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 versus 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 versus increasing the number of protected patches in the network. We discovered that the optimal tradeoff 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 south-western Queensland, Australia. We found that given realistic costs for each action, protection of patches should be prioritised over patch creation for improving the persistence of the greater bilby during the next 20 years.

Introduction

A metapopulation is a collection of interacting subpopulations of the same species, each of which occupies a separate patch of habitat [26, 11, 16, 9]. 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 [22], fish on coral reefs [19] and parasites on hosts [37]. Hence metapopulation models have become a common paradigm for incorporating some spatial structure into population models [9]. 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 [4], the marsh fritillary butterfly (*Euphydyas aurinia*) in Finland [38], the butterfly *Lopinga achine* in Sweden [6], the greater bilby *Macrotis lagotis* in south-western Queensland, Australia [36] and several species, including four endangered polyporous fungi (*Amylocystis lapponica, Fomitopsis rosea, Phlebia centrifuga* and *Cystotereum murraii*), in eastern Finland [12].

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 [18, 20, 24, 5, 10, 33, 34], catastrophes where several patches are disturbed simultaneously [40], age-dependent disturbance [7, 17], and spatially-correlated disturbance [27, 13, 21]. 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 or 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 [28, 23] 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 colonise 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 [26] (corresponding to all patches being immune to disturbance) and the stochastic version of the model of Hess [18] first analysed by Ross [33] 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 south-western Queensland, Australia. The bilby is a type of bandicoot that was once distributed over 70% of the arid and semi-arid 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 south-western Queensland. This decline has resulted in the bilby being classified as *vulnerable* to extinction [3]. 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 [3, 2, 29, 36]. 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 [29, 36]. 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 [32], whether it is better to expand existing patches, link existing patches via corridors, or create a new patch [39], and also to optimising reserve expansion — which areas of habitat should be reserved [15, 14]. 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 maximise the probability of population persistence during the next 20 years. We also considered two approximations which may be useful for addressing the protection versus 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 number of unsuitable patches at time t is $M_u - m(t)$. We now list the possible changes in the state of the system which our model allows 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
Colonisation of unprotected, unoccupied patch	$(m, n, p) \to (m, n+1, p)$	$c\frac{(n+p)}{M}(m - n)$
Local extinction at unprotected, occupied patch	$(m, n, p) \to (m, n-1, p)$	en
Colonisation of protected, unoccupied patch	$(m, n, p) \to (m, n, p+1)$	$c\frac{(n+p)}{M}(M_p - p)$
Local extinction at protected, occupied patch	$(m, n, p) \to (m, n, p-1)$	ep

The parameters of the model are listed in the table below.

Parameters
$e =$ the rate at which a local population becomes extinct
$c =$ the rate at which an empty patch is colonised 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
$M_p =$ the number of protected patches in the system

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 maximising the expected number of occupied patches.

The deterministic approximation of our model, derived from the theory of density-dependent Markov population processes (see [25, 30, 33, 34]), 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 colonisation of suitable, unprotected patches where $z(= p/M)$ is the fraction of occupied, protected patches and c is the patch colonisation 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 colonisation of protected patches where c is the patch colonisation 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 [33], 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 behaviour 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) [8, 40, 31, 23] of the metapopulation for certain parameter values and strategies. The quantities were evaluated by constructing a matrix $Q = (q(i,j), i, j \in S_M)$, 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 $q(i) := \sum_{j \neq i} q(i,j)$ is the total rate at which we move out of state i. Then, the probability distribution of the process at time t, $p(t)$, is given by $p(t) = p(0)\exp(Qt)$, where $p(0)$ is the initial distribution of the process, and exp is the matrix exponential (see, for example, [28, 23]). We evaluated the matrix exponential using the `mexpv` function from EXPOKIT [35], 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 $p(t)$ corresponding to states of extinction. The expected time to extinction was evaluated by solving a system of linear equations: $Q_C \tau = -\mathbf{1}$, where $\mathbf{1}$ is a vector of 1s and Q_C is the matrix Q after removing all rows and columns corresponding to the states of extinction; the expected time to extinction starting from state i is then the i-th element of the vector τ (see, for example, [28, 23]). The quasi-stationary distribution is given by the unique solution $\pi = (\pi_i, i \in C)$ to $\pi Q_C = -\nu\pi$ and $\sum_{i \in C} \pi_i = 1$, where $-\nu$ is the eigenvalue of Q_C with smallest magnitude (see, for example, [31, 23]). This was evaluated numerically using the `eigs` function in Matlab. 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 maximisation 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 unfavourable, 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 [18, 33].

