



# When is landscape matrix important for determining animal fluxes between resource patches?

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## Abstract

It is usually assumed that the fluxes of individuals between the subpopulations in a metapopulation are proportional to the sizes of the departure and arrival resource patches and to the inverse of the distance between these two patches, and therefore, can be described by a regression model, which ignores spatial heterogeneity of the landscape between the resource patches. Recently, Kindlmann et al. [Kindlmann, P., Aviron, S., Burel, F., Ouin A. Can assumption of a non-random search improve our prediction of butterfly fluxes between resource patches? *Ecol. Entomol.*, 29, 447–456] have shown that a spatially explicit model using the non-random dispersal patterns of *Maniola jurtina*, a butterfly species, can explain its fluxes between herbaceous areas in agricultural landscapes much better than the regression model. However, the question still remains, in which particular aspects the regression model reflects the reality satisfactorily and in which ones it fails. To determine these aspects, we analyze here the model developed by Kindlmann et al. [Kindlmann, P., Aviron, S., Burel, F., Ouin A. Can assumption of a non-random search improve our prediction of butterfly fluxes between resource patches? *Ecol. Entomol.*, 29, 447–456] and fit its predictions concerning the dependence of fluxes between individual resource patches on sizes of these patches and on the distance between these patches by the regression model. We conclude that the regression model fails to predict the intensity or fluxes between resource patches, especially when the patches considered are relatively close to each other, so that under optimal conditions the flux could be relatively large. In such cases, the structure of the habitat matrix (e.g. obstacles and/or stepping stones between patches) becomes important.

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## 1. Introduction

Species living in fragmented landscapes usually form a metapopulation—a series of many subpopulations living in spatially isolated resource patches, interconnected by means of migration. Understanding

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the rules of movement of individuals between these subpopulations is crucial for prediction of the dynamics of the metapopulation and conditions for survival of the whole species (Gilpin and Hanski, 1991; Hanski and Gilpin, 1997). We do not know much about how individual animals disperse because of the difficulty in keeping track of dispersing individuals in the field (Zollner and Lima, 1999). Most metapopulation models, therefore, simply assume random movement (Hanski, 1998; Moilanen, 1999). Flux of individuals between subpopulations is then assumed to depend on the sizes of the departure and arrival resource patches and the distance between these two patches. The background ideas are that: (i) population size in the departure patch and, therefore, also the number of emigrants is expected to be proportional to the size of this patch, (ii) the probability that a target (arrival) patch is hit is proportional to its size, (iii) the flux between departure and arrival patches exponentially declines with the distance between these two patches (Wilcox, 1980; Hanski, 1999). This leads to what we will subsequently call “the regression model”, in which the flux of individuals between patches  $i$  and  $j$ ,  $M_{ij}$ , is described by:

$$M_{ij} = aA_iA_j e^{-bD_{ij}}, \quad (1)$$

where  $A_i$  and  $A_j$  are sizes of the departure and arrival patches, respectively,  $D_{ij}$  is distance between these two and  $a$  and  $b$  parameters. This model, therefore, characterizes animal fluxes between patches only by the degree of patch isolation (Verboom and van Apeldoorn, 1990; Moilanen and Hanski, 2001). However, several authors have shown that the intensity of animal fluxes also depends on the presence of corridors or stepping-stones and on heterogeneity of the landscape (Pain et al., 2000; Ricketts, 2001). It is, therefore, questionable, whether formula (1) correctly describes the real fluxes of individuals between the subpopulations, and even if formula (1) is assumed to be a reasonable approximation of the real fluxes, what is the accuracy and what are the limitations of this formula when confronted with real data?

