A practical model of metapopulation dynamics

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Summary

1. This paper describes a novel approach to modelling of metapopulation dynamics. The model is constructed as a generalized incidence function, which describes how the fraction of occupied habitat patches depends on patch areas and isolations.

2. The model may be fitted to presence/absence data from a metapopulation at a dynamic equilibrium between extinctions and colonizations.

3. Using the estimated parameter values, transient dynamics and the equilibrium fraction of occupied patches in any system of habitat patches can be predicted. The significance of particular habitat patches for the long-term persistence of the metapopulation, for example, can also be evaluated.

4. The model is fitted to data from three butterfly metapopulations. The model predicts well the observed minimum patch size for occupancy and the numbers of extinctions and colonizations per year (turnover rate). The results suggest that local populations of the three butterflies in patches of 1 ha, which may support of the order of 1000 adult butterflies, have an expected lifetime of 20–100 years.

Key-words: butterfly ecology, extinction, incidence function, metapopulation dynamics, stochastic model.

Introduction

The most obvious question a metapopulation biologist may expect to be asked is whether some species X is likely to persist, as a metapopulation, in some particular set of habitat patches Y. In the context of conservation biology, the set of patches Y is often a subset of a larger number of larger patches, and the ecologist is asked to predict whether species X, present in the current set of patches, would still persist if some patches were removed or their areas were reduced.

Current analytical models of metapopulation dynamics (e.g. Hanski 1985, 1991; Hastings & Wolin 1989; Hastings 1991; Verboom, Lankester & Metz 1991; Nee & May 1992; Gyllenberg & Hanski 1992; Hanski & Gyllenberg 1993) are not helpful in answering such questions because these models, intended for examining the balance between colonizations and extinctions more generally, do not incorporate specific information about patch locations, and hence do not generate predictions about specific metapopulations. Stochastic patch models (Nisbet & Gurney 1982; Adler 1991) give rough approximations of the numbers of habitat patches and local populations that are necessary for long-term persistence but, once again, space is not explicitly included in these model. Another stochastic model (Adler 1991; Adler & Nürnberg, in press) makes useful qualitative predictions about the effect of patch aggregation on metapopulation persistence, but no quantitative predictions about particular metapopulations are possible. Spatially explicit metapopulation models seem hard to construct using any other approach than numerical simulation. But simulation models, though having the potential to answer quantitative questions of the type posed in the first paragraph (C. Ray & P. Sjögren, unpublished; Hanski & Thomas 1994), are typically tedious to construct, are pestered by many assumptions which are difficult to verify, and include many parameters that are hard to estimate.

The purpose of this paper is to describe a minimalistic model which may provide guidance to quantitative questions about particular metapopulations. The approach is minimalistic in the sense that the number of parameters is curtailed to the minimum, and the information needed about species X is very limited, and of the type that is commonly available: presence/absence ‘snapshot’ data from a set of habitat patches in which the species occurs at equilibrium. A simple stochastic model is fitted to such data to estimate parameter values, which then allow numerical iteration of metapopulation dynamics in other systems of habitat patches. The present approach and models generalize previous...
work (Hanski 1992) which was restricted to simple mainland-island metapopulations (Hanski & Gilpin 1991) and which has been successfully tested with empirical data on small mammals (Peltonen & Hanski 1991).

**Model description**

Let us assume a set of habitat patches $Y$ in which species $X$ occurs at a dynamic colonization–extinction ‘equilibrium’. As the model has no ‘mainland’, where the long-term persistence of the species would be guaranteed, the metapopulation will eventually go extinct. But if the number of patches and the expected fraction of occupied patches are not very small, the metapopulation is expected to converge to a quasi-steady state, which will be called an ‘equilibrium’ state in this paper, before eventual extinction. Nisbet & Gurney (1982) and Adler (1991) give approximations for metapopulation lifetimes in the case of a finite number of equally large patches.

Let us assume that local dynamics, i.e. changes in the sizes of local populations, occur fast in comparison with metapopulation dynamics, colonization of currently empty habitat patches. With this assumption, which is common to all ‘patch’ models of metapopulation dynamics (Hanski 1991), we may ignore local dynamics and focus entirely on the presence or absence of species $X$ in the habitat patches. In view of the practical applications of the model, let us further assume that changes in patch occupancy are scored at discrete time intervals, for instance between successive years. If patch $i$ is empty in year $t$, it will be recolonized with probability $C_i$ by year $t + 1$, and if patch $i$ is occupied in year $t$, it becomes vacant (the population goes extinct) with probability $E_i$ by year $t + 1$. Assuming that $C_i$ and $E_i$ are constant, the occupancy of patch $i$ is described by a linear, first-order Markov chain with two states. Let $J_i$ be the stationary probability that patch $i$ is occupied. This probability, called the incidence (of occupancy) in the ecological literature, is given by the expression

$$J_i = \frac{C_i}{C_i + E_i}.$$  

Eqn 1

Our main task is to make practical yet sensible assumptions about how the extinction and colonization probabilities $E_i$ and $C_i$ depend on measurable environmental variables and on the life-history traits of the species.

