

# Detecting environmental impacts on metapopulations of mound spring invertebrates Assessing an incidence function model

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## Abstract

We use a stochastic patch occupancy model of invertebrates in the Mound Springs ecosystem of South Australia 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 postimpact, 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 with small numbers of patches. © 2001 Elsevier Science Ltd. All rights reserved.

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## 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 for survey work are limited, and it is unlikely that extensive metapopulations can be completely surveyed every year indefinitely.

In a metapopulation setting, detecting an impact requires detecting changes in the probabilities of local extinction and/or 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 international biodiversity significance because of the unique species of flora and fauna that occupy the springs. There are 38 endemic invertebrate species (Ponder, 1986; Ponder et al., 1989; Harris, 1992), and at least three plant species of conservation significance (Kinhill-Stearns, 1984).

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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 and Barron, 1998). Water extraction causes a local drawdown in aquifer pressure leading to reduced spring flow. For the present, we assume that either water extraction or trampling leads to increased probabilities of local extinction for invertebrate populations.

We restrict ourselves here to using two surveys of patch occupancy, pre- and postimpact, to detect impacts. While obviously not optimal, this may well represent the only data available in many realistic circumstances. Preimpact data are especially 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), that can 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 makes this model especially difficult to fit to limited data. Some of the spring groups we are interested in have as few as nine 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. An occupied patch *i* contributes successful colonists to an empty patch *j* with probability (Eq. (1)):

$$p_{i,j} = e^{-\alpha d} \tag{1}$$

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 *j* receives at least one colonist is (Eq. (2)):

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

where *o<sub>i</sub>* is 0 if patch *i* is unoccupied and 1 if it is occupied. We assume that the number of colonists arriving does not affect the probability of colonisation. 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<sub>i</sub>*, is (Eq. (3)):

$$J_i = \frac{\lambda_i}{\lambda_i + \mu} \tag{3}$$

Following Moilanen (1999), we fit the parameters by minimising the difference between the observed patch occupancy values *o<sub>i</sub>* and the incidences *J<sub>i</sub>*:

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

Expression (4) 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 nine patches in Bopeechee Springs (Fig. 1), and *F. zeidleri* occurs in patches 2, 6 and 7. Fitting the IFM to these data using expression (4) 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. In what follows, we first consider the basic dynamics of the model as a whole, particularly to get an idea of how the probability of extinction over a 50-year time period changes with changes in the parameters. Then, we examine the distribution of parameter estimates provided by the IFM from simulated data. Finally, we compare pre- and postimpact parameter estimates to determine whether or not the IFM can detect environmental impacts in metapopulations.

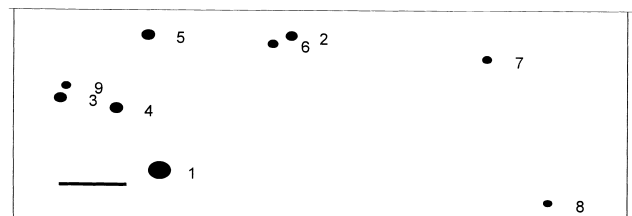


Fig. 1. Spring vent locations at Bopeechee Springs. Size of symbol is proportional to area in meter squared. Scale bar is 100 m.

