

Are patch occupancy data sufficient for inferring metapopulation dynamics using spatially explicit patch occupancy models?*

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Abstract Spatial occupancy data have been widely used to draw inferences about metapopulation dynamics using patch-occupancy models. In the context of conservation biology, parameter estimation of patch-occupancy models is crucial for interpretation of metapopulation dynamics and prediction of a species' response to habitat destruction. In this paper, we explored the uncertainties associated with parameter estimation of a spatially explicit patch-occupancy model, the incidence function model (IFM). By constructing hypothetical networks of habitat patches and metapopulations with known parameters, we could estimate parameters based on maximum likelihood methods using different snapshots from the same metapopulation. Furthermore, we developed a variant IFM with a target-area effect, i. e., the probability of colonization was related to the size of a focal patch as well as spatial isolation. Our results show that estimated parameters based on different snapshots collected from the same metapopulation exhibit considerable variation. For example, estimates from one snapshot may indicate a species with good dispersal and poor local survival probabilities whereas estimates from another snapshot of the same metapopulation may suggest a poor disperser with good local survival probabilities. Failure to include a target-area effect in the model yielded a positive bias for the parameter that scaled extinction probability to patch size. We conclude that inference of metapopulation dynamics based on one snapshot of occupancy data is not reliable [*Acta Zoologica Sinica* 49 (6): 787 - 794, 2003].

Key words Parameter estimation, Uncertainty, Maximum likelihood estimation, Target-area effect

用空间直观模型是否足以从斑块占据性资料中推断集合种群的动态过程?*

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摘要 在集合种群的研究中,经常要根据空间占据性数据应用斑块模型来推断种群的动态过程,在保护生物学应用中,斑块占据性模型的参数估测对于阐释集合种群动态和预测种群对生境破坏的反应极为重要。我们探讨了一种广泛应用的空间直观模型——率函数模型(Incidence function model)中参数估测的不确定性问题,通过构建由50个斑块组成的网络和两个假想的已知参数的集合种群,应用模拟模型产生集合种群随时间变化的斑块占据性数据系列:即快照(snapshot)。然后,根据这些快照,应用率函数模型和最大似然法估测种群动态参数。此外,我们还给出了传统的率函数模型的一个变形,这个变形包含了目标区效应(Target area effect):即一个斑块的占据概率不但取决于空间隔离度,也取决于斑块本身面积的大小。结果表明:根据同一个集合种群不同的快照所估测的参数可以有很大差异,一个快照得出的参数提示的是占据性强但存活率低的集合种群,而另一个快照可能反映的是一个占据性弱但存活率高的集合种群。应用传统的率函数模型于一个包含了目标区效应的集合种群,导致斑块大小相关的灭绝率参数估测的正偏差。因此,仅根据一个快照的空间占据性数据来推测集合种群的过程有很大的不确定性[*动物学报* 49 (6): 787~794, 2003]。

关键词 参数估计 不确定性 最大似然法 目标区效应

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Predicting the probability of persistence for species of conservation concern in a fragmented landscape is a challenging task for wildlife managers. In a network of habitat patches, a spatially structured population, i. e. metapopulation, can persist in a balance of colonization and local extinction (Lande, 1987; Adler, 1994; Hanski, 1998a). Information about population processes such as dispersal is crucial to understanding metapopulation dynamics (Johnson *et al.*, 1990; Ferriere *et al.*, 2000; Nathan, 2001; King *et al.*, 2002). Unfortunately, conservation biologists and wildlife managers often are frustrated by a lack of information about demographic parameters of rare and endangered species. The use of presence/absence data is almost compulsory in many large-scale ecological surveys, as gathering longitudinal data on abundances of multiple species requires enormous resources (Steinberg *et al.*, 1997). Much effort has been made to obtain the information of metapopulation processes based on readily available data of species occupancy (Diamond, 1975; van Dorp *et al.*, 1987; Verboom *et al.*, 1991; Hanski, 1994; Sjogren-Gulve *et al.*, 1996). Patch occupancy models that only rely on distributional data of species in a network of habitat patches are appealing to conservation biologists because of their potential power to predict the fate of endangered species in fragmented landscapes (Wahlberg *et al.*, 1996). Among several commonly used patch occupancy models, the incidence function model (IFM) can be useful for estimating parameters of metapopulation processes based on patch-occupancy data collected at a single point in time (i. e. one snapshot of patch occupancy) and measurable habitat configurations (Hanski, 1994, 1998a). IFMs have been used widely for predicting persistence of metapopulations in fragmented landscapes (Quintana-Ascencio *et al.*, 1996; Wahlberg *et al.*, 1996; Moilanen *et al.*, 1998; Crone *et al.*, 2001).

