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## **A stochastic metapopulation model accounting for habitat dynamics**

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**Abstract.** A stochastic metapopulation model accounting for habitat dynamics is presented. This is the stochastic SIS logistic model with the novel aspect that it incorporates varying carrying capacity. We present results of Kurtz and Barbour, that provide deterministic and diffusion approximations for a wide class of stochastic models, in a form that most easily allows their direct application to population models. These results are used to show that a suitably scaled version of the metapopulation model converges, uniformly in probability over finite time intervals, to a deterministic model previously studied in the ecological literature. Additionally, they allow us to establish a bivariate normal approximation to the quasi-stationary distribution of the process. This allows us to consider the effects of habitat dynamics on metapopulation modelling through a comparison with the stochastic SIS logistic model and provides an effective means for modelling metapopulations inhabiting dynamic landscapes.

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### **1. Introduction**

Understanding the dynamics of populations that inhabit patchy environments is a pivotal problem in ecology. Mathematical modelling of populations has for many years focussed on single unstructured populations. Over the past 20 years there has been growing attention given to the dynamics of populations that occupy isolated patches of habitat. This area is known as metapopulation ecology (see Hanski and Gaggiotti [10]). Whilst many populations exist in patchy environments due to the natural dispersal of their required/preferred landscape, for example those inhabiting lakes, individual hosts or fallen logs, many species that existed as a single group must now exist in a patchy and changing environment due to the destruction of natural habitat. The alarming rate of destruction has resulted in a rapid increase in the number of metapopulations and, as a consequence, increased importance has been placed on understanding the dynamics of such populations.

Classical metapopulation ecology assumes a constant number of patches. However, in many cases the number of suitable patches changes as a result of patches being ephemeral or because they become temporarily unsuitable. A number of authors in the ecological literature have recognised a limitation of the aforementioned

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models: that all patches are assumed to be suitable for occupancy. These include Hess [12], Brachet *et al.* [6], Johnson [13], Keymer *et al.* [14], Amarasekare and Possingham [1], Ellner and Fussmann [9], and Hastings [11].

In addition to the assumption of a constant number of patches, a further simplification of existing models is the absence of stochasticity in the population and patch dynamics. While deterministic models of population dynamics provide much insight to population size (and the influence of model parameters on population size), the incorporation of stochasticity provides additional realism and consequently additional information of interest to modellers. Also, the study of the probability of extinction and expected time to extinction can only be undertaken in a stochastic framework. However, the analysis of stochastic models is more difficult than their deterministic analogues and precise, explicit expressions for quantities of interest are often unattainable. A common approach for obtaining explicit expressions for quantities of interest, while still incorporating stochasticity, is to approximate the original stochastic process with a diffusion process. However, the term “diffusion approximation” is used in some of the ecology literature without specifically identifying any approximation procedure. Practitioners should use such approximations with care, as the assumptions of the model might not always be satisfied in any given situation. We present results that identify diffusion approximations for a wide class of processes through an explicitly defined approximation procedure.

In this paper we consider a metapopulation model that incorporates habitat dynamics. This is the stochastic SIS logistic model with varying carrying capacity. As is common for stochastic population models, the derivation of precise, explicit expressions for quantities of interest is not possible. We obtain explicit expressions for quantities of interest through the use of a diffusion approximation. This is made possible by implementing results of Kurtz [15, 16] and Barbour [2–5]. We present their results in a form that most easily allows their direct application to population models. In particular, we examine diffusion models in the context in which they most naturally arise: as approximations to discrete-state Markovian models, which themselves are often more appropriate in describing the behaviour of the population in question, yet are difficult to analyse from both an analytical and a computational point of view. The results of Kurtz and Barbour allows us to immediately identify the most appropriate approximating diffusion, through an explicitly defined limiting procedure, and to decide whether a diffusion model is appropriate for describing the population in question.

A suitably scaled version of our metapopulation model is shown to converge uniformly in probability, over finite time intervals, to a deterministic model studied previously by Hess [12] and Johnson [13]. This result provides credence to the model studied by Hess and Johnson, since it identifies it as the appropriate approximating model and provides conditions under which the approximation is acceptable. Additionally, by drawing on the work of Kurtz and Barbour, we demonstrate that by removing the trend in the process given by the deterministic approximation just described, and with appropriate scaling, an Ornstein-Uhlenbeck (OU) approximation around a stable fixed point of the deterministic model may be established. The OU process is a stationary, Gaussian and Markovian diffusion process that

experiences drift towards the origin, or in our case towards the fixed point of the approximating deterministic model, proportional to its displacement. It provides explicit expressions for quantities of interest, such as the mean and variance of our metapopulation at any time in its evolution. Additionally, it establishes that the state-probabilities have an approximate normal distribution, that is, we establish a normal approximation to the quasi-stationary distribution. This allows one to assess variation about the deterministic equilibrium and provides a framework for statistical inference.

Our model is presented in Section 2. In Section 3 we recall the definition of density dependence (in the mathematical sense) and present functional limit laws of Kurtz and Barbour in a form appropriate for studying the metapopulation model, and population models in general. These are used in Section 4 to derive the deterministic approximation and our bivariate normal approximation. Finally, in Section 5, we present some numerical results and compare our model with the basic model that assumes no variation in habitat suitability.

