on), and four linear features—two lane banks (L1 and L5) and two road verges (R6 and R9) (see Fig. 1). Two of the studied grasslands (G4 and G10) were mown during the experiment. The other herbaceous patches were not managed during the experiment, except of the grassland G2, which was accidentally grazed by sheep at the end of the study. The mark-release-recapture experiments were conducted from 20 June to 5 July, 7 days before and 7 days after the mowing. The abundance of adults of *Maniola jurtina* was observed to be approximately constant and very large (reaching its seasonal peak) during this period in the same study area during two previous years (Ouin, unpublished data). Thus, the comparisons of butterfly movements before and after mowing of grasslands were not biased by changes in abundance of the adult butterflies. Every day, one mark-release-recapture session was performed between 10 a.m. and 5 p.m. under suitable climatic conditions (Pollard, 1977). One mark-release-recapture session consisted of successive sampling of all herbaceous patches following the same sequence. Each session started in a different patch in the sequence in order to avoid bias due to time of day. During each session, butterflies that were captured for the first time were identified by individual numbers on wing (with odour free pen), and released thereafter. At the same time, their capture

location, i.e., patch number, was recorded. When recapturing butterflies, individual's number and recapture location were recorded. The time spent in each patch was proportional to its surface area (25 min/ha for grasslands and 80 min/ha for linear features, with a minimum of 5 min and a maximum of 20 min) to maintain a constant sampling intensity (Ouin et al., 2004).

The flux from patch *i* to patch *j* was calculated as:

$$M'_{ij} = 100 \times \frac{M_{ij}}{\sum_{k=1}^n M_{ik}}, \quad i \neq j,$$

where  $M_{ij}$  is the number of recaptures in patch *j* (at any time during the experiment) of individuals, which were captured in patch *i*; capture means the first capture of an individual – when it was marked – and recapture the subsequent recapture of this individual (no individual was recaptured more than once in our data) and  $M_{ik}$  is the number of individuals captured in patch *i* and recaptured in patch *i* or any other patch *k*.

Proportion of residents,  $M'_{ii}$ , was estimated for each patch as the proportion of individuals recaptured in the same patch:

$$M'_{ii} = 100 \times \frac{M_{ii}}{\sum_{k=1}^n M_{ik}}$$

Proportion of immigrants,  $I_i$ , was defined for each patch as the percentage of individuals entering patch *i*, out of the total number of recaptured individuals:

$$I_i = 100 \times \frac{\sum_{j=1}^n M_{ji}}{\sum_{k,l=1}^n M_{kl}}$$

Proportion of butterflies captured in patch *i*, out of the total number of captured individuals during the experiment, was

finally defined as the sum of proportion of immigrants  $I_i$  and proportion of residents  $M'_{ii}$ .

### 2.3. The within-year model—first published in Kindlmann et al. (2004)

The studied landscape unit was considered as a mosaic of  $5\text{ m} \times 5\text{ m}$  pixels, so that each of the experimental patches consisted of many pixels. Each of the pixels was characterized according to the value of its land cover in terms of habitat quality for butterflies (Kindlmann et al., 2004): *good* habitat (grassland, grassy field margin, and hedgerow margin) and *bad* habitat (water, woodland and fallow land with high vegetation stands, crop, and road and building). It was assumed that woodlands and fallow land with high vegetation acted as a barrier for butterfly movements, according to the grassland status of the meadow brown. It was assumed that the butterflies are using a non-random, systematic search strategy in which they fly in loops around the starting point and return periodically to it ('homing behaviour'), provided they do not find a *good* habitat (Conradt et al., 2000). The model also assumed that the distance decay curve (dependence of the frequency of flights on their distance) of *M. jurtina* fits a negative exponential function and that the mean flight distance for both males and females is about 70 m, according to findings from Schneider et al. (2003). In the model, this was performed as follows:

- (1) In each step, the direction of flight,  $Dir$ , and its length,  $Length$ , were chosen at random.
- (2) Direction of flight was chosen from a uniform distribution,  $Dir \in (0^\circ; 360^\circ)$ .
- (3) Length of flight,  $Length$ , was chosen from a negative exponential distribution with a constant mean,  $Mean = 70\text{ m}$ , which was chosen as the commonest mean distance of flight of *Maniola jurtina* (Schneider, 2003; Schneider et al., 2003).
- (4) The individual was assumed to move linearly in the direction  $Dir$  for a distance  $Length$ . If at any time during the flight the individual hit a woodland or fallow land, it was assumed to change its direction and perform another flight—this means we returned to point 1. If the individual hit area boundary during the flight, it was allowed to leave the system.
- (5) If the individual starting from pixel  $P_s$  did not hit any woodland or fallow land or area boundary during the flight in the direction  $Dir$  for a distance  $Length$ , and if after having completed the whole flight it arrived to a pixel  $P_a$ , it was assumed to land in  $P_a$ , if either  $P_a$  was *good*, or if  $P_s$  was *bad* (which might have happened, if it hit woodland during the previous flight). If  $P_s$  was *good* and  $P_a$  was *bad*, it was assumed to return to  $P_s$  and land there.
- (6) In the next step, the butterfly was assumed to take off from the point, where it had landed in the previous step, as defined in points 4 and 5, and the whole procedure starting from point 1 was repeated.