As emphasized by Conroy *et al.* (1995), parameter estimation is a necessary and important step in the application of any type of spatially explicit population model. Because any type of patch-occupancy model relies on distributional data of species for parameter estimation, factors leading to variation in patch-occupancy data may introduce uncertainties associated with parameter estimation of IFM. The factors include sampling errors in patch-occupancy data and stochastic dynamics of colonization and extinction. In the field, non-detection of a species' occurrence when it is present at a site may occur due to low density and/or poor efficiency of the sampling method (Gu *et al.**). The sensitivity of parameter estima-

tion of IFMs to non-detection error has been dealt with elsewhere (Moilanen, 2002) and thus will not be considered in this paper. On the other hand, even for a metapopulation at equilibrium there can be considerable variation in spatial pattern of occupancy over time due to inherent stochasticity in colonization and extinction processes. ter Braak *et al.* (1998) has provided an insightful review about the issue. In many metapopulations studied, turnover (extinction of occupied patches and colonization of vacant patches) rates were considerable (Hanski, 1994; Crone *et al.*, 2001). This raises concern about the validity of parameter estimation of the IFM using one snapshot of occupancy data (Moilanen, 1999). For reliable estimation of metapopulation processes with patch occupancy data, multiple snapshots of occupancy are needed (O'Hara *et al.*, 2002; ter Braak *et al.*, 2003). In these studies, Bayesian statistical inference based on Markov chain Monte Carlo (MCMC) has been used to address the uncertainties associated with parameter estimation and missing observations.

In the traditional IFM, colonization and extinction are assumed to be determined by spatial isolation and habitat size, the so-called patch area-isolation paradigm (Hanski, 1998a). Several investigators have reported that processes other than spatial isolation and habitat size play an important role in metapopulation dynamics. For the colonization process, it is likely that a large unoccupied habitat patch has a greater chance of being occupied than a small one, all other things being equal. This is called the target-area effect, a phenomenon widely recognized in island biogeographic surveys (Pokki, 1981; Lomolino, 1990; Gotelli, 1995; Moilanen *et al.*, 2002).

To investigate further the extent of the uncertainty in parameter estimation based on a single snapshot of spatial occupancy data, in this paper, we conducted simulation studies by constructing hypothetical metapopulations with known parameters and processes. Additionally, we present a variant of IFM which incorporates the target-area effect and illustrate the impact of a target-area effect on parameter estimation.

1 Methods

1.1 Hypothetical patch networks

As suggested by Hanski (1994), a suitable situation for parameterization of the IFM is to have a habitat patch network with at least 30 patches, preferably more than 50. Two networks of 50 discrete habitat patches were constructed in a landscape of 100 units long \times 80 units wide. One patch network (Fig. 1a, hereafter referred to as H1) had larger

