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18. Although the samples of $Si(OR)_2PcI_3$ and the tetra-substituted Pc complexes were mixtures of isomers, the molecular compositions for these and the other compounds were established by elemental analysis and mass spectroscopy, and the compounds were also characterized by ultraviolet-visible absorption spectroscopy and proton nuclear magnetic resonance (NMR) spectroscopy. The NMR spectra suggest that $Si(OR)_2PcI_4$ was isolated as a single isomer by crystallization from ether-ethanol solution. We measured the fluence-dependent transmittance of the series of compounds by using 8-ns, 532-nm laser pulses from a frequency-doubled Q-switched Nd:yttrium-aluminum-garnet laser.
19. In the simple fluence-dependent model, the cross section is taken as
$$\sigma(F) = (\sigma_g N_g + \sigma_e N_e)/N_0$$
$$= \sigma_g \exp(-F/F_s) + \sigma_e[1 - \exp(-F/F_s)]$$
where N_g, N_e, and N_0 are the ground state, excited state, and total number densities, respectively. The propagation equation is solved numerically by a finite-element approach where each element is chosen to be optically thin such that beam attenuation within the element can be neglected. The attenuation of the beam is calculated as the pulse is passed sequentially through each element, with the output energy of an element used as the input energy for the next element. See, for example, K. Mansour *et al.*, *Proc. SPIE* **1853**, 132 (1993).
20. Use of tandem cells of a Pc excited-state absorber has achieved a comparable blocking level in a slower optical system (*f*/10), but with the chromophore and the tandem cell device design utilized, the linear transmittance was rather low (20%) [D. J. Hagan *et al.*, *Int. J. Nonlinear Opt. Phys.* **2**, 483 (1993)].
21. For comparison, we calculated that a fully saturated C_{60} limiter with the same N_0 and total path length (L), using parameters in Table 1, would give an attenuation [$1/T = \exp(N_0\sigma_e^{eff}L)$] of 6.2. This value is close to that observed for the homogeneous solution (Fig. 3B), indicating that there is no improvement in nonhomogeneously distributing C_{60} for this $N_0\sigma_e^{eff}L$. A much higher (nonhomogeneously distributed) concentration would be needed to achieve an attentuation of 540 and would result in a linear transmission of 0.12.
22. This work was performed in part at the Jet Propulsion Laboratory as part of its Center for Space Microelectronics Technology and was supported by the Ballistic Missile Defense Organization, Innovative Science and Technology Office, and the U.S. Air Force Wright Laboratory through an agreement with NASA. Work at the Beckman Institute was supported by the Office of Naval Research, the Defense Advanced Research Projects Agency, the Office of Naval Research through the Center for Advanced Multifunctional Molecular Assemblies and Polymers, and the Air Force Office of Scientific Research. P.V.B. is the recipient of a postdoctoral fellowship from the James Irvine Foundation.

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Predicting the Occurrence of Endangered Species in Fragmented Landscapes

Niklas Wahlberg,* Atte Moilanen, Ilkka Hanski

Reliable prediction of metapopulation persistence in fragmented landscapes has become a priority in conservation biology, with ongoing destruction of habitat confining increasing numbers of species into networks of small patches. A spatially realistic metapopulation model, which includes the first-order effects of patch area and isolation on extinction and colonization, has been tested. The distribution of an endangered butterfly was successfully predicted on the basis of parameter values estimated for a well-studied congeneric species. This modeling approach can be a practical tool in the study and conservation of species in highly fragmented landscapes.

Habitat destruction around the world (*1*) often leaves the remaining landscape severely fragmented (*2*), a condition that aggravates the threat to the survival of species that originally occupied more extensive and continuous habitats (*3*). Some species may nonetheless persist as metapopulations (*4*), assemblages of local populations inhabiting networks of habitat patches, even in highly fragmented landscapes. The quantitative understanding of metapopulation dynamics has become critical for the successful management and conservation of scores of endangered species (*5*).