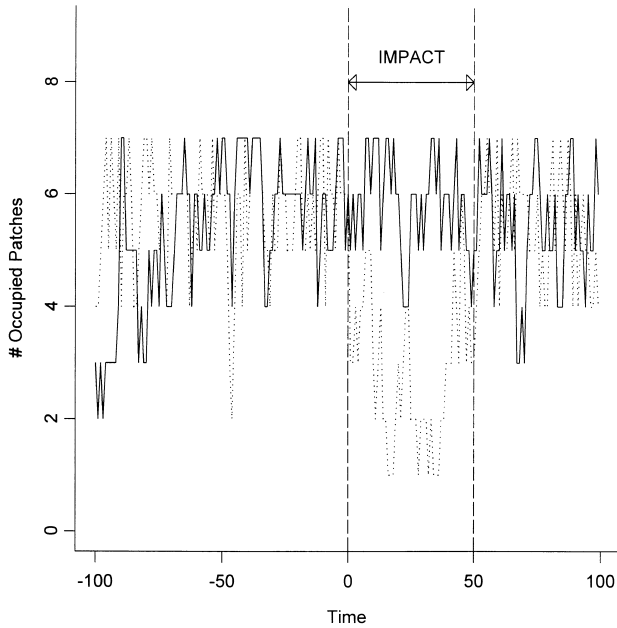


Fig. 2. Time series of the number of occupied patches with (dotted line) and without (solid line) doubling the probability of local extinction for 50 years. Patches 7 and 8 are never occupied in these example trajectories.  $\alpha = 0.015$ ,  $\mu = 0.14$  (0.28).

3.1. Basic dynamics

Starting from the three patches occupied by *F. zeidler* and using the parameters estimated above, the model fluctuates between four and seven patches occupied over a 200-year time span (Fig. 2). If an impact doubles the local

extinction rate at year 0 for 50 years, the stationary distribution shifts downwards, and fluctuates between one and four 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 (Fig. 3). For *F. zeidler*, increasing  $\mu$  from 0.14 to 0.28 increases the probability of global extinction from 20% to greater than 60%.

3.2. Estimating parameters pre- and postimpact

Assuming the parameter estimates obtained from the data are true, we simulated 1000 replicates of the metapopulation with those parameters for 1000 years from randomly chosen starting states. We restarted runs that went extinct before sampling and fit the IFM to the patch occupancy pattern present in the last time step. The distribution of states in the last time step is an estimate of the quasi-stationary distribution, or the distribution of states we expect to see, conditional on the system not having gone extinct.

Many states generate reasonable parameter estimates. However, over 40% of the samples lead to obviously false estimates, including the four most commonly observed states (14.7%). Obviously, false estimates include those with extinction probabilities close to 1 or 0, and extreme

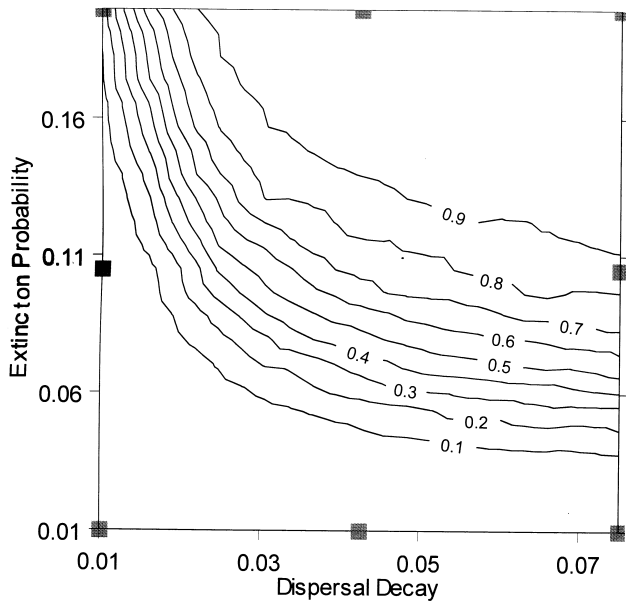


Fig. 3. Probability of extinction within 50 years for *F. zeidler* in the Bopeechee spring group as a function of the dispersal and extinction parameters. The initial patch state is identical with that sampled in 1995.