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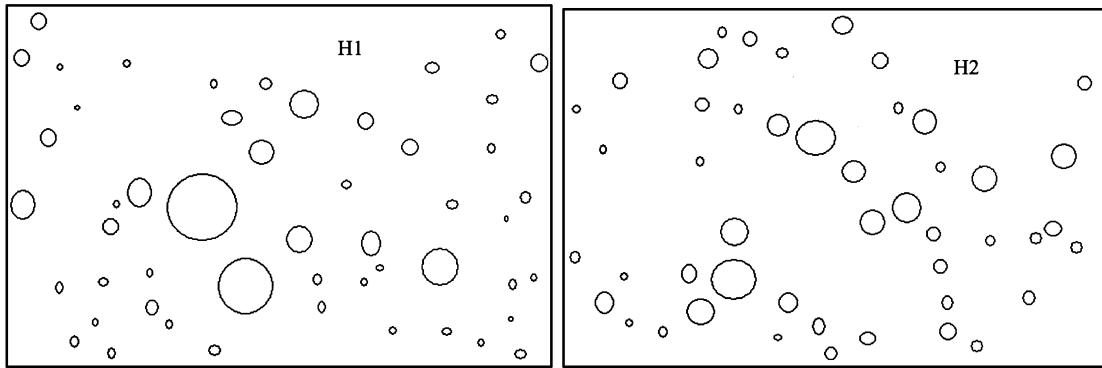


Fig. 1 Two hypothetical networks of habitat patches used for generating simulated data of metapopulation dynamics
Patch size in H1 has a larger variation than that in H2. Circle diameter is scaled by patch size

variation in patch size ($\mu = 11.39$, $\sigma = 38.71$) than the other network of habitat patches (Fig. 1b, referred to as H2) ($\mu = 11.84$, $\sigma = 12.43$). H1 and H2 were roughly the same in total habitat area. The two patch networks were used to compare the effect of a differing range of patch sizes on parameter estimation. To examine whether uncertainties in parameter estimation are affected by species with various life-history features, two hypothetical species were created. Species 1 was a good disperser but was prone to local extinction. Species 2 was a poor disperser but survived well in colonized patches. Dynamics of both species were simulated in H1 and H2, resulting in four combinations of species \times landscape.

1.2 The incidence function model

The IFM was used to simulate metapopulation dynamics. In IFM, the rate of colonization (C_i) of an unoccupied patch is a function of its isolation (S_i) from extant populations:

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

where y is a coefficient for colonization potential and S_i is a measure of spatial isolation of the focal patch i ,

$$S_i = \sum_j p_j \exp(-d_{ij}) A_j \quad (2)$$

where p_j is an indicator (1 = present, 0 = absent) of species occurrence in patch j with habitat area of A_j , d_{ij} is the Euclidean distance between patch i and j , and $1/\mu$ is the mean dispersal distance for members of the species. Extinction probability (E_i) of an occupied patch i is expressed as a function of patch area (A_i):

$$E_i = \frac{e}{A_i^x} \quad (3)$$

where e , the background extinction rate, and x , the strength of area-dependence in extinction rate, are constants to be estimated. For a metapopulation at equilibrium, the probability of occupancy (i. e., inci-

dence) of a patch while taking into account rescue effect (the reduced extinction by immigration) is according to Hanski (1994):

$$J_i = \frac{1}{1 + \frac{e}{S_i^2 A_i^x}} \quad (4)$$

where $e = ey^2$. For a typical IFM, there are four parameters (μ , e , x and y) to be estimated based on patch-occupancy data. Because e and y are combined in equation 4, additional data would be needed to separate the effect of these two parameters, such as the threshold patch size at which the probability of extinction is unity (Hanski, 1994).

Assuming that occurrence of a species among patches was binomially distributed with the probability of occupancy given by equation (4), the log-likelihood is defined as

$$\sum_i [p_i \log J_i + (1 - p_i) \log(1 - J_i)] \quad (5)$$

where $p_i = 1$ for occupied patches and 0 for vacant patches. J_i is the estimated incidence, given by equation 4. We developed a program that estimated parameters based on a Fisher information matrix. This involved calculating second partial derivatives of the log-likelihood of the observation (equation 5) with respect to parameters e and x . The inverse of the Fisher information matrix gives asymptotic estimation of precision of the parameters. Because μ enters in equation (4) through S_i , which in turn depends on concurrent occupancy, we estimated μ by determining the value that maximized equation (5). The precision of estimate μ was obtained by subtracting and adding a small amount, $\pm \delta$, to the maximum likelihood estimate of μ to recalculate the log-likelihood, $\log L_-$ and $\log L_+$. The standard error (std) of μ was estimated as (Bulmer 1979)

$$std = \frac{1}{\sqrt{2 \log L_- - 2 \log L_0 + \log L_+}} \quad (6)$$

where $\log L_0$ is the likelihood given the maximum likelihood estimate of μ . We set $\delta = 0.0001$.

