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METAPOPULATION PERSISTENCE IN A DYNAMIC LANDSCAPE: MORE HABITAT OR BETTER STEWARDSHIP?

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Abstract. Habitat loss and fragmentation has created metapopulations where there were once continuous populations. Ecologists and conservation biologists have become interested in the optimal way to manage and conserve such metapopulations. Several authors have considered the effect of patch disturbance and recovery on metapopulation persistence, but almost all such studies assume that every patch is equally susceptible to disturbance. We investigated the influence of protecting patches from disturbance on metapopulation persistence, and used a stochastic metapopulation model to answer the question: How can we optimally trade off returns from protection of patches vs. creation of patches? We considered the problem of finding, under budgetary constraints, the optimal combination of increasing the number of patches in the metapopulation network vs. increasing the number of protected patches in the network. We discovered that the optimal trade-off is dependent upon all of the properties of the system: the species dynamics, the dynamics of the landscape, and the relative costs of each action. A stochastic model and accompanying methodology are provided allowing a manager to determine the optimal policy for small metapopulations. We also provide two approximations, including a rule of thumb, for determining the optimal policy for larger metapopulations. The method is illustrated with an example inspired by information for the greater bilby, *Macrotis lagotis*, inhabiting southwestern Queensland, Australia. We found that given realistic costs for each action, protection of patches should be prioritized over patch creation for improving the persistence of the greater bilby during the next 20 years.

Key words: dynamic landscape; economic costs; greater bilby; Macrotis lagotis; *metapopulation; optimal management; stochasticity*.

Introduction

A metapopulation is a collection of interacting subpopulations of the same species, each of which occupies a separate patch of habitat (Levins 1969, Gilpin and Hanski 1991, Hanski 1999, Dobson 2003). Habitat loss and fragmentation has created metapopulations where there were once continuous populations. In addition, numerous species naturally occupy landscapes of this type, such as wood roaches in fallen logs (Kambhampati et al. 2002), fish on coral reefs (James et al. 2002), and parasites on hosts (Thrall and Burdon 1997). Hence, metapopulation models have become a common paradigm for incorporating some spatial structure into population models (Ellner and Fussmann 2003). A common type of metapopulation model is a presence/absence model, which tracks only whether or not each patch within the metapopulation is occupied.

Traditional metapopulation models assume that the landscape is static: habitat quality does not change over time. However, landscapes are invariably dynamic. There has been growing interest in empirical studies of metapopulations where patch quality fluctuates, for example, the Sharp-tailed Grouse (*Tympanuchus phasianellus*) in central and northern North America (Akcakaya et al. 2004), the marsh fritillary butterfly (*Euphydyas aurinia*) in Finland (Wahlberg et al. 2002), the butterfly *Lopinga achine* in Sweden (Bergman and Kindvall 2004), the greater bilby *Macrotis lagotis* in southwestern Queensland, Australia (Southgate and Possingham 1995), and several species, including four endangered polyporous fungi (*Amylocystis lapponica*, *Fomitopsis rosea*, *Phlebia centrifuga*, and *Cystotereum murraii*), in eastern Finland (Gu et al. 2002).

There have also been a number of theoretical studies considering the role of habitat disturbance and recovery on metapopulation persistence. These have included metapopulations where patches are affected by different disturbance regimes: independent disturbance events (Hess 1996, Johnson 2000, Keymer et al. 2000, Amarasekare and Possingham 2001, Ellner and Fussmann 2003, Ross 2006*a*, *b*), catastrophes where several patches are disturbed simultaneously (Wilcox et al. 2006), age-dependent disturbance (Brachet et al. 1999, Hastings 2003), and spatially correlated disturbance

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(McCarthy and Lindenmayer 2000, Guichard et al. 2004, Kallimanis et al. 2005). It has been shown that the influence of disturbance on metapopulation persistence is significant. A simplifying feature of many of these models is that they assume every patch of habitat is equally susceptible to disturbance.

The assumption of equal susceptibility of patches to disturbance is unrealistic in situations where management may make a patch less susceptible, or even immune, to disturbance. What if there is a choice between creating a new patch of habitat and reducing the disturbance rate in an existing patch through better stewardship? Existing models do not deal with this issue. We created a new model that accounts for this possibility and explored ways of determining whether it is better to introduce new patches of habitat into the system or protect patches from disturbance in terms of improving population viability.

