

## Dynamic populations in a dynamic landscape: the metapopulation structure of the marsh fritillary butterfly

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The marsh fritillary butterfly *Euphydryas aurinia* is an endangered species in most of northern Europe. We describe the metapopulation structure of *E. aurinia* in Finland, where the species has declined drastically in the past decades. We found two types of habitat patches suitable for the species: semi-permanent meadows and transient clearcuts in the forest. Patch area was the most significant variable predicting the occurrence of *E. aurinia* in a habitat patch. The species tended to be found in young rather than old clearcuts, apparently because the vegetation became too high in the latter. We used the incidence function model to simulate the metapopulation dynamics of *E. aurinia* in its dynamic landscape and discovered that the continued presence of the semi-permanent meadows is essential for the survival of the species in the study area in southeast Finland.

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The theoretical framework for the study of metapopulation dynamics in static patch networks has been well established in the past few years (Hanski 1994, 1999b, Hanski and Gilpin 1997, Moilanen et al. 1998, Hanski and Ovaskainen 2000). However, natural patch networks are often dynamic due to various processes of disturbance and succession. While successional dynamics have received much attention, the dynamics of populations inhabiting dynamic patch networks have only recently been studied in the metapopulation context (Menges 1990, Stelter et al. 1997), and attention is now turning to modelling the dynamics of metapopulations inhabiting such dynamic patch networks (Stelter et al. 1997, Hanski 1999a, Johnson 2000).

Metapopulation models incorporating dynamic landscape structure deal with habitat patches that remain suitable for the focal species for several generations, and thus these models do not consider ephemeral resources that are suitable for only one generation (see

Hanski 1987). During the life-time of a habitat patch, populations are established through colonization, and stochastic extinctions and recolonizations may occur before the patch itself disappears (Harrison 1994, Thomas 1994, Harrison and Taylor 1997, Thomas and Hanski 1997). Empirical studies investigating the effects of patch age structure and succession rates on patch occupancy are few (Johnson 2000), making it difficult to test model predictions. More empirical studies are needed to help us understand how the dynamics of populations are influenced by the dynamics of the habitat (Harrison 1994, Thomas 1994, Thomas and Hanski 1997).

Many species of butterflies occur in early successional habitats and have local population dynamics that are fast with respect to the average life-span of suitable habitat patches (Thomas and Hanski 1997). Therefore, local extinctions may occur for stochastic reasons, but in the long run all local populations go extinct deter-

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ministically. Regional extinction is prevented by new habitat being created to compensate the habitat that has been lost, allowing the species to persist in a given landscape via habitat tracking (Thomas 1994, 1995). Well-documented examples of habitat tracking in butterflies include *Melitaea athalia* (Nymphalidae) (Warren 1991) and *Plebejus argus* (Lycaenidae) (Thomas and Harrison 1992). However, the effects of patch creation and successional disappearance on the dynamics of butterfly metapopulations have not been previously studied in a model context (but see Stelter et al. (1997) for other taxa).

In this paper we report a study on an endangered species of butterfly, the marsh fritillary *Euphydryas aurinia* (Rottenburg), which inhabits early successional habitats in Finland. The numbers of populations of *E. aurinia* have been declining in 17 European countries over the past few decades and the species is listed in Annex II of the 1992 European Community Habitats and Species Directive as “Threatened in Europe” (van Swaay and Warren 1999). In Finland *E. aurinia* has declined drastically over the past 40 yr and is presently restricted to the southeastern part of the country (Fig. 1). Here we document the key features of the dynamic

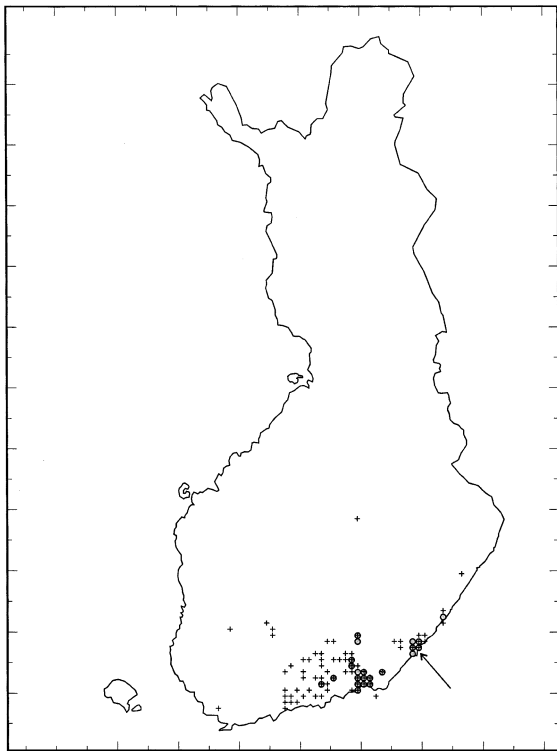


Fig. 1. The distribution of *Euphydryas aurinia* in Finland. The crosses represent records of the species prior to 1988 and the circles represent records from 1988 to 1997. The map has been modified from Huldén et al. (2000). The arrow indicates the study area, which encompassed all the five circles in the cluster.

landscape occupied by the butterfly and patterns in habitat use. We also use a simulation model to investigate several scenarios of patch dynamics and their implications for the long-term persistence of *E. aurinia* in Finland.