Butterflies are an ideal model group for testing these questions, as they typically live in fragmented habitats with networks of local populations. It is also known that butterfly dispersal is affected by resource

patch area, patch isolation, patch quality, and sex (Dover et al., 1992; Hanski, 1994; Hill et al., 1996; Kuussaari et al., 1996; Baguette et al., 1998, 2000; Petit et al., 2001). Conradt et al. (2000) found that the meadow brown (*Maniola jurtina* L.) does not seek habitat by means of random flight. Their experimental butterflies used a non-random, systematic, search strategy in which they flew in loops around the release point and returned periodically to it until a suitable habitat was reached. Schneider et al. (2003) found that the distance decay curve (dependence of the frequency of flights on their distance) of *M. jurtina* fitted a negative exponential function and that the mean flight distance for both males and females was between 60 and 70 m. Most recently, Kindlmann et al. (2004) tested to what extent the non-random dispersal patterns described by Conradt et al. (2000) and Schneider et al. (2003), and the explicit consideration of the landscape mosaic can explain *M. jurtina* fluxes between herbaceous areas in agricultural landscapes. Similar models are now gaining attention (Hanski and Ovaskainen, 2003; Ovaskainen, 2004), as they are able to describe the effect of the habitat matrix (the landscape between the resource patches), which the previous regression models were not able to.

In most cases, Kindlmann et al. (2004) model (further referred to as *Maniola* model) gave either a considerably better, or at least comparable prediction of actual butterfly fluxes than a simple prediction of the regression model based on patch size and distance between patches. That is, the *Maniola* model resulted in smaller residual sums of squared differences between the observed values and those predicted than the regression model. Also, the predictions of the inter-patch fluxes were better correlated (Pearson correlation coefficient) with the empirical data for the *Maniola* model. However, Kindlmann et al. (2004) did not analyze, in which particular aspects the *Maniola* model is better: is it the dependence of predicted butterfly fluxes between individual resource patches on size of the arrival and/or departure patch and/or on distance between these patches, where the regression model fails? Here, we fill this gap.

Our logic is as follows: the *Maniola* model takes into account the matrix, while the regression model does not. Following Kindlmann et al. (2004), we assume the *Maniola* model describes the empirical data sufficiently well. We are thus plotting, how the

fluxes predicted by the *Maniola* model depend on patch size and distance, which was not done in Kindlmann et al. (2004). If these dependencies can be fitted by the appropriate curve, then the regression model suffices. However, if the dependence consists of a “cloud” of points, which cannot be fitted by a curve, then it is evident that something is missing – the fluxes cannot be described only by using patch size and distance – and probably the structure of the matrix has to be taken into account. In such cases, the regression model cannot give a good prediction and the *Maniola* model should be used. We use the *Maniola* model predictions rather than empirical data for comparison with the regression model assumptions, because we could create much more comparison “data” with the model.

## 2. Material and methods

### 2.1. Species and study area

Our model species is the meadow brown (*M. jurtina*), which is one of the most abundant butterfly species in agricultural landscapes. It has one generation per year with adults appearing between mid-June and September and feeds on nectar from flowers. The eggs are laid on a variety of grasses, which are then fed on by the larvae. *M. jurtina* is classified as a sedentary species, with a minimal home range estimated as 0.5 ha (Brakefield, 1982), although in certain cases it can disperse even over several kilometres (Schneider et al., 2003). Landscape elements with tall vegetation such as woodland can act as a barrier to movement (Sutcliffe and Thomas, 1995; Haddad, 1999), leading to changes in flight direction (Fry and Robson, 1994).

The study was conducted in two landscape units in Western France (Northern Brittany), representing fine grain hedgerow network landscapes (*bocage*). The sites differ in the intensity of agricultural production. Site 1 is characterised by a high proportion of large areas of maize and other cereals, compared to site 2 with more grassland. Sampling of butterfly movement and simulations were performed at eight experimental patches in 1998 and 15 in 1999 at each site.

Here, we give only the basic information on both the species and sites necessary for understanding the paper. More details can be found in Kindlmann et al. (2004).

### 2.2. The *Maniola* model

The model was constructed as follows.

The landscape 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 by the type of land cover. “Good” habitats (grasslands, grassy field margins, and hedgerow margins), “bad” habitats (water, crops and roads, and buildings), and “forest” (woodland and fallow land) were distinguished. Landscape composition was different in the 2 years due to crop succession, resulting in different spatial distribution of good and bad habitat for the butterfly. This made it possible to have different cases of landscape composition in the simulations. It was assumed that woodlands acted as a barrier for butterfly movement, according to the grassland status of the meadow brown. Consistently with Conradt et al. (2000), 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, provided they do not find a “good” habitat. 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,  $Dir \in \langle 0; 360^\circ \rangle$ .
- (3) Following Schneider et al. (2003), length of flight, *Length*, was chosen from a negative exponential distribution with a constant mean, *Mean*. *Mean* = 70 m was chosen for the main simulation, as it is the commonest mean distance of flight of *M. 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 land and perform another flight (in principle, this meant change of flight direction, as new *Dir* was repeatedly chosen, until *Dir* pointed outside of the woodland). 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.

