

Patch Dynamics and Metapopulation Theory: The Case of Successional Species

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Abstract

We present a mathematical framework that combines extinction–colonization dynamics with the dynamics of patch succession. We draw an analogy between the epidemiological categorization of individuals (infected, susceptible, latent and resistant) and the patch structure of a spatially heterogeneous landscape (occupied–suitable, empty–suitable, occupied–unsuitable and empty–unsuitable). This approach allows one to consider life-history attributes that influence persistence in patchy environments (e.g., longevity, colonization ability) in concert with extrinsic processes (e.g., disturbances, succession) that lead to spatial heterogeneity in patch suitability. It also allows the incorporation of seed banks and other dormant life forms, thus broadening patch occupancy dynamics to include sink habitats. We use the model to investigate how equilibrium patch occupancy is influenced by four critical parameters: colonization rate, extinction rate, disturbance frequency and the rate of habitat succession. This analysis leads to general predictions about how the temporal scaling of patch succession and extinction–colonization dynamics influences long-term persistence. We apply the model to herbaceous, early-successional species that inhabit open patches created by periodic disturbances. We predict the minimum disturbance frequency required for viable management of such species in the Florida scrub ecosystem.

Introduction

Understanding how populations persist in patchy environments is a central problem in basic and applied ecology. Metapopulation theory focuses on the dynamics of patch occupancy as a function of extinctions and colonizations (Levins, 1969, 1970; Gilpin & Hanski, 1991; Day & Possingham, 1995; Hanski & Gilpin, 1997). An implicit assumption in this framework is that patches themselves do not change in terms of their quality or suitability. The only distinction between patches is whether they are occupied or empty. All empty patches are considered suitable for colonization. This framework emphasizes the life-history attributes of species that influence extinction-colonization dynamics (e.g., longevity, dispersal ability). It does not consider spatial heterogeneity in patch suitability.

Patch dynamics theory on the other hand, focuses on changes in the state of patches themselves (Picket & White 1985; Levin et al., 1993; Wu & Loucks, 1995). Patches are defined in terms of whether they are suitable or unsuitable for colonization. For example, succession, litter accumulation and invasions by natural enemies may cause patches to become unsuitable. Disturbances may reverse these biotic processes and make patches suitable for colonization. This framework emphasizes the role of spatial heterogeneity in extinction-colonization dynamics.

Here, we present a mathematical framework that combines both approaches. This broad perspective is useful for several reasons. First, it introduces an element of spatial heterogeneity to the patchy but spatially homogeneous landscapes envisioned in

metapopulation theory. Second, it emphasizes the temporal scaling of patch dynamics with population dynamics of the species that occupy patches. This scaling relationship is key to understanding how the dynamics of patch suitability (e.g., succession and disturbance) influence extinction-colonization dynamics.

Our approach is two fold. First, we use the framework to make general predictions about how life history and habitat characteristics act in concert to determine long-term habitat occupancy. Second, we apply the theory to a specific biological example: herbaceous, early successional plant species that inhabit gaps maintained by periodic fire in the Rosemary phase of the Florida sand pine scrub. We are particularly interested in predicting the minimum disturbance frequency required for long-term persistence at an acceptable level of patch occupancy.

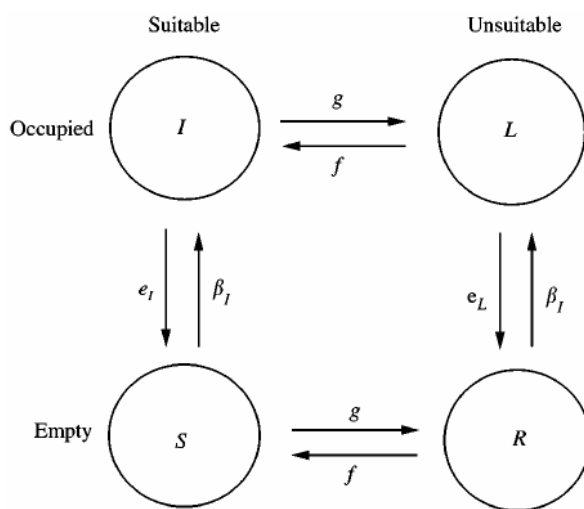


Figure 1. State transitions between the four patch types for a successional species. Note that the resistant patches consist of late-successional vegetation and hence difficult to colonize for early-successional species. Any individuals that colonize resistant patches will stay dormant until a disturbance occurs. Hence $e_L \gg \beta_L$ and $\beta_L \ll \beta_I$, making $\beta_L R I$ a vanishingly small term.

