

# Using individual-based simulations to test the Levins metapopulation paradigm

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## Summary

1. Levins metapopulations have become a standard tool for modelling spatially heterogeneous populations. The acceptance of these models by ecologists may be attributed to their simple structure and their use of presence–absence data.
2. Using structured-metapopulations, which possess stochastic dynamics at the local subpopulation level, the extinction and subsequent recolonization rates can be calculated and compared to those of the classical Levins model.
3. Single-species metapopulations conform to the Levins ideal, validating the widespread use of this conceptual model. However, multispecies systems are shown to deviate in a consistent manner. This deviation, which is explained in terms of a correlation between patch occupancy and average population levels of the species, can be used to identify the signature of enemy–victim interactions.

*Key-words:* Levins metapopulations, local population dynamics, multi-trophic models, stochastic simulations.

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## Introduction

The classical theory of metapopulations (Levins 1969) has been readily accepted and utilized by ecologists (Gilpin & Hanski 1991; Hanski 1994; Hastings & Harrison 1994; Hanski & Gilpin 1997). Metapopulation models have been adapted for a variety of ecological applications and theoretical settings; explaining coexistence and biodiversity (Hanski 1983; Nee & May 1992; Tilman 1994), modelling increased persistence (Sabelis, Diekmann & Jansen 1991; Holyoak & Lawlet 1996; Janssen *et al.* 1997; Stelter *et al.* 1997), predicting the effects of movement and dispersal (Taylor 1990; Rohani & Miramontes 1995) and understanding spatial synchrony (Sutcliffe, Thomas & Moss 1996; Grenfell & Harwood 1997; Sutcliffe *et al.* 1997; Grenfell & Bolker 1998). Thus, determining the accuracy and robustness of these models has important implications across a wide spectrum of research.

The appeal of Levins metapopulations are their intuitive formulation and their use of readily attainable presence–absence data. For a species whose environment can be subdivided into isolated habitats (or patches) the Levins metapopulation model provides an idealized description of how habitat occupancy

changes over time. Levins metapopulation models are based on the assumption that localized extinction of a subpopulation, and then subsequent colonization of the habitat, are slow compared to demographic events. Thus, each patch can effectively be considered to be in one of two states, either empty, or occupied and close to the carrying capacity.

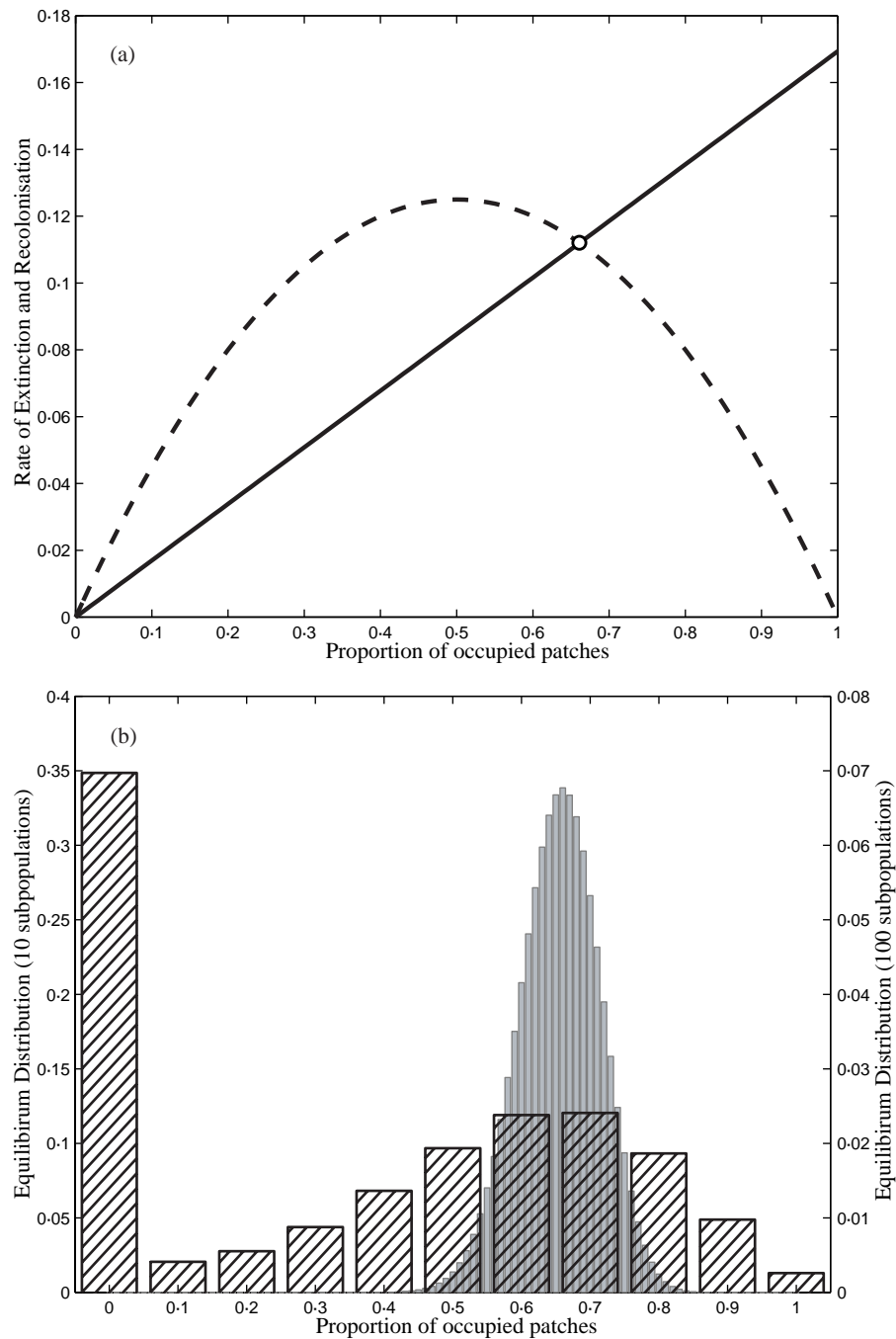
For a Levins metapopulation in which a proportion  $p$  of the patches are occupied, the dynamics are given by