## 2. The Model

Our model is a two-dimensional continuous-time Markov chain defined as follows. Denoting by  $m(t)$  and  $n(t)$ , respectively, the number of suitable patches and the number of occupied patches at time  $t$ ,  $\{p(t) = (m(t), n(t)), t \geq 0\}$  is assumed to be a Markov chain taking values in  $S = \{(m, n) : 0 \leq n \leq m \leq M\}$  with non-zero transition rates

$$q((m, n), (m + 1, n)) = r(M - m), \quad (1)$$

$$q((m, n), (m - 1, n)) = s(m - n), \quad (2)$$

$$q((m, n), (m - 1, n - 1)) = sn, \quad (3)$$

$$q((m, n), (m, n + 1)) = c \frac{n}{M} (m - n), \quad (4)$$

$$q((m, n), (m, n - 1)) = en. \quad (5)$$

The total number of patches in the metapopulation network (or the maximum carrying capacity) is denoted by  $M$ . These rates correspond to: an increase by one in the number of suitable patches due to patch recovery (1), a decrease by one in the number of suitable patches due to landscape dynamics, such as succession, that affects the population inhabiting the patch if occupied ((2) and (3)), an increase by one in the number of occupied patches due to colonisation (4), and, a decrease by one in the number of occupied patches due to local population extinction (5). The parameters  $r$ ,  $s$ ,  $c$  and  $e$  are, respectively, the per patch rate of recovery, the per patch rate of disturbance, the colonisation rate, and, the local population extinction rate.

We are modelling a metapopulation inhabiting a dynamic landscape in which each patch is disturbed independently at rate  $s$ . As habitat is naturally dynamic, this model could be applied to all metapopulations. The model would also be appropriate for metapopulations in successional landscapes where succession is not related to the age of the patch. Thomas and Hanski (Chapter 20 of [10]) provide examples of many species of butterfly that exhibit the kind of behaviour we seek to describe using this model. The model does not account for refuge patches, that is, patches immune to disturbances. Nor does it account for explicit spatial structure or differing patch sizes. Consequently, it does allow us to model a single group of individuals, analogous to the way in which the logistic model is used both for metapopulation and single population modelling. Indeed, the model presented may be used in place of the stochastic SIS logistic model whenever greater flexibility is needed for studying populations that occupy dynamic landscapes.

### 3. Mathematical Framework

This section contains the mathematical framework of the paper. I encourage all mathematically literate modellers to read this section. The results provided may be applied to a wide class of models, in particular those appropriate for modelling an array of population processes involving interactions between population or species types, along with other nonlinearities, and are presented in a form that most easily allows their direct application to such models.

As required for our metapopulation model we restrict our attention to Markov chains with a finite state space. Further technical conditions are required when working with infinite-state processes (see Pollett [19]).

Let  $\{P_\nu, \nu > 0\}$  be a family of continuous-time Markov chains and suppose that  $P_\nu(\cdot)$  takes values in  $S_\nu$ , a finite subset of  $\mathbb{Z}^D$ , and has transition rates  $Q_\nu = (q_\nu(j, k), j, k \in S_\nu)$ . The index parameter  $\nu$  is selected for a particular process by recognising that the approximation is achieved by letting  $\nu$  become large. For our model we use the maximum carrying capacity of the habitat  $M$  as the index parameter.

Kurtz [15] provides us with the following definition of density dependence.

**Definition 3.1.** *A one-parameter family of Markov chains  $\{P_\nu, \nu > 0\}$  with state space  $S_\nu \subset \mathbb{Z}^D$  is called density dependent if there exists a set  $E \subseteq \mathbb{R}^D$  and a continuous function  $f : E \times \mathbb{Z}^D \rightarrow \mathbb{R}$ , such that*

$$q_\nu(k, k+l) = \nu f\left(\frac{k}{\nu}, l\right), \quad l \neq 0.$$

*Remark.* Thus, the family of Markov chains is density dependent if the transition rates of the corresponding “density process”  $X_\nu(\cdot)$ , defined by

$$X_\nu(t) := \frac{P_\nu(t)}{\nu}, \quad t \geq 0,$$

depend on the present state  $k$  only through the density  $k/\nu$ .

The above definition provides an obvious way to associate with the process a density dependent deterministic analogue, namely

$$\frac{d}{dt}X(t) = F(X(t)),$$

where

$$F(x) = \sum_l lf(x, l), \quad x \in E.$$

Its trajectory is “tracked” by the process when  $\nu$  is large. Note that the transitions ( $l$ ) and parameters are not rescaled. The former is due to a notational construct (see Definition 3.1) while the latter is due to a rescaling in the size of the population, not in the rate at which transitions occur. More precisely, we have the following (functional) law of large numbers (Theorem 3.1 of Kurtz [15]) that establishes a deterministic approximation under the conditions stated.

**Theorem 3.2.** *Suppose that  $f(x, l)$  is bounded for each  $l$  and that  $F$  is Lipschitz continuous on  $E$ . Then, if*

$$\lim_{\nu \rightarrow \infty} X_\nu(0) = x_0,$$

we have, for fixed  $\tau > 0$  and for all  $\epsilon > 0$ , that

$$\lim_{\nu \rightarrow \infty} \Pr \left( \sup_{t \leq \tau} |X_\nu(t) - X(t, x_0)| > \epsilon \right) = 0,$$

where  $X(\cdot, x)$  is the unique trajectory satisfying

$$X(0, x) = x,$$

$$X(t, x) \in E, \quad 0 \leq t \leq \tau,$$

$$\frac{\partial}{\partial t}X(t, x) = F(X(t, x)). \tag{6}$$

*Remark.* This law of large numbers tells us that the density process converges (uniformly in probability) over any finite time interval to the deterministic trajectory  $X(t, x)$ , provided that the density process begins close to the initial value  $x_0$  of that trajectory. It will be used in the next section to demonstrate the convergence of a suitably scaled version of our model to the deterministic model studied by Hess [12] and Johnson [13].

Our next result, a functional central limit law, provides a diffusion approximation for the fluctuations of the density process about the deterministic trajectory. It may be deduced from Theorem 3.2 of Pollett [19], which in turn follows from Theorems 3.1 and 3.5 of Kurtz [16].