**Extinction probability**

Let us assume that all the patches have the same quality and hence the same equilibrium density of species $X$. Recalling the assumption that local dynamics occur at a fast time scale in comparison with metapopulation dynamics, the size of the local population in patch $i$, if any exists, is directly proportional to the area of patch $i$, $A_i$. Because the extinction probability $E_i$ typically depends on population size (Williamson 1981; Diamond 1984; Schoener & Spiller 1987; Hanski 1991), we may assume that $E_i$ is a function of $A_i$. Following Hanski (1992), I assume that the extinction probability $E_i$ is given by

$$E_i = \frac{e}{A_i^x} \text{ if } A_i > e^{1/x},$$  

Eqn 2a

$$E_i = 1 \text{ if } A_i \leq e^{1/x},$$  

Eqn 2b

where $e$ and $x$ are two constants. $E_i$ equals unity for $A_i$ equal to or smaller than $e^{1/x}$, which gives the critical patch area, say $A_0$, for which the local population has a unit probability of extinction in 1 year. Parameter $x$ provides the flexibility to describe weaker or stronger dependence of the extinction risk on patch size and hence on population size. When $x$ is large (>1), there is a range of patch sizes beyond which extinction becomes very unlikely, whereas if $x$ is small (<1), there is no such critical patch size and even large populations in large patches have a substantial risk of extinction. Parameter $x$ reflects the severity of environmental stochasticity ($x$ decreases with increasing environmental stochasticity). It goes without saying that parameter $x$ has considerable significance in population and conservation biology (Hanski 1992).

If there is variation in habitat quality which is linearly related to population density, possibly after a suitable transformation, the simplest way to incorporate patch-specific habitat quality into the model is to replace $A_i$ by ‘effective’ area $A'_i$ for patch $i$ with quality $Q_i$. The ‘effective’ area is given by $Q_i A_i/Q^*$, where $Q^*$ is the maximal habitat quality, scaled to equal unity.

**Colonization probability**

The colonization probability $C_i$ is a function of the numbers of immigrants arriving at patch $i$ per year, denoted by $M_i$. Here lie two difficulties. First, finding a reasonable and simple expression for $M_i$ is not easy. Second, even if the size of the metapopulation, as measured by the fraction of occupied patches, remains relatively constant at equilibrium, patches switch from being occupied to being empty, and vice versa, and hence the flow of individuals to patch $i$ varies, depending on exactly which patches happen to be occupied. I assume that year-to-year variation in $M_i$ is, nonetheless, so small that it can be ignored and that equation 1, which assumes constant $M_i$, provides a good approximation. This approximation is unlikely to be misleading when the number of patches is relatively large, which is in any case a necessary requirement for the present modelling approach, and when the species is not very sedentary, in which case most immigrants would originate from a few nearby populations.
Turning to the relationship between the colonization probability $C_i$ and the number of immigrants $M_i$, I assume the following simple relationship,

$$C_i = \frac{M_i^2}{M_i^2 + y^2} \quad \text{eqn 3}$$

This function gives an s-shaped increase in the colonization probability from 0 to 1 with increasing numbers of immigrants. Parameter $y$ determines how fast the colonization probability approaches unity with increasing $M_i$.

Note that equation 3 assumes interactions among the immigrants; if each immigrant would independently establish a new population with a constant probability, an exponential form would be appropriate instead of equation 3. Such interactions are likely to occur in most sexually reproducing organisms, and they give rise to the Allee effect which is the underlying rationale in equation 3. A more mechanistic description of colonization and extinction probabilities would be preferable, but the phenomenological expressions (2) and (3) are adequate for predictive purposes.

The most difficult task is to calculate $M_i$. It seems impractical to derive a formula based on actual movement behaviour of individuals. I will use the following more phenomenological approach, which is nonetheless related to the key elements that must be involved in migration, and which is similar to the formula successfully used by Adler & Nürnberger (in press):

$$M_i = \beta S_i \quad \text{eqn 4}$$

where

$$S_i = \sum p_j \exp\left(-\alpha d_{ij}\right) A_j,$$

and the sum is taken over all patches $j \neq i$, $p_j$ equals 1 for the occupied patches and 0 for the empty patches in year $t$, $d_{ij}$ is the distance between patches $i$ and $j$, and $\alpha$ is a constant setting the survival rate of migrants over distance $d_{ij}$. Constant $\beta$ is a product of several components, including the (constant) density of individuals in the patches, the rate of emigration (the fraction of individuals leaving their natal patch), and the fraction of emigrants moving from patch $j$ in the direction of patch $i$. Clearly, $\beta$ remains generally unknown, but as will be seen below, this causes no problems in the use of the model. $d_{ij}$ is typically measured as the shortest distance between patches $i$ and $j$, but any other measurement that would make better biological sense could be used instead. For instance, one might wish to measure distances around any dispersal barriers. With these assumptions, equation 3 becomes

$$C_i = \frac{1}{1 + \left(\frac{y}{S_i}\right)^2} \quad \text{eqn 5}$$

where $y' = y/\beta$ is a combination of the two parameters. $y'$ describes the colonization ability of the species: good colonizers, which are little affected by isolation, have small $y'$. Note that if the value of $y$ in equation 3 can be established independently, for instance with experiments, one may estimate the numbers of immigrants $M_i$ using equation 4, in which $\beta = y'y'$ ($y'$ is estimated by fitting the model to data as described in the next section).

In the simplest mainland-island situation, all migrants are assumed to originate from the permanent mainland population, which is equally far from all habitat patches; hence, $C_i$ equals a constant $C$ for all $i$. This special case has been previously examined by Hanski (1992).