Our goal is to maximise $(y^* + z^*)[M_p + M_u + N_u + (N_p - M_u)^+]$ 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 optimisation 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 populations 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 optimisation problem is:

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

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 maximises our objective function may be easily evaluated numerically using Matlab or Maple.

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 $(1 - e/c)$ [26, 33], and the equilibrium patch occupancy density for unprotected patches (in isolation) is $[r/(r+s) - (e+s)/c]$ [18, 33]. 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

$$\left(\frac{r}{r+s} - \frac{e+s}{c}\right)\left[N_u + (M_u - N_p)^+\right] + \left(1 - \frac{e}{c}\right)(M_p + N_p), \qquad (8)$$

which we wish to maximise. Once again N_u can be expressed as a function of N_p since we will expend our entire budget B. By differentiating (8) with respect to N_p we arrive at a simple rule of thumb: we should protect patches if

$$\left[\left(1 - \frac{e}{c}\right) - \left(\frac{r}{r+s} - \frac{e+s}{c}\right)\right]\frac{1}{b_p} > \left(\frac{r}{r+s} - \frac{e+s}{c}\right)\frac{1}{b_u}, \qquad (9)$$

otherwise we should create new patches. That is, if the ratio of marginal benefit to marginal cost due to protecting a patch (left-hand side of inequality (9)) is greater than the ratio of marginal benefit to marginal cost due to creating a patch (right-hand side of inequality (9)) 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 prioritise patch creation, and for disturbance rates s greater than s^* we should prioritise patch protection.

Results

Investigation of the system for particular values showed that it settled down to something like a deterministic equilibrium (Figures 1 & 2). However it is not a true equilibrium as the only true equilibrium is extinction of the species. The behaviour exhibited is known as quasistationarity [40, 31].

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 colonisation parameter c and the local extinction rate e, and where possible those that have been used previously (see [36]): $r = 2, s = 2/3, c = 3$ and $e = 1/10$ per year.

Increasing the number of patches protected had a significant positive effect on the persistence of the bilby (Figure 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 (Figures 4 & 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. Figure 4 and Figure 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.

Our next consideration is that of finding an optimal strategy for maximising 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 ([1]). We assumed a fixed budget for the 20 year period of \$12 million, a cost of \$4 million for constructing a new patch suitable for bilby occupancy, and a cost of $\$100,000$ per patch per year (i.e. \$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 of protected patches. 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 \$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 disturbance rate $s = 1/13$ (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 prioritised.

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 colonisation rate $c = 1$, local extinction rate $e = 1/2$, 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 emphasise 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 [33]. This is exemplified by consideration of the optimal decision for the greater bilby population with different rates of disturbance s; whilst the expected number of occupied patches is maximised by creating new patches when the rate of disturbance s is less than approximately 0.46, the probability of extinction is only minimised by creating new patches when the rate of disturbance s is less than approximately 1/13. However, we know from theory [25, 30, 33, 34] 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 $M > 50$.