**Theorem 3.3.** *Suppose that  $f(x, l)$  is bounded for each  $l$ , that  $F$  is Lipschitz continuous on  $E$  and has uniformly continuous first partial derivatives. Suppose also that  $G(x)$ , a  $D \times D$  matrix with elements*

$$g_{ij}(x) = \sum_l l_i l_j f(x, l), \quad x \in E,$$

*is bounded and uniformly continuous on  $E$ . Then, provided*

$$\lim_{\nu \rightarrow \infty} \sqrt{\nu} (X_\nu(0) - x_0) = z, \tag{7}$$

*the family of processes  $\{Z_\nu(\cdot)\}$ , defined by*

$$Z_\nu(t) = \sqrt{\nu} (X_\nu(t) - X(t, x_0)), \quad 0 \leq t \leq \tau,$$

*converges weakly in  $D[0, \tau]$  (the space of right-continuous, left-hand limit functions on  $[0, \tau]$ ) to a Gaussian diffusion  $Z(\cdot)$ , with initial value  $Z(0) = z$  and with characteristic function  $\psi = \psi(t, \theta)$  that satisfies*

$$\frac{\partial \psi}{\partial t}(t, \theta) = -\frac{1}{2} \sum_{j,k} \theta_j g_{jk}(X(t, x)) \theta_k \psi(t, \theta) + \sum_{j,k} \theta_j \frac{\partial F_j}{\partial x_k}(X(t, x)) \frac{\partial \psi}{\partial \theta_k}(t, \theta). \tag{8}$$

*Remark.* (1) It should be noted that the diffusion approximation derived above describes the fluctuations of the density process caused by demographic stochasticity in the evolution of the process, and not fluctuations due to uncertainty in the initial state of the process. The initial state is assumed to be known precisely.

(2) The derivation of equation (8) can be found in [16]. While the equation does specify the distribution of the diffusion, it can only be evaluated explicitly in specific cases. However, one can always obtain the mean and covariance of  $Z(t)$ , given below, and thus, for large  $\nu$ , an approximate formula for the mean and covariance of the density process  $X_\nu(t)$ .

Using equation (8) we can determine the mean and covariance of  $Z(t)$ . These are given by

$$\mu_t := E(Z(t)) = M_t z$$

and

$$\Sigma_t := \text{Var}(Z(t)) = M_t \left( \int_0^t M_\nu^{-1} G(X(\nu, x_0)) \left( M_\nu^{-1} \right)^T d\nu \right) M_t^T,$$

respectively, where

$$M_t = \exp \left( \int_0^t B_\nu d\nu \right)$$

and

$$B_t = \nabla F(X(t, x_0)).$$

While we have derived explicit expressions for the time-dependent fluctuations about the deterministic path, the required integration often leads to formulae that are too complicated to be of practical use. However, if  $x_0$  is chosen as an equilibrium point of the limiting deterministic model defined by equation (6), then the diffusion approximation can be strengthened by identifying an approximating OU process. That is, if we now model fluctuations about the equilibrium point of the deterministic model, instead of the fluctuations about the deterministic trajectory, we can derive simple explicit formulae for the mean and covariance of our density process. This is achieved as follows.

**Corollary 3.4.** *If  $x_0$  satisfies  $F(x_0) = 0$  then, under the conditions of Theorem 3.3, the family  $\{Z_\nu(\cdot)\}$  defined by*

$$Z_\nu(t) = \sqrt{\nu}(X_\nu(t) - x_0), \quad 0 \leq t \leq \tau,$$

*converges weakly in  $D[0, \tau]$  to an OU process  $Z(\cdot)$ , with initial value  $Z(0) = z$ , and with local drift matrix  $B = \nabla F(x_0)$  and local covariance matrix  $G(x_0)$ . In particular,  $Z(t)$  has a normal distribution with mean  $\mu_t = \exp(Bt)z$  and covariance*

$$\Sigma_t = \exp(Bt) \left( \int_0^t \exp(-Bw)G(x_0) \exp(-B^T w)dw \right) \exp(B^T t).$$

We can conclude that, for large  $\nu$ ,  $X_\nu(t)$  is approximately normally distributed with a “working approximation” for the mean given by

$$E(X_\nu(t)) \approx x_0 + \exp(Bt)(X_\nu(0) - x_0), \quad (9)$$

obtained by setting  $z$  equal to  $\sqrt{\nu}(X_\nu(0) - x_0)$ , and with covariance matrix given by

$$\text{Var}(X_\nu(t)) \approx \frac{1}{\nu} \Sigma_t.$$

*Remark.* For our model the fixed point of interest is asymptotically stable, that is we have  $x_0$  asymptotically stable. Results of Barbour [2–5] show us that this is not a requirement for the above approximations to hold. In fact the OU approximation is often very accurate in modelling the fluctuations about unstable equilibrium points and centres. As emphasised by Pollett [19, 20], this is particularly important in situations of quasi-stationarity (see for example [18]).

#### 4. Diffusion Approximation of the Metapopulation Model

If we take  $M$ , the total number of patches in the metapopulation network, as our index parameter and define the scaled process  $x_M(t) = \{u(t), v(t)\} = \{m(t)/M, n(t)/M\}$ , with components being the fraction of suitable habitat and the fraction of occupied habitat, respectively, then Theorem 3.2 establishes the unique approximating deterministic model:

$$\frac{du}{dt} = r - (r + s)u \quad (10)$$

and

$$\frac{dv}{dt} = cv(u - v) - (e + s)v. \quad (11)$$

This is the deterministic model studied by Hess [12] and Johnson [13] and thus provides credence to their work, since it identifies the model as the appropriate approximating model and provides conditions under which the approximation is acceptable. This system has solution

$$u(t) = \frac{r}{r + s} + K_1 \exp(-(r + s)t) \quad (12)$$

and

$$v(t) = \frac{\exp\left(\int(-s + cu(t) - e)dt\right)}{\int(c \exp(\int(-s + cu(t) - e)dt)) dt + K_2}, \quad (13)$$

where  $K_1$  and  $K_2$  are constants of integration determined by initial conditions. The latter of these equations can be evaluated numerically. However, it can be seen that the equilibrium fraction of suitable habitat is

$$u^* = \frac{r}{r + s}$$

and the corresponding equilibrium fraction of occupied habitat is either

$$v_{trivial}^* = 0$$

or

$$v^* = \frac{r}{r + s} - \frac{e + s}{c},$$

with the trivial equilibrium losing stability to the nontrivial one when the latter is positive. Thus, this provides us with a simple condition for persistence of the species in the deterministic case, namely