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 both experimental landscapes and in each of the experimental patches within the landscape, an initial position of the butterfly was chosen at random and the procedure described above (points 1–6) was performed 1000 times, so simulating 1000 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 landscape and each patch selected.  $M_{ij}$  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  $j$  during the simulation.

The patterns of “good” and “bad” habitats slightly differed between years 1998 and 1999 in the landscape studied because of agricultural practices like, e.g. ploughing, which converted meadows (“good” habitat) into arable fields (“bad” habitat), etc. Thus, the model predictions for landscape patterns in 1998 and 1999 were verified using the empirical data and model predictions separately for each of these years. Here, we analyze the predictions of the *Maniola* model concerning the dependence of fluxes between resource patches (sets of connected pixels of the same habitat) on sizes of these patches and on the distance between these patches.

### 2.3. Simulations in random landscapes

It is difficult to collect empirical data in more than two landscape units. To get an idea about the fluxes for a broader range of landscapes, we ran the *Maniola* model for a series of randomly constructed landscapes, following the algorithm suggested by Wiegand

et al. (1999). Each of the landscapes consisted of  $210 \times 210$  pixels with  $F$  forests (we used  $F = 0, 3, 6, 9$ ) and  $G$  good habitats (we used  $G = 0, 3, 6, 9$ ). For each combination of the numbers  $F$  and  $G$ , we constructed 10 random landscapes as follows:

- (i) Random numbers  $x_f(i), y_f(i), x_g(j), y_g(j)$  were chosen from the uniform distribution on  $\langle 0;210 \rangle$  and random numbers  $h_f(i), h_g(j)$  were chosen from the uniform distribution on  $\langle Ah - Avh; Ah + Avh \rangle$  for  $i = 1, \dots, F$  and  $j = 1, \dots, G$ .
- (ii) We created three-dimensional surfaces by superimposing a high number of two-dimensional Gaussian functions:

$$f(x, y) = \sum_{i=1}^F h_f(i) \times e^{-Aw((x-x_f(i))^2+(y-y_f(i))^2)} \tag{2}$$

and similarly,

$$g(x, y) = \sum_{j=1}^G h_g(j) \times e^{-Aw((x-x_g(j))^2+(y-y_g(j))^2)} \tag{3}$$

- (iii) Next, we placed horizontal planes at the elevation  $C$  producing two elevational zones in the landscape: high, and low. Pixels in the landscape with coordinates  $(x,y)$  were assumed to be a “forest”, if  $f(x,y) > C$ , a good habitat, if  $f(x,y) \leq C$  and  $g(x,y) > C$ , and a bad habitat otherwise.
- (iv) Finally, pixels  $(x,y) \in \langle 61;80 \rangle \times \langle 61;80 \rangle$  and  $(x,y) \in \langle 131;190 \rangle \times \langle 131;190 \rangle$  were assumed to be good habitats, independently of the algorithm (1)–(3) above and assumed to be departure and arrival patches, respectively. The experimental butterflies were placed at pixel  $\langle 70;70 \rangle$  at the beginning of each simulation.

The values of  $Ah = 20, Avh = 20, Aw = 0.005$  used in the simulations were chosen by trial and error to provide landscapes with the average forest and/or good habitat diameter equal to about 20 pixels, which is about 10% of the diameter of the total study area. The sizes and distance of the departure and arrival patches were chosen by trial and error, so that the flux between the patches was relatively large.