We used a continuous-time Markov chain (Norris 1997, Keeling and Ross 2008) to model a metapopulation in which a number of patches are immune to disturbance, with the remaining patches susceptible to independent disturbance events. We assumed that when a patch is disturbed it becomes temporarily unsuitable for occupancy. If a patch is occupied when disturbed, the population occupying that patch becomes locally extinct. Unsuitable patches recover independently of other patches at a constant rate. Each occupied patch may provide propagules that colonize suitable unoccupied patches, and may also become unoccupied in the absence of a disturbance and independently of other patches through a local extinction event, which results in the patch itself remaining suitable for occupancy. This model encompasses both the stochastic version of the classical metapopulation model of Levins (1969) (corresponding to all patches being immune to disturbance) and the stochastic version of the model of Hess (1996), first analyzed by Ross (2006*a*) where all patches are susceptible to disturbance.

We investigated the influence of both the number of patches and the number of patches protected from disturbance on population persistence in a dynamic landscape. In particular, we considered the influence of protected patches on the greater bilby population of southwestern Queensland, Australia. The bilby is a type of bandicoot that was once distributed over 70% of the arid and semiarid regions of Australia, but is now largely restricted to the Tanami Desert in the Northern Territory, the Gibson and Great Sandy Deserts of Western Australia, and one isolated population between Boulia and Birdsville in southwestern Queensland. This decline has resulted in the bilby being classified as vulnerable to extinction (Australasian Marsupial and Monotreme Specialist Group 1996). The reduction in the bilby's range is a result of habitat modification by cattle and rabbits, as well as from predation by cats, dingoes, and foxes (Southgate and Possingham 1995, Australasian Marsupial and Monotreme Specialist Group 1996, Pavey 2005). The particular bilby population we considered consists of approximately 600–700 individuals distributed predominantly as four distinct, interacting subpopulations. Each of these populations is subject to habitat modification by cattle and rabbits, and the patches can also become unsuitable for occupancy due to predation. In addition to these processes, each patch may also be subject to flooding, drought, and fire. Management strategies for increasing the persistence of the species are currently being considered and some of these have recently been implemented (Southgate and Possingham 1995, Pavey 2005). Our results are illustrated with respect to the greater bilby, however our methodology is applicable to any metapopulation.

The optimal management of metapopulations has received considerable attention to date. In particular, consideration has been given to whether to make a new patch of habitat or reintroduce a species to a suitable but empty patch (Possingham 1996), whether it is better to expand existing patches, link existing patches via corridors, or create a new patch (Westphal et al. 2003), and also to optimizing reserve expansion by determining which areas of habitat should be reserved (Haight et al. 2002, 2004). These latter studies also incorporated the monetary costs of the various actions into the decision theory framework. As far as we know no one has considered the optimal decision of whether to make a new patch of habitat or protect an existing patch from disturbance within an economic framework.

We assumed that, given a fixed budget, the manager had two options: creating new patches or protecting patches. Specifically we addressed the question: How many patches of habitat should be created and/or protected to maximize the probability of population persistence during the next 20 years. We also considered two approximations which may be useful for addressing the protection vs. creation question for systems with larger numbers of patches. Finally, we considered the question of what reduction in the disturbance rate (over all the patches in the metapopulation) would have the same impact on viability as protecting a given number of patches.

Models

Stochastic model for small metapopulations

We used a continuous-time Markov chain model to describe the dynamics of a presence–absence metapopulation in a dynamic landscape. A continuous-time Markov chain is defined by the rates of transition between the possible states of the system. Let $m(t)$ be the number of suitable, unprotected patches, $n(t)$ the number of occupied, unprotected patches, and $p(t)$ the number of occupied, protected patches at time t. Then $\{(m(t), n(t), p(t)), t \geq 0\}$ is assumed to be a Markov chain taking values in the set of all possible values $S_M = \{(m, n, p) \in \mathbb{Z}^3: 0 \leq n \leq m \leq M_u, 0 \leq p \leq M_p\}$, where M_u is the number of unprotected patches and M_p is the number of protected patches ($M := M_u + M_p$). The

TABLE 1. Possible changes in the state of the system and the corresponding positive transition rates between states.

Event	Transition	Rate
Recovery of unsuitable, unprotected patch	$(m, n, p) \to (m+1, n, p)$	$r(M_u - m)$
Disturbance of unoccupied, unprotected patch	$(m, n, p) \to (m-1, n, p)$	$s(m-n)$
Disturbance of occupied, unprotected patch	$(m, n, p) \to (m-1, n-1, p)$	sn
Colonization of unprotected, unoccupied patch	$(m, n, p) \to (m, n+1, p)$	$c[(n+p)/M](m-n)$
Local extinction at unprotected, occupied patch	$(m, n, p) \to (m, n-1, p)$	en
Colonization of protected, unoccupied patch	$(m, n, p) \to (m, n, p+1)$	$c[(n+p)/M](M_p - p)$
Local extinction at protected, occupied patch	$(m, n, p) \to (m, n, p-1)$	ep

Note: Parameters are e, the rate at which a local population becomes extinct; c, the rate at which an empty patch is colonized by an occupied patch; s, the rate at which a patch becomes unsuitable for occupancy; r, the rate at which a patch recovers to become once again suitable for occupancy; M, the total number of patches in the system; M_u, the number of unprotected patches in the system; and M_p, the number of protected patches in the system.

number of unsuitable patches at time t is $M_u - m(t)$. The possible changes in the state of the system that our model allows and the corresponding positive transition rates between states are listed in Table 1.

