

## THE ROLE OF HABITAT DISTURBANCE AND RECOVERY IN METAPOPULATION PERSISTENCE

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**Abstract.** Classical metapopulation theory assumes a static landscape. However, empirical evidence indicates many metapopulations are driven by habitat succession and disturbance. We develop a stochastic metapopulation model, incorporating habitat disturbance and recovery, coupled with patch colonization and extinction, to investigate the effect of habitat dynamics on persistence. We discover that habitat dynamics play a fundamental role in metapopulation dynamics. The mean number of suitable habitat patches is not adequate for characterizing the dynamics of the metapopulation. For a fixed mean number of suitable patches, we discover that the details of how disturbance affects patches and how patches recover influences metapopulation dynamics in a fundamental way. Moreover, metapopulation persistence is dependent not only on the average lifetime of a patch, but also on the variance in patch lifetime and the synchrony in patch dynamics that results from disturbance. Finally, there is an interaction between the habitat and metapopulation dynamics, for instance declining metapopulations react differently to habitat dynamics than expanding metapopulations. We close, emphasizing the importance of using performance measures appropriate to stochastic systems when evaluating their behavior, such as the probability distribution of the state of the metapopulation, conditional on it being extant (i.e., the quasistationary distribution).

**Key words:** colonization; disturbance; extinction; fire; habitat; metapopulation; persistence; quasistationary; succession.

### INTRODUCTION

Studying population dynamics in space has become increasingly important for all aspects of population management, including harvesting, conservation, and control (Shea et al. 1998). Metapopulations, a common representation for spatially structured populations, are sets of populations, each vulnerable to extinction, and connected by dispersing individuals (Levins 1969, Hanski and Simberloff 1997). The classical metapopulation model has been with us for over 50 years, and has seen much refinement and application (Andrewartha and Birch 1954, Levins 1969, Hanski and Simberloff 1997). However, much of the development of the theory has assumed that the landscape is static.

Empirical evidence indicates that habitats are not static, that, over longer timescales, many metapopulations are driven by habitat dynamics, e.g., disturbance followed by succession, not subpopulation processes, such as extinction and colonization (Harrison and Taylor 1997, Thomas and Hanski 2004). For instance, nearly all extinctions of British butterflies are due to habitat

conversion, not chance local extinction (Thomas 1994). In fact, the persistence of species that utilize early or midsuccessional habitats (e.g., Wahlberg et al. 2002, Biedermann 2004) or those that negatively impact their habitat (e.g., Fryxell 2001) appears to be a function of habitat dynamics, not colonization and extinction. This is not to say that colonization and extinction are not important processes in metapopulation systems, as there is substantial evidence for their role, but that the long-term dynamics are framed by changes in habitat suitability (Harrison and Taylor 1997, Elmhagen and Angerbjorn 2001). Our interest in spatial population models that allow for habitat dynamics emerges from attempts to model arboreal marsupials, which depend on mature forests, in managed landscapes (Possingham et al. 1994, Lindenmayer and Possingham 1996). Disturbances such as fire and logging invariably cause local extinctions, and thus empty patches are frequently not suitable for recolonization. This problem forced us to build the first spatially explicit simulation model that allowed for habitat dynamics (Possingham and Davies 1995).

The mismatch between theory and reality is stimulating a burst of new theory attempting to integrate habitat and metapopulation dynamics (Gyllenberg and Hanski 1997, Brachet et al. 1999, Johnson 2000, Keymer et al. 2000, Amarasekare and Possingham 2001, Ellner and Fussman 2003, Biedermann 2004). This emerging body of theory relies on deterministic dif-

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ferential equations to represent metapopulations in habitats with successional dynamics. While the approaches and analyses vary widely, a general conclusion emerges: metapopulation persistence, or patch occupancy, is critically dependent on the relative rates of colonization and habitat turnover. This key to persistence has an analogy in disease ecology—an occupied patch needs to colonize, on average, at least one other patch before it becomes extinct itself (Anderson and May 1991, Nee 1994, Gyllenberg and Hanski 1997, Dobson 2003). However, while much of the theory points to the importance of the rate of habitat turnover, the models include turnover only in a very simplistic way, assuming a constant rate or probability of patch succession to an unsuitable state, and generally in the absence of stochasticity (except simulations included in Keymer et al. 2000, Ellner and Fussman 2003).