In each of the 10 experimental patches within the landscape unit, an initial position of the butterfly was chosen at random and the procedure described above (points 1–6) was

performed 10–100 times with step 10, so simulating 10–100 flights of one butterfly, the first one starting in the pixel selected, the second one starting in the pixel, where the butterfly landed after having performed the first flight (as defined in points 4 and 5), etc. This was repeated 1000 times for each patch selected. As the changes in the number of flights did not qualitatively affect the outcome, we publish only results for 10 flights. Point 2 above means that the experimental butterflies were not assumed to be able to learn from unsuccessful flights, as follows from Conradt et al. (2000). Note that different types of behaviour described in points 4 and 5 above reflect two different situations: hitting woodland or fallow land during the flight is only a signal to changing flight direction and continuing the search, while arrival to a bad pixel at the end of the flight is a signal to return to the takeoff pixel. Because linear movements are simulated at each step, the model does not exactly mimic real flights in loops, but it still expresses the 'homing behaviour' depicted by Conradt et al. (2000).

The predicted flux from patch  $i$  to patch  $j$   $N_{ij}$  was then calculated as the number of times any of the experimental butterflies, the initial position of which was in patch  $i$ , landed in patch  $j$  after having completed 10 flights. In order to make this value comparable with the empirical fluxes,  $M'_{ij}$ , and with the empirically obtained proportions of residents,  $M'_{ii}$ , we used the transformation

$$N'_{ij} = 100 \times \frac{N_{ij}}{\sum_{k=1}^n N_{ik}},$$

and compared the predicted fluxes  $N'_{ij}$ , with  $M'_{ij}$ .

To simulate the effect of mowing, unmown grasslands were considered as a *good* habitat, while mown grasslands were considered as a *bad* habitat. We considered three scenarios: mowing *before* the butterflies begin to activate on wing, in which case the mown grassland was considered as *bad* habitat during all 10 flights, mowing *during* the season, in which case the mown grassland was considered as a *good* habitat during the first 5 flights, and as a *bad* habitat during the last 5 flights, and mowing *after* the season of butterfly activity (equivalent to *absence* of mowing from the point of view of the butterfly), in which case the grassland was considered as *good* habitat during all 10 flights.

### 2.4. Comparison of the model predictions with empirical data

Although the model predictions have already been validated using empirical data in static landscapes (Kindlmann et al., 2004), we did not know whether the model could satisfactorily predict changes in butterfly fluxes and distribution following changes in habitat quality. The model predictions were therefore compared with the empirical data on mown meadows. Similarity between the matrices of predicted vs. observed fluxes, i.e., between the matrices  $N = (N'_{ij})$  and  $M = (M'_{ij})$  was then tested by means of Mantel's test (Mantel, 1967). Significance levels were determined by performing 1000 permutations for the test (Manly, 1998). Only the similarity of inter-patch fluxes between the observed and predicted values was compared and therefore the diagonals of the matrices (proportions of residents) were deleted from the permutation tests.

In addition, to compare the goodness-of-fit of the model, residual sums of squares of non-diagonal terms for the pairs of matrices *N* and *M* (measure of fit of the model) were calculated.

Pearson's correlation coefficients in the SYSTAT (Systat Software Inc., USA) package were used to calculate the correlations between the proportions of residents and immigrants predicted by the model and those observed, and between the inter-patch fluxes and those predicted by the model.

2.5. Between-years model

To simulate the between-years dynamics of the butterflies, we assumed that the number of butterflies, which appear in the patch the next year is proportional to  $N'_{ij}$  (immigrants and residents), with the constant of proportionality equal to *K*. The constant *K* is positively associated with, but not equal to, the number of flights performed by the adult, butterfly fecundity and larval survival to adult age. Provided the sex ratio is constant during the season and close to 1:1, this is a reasonable assumption. All the simulations were performed for three different values of the constant *K* (*K* = 1000, 800, and 600). As we did not have any information about its actual value, the choice was based on expert opinion, based on preliminary model runs—the range from 600 to 1000 hit the switching point from mowing-independent population extinction to mowing-independent population growth (for *K* > 1000 the population always increases, for *K* < 600 the population always decreases within the chosen mowing regimes). We iterated each scenario for 10 years, in order to see the long-term effect of different management regimes on the population dynamics of the butterflies.

