

# Detecting Environmental Impacts on Metapopulations of Mound Spring Invertebrates: Assessing the Incidence Function Model

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**Abstract** We use a stochastic patch occupancy model of invertebrates in the Mound Springs ecosystem of SA to assess the ability of incidence function models to detect environmental impacts on metapopulations. We assume that the probability of colonisation decreases with increasing isolation, and the probability of extinction is constant across spring vents. We run the models to quasi-equilibrium, and then impose an impact by increasing the local extinction probability. We sample the output at various times pre- and post-impact, and examine the probability of detecting a significant change in population parameters. The Incidence Function Model approach turns out to have little power to detect environmental impacts on metapopulations.

## 1. INTRODUCTION

Detecting impacts on populations is an important and well studied part of environmental impact assessment. However, many populations exist as networks of smaller populations, called metapopulations. Metapopulations arise either naturally or through habitat fragmentation. To our knowledge, there is little theory on how to detect environmental impacts on metapopulations. Usually metapopulation survey data is limited to the presence or absence of a species in a subpopulation. Moreover, resources are limited, and it is unlikely that extensive metapopulations can be completely surveyed every year indefinitely. When should a metapopulation be sampled to detect an impact that significantly increases the probability of global extinction?

In a metapopulation setting, detecting an impact requires measuring changes in the probabilities of extinction and recolonisation of subpopulations. Cooper and Mangel [1998] and Thrall et al. [1998] showed that detailed observations of single subpopulations can lead to misleading conclusions when metapopulation dynamics are ignored, because the local dynamics do not necessarily provide information about the dynamics of the system as a whole. Furthermore, once an impact has occurred, it may take some time before the occupancy pattern reaches a new quasi-stationary distribution [Pollett 1997]. As a result, presence/absence surveys of a metapopulation immediately after a putative impact may have very little power to detect changes in the parameters of the system. We explore some of these issues using

a particular metapopulation system, aquatic invertebrates in the Mound Springs of South Australia.

Mound springs arise around the margins of the Great Artesian Basin (GAB) in central Australia where underground aquifers are close to the surface, and pressurised water leaks through faults to emerge as spring vents. The wetlands associated with spring vents range in size from a few square metres to several hectares. Individual spring vents tend to occur in clusters, known as spring groups, varying in size from 1 to over 200 spring vents. The aquatic ecosystem associated with the springs is of national biodiversity significance because of the unique species of flora and fauna that occupy the springs. There are 38 endemic invertebrate species [Harris 1992, Ponder 1986, Ponder et al. 1989], and at least 3 plant species of conservation significance [Kinhill-Stearns 1984].

The main threats to individual spring vent populations are trampling by stock and water extraction. GAB water is extracted through bores for many uses, the biggest user being pastoralism [85%; Cox et al. 1998]. Water extraction causes a local drawdown in aquifer pressure leading to reduced spring flow. For the present, we assume that either impact leads to increased probabilities of local extinction for invertebrate populations.

We restrict ourselves here to using two surveys of patch occupancy, pre- and post-impact, to detect impacts. While obviously not optimal, this may well represent the only data available in many

realistic circumstances. Pre-impact data in particular are scarce.

## 2. PATCH OCCUPANCY MODEL

First, we need a model describing how the occupancy of patches by individual species changes with time. Hanski [1994] described a simple stochastic model for metapopulations, the Incidence Function Model (IFM), designed to be parameterised with single surveys of patch occupancy data. The primary advantage of the IFM is that it needs very little data, and is widely accepted in the conservation biology literature. Day and Possingham [1995] and ter Braak et al. [1998] showed that the IFM has some poor statistical properties, in addition to having five or more parameters. The large number of parameters make this model especially difficult to fit to limited data. Some of the spring groups we are interested in have as few as 9 patches. We developed a version of the IFM with only two parameters, one each for colonisation and extinction. We use this model to assess the ability of the IFM approach to produce useable parameter estimates for our system.