The development of models that integrate metapopulation and habitat dynamics is not solely a theoretical curiosity, simulations of metapopulation and habitat dynamics for management are increasingly common (for examples using RAMAS Landscape, see Akcakaya et al. [2004] [program available online]).<sup>5</sup> These models provide realistic tools for evaluating management, such as logging, fire suppression, and grazing, which generally affects habitat dynamics. However, in the absence of well-developed theory on how systems that involve both metapopulation and habitat dynamics should behave, it is difficult to assess the generality of patterns and predictions emerging from these complex simulation models (for an exchange on this topic see Bagueette [2004], and Hanski [2004]).

In this paper, we construct a stochastic spatial population model incorporating both metapopulation processes and habitat dynamics. We analyze the effect of the habitat dynamics, governed by patch disturbance and recovery, on extinction risk and the probability distribution of the state of the system, assuming it is not extinct (the quasistationary distribution). In particular, we concentrate on how changes in the pattern of turnover in habitat, as determined by the rates and intensity of patch disturbance, and the rate of recovery, affect the dynamics of the metapopulation. In contrast to previous work, our model is stochastic, which implies that metapopulation extinction occurs eventually in all cases. Thus, the important performance measures are ones that represent the time course of this process and the states we might expect the system to be in prior to metapopulation extinction.

## THE MODEL AND ANALYSIS

### Model structure

Metapopulations are modeled using a two-dimensional continuous-time Markov chain. The state of the system, the number of suitable and occupied patches,  $(s, o)$ , is determined by a habitat process  $S(t)$  and by

<sup>5</sup> (<http://www.ramas.com/landsc.htm>)

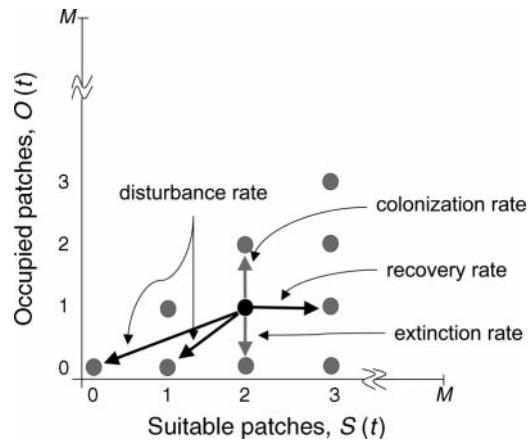


FIG. 1. Potential transitions in the stochastic metapopulation-habitat model. Metapopulation rates are illustrated by gray arrows, habitat by black arrows;  $M$  is the total number of patches, suitable and unsuitable.

a metapopulation process  $O(t)$ . The habitat state changes according to two processes, disturbance and recovery (Fig. 1).

The metapopulation process can change the number of occupied patches, up or down, by no more than one unit at a time, analogous to the familiar birth-death model (Fig. 1; for an introduction to birth-death models, see Taylor and Karlin [1998]). By contrast, habitat disturbance is a catastrophic process, hence disturbance can instantaneously reduce the number of suitable patches (and thus occupied patches) by more than one. We assume each patch recovers independently, and thus allow recovery of at most one patch at a time.

These assumptions regarding single changes within an infinitesimal unit of time are standard assumptions for continuous time Markov chains, and still allow many events to occur over a longer period, such as a year. Importantly, we assume that the patches are identical, and thus all of the rates are independent of which patches are being affected.

In the absence of changes in the habitat, the metapopulation follows the classic metapopulation dynamics of extinction and colonization (Fig. 1). We can represent the rate of extinction, passing from state  $(s, o)$  to state  $(s, o - 1)$ , as

$$(s, o) \rightarrow (s, o - 1) = eo. \quad (1)$$

The constant per capita extinction rate,  $e$ , results in the rate of extinctions increasing with the number of occupied patches. Similarly, the rate at which new patches are colonized is the rate at which the number of occupied patches increases by one:

$$(s, o) \rightarrow (s, o + 1) = c \frac{o(s - o)}{M} \quad (2)$$

where  $c$  is the density-dependent per capita rate of colonization and  $M$  is the total number of patches, suitable and unsuitable.