$$\frac{dp}{dt} = cp(1-p) - ep \quad \text{eqn 1}$$

The rate of extinction is therefore  $ep$ , which assumes that occupied patches go extinct at a constant rate independent of the state of the other subpopulations. The rate of colonization is  $cp(1-p)$ ; this assumes that empty patches ( $1-p$ ) are colonized at a rate proportional to the number of occupied patches ( $p$ ). These two rates (shown in Fig. 1a) determine the entire dynamics. Because the deterministic form of the Levins model (eqn 1) is identical to equations for logistic growth, its dynamical behaviour is well understood. When  $e$  is less than  $c$  the dynamics converge to an equilibrium density of occupied sites  $p^* = 1 - e/c$ , otherwise the entire population rapidly goes extinct.

In any real ecological setting, there will only be a finite number ( $N$ ) of subpopulations, and so stochastic fluctuations in the number of occupied patches can be expected (Bartlett 1956; Bailey 1964; Nisbet & Gurney 1982; Mollison 1986; Renshaw 1991; Jetschke 1992;

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**Fig. 1.** Behaviour of the Levins metapopulation equation. (a) The colonization rate (dashed line) and extinction rate (solid line) from equation 1 ( $e = 0.17$ ,  $r = 0.5$ ). The circle denotes the deterministic fixed point. (b) The long-term distribution of occupied habitats predicted by the stochastic version of the Levins model. Two distributions are shown,  $N = 10$  (hashed bars) and  $N = 100$  (grey bars). ( $e = 0.17$ ,  $r = 0.5$ ,  $\epsilon = 10^{-3}$ ).

Mangel & Tier 1993). Using the deterministic Levins model (eqn 1) as a template, it is possible to formulate equations for the probability,  $P(n)$ , of having  $n$  habitats occupied.

$$\frac{dP(n)}{dt} = e(n+1)P(n+1) + c(n-1)\left(1 - \frac{n-1}{N}\right)P(n-1) - \left[en + cn\left(1 - \frac{n}{N}\right)\right]P(n) \quad \text{eqn 2}$$

As these equations model a stochastic process, we find that the eventual solution is for the entire metapopulation to become extinct. However, if we allow a very small amount of immigration ( $\epsilon$ ) from an external source, then a meaningful equilibrium distribution can be found. Examples of the equilibrium distribution are given in Fig. 1b. When there are few potential habitats ( $N$  is small) the equilibrium distribution is wide and there are many global extinctions (when all patches are unoccupied). In contrast, when there are many

available patches ( $N$  is large) the distribution is close to normal, global extinctions are extremely rare and the immigration rate ( $\epsilon$ ) has little effect. We note that the long-term distribution obtained when immigration is included may be different from the so-called quasi-equilibrium distribution (Vandoorn 1991) where the results are conditional on the population being extant. However, for large numbers of patches when the bulk of distribution is far from zero these differences are minor.

The aim of this paper is to compare the theoretical predictions from metapopulation models where habitats are considered to be either empty or occupied (such as eqns 1 and 2), with more complete simulations where the number of individuals within each local subpopulation is modelled stochastically (Lande, Engen & Saether 1998; Hastings & Wolin 1989; Levin, Powell & Steele 1993; Mangel & Tier 1993; Grenfell, Bolker & Kleczkowski 1995; Burkey 1997). Such models, with stochastic local dynamics, will be referred to as structured metapopulations to differentiate them from the standard Levins metapopulation. Throughout, it is informative to compare the observed rates of subpopulation extinction and colonization from the structured metapopulation simulations ( $R_e$  and  $R_c$ ) with the theoretical values from the Levins model. This ratio defines the rate modifiers  $\gamma_e$ ,

$$\gamma_e = \frac{R_e(p)}{p} \quad \gamma_c = \frac{R_c(p)}{p(1-p)} \quad \text{eqn 3}$$

#### SINGLE SPECIES MODELS

One of the simplest structured metapopulation models has its local dynamics generated by the stochastic logistic equation. If the local subpopulation consists of  $m$  individuals, then the birth and death rates per individual are,

$$\text{birth}(m) = B_0 \quad \text{death}(m) = D_0 + mD_1 \quad \text{eqn 4}$$

So births are assumed to be density-independent, whereas deaths have a density-dependent component. In a deterministic setting, such local dynamics lead the standard logistic model with convergence to a carrying capacity. When the dynamics are stochastic, such that each event occurs at random but with an underlying rate (Renshaw 1991), a distribution of population sizes arises – although without imports the local population is doomed to eventual extinction. (It is interesting to note the differences between the models for patch occupancy (eqn 1) and logistic dynamics (eqn 4). Although both models possess deterministic equations of the same form, density dependence enters in different ways and this can have striking effects on the stochastic dynamics.)