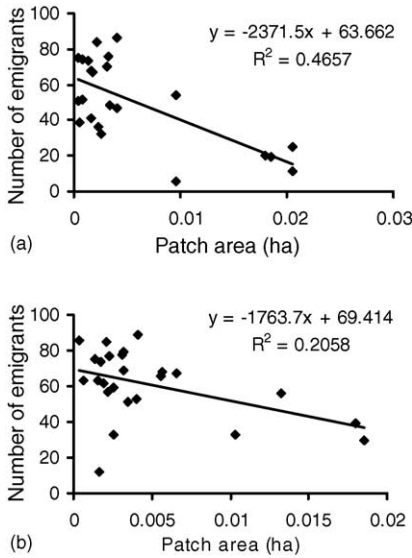


Fig. 1. Dependence of the number of emigrants from the departure patch on the size of the departure patch fitted by a straight line for each site separately (top: site 1; bottom: site 2), as predicted by the *Maniola* model for the years 1998 and 1999. Fitted parameters and  $R^2$  are in the inset.

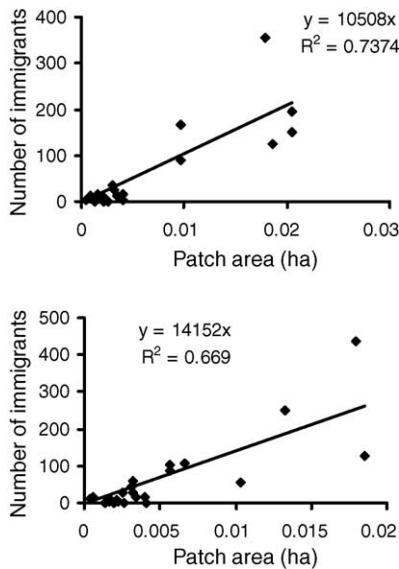


Fig. 2. Dependence of the number of immigrants to the arrival patch on the size of the arrival patch fitted by a straight line for each site separately (top: site 1; bottom: site 2) for the years 1998 and 1999 lumped, as predicted by the *Maniola* model. Fitted parameters and  $R^2$  are in the inset.

### 3. Results

Fig. 1 shows the dependence of the number of emigrants from the departure patch on the size of the departure patch as predicted by the *Maniola* model for the years 1998 and 1999 for each site separately and for both years lumped. The dependence can be fitted by a straight line but the regression explains only 21–46% of the total variance ( $R^2 = 0.46$  for site 1 and  $R^2 = 0.21$  for site 2). Contrary to formula (1), the number of emigrants declines, as patch size increases.

Fig. 2 shows the dependence of the number of immigrants to the arrival patch on the size of the arrival patch as predicted by the *Maniola* model for the years 1998 and 1999 for each site separately and for both years lumped. The dependence is conspicuously linear with zero intercept ( $R^2 = 0.73$  for site 1 and  $R^2 = 0.67$  for site 2), thus in a very good accord with formula (1).

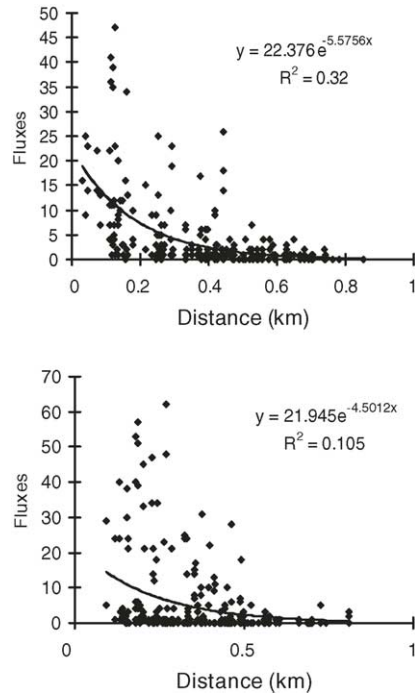


Fig. 3. Dependence of the flux of individuals between resource patches per unit area of the arrival and departure patches on the distance between these patches fitted by a negative exponential for each site separately (top: site 1; bottom: site 2), as predicted by the *Maniola* model for the years 1998 and 1999. Fitted parameters are in the insets.



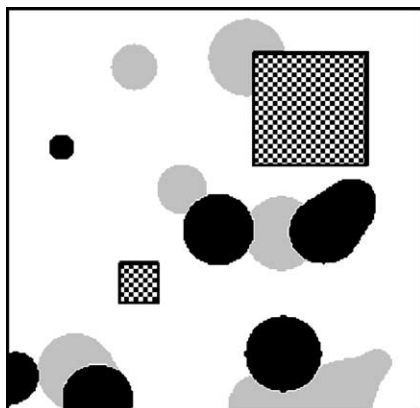


Fig. 4. One example of a random landscape created by our algorithm described in Section 2.3, points (i–iv). Light shading, forest; heavy shading, good habitat; checker cross shading, arrival and departure patches.