Our model also includes transitions in the number of suitable patches due to disturbance. We formulate the loss of suitable patches through disturbances as a two-part process. We assume disturbances occur at a constant rate,  $d$ . Given that a disturbance occurs, some number of suitable unoccupied patches,  $x$ , and suitable occupied patches,  $y$ , become unsuitable. Any occupied patches that become unsuitable also become unoccupied. We can represent the rate of transitions in the number of suitable and occupied patches, due to disturbance, as

$$(s, o) \rightarrow [s - (x + y), o - y] \\ = d \Pr\{X = x | s, o\} \Pr\{Y = y | o\}. \quad (3)$$

We assume that, given a disturbance, each patch has a constant probability,  $p$ , of becoming unsuitable. Thus, the probability of  $y$  occupied patches becoming unsuitable follows a binomial distribution, as

$$\Pr\{Y = y | o\} = \binom{o}{y} p^y (1 - p)^{o-y}. \quad (4)$$

Similarly, the probability of  $x$  suitable, but unoccupied, patches becoming unsuitable is also binomially distributed, as

$$\Pr\{X = x | s - o\} = \binom{s - o}{x} p^x (1 - p)^{(s-o)-x}. \quad (5)$$

The expected number of suitable patches lost in any disturbance will thus be  $ps$ , and the expected number of occupied patches lost will be  $po$ .

We assume patches recover independently at a constant rate,  $r$ . The rate at which single suitable patches are added is then the product of the recovery rate and the number of unsuitable patches in the system:

$$(s, o) \rightarrow (s + 1, o) = r(M - s). \quad (6)$$

Thus the time required to observe one patch recover (proportional to the reciprocal of the above rate) is relatively short when there are few suitable patches, but increases as a higher fraction of the total patches become suitable

#### *Parameters and exploration*

We assume a metapopulation with 20 patches, small enough to make computation quick but large enough to be reasonably realistic. We use a baseline scenario with the following parameters: colonization rate ( $c$ ) = 2, extinction rate ( $e$ ) = 1, disturbance rate ( $d$ ) = 0.05, disturbance intensity ( $p$ ) = 0.25, and recovery rate ( $r$ ) = 0.1 as a point of departure.

We modify this baseline scenario to explore the impact of habitat dynamics across four basic types of metapopulations, which are differentiated by the ratio of colonization to extinction (declining vs. expanding), and by the magnitude of the sum of the colonization and extinction rates relative to the sum of the habitat rates (slow vs. fast). The parameters for the metapop-

ulation process are: declining metapopulation,  $c = 0.5$ ,  $e = 2$ ; slow stable metapopulation,  $c = 0.5$ ,  $e = 0.5$ ; fast stable metapopulation,  $c = 2$ ,  $e = 2$ ; and expanding metapopulation,  $c = 2$ ,  $e = 0.5$ .

We examine the impacts of different types of patch turnover on metapopulations by varying the three habitat parameters: disturbance rate, disturbance intensity, and patch recovery rate, in a pairwise fashion. To do this, we hold one rate constant, vary a second, and adjust the third rate such that the rates balance at a fixed number of suitable patches ( $0.5M$ ). In a deterministic system, this state ( $0.5M$ ) would be the equilibrium number of suitable patches. For instance, for the analysis of the disturbance/recovery rate trade-off we varied the disturbance rate  $d$ , and compensated by adjusting the patch recovery rate  $r$  such that the equation

$$r = dp \left( \frac{s}{M - s} \right) \quad (7)$$

is always true. Using Eq. 7, we can find the value of any of the rates given the other two and a value for  $s$  ( $0.5M$ ). This allows us to also explore effect of habitat turnover as disturbance rate  $d$  increases, compensated by decreasing intensity  $p$ , and as intensity increases  $p$ , compensated by increasing recovery rate  $r$  as described above.

We focus primarily on two measures of the performance of the metapopulation: the mean time to extinction and the quasistationary distribution. The mean time to extinction is fairly straightforward, and has been used widely in ecological modeling. Although there are concerns with its use for representing persistence, it does provide a summary measure that is relevant for ecologists (Ludwig 1996, McCarthy et al. 2005). As alluded to above, the quasistationary distribution is the probability distribution of the state,  $(s, o)$ , of the metapopulation system, given that it is extant, after the effects of the initial conditions have disappeared (Day and Possingham 1995, Pollett 2001). In our case, this could be envisioned as a probability surface, with the  $x$ - and  $y$ -axes representing the number of suitable and occupied patches respectively, and the elevation of the surface representing the probability of any given state,  $(s, o)$ . Roughly speaking, a quasistationary distribution can tell an ecologist what they should anticipate seeing, when observing an established metapopulation for the first time.

## RESULTS

We first discuss the basic behavior of the model, including the dynamics of the deterministic analogue and time to extinction. We then examine the impacts of habitat dynamics on metapopulation persistence, and on the conditional probability distribution of metapopulation state.