Colonisation probabilities depend on the state of the system, with the probability that an occupied patch  $i$  contributes successful colonists to an empty patch  $j$  given by

$$p_{i,j} = e^{-\alpha d} \quad (1)$$

where  $d$  is the euclidean distance in metres between the vents, and  $\alpha$  is the rate at which colonisation declines with distance. When  $d=0$  the probability of colonisation is 1. The probability that an empty patch  $i$  receives at least one colonist is:

$$\lambda_j = 1 - \prod_{i=1, i \neq j}^n (1 - p_{i,j}) o_i \quad (2)$$

where  $o_i$  is 0 if patch  $i$  is unoccupied and 1 if it is occupied. The probability of local extinction  $\mu$  is assumed to be the same for all patches. There can be more than one turnover per time step.

The key assumption that allows the incidence function model to be fit to a single patch occupancy survey is to assume that each patch is at the equilibrium of a two state markov chain (occupied/unoccupied) with the transition matrix:

present state	future state	
	unoccupied	occupied
unoccupied	$1 - \lambda_i$	$\lambda_i$
occupied	$\mu_i$	$1 - \mu_i$

The equilibrium probability that the patch is occupied, the incidence  $J_i$ , is

$$J_i = \frac{\lambda_i}{\lambda_i + \mu} \quad (3)$$

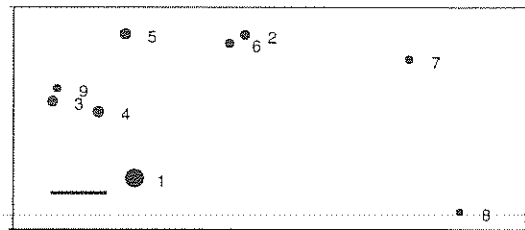
The parameters are fit by minimising the difference between the observed patch occupancy values  $o_i$  and the incidences  $J_i$ :

$$\min \sum_{all i} -o_i \log_e(J_i) - (1 - o_i) \log_e(1 - J_i) \quad (4)$$

This expression is technically a pseudo-likelihood, rather than a likelihood, because the IFM ignores spatial and temporal autocorrelation in patch occupancy.

## 3. RESULTS

We test our model on the patch occupancy data for the hydrobiid snail *Fonscochlea zeidleri* in the Bopeechee Springs group. There are 9 patches in Bopeechee springs (Figure 1), and *F. zeidleri* occurs in patches 2, 6, and 7. Fitting the IFM to these data gives estimates of  $\alpha = 0.015$  and  $\mu = 0.14$ . These parameters give colonists a 22% chance of reaching a patch 100 m away, and each patch has a 14% chance of going extinct each year.

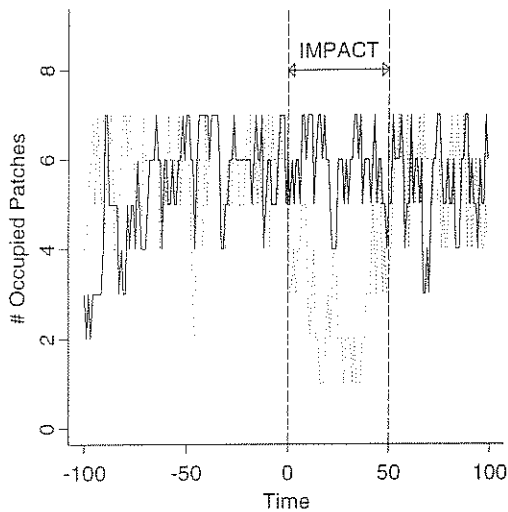


**Figure 1** Spring vent locations at Bopeechee springs. Coordinates in m. Size of symbol is proportional to area in  $m^2$ . Scale bar is 100 m.