Simulations of metapopulation dynamics were conducted for 200 time units with known parameters (for species 1 and 2, α , e and x were 0.18, 15, 0.7 and 0.28, 5, 1.5, respectively). Initially all patches were occupied. Patch occupancy for use in estimating parameters of the IFM was sampled from time units 100 to 200, after metapopulations had reached quasi-equilibrium states.

1.3 IFM with target-area effect

A simple way to incorporate target-area effects is to assume that colonization probability is not only dependent on spatial isolation but also is related to the focal patch size. Studies have shown that island geometry, for example, island width perpendicular to the line of immigration, could be important in affecting immigration rates (Lomolino, 1990). Therefore, equation 1 becomes:

$$C_i = \frac{1}{1 + \frac{y^2}{A_i^b S_i^2}} \tag{7}$$

where b is constant scaling colonization probability to the focal patch size. Note that the effect of spatial isolation and the focal patch size is multiplicative. Consequently, equation 4 was modified to account for the target-area effect as:

$$J_i = \frac{1}{1 + \frac{e}{S_i^2 A_i^{b+x}}} \tag{8}$$

Clearly, an estimate of x derived using the traditional IFM in truth is a combination of x and b in the presence of the target-area effect.

2 Results

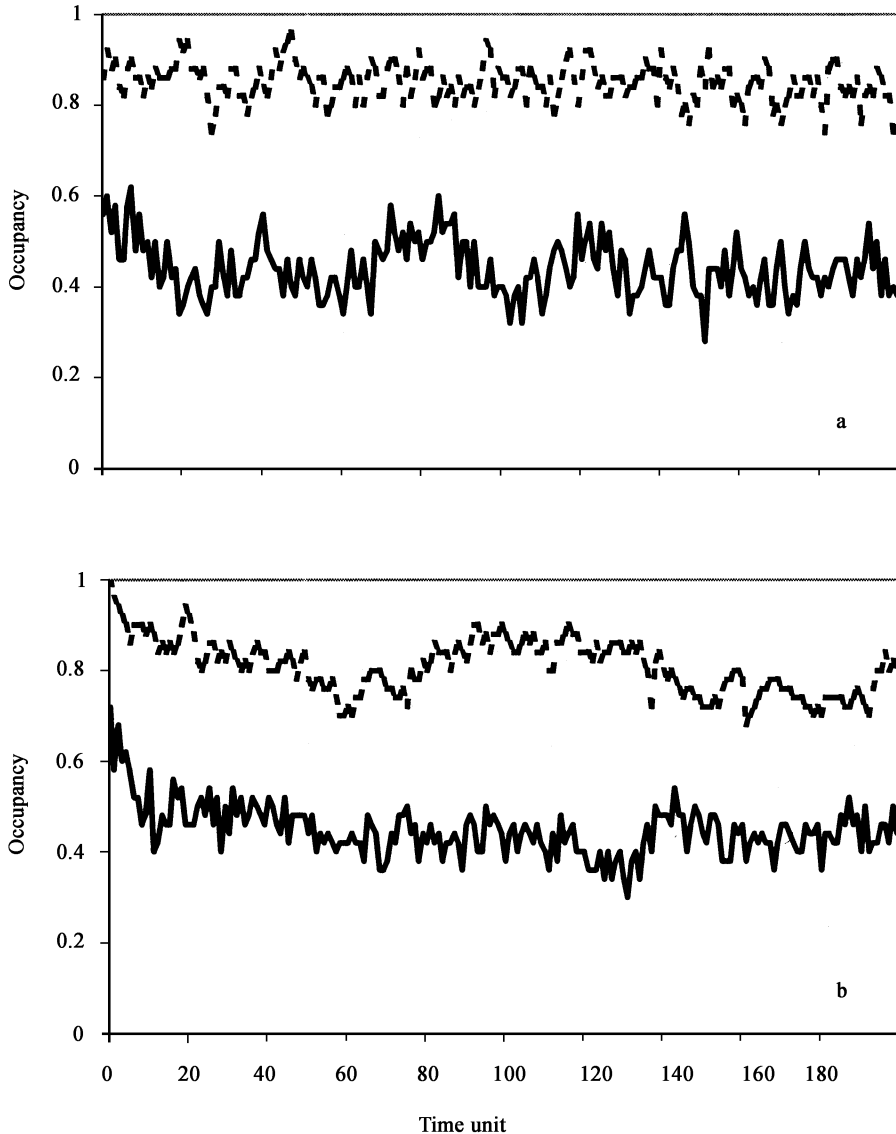


Fig. 2 Simulated patch occupancy of two hypothetical species (panel a, species 1 and panel b, species 2) in two patch networks
Solid lines and dotted lines for H1 and H2 respectively

2.1 Effect of stochasticity in metapopulation dynamics on parameter estimation

The predicted occupancy of metapopulations with various life-history features in the landscape was displayed in Fig. 2. Both species had a higher occupancy in H2, the network with more homogeneous patch sizes, than in H1, the network with greater variation in patch size. This was due to many small patches in H1 that had high extinction probabilities. Turnover rates were around 20% and 10% for Species 1 and 2, respectively. Occupancy by species 1, the good disperser prone to local extinctions, oscillated more than that of species 2 (Fig. 2).