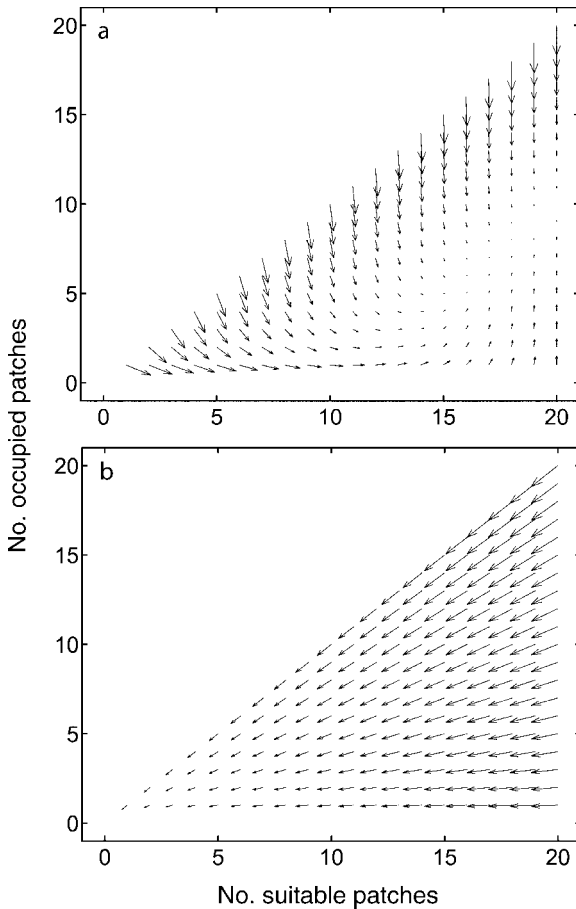


FIG. 2. Rate fields in the base model (a) between disturbances, and (b) during a disturbance. Parameters in this model are: density-dependent per capita rate of colonization,  $c = 2$ ; constant per capita extinction rate,  $e = 1$ ; constant rate of disturbance,  $d = 0.05$ ; probability of a patch becoming unsuitable (disturbance intensity),  $p = 0.25$ ; patch recovery rate,  $r = 0.1$ .

#### Base model behavior

The rate field of the base model is the expected magnitude and direction of the drift in the stochastic process, and provides a guide to the dynamics (Fig. 2). After a disturbance, the metapopulation/habitat system tends toward the deterministic steady state with all patches suitable, and some fraction occupied, or to metapopulation extinction (Fig. 2a). Eventually, another disturbance occurs and reduces the number of suitable and occupied patches (Fig. 2b).

To get a feel for the system dynamics, it is instructive to look at the average rate field and identify steady states of the system (Fig. 3a). However, these are averages across the two processes above and the model may rarely visit those steady states. In this case (Fig. 3a), the system has two steady states: one close to (18,0), representing a steady state in the habitat dynamics following metapopulation extinction, and another stable one near (18,8)—eight of 18 suitable patch-

es occupied. From most initial points, the system will tend toward the stable point with an extant metapopulation, but if the system starts with fewer than 10 suitable patches, patch occupancy decreases, and extinction is likely.

Mean time to extinction in the stochastic model reflects the rate field, with rapid extinction from initial states of 10 suitable patches or less (Fig. 3b). Interestingly, there is little effect of the number of occupied patches on mean time to extinction at these low numbers of suitable patches. Mean time to extinction is relatively independent of the number of occupied patches, even when all suitable patches are initially occupied, i.e., at saturation. Similarly, at higher numbers of suitable patches, persistence is largely independent of the number occupied, suggesting that habitat dynamics dominate.

#### Effects of habitat dynamics

We compare effects of habitat dynamics on metapopulation dynamics in three ways: (1) increasing the