Fig. 3 shows the dependence of the flux of individuals between resource patches per unit area of the arrival patch on the distance between these patches as predicted by the *Maniola* model for the years 1998 and 1999 for each site separately and for both years lumped. The dependence was fitted by a negative exponential, but the fit was very bad and explained only 10–32% of the total variance ( $R^2 = 0.32$  for site 1 and  $R^2 = 0.10$  for site 2). An especially large scatter between flux values was observed for low values of the inter-patch distance (<0.5 km).

One example of the random landscape created by our algorithm is shown in Fig. 4. Fig. 5 then shows the number of butterflies out of the 10,000 individuals (1000 for each of the 10 random landscapes) that

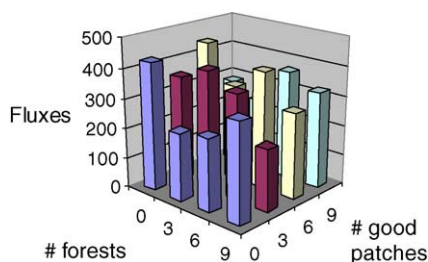


Fig. 5. Dependence of the flux of individuals between resource patches on the number of forests and good habitats in the habitat matrix (landscape between the resource patches) as predicted by the *Maniola* model for random landscapes created by the algorithm (i–iv).

Table 1  
Results of ANOVA with butterfly fluxes as dependent variable and number of forests and number of good habitats as factors for the simulations using random landscapes

Source of variation	SS	d.f.	MS	F	P-value	F <sub>crit</sub>
Forests	85,185	3	28,395	0.34	0.80	2.67
Good patches	213,385	3	71,128	0.85	0.47	2.67
Interaction	496,646	9	55,183	0.66	0.75	1.95
Within	12,090,678	144	83,963			
Total	12,885,894	159				

reached the arrival patch in our simulations, for each combination of the number of forests and good habitats. Analysis of variance with factors number of forests and number of good habitats (Table 1) shows that neither of the factors, nor their interactions significantly influenced the butterfly fluxes in our simulations.

#### 4. Discussion

Only the dependence of the number of immigrants to the arrival patch on the size of the arrival patch was in good accord with the formula (1). Thus, providing all other things are equal, size of the arrival patch is directly proportional to the number of immigrants arriving to this patch, in accord with the assumption of the formula (1).

In our simulations, the number of “empirical butterflies” was independent of the size of the departure patch, but the proportion of them that left the patch and became “emigrants” declined with the size of the patch. This result is quite logical, as especially individuals that are in the centre of the patch seem to be less likely to emigrate from large compared to small patches—especially when the large patch is circular shaped (Fig. 6). This is consistent with results of previous studies, which found inverse relationships between patch size and emigration of butterflies (Hill et al., 1996; Kuussaari et al., 1996; Sutcliffe et al., 1997; Baguette et al., 2000; Petit et al., 2001; Wahlberg et al., 2002). The negative association between the number of emigrants and size of the departure patch thus becomes especially important for species with low mobility, in which the average flight distance is low relatively to the size of the patch in

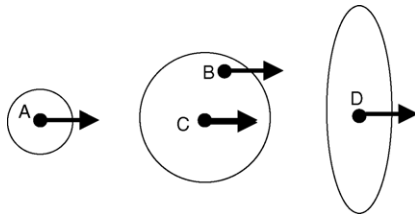


Fig. 6. Illustration of the possible causes of the decline of the flux of individuals from the departure patch on the size of the departure patch. Assuming same lengths of flights, butterfly A, sitting in the centre of its patch, will leave its small patch, and so will butterfly B sitting at the edge of the large patch and butterfly D sitting in the centre of its large, but oval-shaped patch. However, butterfly C sitting in the centre of its large patch will remain in its patch even after the flight.

which they are staying. However, if one takes into account that population size in a patch is not independent of, but positively associated with the size of this patch, then the number of emigrants may even increase with patch size, as assumed by formula (1).