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 maximising 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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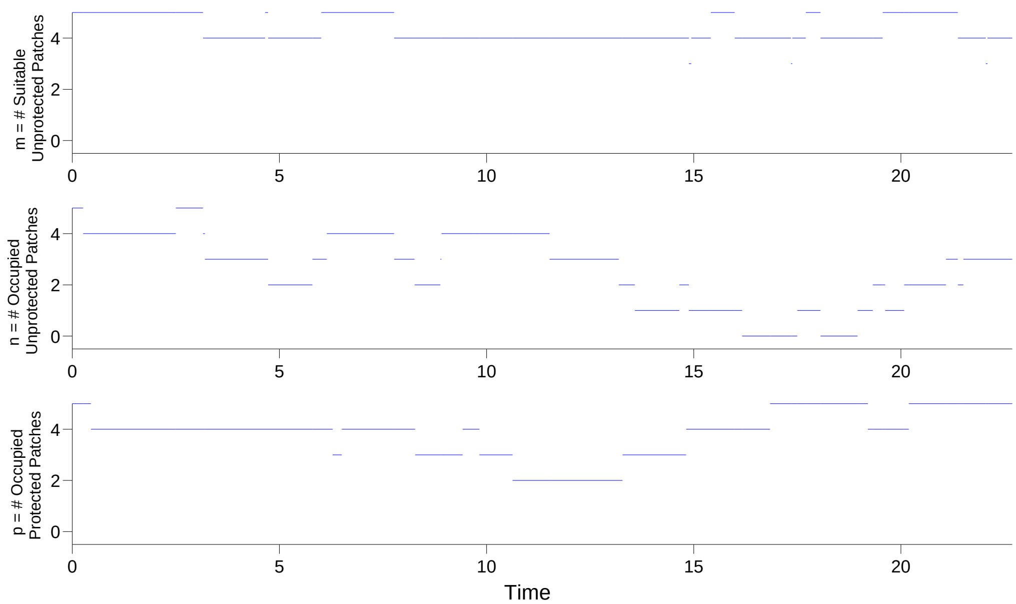

Figure 1:

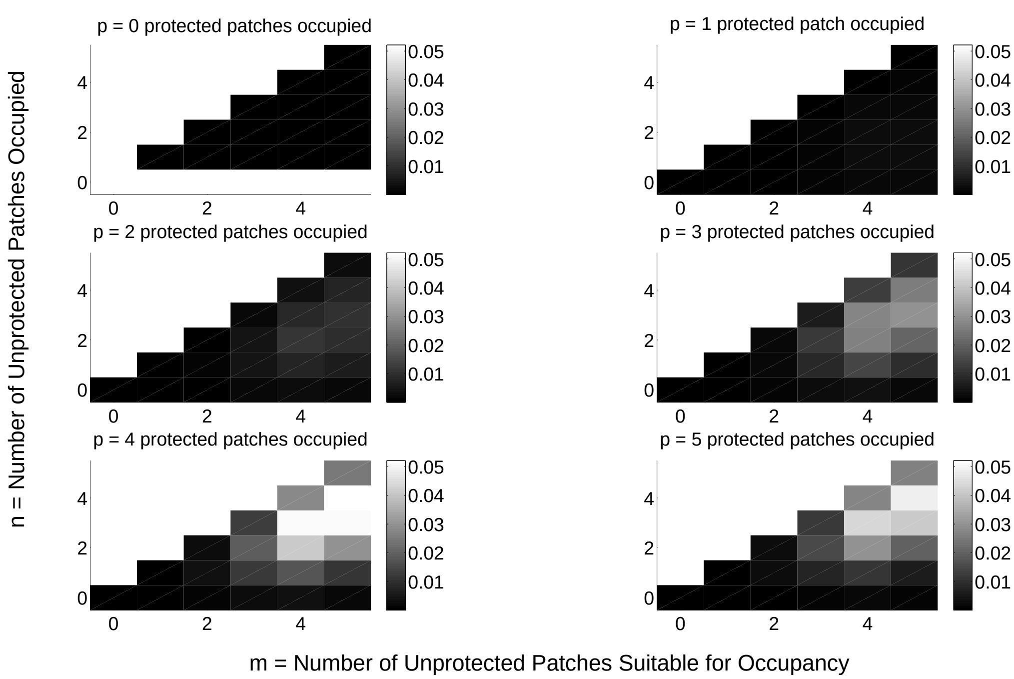

Figure 2:

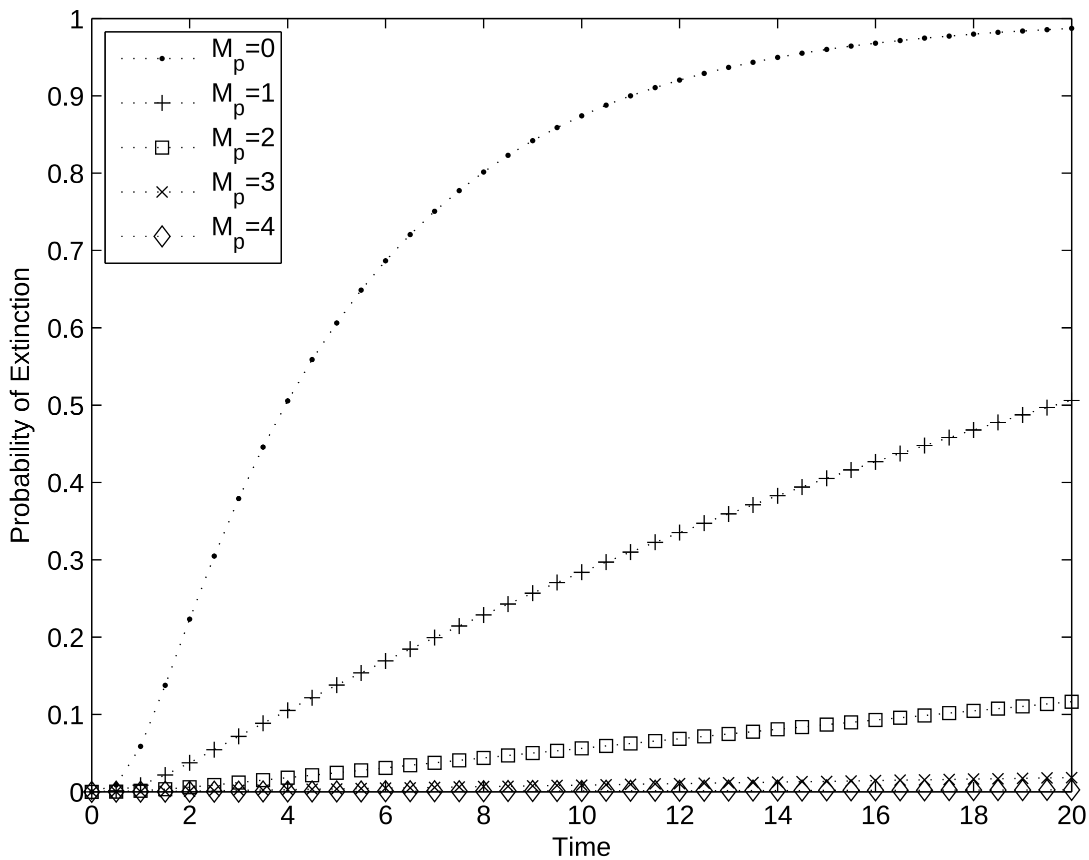
M_p=0
M_p=1
M_p=2
M_p=3
M_p=4
Probability of Extinction
Time
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
2
4
6
8
10
12
14
16
18
20

Figure 3:

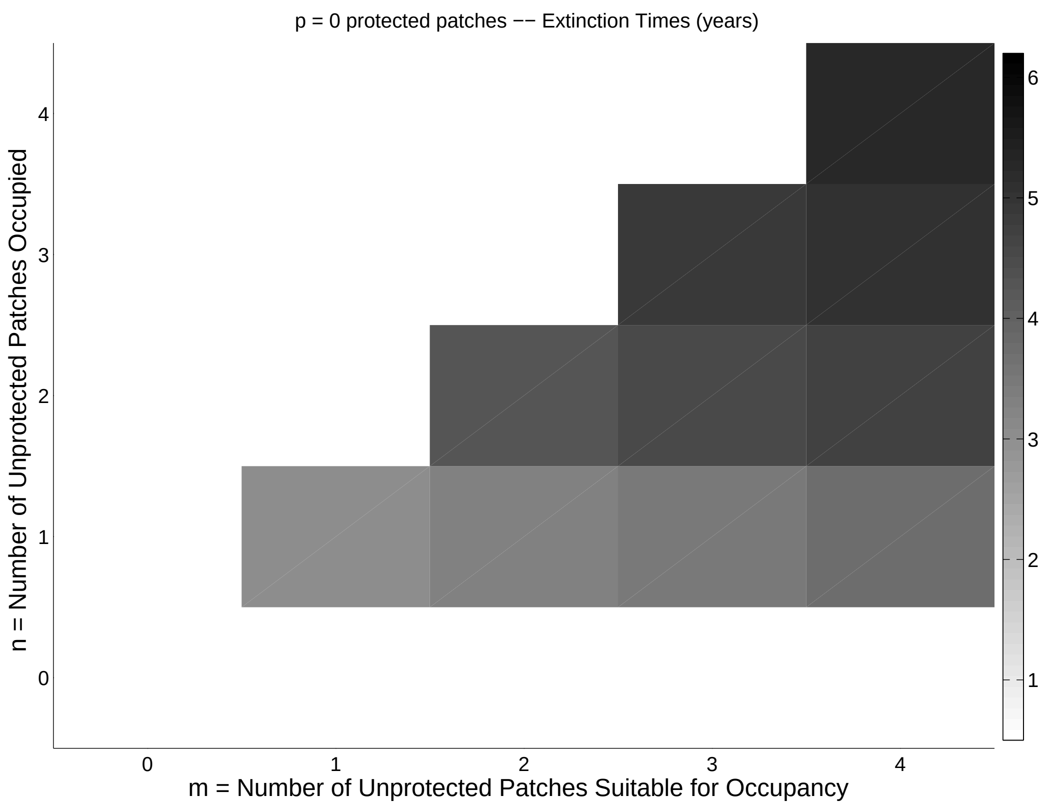
p = 0 protected patches −− Extinction Times (years)
n = Number of Unprotected Patches Occupied
m = Number of Unprotected Patches Suitable for Occupancy
0
1
2
3
4
6
5
4
3
2
1