Interaction between the patches is assumed to be driven by global movement, such that individuals leave their home patch at a rate  $\sigma$  and disperse into any patch. In many real ecological systems we can expect

the movement rates between patches to have some local component such that dispersal is more likely between nearby patches (Adler & Nüernerger 1994; Hanski 1994; Kot, Lewis & van den Driessche 1996; Hanski & Ovaskainen 2000). However, the assumption of global movement still allows spatial heterogeneities to develop, provides a reasonable approximation to the dynamics of many species, and means that the same equations hold for all subpopulations – this vastly simplifies the modelling and the interpretation of results. The effects of local movement are considered briefly in the discussion.

As this is a stochastic system, permanent extinctions of the entire metapopulation are again a possibility, to prevent this a small amount of immigration at a rate  $\epsilon$  per patch is introduced. The underlying deterministic dynamics of this system are therefore given by,

$$\frac{dx_i}{dt} = B_0x_i - (D_0 + D_1x_i)x_i - \sigma x_i + \frac{\sigma}{N} \sum_{j=1}^N x_j + \epsilon \quad \text{eqn 5}$$

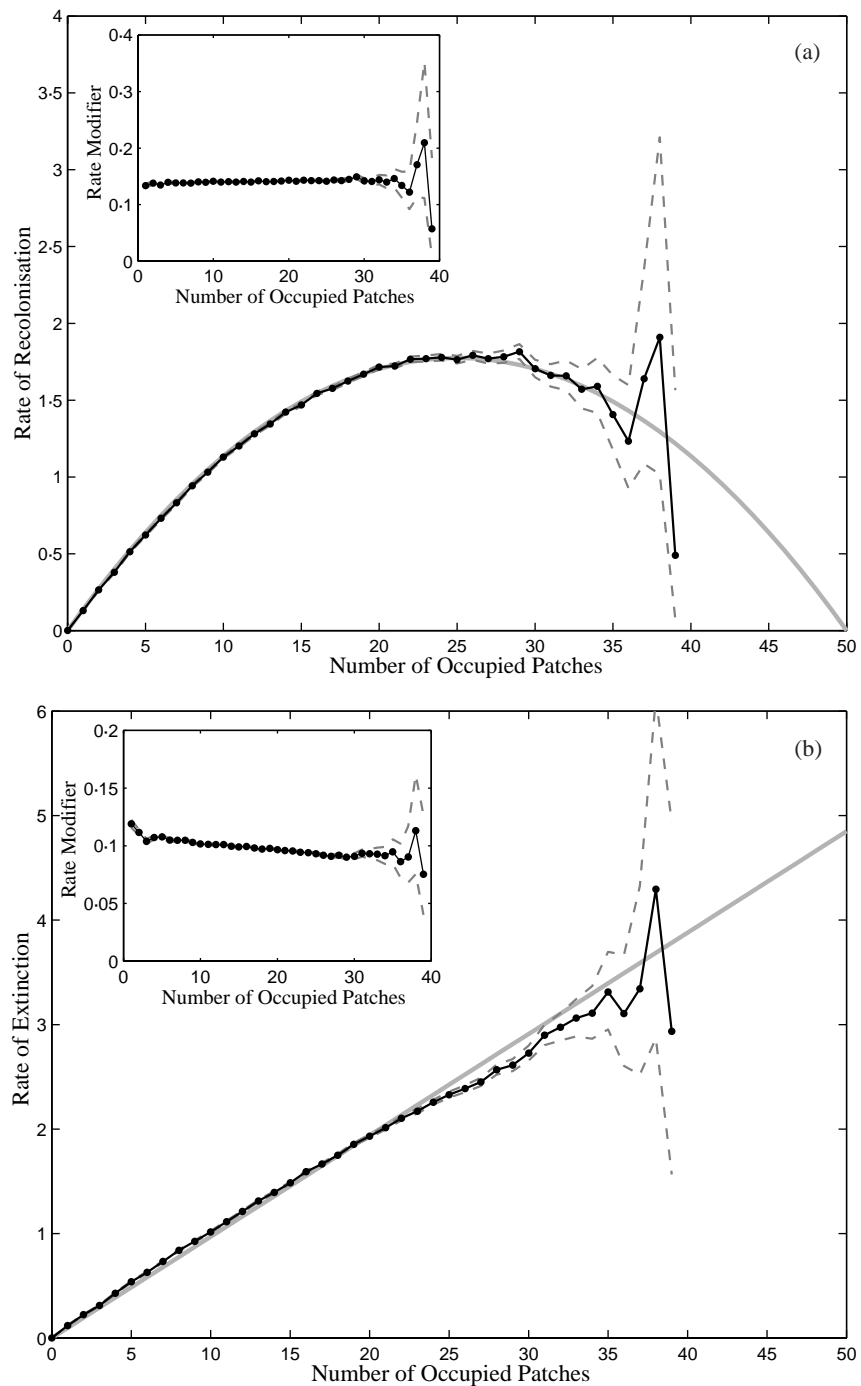
where  $x_i$  is the level of individuals in patch  $i$ . Simulation of this deterministic system, leads to convergence to the same equilibrium value in all patches  $\left(x_i \rightarrow x^* \approx \frac{D_1}{B_0 - D_0}\right)$ , so heterogeneities are soon lost. Thus, stochasticity is necessary to maintain spatial heterogeneity.