$$\frac{r}{r + s} > \frac{e + s}{c}. \quad (14)$$

That is, if condition (14) is satisfied we have a stable positive fixed point, otherwise we have population extinction. This persistence condition, and model, is intuitively

appealing for a number of reasons. Firstly, as we will see in the next section, when disturbance is absent from our model, the fixed points and the persistence condition collapse to those given by the classical metapopulation model of Levins [17]. This allows us to identify the impact of habitat dynamics on metapopulation patch suitability and occupancy. Also, we note that the ratio  $c/(e + s)$  may be viewed analogously to the basic reproduction ratio  $R_0$  in epidemiology, that is, the expected number of infections in a completely susceptible population, given a mean lifetime of  $1/(e + s)$  (see Diekmann *et al.* [8]). In our model, this corresponds to the expected number of colonisations in a completely suitable unoccupied landscape. Our condition (14) can thus be interpreted as requiring the ratio  $c/(e + s)$ , multiplied by the equilibrium fraction of suitable habitat  $r/(r + s)$ , to be greater than 1, a result that is completely analogous to those for models of infection from epidemiology.

To simplify and improve interpretation of the results which follow, we reparameterise the model by introducing the new quantities

$$\rho = \frac{r}{r + s}$$

and

$$\theta = \frac{c}{e + s}.$$

Both are dimensionless. The parameter  $\rho$  is the equilibrium fraction of suitable habitat from the deterministic model and is thus less than or equal to one. The parameter  $\theta$  is strictly positive and, as discussed, can be viewed analogously to the basic reproduction ratio  $R_0$  in epidemiology.

Now, considering fluctuations about the equilibrium point  $x^*$  of the limiting deterministic model, we may establish a bivariate OU approximation for the fractions of suitable and occupied patches in the metapopulation network using Corollary 3.4. With  $x_M(t)$  defined as before, and provided

$$\lim_{M \rightarrow \infty} \sqrt{M}(x_M(0) - x^*) = z,$$

the family  $\{Z_M(\cdot)\}$ , defined by  $Z_M(t) = \sqrt{M}(x_M(t) - x^*)$ ,  $0 \leq t \leq \tau$ , converges weakly in  $D[0, \tau]$  to an OU process  $Z(\cdot)$  with initial value  $Z(0) = z$ , and with local drift matrix

$$B = \nabla F(x^*) = \begin{pmatrix} -(r + s) & 0 \\ c \left( \frac{r}{r+s} \right) - (e + s) & -c \left( \frac{r}{r+s} \right) + (e + s) \end{pmatrix} \tag{15}$$

and local covariance matrix

$$G = G(x^*) = \begin{pmatrix} \frac{2sr}{r+s} & s \left( \frac{r}{r+s} - \frac{e+s}{c} \right) \\ s \left( \frac{r}{r+s} - \frac{e+s}{c} \right) & 2(e + s) \left( \frac{r}{r+s} - \frac{e+s}{c} \right) \end{pmatrix}. \tag{16}$$

In particular,  $Z(t)$  is normally distributed with mean  $\mu_t = \exp(Bt)z$  and covariance

$$\Sigma_t = \exp(Bt) \left( \int_0^t \exp(-Bw)G \exp(-B^T w)dw \right) \exp(B^T t).$$

In practice  $M$  will be large and of fixed size. Thus, we obtain a “working approximation” for the mean by setting  $z$  equal to  $\sqrt{M}(x_M(0) - x^*)$ . This provides the approximation

$$E(x_M(t)) \approx x^* + \exp(Bt)(x_M(0) - x^*) \tag{17}$$

and

$$\text{Var}(x_M(t)) \approx \frac{1}{M} \Sigma_t.$$

The appendix contains the full time-dependent OU approximation. However, the quantities of most interest are the long-term mean and the long-term covariance matrix of this approximation. The bivariate normal approximation to the quasi-stationary distribution has mean

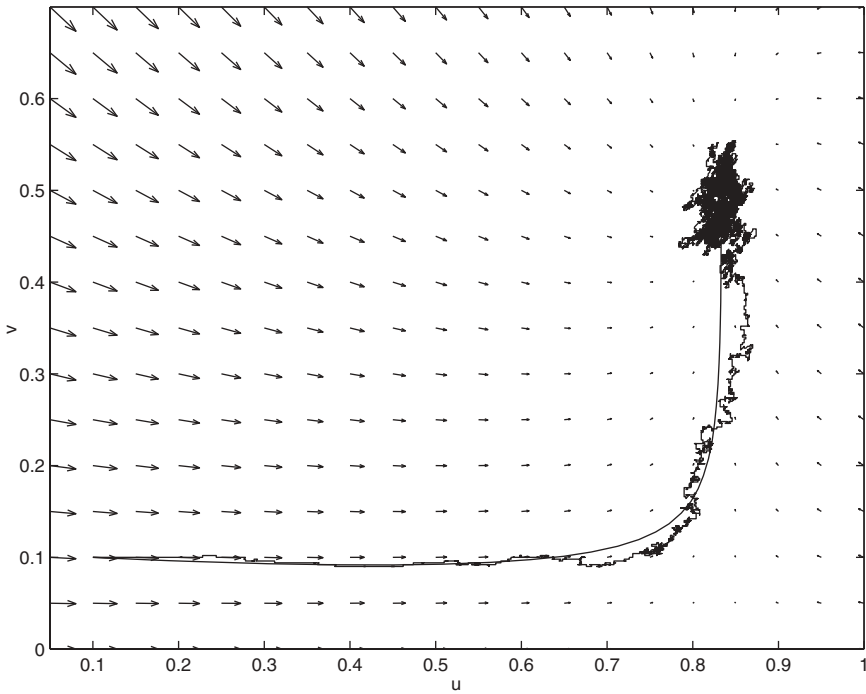
$$\mu = (u^*, v^*) = \left( \rho, \rho - \frac{1}{\theta} \right)$$

and covariance matrix

$$\frac{1}{M} \Sigma = \frac{1}{M} \begin{pmatrix} \rho(1 - \rho) & \frac{(1 - \rho\theta)(\rho - 1)(r + c\rho^2)}{r\theta + c\theta\rho^2 - c\rho} \\ \frac{(1 - \rho\theta)(\rho - 1)(r + c\rho^2)}{r\theta + c\theta\rho^2 - c\rho} & \frac{\rho(r\theta^2 + r\theta + c\theta^2\rho^2 + c\theta\rho^2 - r\theta^2\rho - c - c\theta^2\rho^3)}{\theta(r\theta + c\theta\rho^2 - c\rho)} \end{pmatrix}.$$