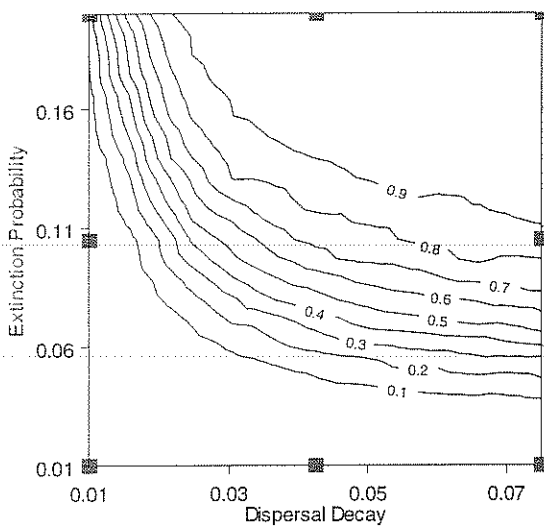
### 3.1 Basic Dynamics

Starting from the 3 patches occupied by *F. zeidleri*, and using the parameters estimated above the model fluctuates between 4 and 7 patches occupied over a 200 year time span (Figure 2). If an impact doubles the local extinction rate at year 0 for 50 years, the stationary distribution shifts downwards, and fluctuates between 1 and 4 patches occupied, occasionally going extinct.

Generally the higher the local extinction probability, or the quicker the colonisation probability decays, the greater the probability that the system goes extinct within 50 years (Figure 3). For *F. zeidleri*, increasing  $\mu$  from 0.14 to 0.28 increases the



**Figure 2** Time series of the number of occupied patches with (dotted line) and without (solid line) doubling the probability of local extinction for 50 years. Patches 7 and 8 are never occupied in these example trajectories.  $\alpha = 0.015$ ,  $\mu = 0.14$  (0.28)

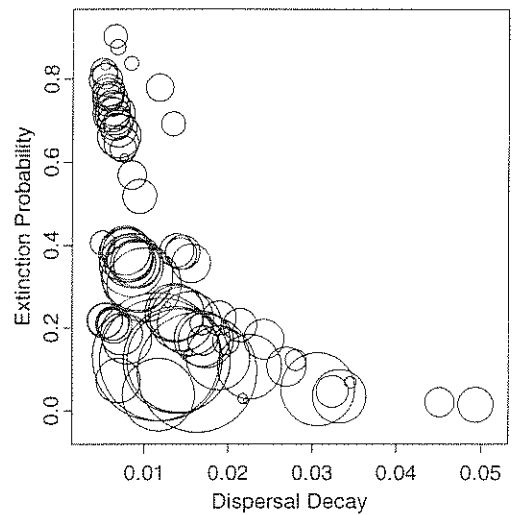


**Figure 3** Probability of extinction within 50 years for *F. zeidleri* in the Bopeechee spring group as a function of the dispersal and extinction parameters. The initial patch state is identical with that sampled in 1995.

probability of global extinction from 20% to greater than 60%.

### 3.3 Estimating Parameters Pre- and Post-Impact

We ran our model for 1000 years from randomly chosen starting states, and fit the IFM to the patch



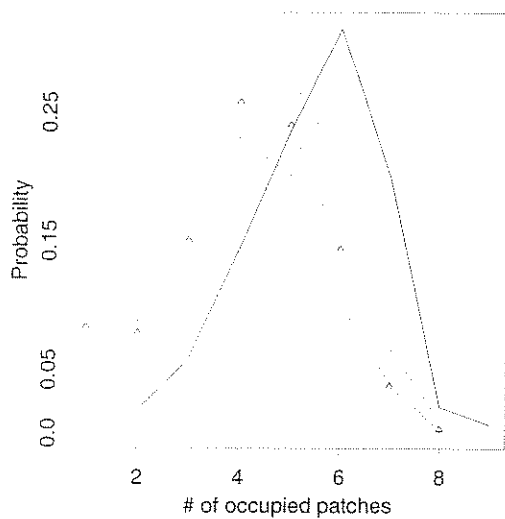
**Figure 4** Parameter estimates for 1000 replicate runs of the model. Each circle is proportional to the frequency of the state that generates that pair of estimates.

occupancy pattern present in the last time step. We discarded runs that went extinct before sampling.