Figure 4:

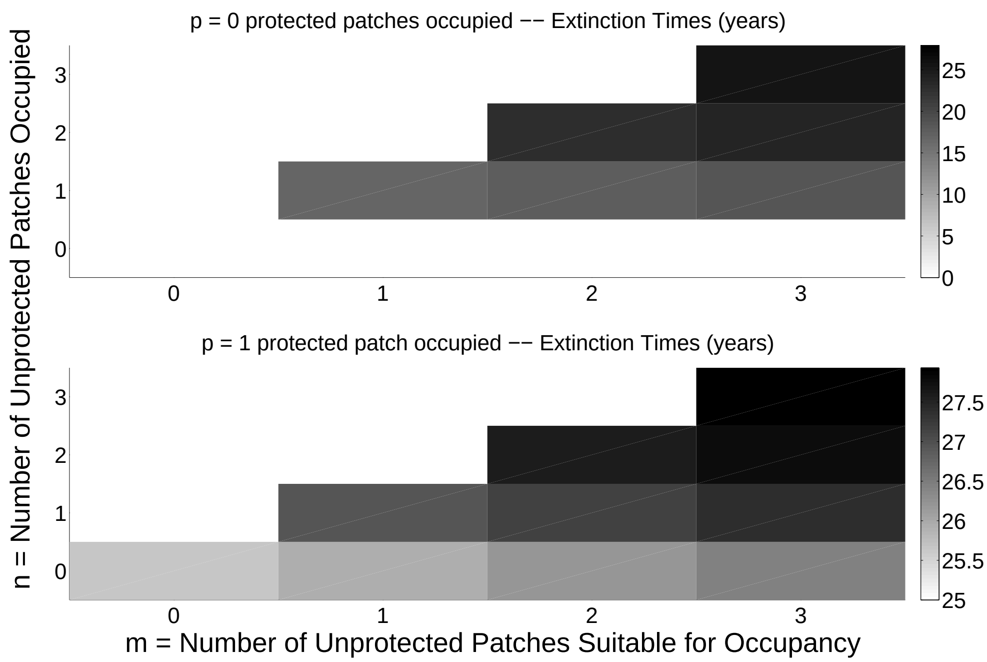
p = 0 protected patches occupied −− Extinction Times (years)
p = 1 protected patch occupied −− Extinction Times (years)
n = Number of Unprotected Patches Occupied
m = Number of Unprotected Patches Suitable for Occupancy
0
1
2
3
25
20
15
10
5
27.5
27
26.5
26
25.5

Figure 5:

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. Parameters are colonisation 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 $M_p = 5$.

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 Figure 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 varies from plot to plot.