Thus we have obtained explicit expressions for the mean and variance of our metapopulation model via our bivariate OU approximation. The long-term covariance matrix is of additional interest because it provides the variance of the number of occupied patches. This variance can be compared with the variance obtained for the stochastic SIS logistic model in order to investigate the effect of habitat dynamics on metapopulation dynamics. A comparison showing this effect will be illustrated in Section 5 (Figure 5).

Although one would expect a diffusion approximation derived using Theorem 3.3 to provide a better approximation of the distribution of  $x_M(t)$  for  $t$  small (since it concerns the random fluctuations about the deterministic trajectory), the OU approximation has the advantage of there being explicit formulae for the mean and covariance. Further, the trajectories of our process move rapidly towards the fixed point (see Figure 1 in Section 5), and thus the OU approximation (concerning random fluctuations about the equilibrium point) is more important in describing the fluctuations of the process. This is in contrast to results of Clancy *et al.* [7], who required the diffusion approximation detailed in Theorem 3.3, due to the slow spiralling approach of trajectories towards the vicinity of the equilibrium point. Also, the use of the OU approximation allows us to implement results of Barbour [2–5] which show for how long the distributional approximation is valid.



**Fig. 1.** Simulation of the process with  $r = 0.5, s = 0.1, c = 0.6, e = 0.1, M = 500$ , for 10,000 transitions, the deterministic trajectory from same initial point, and the gradient field.

A convenient change of coordinates (see Barbour [2–5]) is achieved by setting

$$W_\nu(t) = AZ_\nu(t),$$

where the rows of  $A$  correspond to the left-eigenvectors of  $B$  (provided, as is the case for our model, the eigenvalues of  $B = \nabla F(x^*)$  are real). The sequence  $\{W_\nu(\cdot)\}$  converges weakly to an OU process  $W(\cdot)$ , which, in our two-dimensional case, has local drift matrix  $\Lambda = \text{diag}(\lambda_1, \lambda_2)$ , where  $\lambda_1$  and  $\lambda_2$  are the (strictly negative and distinct) eigenvalues of  $B$ , and local covariance matrix  $H = AGA^T$ . The individual components of this process are themselves OU processes. This transformation allows us to apply results of Barbour [2–5] that address the question of how long the OU process  $W(\cdot)$  provides an adequate distributional approximation for  $W_\nu(\cdot)$ . His result shows that the time till  $W_\nu$  first crosses the contour

$$\sum_{k=1}^2 \sqrt{(2C_{kk}/W_{(k)}^2)} \exp(W_{(k)}^2/2C_{kk}) = \frac{\exp(c_\nu^2)}{c_\nu}$$

(which, to order  $c_\nu^{-1}$ , delimits the rectangle  $|W_{(k)}| \leq c_\nu \sqrt{2C_{kk}}, k = 1, 2$ ), where  $\{c_\nu\}$  converges to  $\infty$  and  $C_{ij} = -H_{ij}/(\lambda_i + \lambda_j)$ , is approximately exponentially distributed. This result answers the question of “how long” because it establishes that, provided  $c_\nu = o(\nu^{1/8})$ , the expected time until exit is asymptotically

$$\frac{1}{2|\lambda_1 + \lambda_2|c_v} \sqrt{\pi} \exp(c_v^2).$$

Barbour also obtains results which show that the exit times,  $\tau_d$ , in each dimension,  $d = 1, 2$ , from regions approximating

$$|W_{(k)}| \leq (c_v + 1 - \delta_{kd})\sqrt{2C_{kk}}, \quad k = 1, 2,$$

where  $\delta_{kd}$  is the Kronecker delta, is again approximately exponentially distributed. With the previous condition imposed on  $c_v$  again, the mean time until exit is asymptotically

$$\frac{1}{2|\lambda_d|c_v} \sqrt{\pi} \exp(c_v^2).$$

Thus, the time taken for  $W_M$  to first cross the contour

$$\sum_{k=1}^2 \sqrt{(2C_{kk}/W_{(k)}^2)} \exp(W_{(k)}^2/2C_{kk}) = \frac{\exp(c_M^2)}{c_M},$$

or exit regions approximating

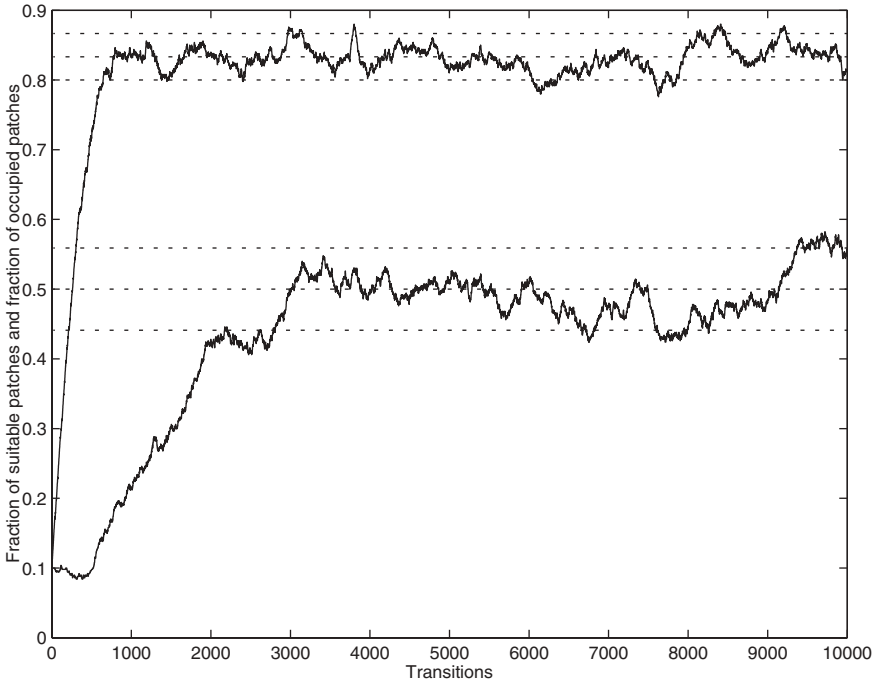
$$|W_{(k)}| \leq (c_M + 1 - \delta_{kd})\sqrt{2C_{kk}},$$