## Material and methods

### Study species

*Euphydryas aurinia* is a univoltine butterfly belonging to the family Nymphalidae. In Finland the adults fly from the beginning of June until the beginning of July (Klemetti and Wahlberg 1997). In northern Europe the species is monophagous on *Succisa pratensis* (Dipsacaceae), on which females lay their eggs in large batches of ca 300 eggs (Porter 1981, Klemetti and Wahlberg 1997). Females may lay several batches of eggs, but the first batch is typically laid in the natal habitat patch as newly-eclosed females are so egg-laden that they are not able to fly long distances (Porter 1981). The larvae are gregarious in the autumn and spin a large silken web around the leaves of their host plant within which they feed. Larvae diapause within a winter web, which is constructed on the host plant. In the spring, the larvae are initially gregarious and, by basking together in large groups, they are able to raise their body temperature well above the ambient (Porter 1982). In the course of the spring the larval groups break up and the final instar larvae tend to feed singly. The larvae are attacked by the braconid parasitoid *Cotesia bignellii* (Hymenoptera: Braconidae) in Finland (Komonen 1997).

### Study system

We surveyed all suitable habitat patches for *E. aurinia* within an area of 150 km<sup>2</sup> in the Joutseno region of southeastern Finland (Fig. 1) with the aid of 1:20 000 topographical maps. Our study area was bounded by Lake Saimaa to the north, by the border between Finland and Russia to the east, by extensive bogs to the south and a dry esker to the west. All open habitat with the larval host plant present was regarded as suitable for the species. Two different types of habitat patches were identified, meadows and clearcuts (see Results). Patches were easily delimited from the surrounding habitat (usually forest). All suitable habitat patches were drawn onto the maps, their spatial coordinates were determined and the areas of the patches were calculated using GIS with the aid of digitized maps. The presence of *E. aurinia* was surveyed in the spring 1996 by searching for postdiapause larvae during the period 5–19 May. Larvae had dispersed towards the end of the period and the presence of *E. aurinia* was

inferred from feeding marks on *Succisa pratensis* in association with larval faeces. We have not observed any other comparable insect feeding on this plant in the spring and are confident that the feeding marks were left by *E. aurinia* larvae. The patches were resurveyed in late summer 1996 from 18 to 30 August by searching for larval webs on the host plants. However, due to time constraints and high vegetation making larval webs difficult to find, the presence of *E. aurinia* in some patches may have been missed in the latter survey.

In addition to the coordinates and the area of each patch, we recorded the percentage of different habitat types (forest, agricultural field, etc.) bordering the focal patch, the quality of the patch on a scale from 1 (open, low vegetation) to 3 (overgrown), and the number of flowering *S. pratensis* plants in the patch. We assume that the number of flowering host plants is a good measure of the total number of host plants in the patch.

### Analyses of patch variables

We investigated the effects of the patch variables on the probability of a patch being occupied by *E. aurinia* using logistic regression. The explanatory variables were patch area in ha, density of flowering *S. pratensis* plants per ha, connectivity of the patch, quality of the patch (1 = open, low vegetation; 2 = open, high vegetation; 3 = overgrown), and percentage of open habitat bordering the patch. Connectivity was calculated using the S index of Hanski (1994) (see eq. 4 below for the definition of S). The significance of each variable was evaluated based on the difference between a model with and without it, tested against a  $\chi^2$ -distribution. During the course of our survey, we discovered that a large proportion of the suitable habitat patches for *E. aurinia* were located on clearcuts. For these habitat patches we were able to determine the age of the patch from data provided by the Joutseno Forestry Association. We investigated the effect of patch age on the incidence of *E. aurinia* and the density of the host plant. Age could not be entered as a variable in the logistic regression model as we do not have information about the age of suitable habitat patches that were not on clearcuts (see Results).