Simulating the structured metapopulation stochastically, we can record the average rates of extinction and colonization ( $R_e(p)$  and  $R_c(p)$ ) for every possible proportion of occupied patches ( $p$ ). For consistency with the Levins model, any colonizations due to the immigration rate,  $\epsilon$ , are not incorporated into the results. From Fig. 2 we can clearly see that the classical Levins metapopulation (eqn 1) is an extremely good description of the dynamics of patch occupancy as there is close agreement between the rates ( $R_e$  and  $R_c$ ) and the expected curves. This is confirmed by plotting the rate modifiers ( $\gamma_e$  and  $\gamma_c$ ) which show little variation across all levels of patch occupancy, although there is a small but significant decline in  $\gamma_e$  as the patch occupancy increases.

Figure 2 and the following figures all show the average rates of colonization or extinction; these are calculated as,

$$R_c(p) = \frac{\text{Number of extinctions at occupancy } p}{\text{Time spent at occupancy } p} \quad \text{eqn 6}$$

and similarly for  $R_e$ . The dotted lines show are the 95% confidence intervals for the average rate. We note that the distribution of times for an event to take place is exponentially distributed (as predicted by theory). However, we are not interested in the confidence intervals for a single event, but instead we consider what fixed rate could give rise to the observed dynamics. These results are from computer simulations where obtaining long time-series is trivial, obviously for real



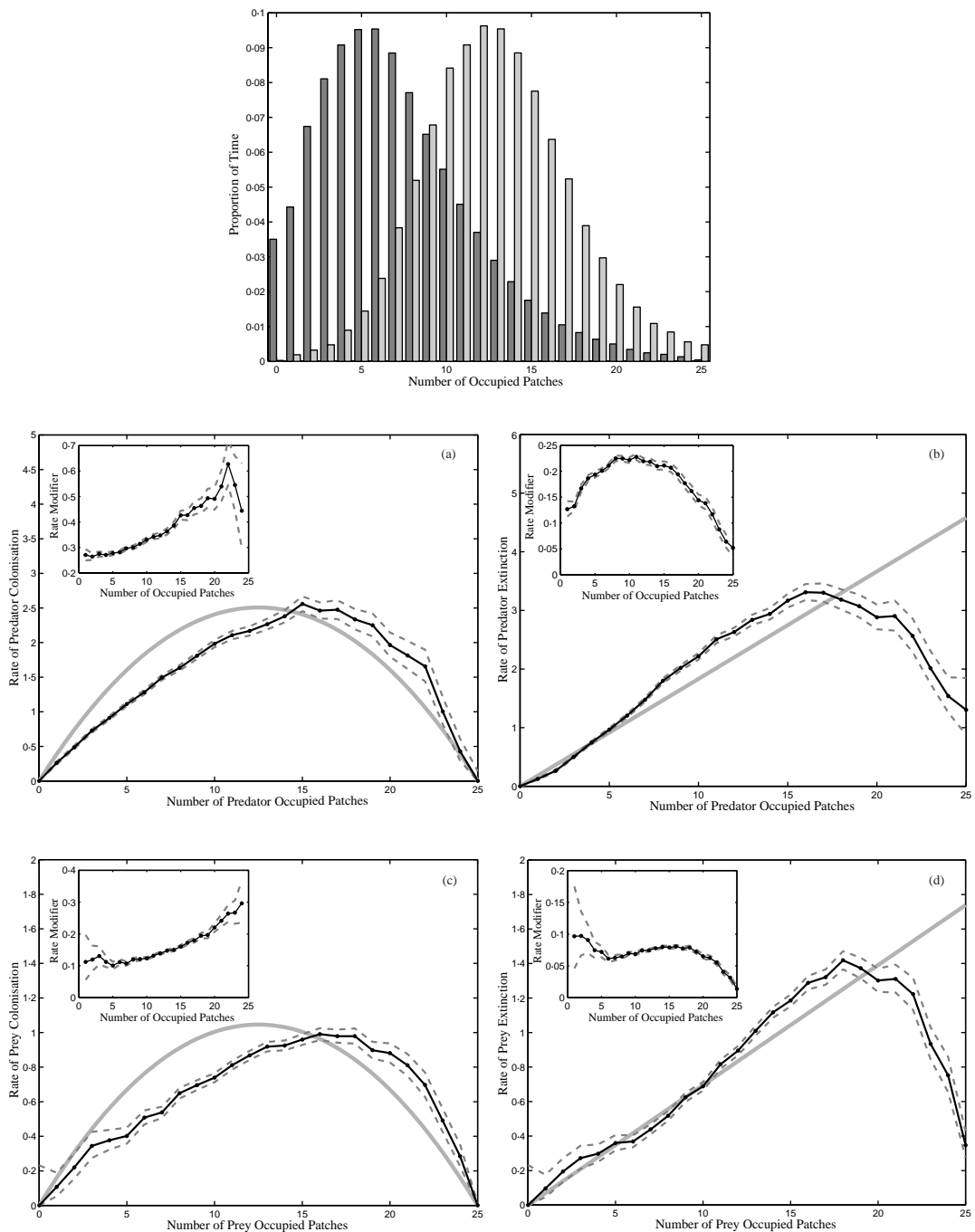
**Fig. 2.** The rates of (a) colonization and (b) extinction for the single-species model. The black dots give the average rate at which events occur, the dashed lines are the 95% confidence intervals and the grey lines are the best fit of the classic Levins equations. Colonizations due to external imports have been ignored. Finally, the inset graphs give the rate modifiers,  $\gamma_c$  and  $\gamma_e$ . (The results are the average of one million time steps,  $B = 2$ ,  $D_0 = 1.5$ ,  $D_1 = 0.025$ ,  $\sigma = 0.01$ ,  $\epsilon = 10^{-3}$ , number of subpopulations  $N = 50$ .)

ecological systems where less data is available the size of the confidence intervals will be larger.