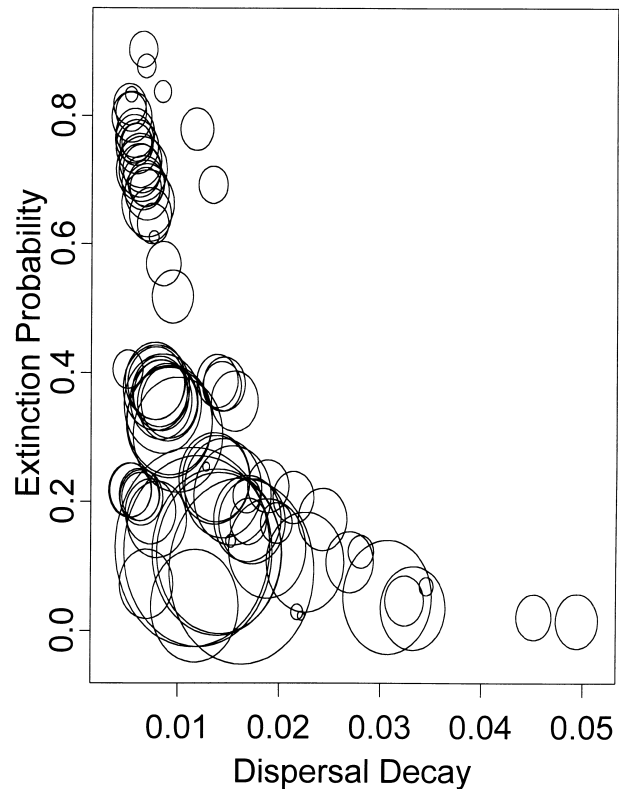


Fig. 4. Parameter estimates for 1000 replicate runs of the model. Each circle is proportional to the frequency of the state that generates that pair of estimates.

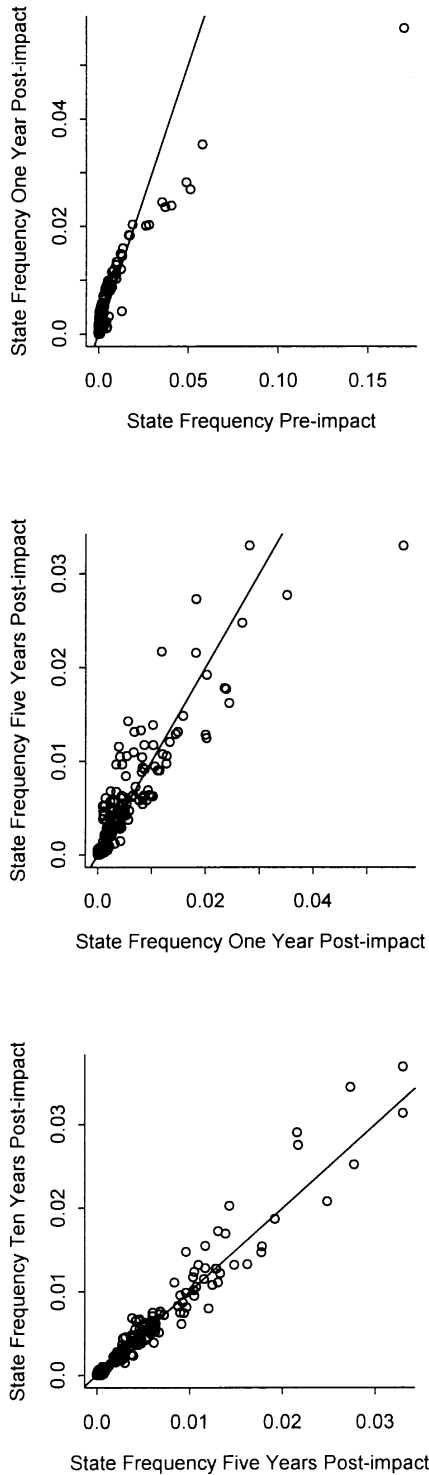


Fig. 5. Changes in the distribution of nonextinct system states 1, 5 and 10 years postimpact. Each point is the relative frequency of a single state of the system, measured at the impact (*x*-axis) and *t* years later (*y*-axis). When the system reaches a quasi-stationary distribution, the frequencies of each state should plot around the indicated one-to-one line, because by definition the relative frequency of extant (nonextinct) states is not changing if the system is exhibiting quasi-stationarity.