### Analyses of metapopulation dynamics

We analyzed the dynamics of the *E. aurinia* metapopulation in the study area using the incidence function model (IFM) (Hanski 1994). The IFM is a stochastic patch occupancy model in which the presence/absence of a species in a habitat patch is modelled. The incidence  $J_i$  in patch  $i$  depends on colonization ( $C_i$ ) and extinction probabilities ( $E_i$ ) in the following manner,

$$J_i = \frac{C_i}{C_i + E_i - C_i E_i} \quad (1)$$

The intrinsic probability of extinction of a local population is a function of population size (which is assumed to be proportional to patch area  $A_i$ ) and is thus patch specific,

$$E_i = \frac{e}{A_i^x}, \quad (2)$$

where  $A_i$  is the area of patch  $i$ , and  $e$  and  $x$  are two parameters. The colonization probability of an empty patch is dependent on the connectivity of the patch in the following manner,

$$C_i = \frac{S_i^2}{S_i^2 + y^2}, \quad (3)$$

where  $y$  is a parameter and  $S_i$  is a measure of connectivity,

$$S_i = \sum_{i \neq j} p_j \exp(-\alpha d_{ij}) A_j^b. \quad (4)$$

In the latter formula,  $p_j$  is the incidence of the species in patch  $j$  (here 0 or 1, because data were available for only 1 yr),  $\alpha$  is a parameter that determines the effect of distance on colonization,  $d_{ij}$  is the distance between patches  $i$  and  $j$ ,  $A_j$  is the area of patch  $j$  and  $b$  is parameter that transforms patch area to expected emigration rate. Equation 1 includes the "rescue effect" (Brown and Kodric-Brown 1977, Hanski 1994), which describes the reduced probability of local extinction in populations that are well connected to other populations and hence receive substantial immigration to boost the local population size.

Parameterizing the IFM (or any other metapopulation model) when the landscape is dynamic is not a trivial procedure, since patterns of patch occupancy may not depend on the current landscape configuration. We first parameterized the IFM for *E. aurinia* with the MC method of Moilanen (1999), using the snapshot of presence/absence obtained from the spring survey. This procedure assumed a static patch network. For the MC method to work with one snapshot, one has to place a limit on the maximum number of turnover events that can occur in one generation (Moilanen 1999). We limited the maximum number of turnovers to 10, which is a value consistent with the turnover rate inferred from the comparison of the spring and autumn surveys (see Results). We used 5500 function evaluations during parameter estimation and repeated this 5 times. In order to tease apart the values of  $e$  and  $y$  from the product  $ey^2$  (see Hanski (1994) for details), we assumed the minimum patch area ( $A_0$ ), where the extinction risk in one time step is equal to 1

(see eq. 2), to be 1500 m<sup>2</sup>. This is roughly the minimum size of the occupied patches.

The dynamic nature of the *E. aurinia* patch network made rigorous parameter estimation of the IFM impossible. In this case, the observed pattern of patch occupancy is not only a reflection of patch connectivities and areas, which is the basic assumption of the IFM, but also depends on the past history of the landscape structure. The above procedure for estimating parameter values assumes a static patch network. We next manually adjusted the parameter values for the meta-population model to predict realistic dynamics in a dynamic landscape. We did this by reducing the value of parameter  $\gamma$  (thus increasing colonization efficiency) until the predicted level of patch occupancy in a baseline dynamic landscape was around the observed level (see below).

We then investigated five scenarios of landscape change by simulating the IFM. The two different patch types that are present in the study area, meadows and clearcuts, were included in the simulations with different patch dynamics. Meadows were either left unchanged (assuming continuous grazing) or they were allowed to disappear (overgrow) at a constant rate. Clearcuts had similar dynamics to those observed in the field, i.e. the quality of a suitable habitat patch was high for the first 4 yr after which it declined to 0 in 14 yr (see Results). New clearcuts were created at a similar rate to the actual rate over the past decade, which was calculated from the distribution of clearcut ages in our data set. The number of new clearcuts in the study area was assumed to be normally distributed with a mean 6 and a standard deviation 4. We did not vary this rate. New clearcuts had an area that was selected randomly from the observed frequency distribution of patch areas. Simulations were started with the observed pattern of patch occupancy. All scenarios were iterated for 100 generations and the first 50 generations were omitted in the analyses to allow the simulation to achieve a quasi-stationary state.

Scenario 1: the baseline dynamics. Dynamic patch network with meadow habitats remaining unchanged, with clearcuts becoming overgrown and new clearcuts being created at random locations in the landscape.

Scenario 2. Dynamic patch network with meadows becoming overgrown and thereby losing area at a rate of 5% yr<sup>-1</sup> (after generation 50). Clearcuts as in Scenario 1.

