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Patch-occupancy dynamics in fragmented landscapes

Ilkka Hanski

Ecologists are often faced with the dilemma of holding only observational data on patterns, while being hard pressed to say something about the processes that have supposedly produced these patterns. A popular example is the pattern of habitat patch occupancy of species living in fragmented landscapes, and the processes of stochastic population extinction and patch recolonization. Patch-occupancy dynamics is a fashionable^{1–3}, though still controversial^{4,5}, issue in conservation biology, where there is the additional difficulty that experimentation would often be unethical as well as impractical. The purpose of this review is to summarize the kind of pattern data that ecologists interested in 'patch-occupancy dynamics' have accumulated, and to outline a recent approach to modelling of occupancy data for the purpose of answering questions about the dynamics.

Patterns of patch occupancy

It has been said that the increase in species number with increasing (island) area is one of the few valid

Recent work on the dynamics of species living in fragmented landscapes has produced much information on patterns of habitat patch occupancy in a wide range of organisms. Building on an elementary Markov chain model of patch occupancy, a family of incidence–function models can be constructed for particular kinds of metapopulations. These models can be parameterized with field data on patch occupancy, and the models can be used to make quantitative predictions about specific metapopulations. This approach provides a potentially powerful tool for the management of reserve networks and species living in fragmented landscapes.

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generalizations in ecology. The species–area relationship, and the analogous species–isolation relationship (decreasing species number with increasing isolation) were two critical building blocks on which the equilibrium theory of island biogeography⁶ was established. These multi-species patterns tend to emerge from regularities in the occurrence of individual species on true or habitat islands varying in area and isolation. Below, I use the shorthand term '(habitat) patch' for islands and also discrete fragments of a particular kind of habitat.

Patterson^{7,8} has drawn attention to significant 'nestedness' of species occurrences in habitat patches. Theoretically, species might occur as if randomly placed

in patches, with the constraint that smaller patches have a smaller probability of having any one of the species than larger patches. But this is not the pattern typically observed. In reality, each species tends to occur in patches exceeding an apparent threshold value in size. This threshold area varies among the species, which produces the more-or-less regular increase in species number with increasing area. That is, species that are present in a

particular patch are a subset of the species found in still larger patches. Various community-level indices have been used to characterize the degree of nestedness in species assemblages (reviews in Refs 9,10).

Examining the distributional ecology of individual species rather than entire communities, Diamond¹¹ coined the term 'incidence function' to describe the generally increasing probability of occurrence (or incidence) of a species in patches with increasing area (or total species number). The statistical significance of incidence patterns in individual species has been tested with the Mann-Whitney U-test¹² and related tests¹³ and with logistic regression^{14,15}. Empirical results for a wide range of organisms, but especially birds¹⁶, small mammals¹⁷⁻²⁰ and insects^{15,21,22}, confirm that the incidence of occupancy typically increases with increasing patch area and with decreasing isolation (Fig. 1a-f gives a range of examples).

Processes of patch occupancy

Patterns of patch occupancy may be affected by all sorts of factors, including unique historical events and variation in habitat quality (for an illuminating example

see Ref. 23), but here I consider only situations where the two principal processes in patch occupancy are stochastic extinction and recolonization. Recent empirical studies have related the rates of these processes to patch area and isolation.

Most organisms have limited powers of dispersal. It is therefore expected that the rate of recolonization of presently empty patches would decrease with increasing isolation. Other things being equal, small patches can only have small populations, which have a higher risk of extinction than large populations²⁴⁻²⁶. Hence, the extinction rate is generally expected to decrease with increasing patch area. These expectations are amply supported by empirical data (Fig. 1g-l). Decreasing rate of recolonization with increasing isolation and decreasing rate of extinction with increasing patch area are very robust results, applying to the vast majority of species, regardless of the details of their ecology.