There was considerable variation in individual parameters estimated from a sequence of occupancy data of the same metapopulation, despite relatively small variation in occupancy (Table 1). Interpretation of metapopulation dynamics based on these estimates could be inconsistent. For example, parameters in the second ($\alpha = 0.25$, $e = 1.532$, $x = 0.87$) and third row ($\alpha = 0.07$, $e = 1504.92$, $x =$

0.211) of Table 1 specified species with fundamentally different characters in term of dispersal ability and proneness to extinction. Significant correlations between α and e and between α and x were detected in 100 repeats of estimates for both species in the two habitat networks (Table 2).

Despite the large variation in individual parameter estimates from consecutive snapshots of occupancy, the averages of the estimates from 100 replicates of estimated parameters were seemingly unbiased for parameters α and x . However, there were substantial positive biases in estimates of e (Table 3). The bias of estimates of α was larger for the species in H1 than H2 (Table 3). Both species exhibited similar levels of uncertainties in term of parameter estimation. Because e is a combination of α and y that reflect extinction and colonization effect, respectively, it is impossible to ascertain the relative role of the two parameters in generating the huge bias in estimated e based on only occupancy data.

Table 1 Parameter estimation based on 10 consecutive snapshots time units of 120 - 129 of occupancy sampled from a simulated metapopulation of hypothetical species 1

Occupancy	Number of turnovers		Std	e	Std e	x	Std x
Patch network H1							
0.6	10	0.12	0.010	125.42	60.54	0.648	0.321
0.56	10	0.25	0.018	1.532	0.825	0.870	0.376
0.6	10	0.07	0.006	1504.92	618.94	0.211	0.228
0.62	9	0.12	0.010	102.27	51.30	0.669	0.346
0.54	6	0.09	0.008	779.22	333.47	0.300	0.238
0.52	9	0.08	0.007	1318.53	560.53	0.184	0.219
0.48	10	0.1	0.008	662.99	292.42	0.263	0.231
0.52	10	0.23	0.016	2.011	1.230	0.284	0.325
0.48	10	0.19	0.013	15.38	8.362	0.271	0.275
0.54	7	0.13	0.010	100.86	50.68	0.311	0.278
Patch network H2							
0.8	6	0.19	0.014	17.63	19.97	0.823	0.602
0.82	5	0.15	0.012	133.16	133.74	1.176	0.576
0.86	4	0.24	0.022	8.459	10.66	1.626	0.782
0.9	6	0.16	0.016	56.13	69.94	1.480	0.828
0.9	4	0.16	0.016	40.04	50.03	1.249	0.786
0.86	4	0.25	0.018	1.877	2.402	0.919	0.706
0.82	8	0.17	0.013	5.571	6.420	-0.190	0.542
0.84	9	0.19	0.014	9.054	10.226	0.499	0.599
0.84	6	0.32	0.021	1.123	1.428	1.778	0.752
0.76	8	0.24	0.015	4.059	5.000	0.640	0.628