Scenario 3. Dynamic patch network with meadows becoming overgrown as in Scenario 2 and with clearcuts becoming overgrown. New clearcuts are created within 3 km of an occupied patch.

Scenario 4. Dynamic patch network with meadows becoming overgrown as in Scenario 2 and with clearcuts becoming overgrown. New clearcuts are created within 1 km of an occupied patch.



Fig. 2. The patch network of *Euphydryas aurinia* in SE Finland. The actual shapes and relative sizes and locations of the patches are shown. Black and white patches represent patches that were found to be occupied versus empty in the spring survey. Patches that are located within a grey area are meadows, while all other patches are clearcuts. The grey areas do not represent any particular habitat.

Scenario 5. Dynamic patch network with meadows becoming overgrown as in Scenario 2 and with clearcuts becoming overgrown. New clearcuts are created within 1 km of an existing habitat patch (not necessarily occupied).

## Results

### Patterns in habitat use

We found a total of 114 suitable habitat patches in the spring survey, of which 55 were occupied by *E. aurinia* (Fig. 2). In the late summer survey we recorded the presence of *E. aurinia* in 42 patches. Five patches had been colonized and local extinction appeared to have occurred in 18 patches. However, this latter figure is likely to be an overestimate because of the difficulty in ascertaining the presence of the butterfly in the autumn

Table 1. Logistic regression model for the occurrence of *Euphydryas aurinia* in a set of 114 habitat patches. Patch area is given in ha, *Succisa* ha<sup>-1</sup> is the density of the host plants per ha, connectivity is measured by the S<sub>i</sub> index (see text for details), quality is the state of the patch (1 = open, low vegetation; 2 = open, high vegetation; 3 = overgrown), and boundary is the proportion of open habitat bordering the patch. The change in deviance when a given term is dropped from the full model is  $\chi^2$ -distributed with 1 degree of freedom.

Independent variable	Coefficient (SE)	Odds ratio (95% confidence interval)	Model improvement (change in deviance)*	
			$\chi^2$	p
Constant	-5.89 (1.74)			
Area (ha)	1.98 (0.46)	7.26 (2.95-17.84)	40.03	<0.001
<i>Succisa</i> ha <sup>-1</sup>	0.02 (0.01)	1.02 (1.01-1.03)	39.86	<0.001
Connectivity	0.04 (0.05)	1.04 (0.94-1.16)	0.57	0.450
Quality	0.42 (0.48)	1.52 (0.59-3.92)	0.77	0.380
Boundary	-0.29 (0.94)	0.74 (0.12-4.70)	0.10	0.752

\* Deviance of full model 94.70, DF = 107.

survey (see Material and methods). In our analysis, we assume that the true number of turnover events between two generations is 10 (this assumption is not critical for parameter estimation as will be shown in the next section).

The habitat patches could be divided into three categories, 68 patches were on clearcuts, 31 patches were on moist meadows and 15 patches were on other open habitats, such as under powerlines or on land over gaslines. For further analyses the latter two categories were combined and are referred to as meadows. In the spring survey, 24 of the occupied patches were meadows and 31 were clearcuts, while in the late summer survey the numbers were 16 and 26, respectively. Four of the five colonizations occurred on clearcuts. The proportions of occupied meadows and clearcuts do not differ from each other ( $2 \times 2$  tables, Pearson's  $\chi^2 = 0.48$ ,  $p = 0.49$ ). The mean, median and maximum patch areas were 1.35, 0.81 and 16.84 ha, respectively.

The most important variables explaining the presence of *E. aurinia* in a patch were patch area and the density of host plants (Table 1), such that the larger the patch and the more host plants per ha, the more likely the patch was to be occupied by the butterfly. The odds ratios (Table 1) characterize the quantitative effects of the explanatory variables on the occurrence of *E. aurinia* in a patch. Thus, when patch area increases by one unit (1 ha), there is a sevenfold increase in the probability of occupancy (odds ratio 7.26). Similarly, increasing the number of host plants per ha by one increases the probability of a patch being occupied by 2% (odds ratio 1.02). Inclusion of the other three variables (connectivity, patch quality and the proportion of open patch boundary) did not significantly improve the fit of the logistic regression model.

The age of the clearcut had a clear effect on the occupancy by *E. aurinia* (Fig. 3). The fraction of occupied patches was very low soon after clearcutting, peaked at 3 yr and decreased rather monotonically after that. Many clearcuts become immediately suitable habitat for *E. aurinia*, as *Succisa pratensis* apparently has a

seedbank in the soil (Klemetti and Wahlberg unpubl.). Succession is subsequently rapid as clearcuts are planted with tree seedlings (usually spruce *Picea abies* L.), and the quality of the patches starts to decline a few years after the clearcut. Patch quality is not a function of the density of host plants only, which does not change greatly with the age of the patch (Fig. 4). Shading by tree seedlings substantially decreases habitat quality. The four clearcuts that were colonized over the summer were 2 and 3 yr old, while the apparent extinctions on clearcuts occurred in all age classes (3, 4, 5, 6, 7, 8, 10, 12 and 14 yr).