The Model

In classical metapopulation theory the landscape consists of only two types of patches: occupied patches and suitable but empty patches (Levins, 1969, 1970; Levins & Culver, 1971; Slatkin, 1974; Hastings, 1980). In patch dynamics theory the landscape also consists of two types of patches: those that are suitable for colonization and those that are unsuitable (Pickett & White, 1985; Levin et al., 1993; Wu & Loucks, 1995). Merging the two perspectives leads to a landscape characterized by four types of patches: occupied-suitable, unoccupied-suitable, occupied-unsuitable and unoccupied-unsuitable.

We introduce a patch nomenclature that is drawn from epidemiological theory (May & Anderson, 1979; Anderson & May, 1991). Lawton et al. (1994) and Nee (1994) noted a direct analogy between the metapopulation and epidemiological approaches: occupied patches are the equivalent of infected individuals (I), and empty patches, the

susceptible individuals (S). Here we extend this analogy. We use an early-successional species as an example.

For an early successional species empty, unsuitable patches are those that are dominated by late successional species. Such patches are the equivalent of individuals that are resistant or become temporarily immune to the disease (type R; Fig. 1). Disturbances such as fire will convert resistant patches to empty but suitable patches (type S). These patches are now susceptible to colonization by the early successional species. Once colonized, they become infected patches (type I).

Over time, patches occupied by the early successional species will be invaded by late-successional species. Litter accumulation and shading by these competitive dominants will make the patch unsuitable for seedling recruitment (Rees & Paynter, 1997). Individuals will senesce and eventually above-ground plant parts will die, giving the appearance of local extinction (Noble & Slatyer, 1981). However, the patch may contain a seedbank or some other dormant form of the life cycle (Zammit & Zedler, 1993). Such patches could also be thought of as refuges from predators or pathogens where the plant can survive but cannot reproduce. Pursuing the epidemiological analogy, a patch of this sort would be equivalent to a latent individual (type L) that is infected but cannot transmit the disease (cf. Grenfell & Harwood, 1997). Latent patches are essentially sink populations in time or space. Disturbances that reverse the successional process (e.g., fire) can bring the seeds out of dormancy and revert latent patches to the occupied, suitable patches (type I). Extinction of seed banks or other dormant life stages from latent patches will in turn give rise to resistant patches. Fire can complete the cycle by converting resistant patches to empty but suitable patches (Fig. 1). Note that only infected patches can create latent or infected patches, and that the rate at which patches become suitable or unsuitable is independent of whether or not it is occupied. In other words, patch occupancy is a function of the species' biology (e.g., fecundity, longevity, colonization ability) while patch availability is a function of processes extrinsic to the species (e.g., disturbance, litter accumulation, invasion by competitive dominants, and predation).

We use a system of differential equations to represent the dynamics of the four patch-type system:

$$\begin{aligned}\frac{dI}{dt} &= \beta_I SI - e_I I + fL - gI, \\ \frac{dS}{dt} &= e_I I - \beta_I SI + fR - gS, \\ \frac{dL}{dt} &= gI - fL - e_L L + \beta_L RI, \\ \frac{dR}{dt} &= gS - fR + e_L L - \beta_L RI.\end{aligned}\quad (1)$$

Here f is the disturbance frequency and g , the rate of habitat succession. Quantities e_I and e_L represent local extinction rates, and β_I and β_L the per patch colonization rates of

infected and latent patches, respectively. As in epidemiological theory (May & Anderson, 1979; Anderson & May, 1991; Grenfell & Harwood, 1997), the total number of patches in the system is assumed to be constant such that $I + S + L + R = P$. Alternatively, $I, S, L,$ and R can be thought of as the frequency of each patch type in the landscape in which case $I + S + L + R = 1$.