To be emphatic, we assumed that protected patches are immune to disturbances; our decision, which is presented later in the paper, is whether to create/acquire new patches of habitat (increase M_u) which are susceptible to disturbance events, or to protect patches from disturbance events (increase M_p and decrease M_u), given budgetary constraints.

Deterministic model for large metapopulations

Obviously the question of interest—protect or create?—will also be of interest for populations inhabiting larger metapopulation networks. In these situations the number of patches may be so large that numerical calculations required for analysing the full stochastic model are infeasible. For this reason, we also considered a deterministic model that approximates the optimal decision by maximizing the expected number of occupied patches.

The deterministic approximation of our model, derived from the theory of density-dependent Markov population processes (see Kurtz 1970, Pollett 1990, Ross 2006*a*, *b*), consists of a system of three differential equations. The first equation,

$$\frac{dx}{dt} = r(\rho_u - x) - sx$$

describes the dynamics of the fraction $x(=m/M)$ of suitable patches; the first term on the right-hand side $r(\rho_u - x)$ corresponds to recovery of unsuitable, unprotected patches where r is the rate of patch recovery and ρ_u is the proportion of unprotected patches, and the second term on the right-hand side sx corresponds to disturbance of suitable (unprotected) patches where s is the rate of habitat disturbance. The second equation,

$$\frac{dy}{dt} = c(y+z)(x-y) - (e+s)y$$

describes the dynamics of the fraction $y(=n/M)$ of occupied, unprotected patches; the first term on the right-hand side $c(y+z)(x-y)$ corresponds to colonization of suitable, unprotected patches where $z(=p/M)$ is the fraction of occupied, protected patches and c is the patch colonization rate, and the second term on the right-hand side $(e+s)y$ corresponds to local extinction and disturbance where e is the local patch extinction rate and s is the rate of habitat disturbance. The final equation,

$$\frac{dz}{dt} = c(y+z)(\rho_p - z) - ez$$

describes the dynamics of the fraction $z(=p/M)$ of occupied, protected patches; the first term on the right-hand side $c(y+z)(\rho_p - z)$ corresponds to colonization of protected patches where c is the patch colonization rate and ρ_p is the proportion of protected patches, and the second term on the right-hand side ez corresponds to local extinction where e is the local patch extinction rate.

From this system of differential equations, we can show that the equilibrium density of suitable habitat x^* is given by

$$x^* = \frac{r\rho_u}{r+s}.$$

This is identical to the equilibrium density of suitable habitat for the classical metapopulation in dynamic landscape model considered by Ross (2006*a*), multiplied by the proportion of patches that are susceptible to disturbance events ρ_u. The equilibrium density of occupied, unprotected patches y^*, and the equilibrium density of occupied, protected patches z^*, may also be evaluated, but the expressions are rather cumbersome and are presented in the Appendix. For future reference note that $y^* + z^*$ is the equilibrium density of occupied patches.

METHODS

Stochastic

We determined the dynamic behavior of our model, along with the extinction probability, the expected time to extinction, and the quasi-stationary distribution (the distribution of the process conditioned on the population being extant) (Day and Possingham 1995, Pollett 1996, Wilcox et al. 2006, Keeling and Ross 2008) of the metapopulation for certain parameter values and strategies. The quantities were evaluated by constructing a matrix $\mathbf{Q} = (q(i, j), i, j \in S_M)$, where $q(i, j)$ is the rate of transition from state i to state j, for $j \neq i$, and $q(i, i) = -q(i)$, where $q(i) := \Sigma_{j \neq i}\, q(i, j)$ is the total rate at which we move out of state i. Then, the probability distribution of the process at time t, $\mathbf{p}(t)$, is given by $\mathbf{p}(t) = p(0)\exp(\mathbf{Q}t)$, where $p(0)$ is the initial distribution of the process, and exp is the matrix exponential (see, for example, Norris 1997, Keeling and Ross 2008). We evaluated the matrix exponential using the mexpv function from EXPOKIT (Sidje 1998), a numerical package for efficiently computing the matrix exponential. The probability of extinction by time t is then the sum of the elements of the vector $\mathbf{p}(t)$ corresponding to states of extinction. The expected time to extinction was evaluated by solving a system of linear equations: $\mathbf{Q}_C\tau = -\mathbf{1}$, where $\mathbf{1}$ is a vector of 1s and $\mathbf{Q}_C$ is the matrix $\mathbf{Q}$ restricted to the non-extinct states C (all rows and columns of $\mathbf{Q}$ corresponding to the states of extinction are removed); the expected time to extinction starting from state i is then the ith element of the vector τ (see, for example, Norris 1997, Keeling and Ross 2008). The quasi-stationary distribution is given by the unique solution $\pi = (\pi_i, i \in C)$ to $\pi\mathbf{Q}_C = -\upsilon\pi$ and $\Sigma_{i \in C}\, \pi_i = 1$, where $-\upsilon$ is the eigenvalue of $\mathbf{Q}_C$ with smallest magnitude (see, for example, Ross 2006*a*, Keeling and Ross 2008). This was evaluated numerically using the eigs function in Matlab (MathWorks, Natick, Massachusetts, USA). To employ these methods of numerical evaluation, we needed to transform the state space S_M to a (one-dimensional) set of the form $S = \{1, 2, \ldots, N\}$. The transformation we adopted is presented in the Appendix.