### Parameter estimation

We first estimated parameter values from the observed occupancy pattern, assuming the network to be static.

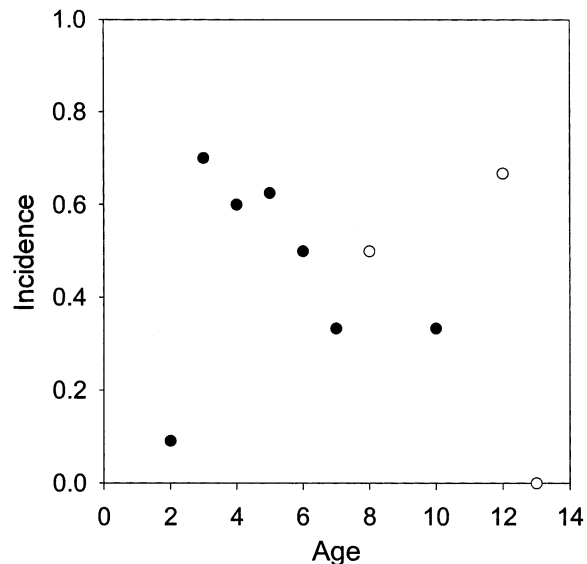


Fig. 3. The fraction of occupied patches in clearcuts of different ages.  $n \geq 6$  for filled dots and  $n \leq 4$  for open dots.

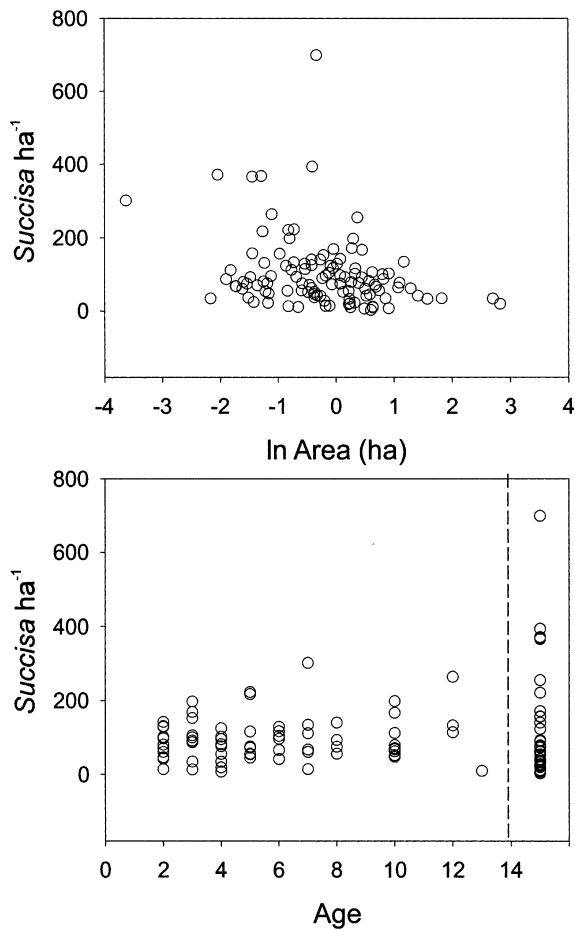


Fig. 4. The effects of age of clearcuts on the density of host plants in the habitat patches for *Euphydryas aurinia*. The density of host plants in meadows is shown to the right of the dashed line.

These parameters (Table 2) predicted “realistic” dynamics when the model was iterated in the patch network without allowing for landscape dynamics (Fig. 5). We investigated the effect of limiting the number of turnover events per year to 10 by estimating parameter values for turnover limits of 15, 20, 25 and 30. The

Table 2. Parameter values for the incidence function model used to analyze the metapopulation dynamics of *Euphydryas aurinia* in Finland. These values were estimated from the observed patch occupancy assuming a static patch network. Parameter values for *Melitaea cinxia* were taken from Hanski et al. (1996). Spatial units are km and ha.

Parameter	<i>E. aurinia</i> (static network)	<i>M. cinxia</i>
$\alpha$	0.42	1
$x$	1.30	0.952
$y$	48.13*	4
$e$	0.08	0.01

\* This value was reduced to 4 while adjusting the model to the dynamic landscape (see text).