Recently, Hanski developed a spatially realistic metapopulation model, called the incidence function model (*6*), which strives to combine generality and realism in a framework that allows parameter estimation and quantitative prediction for real metapopulations (*6, 7*). In the incidence function model (*8*), the probability of local extinction is determined by the size of the respective habitat patch, which assumes a positive relation between expected population size and patch area. Such a relation is commonly observed for animals (*9*). The probability of colonization of an empty patch is determined by its isolation from the occupied patches and by the sizes of these patches. Our recent studies of the Glanville fritillary butterfly (*Melitaea cinxia*) demonstrated that the effects of patch area and isolation dominate in the dynamics of its metapopulations, with factors that describe the quality of the habitat patches and the surrounding landscape exerting only relatively minor effects (*7, 10*). Other studies have reached similar conclusions (*11*), although often some attribute of patch quality has also been found to have a significant effect (*12*).

The parameters of the incidence function model can be estimated from a snapshot of patch occupancies (*8*). In making these estimates, we also assumed that the metapopulation from which the snapshot was taken was not far away from a stochastic steady state. This may be a problematic assumption for endangered species, many of which may be declining after recent habitat destruction. Often it is also difficult to collect sufficient data on rare species to estimate the parameters of any model. In this study, we used extensive data on metapopulation dynamics to test whether parameter values estimated for an unendangered butterfly species can be used as surrogates when data are unknown for a rare and endangered congeneric species.

The false heath fritillary butterfly, *Melitaea diamina*, is an endangered species in Finland (*13*) and within much of its range in Europe (*14*). It occurs on moist meadows with the larval host plant *Valeriana sambucifolia*. In spring 1995, we surveyed its only well-known metapopulation in Finland for all suitable habitat patches (*15*). Within an area of 600 km^2 we located 94 suitable patches, of which 35 were found to be occupied (*16*). It is unlikely that there are any other populations outside the study area within several hundred kilometers (*17*). *Melitaea diamina* is ecologically similar to the congeneric *M. cinxia* (*18*), which we have studied intensively in a large network of ~1600 habitat patches (*7, 19*). We have estimated the parameters of the incidence function model for *M. cinxia* (*7*), and we now use the published parameter val-

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Department of Ecology and Systematics, Division of Population Biology, Post Office Box 17 (Arkadiankatu 7), FIN-00014 University of Helsinki, Helsinki, Finland.

*To whom correspondence should be addressed. E-mail: nwahlber@helsinki.fi

Table 1. Estimated parameter values (with standard errors) and simulation results. The parameters were estimated for four butterfly species (*8, 21*). For each parameter set 20 replicate simulation runs were performed (*20*). The *ML* value reported here is the log-likelihood error during model iteration, which can be calculated from Eq. 4 in (*8*) by using J_i values determined from the simulation runs as the proportions of time each patch was occupied during iteration. The product *ML* measures the correspondence between predicted and empirically observed patch occupancies (Fig. 1); smaller values indicate better fit. Quantities P and P_A are the fractions of patches and the pooled patch area occupied during the simulation, respectively.

Species	Parameter values (SE)					Fraction of habitat occupied (mean ± SD)	
	x	ey^2	e	y	ML	P	P_A
Melitaea diamina	0.884 (0.257)	0.182 (0.105)	0.014	3.62	66.8 ± 6.4	0.36 ± 0.05	0.44 ± 0.07
Melitaea cinxia	0.952 (0.271)	0.158 (0.166)	0.010	3.97	65.3 ± 8.1	0.40 ± 0.02	0.50 ± 0.04
Scolitantides orion	0.964 (0.482)	0.239 (0.323)	0.009	5.04	65.4 ± 9.3	0.33 ± 0.04	0.45 ± 0.08
Hesperia comma	0.975 (0.206)	0.830 (0.400)	0.009	9.65	85.8 ± 11.9	0.19 ± 0.02	0.32 ± 0.06

ues for M. *cinxia* to predict the dynamics of M. *diamina* in the patch network surveyed in 1995 (*20*).