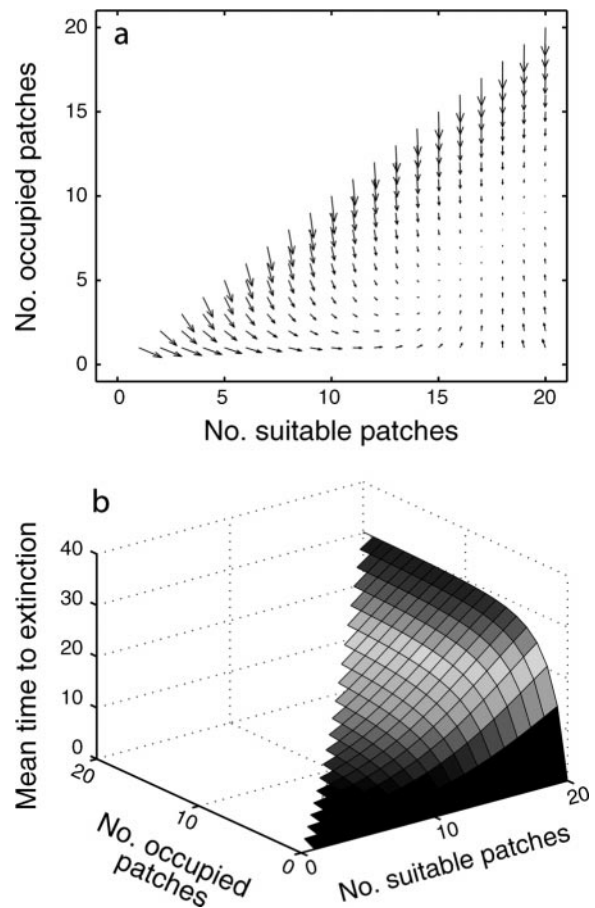


FIG. 3. Dynamics and persistence in the base model. (a) Average rate field for the deterministic analogue; (b) mean time to extinction from each possible starting state. Parameters in this model (defined in Fig. 2 legend) are  $c = 2$ ,  $e = 1$ ,  $d = 0.05$ ,  $p = 0.25$ , and  $r = 0.1$ .

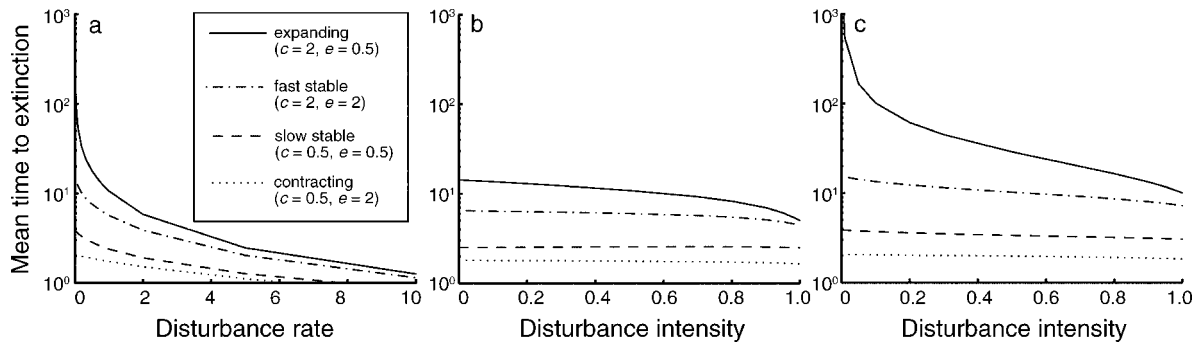


FIG. 4. Expected persistence time for different types of metapopulations with varying habitat dynamics. Panels illustrate the effect of different types of changes in habitat turnover: (a) the effect of increasing the disturbance rate and compensating by increasing the recovery rate; (b) the effect of increasing disturbance intensity and decreasing frequency; and (c) the effect of increasing intensity and increasing recovery rate. Note the y-axis log scale. Metapopulation parameters are defined in Fig. 2. See Eqs. 4–7 for explanations of the types of habitat turnover and definitions of the various rates.

disturbance rate and compensating by increasing the recovery rate; (2) increasing the disturbance intensity, and decreasing the disturbance rate; and (3) increasing the disturbance intensity, and increasing the recovery rate. In each case, the compensation means that the average number of suitable patches remains constant so the effects we see are determined by details of the disturbance process (see Eq. 7). We examine the effect of altering habitat patch turnover in each of these three ways for four types of metapopulations: (1) contracting, (2) slow stable, (3) fast stable, and (4) expanding.

#### *Mean time to extinction*

Increasing the rate of disturbance, while increasing the recovery rate to maintain the same steady-state number of suitable patches, results in a decrease in mean time to extinction for all four types of metapopulations (Fig. 4a). This is expected, as variability in the number of suitable patches will increase with the habitat process rates, resulting in a higher likelihood of reaching states from which extinction is probable. Intriguingly, the influence of increasing the habitat dynamic rates changes depending on the kind of metapopulation. The expanding metapopulations are most strongly affected, experiencing a strong initial decrease in mean time to extinction as the rate of disturbance increases, which then tapers off (Fig. 4a). The slow stable metapopulations follow a similar, but less pronounced pattern (Fig. 4a). By comparison, the other two types of metapopulations exhibit far less substantial declines in mean time to extinction (although they already exhibited lower mean times to extinction). In all four cases, the negative effect of increasing the disturbance rate is strongest at small values and subsequently decreases.