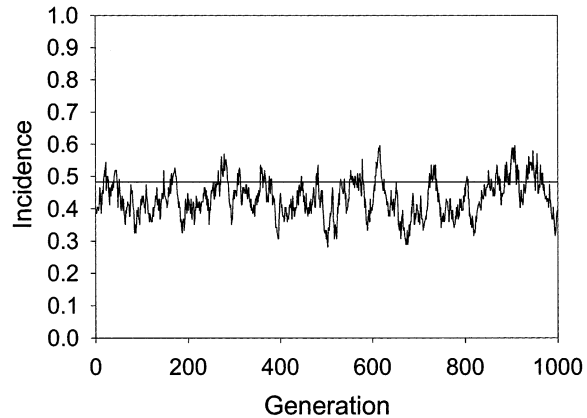


Fig. 5. The predicted dynamics of *Euphydryas aurinia* assuming a static patch network (parameter values in Table 2). The straight line gives the observed fraction of occupied patches in the spring 1996, while the time series gives the predicted fraction of occupied patches in one model run.

point estimates thus obtained did not differ significantly (were within the 95% confidence limits) from those reported in Table 2 under the static network, except for parameter  $x$ , which decreased as the maximum number of turnover events increased. For comparison, Table 2 also shows the parameter values that have been rigorously estimated for a related species *Melitaea cinxia* (Hanski et al. 1996).

We attempted to simulate the dynamic patch network as realistically as possible. Based on information in Fig. 3 and field observations, patch quality in clearcuts was assumed to immediately reach the relative value of 1, and to remain at that level for 4 yr, after which the quality deteriorated exponentially to 0 at 14 yr. The patch area is multiplied by this measure of relative value to give the effective patch area of clearcuts in each age class.

For the dynamic landscape, a value of  $y$  that was one order of magnitude smaller than the estimated one (assuming a static patch network) predicted well the average observed incidence. We thus use below parameter values originally estimated for *E. aurinia* (Table 2), but with  $y$  set at the value of 4.

The adjusted parameter values predicted an increase in the average incidence of *E. aurinia* in the clearcuts until age class 4, after which there was a decline in average incidence towards older clearcuts (Fig. 6, open circles). These dynamics are realistic though the predicted incidence does not decline as fast as observed empirically. One plausible explanation is that patches in the older age classes do not receive immigrants that might colonize otherwise empty patches. This hypothesis is based on female behaviour (females lay their first egg batch in their natal patch; Porter (1981)) and the assumption that old clearcuts might not be perceived by migrating females to be patches at all. In simulations, we assumed that patches  $> 6$  yr received no immi-

grants. With this assumption the average incidence declines rapidly to zero roughly as found empirically (Fig. 6, filled circles).

### Simulation of different landscape scenarios

The parameter values estimated on the assumption of a static network (Table 2) predicted metapopulation extinction in our baseline dynamic landscape (Fig. 7A). The parameter values adjusted for the baseline dynamic landscape (Scenario 1) predicted metapopulation dynamics as shown in Fig. 7B. In this scenario, the metapopulation continues to occupy roughly half of the patches in a stable manner. However, the metapopulation loses its stability when meadows are allowed to overgrow at a rate of  $5\% \text{ yr}^{-1}$  (Scenario 2), and it declines to extinction once the meadows are no longer of sufficient size to have a low extinction risk (Fig. 7C). Creating an aggregated network of clearcuts can keep the metapopulation alive for longer even though the meadows disappear. When the new clearcuts were always located within 3 km of the patches occupied by *E. aurinia* (Scenario 3), the predicted dynamics had high amplitude and the metapopulation declined more slowly than in the previous scenario (Fig. 7D). The decline was further slowed down when the new clearcuts were located within 1 km of occupied patches (Scenario 4), though the amplitude remained high (Fig. 7E). By restricting new clearcuts to be created within 1 km of randomly chosen patches, without regard to the status of *E. aurinia* in those patches (Scenario 5), the decline was similar to that in Scenario 3 (Fig. 7F).

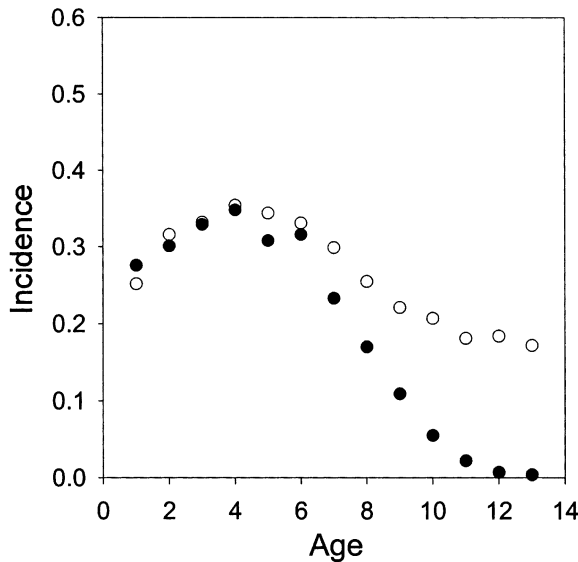


Fig. 6. The predicted incidences in the different age classes of clearcuts when patches older than 6 yr are allowed to be colonized (open circles) and when immigration into these patches is not allowed (closed circles).