The Levins metapopulation model (Levins, 1969, 1970) arises as a special case of eqn (1) when we ignore the distinction between suitable and unsuitable patches. Equation (1) has two fixed points, a trivial fixed point with the successional species absent:

$$I_1^* = 0, \quad L_1^* = 0,$$

$$S_1^* = \frac{f}{f+g}, \quad R_1^* = \frac{g}{f+g} \quad (2)$$

and an internal fixed point with the successional species present in both active and dormant stages:

$$I_2^* = \frac{-b + \sqrt{b^2 - 4ac}}{2a},$$

$$S_2^* = \frac{b + 2\beta_I\beta_L\left(\frac{f}{f+g}\right) - \sqrt{b^2 - 4ac}}{2a},$$

$$R_2^* = \frac{\beta_L(e_I(f + e_L) + g(e_L - f)) - \beta_I(f + e_L)\left(\beta_L\left(\frac{f}{f+g}\right) + (f + e_L)\right) + \sqrt{b^2 - 4ac}}{2\beta_L^2 f},$$

$$L_2^* = 1 - I_2^* - S_2^* - R_2^*,$$

where

$$a = \beta_I\beta_L,$$

$$b = \beta_I(f + e_L) + \beta_L(e_I + g) - \beta_I\beta_L\left(\frac{f}{f+g}\right)$$

and

$$c = (f + e_L)\left(e_I - \beta_I\left(\frac{f}{f+g}\right)\right) + g\left(e_L - \beta_L\left(\frac{f}{f+g}\right)\right). \quad (3)$$

From eqn (3) it can be seen that $I_2^* > 0$ if $c < 0$. By transforming c , we get the following criterion for a positive internal fixed point:

$$-\frac{(\beta_I - e_I)}{(f + g)} \left(f^2 + f \left(e_L + g \frac{\beta_L - (e_I + e_L)}{\beta_I - e_I} \right) - \frac{ge_L(g + e_I)}{\beta_I - e_I} \right) < 0. \quad (4a)$$

In the absence of succession, disturbance or other factors that influence patch suitability, eqn (4a) simplifies to $\beta_I - e_I > 0$, the persistence criterion of the classical Levins metapopulation model. For instance, when $g = 0$ and $e_L = 0$, patches are always suitable and hence latent and resistant patches do not exist. When $g > 0$ however, persistence additionally requires positivity of the second-order polynomial in f . This will occur as long as

$$f > - \left(\frac{e_L}{2} + g \frac{\beta_L - (e_I + e_L)}{2(\beta_I - e_I)} \right) + \sqrt{\left(\frac{e_L}{2} + g \frac{\beta_L - (e_I + e_L)}{2(\beta_I - e_I)} \right)^2 + \frac{ge_L(g + e_I)}{\beta_I - e_I}}. \quad (4b)$$

In the presence of succession, metapopulation persistence requires that the disturbance frequency f exceeds the minimum specified by eqn (4b).

Note that $I^* + S^* = f / (f + g)$ and $L^* + R^* = g / (f + g)$. This is because the transition between suitable and unsuitable patches is independent of whether patches are occupied or empty. Hence it is always true that the fraction of suitable patches is $f / (f + g)$ and the fraction of unsuitable patches is $g / (f + g)$. Moreover, $0 < I_2^* \leq f / (f + g)$ necessarily implies $0 \leq S_2^* < f / (f + g)$, $0 \leq R_2^* < g / (f + g)$, and $0 < L_2^* \leq g / (f + g)$.

Local stability of the two fixed points determines whether successional species can invade and persist in the landscape. An unstable trivial fixed point implies invasibility, while a stable internal fixed point implies long-term persistence.