**PARAMETER ESTIMATION**

Substituting expressions (2) and (5) into equation 1 gives a model for the probability of patch $i$ being occupied as a function of its size and spatial location with respect to the occupied patches,

$$J_i = \frac{1}{1 + \left(1 + \left(\frac{y'}{S_i}\right)^2\right)^{\frac{e}{A_i}}} \quad \text{eqn 6}$$

This model may be fitted to empirical data on patch occupancy for a given value of $\alpha$ and using $p_i$ as a dependent variable instead of the unknown $J_i$. The model is fitted with non-linear regression using maximum likelihood estimation (see legend to Fig. 1).

To summarize the kind of data that are required for this model, one needs to know patch areas $A_i$, their spatial locations, to calculate the pairwise distances $d_{ij}$, the presence or absence of the species in the patches in the year of the survey $p_i$, and the value of parameter $\alpha$, which sets the distribution of migration distances. The remaining parameters $y'$, $e$ and $x$ are estimated using equation 6. In principle, one could estimate also the value of $\alpha$ from the presence/absence data by fitting equation 6 for different values of $\alpha$ and selecting the best-fitting value, but for two reasons a more preferable approach is to obtain an independent estimate of $\alpha$ using, e.g. mark–recapture data. First, this will reduce the number of parameters that remain to be estimated from the presence/absence data. And second, it is important to check that migration is sufficiently restricted to make the metapopulation approach reasonable in the first place (note that even if individuals would completely redistribute themselves in each generation, contrary to what is assumed here, patch occupancy might still show an area and perhaps even an isolation effect). Fortunately, as will be demonstrated in the section on butterfly metapopulations, the use of equation 6 is not overly sensitive to the exact value of $\alpha$.

A very attractive feature of equation 6 is that it allows, in principle, independent estimation of
Fig. 1. The value of the maximum likelihood (ML) function which was minimized by the Quasi-Newton method in parameter estimation for Examples A and B in Table 1 (panels a and c), and the respective predicted turnover rates (number of events per generation, panels b and d), against the logarithm of the extinction parameter $e$. The ML function is defined as

$$-\sum p_i \ln \bar{J}_i + (1 - p_i) \ln (1 - \bar{J}_i),$$

where $p_i = 1$ for occupied and 0 for empty patches, and $\bar{J}_i$ is the estimated incidence, given by equation 6. For further discussion see the text.

the parameters which describe colonization ($\alpha$ and $y'$) and extinction ($e$ and $x$). In practice, however, parameter estimation with equation 6 may be expected to work only when the rates of colonization and extinction are not too high nor too low. The former case is discussed in the next section; here I describe a problem with low rates.

When the colonization rate is low, for instance because emigration rate is low, it becomes impossible to obtain reliable estimates of $y'$ and $e$ independently. To see this, note that the denominator in equation 6 can be written as $1 + (S_i^2 + y'^2)e/(S_i^2A_i^2)$, which is approximately $1 + (y'^2e)/(S_i^2A_i^2)$ when $S_i$ is small in comparison with $y'$. Table 1 gives two examples. The data for these examples were generated by assuming the patches in the Melitaea cinxia metapopulation, which will be analysed below in the section on butterfly metapopulations, and using equations 2 & 5 to numerically iterate metapopulation dynamics from an initial set of $p_i$ values. Data were obtained from generation 100, when the dynamics had reached an equilibrium state. Table 1 shows that in one case (Example A) parameter estimation was apparently successful, whereas in the other case it failed entirely. But in Example A the maximum likelihood function which was minimized in parameter estimation reached only a local minimum (Fig. 1a). In both cases the problem lies in the low rate of colonization, which makes it impossible to distinguish among different combinations of $y'$ and $e$. However, reasonably accurate parameter estimates can be obtained with extra information on population turnover. Figure 1 shows the predicted turnover in the two examples against the extinction parameter $e$. The observed turnover was 0-4 and 1-4 events per generation in Examples A and B (mean values for generations 91–100; the respective ranges of turnover events per generation were 0–1 and
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have undesirable consequences for the modelling of 
where \( z \) is another constant. This may, however, 
the term \( S_i^2 \) in equation 8 would be replaced by \( S_i^2 \), 
where \( e' = ey'^2 \). Equation 3 could, of course, be 
generalized to other powers than 2, in which case 
the counterintuitive prediction is that equation 6 
approaches 0.5, though intuitively one might expect 
it to approach unity, in spite of high extinction rate, 
because of high colonization rate. The reason for 
the counterevidence is that equation 6 does not allow for 'simultaneous' extinctions and 
and colonizations, which would leave the patch occupied. 
To take into account such a 'rescue effect' (Brown & 
Kodric-Brown 1977; Hanski 1991), let us change the 
realized extinction probability to \((1 - C)E \) \( \), where \( E \) now stands for the extinction probability in the 
absence of migration. This is another extreme 
assumption, most likely to apply in cases where 
extinctions typically occur before recolonizations in 
the annual cycle of events. Equation 1 then becomes 

\[
J_i = \frac{C_i}{C_i + E_i - C_i E_i} , \quad \text{eqn 7}
\]

Notice that the product \( C_i E_i \) is a measure of the 
strength of the rescue effect. The rescue effect is especially important for small patches (with large \( E \)) which are located close to large populations 
giving a large \( C_i \). Equation 6 now becomes 

\[
J_i = \frac{1}{1 + \frac{e'}{S_i^2 A_i^2}} , \quad \text{eqn 8}
\]

where \( e' = ey'^2 \). Equation 3 could, of course, be 
generalized to other powers than 2, in which case 
the term \( S_i^2 \) in equation 8 would be replaced by \( S_i^2 \), 
where \( z \) is another constant. This may, however, 
have undesirable consequences for the modelling of 
transient metapopulation dynamics (see the section 
on butterfly metapopulations below).