$\alpha = 0.18$, $e = 15$, $x = 0.7$ in the two networks of habitat patches

Table 2 Correlations between parameters of incidence function models estimated from 100 repeats of parameter sets

	H1		H2	
	Species 1	Species 2	Species 1	Species 2
vs. e	- 0.64**	- 0.57**	- 0.35**	- 0.52**
vs. x	0.27**	0.52**	0.38**	0.62**
e vs. x	- 0.24*	- 0.17	- 0.44**	0.15

*: Significant at $P=0.05$ ** : Significant at $P=0.01$

2.2 Impact of target-area effect on parameter estimation

As expected, the presence of the target-area effect yielded positively biased estimates of x (Table 3). The degree of the bias was associated with the strength of the target-area effect, represented by the coefficient b .

3 Discussion

Our simulations demonstrate that estimated parameters varied from one snapshot to another even when sampled from the same metapopulation at quasi-equilibrium. Such inaccuracy in parameter estimation might be negligible if the IFM were used to predict the probability of long-term persistence in the same landscape without disturbance. However, it could produce erroneous predictions regarding the response of a metapopulation to landscape change, because parameters of the IFM characterize a species' ability to respond to habitat loss and fragmentation. Predictions regarding the species' response to habitat change could differ radically, depending on which snapshot (e.g., year of sampling) was used to derive parameter estimates. A snapshot yielding large estimated values of e and x would be interpreted as characterizing a species with poor dispersal and good survival ability. Such a species responds differently to habitat loss and fragmentation than a species with good dispersal and poor survival ability, characterized by small e and x . Although the estimated parameters of e and x averaged over 100 snapshots were unbiased (Table 3), estimates from one snapshot of patch occupancy data often were unreliable. Our results highlight the difficulty associated with utilization of the IFM without much empirical data to verify the predictions. We echo concerns raised by other investigators that data on patch occupancy are insufficient to unravel underlying population processes (ter Braak *et al.*, 1998; Tyre *et al.*, 2001; Clinchy *et al.*, 2002).

Based on the patch area-isolation paradigm, the traditional IFM makes simplifications to facilitate parameter estimation. In some situations, these approximations have been useful in predicting species occupancy (Hanski, 1992; Wahlberg *et al.*, 1996).

However, recent studies have underscored the need to expand the IFM paradigm to include other factors which are important for metapopulation dynamics (Fleishman *et al.*, 2002; Harding *et al.*, 2002). For example, using a decade of census data for stream fishes, Gotelli *et al.* (1999) showed that annual probabilities of colonization and extinction were related to position in the stream gradient. For most species, colonization was less likely and extinction more likely in upstream than downstream sites. Therefore, spatial variability in colonization and extinction should be incorporated for populations that are distributed across environmental gradients (Gotelli *et al.*, 1999). Habitat quality, rather than patch area and isolation, has been shown to be related to occupancy, colonization and extinction in a riparian-obligate butterfly metapopulation (Fleishman *et al.*, 2002).

A target-area effect on colonization has been widely recognized in island biogeography (Gotelli, 1995; Moilanen *et al.*, 2002). Increases in species richness with increasing area might result partly from a positive correlation between immigration rates and island size (Gilpin *et al.*, 1976; Simberloff, 1976). Larger islands may serve as more effective target areas for potential immigrants because they are more likely to be seen (by active dispersers) or intercepted (by passive dispersers) (Lomolino, 1990). Habitat features related to target-area effect are different for these two different types of dispersers. An island width perpendicular to the line of immigration is more important than patch area for active dispersers, whereas the latter plays a more important part in colonization by passive dispersers (Lomolino, 1990). Therefore, large patches have two advantages over small ones in colonization-extinction dynamics of a metapopulation, i.e. smaller extinction probability and larger colonization probability. If these two effects are both related to patch size, as assumed in our modified IFM, they cannot be distinguished without additional information. Empirical data documenting the correlation between numbers of immigrants and patch size could be used to estimate b independently. Ignoring a target-area effect when it was present yielded a positive bias in estimates of x (Table 3). The bias increased with increasing magnitude of the target-area effect (results not shown). The parameter x has been designated as an important indicator of environmental stochasticity (Hanski, 1998a) and has been linked to demographic parameters of local populations (Hanski, 1998b). Thus, overestimates of x induced by neglecting target-area effects would lead to misinterpretation of a species' response to habitat and environmental change.