We first investigate whether the successional species can invade when rare. Invasion will succeed if the dominant eigenvalue of the Jacobian matrix is positive when evaluated at the trivial fixed point.

The Jacobian of eqn (1) with $L = 1 - S - R$ is

$$\begin{bmatrix} -e_I - f - g + \beta_I S^* & \beta_I I^* - f & -f \\ e_I - \beta_I S^* & -g - \beta_I I^* & f \\ -e_L - \beta_L R^* & g - e_L & -e_L - f - \beta_L I^* \end{bmatrix}.$$

The eigenvalues of the Jacobian evaluated at

$(I_1^* = 0, S_1^* = f/(f + g), L_1^* = 0, R_1^* = g/(f + g))$
 are: $-f - g, (-x - \sqrt{x^2 - 4y})/2$ and $(-x + \sqrt{x^2 - 4y})/2$ where

$$x = -\beta_I \left(\frac{f}{f + g} \right) + e_I + e_L + f + g$$

and

$$y = (f + e_L) \left(e_I - \beta_I \left(\frac{f}{f + g} \right) \right) + g \left(e_L - \beta_L \left(\frac{f}{f + g} \right) \right).$$

Note that $x^2 > 4y$ for all positive values of β_I, β_L, f and g . All eigenvalues are therefore real, and the transition from stability to instability involves a zero real root (Gurney & Nisbet, 1998). Hence, the system defined by eqn (1) does not exhibit oscillatory instability.

The dominant eigenvalue is $(-x + \sqrt{x^2 - 4y})/2$, and its sign is determined by the magnitude of y . For instance, when $y = 0$ the dominant eigenvalue is negative and the trivial fixed point $[I_1^* = 0, S_1^* = f/(f + g), L_1^* = 0, R_1^* = g/(f + g)]$ is stable to invasion by the successional species. When $y < 0$, the dominant eigenvalue is positive and the successional species can invade when rare. The invasion criterion is therefore

$$\beta_I \left(\frac{f}{f + g} \right) + \beta_L \left(\frac{g}{f + g} \right) > e_I \rightarrow \frac{e_L}{f} \left(e_I + g - \beta_I \left(\frac{f}{f + g} \right) \right). \quad (5)$$

A few manipulations reveal that the invasion criterion [eqn (5)] is the same as the persistence criterion derived previously [eqn (4a)]. Conditions that allow the successional species to maintain a non-zero abundance also ensure its invasion and spread.

The invasion criterion is a necessary but not sufficient condition for long-term persistence. We next investigate the local stability of the internal fixed point.

The eigenvalues of the Jacobian are the roots of the characteristic equation

$$\lambda^3 + A_1 \lambda^2 + A_2 \lambda + A_3 = 0,$$

where

$$A_1 = e_I + e_L + 2(f + g) + I_2^*(\beta_I + \beta_L) - \beta_I S_2^*,$$

$$\begin{aligned} A_2 = & (f + g)^2 + e_I(e_L + 2f + g) + e_L(f + 2g) \\ & - \beta_I \beta_L I_2^* S_2^* - (\beta_I(e_L + 2f + g)) S_2^* \\ & - \beta_L f R_2^* + \beta_I \beta_L I_2^{*2} \\ & + (\beta_I(e_L + 2f + g) + \beta_L(e_I + f + 2g)) I_2^* \end{aligned}$$

and

$$\begin{aligned} A_3 = & (f + g)(\beta_I \beta_L I_2^{*2} + (\beta_I(f + e_L) + \beta_L(g + e_I)) \\ & - \beta_I \beta_L S_2^*) I_2^* + e_I(f + e_L) + g e_L \\ & - \beta_I S_2^*(f + e_L) - \beta_L f R_2^*. \end{aligned}$$

The Routh-Hurwitz criteria for the stability of the equilibrium are $A_1 > 0$, $A_3 > 0$ and $A_1 A_2 - A_3 > 0$ (May, 1974; Gurney & Nisbet, 1998). As mentioned previously, the transition from stability to instability involves a zero real root rather than a complex root with zero real parts. Since there is no oscillatory instability involved, the important criterion for stability is $A_3 > 0$ (Gurney & Nisbet, 1998).