Similar results to those of Fig. 2 are found for a wide range of parameters and various forms of density dependence, suggesting that for continuous-time one-species models the standard Levins metapopulation model provides a surprisingly good description of patch occupancy, even for structured metapopulations with the added complexity of local stochastic dynamics.

### Multi-species models

By far the most common two-species model is the Lotka–Volterra equation for the interaction of predators and prey (Lotka 1925; Volterra 1926), which has been applied to a wide variety of settings (Hastings 1978; DeRoos, McCauley & Wilson 1991; McLaughlin & Roughgarden 1991; Sabelis *et al.* 1991; Wilson, DeRoos & McCauley 1993). This simple model will be used as the basis for the



**Fig. 3.** Results from the two-species stochastic predator–prey model. (a) The number of patches occupied by predators (dark bars) and prey (light bars). The remaining graphs show the rates of colonization by predators (b) or prey (d), and extinction of predators (c) or prey (e). Again, the inset graphs show the rate modifiers. (The results are the average of 50 thousand time steps,  $B = 2$ ,  $D_V = 5 \times 10^{-4}$ ,  $C_V = 0.05$ ,  $C_P = 0.01$ ,  $D_P = 2$ ,  $\sigma_V = 10^{-4}$ ,  $\sigma_P = 0.01$ ,  $\epsilon_V = \epsilon_P = 0.01$ ,  $N = 25$ .)

local stochastic dynamics of a structured metapopulation to investigate the behaviour of such multi-trophic systems. The underlying deterministic equations for the abundance of predators ( $P_i$ ) and prey ( $V_i$ ) in patch  $i$  are,

$$\begin{aligned} \frac{dV_i}{dt} &= BV_i - D_V V_i^2 - C_V V_i P_i - \sigma_V V_i + \frac{\sigma_V}{N} \sum_{j=1}^N V_j + \epsilon_V \\ \frac{dP_i}{dt} &= C_P V_i P_i - D_P P_i - \sigma_P P_i + \frac{\sigma_P}{N} \sum_{j=1}^N P_j + \epsilon_P \end{aligned} \quad \text{eqn 7}$$

This model differs from the standard Lotka–Volterra models in that the prey suffer a slight density-dependent death rate; this prevents unbounded exponential growth if the predators become locally extinct. The simulation results for the stochastic structured metapopulation model are shown in Fig. 3.

More careful consideration of the concepts underlying Levins metapopulations would lead us to develop an expanded form of the model for two-species systems. In a predator–prey metapopulation four types of

subpopulation can exist, those with prey only ( $v$ ), those with predators only ( $p$ ), those with both predators and prey ( $b$ ) and empty patches ( $1 - v - p - b$ ). Hence, the Levins metapopulation model for this system should be,

$$\begin{aligned}\frac{dv}{dt} &= (c_v v + C_v b)(1 - v - p - b) + E_p b - e_v v \\ \frac{dp}{dt} &= (c_p p + C_p b)(1 - v - p - b) + E_v b - e_p p \quad \text{eqn 8} \\ \frac{db}{dt} &= (c_v v + C_v b)v + (c_p p + C_p b)p - (E_p + E_v)b\end{aligned}$$

The eight parameters of these metapopulation equations can again be readily estimated from the structured metapopulation simulations by observing the rates at which events occur. However, even using this more complex set of equations we cannot achieve a good fit to the simulation results for the structured model. More detailed numerical studies reveal that the four parameters  $c_p$  (colonization by predators from predator only patches),  $C_p$  (colonization by predators from patches with both species),  $E_v$  (extinction of prey from patches with both species) and  $e_p$  (extinction of predators from predator only patches) all show significant variation with the proportion of patches in each state.

The results of the simulations could now be compared with the three-dimensional metapopulation model (eqn 8); however, it is simpler and more biologically appealing to retain the structure of the standard Levins model (eqn 1). We therefore treat the two populations, predators and prey, as independent and compare the average rates of colonization and extinction to the single-species Levins model. This approach has the added advantage that the analysis can be compared to field data where only a single species (out of an entire community) has been recorded.

The distribution of patch occupancy (Fig. 3a) shows that a wide range of states exist, although the prey clearly show higher occupancy rates than the predator. The predator is globally extinct for about 3.5% of the time and therefore relies on external rescue effects to persist over long time-scales. The four rates (Fig. 3b–e) all show significant departures from the Levins model behaviour. When more patches are occupied, the colonization rates for both predators and prey (Fig. 3b,d) are higher than expected; this is clear from the increasing trend in the rate modifier  $\gamma_c$ . For the extinction rate (Fig. 3c,e) the behaviour is less clear, but both rate modifiers  $\gamma_e$  show a significant drop for large numbers of occupied patches. In conclusion, we therefore see fewer colonizations than expected when there are fewer occupied patches, and more colonizations and less extinctions than expected when most patches are occupied. This leads to a wider distribution of patch occupancy than would be predicted by a stochastic version of the Levins metapopulation model (eqn 2).