It should not come as a surprise that a simple stochastic model incorporating isolation-dependent recolonization rate and patch-area-dependent extinction rate predicts the observed patterns of patch occupancy (see Box 1):

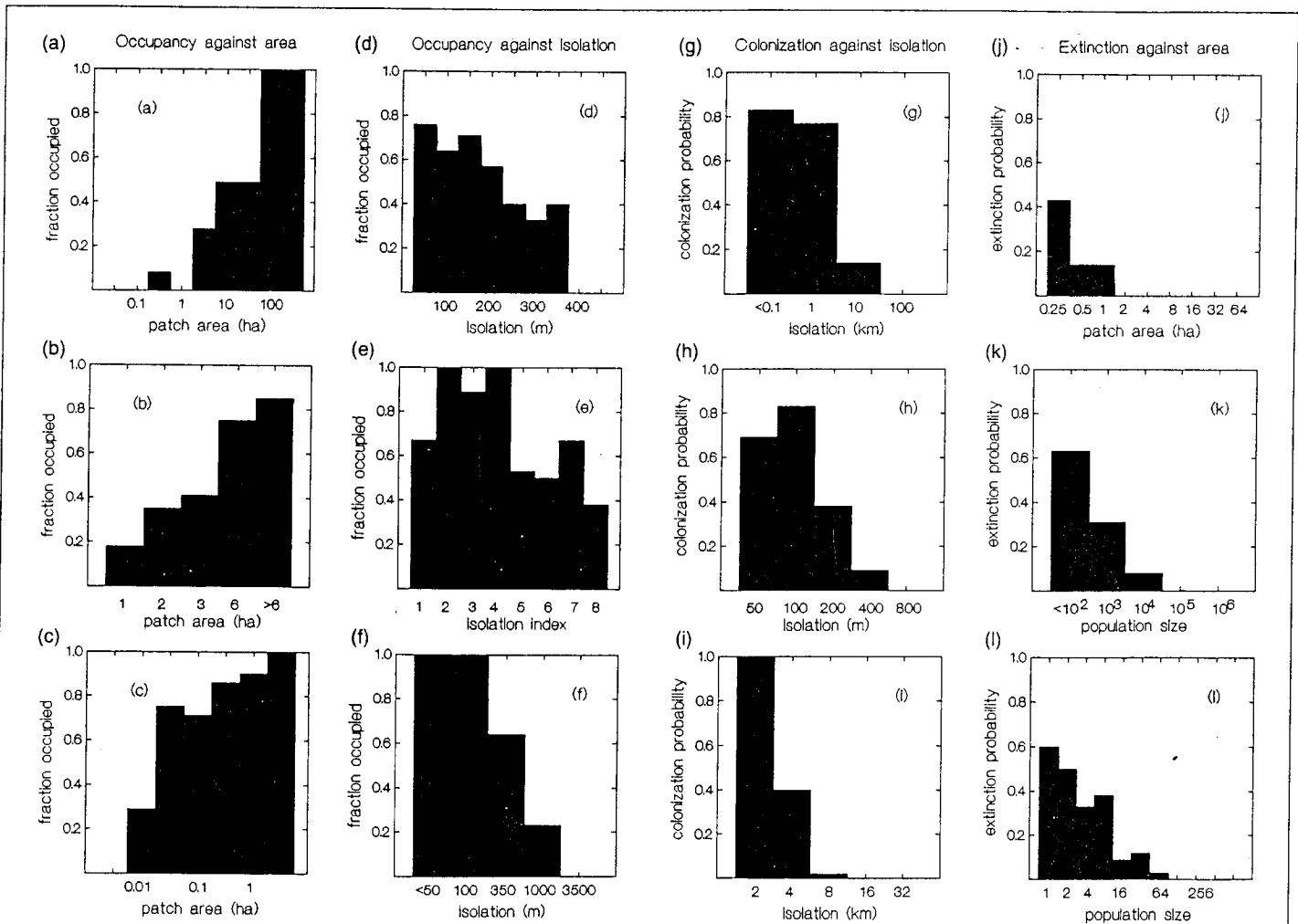


Fig. 1. Metapopulation patterns and processes: (a) the masked shrew (*Sorex caecutiens*) on small islands in lakes in Finland ($n = 68$ islands³²); (b) the nuthatch (*Sitta europaea*) in small woodlots in the Netherlands ($n = 68$ woodlots³³); (c) the butterfly *Hesperia comma* on dry meadows in England ($n = 67$ meadows; C. D. Thomas, unpublished); (d) the pika (*Ochotona princeps*) in discrete habitat patches in California ($n = 78$ patches³⁴); (e) the butterfly *Scolitantides orion* in discrete habitat patches in Finland [$n = 72$ patches, isolation measured by S_p , eqn (4); P. Saarinen, unpublished]; (f) the common shrew (*Sorex cinereus*) on islands in North America ($n = 39$ islands, omitting the smallest one; combined from Refs 27 and 35); (g) the butterfly *Hesperia comma* on dry meadows in England ($n > 100$ meadows, colonization over nine years³⁶); (h) the cricket *Metrioptera bicolor* in discrete habitat patches in Sweden ($n = 43$ patches, colonization in one year³⁷); (i) the butterfly *Euphydryas editha* in discrete habitat patches in California ($n = 59$ patches, colonization over nine years²³); (j) the cricket *Metrioptera bicolor* in discrete habitat patches in Sweden ($n = 90$ patches, extinction in one year³⁷); (k) pooled data for four species of spiders (*Metepeira datona*, *Gasteracantha cancriformis*, *Argiope argentata* and *Eustala cazieri*) on small islands in the Bahamas ($n = 222$ island-populations, extinctions in four years²⁶); (l) the butterfly *Phebejus argus* in discrete habitat patches in the UK ($n = 55$ patches; extinctions in seven years³⁸).

Box 1. Markov chain model for patch occupancy

The elementary incidence-function model is a linear, first-order Markov chain with two states, the presence or absence of a species in patch i . It is assumed that if patch i is currently empty, it has a constant probability C_i of becoming recolonized in unit time; and if patch i is currently occupied, it has a constant probability E_i of becoming empty (population goes extinct). The incidence of the species in patch i , defined as the stationary probability of occupying patch i , is then given by³¹:

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