This simulation was repeated for the following scenarios:

- No disturbance: no grassland mown during the 10 years.
- Low disturbance intensity: part of grasslands mown each year during the 10 years, representing about 20% of the area covered by all grasslands.
- High disturbance intensity: part of grasslands mown each year during the 10 years, representing about 80% of the area covered by all grasslands.

In the scenario with low disturbance intensity, the landscape still has numerous patches of good habitat (grasslands), while in the scenario with high disturbance intensity, almost exclusively linear good habitats (field margins and road verges) remain in the landscape. In each of the last two scenarios, mowing at the beginning, during, and at the end of the season (the last option is equivalent to absence of mowing) was considered. For each scenario and each time of mowing, the relative variation of butterfly abundance between the 1st and the 10th year of simulations in patch *i*,  $R_i$ , was then calculated as

$$R_i = \frac{(\text{number of individuals in year 10}) - (\text{number of individuals in year 1})}{\text{number of individuals in year 1}} \times 100$$

3. Results

3.1. Comparison of the observed numbers of captures and predicted butterfly numbers within a year

One thousand one hundred and twelve butterflies were captured during the mowing experiment in summer 2000. Thirty percent of marked butterflies (329 individuals) were recaptured, among which 167 individuals were found to move between empirical patches.

Predicted numbers of butterflies in patches were statistically significantly positively correlated with the observed numbers of captures, both before and after mowing (Pearson correlations: before mowing:  $r=0.72$ ,  $P<0.05$ ; after mowing:  $r=0.42$ ,  $P<0.05$ ). Fig. 2 shows the comparison of the observed numbers of captures and the predicted numbers of butterflies in the patches, measured as the sum of  $\sum_i N'_{ii}$  (residents) and  $\sum_j N'_{ji}$  (immigrants), in the periods before and after mowing. A striking similarity of the model predictions and empirical data is evident. According to the Mantel's tests, the probabilities that the predicted fluxes differ from the observed ones are  $P<0.001$ , for both before and after mowing. Thus, similarly to Kindlmann et al. (2004), it can be concluded that the model satisfactorily mimics the real situation.

As observed during the experiment, the model predicted a high aggregation of butterflies in some grasslands (especially in G2), compared with linear features, i.e., road verges and lane banks. This could be interpreted as a lower residency of butterflies in linear features due to lower habitat quality. Because the studied linear features had higher vegetation quality than

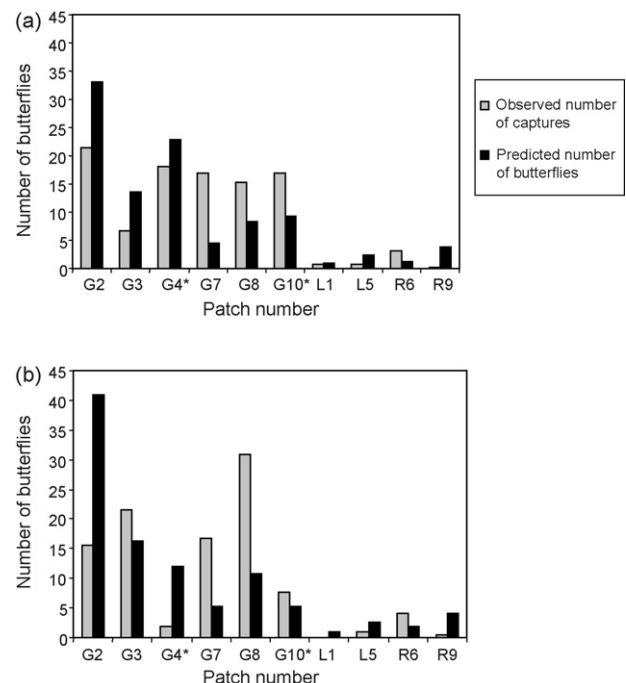
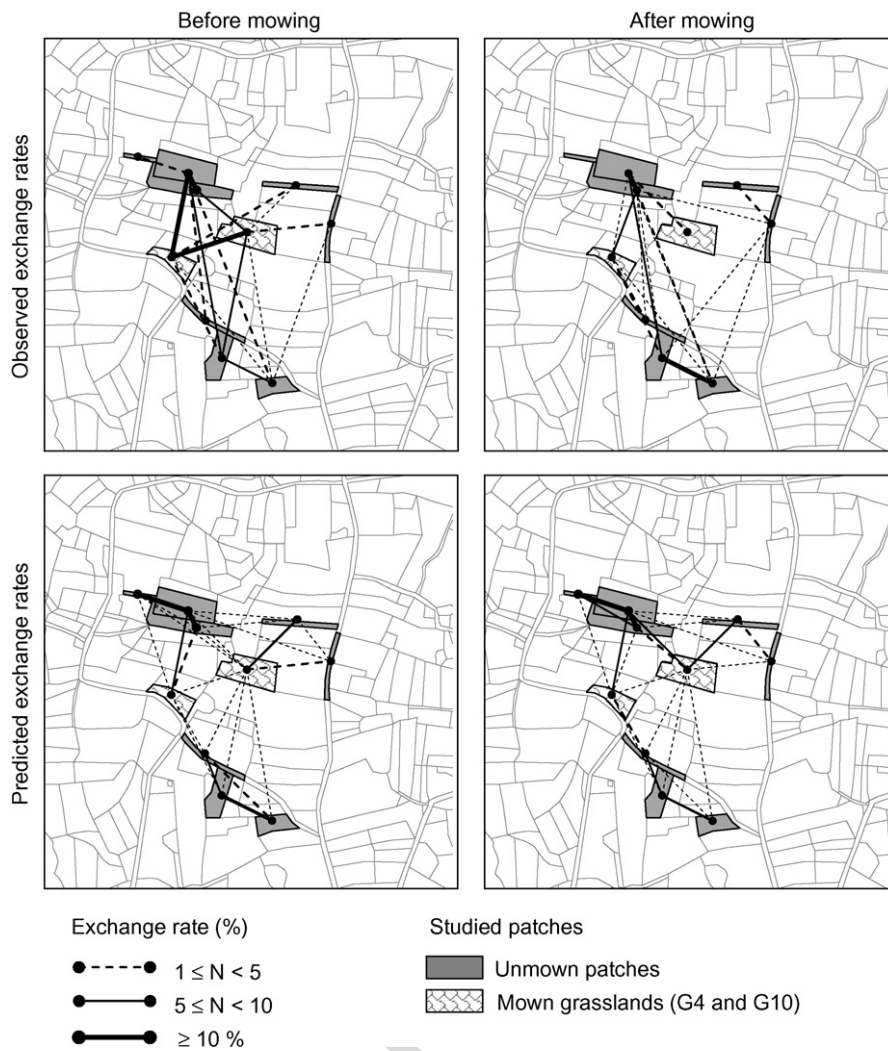