The model predicted very successfully the pattern of patch occupancy in M. *diamina* (Fig. 1, A and B). The observed fraction of occupied patches was 0.37, whereas the predicted value was 0.40 ± 0.04 (mean ± 2 SD). The successful prediction is essentially due to three clusters of patches, which had high incidences in the model prediction and a high rate of occupancy in reality. We ran the model with three other sets of parameter values estimated for three species of butterflies (*21*) (Table 1). Parameter values for *Scolitantides orion* slightly underestimated the distribution of M. *diamina* in its patch network (Fig. 1C), whereas parameter values estimated for *Hesperia comma* more clearly underestimated patch occupancy in M. *diamina* (Fig. 1D), possibly because these species appear to be poorer colonizers than the two *Melitaea* species (as suggested by the larger values of y in Table 1). Thus, although parameter values of a congeneric species correctly predicted habitat occupancy in M. *diamina*, parameters of unrelated species may not do so. Although many butterfly species have been studied intensively in recent years (*22*), these studies have not covered sufficiently large patch networks to allow us to estimate the parameters of the incidence function model for species other than those in Table 1.

These results have three important implications. First, the results support the notion that metapopulation dynamics in highly fragmented landscapes are dominated by the effects of patch area and isolation on local extinctions and colonizations (*7, 23*). Second, the successful application of the model implies, although it does not suffice to prove, that the metapopulation of the endangered butterfly M. *diamina* is close to a stochastic steady state, apparently because of fast population turnover rate in relation to the rate of environmental change (*24*). And third, the results demonstrate the potential value of using information for a more abundant and widespread congeneric species to estimate the

Fig. 1. Patterns of patch occupancy in the *M. diamina* metapopulation. (**A**) A map of the observed patch occupancy of *M. diamina* in the Tampere region of Finland. Filled and empty circles indicate occupied and empty patches, respectively. The size of the circle is proportional to the area of the patch. (**B**) The predicted incidences of patch occupancy for *M. diamina*, based on the incidence function model with parameter values estimated for *M. cinxia*. (**C**) Same as (B) but for *Scolitantides orion*. (**D**) Same as (B) but for *Hesperia comma*. The shading of the circles indicates the incidence (long-term probability of occupancy) of individual patches: shade gradient from white (incidence = 0.0) to black (incidence = 1.0).