Recall that the extinction probability E_i tends to decrease with increasing patch area (Fig. 1j-l) because small patches tend to have small populations which are vulnerable to extinction, and the colonization probability C_i tends to decrease with increasing isolation (Fig. 1g-i) because the numbers of immigrants reaching patch i decrease with increasing isolation. The elementary model thus predicts the generally observed patterns of decreasing patch occupancy with decreasing patch area (Fig. 1a-c) and increasing isolation (Fig. 1d-f).

decreasing incidence of occupancy J_i with increasing isolation and decreasing area of patch i . This result parallels the predictions of the familiar MacArthur-Wilson model⁶ for species number on islands varying in size and isolation. Despite its generality and simplicity, this elementary model easily leads to more specific, quantitative models that may help ecologists to use pattern data on patch occupancy to make novel predictions about dynamics.

Constructing more specific models

Quantitative incidence-function models may be constructed by making specific assumptions about how the isolation and area of patch i affect the probabilities of recolonization and extinction, C_i and E_i (Box 1). Let us recall the situation which was in the minds of Robert MacArthur and Edward Wilson when they developed their equilibrium theory of island biogeography⁶: a set of islands located off the mainland. In this case, all migration leading to recolonization occurs from the mainland to the islands. The mainland may be a true mainland or a very large habitat patch surrounded by smaller patches (such as has been described for the butterfly *Euphydryas editha*²³). Habitat patches (islands) vary in area A_i and isolation D_i (distance from the mainland).

Box 2 describes a set of simple assumptions to transform the elementary model (see Box 1) for such mainland-island metapopulations. These assumptions lead to the model:

$$J_i = \left(1 + \frac{\mu e^{\beta D_i}}{A_i^x} \right)^{-1} \quad (2)$$

where μ , β and x are three fitted parameters.

A very attractive feature of this model is that it can be fitted to simple 'snapshot' data on patch occupancy to estimate the parameter values of the extinction and recolonization probabilities E_i and C_i (Box 2). Figure 2 and Box 3 give two examples of using this equation to model the occurrence of shrews on small islands. In Box 3, the model-predicted extinction and recolonization probabilities are compared with probabilities estimated directly in an independent five-year study. The match between the predicted and estimated probabilities is striking.