A general drawback of equation 8 in comparison 
with equation 6 is that the parameters of the colonization 
and extinction rates can never be estimated independently with equation 8, in which \( e \) and \( y' \) 
appear as the product \( e' = ey'^2 \). Therefore, without 
using some extra information it is not possible to 
calculate the extinction and colonization probabilities 
with the estimated parameter values. The most 
practical way to tease apart the two rates is to collect 
data on patch occupancy in another year, or in several 
years, and to use data on observed population turnover to calculate the values of \( y' \) and \( e \). Denoting by \( T \) 
the total number of turnover events (extinctions 
and colonizations) per year, we can use the equality 

\[
T = \sum (1 - C_i) E_i p_i + C_i (1 - p_i) \quad \text{eqn 9}
\]

with the expressions for \( C_i \) and \( E_i \), to obtain 

\[
T = \sum \frac{1}{S_i^2 + y'^2} \left[ S_i^2 (1 - p_i) + \frac{e' p_i}{A_i} \right] , \quad \text{eqn 10}
\]

from which the value of \( y' \) can be found numerically 
(note that the values of \( e' \) and \( x \) have already been 
obtained from equation 8). Having thus obtained 
the value of \( y' \), one may calculate the value of \( e \) 
from \( e = e' y'^2 \). Now we have estimates of all the 
parameter values and may numerically iterate the 
dynamics of the metapopulation in any system of 
habitat patches.

**Application to butterfly metapopulations**

In this section I report the results of fitting equations 
6 and 8 to data from three exceptionally well-studied 
butterfly metapopulations. The species are the 
Glanville fritillary *Melitaea cinxia* L. from South 
Finland (details in Hanski, Kuussaari & Nieminen 
1994), the silver-spotted skipper *Hesperia comma* 
L. from South England (Thomas & Jones 1993) and 
the chequered blue *Scolitantides orion* Pallas from 
South Finland (P. Saarinen, unpublished data). The 
first two metapopulations have been analysed with 
a spatially explicit, nine-parameter simulation 
model by Hanski & Thomas (1994). The three 
metapopulations include 50–70 habitat patches, 
with mean areas of 0.1–0.9 ha, and located within 
total areas in the range 20–100 km² (Table 2). The 
mean \( S \) values vary from 0.5 in *S. orion* to \( c. 2.0 \) in 
*M. cinxia* and *H. comma*. The smaller values for 
*S. orion* primarily reflect the smaller patch areas in 
this metapopulation than in the two other species. 
The observed fractions of occupied patches were 
0.84, 0.80 and 0.63 in the three species in the respective 
year of the survey (Table 2).

The results of fitting equation 6 to these data are 
summarized in Table 2. The estimated \( e \) values, 
which give the per year extinction probability in a 
patch of 1 ha, are all close to each other, ranging

### Table 1. Results of fitting equation 6 to two sets of simulated data. The data were generated by assuming the 50 habitat patches in the *Melitaea cinxia* metapopulation, discussed in the section on butterfly metapopulations. Estimate 1 gives the values obtained from fitting equation 6 to the data. Estimate 2 was obtained by fixing the value of \( e \) in equation 6 based on the observed population turnover (Fig. 1)

<table>
<thead>
<tr>
<th>Example</th>
<th>Parameter</th>
<th>True value</th>
<th>Estimate 1</th>
<th>Estimate 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>( y' )</td>
<td>10</td>
<td>4.52</td>
<td>3.55</td>
</tr>
<tr>
<td></td>
<td>( e )</td>
<td>0.002</td>
<td>0.005</td>
<td>0.008</td>
</tr>
<tr>
<td></td>
<td>( x )</td>
<td>0.5</td>
<td>0.57</td>
<td>0.55</td>
</tr>
<tr>
<td>B</td>
<td>( y' )</td>
<td>10</td>
<td>0.12</td>
<td>3.32</td>
</tr>
<tr>
<td></td>
<td>( e )</td>
<td>0.002</td>
<td>0.79</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>( x )</td>
<td>1.0</td>
<td>2.04</td>
<td>1.30</td>
</tr>
</tbody>
</table>
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Table 2. Results of fitting equation 6 to three butterfly metapopulations (see Figs 2–4). \( P^* \) is the observed fraction of occupied patches. The value of \( a \) was set at 2 in each case. Parameter estimates are given with their asymptotic standard errors (in parentheses)