Fig. 2 – Numbers of butterflies in empirical patches captured in 2000 and predicted by the model before mowing (a, top) and after mowing (b, bottom). G: grassland, L: lane, R: road verge. \* refers to mown grasslands (G4 and G10).

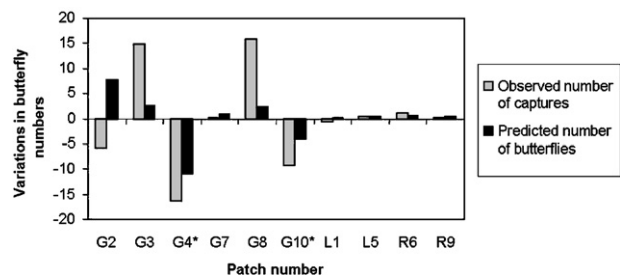


**Fig. 3 – Exchange rates (fluxes in both directions summed) of butterflies between empirical patches observed in 2000 and predicted by the model before (left) and after mowing (right).**

grasslands (Ouin et al., 2004), the results suggest more that they were less accessible for butterflies (the butterflies found them less frequently). It is also evident that the predicted distribution of individuals depends on interactions between butterfly movements and the landscape pattern. The examination of observed and predicted exchanges (fluxes in both directions summed) of butterflies between patches in Fig. 3 shows that the exchange rates were higher between proximate grasslands before mowing (i.e., between grasslands G2, G3, G4, G10 and between grasslands G7 and G8), probably because of a lower inter-patch distance. Exchanges between distant grasslands or linear features were often reduced.

Fig. 4 shows the differences between the numbers of butterflies in individual patches before and after mowing, as they were observed and as the model predicted them. Again, the predicted values were significantly correlated with the empirical ones (Pearson correlation:  $r = 0.58, P < 0.05$ ). It is clearly seen that the butterfly captures in the mown grasslands G4 and G10 decreased considerably, while those in unmown grasslands (especially in G3 and G8) increased and those in linear habitats (road verges and lane banks) were almost unchanged. This can

be related to the changes, which occurred in butterfly fluxes after mowing. Fig. 3 shows a strong reduction of exchanges between the mown grasslands (especially G4) and proximate herbaceous patches after mowing. Butterfly fluxes from the



**Fig. 4 – Variations in butterfly abundance in empirical patches, measured as differences between the numbers of butterflies in individual patches before and after mowing observed in 2000 and predicted by the model. G: grassland, L: lane, R: road verge. \* refers to mown grasslands (G4 and G10).**

proximate patches (e.g., G2) were mainly redistributed towards the more distant grasslands (G7 and G8), and to a lesser extent towards some linear features (especially R6). Thus, the butterflies probably flew along the different linear features to reach the remnant suitable grasslands.