Using the parameter estimates from the data in Fig. 2, one may draw interesting inferences about colonization rate over distances that are so large that direct estimation is

Box 2. Mainland-island incidence-function model

Let us assume that all migration to a set of habitat patches ('islands') occurs from one very large population which is invulnerable to extinction (the 'mainland'). The habitat patches have different areas A_i and degrees of isolation D_i , the latter being measured by the distance from the mainland. To keep the model simple, let us assume, without twisting the facts too much, that the colonization probability C_i is a negative exponential function of distance from the mainland, $C_i = q \exp(-\beta D_i)$, where q and β are two parameters. This relationship can be further simplified for species that are common on the mainland, in which C_i approaches one when D_i approaches zero (for these species $q = 1$; q is thus the probability of colonization of patch i when isolation is zero). Here I ignore the generally relatively weak dependence of C_i on patch area A_i . The extinction probability, in contrast, strongly depends on patch area but not on isolation (extinction probability may depend on isolation if there is strong rescue effect³⁰). One possible two-parameter function relating extinction risk to patch area is $E_i = \mu/A_i^x$ (Ref. 32).

With these assumptions, the elementary incidence function model (1) turns to:

$$J_i = \left(1 + \frac{\mu e^{\beta D_i}}{A_i^x} \right)^{-1} \quad (2)$$

To fit eqn (2) to empirical data, one needs to know the patch areas and isolations, A_i and D_i , as well as the pattern of occupancy of the species in the patches at one point in time, p_i (for presence $p_i=1$, for absence $p_i=0$). The unknown incidence J_i in eqn (2) is replaced by p_i for the purpose of maximum-likelihood estimation of the model parameters. Additionally, one has to make the assumption that the species occurs in a stochastic steady state in the patches (i.e. no increasing or decreasing trend in the number of occupied patches).

not possible. For instance, we may infer from the value of β that the per-year colonization probabilities of islands located 1, 2 and 4 km from the mainland are 0.06, 0.004 and 0.00001. As the islands are roughly 5000 years old²⁷, these values suggest that an island located 2 km from the mainland has almost certainly been colonized by the shrew at least once, but an island 4 km from the mainland has only a 5% probability of colonization in 5000 years. Therefore, these results suggest that the critical isolation of post-glacial islands for the presence of *Sorex* shrews is >2 but <4 km. This conclusion is in agreement with observations of dispersal distances in shrews^{18,28,29}.

Metapopulations without a mainland

Mainland-island metapopulations are especially tractable because of the simplifying assumption that all migration occurs from the mainland to the islands. Many networks of habitat patches, despite differences in patch areas, do not have a 'mainland' (a very large patch), and migration occurs among many habitat patches. This creates a problem for modelling the colonization probabilities C_i , which now depend on exactly which other patches are presently occupied and are therefore potential sources of migrants. The set of occupied patches varies at the stochastic steady state, which the metapopulation may reach before eventual extinction, hence the C_i values also vary in time. This is contrary to the assumptions

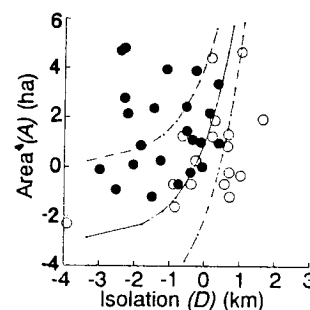


Fig. 2. Island areas (A_i), isolations (D_i) and occupancies (p_i) in the pooled data for the common shrew (*Sorex cinereus*) from Refs 27 and 35. Occupied islands are shown by black dots, unoccupied islands by circles. The three lines are the $J_i = 0.9$ (upper broken), $J_i = 0.5$ (solid line) and $J_i = 0.1$ (lower broken) incidence lines from eqn (2). The parameter estimates, with asymptotic standard errors in brackets, are: $\mu = 0.119$ (0.089), $\beta = 2.824$ (0.952) and $x = 0.709$ (0.320), where $n = 40$.

Box 3. Comparison between predicted and observed per-year colonization and extinction probabilities in three species of *Sorex* shrews

The predicted values come from fitting the mainland-island incidence-function model (eqn 2) to occupancy data from 68 islands. Island isolation varied relatively little in this system (significant effect only in *S. araneus*). Hence, parameter β (Box 2) was set to zero. To tease apart the values of μ and q , which now cannot be estimated independently, it was assumed that the critical island area for which $E_i=1$ is 0.5 ha [for *S. araneus* the respective value calculated from eqn (2) with the effect of isolation included was 0.66 ha]. The colonization and extinction rates were measured directly in an independent study of 17 islands surveyed for five years^{20,32}. The predicted extinction probability is for an island of 1.6 ha, which is the median size of the 17 islands.