<table>
<thead>
<tr>
<th></th>
<th>M. cinxia</th>
<th>H. comma</th>
<th>S. orion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of patches</td>
<td>50</td>
<td>64</td>
<td>70</td>
</tr>
<tr>
<td>( P^* )</td>
<td>0.84</td>
<td>0.80</td>
<td>0.63</td>
</tr>
<tr>
<td>Mean ( A ) (ha) ± SD</td>
<td>0.41 ± 0.81</td>
<td>0.94 ± 1.39</td>
<td>0.10 ± 0.10</td>
</tr>
<tr>
<td>Mean ( S ) ± SD</td>
<td>2.27 ± 1.33</td>
<td>2.15 ± 1.27</td>
<td>0.45 ± 0.32</td>
</tr>
<tr>
<td>( y' )</td>
<td>0 (0.182)</td>
<td>2.663 (1.713)</td>
<td>0.173 (0.103)</td>
</tr>
<tr>
<td>( e )</td>
<td>0.044 (0.035)</td>
<td>0.010 (0.011)</td>
<td>0.036 (0.049)</td>
</tr>
<tr>
<td>( x )</td>
<td>0.501 (0.203)</td>
<td>1.009 (0.222)</td>
<td>0.790 (0.434)</td>
</tr>
<tr>
<td>ML function*</td>
<td>19.1</td>
<td>20.3</td>
<td>39.4</td>
</tr>
<tr>
<td>Predicted ( A_0 ) (m²)</td>
<td>20</td>
<td>104</td>
<td>149</td>
</tr>
<tr>
<td>Observed ( A_0 ) (m²)</td>
<td>12</td>
<td>200</td>
<td>200</td>
</tr>
<tr>
<td>Predicted turnover</td>
<td>16</td>
<td>6</td>
<td>27</td>
</tr>
<tr>
<td>Observed turnover</td>
<td>9(^\dagger)</td>
<td>NA</td>
<td>22(^\dagger)</td>
</tr>
</tbody>
</table>

* Maximum likelihood (ML) function was minimized in parameter estimation (for its definition see legend to Fig. 1).
\(^\dagger\) Based on the presence of adult butterflies in 1991 and 1992. Because \( y' = 0 \), the predicted number of colonizations is the number of empty patches in 1991 (cf. equation 3), which is probably an overestimate.
\(^\dagger\) Based on the presence of eggs in 1991 and 1992. NA = data not available.

from 1 to 5%. These values agree well with the existing information about turnover rates in butterfly populations (Thomas 1993; Thomas, Thomas & Warren 1992). The more detailed simulation model with nine parameters gave the respective extinction probabilities as 0.6 and 0.8% for \( M. \) cinxia and \( H. \) comma, respectively, with about 1000 individuals per ha at local equilibrium (Hanski & Thomas 1994).

The \( x \) values range from 0.5 to 1.0, which are consistent with the generally important role of environmental stochasticity in insect population dynamics (Hanski 1992). \( Melitaea \) cinxia has the smallest \( x \) value, which may reflect its biology: \( M. \) cinxia is the only species among the three species with gregarious larvae, which are expected to increase variability in population size (Hanski 1987), as the survival probabilities of same-group larvae are to some extent correlated. The estimated value of \( y' \) is 0 for \( M. \) cinxia, suggesting that in this metapopulation colonization is very rapid and, taking the estimate \( y' = 0 \) at its face value, independent of isolation. The average degree of isolation was indeed low in this metapopulation, most local populations being located less than 300 m from the nearest occupied patch (Hanski et al. 1994).

The values of \( e, x \) and \( y' \) were estimated by assuming that \( \alpha = 2 \), which value is based on the results of an extensive mark–recapture study on \( M. \) cinxia (Hanski et al. 1994). Table 3 shows that the values of the extinction parameters \( e \) and \( x \) were not sensitive to the value of \( \alpha \) within a realistic range. The value of \( y' \) obviously depends on \( \alpha \). These results are encouraging, in view of the general difficulty of accurately estimating \( \alpha \).

Using the estimated parameter values, the critical patch areas \( A_0 \) for which the per-year extinction probability equals one can be calculated. These values are in good agreement with the observed minimum areas of occupied patches (Table 2). As the equilibrium local population density is around 1000 butterflies per ha in \( M. \) cinxia and \( H. \) comma (Hanski & Thomas 1994), the \( A_0 \) corresponds to population sizes of 2–15 adult butterflies. Taking further into account that, typically, only a third of adult butterflies are likely to be alive at the same time, these estimates of the critical minimum population sizes are in accordance with our expectations.

One may also calculate a prediction for the number of extinctions and colonizations in 1 year, starting from the set of occupied patches which was used to estimate the parameter values. These values can be compared with observed values in \( M. \) cinxia and \( S. \) orion, for which occupancy data are available for 2 years. The agreement is very good for \( S. \) orion, somewhat less good for \( M. \) cinxia (Table 2). In both species the predicted number of turnover events (colonizations and extinctions) is greater than the observed one, perhaps because the latter is affected by the rescue effect, which is not included in equation 6 (but see below).

Figures 2–4 show the patch areas \( A_i \), isolations \( S_i \) and patch occupancies \( p_i \) in the three metapopulations, with the line \( J_i = 0.5 \) drawn for the parameter values shown in Table 2. Figure 5 shows the maximum likelihood function which was minimized in parameter estimation, against the value of \( e \). In all cases the function reached a distinct minimum.

In all three metapopulations there are several small patches located close to large ones (Figs 2–4),
suggesting that the rescue effect may play a significant role. I therefore fitted equation 8 to these data, and calculated the values of \( y' \) and \( e \) using equation 10 and the observed number of turnover events in \( M. \ cinxia \) and \( S. \ orion \). The numerical results are given in Table 4, and Figs 2–4 show the respective lines of \( J_i = 0.5 \) incidence based on three models: equation 6 (continuous line), equation 8 with the estimated \( z \) value (broken line) and equation 8 with \( z = 2 \) (dashed line). For the statistics see Tables 2 and 4.