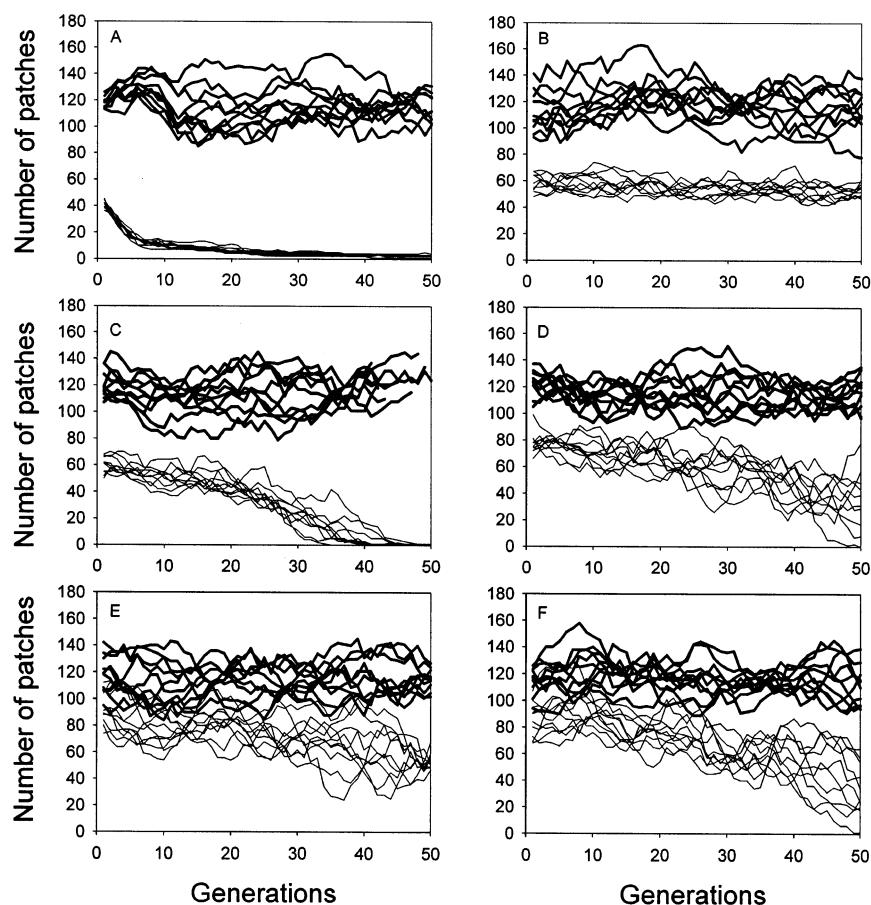
### Discussion

In our study area, *E. aurinia* exists in a patch network that is composed of both transient and more persistent habitat patches. Local populations inhabiting these patches have a distinct risk of extinction, either for stochastic or deterministic reasons (through succession of the transient habitats). This situation is different from other metapopulations of *E. aurinia* earlier studied by Warren (1994) and Lewis and Hurford (1997), which inhabit habitat patch networks that can be considered as static in relation to the life-times of the populations (see Thomas 1995, Hanski 1999b).

The situation we have described here is relatively common in many endangered butterfly species, which in Europe are largely confined to man-made habitats (Thomas 1993). One of the best studied examples is *Melitaea athalia* in Britain, which inhabits coppiced woodlands (Warren 1991). The local populations of these butterflies are able to colonize coppiced areas in the forest as soon as they are created from populations occurring in more permanent open areas. The coppiced areas remain suitable for several years, after which local populations of *M. athalia* necessarily go extinct. The occurrence of *M. athalia* in the woodland is dependent on a sufficiently fast rotation of coppicing such that enough suitable habitat is available at any one time (Warren 1991).