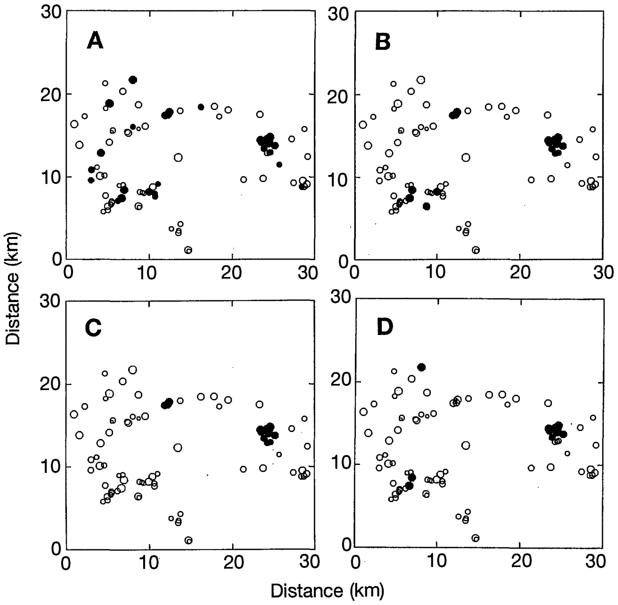
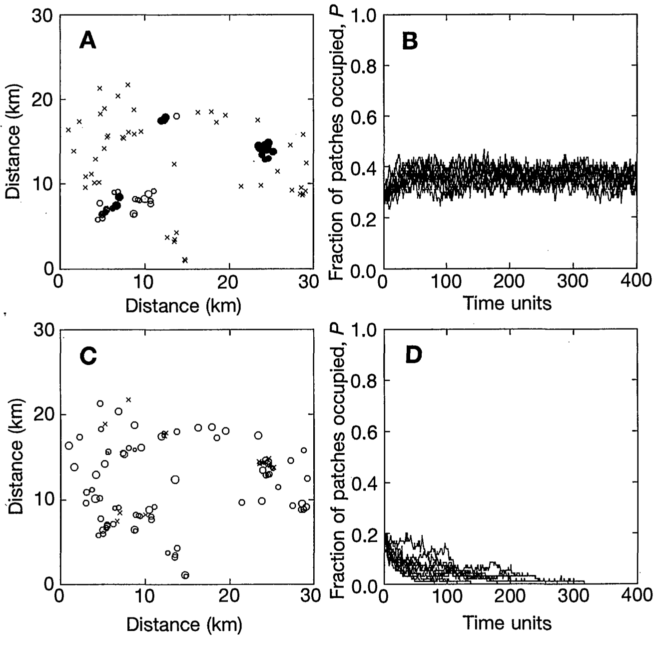


Fig. 2. Consequences of habitat destruction in the *M. diamina* metapopulation. (**A**) Consequence of the destruction of 47 patches around the edges of the network described in Fig. 1A (55% of the total area of 0.59 km^2 destroyed). Each destroyed patch is represented by an ×. The shading of the patches is as in Fig. 1B. (**B**) The results of 10 replicate simulations for the patch network in (A). In each simulation the incidence function model was iterated for 400 time units starting from the observed patch occupancy pattern shown in Fig. 1A. (**C**) Same as (A), except that 15 patches were destroyed in areas critical to the persistence of the *M. diamina* metapopulation (44% of the total area destroyed). (**D**) Same as (B), but for the network described in (C).



parameters of predictive models for endangered species, although clearly this approach must be used with great caution (*25*).

Because the incidence function model successfully predicted the occupancy pattern of *M. diamina* with surrogate parameters (Fig. 1, A and B), it would be justified to use the model as a practical management tool in this case. By changing the number, areas, and spatial locations of the habitat patches in the model, the likely consequences of habitat alteration to the long-term survival of the species may be explored. As an example, we simulated the destruction of patches in the *M. diamina* network either around the edges of the network (Fig. 2A) or in more central positions (Fig. 2C). Destroying patches around the edges had little effect on long-term occupancy in the remaining patches (Fig. 2B). In this instance, the destroyed patches were generally so isolated that they played only a small role in the dynamics of the metapopulation as a whole. In contrast, destroying patches in more central positions of the network caused the metapopulation to collapse (Fig. 2D).

With such numerical exercises, patches and regions that are particularly significant to the survival of the species may be identified, although the possible value of patches that are deemed less critical for metapopulation survival by this analysis must also be considered. We would stress that comparable results are not obtained with models that are spatially implicit or spatially explicit but unrealistic, such as the Levins model or stepping-stone models (*26*).

Our results demonstrate that the incidence function model is a practical tool that can be used to predict the occurrence of butterflies and similar taxa in fragmented landscapes (*7*). The model is sufficiently simple to make parameter estimation realistic for many species. Furthermore, as a first approximation, a single set of parameter values may be used for a group of related species, such as the butterflies in Table 1, with qualitatively although not necessarily quantitatively correct predictions about metapopulation responses in changing landscapes.