Fitting a modified version of equation 8 with the power 2 in the colonization function (equation 3) replaced by parameter \( z \) produced the \( z \) values of 0.47, 1.64 and 0.87 in \( M. \ cinxia \), \( H. \ comma \) and \( S. \ orion \) (Table 4, see also Figs 2–4). The low value for \( M. \ cinxia \) is consistent with the estimated \( y' = 0 \) from equation 6 (Table 2), indicating little role for isolation in colonization. But a problem with the \( M. \ cinxia \) data set is that most patches were occupied in the year of the survey (Fig. 2), and isolation may well be more important in this metapopulation than the fraction of occupied patches is lower. In any case, I prefer to use the power 2 in equation 3 systematically, because this makes good biological sense, and represents a useful parameterization of the model for subsequent simulation of transient dynamics, as demonstrated in the next section.

**Using the estimated parameter values to predict metapopulation dynamics**

When the parameters of equations 2 and 5 have been estimated from a metapopulation at equilibrium, it is possible to iterate the dynamics of the species in any set of habitat patches with known values of \( A_j \) and patch locations, and starting from any configuration of occupied patches \( p_i \) (note that when the \( p_i \) and patch locations are known, one may calculate the \( S_j \) values). The iterations proceed by generating stochastic extinctions and colonizations of the currently occupied and empty patches, respectively, according to equations 2 & 5. Such iterations will generate predictions both about the transient dynamics and about the ultimate equilibrium patch occupancy. I will next give some examples on the butterfly metapopulations.
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The model predictions for *Hesperia comma* can be tested with another metapopulation of the same species, which has been expanding since 1982. Thomas & Jones (1993) describe how an improvement in patch quality in the 1970s was followed in the 1980s by an increase from three to 21 occupied patches in a system of 54 patches in 9 years. Assuming that the metapopulation from which the parameter values were estimated (Fig. 3) was at equilibrium, we may predict, with the present model, the expected increase in patch occupancy in 9 years, starting from the three patches which were occupied in reality in 1982. In 100 numerical iterations for 9 years, the mean number of occupied patches increased to 11.4 (SD = 1.2) in 9 years, with a maximum of 16 patches occupied. This is somewhat less than the observed 21 patches. On the other hand, the nine-parameter simulation model (Hanski & Thomas 1994) also predicted a lower mean number of occupied patches after 9 years (nine patches) than was actually observed. As both models used data from the metapopulation at equilibrium (Fig. 3) to predict the dynamics in the expanding metapopulation, a possible explanation of the difference between the predictions and observations is that, in fact, the metapopulation in Fig. 3 was not at equilibrium but was also expanding, though only slowly. Some observations support this conclusion (Thomas & Jones 1993; Hanski & Thomas 1994). On the other hand, the discrepancy may also reflect the general difficulty of deducing the rate of expansion into a network of empty habitat patches, which may be much affected by occasional long-distance migration, from the knowledge of equilibrium metapopulation patterns, which are mostly affected by short-distance migration.

Only single metapopulations of *Melitaea cinxia* and *Scolitantides orion* have been studied so far, hence no direct tests of predicted transient or equilibrium dynamics are yet possible. But recollect that equation 6 predicted quite well the minimum size of the occupied patches and the per-year turnover rate in these species (Table 2). We may also produce predictions on e.g. how the equilibrium number of occupied patches would respond to a constant reduction in patch areas. Figure 6 shows the results of such calculations for *M. cinxia*. It is apparent that if the patch areas were reduced to less than 30% of their present areas, the metapopulation would go extinct. This prediction is compared, in Fig. 6, with...
Fig. 6. The predicted fraction of patches occupied at equilibrium (after 100 generations) in the *Melitaea cinxia* metapopulation when the areas of all patches were reduced to a constant fraction of the original area (on the horizontal axis). The black dots give three replicate predictions based on equation 8. The open circles give the same prediction (three replicates) based on a more detailed, nine-parameter simulation model (Hanski & Thomas 1994). The difference between the two predictions is discussed in the text. Iterations were started with half of the patches occupied.

A similar prediction based on the more detailed, nine-parameter simulation model (Hanski & Thomas 1994), which includes local dynamics and an explicit description of migration. The more complex model predicts accurately the observed effects of patch area and isolation on both patch occupancy and local density (Hanski & Thomas 1994). The predicted pattern is the same, but in the more complex model the metapopulation went extinct already when patch areas were halved (Fig. 6).

The difference in the predictions of the two models was expected. The nine-parameter simulation model describes local dynamics, and takes into account the fact that newly established local populations are typically small and hence more vulnerable to extinction than the respective populations at local equilibrium. The present models ignore local dynamics. Because these models were fitted to data on patch occupancy at equilibrium, the model predictions are expected to be valid for situations in which the population size distribution is comparable to that at equilibrium. In expanding metapopulations there are relatively more small populations than at equilibrium, and hence the model may underestimate the extinction rate and overestimate the colonization rate. This problem is more severe the higher the rate of population turnover; in other words, the more similar are the time-scales of local and metapopulation dynamics. To remedy this problem, local population growth has to be included in the model which, however, introduces at least one more parameter and makes the parameter estimation more complex (Hanski, unpublished).