**3.2. Predicted long-term effect of agricultural practices on butterfly population dynamics**

Fig. 5 shows the development of the butterfly population under the two scenarios of disturbance intensity (20 and 80% of grasslands mown, respectively), the differing management regimes: no grasslands mown (equivalent to late mowing), grasslands mown each year during the period of butterfly activity, and grasslands mown early (before the adult butterflies begin to fly) each year, and three different values of the constant  $K$  ( $K = 1000, 800,$  and  $600$ ). Quite clearly, there are dramatic differences in the fate of the population between the different management regimes.

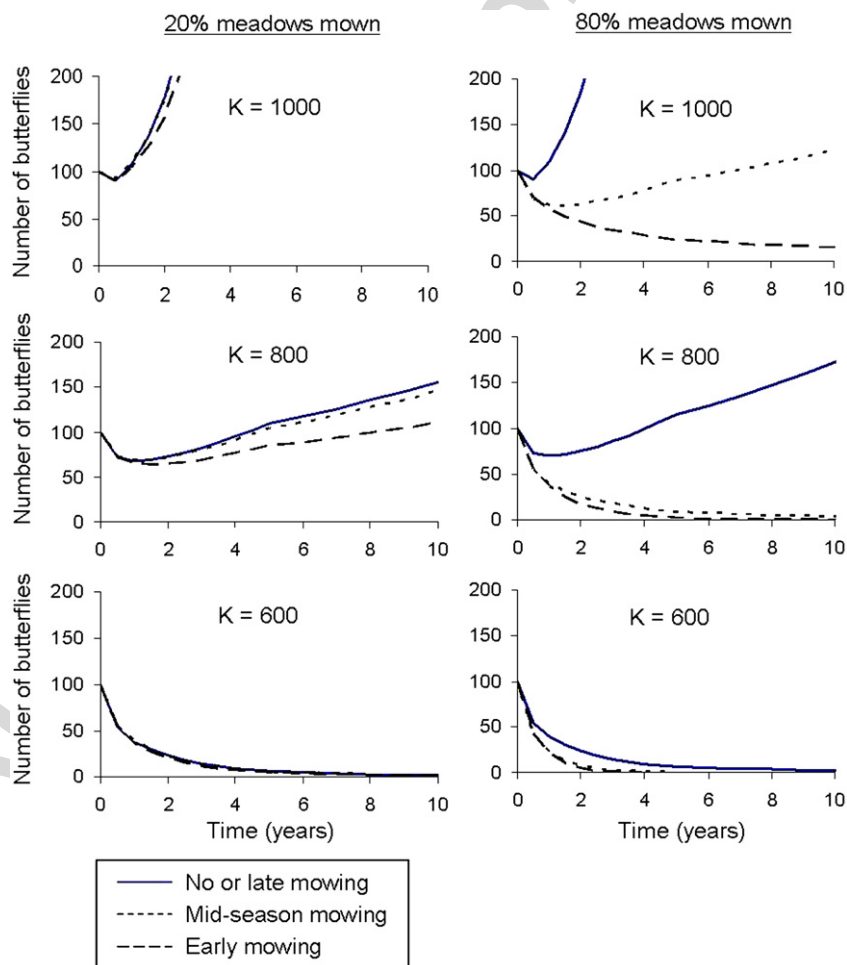
Absence of mowing resulted in a conspicuous increase in total butterfly numbers for  $K = 1000$ , their moderate increase for  $K = 800$ , and their decline for  $K = 600$ . Expressed in biological terms: the butterfly population increased, when butterfly

fecundity was large and/or their juvenile mortality was small and vice versa.

Repeated mowing over the years had differential effects on the development of the butterfly population depending on mowing intensity. Under repeated low intensity mowing (20% of grasslands mown), butterfly abundance could increase over the years for  $K = 1000$  and  $800$ , while for  $K = 600$  low intensity mowing led to a drop in butterfly numbers (Fig. 5). On the contrary, intensive mowing (80% of grasslands mown) early in the season always had fatal effects on the survival of the butterfly metapopulation, expressed by the severe drop in total butterfly numbers (Fig. 5). The model predicted almost complete extinction of the butterfly metapopulation after 3 or 5 years of repeated mid-season mowing for  $K = 600$  and  $800$ , but a slight increase of butterfly numbers for  $K = 1000$ .