in either dimension  $d = 1, 2$ , is of order  $c_M^{-1} \exp(c_M^2)$  whenever  $c_M = o(M^{1/8})$ . Hence, it is asymptotically larger than any power of  $M$  if, for example,  $c_M = 0(M^{1/8} / \log M)$ .

It should be emphasised that the above result provides a qualitative indicator of the length of time for which the OU process provides an effective approximation of the metapopulation process. Since the metapopulation model is a finite state Markov chain, with an absorbing axis corresponding to all patches being unoccupied, we know that the metapopulation itself will become extinct in finite time. The importance of the result is that it shows that the time scale over which the metapopulation persists is typically large enough that the diffusion approximation can be taken as an effective description of the metapopulation dynamics. Additionally, as Barbour [2–5] states, although this may well be enough to justify treating the normal approximation around  $x^*$  as the true equilibrium distribution, it does not yield the distribution of the time until extinction, which, due to the scaling by  $v^{1/2}$  in deriving the OU approximation, would require  $c_v = o(v^{1/2})$ .

### 5. Numerical Results and Discussion

Figure 1 illustrates a typical realisation of our metapopulation process. It depicts a simulation of 10,000 transitions and the corresponding deterministic trajectory. We can see from the trajectory shown, and the gradient field, that any trajectory will move rapidly towards the vicinity of the equilibrium point. Thus, as discussed in the last section, Theorem 3.2 and Corollary 3.4 give credence to the use of the OU approximation to describe the behaviour of the process. Figure 2 isolates the behaviour of the fraction of suitable and the fraction of occupied habitat corresponding to



**Fig. 2.** Fractions of suitable and occupied patches from the simulation, together with equilibrium fractions and  $\pm 2$  standard deviation bands determined by the OU approximation.

the simulation in Figure 1. The usefulness of the variances determined by the OU approximation is also demonstrated by way of bands corresponding to  $\pm 2$  standard deviations for each of the fractions.

Figure 3 shows a simulation of our process and the corresponding contours of the OU Gaussian diffusion approximation.

Of considerable interest is a comparison of our model to the stochastic SIS logistic model to investigate the effect of habitat dynamics on metapopulation dynamics. The stochastic SIS logistic model has non-zero rates

$$q^L(n, n + 1) = c \frac{n}{M} (M - n)$$

and

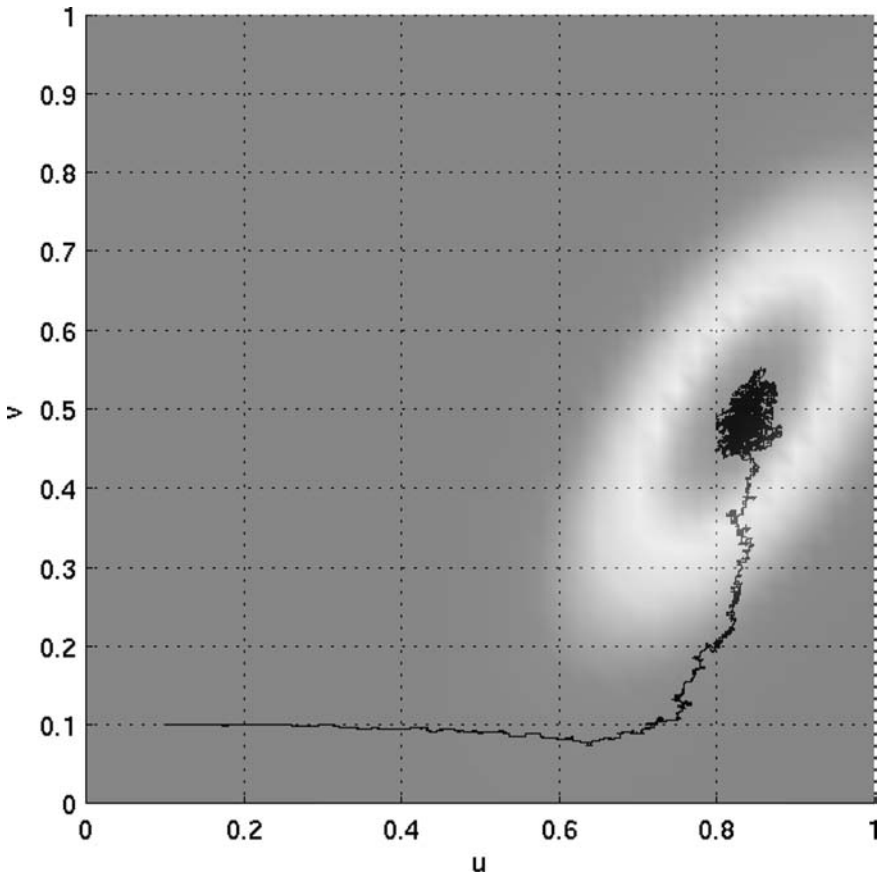
$$q^L(n, n - 1) = en.$$

Therefore, the model is density dependent with  $E = [0, 1]$  and

$$f^L(x, l) = \begin{cases} cx(1 - x) & \text{if } l = 1 \\ ex & \text{if } l = -1. \end{cases}$$