**Errors in Parameter Estimation**

The parameter estimates in Tables 2 & 4 have relatively large standard errors and wide confidence limits, but it is difficult to assess from these results how well the model actually performs. One important question is how sensitive the parameter estimates are to changes in the exact set of occupied patches, which will change even at equilibrium. To examine this question, I generated a hypothetical data set for a system of 50 patches, sampled patch occupancy in generations 91–100, when an equilibrium level of patch occupancy appeared to have been reached, and fitted equation 8 to these data with the help of equation 10 and the number of turnover events in the model output between generations $t$ and $t + 1$.

Figure 7 shows the patch areas $A_i$, isolations $S_i$ and patch occupancies $p_i$ in generation 91, with the lines $J_i = 0.5$ calculated for the true parameter values (which were used to generate the data) and for the 10 sets of estimated parameter values. Notice that because patch occupancy changed from generation to generation, the pattern of occupancies shown in Fig. 7 is valid for generation 91 only.

The estimated $J_i = 0.5$ lines all lie a little to the left of the 'correct' line for large and very isolated patches, which suggests that these patches, the ones with the lowest turnover rate, had not yet reached an equilibrium after 100 generations (iterations were started with all patches occupied). In the bottom right corner of the figure, with small and little-isolated patches, there is much variation in the $J_i = 0.5$ lines based on different parameter estimates (Fig. 7). This is not surprising, because these are the patches with the highest turnover rate, and there happened to be relatively few patches in this region.

**Table 3. Parameter estimates for *H. comma* and *S. orion* (equation 6) for different values of $\alpha$. The more detailed results in Table 2 are for $\alpha = 2$. Results for *M. cinxia* were unaffected by $\alpha$, because in each case $y' = 0**

<table>
<thead>
<tr>
<th>Species</th>
<th>$\alpha$</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>H. comma</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$y'$</td>
<td>NC</td>
<td>2.663</td>
<td>0.877</td>
<td>0.371</td>
<td>0.123</td>
<td></td>
</tr>
<tr>
<td>$e$</td>
<td>NC</td>
<td>0.010</td>
<td>0.011</td>
<td>0.011</td>
<td>0.014</td>
<td></td>
</tr>
<tr>
<td>$x$</td>
<td>NC</td>
<td>1.009</td>
<td>1.111</td>
<td>1.187</td>
<td>1.203</td>
<td></td>
</tr>
<tr>
<td>ML function</td>
<td></td>
<td>20.3</td>
<td>19.0</td>
<td>18.5</td>
<td>18.5</td>
<td></td>
</tr>
<tr>
<td><strong>S. orion</strong></td>
<td></td>
<td>0.737</td>
<td>0.173</td>
<td>0.063</td>
<td>0.020</td>
<td>0.002</td>
</tr>
<tr>
<td>$y'$</td>
<td></td>
<td>0.036</td>
<td>0.036</td>
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<td>0.035</td>
<td>0.055</td>
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<tr>
<td>$e$</td>
<td></td>
<td>0.753</td>
<td>0.790</td>
<td>0.853</td>
<td>0.867</td>
<td>0.800</td>
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<tr>
<td>$x$</td>
<td></td>
<td>39.6</td>
<td>39.4</td>
<td>40.0</td>
<td>41.0</td>
<td>41.4</td>
</tr>
</tbody>
</table>

NC, no convergence in parameter estimation.
A model of metapopulation dynamics

Table 4. Results of fitting equation 8 to the three butterfly metapopulations. The values of $y'$ and $e$ were obtained from equation 10 using the observed value of turnover events per year ($T$). The value of $a$ was set at 2 in each case. Parameter estimates are given with their asymptotic standard errors (in parentheses). The last line gives the estimated value of $z$ in a modified version of equation 8, with $S_i^2$ replaced by $S_i^*$ (see the text).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$M. \ cinxia$</th>
<th>$H. \ comma$</th>
<th>$S. \ orion$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$e'$</td>
<td>0.026 (0.027)</td>
<td>0.084 (0.048)</td>
<td>0.0014 (&lt;0.001)</td>
</tr>
<tr>
<td>$x$</td>
<td>0.891 (0.263)</td>
<td>1.103 (0.234)</td>
<td>1.339 (0.135)</td>
</tr>
<tr>
<td>ML function</td>
<td>22.6</td>
<td>20.7</td>
<td>42.9</td>
</tr>
<tr>
<td>$T$</td>
<td>9</td>
<td>NA</td>
<td>22</td>
</tr>
<tr>
<td>$y'$</td>
<td>1.340</td>
<td>(3-190)*</td>
<td>0.259</td>
</tr>
<tr>
<td>$e$</td>
<td>0.014</td>
<td>(0-008)*</td>
<td>0.021</td>
</tr>
<tr>
<td>$z$</td>
<td>0.469 (0.459)</td>
<td>1.636 (0.460)</td>
<td>0.869 (0.308)</td>
</tr>
<tr>
<td>ML function</td>
<td>18.7</td>
<td>20.5</td>
<td>37.7</td>
</tr>
</tbody>
</table>

* Assuming $T = 4$ (=assuming the same ratio of observed to predicted turnover events as in $M. \ cinxia$ and $S. \ orion$).