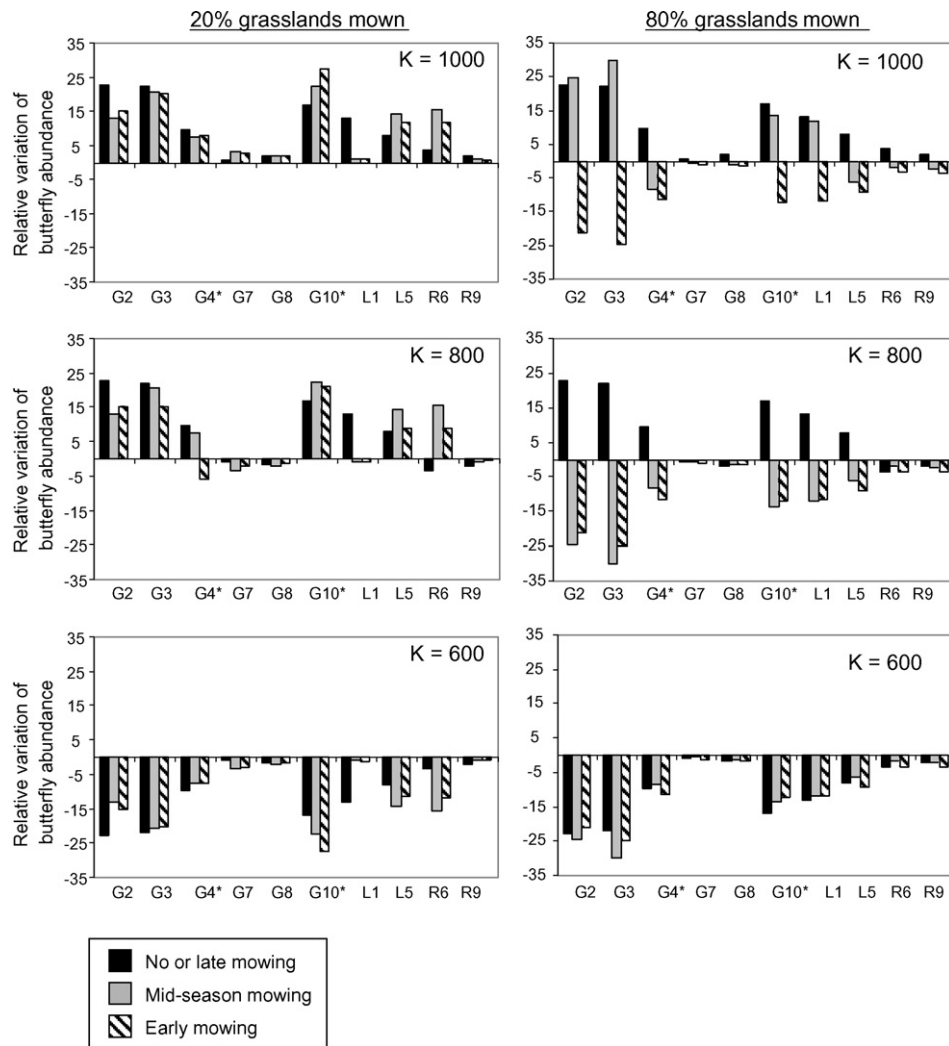
**3.3. Long-term dynamics of butterfly populations in individual patches**

Fig. 6 shows the relative variation of butterfly abundance in individual patches between the 1st and the 10th year of simulations,  $R_i$ , for low (20% of grasslands mown) and high intensity of disturbance (80% of grasslands mown), under the three



**Fig. 5 – Model prediction of butterfly metapopulation dynamics for the two scenarios (left: 20% of grasslands mown; right: 80% of grasslands mown) depending on the different management regimes (no or late mowing, mid-season mowing, early mowing) and the values of the constant  $K$  ( $K = 1000, 800,$  and  $600$ ).**





**Fig. 6 – Relative variation of butterfly abundance in individual patches between the 1st and the 10th year of simulation,  $R_i$ , for the two scenarios (left: 20% of grasslands mown; right: 80% of grasslands mown) depending on the different management regimes (no or late mowing, mid-season mowing, early mowing) and the values of the constant  $K$  ( $K = 1000$ , 800, and 600). G: grassland, L: lane, R: road verge. \* refers to mown grasslands (G4 and G10).**

management regimes (no or late mowing, mid-season mowing and early mowing) and for  $K = 1000$ , 800, and 600. Clearly, the relative changes in butterfly numbers were different in different patches, depending on the intensity of disturbance and the type of management regimes. This suggests that different patches are differentially isolated for butterflies.

Absence of mowing during the 10 years led to an increase in butterfly numbers in all patches for  $K = 1000$ , which was more pronounced in some grasslands (especially G2, G3 and G10), compared with more isolated grasslands (grasslands G7 and G8) and linear features (Fig. 6). This confirms that the latter patches were less accessible for butterflies. The pattern predicted for  $K = 800$  was similar, the exception being a slight drop of butterfly numbers in some linear features and in grasslands G7 and G8. For  $K = 600$ , absence of mowing induced a decrease in butterfly abundance, proportionally more severe in the less isolated patches, in accordance with the overall decline of the butterfly population (Fig. 6).