A little manipulation reveals that $A_3 > 0$ if

$$I_2^* > \frac{-b' + \sqrt{b'^2 - 4a'c'}}{2a'},$$

where

$$a' = \beta_I \beta_L,$$

$$b' = \beta_I(f + e_L) + \beta_L(g + e_I) - \beta_I \beta_L S_2^*$$

and

$$c' = (f + e_I)(e_I - \beta_I S_2^*) + g e_L - \beta_L f R_2^*. \quad (6)$$

But, $I_2^* = (-b + \sqrt{b^2 - 4ac})/2a$ with a , b and c defined as in eqn (3). Also $S_2^* < f/(f + g)$ and $R_2^* < g/(f + g)$. Comparing eqns (3) and (6) reveals that $b < b'$ and $c < c'$. Hence, the inequality in eqn (6) is always satisfied. The internal fixed point is stable when it exists.

In summary, when the internal fixed point is positive (persistence), the trivial fixed point becomes unstable, i.e., the successional species can invade when rare. The internal fixed point, when positive, is asymptotically stable.

We next investigate how the four key parameters (colonization rate, extinction rate, disturbance frequency and rate of habitat succession) influence equilibrium patch occupancy. The functional form of I_2^* reveals that it depends only on the ratios f/β_I , g/β_I , e_I/β_I , e_L/β_I and β_L/β_I . We use $1/\beta_I$ as the time scale and analyse I_2^* in terms of these scaled parameters. This approach allows us to emphasize the temporal scaling of patch dynamics with extinction-colonization dynamics.