Deterministic

We formulated the problem as a constrained maximization problem, assuming that the number of occupied patches, and number of new patches and protected patches, are all real valued, and used the deterministic approximation to determine the strategy which resulted in the maximum expected number of occupied patches. It is possible, if the habitat dynamics are particularly unfavorable, that adding a new (unprotected) patch to the system decreases population viability. In such a situation the optimal strategy is obvious: protect patches, and create/acquire new patches only if there is sufficient funds to also protect them. Here we considered the more likely case where both protecting patches and creating/acquiring new patches increases population viability (which simplifies calculations as shown in the next paragraph); a sufficient condition for this to occur is $r/(r + s) > (e + s)/c$, which is the condition for the existence of a positive equilibrium patch occupancy density for a metapopulation system consisting of only unprotected patches (Hess 1996, Ross 2006*a*).

Our goal is to maximize $(y^* + z^*)[M_p + M_u + N_u + (N_p - M_u)^+]$ by creating a number N_u of new, unprotected patches and a number N_p of (possibly new) protected patches, where $(\delta)^+$ is δ if $\delta > 0$ and 0 otherwise. Note that y^* and z^* are also functions of both N_u and N_p through ρ_u, ρ_p, and M. This optimization will be subject to the budgetary constraint $B \geq b_u N_u + b_p N_p + b_u(N_p - M_u)^+$, where B is the overall budget, b_u is the cost of creating/acquiring a new, unprotected patch, and b_p is the cost of protecting an existing (or newly created) patch from disturbance (note that budget and costs are for the whole time horizon of interest, which is 20 years here). Since we assume that all variables are real valued and that additional expenditure always increases the population's viability, we will always expend the entire budget, so the inequality in the budget constraint becomes an equality. Thus, we may express N_u as a function of N_p:

$$N_u = \frac{B - b_p N_p}{b_u} - (N_p - M_u)^+$$

allowing us to express our objective function as a function of N_p only. The optimization problem is

$$\text{maximize}(y^* + z^*)[M_p + M_u + N_u + (N_p - M_u)^+]$$

where y^*, z^*, and N_u are functions of N_p, subject to $0 \leq N_p \leq N_p^{\max}$. N_u may then be determined from the budgetary constraint equation. An expression for the value of N_p that maximizes our objective function may be easily evaluated numerically using Matlab or Maple (Maplesoft, Waterloo, Ontario, Canada).

Rule of thumb

We developed a simple rule of thumb for determining whether to protect patches from disturbance or create new patches of habitat. The rule of thumb was derived by ignoring the effect of protected patches on the unprotected patches' equilibrium occupancy, and vice versa, thus simplifying the expression for the expected number of occupied patches. The equilibrium patch occupancy density for protected patches (in isolation) is $(1 - e/c)$ (Levins 1969, Ross 2006*a*), and the equilibrium patch occupancy density for unprotected patches (in isolation) is $[r/(r + s) - (e + s)/c]$ (Hess 1996, Ross 2006*a*). With our independence assumption, the resulting equilibrium patch occupancy owing to creating N_u new patches and protecting N_p patches from disturbance is given by

$$\left(\frac{r}{r+s} - \frac{e+s}{c}\right)[N_u + (M_u - N_p)^+] + \left(1 - \frac{e}{c}\right)(M_p + N_p)$$

which we wish to maximize. Once again N_u can be expressed as a function of N_p since we will expend our entire budget B. By differentiating with respect to N_p we arrive at a simple rule of thumb: we should protect patches if

$$\left[\left(1 - \frac{e}{c}\right) - \left(\frac{r}{r+s} - \frac{e+s}{c}\right)\right]\frac{1}{b_p} > \left(\frac{r}{r+s} - \frac{e+s}{c}\right)\frac{1}{b_u}.$$