Table 1

Changes in estimated parameters 10 years postimpact. Three combinations did not change state

| Local extinction ( $\mu$ ) | Dispersal decay ( $\alpha$ ) |           |
|----------------------------|------------------------------|-----------|
|                            | Improved (%)                 | Worse (%) |
| Improved                   | 17                           | 46        |
| Worse                      | 34                           | 3         |

colonisation parameters leading to colonisation probabilities close to 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. The most common state has all patches occupied except the two most isolated. In this case, the estimation fails because the best way to fit this pattern is to set the extinction and colonisation probabilities to 0. We exclude all obviously false estimates in what follows. The parameters in the model are inversely correlated (Fig. 4). The estimated parameters lead to 50-year extinction probabilities ranging from <10% to >90% (see Fig. 3).

Assuming that sensible estimates, good or bad, can be obtained from a preimpact 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, postimpact snapshot. We discard any combinations where one or both states lead to nonsensical parameter estimates.

The distribution of system states shifts markedly after only 1-year postimpact, with low frequency states increasing in frequency and the most common states reducing in frequency (Fig. 5). From 1 to 5 years, the frequency of the most common state is still changing rapidly, although most other states have settled down. From 5 to 10 years post-impact, there is little systematic change in the frequencies of system states. This suggests that by 10 years postimpact the system is approaching a new quasi-stationary distribution.

We compared the estimated parameters of the system pre- and 10 years postimpact for those combinations of parameters where both states yielded sensible estimates (Table 1). The results for 1 and 5 years postimpact were similar. Most pairs of surveys indicated that one parameter had deteriorated, while the other had improved. A reduction in the extinction rate was slightly less likely to be detected than a reduction in the colonisation rate. Regardless of whether a change in one parameter is detected, it is usually at least partially compensated for by an improvement in the other parameter.

These results can at best be described as ambiguous. For comparison, we repeated the process for a 10-year time span without increasing the extinction rate between the two snapshots (Table 2). The same pattern is reflected in the results, suggesting that IFM estimates are not detecting an

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

| Local extinction ( $\mu$ ) | Dispersal decay ( $\alpha$ ) |           |
|----------------------------|------------------------------|-----------|
|                            | Improved (%)                 | Worse (%) |
| Improved                   | 10                           | 41        |
| Worse                      | 42                           | 7         |

impact, but that the changes reflect the variation inherent in the estimation procedure.

### 3.3. Patch suitability

An alternative explanation for the presence of *F. zeidleri* in only three out of the nine spring vents is that the other vents are not suitable habitat. We can only assess this alternative qualitatively at this stage by considering the distribution of other species in the vents of the Bopeechee group. *F. zeidleri* shares vents 2 and 6 with another hydrobiid, *F. accepta*, which is also found in all other patches except 7 and 9. In addition, the mound springs endemic ostracod *Ngarawa dirga* shares patches 2 and 7 with *F. zeidleri*, and is also found in all other patches except 6 and 9. It is possible that these two species have a broader physiological tolerance than *F. zeidleri*, but this overlap in occupancy extends throughout the springs in the Lake Eyre region. Patch 9 is not occupied by any of the mound springs invertebrates, and is the smallest, most isolated patch with the highest pH and conductivity in the Bopeechee group. However, *F. zeidleri* occurs in spring vents with higher conductivity and pH in other nearby groups, so these features should not exclude it from patch 9. We conclude tentatively that the vents in the Bopeechee group unoccupied by *F. zeidleri* are potential habitat patches for the species.

## 4. Conclusions

The primary conclusion is that the IFM method is inadequate 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. 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 four or five 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. This is likely to be a problem for other estimation procedures (Moilanen, 1999).

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 parameter estimates, and the fact that many states of the system generate nonsensical results. The different states of the system appear to fluctuate along the lines of equal extinction probability in Fig. 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 simple 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.

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