When mowing intensity was low and  $K = 1000$ , then early and mid-season mowing led to an increase in butterfly numbers in all patches, which was especially pronounced in the more accessible ones (e.g., grasslands G2, G3, G10) (see Fig. 6). When mowing intensity was low and  $K = 800$ , butterfly numbers dropped slightly in the more isolated patches (grasslands G7 and G8, road verge R9) and increased in other patches (Fig. 6). When mowing intensity was low and  $K = 600$ , butterfly numbers declined in all patches, proportionally more pronounced so in the less isolated ones (Fig. 6).

For high intensity of disturbance and  $K = 1000$ , mid-season mowing during the 10 years resulted in a drop of butterfly numbers in the isolated patches and an increase of butterfly populations in accessible grasslands (Fig. 6). For other scenarios of management regimes (mid-season mowing for  $K = 800$  and 600, and early mowing for all three  $K$  values), mowing at high intensity resulted in a decline of butterfly populations

proportionally higher in the less isolated patches, in accord with the predicted population extinction (Fig. 6).

## 4. Discussion

### 4.1. Predicted effects of repeated disturbances on the long-term dynamics of butterfly populations

Our model predicts that farming practices such as mowing might lead to significant changes in the abundance of butterfly populations and affect their long-term survival. These changes are dependent on two factors: the amount of grasslands in the landscape mown each year, i.e., the intensity of disturbance, and the timing of mowing in the period of butterfly activity.

According to the assumptions made in the model, the predicted distribution of butterflies in the landscape reflects their ability to reach herbaceous habitats, i.e., the connectivity of the landscape: it depends on the presence of stepping-stone habitats (grasslands) and of corridors (field margins) between resources patches, but also on the presence of landscape elements that act as barriers for butterfly movements—woodlands in our case (Kindlmann et al., 2004). The model predicted that mowing of herbaceous patches results in isolation of butterfly populations in some herbaceous patches over years, which leads to population decline and ultimate extinction. Disturbances cause changes in spatial heterogeneity of landscapes and in the distribution of habitat patches at the landscape scale (Denslow, 1985). In our case, mowing of grasslands led to significant changes in landscape connectivity and modified the chance for butterflies to reach suitable resource patches—the mown areas impeded butterfly movements between the remnant resource patches. The predicted response of butterfly populations to mowing differed depending on the amount of disturbed habitats in the landscape: low disturbance intensity (20% of grasslands mown) allowed persistence or even expansion of butterfly populations, while high disturbance intensity (80% of grasslands mown) did not. This can be attributed to the different landscape patterns caused by mowing in the two scenarios. Low disturbance intensity allowed persistence of some large herbaceous patches, whereas under the high disturbance scenario almost exclusively non-productive landscape elements such as hedgerows, field margins and road verges remained as suitable habitats. Thus it seems that butterfly populations are sensitive to the degree of change in landscape connectivity caused by the amount of disturbed habitats in the landscape. Although non-productive landscape elements can play an important role for butterflies as corridors or habitats (Dover, 1989, 1996; Fry and Robson, 1994; Geertsema and Sprangers, 2002), they may not be sufficient for a long-term survival of butterfly populations.

Understanding the effects of landscape pattern on ecological processes and their changes is one of the major challenges in landscape ecology and conservation biology. Until now, most studies have focused on changes in uncultivated habitats, e.g., forests, but few have considered the role of farming activities in the landscape dynamics (Baudry et al., 2003). Our study suggests that farming practices should be considered

explicitly to understand how the landscape dynamics could affect survival of species associated with agricultural habitats, especially those with low mobility. *Maniola jurtina* does not have strong requirements for oviposition or for larval and adult food (Feber, 1993). However, it has a limited mobility in comparison with other common farmland butterfly species. Temporal changes in spatial structure of agricultural land act against the persistence of populations of less mobile species (Feber and Smith, 1995). Major disruptions caused by farming practices, which characterise agricultural habitats, make the supply of resources unpredictable (MacDonald and Smith, 1991). Habitat may therefore be under-utilised simply because many butterfly species are insufficiently mobile to respond to the changing distribution of resources.

Our model predicts that timing of mowing in the season is crucial for the persistence of butterfly populations, early-season mowing having the strongest negative impact. Our results are consistent with the previous knowledge on the effect of timing of farming practices. Mowing in summer can affect species that are on the wing at that time (Feber et al., 1996). Badly timed grazing or mowing will produce inappropriate conditions for butterflies, which will cause butterfly populations to collapse (Oates, 1995). Grasslands, which are cut late or in mid-summer, can support vast populations of grassy-feeding species such as *Maniola jurtina* (Oates, 1995). Late cutting has two advantages for butterflies: it provides a continuous supply of nectar resources and undisturbed habitat in which females can oviposit and/or the larvae can feed or complete their development (Feber and Smith, 1995). Managing herbaceous habitats by late cutting is thus advocated for enhancing biodiversity (Council of Europe, 1997; Chaïb and de Manneville, 2003).