Otherwise we should create new patches. That is, if the

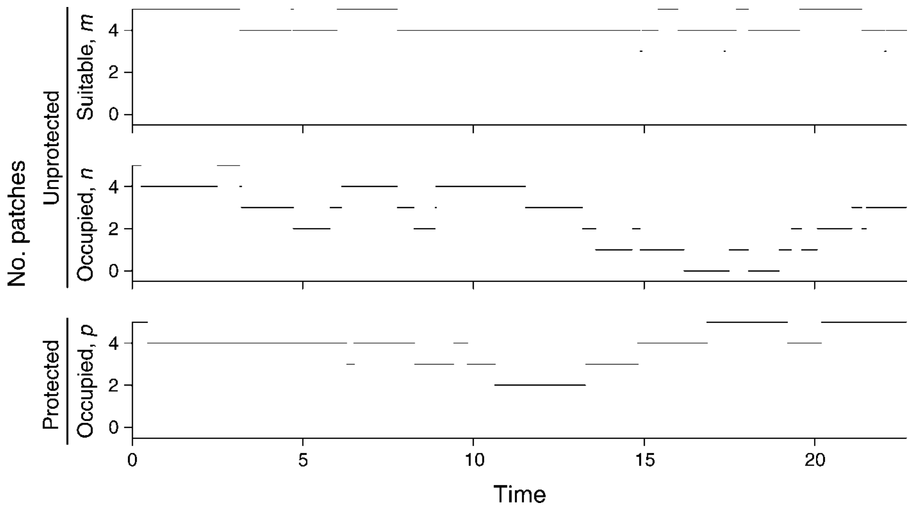

FIG. 1. The evolution of the number of suitable patches, denoted by m (of those unprotected), the number of these suitable patches that are occupied, denoted by n, and the number of protected patches occupied, denoted by p, through time, from an initial number of (5, 5, 5) in each class, respectively. Parameter values are colonization rate $c = 0.6$, local extinction rate $e = 0.1$, rate of patch recovery $r = 0.6$, rate of habitat disturbance $s = 0.1$, total number of patches $M = 10$, and number of protected patches $M_p = 5$.

ratio of marginal benefit to marginal cost due to protecting a patch (left-hand side of this inequality) is greater than the ratio of marginal benefit to marginal cost due to creating a patch (right-hand side of this inequality) then we should protect patches, otherwise we should create more habitat. This may also be rearranged to evaluate the critical cost ratio b_u/b_p so that the influence of changing costs on the optimal management policy may be investigated.

From the above rule of thumb, we can determine an explicit approximation for the threshold disturbance rate s^* for which the optimal policy changes from patch creation to patch protection (assuming all other rates are unchanged):

$$s^* = \frac{a + \sqrt{a^2 + 4b_p r(c-e)(b_p + b_u)}}{2(b_p + b_u)}$$

where $a = -(b_p r + b_u r + b_p e + b_u c)$. For disturbance rates s less than s^* we should prioritize patch creation, and for disturbance rates s greater than s^* we should prioritize patch protection.

RESULTS

Investigation of the system for particular values showed that it settled down to something like a deterministic equilibrium (Figs. 1 and 2). However it is not a true equilibrium as the only true equilibrium is extinction of the species. The behavior exhibited is known as quasi-stationarity (Pollett 1996, Wilcox et al. 2006).

Case study: the greater bilby

We then considered the greater bilby metapopulation described in the introduction. We assumed realistic values for the recovery rate r, the disturbance rate s, the colonization parameter c, and the local extinction rate e, and where possible those that have been used previously (see Southgate and Possingham 1995): $r = 2$, $s = 0.67$, $c = 3$, and $e = 0.10$ per year.

Increasing the number of patches protected had a significant positive effect on the persistence of the bilby (Fig. 3). Protecting only one of the four patches resulted in a substantial decrease in the extinction probability, from close to 1 to 0.506. Additionally, protecting all four patches from disturbance resulted in the probability of extinction in 20 years reduced from almost certain extinction to a small likelihood of extinction: 0.0024. This dramatic decrease highlights the potential importance of protecting patches from disturbance as a means of increasing population persistence and thus biodiversity, in particular for species that are heavily influenced by the dynamics of the landscape they inhabit. As a comparison, if we were to add an additional three patches of habitat and translocate species to these patches, the probability of extinction would be reduced to only 0.84.

Another common measure of population persistence is the expected time to extinction (Figs. 4 and 5). Similar results to that for the probability of extinction can be found; the protection of patches dramatically increased the persistence time of the bilby, in this case by a factor of approximately four (cf. Figs. 4 and 5). Once again, when landscape dynamics are important, the protection of patches has a significant influence on increasing the expected time to extinction of species.

The above methods provide valuable information concerning the effectiveness of various management options. However, they ignore the different costs of each action, and hence are not useful for real-world management decision making.