We now consider the average population levels as a function of the number of occupied patches (Fig. 4) in order to explain the behaviour of the modifiers. The

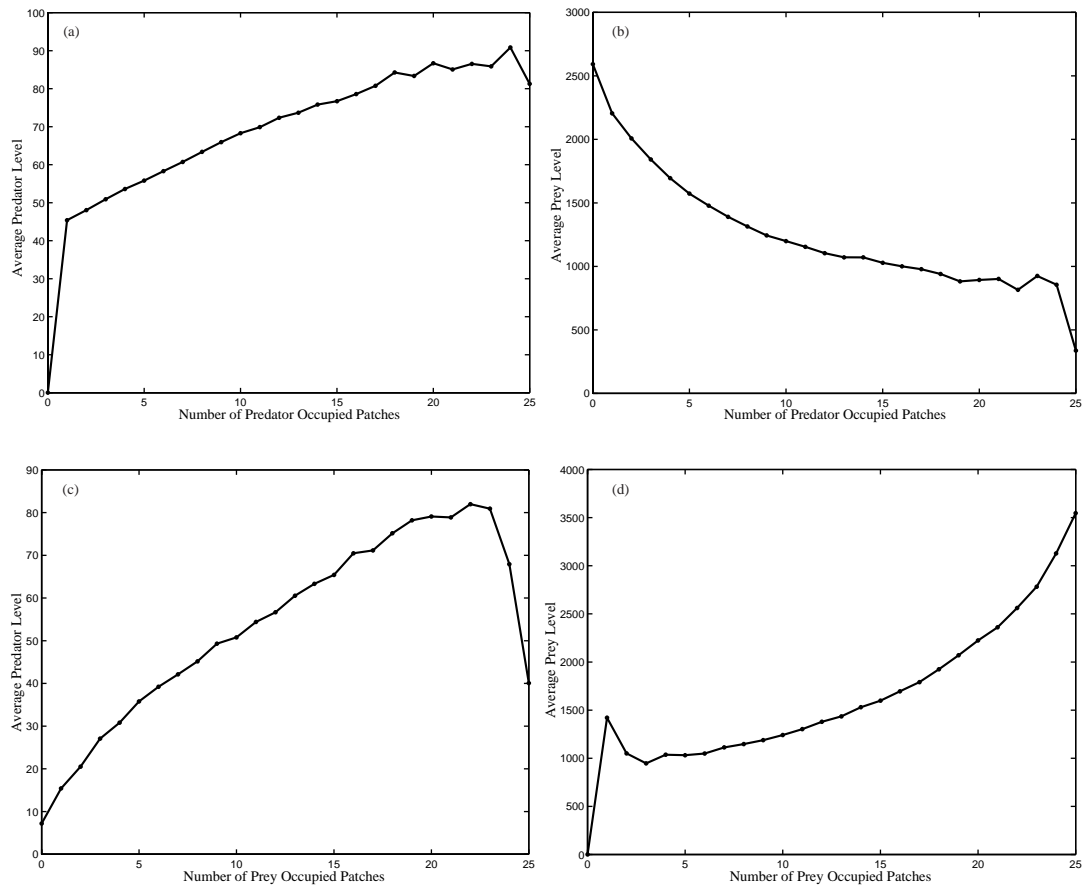
Levins model implicitly assumes that the population levels are invariant and close to the carrying capacity, which is clearly not true for the structured model due to the stochastic behaviour within the patches. Standard theory tells us that the extinction rate should decrease exponentially with the expected number of individuals in a local subpopulation (Bailey 1964; Shaffer & Samson 1985; Lande 1993; Caughley 1994; Foley 1994), and that colonizations should increase when there are more individuals dispersing into other patches. Hence, the increase in the number of organisms per occupied patch (Fig. 4a,d) explains much of the behaviour of the rate modifiers. However, the reduced value of the extinction rate modifier ( $\gamma_e$ ) for low patch occupancy can be explained by the abundance of the other species (Fig. 4b,c). We note that the opposite trends in Fig. 4b,c are due to the opposite effects of interspecies interaction that characterize natural enemy systems (more predators decrease the numbers of prey, whereas more prey increases the number of predators).

It is therefore the correlations between patch occupancy and average abundance that lead to the breakdown of the standard Levins metapopulation model. We stress that these correlations arise from the interaction between stochasticity and the boom–bust dynamics of natural enemy systems, which can be compared to the stochastic resonance effect (Bartlett 1956; Renshaw 1991). The introduction of a predator into a prey-only patch will produce a local boom in predator numbers that will spread to other patches and may drive the local prey population extinct. Such stochastically driven cycles can also be observed in the patch occupancy dynamics, although of much lower amplitude and far more irregular.

#### DISCRETE-TIME MODELS

So far, only continuous-time models have been considered. Although all ecological systems operate in continuous time, most ecological data are sampled at regular intervals. This, together with the seasonality often observed in population dynamics, means that discrete-time models have an important role in ecology. The discrete-time models used here to generate the stochastic local subpopulation dynamics consist of two phases: a demographic phase when birth, death and other within-patch events occur, and a movement phase when individuals disperse between patches (cf. Hassell, Comins & May 1991). Extinction and colonization events are determined by the state of the patches at the end of each time-step. Therefore, if a subpopulation is driven to extinction during the demographic phase but colonized during the movement phase, these events are ignored as they would not readily be detected by a periodic ecological survey.