The incidence function model that we used to analyze the dynamics of *E. aurinia* in its dynamic landscape has been successfully used in several studies of butterflies (Hanski 1994, Hanski et al. 1996, Wahlberg et al. 1996), and it proved to be a helpful model also in the present case. However, the estimation of the parameter values from the empirical observations was difficult, and our modelling results are dependent on the parameter values used. Encouragingly, the parameter values obtained reflect known differences between the biology of *E. aurinia* and *M. cinxia* (Hanski et al. 1996). The parameters related to extinction yield higher extinction rate for *E. aurinia* than for *M. cinxia*, apparently because the habitat patches are an order of magnitude larger in the *E. aurinia* system without there being a corresponding difference in population sizes. In other words, population density was much lower in *E. aurinia* than in *M. cinxia*. In *E. aurinia*, the effect of distance on the probability of colonization ( $\alpha$ ) is about half of that estimated for *M. cinxia*, in accord with the results of a mark-recapture study of these two butterfly species (Wahlberg et al. 2002). The efficiency with which *E. aurinia* colonizes empty patches in relation to connectivity (parameter  $\gamma$ ) is probably similar to that in *M. cinxia*. Both species are known to lay batches of up to 300 eggs (Wahlberg 2000), which may increase the probability of a single female to found a population in an empty habitat patch.

Fig. 7. The dynamics of an *Euphydryas aurinia* metapopulation in Finland under different landscape scenarios. In each panel, the thick line shows the number of patches in the dynamic patch network and the thin line shows the number of occupied patches, both for ten replicate simulations. A) Scenario 1, meadows remain unchanged, clearcuts created in random locations (see text for details), metapopulation dynamics simulated with unadjusted parameter values given in Table 2. B) Scenario 1, metapopulation dynamics simulated with adjusted parameter values. C) Scenario 2, meadows become overgrown, clearcuts created in random locations. D) Scenario 3, meadows become overgrown, clearcuts created within 3 km of occupied patches. E) Scenario 4, meadows become overgrown, clearcuts created within 1 km of occupied patches. F) Scenario 5, meadows become overgrown, clearcuts created within 1 km of randomly chosen patches.



The observation that the incidence of *E. aurinia* in clearcuts is dependent on the age of the clearcut (Fig. 3) led us to assume a model of succession that leads to the dynamics shown in Fig. 6. Our assumption that older “patches” are no longer perceived as patches by migrating females means that older patches are not recolonized if the respective local populations go extinct. The empirical observations showed higher incidences in the older patches (Fig. 3) than the model of succession predicts (the closed circles in Fig. 6). However, the survey of older habitat patches was highly biased and many patches in the older age classes were not classified by us as suitable habitat. Thus the observed incidences in the older age classes are necessarily overestimates due to our surveying methods. In this study we bring forth a possibility that has not been considered in the literature, i.e. that after a certain successional age habitat patches may support local populations even though they may not be available for recolonization, should the local population go extinct. Without taking this into account, one would overestimate the capacity of the patch network to support a viable metapopulation.

The conservation implication of our simulation results is that meadows are important for the persistence of *E. aurinia* in southeast Finland. This result was

robust to the parameter values used, as similar results were obtained over a wide range of parameter values tested while adjusting the IFM for the dynamic landscape. If the meadows were to disappear, the only salvation for the species appears to be aggregating clearcuts in the landscape or, of course, preventing forest regrowth in some clearcuts that would hereby be turned to effective meadows. Since aggregating of new clearcuts may not be logistically possible (forests must grow for at least 70 yr before they can be cut), the only reasonable conservation action would be to preserve the meadows as suitable habitat, that is, prevent them from becoming overgrown. The meadows would then act as refuges, from which *E. aurinia* can colonize clearcuts that appear in the landscape without regard to the presence of the butterfly.

Our study is an example of a species that inhabits a habitat patch network which is a mixture of successional and more static patches. The meadows can be seen as static as they have earlier been kept open for agricultural reasons (natural pastures for cattle and a source of cattle fodder). Such habitats are known as plagioclimax habitats (Thomas 1995), in which natural succession is prevented. With the cessation of traditional agricultural practices in modern times, natural

succession now threatens the habitat of many species of butterfly (Warren 1993). To successfully apply the metapopulation concept to these species for conservation purposes, it is necessary to account for the dynamic nature of their habitats (Thomas 1983, Thomas et al. 1986, Warren 1991, Thomas 1994). Our study is the first to analyze the metapopulation dynamics of an endangered species in a highly fragmented and dynamic landscape using a dynamic model. Our analyses have necessarily been somewhat ad hoc, as the theoretical framework for dynamic metapopulations in dynamic landscapes is still in its infancy (Hanski 1999a, Johnson 2000). However, our results are relevant for both the conservation of *E. aurinia* in Finland and for the continued development of the theory. We hope that this example encourages others to apply the metapopulation concept to species living in dynamic landscapes.

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