Figure 8 shows the transient and equilibrium dynamics predicted by the true parameter values and by the estimated parameter values in another system of 50 patches (the observed set of 50 patches in the Melitaea cinxia metapopulation). Note that the results are practically identical. In all but one case the metapopulation expanded from the initial state of one patch occupied to $\geq 40$ occupied patches in 50 generations, though there was much variation in the time it took to increase from one to $\geq 40$ patches occupied. The number of turnover events remained fairly constant, indicating higher relative turnover rate during metapopulation expansion than at equilibrium (turnover events per year per number of occupied patches).

Discussion

The use of regression models to characterize the effects of patch area and isolation on occupancy is a common practice in the metapopulation literature (Van Dorp & Opdam 1987; Lomolino, Brown & Davis 1989; Taylor 1991; Sjögren 1991; Peltonen & Hanski 1991; Thomas & Jones 1993; Thomas 1993). The unique feature of the present approach is that the models are based on ecological considerations and were developed in a population dynamic context.

The advantages are twofold. First, the parameter estimates have a meaningful biological interpretation, which in itself may be helpful, especially in comparisons of several metapopulations of one or more species. Secondly, and more important, the parameter estimates allow numerical iterations of the dynamics of the species in any system of habitat patches, thus generating predictions that are potentially of substantial value. The applications are countless. For instance, one may evaluate the relative 'value' of different habitat patches to long-term persistence of a metapopulation; examine the expected consequences of different management practices using experiments of the type described in Fig. 6; ask whether a presently vacant system of habitat patches would be colonized by a species following international introduction, and where exactly the initial propagule should be placed to maximize the probability of successful metapopulation establishment?

That is the good news. The bad news is that as so little is required in terms of data, one would be unwise to make too grandiose claims about the performance of the model. There is no need to emphasize the caution with which predictions of simple models should be treated. But complex models also have problems, and the great advant-

![Fig. 7. A hypothetical data set of 50 patches with a log-normal patch size distribution and random spatial locations within a 5 x 5 km² area. Metapopulation dynamics were iterated, starting with all patches occupied, and using the following parameter values: $a = 2$, $e = 0.01$, $x = 1$ and $y' = 1$. Equation 8 was fitted to data sampled from generations 91-100 (10 data sets), using equation 10 with the observed number of turnover events between two successive years (mean number 5-7 events, range 2-10). The $J_f = 0-5$ lines shown in the figure are based on the true parameter values (continuous line) and the 10 sets of estimated parameter values (broken lines). Patch occupancy is shown for generation 91.](image-url)
Fig. 8. Iterated metapopulation dynamics in the network of 50 patches occupied by *Melitaea cinxia* using the parameter values estimated from the hypothetical data set described in Fig. 7. Panel (a) shows 10 replicate trajectories based on the parameter values which were used to generate the data in Fig. 7, and panel (c) shows the trajectories based on the 10 sets of parameter values estimated from the data thus generated. In both cases the metapopulation was started with the same single patch occupied. Panels (b) and (d) show the numbers of turnover events per generation in the two cases.

The age of simple models is that their predictions are often easier to test and interpret than are the predictions of complex models. Furthermore, if the purpose is to compare, e.g. the consequences of two different changes in patch configuration, predictions based on the present model are likely to be qualitatively correct even if the quantitative predictions, especially about transient dynamics, might be somewhat in error.

The present modelling approach is particularly attractive because it only requires presence/absence census data, a ‘snapshot’ of patch occupancy at one point in time, which is generally easy to obtain. However, this approach is not likely to yield reliable results if the number of patches is small, or if the species occupies nearly all, or is absent in nearly all patches; in which case there is little information about the effects of patch area and isolation on occupancy, and hence little information embedded in the patterns about the rates of colonization and extinction. I recommend that the number of patches should be at least 30, preferably more than 50; that the fraction of occupied patches at equilibrium should be >0.2 and <0.8; and that there should be ample variation in patch sizes and isolations. No definite criteria for the kind of data that are acceptable can be given, however, because the different features of the data have interactive consequences for model performance. Instead of applying the model mechanistically, it is necessary to guard for potential problems due to idiosyncratic patch configurations. It is also worth iterating the key assumption on which parameter estimation is based; namely, that the metapopulation is at a colonization–extinction equilibrium. Unfortunately, it may often be difficult to ascertain whether this assumption is met and, even worse, this assumption is unlikely to be valid for many endangered and declining species, for which one would wish to apply the model. In these cases the only possibility would be to locate a conspecific metapopulation at equilibrium elsewhere, or to use data on an ecologically similar species with metapopulations at equilibrium.

The only way to find out the real predictive value
of a model is to test it with several sets of appropriate data. Although no ideal data for this purpose were available, the results on butterfly metapopulations described in this paper are encouraging. The results for the three species of butterfly were unexpectedly parallel, which raises the possibility that one could actually use one set of parameter values for these and similar species to generate rough predictions about particular networks of habitat patches and about particular metapopulations. Based on the present results, I suggest using for this purpose equation 8, which includes the rescue effect, with the following parameter values (patch areas in ha and distances in km): \( a = 2 \), \( y' = 1 \), \( e = 0.01 \), and \( x = 1 \).

Acknowledgements

I thank Mats Gyllenberg for useful discussion and comments, Fred Adler and Chris Thomas for comments on the manuscript, and Chris Thomas and Pekka Saarinen for permission to use their butterfly data.

References


Received 14 December 1992; revision received 3 March 1993