Figure 5 shows the results from stochastic metapopulation simulations based on the discrete-time Ricker map and the Nicholson–Bailey model (Appendix 1 gives a detailed formulation). Although the local



**Fig. 4.** The average number of predators (a and c) and prey (b and d) in patches occupied by that species as functions of the number of occupied patches (parameters as in Fig. 3).

dynamics of these models are very different in character to the continuous-time logistic and Lotka–Volterra models, the rate modifiers show very similar behaviour. The single-species Ricker map (Fig. 5a,b) is again a remarkably good fit to the underlying form of the Levins metapopulation equations, and has rate modifiers  $\gamma_c$  and  $\gamma_e$  that remain constant across all levels of occupation. By contrast, the Nicholson–Bailey simulation shows significant deviation away from the Levins model, predicting many more colonizations and far fewer extinctions when most patches are occupied (Fig. 5c,d). This behaviour is very similar to the results for the Lotka–Volterra system, and comparable dynamics occur across the entire range of natural-enemy models and parameters that have been tested.

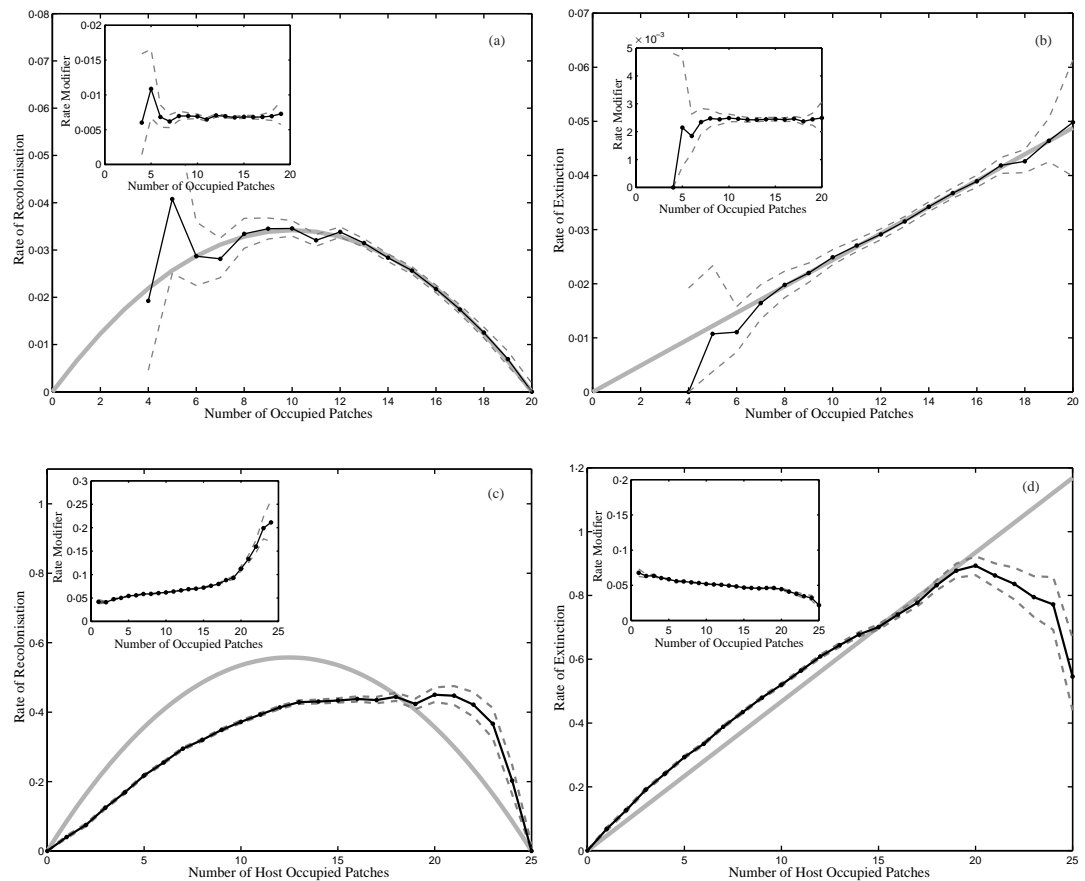
### Discussion

Levins metapopulation models have been used for a variety of organisms that can be considered as occupying discrete habitats (Schoener 1991; Ouborg 1993; Stelter *et al.* 1997; Nieminen & Hanski 1998; Esler 2000; Singer, Bleich & Gudof 2000; Swenor, Logan & Hornocker 2000). Such models are formulated under the assumption that extinctions and colonizations are very infrequent events compared to the organism’s demographic dynamics. Here, by using stochastic

simulations, the accuracy and robustness of the Levins model has been tested.

Stochasticity refers to elements of chance entering into our models. This paper has concentrated on demographic stochasticity, when each event (such as birth, death, movement or predation) occurs at random but with a given underlying rate. By including demographic stochasticity, the populations can be individual-based such that each subpopulation contains an integer number of creatures, and chance events can force the population level to zero causing an extinction. The inclusion of demographic stochasticity can have many other dynamical effects (Wilson 1998), but here we are solely interested in the extinction rate that emerges from the local dynamics.