Species	Colonization probability		Extinction probability	
	Predicted	Measured	Predicted	Measured
<i>S. araneus</i>	0.26	0.20	0.07	0.04
<i>S. caecutiens</i>	0.03	0.05	0.35	0.33
<i>S. minutus</i>	0.18	0.13	0.59	0.46

Box 4. Colonization probability in metapopulations without a mainland

The colonization probability C_i must be a function of the numbers of immigrants arriving at patch i per year, say M_i . If each immigrant establishes a new local population in an empty patch independently of each other, then $C_i=1-\exp(-yM_i)$, where y is a parameter. Often the probability of population establishment depends on the size of the propagule (M_i), and a better assumption is, for example, the following:

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

This function gives an S-shaped increase in the colonization probability from zero to one with increasing numbers of immigrants. Finally, to relate M_i to the sizes and locations of the existing local populations, let us assume that:

$$M_i = \gamma S_i \quad (4)$$

where

$$S_i = \sum_{j=1}^n p_j e^{-\alpha d_{ij}} A_j$$

p_j equals one for the occupied patches and zero for the empty patches, d_{ij} is the distance between patches i and j , and α is a constant setting the survival rate of migrants over distance d_{ij} . γ is a constant which 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 . With these assumptions:

$$C_i = \frac{1}{1 + \left[\frac{y'}{S_i} \right]^2} \quad (5)$$

where $y' = y/\gamma$ is a combination of the two parameters.

of the elementary model (Box 1). However, this variation is often quite small and can be ignored. Box 4 outlines a set of assumptions about C_i which lead to the following incidence-function model for metapopulations without a mainland:

$$J_i = \left[1 + \left[1 + \left(\frac{y'}{S_i} \right)^2 \right] \frac{\mu}{A_i^x} \right]^{-1} \quad (6)$$

(for the explanation of y' and S_i see Box 4).

This model may be fitted to empirical patch occupancy data in the same manner as the mainland-island model, eqn (2). Hanski³⁰ gives examples of using this model for three butterfly metapopulations, with further discussion on model assumptions, data requirements and confidence intervals around the predictions.

Applications in conservation biology

Let us return to the elementary model described in Box 1. Having estimated the parameters relating the probabilities E_i and C_i to patch areas A_i and isolations D_i , it is a simple matter numerically to iterate the dynamics of patch occupancy in any network of habitat patches, starting from an arbitrary set of patch occupancies. That is, in each generation, each occupied patch is allowed to go extinct with probability E_i (depends on patch area), and each empty patch is recolonized with probability C_i (depends on isolation, which may depend on the current set of occupied patches, Box 4). Repeating these calculations for many generations generates a trajectory of patch occupancy. One may assess the risk of metapopulation extinction and the size of the metapopulation at the stochastic steady state. All sorts of numerical experiments can be carried out; for instance, one may assess how much metapopulation extinction risk is increased by removing some particular patches. Conservation biologists might be especially interested in comparing the predicted consequences of alternative changes in the network of habitat patches.

Figure 3 gives an example based on a real metapopulation of the butterfly *Melitaea cinxia* in Finland²¹, living in a network of 50 small patches (dry meadows, mostly <1 ha). The parameter values of a modified version of eqn (6), which takes into account the rescue effect³⁰, were estimated from data collected in 1991, when 42 of the 50 patches were occupied. Based on these values, I generated two indices for each patch, which reflect one aspect of their relative 'importance' for metapopulation persistence: (1) the estimated probability of successful reinvasion into the patch network from the focal patch, following extinction from all other patches; (2) the number of extant populations 20 generations after the reinvasion (if successful). The results indicate that the species would invade the patch network with a high probability from six patches; no reinvasion is predicted from 20 patches, whereas the result was intermediate in the remaining 24 patches (Fig. 3). In this case, the estimated probabilities of reinvasion were mostly affected by patch areas, but the number of patches occupied after 20 generations was also significantly affected by patch isolation. Qualitatively these results are not unexpected, but it may often be valuable to have a quantitative, rather than a subjective, assessment of the relative 'significance' of particular habitat patches.