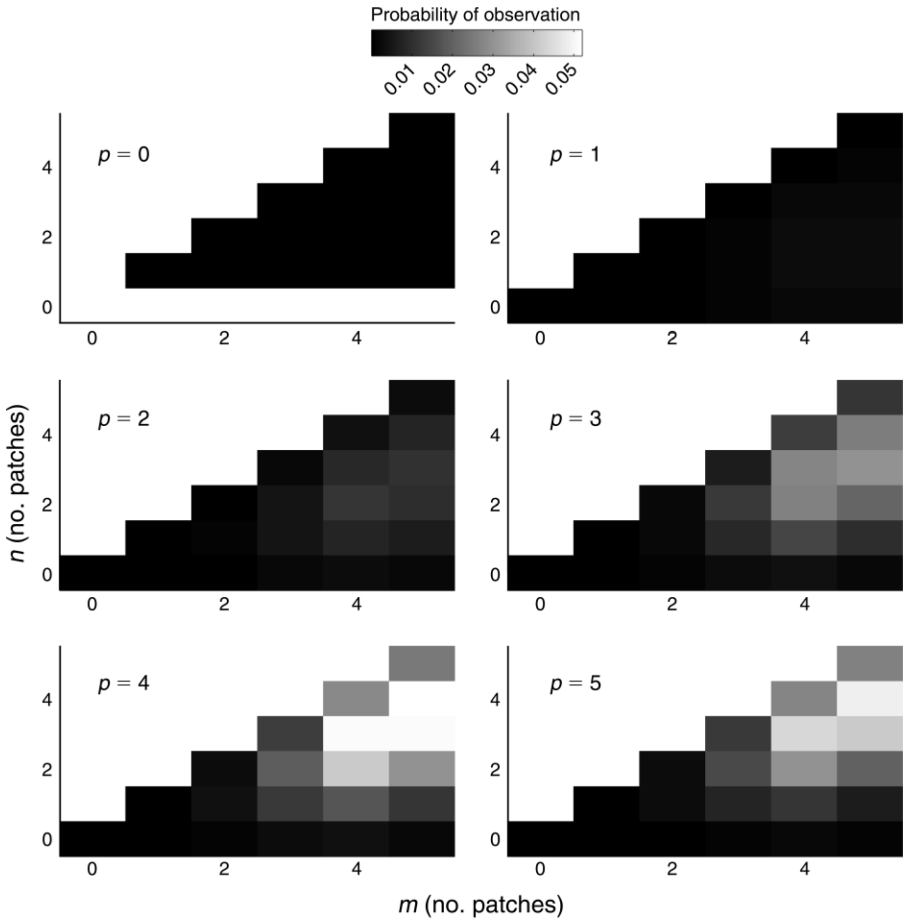

FIG. 2. Plots of the quasi-stationary distribution (the number in each class conditional upon non-extinction) of the stochastic model for a metapopulation in a dynamic landscape, with parameter values corresponding to those used in Fig. 1. Each cell represents the probability of observing a particular (m, n, p) combination, given that the species in question has not become extinct; m and n vary along the horizontal and vertical axes, respectively, of each plot, and p (the number of protected patches occupied) varies from plot to plot.

Our next consideration is that of finding an optimal strategy for maximizing the greater bilby's persistence over the next 20 years with the constraint of a fixed budget.

Our possible management actions consist of increasing the number of patches in the network or increasing the number of protected patches in the network. We determined the best combination of these actions, given realistic relative costs for each (Queensland Government Natural Resources and Mines, *unpublished data*). We assumed a fixed budget for the 20-year period of AU$12 million, a cost of AU$4 million for constructing a new patch suitable for bilby occupancy, and a cost of AU$100 000 per patch per year (i.e., AU$2 million over 20 years) for protection of an existing patch from habitat degradation and predation. Here, we have assumed protection ensures no modification to habitat. In reality, there will still be some modification, and there is likely to be a relationship between the cost and the rate of such disturbance. Further research will investigate such issues. With these plausible parameter values we found that the optimal strategy for increasing viability is to construct one new patch of habitat and to protect four of the five patches, at a total cost of AU$12 million. The implementation of this strategy resulted in the probability of extinction at the end of the 20-year period decreasing from close to 1 to 0.002.

The optimal strategy found here is typical for similar budgets and action costs for the bilby, and other metapopulations that are highly influenced by their landscape dynamics. The first priority is the protection of patches from disturbance, and then, if additional funding remains, we should construct new habitat and protect these new patches simultaneously.