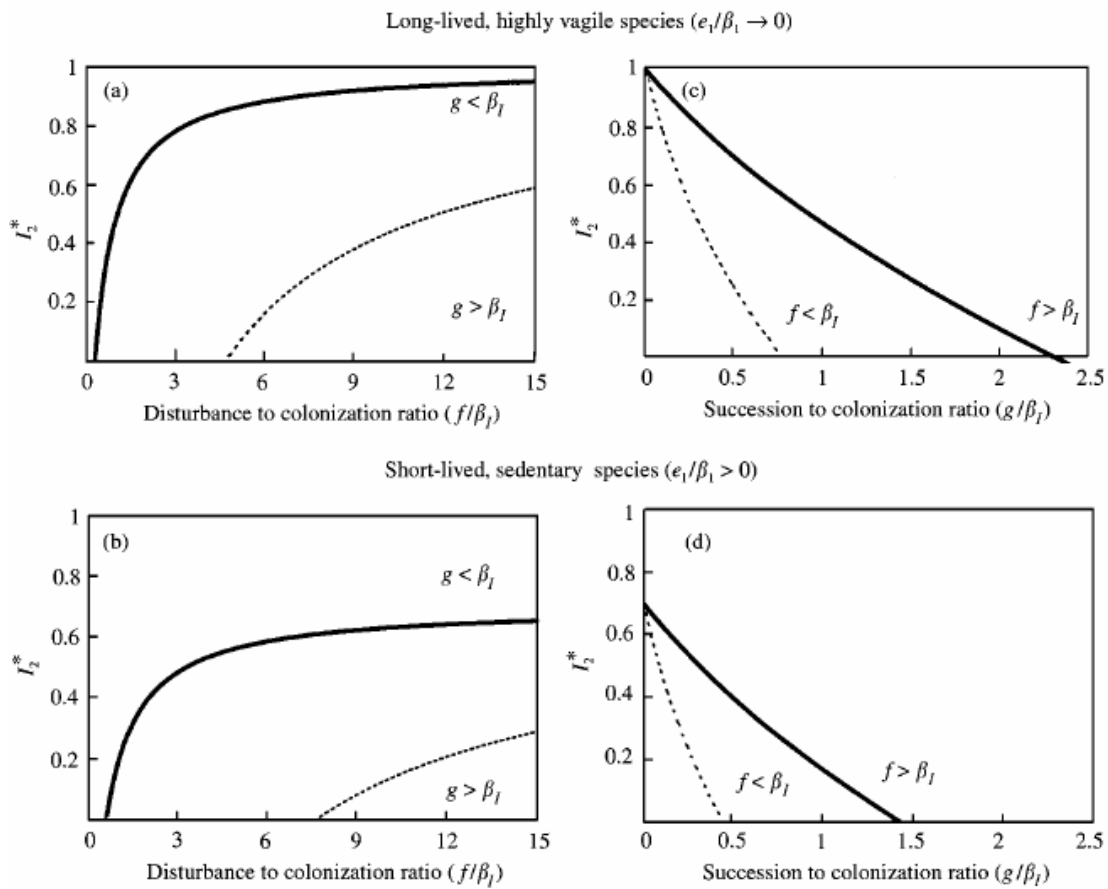


Figure 2. Change in equilibrium patch occupancy (I_2^*) with ratios of key parameters. Panel (a) depicts the relationship between I_2^* and f/β_I for $g/\beta_I < 1$ (solid curve) and $g/\beta_I > 1$ (dashed curve) when $e_I/\beta_I = 0$. Note that when $g \rightarrow 0$ or $f \rightarrow \infty$, $I_2^* \rightarrow 1 - e_I/\beta_I$, the equilibrium fraction of occupied patches in the Levins model. Panel (b) illustrates the same set of relationships when $e_I/\beta_I = 0$. Panels (c) and (d) depict how I_2^* changes with g/β_I for $e_I/\beta_I = 0$ and $e_I/\beta_I > 0$, respectively. In each panel, the solid curve is for $f/\beta_I > 1$ and the dashed curve, $f/\beta_I < 1$. Other parameter values are as follows: $\beta_L/\beta_I = 0.001$, $e_L/\beta_I = 0.5$.

Figure 2 summarizes the main results of this analysis. Panels 2a and 2b illustrate how the scaling of disturbance frequency and per patch colonization rate of occupied, suitable patches (f/β_I) influences equilibrium patch occupancy (I_2^*). Note that the colonization rate depends on the life history attributes of the species such as fecundity

and dispersal, while disturbance frequency is determined by processes extrinsic to the species' biology. The key result here is the asymptotic relationship between I_2^* and f/β_I . In other words, increasing the disturbance frequency relative to the colonization rate yields diminishing returns on I_2^* . The exact nature of this relationship depends on how the rate of succession of the habitat scales with the colonization rate (g/β_I). For instance, when succession rate is low relative to colonization rate, the species will establish even at very low values of f/β_I . On the other hand, when the rate of habitat succession is faster than the species' ability to colonize new patches, then there is a threshold value of f/β_I below which the species will not be able to establish itself [compare the two curves in Fig. 2(a)]. This threshold can be calculated using the persistence criterion in eqn (4):

$$\left(\frac{f}{\beta_I}\right)_{cr} = -\left(\frac{e_L}{2\beta_I} + g \frac{\beta_L - (e_I + e_L)}{2\beta_I(\beta_I - e_I)}\right) + \sqrt{\left(\frac{e_L}{2\beta_I} + g \frac{\beta_L - (e_I + e_L)}{2\beta_I(\beta_I - e_I)}\right)^2 + \frac{ge_L(g + e_I)}{\beta_I^2(\beta_I - e_I)}} \quad (7)$$

The qualitative nature of the relationship between I_2^* and f/β_I does not depend on the scaling relationship between extinction rate and the colonization rate. For example, species that are highly vagile or long-lived ($e_I/\beta_I \rightarrow 0$), exhibit the same asymptotic relationship as do species that are relatively sedentary or short-lived [$e_I/\beta_I > 0$; compare Figs 2(a) and (b)]. There is a quantitative difference in that the former will occupy a higher proportion of the habitat at equilibrium compared to the latter for all values of f/β_I . Figures 2(c) and (d) illustrate how the scaling of habitat succession rate with colonization rate influences equilibrium patch occupancy. Equilibrium patch occupancy declines as the rate of succession increases relative to colonization rate.