The effect of timing of mowing on the survival of the butterfly populations can sometimes have quite unexpected effects on the optimal management regimes of certain specific conservation areas, where protection of different species is the aim. For example, we know of a nature reserve (Milikovice in the Czech Republic) that contains an endangered orchid, *Dactylorhiza majalis*, and an endangered butterfly, *Maculinea telejus*. The larvae of the latter live on *Sanguisorba officinalis*, which flowers in July, while *D. majalis* is in bloom in June. As *D. majalis* requires regular mowing for its proper development and long-term survival, the site has been regularly mown after *D. majalis* had fruited, but sometimes before *S. officinalis* had finished flowering. This management resulted in a flourishing population of *D. majalis*, but – because of its host plant was cut – a decline in abundance of *M. telejus* after about 10 years (Kindlmann, unpublished).

### 4.2. Understanding species dynamics in agricultural landscapes: limitations and contributions of the present modelling approach

Our modelling approach has some limits. We aimed at simulating a non-random, systematic search strategy in which butterflies fly in loops around the starting point and return periodically to it, provided they do not find a good habitat. Actually, the model mimics more the ‘homing behaviour’ of butterflies than real flights in loops, since each movement step is straight. Even if our modelling of the butterfly move-

ment is a simplification of the flying behaviour depicted by Conradt et al. (2000), it still reflects satisfactorily the movements and distribution of *M. jurtina*. Furthermore, butterfly movements were simulated with a flight length chosen from a negative exponential distribution with a constant mean of 70 m. However, longer flight distance and a broad variation in the mean distance of flight for this species have been observed (Schneider, 2003). A previous sensitivity analysis of the model to this parameter (varied by 5 m from 5 to 100 m) showed a very weak dependence of the results on the mean flight distance (Kindlmann et al., 2004). Finally, the values of the parameter  $K$  were chosen arbitrarily ( $K=1000, 800, \text{ and } 600$ ) and so was the number of flights performed by one butterfly (10–100 in our simulations). We do not have any information about their actual values for *Maniola jurtina*, but our sensitivity analysis suggests that changes in the number of flights within the range from 10 to 100 do not affect the qualitative behaviour of the model. The model appeared to be sensitive to the value of  $K$  as demonstrated by the different predicted patterns for the three tested values. Nevertheless, the values of reproductive success of *Maniola jurtina* in the between-years model remain meaningful from a qualitative point of view, as illustrated by our results.

We have modelled farming practices (mowing) simply by assuming that the corresponding habitat character changes from being *good* to being *bad* and by appropriate timing of this change in the simulation without integrating highly detailed data on the quality of resources like changes in nectar and host resources into the model. Comparison of the actual and predicted fluxes within a year lends a strong support for this simple approach. Spatially explicit models of population distribution and dynamics at the landscape scale often ignore the impacts of changes in habitat quality under disturbance (e.g., Hanski and Thomas, 1994; Hanski et al., 1998; Roland et al., 2000), whilst models testing the impacts of landscape dynamics build predictions based only on patch size and isolation (e.g., Bergman and Kindvall, 2004; Schtickzelle and Baguette, 2004). Based on simple assumptions and on a limited number of inputs parameters, our modelling approach combined both a spatially explicit description of the landscape and the integration of habitat variability over time.

An interesting support for the model follows from Fig. 2: The most conspicuous discrepancy between the model predictions and empirical data is the prediction that butterfly abundance in grassland G2 after mowing should be larger than that before, while the empirical data show exactly the opposite. Grassland G2 has been grazed at low intensity by sheep towards the end of the experiment. Thus butterflies, which have left the mown patches, if arrived to this patch, did not find suitable habitat conditions (inappropriate vegetation height or nectar availability) to stay here and continued in searching for a patch with better resource quality.

Our scenarios of farming disturbance were very simple in comparison with what really happens in agricultural landscapes. The agricultural landscape is characterised by a shifting mosaic of land-uses caused by different farming practices. Furthermore, timings of farming practices are highly fluctuating depending on the phenology of the different crops and decisions of individual farmers. Our modelling approach permits to generalize and predict how farming practices influ-

ence herbivorous insect population dynamics via the changes in the amount and spatial organisation of herbaceous patches in the agricultural mosaic. Generalization of our results to higher trophic levels may, however, be problematic, as insect parasites or predators and species with a different food range may be differentially susceptible to disturbance (Steffan-Dewenter, 2003; Thies et al., 2003). According to the percolation theory (With et al., 1997; With and King, 1999), landscape connectivity decreases non-linearly with the decreasing amount of habitats and movements between fragments are inexistent under a defined threshold. We tested two contrasted scenarios of disturbance intensity, but it would be interesting to extend the simulations to a large variation of disturbance intensity to determine whether such threshold exists for butterfly persistence.

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