If landscape dynamics are relatively unimportant (or slow) compared to metapopulation dynamics, the main priority is to construct additional patches. For the greater bilby population, there is a threshold around the

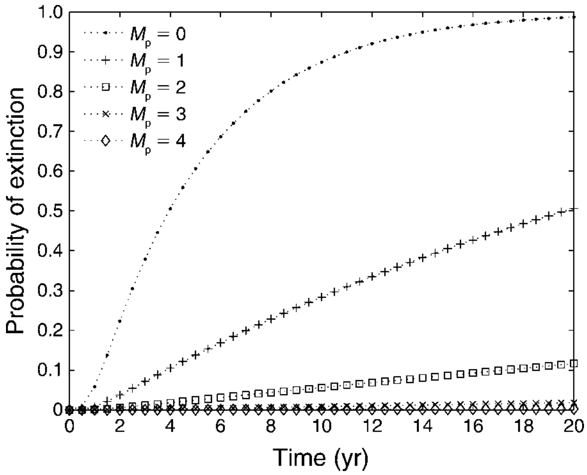

FIG. 3. The probability of extinction over a 20-year period for the greater bilby with different numbers of protected patches. Each set of points corresponds to a different number of protected patches, with a fixed total number of patches (four), a fixed initial number of suitable patches (four), and a fixed initial number of occupied patches (four), with all protected patches being occupied initially. Parameter values are colonization rate $c = 3$, local extinction rate $e = 0.1$, rate of patch recovery $r = 2$, rate of habitat disturbance $s = 0.67$, total number of patches $M = 4$, and number of protected patches $M_p = 0, 1, 2, 3, 4$, respectively.

disturbance rate $s = 0.08$ (assuming all other rates are unchanged). For patch disturbance rates less than this threshold the priority is to create new patches, and for patch disturbance rates above the threshold protection of patches should be prioritized.

Finally, as a comparison, the two other plausible management strategies over the 20-year period, with the given budget and costs, are to either add an extra three subpopulations to the metapopulation or to add two additional patches and protect two of the resulting six patches. These result in the probability of extinction decreasing to 0.844 and 0.071, respectively, both considerably higher than that of the optimal strategy.

For purposes of demonstrating the usefulness and accuracy of the approximations, we considered a metapopulation with a larger number of patches $M = 20$ and with colonization rate $c = 1$, local extinction rate $e = 0.50$, rate of habitat recovery $r = 1$, and with the same cost of patch protection $b_p = 2$, cost of patch creation $b_u = 4$, and budget $B = 12$. For a metapopulation with these rates and costs, there exists a threshold at habitat disturbance rate $s \approx 0.057$; for rates of disturbance $s > 0.057$ we should protect patches, otherwise we should create more habitat.

Deterministic approximation

The optimal decision for the bilby population derived from using our deterministic approximation is in agreement with that found using the full stochastic model; create one new patch and protect four of the five patches.

We emphasize that care should be taken when using this approximation for small metapopulations, as it only uses the expected number of occupied patches and in no way accounts for stochasticity in the process. This is important as it has been identified that habitat disturbance always increases the variability in patch occupancy dynamics (Ross 2006*a*). This is exemplified by consideration of the optimal decision for the greater bilby population with different rates of disturbance s; while the expected number of occupied patches is maximized by creating new patches when the rate of disturbance s is less than approximately 0.46, the probability of extinction is only minimized by creating new patches when the rate of disturbance s is less than ~0.08. However, we know from theory (Kurtz 1970, Pollett 1990, Ross 2006*a*, *b*) that, as the population size increases, the deterministic approximation will become more accurate and consequently the deterministic approximation presented should provide accurate results for population management in situations where the exact computational approach is infeasible.

For our example of a metapopulation with a larger number of patches ($M = 20$), the deterministic approximation predicts a threshold rate of disturbance of $s \approx 0.083$, which is much closer to the exact threshold at rate of disturbance $s \approx 0.057$, demonstrating that the approximation improves with increasing patch numbers. We recommend that the exact computational approach be used when it is feasible to do so, which depends upon the hardware available, time frame used, and management options available. However, this deterministic approximation, and the rule of thumb to follow, should provide accurate results for metapopulations with more than 50 patches, that is, $M > 50$.

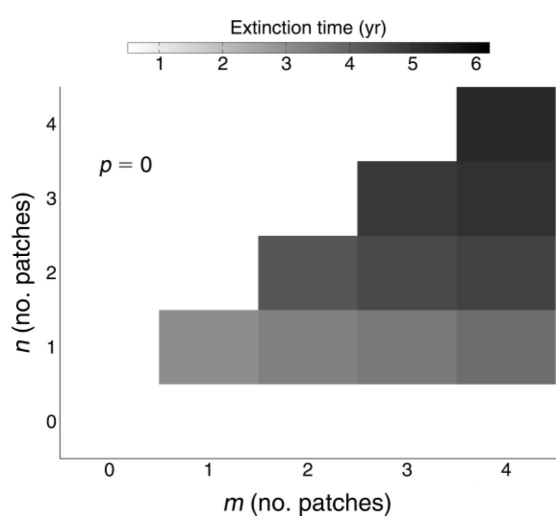

FIG. 4. The expected time to extinction for the greater bilby with no protected patches. Parameter values are colonization rate $c = 3$, local extinction rate $e = 0.1$, rate of patch recovery $r = 2$, rate of habitat disturbance $s = 2/3$, total number of patches $M = 4$, and no protected patches ($M_p = 0$).