This decline is faster than linear when disturbance frequency is low relative to the colonization rate. It is roughly linear when disturbance frequency is high [Fig. 2(c)]. As before, the scaling of e_I with β_I does not change the qualitative nature of the relationship between I_2^* and g/β_I . It merely lowers the equilibrium patch occupancy for relatively sedentary or short-lived species (cf. Figs 2(c) and (d)).

These results can be compared with predictions of classical metapopulation theory (Levins, 1969, 1970; Gilpin & Hanski, 1991). Metapopulation theory predicts that a species will persist in the landscape as long as the colonization rate exceeds the extinction rate ($e_I/\beta_I < 1$). In our model where patches may change from being suitable to unsuitable on a time scale comparable to extinction-colonization dynamics, persistence will additionally depend on the (i) net rate at which suitable patches arise in the landscape relative to the species' colonization ability, and (ii) longevity of dormant stages of the life cycle relative to the disturbance frequency.

Biological Examples

The framework we have presented captures the essence of some patchily distributed communities. For example, the Florida scrub is a shrubdominated habitat that is subject to periodic burns (Quintana-Ascencio & Menges, 1996; Menges & Kimmich, 1996). The dominant shrub, Florida rosemary (*Ceratiola ericoides*) is eliminated almost completely by fire, and recovers slowly from a soil seed bank. Herbaceous perennials such as the endemic *Eryngium cuneifolium* are restricted to the open patches created by fires. This is largely due to below-ground competition and allelopathy from the dominant shrubs (Menges & Kimmich, 1996). The herbs increase in abundance when openings are created by fires. As time since fire increases the shrubs start to spread into the open patches, leading to dramatic reductions in survival and fecundity of *E. cuneifolium* and other gap-dependent species (Abrahamson et al., 1984; Johnson & Abrahamson, 1990; Menges & Kohfeldt, 1995). Coexistence of herbs and shrubs thus requires frequent fires relative to the longevity of the herbs and the rate at which the dominant shrubs colonize open patches (Menges & Kimmich, 1996).

A similar situation occurs in the fire-prone shrublands and woodlands of south-eastern Australia (Keith & Bradstock, 1994; Gill et al., 1995; Keith, 1996). Dominant shrubs that are serotinous, obligate seeders decline when fires are frequent relative to juvenile longevity. In contrast, legumes that have buried, dormant seeds are stimulated to germinate by fire (Bradstock et al., 1998). A third example comes from the wetland prairies of the Willamette valley in western Oregon (Pendergrass et al., 1999). Prairie plant species such as the endangered Bradshaw's parsley (*Lomatium bradshawii*) are adapted to survive frequent disturbances created by fall season fires. In the absence of natural and anthropogenic fires, woody species encroach and threaten to displace prairie natives such as *L. bradshawii* (Pendergrass et al., 1999).

As the above examples suggest, periodic disturbances are necessary for the persistence of early successional species such as the Florida scrub endemics and the prairie plant species of western Oregon. Proper management of such species requires knowledge of the minimum disturbance frequency that allows long-term persistence. We use the theory developed above to address this problem for the herbaceous endemic *E. cuneifolium*. We take two approaches. First, we compute the minimum fire frequency f_p^* required for long-term persistence ($I_2^* > 0$). Second, we derive the minimum fire frequency f_x required for maintaining the population at a prescribed level of occupancy ($I_2^* > x$, $x = 0.1, 0.2$, etc.). We set $x = 0.1$ for illustrative purposes. For species such as *E. cuneifolium* that have restricted ranges, 10% occupancy provides a more realistic criterion for persistence in a stochastic environment. The open patches colonized by *E. cuneifolium* are eventually crowded out by invading shrubs. Hence opportunities for natural extinction of these patches are not realized (i.e., $e_I = 0$). Colonization rate of latent patches b_L could conservatively be assumed to be zero. Data on time since fire and *E. cuneifolium* mortality due to encroachment by shrubs (Menges & Kimmich, 1996) suggests above-ground extirpation 20-40 years post-fire, yielding a maturation rate g in the range 0.025-0.05 per year. We were unable to find published information on the rate at which open patches are colonized by *E. cuneifolium* (β_I) and the longevity of the seed bank ($1/e_L$). These are typically the parameters that are hard to estimate in the field. We explore the sensitivity of f_p^* and f_x to variation in β_I and e_L .