In contrast, when we increase the intensity of disturbances and compensate by decreasing their frequency, we find that the negative effect on the mean time to extinction is increasingly strong (Fig. 4b). Again, this effect is strongest for the expanding meta-

population, which has a marked downward trend in mean time to extinction as intensity increases. The causal interpretation based on variance does not appear to hold in this case. Reducing the disturbance rate but increasing their size may or may not increase the habitat process variance depending upon the parameter values. However, increasing the disturbance size increases the chance the metapopulation will be pushed into states where drift favors extinction (Fig. 3a). So, independent of the effect of more variability in the number of suitable patches, an increase in disturbance intensity will decrease persistence even where the mean number of suitable patches remains constant.

Similar to the previous two comparisons, when we increase disturbance intensity and compensate by increasing the recovery rate, the different metapopulations react to different degrees, but in a similar manner (Fig. 4c). Mean time to extinction declines rapidly as disturbance intensity increases at low levels. This negative effect then lessens as intensity increases. As before, this effect is driven by an increased chance of visiting states that drift toward extinction, due to the increase in disturbance intensity.

#### *Quasistationarity*

For all three types of variation in habitat turnover discussed in the previous section, if disturbances are infrequent or mild, our metapopulation/habitat system has a unimodal quasistationary distribution (Fig. 5a–c). These probability distributions have strong peaks (are concentrated on a relatively small subset of the state space). The quasistationary distributions change radically as the pattern of turnover in habitat changes (Fig. 5d–f). Increasingly frequent disturbances, compensated for by an increasingly quick recovery, yield distributions of extant metapopulations that remain unimodal, but shift towards lower patch occupancy, with increased variability in the number of suitable patches (Fig. 5g). In contrast, for both intensity/recovery and intensity/frequency trade-offs in habitat dynamics, the