Thus, the approximating deterministic model is determined by  $F^L$ , given by

$$F^L(x) = cx(1 - x) - ex,$$



**Fig. 3.** Simulation of the process together with contours of the approximating bivariate normal distribution.

which has equilibrium points at

$$x_{trivial}^* = 0$$

and

$$x^* = 1 - \frac{e}{c}.$$

We can compare this equilibrium fraction of occupied patches to that given by our model, namely

$$v^* = \frac{r}{r+s} - \frac{e+s}{c}.$$

In agreement with Hess [12] and Johnson [13], it can be seen that disturbance affects the equilibrium fraction in two ways. Firstly, it reduces the fraction of suitable habitat ( $1$  compared with  $u^*$ ) and secondly it increases the extinction rate of

the metapopulation by adding the habitat destruction component  $s$  to the standard extinction rate  $e$ . The stochastic SIS logistic model also has

$$B^L = e - c,$$

which gives the deterministic persistence condition of  $c > e$ . It can be seen that if  $s = 0$  the persistence condition derived for our model, equation (14), reduces to the same persistence condition and also the same equilibrium fraction of occupied patches.

Further to this, we can consider two situations that might arise from using the existing stochastic SIS logistic model. Firstly, since there is no modelling of habitat dynamics, it might be assumed that all  $M$  patches are suitable for occupancy. It would then also be assumed that the extinction of local populations is occurring at rate  $e + s$ . This situation modelled with the stochastic SIS logistic model results in an equilibrium fraction of occupied habitat given by

$$x_{eq}^* = 1 - \frac{e + s}{c}$$

and the persistence condition

$$c > e + s.$$

Therefore, we would incorrectly overestimate the expected proportion of occupied habitat and could possibly make incorrect decisions concerning the persistence of the metapopulation. The second situation is one in which data leads to an estimate of the average fraction of suitable habitat to be approximately

$$\frac{r}{r + s}.$$

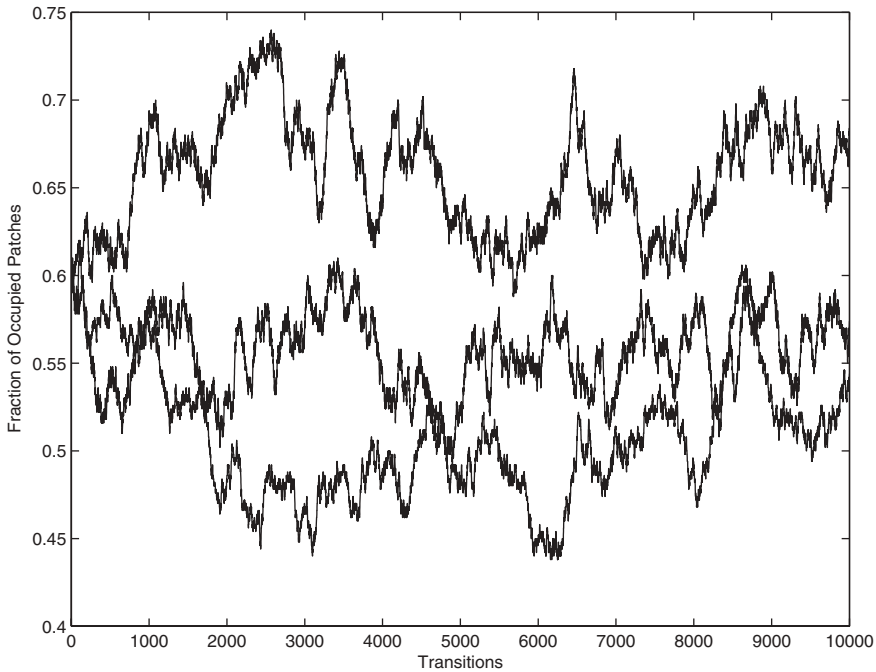
Combining this with the stochastic SIS logistic model gives the equilibrium fraction of occupied habitat as

$$x_{eq}^* = \frac{r}{r + s} \left[ 1 - \frac{e + s}{c} \right]$$

and the same persistence condition

$$c > e + s.$$

Thus, we would still incorrectly overestimate the expected proportion of occupied habitat and could possibly make incorrect decisions concerning the persistence of the metapopulation. Therefore, in general, using existing models that do not explicitly model habitat dynamics will overestimate the average proportion of occupied patches and will provide incorrect persistence conditions for certain parameter regions. Figure 4 illustrates this reduction in patch occupancy density via a comparison of our model to the stochastic SIS logistic model for each of the scenarios outlined above.

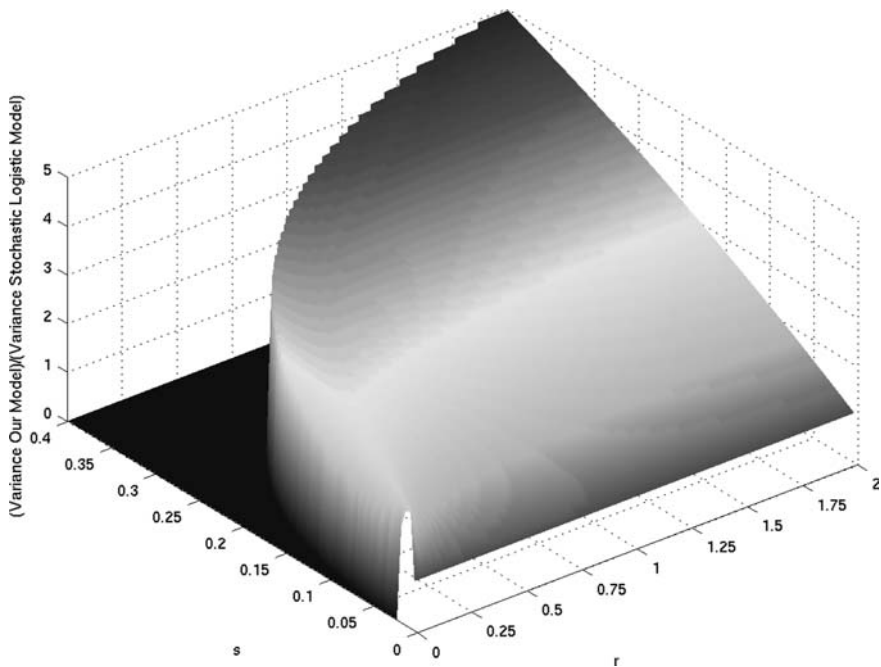


**Fig. 4.** Simulation of the stochastic SIS logistic model with extinction rate  $e + s$ , with extinction rate  $e + s$  and reduced habitat, and our new model, respectively from top to bottom.