A variety of single-species systems, in both continuous and discrete time, were simulated in a stochastic metapopulation framework with global coupling. From these simulations the rates of colonization and extinction were measured, and found to agree well with the Levins formulation. In particular, the rate modifiers (defined as actual rate divided by theoretical rate) show little variation with the number of occupied patches. This vindicates the use of Levins metapopulations in many applications, such that the population-level dynamics can be simulated while the individual-level dynamics are ignored.



**Fig. 5.** Results from the discrete-time Ricker map (a and b) and the Nicholson–Bailey model (c and d). The Ricker map fits the expected rates from the Levins metapopulation model, as seen by the constant rate modifiers. (The results are the average of one million time steps,  $r = 4$ ,  $K = 5.27$ ,  $\sigma = 10^{-3}$ ,  $\varepsilon = 10^{-3}$  and  $N = 20$ .) The rates from the Nicholson–Bailey model show similar deviations away from the Levins model, as were observed for the Lotka–Volterra simulation. (The results are the average of one million time steps,  $b_H = 1.01$ ,  $a = 0.01$ ,  $s_p = 0.99$ ,  $\sigma_p = 0.1$ ,  $\sigma_H = 10^{-3}$ ,  $\varepsilon_p = \varepsilon_H = 0.01$  and  $N = 25$ .)

For two-species natural-enemy systems, the rates shows consistent deviations from the Levins ideal across a wide variety of models and parameters. In general, the rate of colonization is skewed; the maximal rate occurs for higher levels of occupation than the Levins model predicts. Hence, we see more colonizations at high occupancy and fewer at low occupancy compared with the standard theory. The main feature of the extinction rates is their dramatic decline for high patch occupancy. The effect of these deviations is to produce distributions of patch occupancy with much higher variance than the stochastic Levins model (eqn 2) would predict; this is because situations where the vast majority of patches are either all occupied or all extinct persist far longer in the stochastic structured metapopulation.

The change in rate modifiers can be linked to the change in the average level of each species over all patches in which they occur. For natural-enemy systems there is a clear variation in species levels as the occupancy changes. This can be thought of as an interaction between the dynamics at global and local scales, which is equivalent to a positive correlation in the level of abundance between patches. These correlations

between local and global populations are only observed in the natural-enemy simulations, and may be attributable to their oscillatory ‘boom–bust’ nature, as the presence of many predators (parasitoids) can rapidly drive the prey (hosts) extinct. Similar qualitative differences have also been identified between the persistence behaviour of single-species and natural-enemy metapopulations (Keeling 2000), and again this is attributable to the build-up of strong correlations and interactions between subpopulation and metapopulation dynamics.

From these general results we find that comparing the actual rates of colonization and extinction with those assumed by the Levins model can also act as an informative tool. For field data this comparison allows us to assess whether a species exists in isolation or whether a specialist natural enemy plays an important role in its survival and dynamics. A good example of this might be the effects of a lethal disease, or a highly specialized predator. The interaction of prey with a generalist predator is unlikely to give rise to boom–bust cycles – as low numbers of the prey species is unlikely to cause a crash in predator numbers – and hence such a system will be much closer to the Levins model.

The basic Levins metapopulation model is obviously an idealized representation and many other complicating factors (in addition to stochastic local dynamics) may be included. Structured metapopulation models have been developed that consider the additional effects of populations of differing carrying capacities, localized movement of individuals, and global fluctuations in the parameters (mimicking the effects of weather). Preliminary analysis has shown that even with these profound modifications the basic form of the Levins model still holds for the vast majority single-species systems.

This research into the effects of local stochastic dynamics complements the recent work into the effects of spatial structure (Hanski & Ovaskainen 2000) showing that the basic structure of the Levins metapopulation model is valid across a wide range of applications and conditions.

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## Appendix

The stochastic Ricker map is defined by a phase of reproduction and death followed by random movement. Starting with a population of size  $x_i$  in patch  $i$ , the number of individuals after the reproduction and death phase is  $y_i$ .

$$y_i(t) = B\left(\exp\left[\frac{-x_i}{K}\right], P(rx_i)\right) + P(\epsilon)$$

where  $P(m)$  is drawn from a Poisson distribution with mean  $m$ , and  $B(p, n)$  is drawn from a binomial distribution. To calculate  $x_i(t + 1)$ , individuals are allowed to disperse with a probability  $\sigma$ ; the number of individuals

leaving a patch is therefore drawn from another binomial distribution  $B(\sigma, y_i(t))$ .

The stochastic Nicholson–Bailey model can be created in a similar manner. With  $H_i(t)$  and  $P_i(t)$  being the number of hosts and parasitoids in patch  $i$  at time  $t$ , the interaction phase is governed by,

$$\begin{aligned} h_i(t) &= B(\exp[-aP_i(t)], Q_i) \\ p_i(t) &= B(s_p, Q_i - h_i(t)) \end{aligned}$$

where  $Q_i = P(b_H H_i(t))$ .

So  $Q$  is the number of host eggs laid that year. Then  $H_i(t + 1)$  and  $P_i(t + 1)$  are derived from  $h_i(t)$  and  $p_i(t)$  by allowing hosts and parasitoids to disperse with probabilities  $\sigma_H$  and  $\sigma_P$ , respectively.