Many common states generate reasonable parameter estimates. However, over 40% of the samples lead to obviously false estimates, including the most commonly observed state. Obviously false estimates include those with extinction probabilities  $\approx 1$  or 0, and extreme colonisation parameters leading to colonisation probabilities  $\approx 1$  or 0. States with only one patch occupied, or all patches occupied always generate bad estimates. Beyond that, there are no obvious characteristics distinguishing states that generate good results from those generating bad results. We exclude all obviously false estimates in what follows. The parameters in the model are inversely correlated (Figure 4). The estimated parameters lead to 50 year extinction probabilities across the full range from <10% to >90%.

Assuming that sensible estimates, good or bad, can be obtained from a pre-impact snapshot of patch occupancy, the next question is how well a change in those rates can be detected. We ran the model as before, taking a snapshot at year 1000. We then doubled the local extinction rate (to 0.28) and ran the model for another 1, 5 or 10 years before taking a second, post-impact snapshot. We discard any combinations where one or both states lead to non-sensical parameter estimates.

The distribution of system states shifts markedly post-impact, even after only one year (Figure 5). The mode of the distribution did not shift between



**Figure 5** Distribution of system states represented only by the number of occupied patches. Pre-impact = Solid Line. 1 Year post-impact = dotted line. 5 years post-impact = dotted line and triangles. 10 years post-impact = dotted line and pluses.

years 5 and 10, although the curve as a whole drops, and the probability mass in states with one patch occupied increases dramatically. This suggests that by 10 years post-impact the system has settled into a new quasi-stationary distribution.

We compared the estimated parameters of the system pre- and ten years post-impact for those combinations of parameters where both states yielded sensible estimates (Table 1). The results for one year and five years post-impact were similar. Most pairs of surveys indicated that one parameter had deteriorated while the other had improved. For comparison, we repeated the process for a ten year time span without an impact (Table 2). The same pattern is reflected in the results, suggesting that this method is not detecting an impact.

#### 4. CONCLUSIONS

The primary conclusion is that the IFM method is useless for detecting impacts on metapopulation parameters, at least in the mound springs system. There are at least two possible reasons.

First, the number of patches (9) in the system we are interested in is much smaller than patch systems to which the IFM model has been applied in the past. The primary assumption in the IFM model is that the colonisation rates do not change with time.

**Table 1** Changes in estimated parameters ten years post-impact. Three combinations did not change state.

Extinction ( $\mu$ )	Dispersal Decay ( $\alpha$ )	
	Improved	Worse
Improved	17%	46%
Worse	34%	3%

**Table 2** As for Table 1 but without an increased local extinction rate.

Extinction ( $\mu$ )	Dispersal Decay ( $\alpha$ )	
	Improved	Worse
Improved	10%	41%
Worse	42%	7%

In a system with many patches, this may be largely true on average, especially if there are patches present that are largely immune to extinction ('mainlands' in the island biogeography sense). With a small number of patches, the change in colonisation rate for an empty patch with 4 or 5 other patches colonised could be quite large.

Second, the IFM assumes that each patch is occupied with its 'equilibrium' frequency, presupposing that the parameters of the system are not changing. However, this is definitely not the case when an environmental impact has been imposed on the metapopulation in between two sample points.

Application of the IFM often detects a change in both parameters, in opposite directions. This disappointing and paradoxical result arises from the strong correlation between the parameters, and the fact that many states of the system generate non-sensical results. The different states of the system appear to fluctuate along the lines of equal extinction probability in Figure 3 — an increase in colonisation ability can be compensated for by a decrease in extinction probability.

Our future work will concentrate on two fronts. First, developing stochastic models incorporating the known biology into colonisation and extinction mechanisms in a simply way. Second, developing better methods of using survey data to fit parameters to the models. This will likely include making use of quasi-stationary distributions to calculate likelihoods for initial surveys, and Markov Chain Monte Carlo.

## 5. ACKNOWLEDGEMENTS

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