As mentioned earlier, the explicit expression for the variance in the number of occupied patches allows us to investigate the effect of ignoring habitat dynamics upon the variability of metapopulation occupancy dynamics. It can be seen from Figure 5 that the relative increase in variance of our model compared to the stochastic SIS logistic model is increasing as the rate of disturbance increases, that is, with  $s$ . For the parameters used in the simulations there is an approximate increase in variance of occupied patches by a factor of 2.6. This is a significant increase in variance and emphasises the importance of quantifying stochasticity in both habitat and population dynamics.

## 6. Conclusion

We have presented a stochastic metapopulation model that accounts for habitat dynamics. Results of Kurtz and Barbour, that provide deterministic and diffusion approximations for a wide class of stochastic models, were presented in a form that most easily allows their direct application to population modelling. These results were used to demonstrate convergence (uniformly in probability over finite time intervals) of a suitably scaled version of the metapopulation model to a deterministic model studied previously in the ecological literature by Hess [12] and Johnson [13].



**Fig. 5.** Ratio of variance in occupied patches for our model to that of the stochastic SIS logistic model with  $c = 0.6$  and  $e = 0.1$ .

We extended their work by also establishing a bivariate normal approximation for the patch suitability and patch occupancy densities, conditional upon non-extinction. That is, we established a bivariate normal approximation to the quasi-stationary distribution of the original process. This allowed us to quantify the effect of habitat dynamics on the variability of patch occupancy dynamics through a comparison with the stochastic SIS logistic model. Additionally, we have provided an effective means for modelling metapopulations occupying landscapes that are ephemeral or subject to temporary unsuitability and have established a framework for statistical inference for fitting the model to real metapopulation data, thus allowing population viability analyses of such metapopulations. The approach and techniques presented in this paper have wide applicability and should be of interest to most biological modellers.

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### 7. Appendix

The time-dependent mean and covariance matrix of the OU approximation are given by

$$\mu_t = \begin{pmatrix} \exp\left(-\frac{tr}{\rho}\right) & 0 \\ \frac{c}{\rho}(\theta\rho - 1) \left[ \exp\left(\frac{tc(1-\theta\rho)}{\theta}\right) - \exp\left(-\frac{tr}{\rho}\right) \right] \exp\left(\frac{tc(1-\theta\rho)}{\theta}\right) \end{pmatrix}^z$$

and

$$\frac{1}{M} \Sigma_t = \frac{1}{M} \begin{pmatrix} (\rho - 1)\rho \left( \exp\left(-\frac{2tr}{\rho}\right) - 1 \right) \chi_t & \\ & \Omega_t \end{pmatrix},$$

respectively, where

$$\chi_t = \frac{\eta + \xi \exp\left(-\frac{2tr}{\rho}\right) + \zeta \exp\left(\frac{-t(r\theta + c\theta\rho^2 - c\rho)}{\rho\theta}\right)}{(r\theta + c\rho - c\theta\rho^2)(r\rho + c\theta\rho^2 - c\rho)},$$

in which

$$\eta = \frac{(c\rho^2\theta - c\rho - r\theta)(\theta\rho - 1)(\rho - 1)(r + c\rho^2)}{\rho^{12}}$$

$$\xi = \frac{c(1 - \rho)(c\rho - r\rho + r\theta^2\rho - c\theta\rho^2 + c\theta^2\rho^3)}{\rho^{10}}$$

and

$$\zeta = \frac{r(\rho - 1)(\theta\rho - 1)(r\theta + c\theta\rho^2 + c\rho)}{\rho^{12}},$$

and, the entry corresponding to the variance in the occupied patches is given by

$$\Omega_t = \frac{\Delta + \epsilon \exp\left(-\frac{2tr}{\rho}\right) + \phi \exp\left(t\left(\frac{c\rho - c\theta\rho^2 - r\theta}{\rho\theta}\right)\right) + \Theta \exp\left(2tc\left(\frac{\rho\theta - 1}{\theta}\right)\right)}{\theta(r\theta + c\rho - c\theta\rho^2)^2(r\theta - c\rho + c\theta\rho^2)},$$

where

$$\Delta = \frac{(r\theta + c\rho - c\theta\rho^2)^2(r\theta^2 + r\theta - r\theta^2\rho - c + r\rho^2\theta^2 + c\rho^2\theta + c\rho^3\theta^2)}{\rho^{15}}$$

$$\epsilon = \frac{c^2\theta(1 - \rho)(\theta\rho - 1)^2(r\theta + c\theta\rho^2 - c\rho)}{\rho^{13}}$$

$$\phi = \frac{2cr\theta(\rho - 1)(\theta\rho - 1)^2(r\theta + c\theta\rho^2 + c\rho)}{\rho^{15}}$$

and finally

$$\Theta = (c\rho - r\theta - c\theta\rho^2) \left[ \frac{(2c^2\theta\rho^2 - c\rho - c^2\theta^2\rho^3 - cr\theta - cr\rho\theta + cr\rho\theta^2 + cr\rho^2\theta^2 + r^2\rho\theta^3 - r^2\theta^2)}{\rho^{15}} \right].$$

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