The successful application of the incidence function approach requires that the habitat of the focal species occurs in discrete and relatively small patches and that these patches have local breeding populations as stipulated by metapopulation models in general. The incidence function model cannot be applied to species with entirely different spatial structures, such as patchy populations but with panmictic reproduction. With these caveats, the incidence function approach may serve as the basis for a practical and predictive theory of the metapopulation dynamics of species living in networks of discrete and small habitat patches.

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8. The long-term probability of patch *i* being occupied, called the incidence J_i, is given by

$$J_i = \frac{C_i}{C_i + E_i - C_iE_i} \tag{1}$$

where E_i and C_i are the extinction and colonization probabilities, respectively, in unit time, and the term C_iE_i accounts for the rescue effect (*6*). Quantities E_i and C_i are expressed as functions of patch area (A_i; $E_i = e/A_i^x$) and isolation [S_i; $C_i = S_i^2/(S_i^2 + y^2)$], as further explained in (*6*), which leads to

$$J_i = \left[1 + \frac{ey^2}{S_i^2A_i^x}\right]^{-1} \tag{2}$$

where

$$S_i = \sum_{i \neq j} p_j e^{-\alpha d_{ij}} A_j^{\,b} \tag{3}$$

and $p_j = 1$ for occupied and 0 for empty patches, d_{ij} is the distance between patches *i* and *j*, α determines the effect of distance on colonization, and *b* transforms patch area to expected population size [values for α and *b* are typically estimated from mark-recapture studies and real population sizes, respectively (*6*)]. Paramater *x* determines how fast the risk of extinction increases with patch area. Thus, the basic data essential to the use of the model are the areas and spatial coordinates of patches (the latter are used to calculate the d_{ij} values). Equation 2 can be linearized with the logit-transformation and fitted to data on patch occupancy (the *p* values). Maximum likelihood parameter estimates for *x* and the product ey^2 are obtained by minimizing the function

$$ML = -\sum p_i \ln J_i + (1 - p_i) \ln(1 - J_i) \tag{4}$$

To tease apart the parameters of extinction and colonization rates from the product ey^2, it is possible to use information on the minimum patch area A_0, for which extinction occurs with probability 1 in unit time in the absence of immigration. The value of *e* is derived from $e/A_0{}^x = 1$, that is, $e = A_0{}^x$. The quantity A_0 may be estimated as the minimum occupied patch area, or an estimate of population turnover rate in unit time may be used. For details, see (*6, 7*).
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15. We surveyed an area 20 km by 30 km in the field in May 1995 with the help of 1:20,000 topographical maps. All suitable habitat patches were drawn onto the maps, and their spatial coordinates were determined. The areas of the patches were estimated either in the field or on the maps. The median area of the patches is 0.2 ha (range, 0.005 to 4.0 ha).
16. All suitable patches were resurveyed during the butterfly flight season in June through July 1995. A constant search time relative to patch area was used. In the case of empty patches, additional time was allocated to search for the species to ensure its absence. On the basis of our experience with the congeneric *M. cinxia* (*7*), we are confident that this survey yielded a reliable snapshot of the presence or absence of the species in the patches.
17. *Melitaea diamina* occurs in two areas other than our study area in the Tampere region of Finland. The other known metapopulations occur on the west coast (Kristiinankaupunki and Merikarvia), several hundred kilometers away from Tampere.
18. Before this study, nothing was known about the biology of *M. diamina*. As a part of this study, we investigated its larval biology and adult reproductive biology.
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20. We iterated the incidence function model using the reported parameter values, and the values of *ML* and the fractions of patches occupied (*P* and P_A) were calculated from these results. Each simulation run (600 time units) was started with the observed patch occupancy pattern for *M. diamina*. The results for the first 100 time units were omitted from the calculations to give the metapopulation time to reach stochastic equilibrium.
21. The following parameter values were used for all species as explained in (*7*): α = 1.0, *b* = 0.5, and A_0 = 79 m^2. The observed turnover rate between 2 years for *M. cinxia* (*6*) was used to estimate A_0.
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