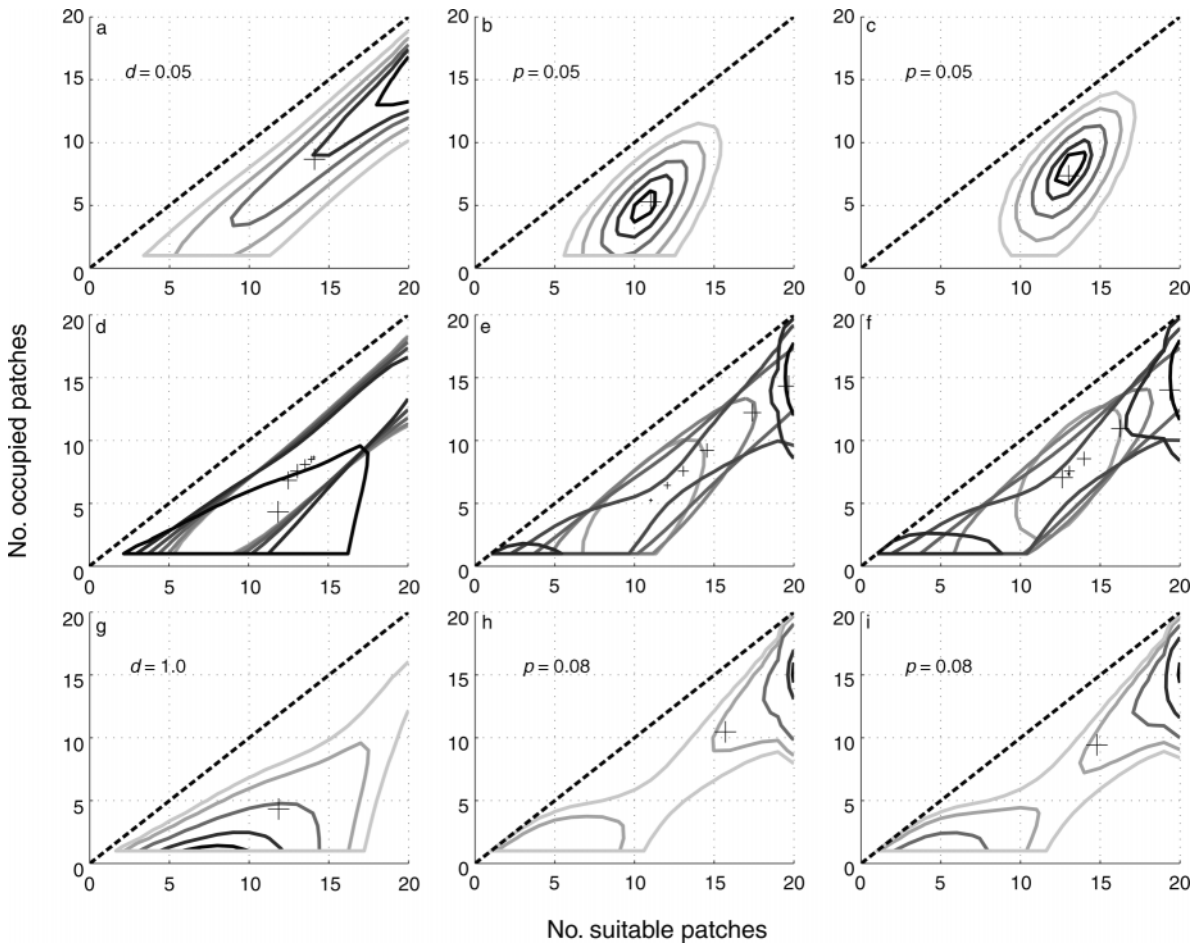


FIG. 5. Probability distributions of metapopulation and habitat states, conditional on the metapopulation being extant, as habitat dynamics change. Columns of panels illustrate the effect of different types of changes in turnover. Panels (a), (d), and (g) show the effect of increasing the disturbance rate and compensating by increasing the recovery rate; (b), (e), and (h) show the effect of increasing disturbance intensity and decreasing frequency; and (c), (f), and (i) show the effect of increasing intensity and increasing recovery rate. In each column, the middle panel shows the 75% isolines of probability for the states that contain the greatest probability mass. The markers (+ symbols) show the mean for each distribution. Marker size and isoline weight increase as the rate or intensity increases. The top and bottom rows of panels show the distribution for a single set of parameters, with the top corresponding to the lowest level of the rate or intensity and the bottom corresponding to one of the higher rates. Isolines in these panels represent cumulative probabilities for states containing the largest probability mass, in decreasing order of weight the isolines represent probabilities of 0.1, 0.25, 0.5, 0.75, and 0.9. The base rates for the model runs were  $c = 2$ ,  $e = 0.5$ ,  $d = 0.1$ ,  $p = 0.5$ , and  $r = 0.05$ . Habitat turnover dynamics were adjusted holding the metapopulation rates and one of the three habitat rates constant. The rates in the middle row of panels, in increasing order of line weight, are as follows: (d) 0.05, 0.06, 0.07, 0.10, 0.17, 1.00; (e) and (f) 0.05, 0.30, 0.50, 0.70, 0.90, 0.99.

quasistationary distributions shift from being unimodal at low disturbance intensities to bimodal at high intensities (Fig. 5h, i). At the same time, the mean for the distributions moves to higher values of occupancy and suitability (Fig. 5e, f). This suggests that these systems spend most of their time in a nearly saturated state (almost all habitat suitable, and most of it occupied), except following disturbances, when they make a visit to low levels of suitability and occupancy, subsequently either going extinct or moving relatively quickly back to the nearly saturated state.

## DISCUSSION

We found habitat turnover strongly affected persistence (Fig. 4). More interestingly, intensifying habitat turnover in different ways, while keeping the mean number of suitable patches constant, results in varying declines in persistence by the metapopulation system. In some cases this nonlinear relationship was a decreasing function of the rate we modified (frequency/recovery trade-offs), while in others it was an increasing function (intensity/frequency) or both (intensity/recovery), depending on the value of the rate in ques-

tion. The effect on persistence times of changing habitat dynamics was nonlinear in all of the cases we investigated. Different metapopulation types (contracting, expanding, fast and slow stable) differed only in the degree of their response to habitat turnover, with the most persistent metapopulations suffering the sharpest impacts of increases in disturbance rates or intensity.

These results extend those from simpler analytic models, which model habitat transitions deterministically using a constant rate, instead of periodic disturbances (Brachet et al. 1999, Johnson 2000, Keymer et al. 2000, Amarasekare and Possingham 2001, Ellner and Fussman 2003). In those analyses, mean patch lifetime and its size relative to colonization and/or extinction rate determined persistence. In our model, mean lifetime for a patch is  $1/dp$ , the inverse of the arrival rate of disturbances multiplied by the probability that a patch is lost if a disturbance occurs. This means that, for some of the patch dynamics we compared, patch lifetime varied, while for others it was constant. Trade-offs between disturbance frequency or intensity and recovery result in varying patch lifetimes (Fig. 4a, 400–4 time units; Fig. 4c, 40–2 units). In contrast, the trade-off between frequency and intensity maintains a constant mean patch lifetime (Fig. 4b, 10 time units). We find that not only does mean patch lifetime matter, but also that the pattern of turnover is very important in determining how persistence varies with patch lifetime.