Table 3 Parameter estimates of the incidence function models

	Given values of parameters	Mean	Standard deviation ?	min	max
Habitat 1					
Species 1					
	0.18	0.183	0.054	0.07	0.28
<i>e</i>	15	117.43	260.82	0.655	1 504.91
<i>x</i>	0.7	0.616	0.327	- 0.289	1.541
Species 2					
	0.26	0.250	0.054	0.14	0.37
<i>e</i>	5	32.23	79.91	0.502	547.93
<i>x</i>	1.3	1.263	0.382	0.535	2.793
Habitat 2					
Species 1					
	0.18	0.1828	0.042	0.13	0.32
<i>e</i>	15	43.09	76.28	0.332	424.02
<i>x</i>	0.7	0.783	0.738	- 0.764	2.959
Species 2					
	0.28	0.2834	0.045	0.16	0.43
<i>e</i>	5	6.779	11.91	0.833	72.35
<i>x</i>	1.3	1.279	0.579	- 0.041	2.618
Habitat 1 with target area effect					
	$b = 0.7$				
Species 1					
	0.2	0.193	0.063	0.08	0.33
<i>e</i>	15	284.91	962.37	0.485	7 911.12
<i>x</i>	0.5	1.130	0.382	0.412	2.325
Species 2					
	0.28	0.278	0.063	0.13	0.42
<i>e</i>	5	23.65	63.01	0.458	411.15
<i>x</i>	1.3	1.995	0.661	0.863	4.060

Statistics were obtained from 100 repeats of parameters estimated from sequences of occupancy sampled from time unit 100 to 200

Crone *et al.* (2001) estimated parameters based on the patch-occupancy data from a six-year survey of vole populations in Tvarminne archipelago, Finland. Likelihood ratio tests were used to choose between nested models that assumed various processes underlying metapopulation dynamics. We found that there were substantial variations in log-likelihoods calculated from various snapshots sampled from the same metapopulations. Given the substantial variation in log-likelihoods calculated from various snapshots of patch-occupancy data, caution is warranted in model selection solely based on log-likelihood ratio tests. Moreover, equifinality, a phenomenon recognized in mechanistic modeling of complex ecological systems, indicates that various models can fit to the same data

set with similar levels of goodness-of-fit but fundamentally different interpretations (Beven *et al.*, 2001). There are many different model structures and many different parameter sets within a chosen structure that may be acceptable in reproducing the behavior of the system. For example, incorporation of spatially correlated extinction could readily explain the pattern of patch occupancy typically cited as evidence of the preeminent importance of dispersal in metapopulation dynamics (Clinchy *et al.*, 2002).

The inherent stochasticity induced by colonization-extinction dynamics may prevent reliable estimation of metapopulation processes based solely on one snapshot of occupancy data and landscape configuration, especially for small patch networks. Presum-

ably, stochasticity will be less influential as the number of patches increases. Since a single snapshot of occupancy is insufficient to reliably specify IFMs, multiple surveys of species occupancy would be necessary to improve statistical inference about metapopulation dynamics (O'Hara *et al.*, 2002; ter Braak *et al.*, 2003). An advantage of multiple surveys is that turnovers of recolonization of vacant patches and extinction of occupied patches can be estimated. These allow one to separately estimate colonization and extinction parameters, thus increasing the resolution of statistical inference (Sjogren-Gulve *et al.*, 1996).

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