It was complicated to quantify the dependence of the flux of individuals between resource patches on the distance between these patches. Consistent with the assumptions of the formula (1), fluxes between distant patches were always low, as such is the probability that the butterfly will end at a distant patch. However, fluxes between close patches were sometimes very large and sometimes very small. This is probably the case, in which habitat matrix plays the largest role. Characteristics of the landscape between resource patches may result in effective isolation of a patch that is greater or lower than that expected based only on distance (Roland et al., 2000; Ricketts, 2001). Here, fluxes of the meadow brown between close patches, although potentially large, can be negatively affected by obstacles (e.g. woodland areas) on the way, or by the relative position of the arrival patch, as illustrated in Fig. 7. Here, a butterfly sitting in patch X can easily reach patches A and C. It is more difficult for the butterfly to reach patch D, although similar in size and distance from X to patch C, but differing in its relative position to the departure patch, X: the angle, under which patch D is “observed” by the butterfly sitting in X, is smaller compared to that for patch C (the “angles” are indicated by light shading in Fig. 7). It is very difficult for the butterfly to reach patch B, although the same distance from X and of the same size as patch A, because of the obstacle Z on the way.

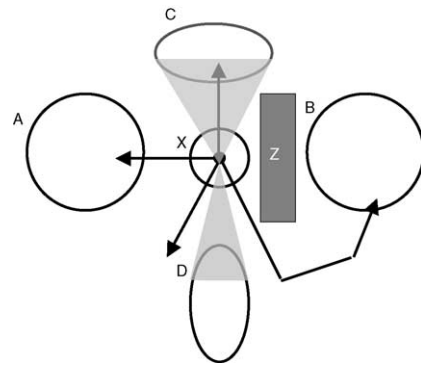


Fig. 7. Illustration of the possible causes of the scatter in dependence of the flux of individuals between resource patches on the distance between these patches for low inter-patch distances. The angle, under which patch D is “observed” by the butterfly sitting in X, is smaller compared to that for patch C (indicated by light shading). Z is an obstacle on the way from X to B. See text for further explanation.

Thus, patch B cannot be reached by a single flight, which lowers the flux between X and B.

The inclusion of the effect of habitat matrix becomes especially important when the habitat consists of a relatively dense network of resource patches that can be easily reached under optimum circumstances. Presence of obstacles and/or the shape of the arrival patch can then substantially affect the flux of individuals between patches.

The intensity of fluxes between patches becomes especially important for the population dynamics and probability of survival of the species under consideration, when (A) the species has typically a low population density in a patch, and/or when (B) the network of resource patches is not very dense because of either large inter-patch distances, or because of low mobility of the species. If (B) is satisfied, then inter-patch migration is extremely small; the metapopulation consists rather of many isolated populations, which – especially if (A) is also satisfied – are prone to extinction. The positive effects of metapopulation dynamics (like recolonization of patches, where the species became extinct for some reason) cannot counteract this because of low degree of inter-patch migration. According to the results presented here, habitat matrix plays only a minor role in such cases, as the fluxes are small. If (A), but not (B) is satisfied, then habitat matrix is important, as our results indicate it can strongly affect fluxes between patches, and

therefore, recolonization of empty patches. If neither (A) nor (B) is satisfied, the species is usually not endangered.

The information in Table 1 gives some insight into the analysis of butterfly movements in random landscapes. Lack of influence of the number of forests and good habitats plus the large residual variance indicate that it is the relative position of individual components of the habitat matrix rather than their abundance, which determines butterfly fluxes between resource patches.

To summarize, the regression model, which ignores spatial heterogeneity of the landscape between resource patches, fails to predict the intensity or fluxes between resource patches especially when the patches considered are relatively close to each other, so that under optimal conditions the flux could be relatively large. In such cases, the structure of the habitat matrix (e.g. obstacles and/or stepping stones between patches) becomes important. It is a challenge for the future to develop a theory of fluxes between patches that will encompass more of habitat matrix than just distance between patches and their sizes. However, because of the enormous variability of possible landscape patterns the ultimate goal may never be achieved.

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