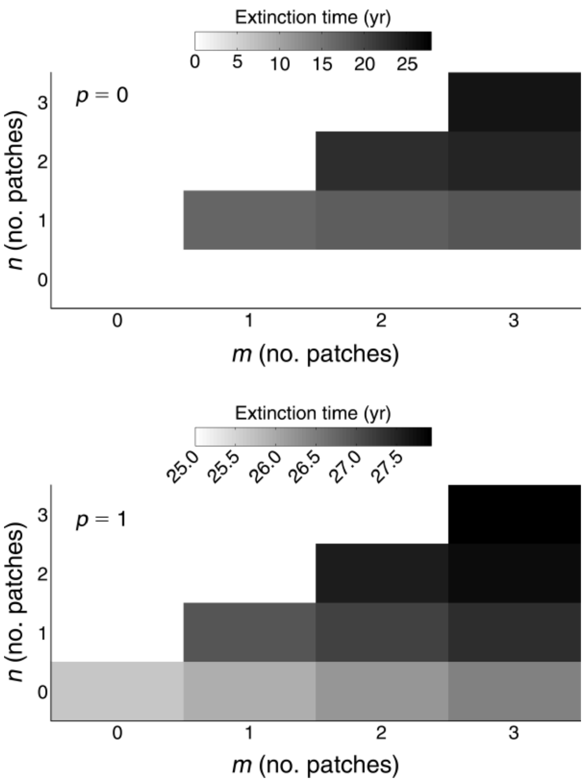

FIG. 5. The expected time to extinction for the greater bilby with one protected patch. Parameter values are colonization rate $c = 3$, local extinction rate $e = 0.1$, rate of patch recovery $r = 2$, rate of habitat disturbance $s = 2/3$, total number of patches $M = 4$, and one protected patch ($M_p = 1$). (Note the different extinction scales for the subplots.)

Rule of thumb

The rule of thumb appeared to be very robust and provided estimates in very good agreement with the deterministic approximation; for the bilby population it predicted that when the disturbance rate s increases over approximately 0.43, patch creation is optimal and, for our larger metapopulation example, it predicted that when the disturbance rate s increases over approximately 0.087, patch creation is optimal (the respective disturbance rate thresholds s^* using the deterministic approximation are $s^* \approx 0.46$ for the bilby population and $s^* \approx 0.083$ for our larger metapopulation example). It suffers from the same failings as the full deterministic approximation, in that it does not account for stochasticity in the process and assumes continuous numbers of individuals, and thus it should be used with care for metapopulations with a small numbers of patches.

Partial protection

Finally we considered the question: What reduction in the disturbance rate s (over all the patches in the metapopulation) would have the same impact on the viability of the bilby population (in terms of 20-year survival probability) as protecting a given number of patches? Such a reduction corresponds to the partial protection of all patches within the metapopulation network. To match the same probability of extinction in 20 years from protecting one patch we would need to reduce the rate of disturbance s from 0.66 to approximately 0.28. For two protected patches, it would need to be reduced to approximately 0.13, and for three protected patches it would need to be reduced to approximately 0.05. Thus, it appears that it is more effective (in this situation) to focus protection on a smaller number of patches, consequently protecting them completely, than averaging this protection amongst all patches (assuming equal cost).

CONCLUSION

Our analysis has identified the importance of protected patches on metapopulation viability in a dynamic landscape. In particular, it has identified the significance of this strategy for metapopulations that are strongly influenced by the dynamics of the landscape they inhabit, such as the greater bilby. The optimal strategy for maximizing metapopulation viability, given a fixed budget and costs for each of two management actions (constructing new patches or protecting patches), was found to depend upon all of the parameter values and costs associated with the species under consideration. In simple cases, the optimal strategy was found to be the obvious one: protect patches when landscape dynamics dominate metapopulation persistence and create patches otherwise. For interesting cases with metapopulation and landscape dynamics occurring on similar time scales, the optimal strategy is not easily deduced without a full exploration of the model. However, we have provided two approximations, including a simple rule of thumb, that are useful for metapopulations consisting of a large number of patches. We have presented, in detail, the optimal strategy for improving the viability of the greater bilby *Macrotis lagotis*; and this methodology can be applied to any metapopulation.

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APPENDIX

Deterministic fixed points and the transformation (*Ecological Archives* A018-018-A1).