Our observation is related to the finding, in successional models, that longer “refractory” periods, i.e., the time a patch remains unsuitable, reduce persistence (Ellner and Fussman 2003). In the successional case, a longer refractory period means a higher fraction of the patches are unsuitable. This is similar to increasing the disturbance intensity in our system, which results in a larger fraction of patches being unsuitable simultaneously (Fig. 4b and c). This effect is reflected in the quasistationary distributions where large infrequent disturbances result in distributions with little variability in the number of suitable patches (Fig. 5h). However, if we modify the “refractory” period directly, by increasing the recovery rate while compensating by increasing disturbance frequency or intensity, persistence actually increases with the refractory period (Fig. 4a and c). Thus, the effect of the refractory period observed elsewhere (Ellner and Fussman 2003) is probably due to synchronization of the state of the patches, not specifically the period of time they are unsuitable. Similar persistence reductions due to synchronization have been observed, due to spatial correlations, and the reduction of persistence with increasing patch synchronization may be a general effect (Johst and Drechsler 2003).

Our results provide guidance on the impacts of habitat dynamics on persistence in natural systems. For instance, fires vary in frequency, spatial extent (inten-

sity in our model) and recovery rate (Clark 1990, Clark and Royall 1996, Clark et al. 2002). In systems where fire affects habitat suitability, for instance, for collared lizards (Brisson et al. 2003) or marsupials in forests (McCarthy and Lindenmayer 2000), habitat dynamics are clearly important for persistence. These dynamics are amenable to management via controls on logging patterns, prescribed burning, and fire suppression activities. Our results illustrate that the largest gains in persistence will depend on the rates of disturbance and recovery, and the fraction of patches that are lost in a disturbance. If fires are very large in spatial extent, affecting most patches, controlled burns will achieve the largest persistence increases (increasing frequency but decreasing intensity; Fig. 5b). However, reducing the spatial extent of fires by controlled burning (lower intensity, higher frequency) will have diminishing effects at lower intensities. By contrast, if fires are typically localized (low intensity), increasing patch recovery rate, by seeding or fertilizer treatments, will yield the largest persistence gains (Fig. 5c). Clearly, this example ignores the spatial structure in the disturbance; however, simulation models have shown disturbance structure to have little effect (McCarthy and Lindenmayer 2000).

Examining the quasistationary distributions across the range of habitat dynamics suggests that habitat turnover patterns have a big impact not only on persistence, but also on the system state. The distributions are unimodal at low disturbance rates or intensities. However, as habitat turnover increases the distributions either tend toward the lowest states (i.e., toward metapopulation extinction) or become bimodal. The shift to a bimodal quasistationary distribution for the metapopulation/habitat system is a result of rare large disturbances moving the system away from the deterministic steady state, at which point it either goes extinct or rapidly moves toward the steady state. Although such metapopulations may appear to be relatively stable (i.e., near the upper mode of the quasistationary distribution), periodically they will be in an extremely precarious state, from which long-term persistence may be very unlikely. Returning to the fire example above, for metapopulations with these bimodal quasistationary distributions periodic management might be very effective, focusing on preventing extinctions when a metapopulation is in a temporarily depressed state. By contrast, extinction risk is fairly similar over time for the unimodal metapopulations, and continual management may be a better option (Mangel and Tier 1993).

Estimation of colonization and extinction rates from empirical data is problematic in the presence of habitat dynamics (for an empirical example, see Biedermann [2004]). If metapopulation rates are estimated from patch occupancy data, systems with the same colonization and extinction rates may yield substantially different estimates (compare Fig. 5a–c). Even if the metapopulation rates are estimated from turnover events,

they will only be correct if they are from a period between habitat fluctuations, and will still not accurately represent the long-term dynamics. Existing suggestions for incorporating habitat suitability rely on determining habitat age, and thus incorporating their dynamics (Johnson 2000, Hastings 2003). However, if transitions in patch suitability are due to stochastic factors instead of deterministic aging, or age and/or suitability is difficult to determine, this approach may not be feasible (Biedermann 2004, Thomas and Hanski 2004). Developing and parameterizing models, such as ours, which incorporate both habitat and metapopulation dynamics is an important future step for empirical metapopulation ecology.

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