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 (4), a fixed initial number of suitable patches (4) and a fixed initial number of occupied patches (4), with all protected patches being occupied initially. Parameters are colonisation 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 number of protected patches $M_p = 0, 1, 2, 3, 4$ respectively.

Fig. 4. The expected time to extinction (years) for the greater bilby with no protected patches. Parameter values are colonisation 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 (years) for the greater bilby with one protected patch. Parameter values are colonisation 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 different scale for each subplot.)

Appendix

The deterministic system

The deterministic system which arises in the limit as the number of patches tends to infinity and the proportions of protected and susceptible patches remain constant is

$$\begin{aligned}
\frac{dx}{dt} &= r(\rho_u - x) - sx, \\
\frac{dy}{dt} &= c(y+z)(x-y) - (e+s)y, \\
\frac{dz}{dt} &= c(y+z)(\rho_p - z) - ez.
\end{aligned}$$

Setting the three derivatives equal to 0 and solving for $w^* = (x^*, y^*, z^*)$ we get the trivial fixed point $w_0^* = (\frac{r\rho_u}{r+s}, 0, 0)$ and also $w_1^* = (x_1^*, y_1^*, z_1^*)$, where

$$\begin{aligned}
x_1^* &= \frac{r\rho_u}{r+s}, \\
y_1^* &= \frac{(e+s)(r+s)(c(\rho_p - \alpha_1) - e) + cre\rho_u}{ec(r+s)}, \\
z_1^* &= \alpha_1,
\end{aligned}$$

and α_1 is a root of

$$\begin{aligned}
\alpha(z) &= sc(r+s)z^2 + ((r+s)(se - 2sc\rho_p) - ce(r + s\rho_p))\, z \\
&\quad + ce\rho_p(r + s\rho_p) + \rho_p(r+s)(sc\rho_p - se - e^2).
\end{aligned}$$

We can see immediately that in order for this fixed point to be in the appropriate state space $\bar{S} = [0, \rho_u]^2 \times [0, \rho_p]$ it is necessary that $\alpha_1 \in [0, \rho_p]$. In addition we observe numerically that if α has two roots in the interval $[0, \rho_p]$ then using the larger root results in y_1^* being negative. The fixed point w_1^* we seek is therefore that obtained by taking α_1 as the smallest root of $\alpha(z)$ in the interval $[0, \rho_p]$, and if α has no such root then w_0^* is the only fixed point in $\bar{S}$. One can then determine the stability of these fixed points by looking at the eigenvalues of the Jacobian matrix

$$J(x,y,z) = \begin{pmatrix} -(r+s) & 0 & 0 \\ c(y+z) & c(x-2y-z)-e-s & c(x-y) \\ 0 & c(\rho_p - z) & c(\rho_p - 2z - y) - e \end{pmatrix}.$$

Although some progress can be made in this direction analytically, the formulae so derived are cumbersome and relatively uninformative, so we evaluated the fixed points and determined their stability numerically.

The transformation

Here we describe the transformation used to map the state space S to a set of the form $\{1, 2, \ldots, N\}$, so that numerical calculations could be performed. The state space S is the triangular prismoidal set $S = \{(m,n,p) \in \mathbb{Z}^3 : 0 \leq n \leq m \leq M_u, 0 \leq p \leq M_p\}$ and we wished to transform this to a set of the form $\{1, 2, \ldots, N\}$. It can be easily shown that $N = (M_p+1)(M_u+1)(M_u+2)/2$. One mapping which achieves this is $(m,n,p) \to m + 1 + n\left(M_u - \frac{n-1}{2}\right) + p(M_u+1)(M_u+2)/2$, which has the additional property that the absorbing (extinct) states $(m,0,0)$ map to $\{1, 2, \ldots, M_u+1\}$, which simplified coding.

We also needed to invert this transformation following computations. To do this we firstly noted that the transformation is of the form $y = f_1(n,m,M_u) + pf_2(M_u)$, so that $p = y - 1 \pmod{(M_u+1)(M_u+2)/2}$, and then $j = y - p(M_u+1)(M_u+2)/2$ is sufficient to determine $m, n \in \{0 \leq m \leq n \leq M_u\}$. We did this by checking successive possible values of n, and subsequently found m.