The incidence-function approach has the potential to develop into a helpful tool in population biology and conservation biology, allowing ecologists to use widely available information on patch occupancies to answer, realistically, vital questions about metapopulation dynamics. A particular strength of this approach is that it allows the investigation of processes at spatial and temporal scales that are relevant to conservation biology but difficult to tackle with other approaches. Admittedly, not all organisms living in fragmented landscapes conform to the kind of stochastic extinction-recolonization dynamics assumed in the model, but many do. Although, generally, other factors apart from patch areas and isolations need to be considered, areas and isolations can seldom be ignored.

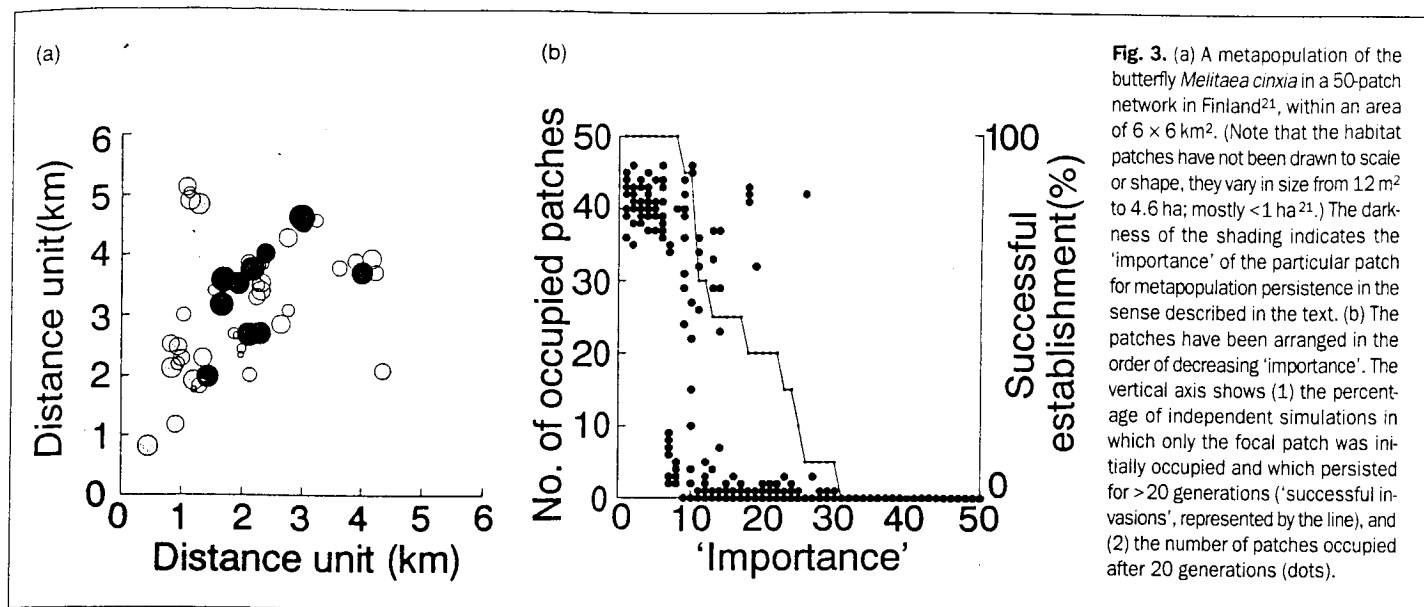


Fig. 3. (a) A metapopulation of the butterfly *Melitaea cinxia* in a 50-patch network in Finland²¹, within an area of 6 × 6 km². (Note that the habitat patches have not been drawn to scale or shape, they vary in size from 12 m² to 4.6 ha; mostly <1 ha²¹.) The darkness of the shading indicates the 'importance' of the particular patch for metapopulation persistence in the sense described in the text. (b) The patches have been arranged in the order of decreasing 'importance'. The vertical axis shows (1) the percentage of independent simulations in which only the focal patch was initially occupied and which persisted for >20 generations ('successful invasions', represented by the line), and (2) the number of patches occupied after 20 generations (dots).

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