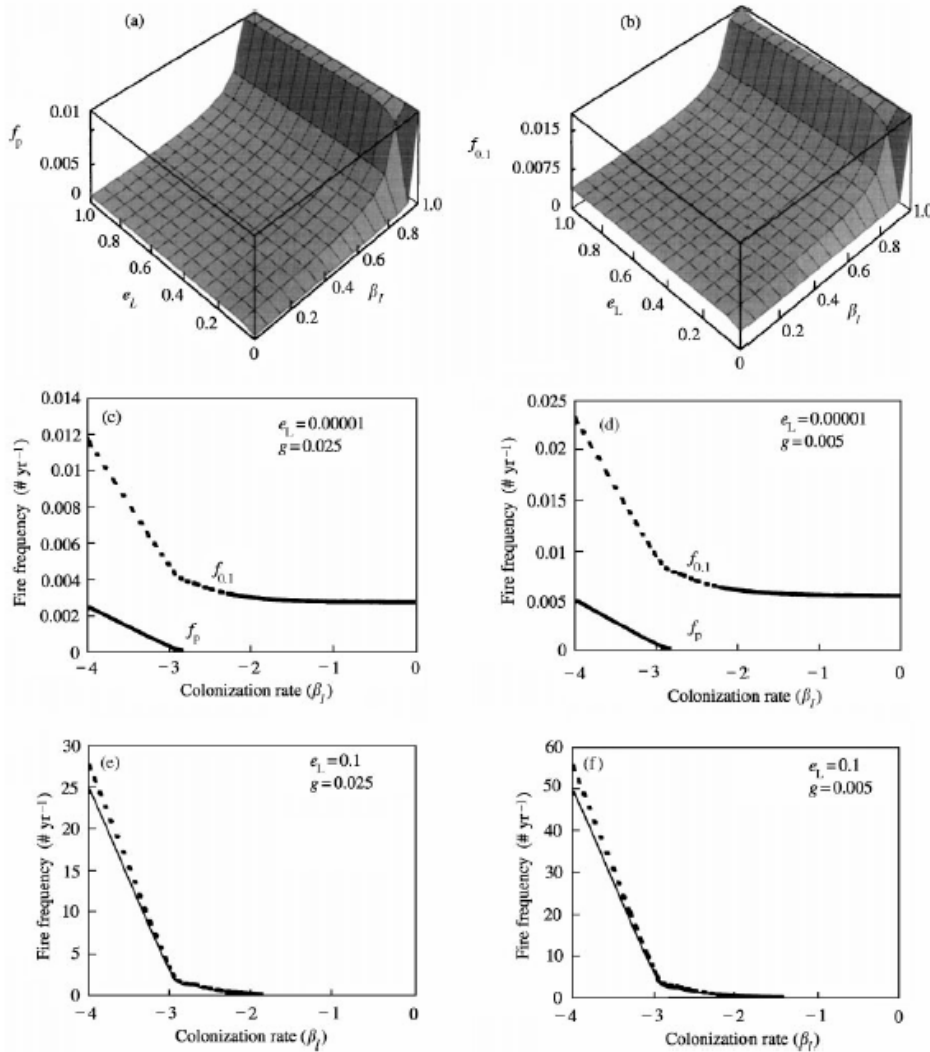


Figure 3. Minimum fire frequency required for persistence [f_p , (a)] and 10% habitat occupancy [$f_{0.1}$, 3(b)] as a function of seed bank longevity (e_L) and colonization rate of empty, suitable patches (β_I). Parameter values are based on available information: $e_L = 0$, $\beta_L = 0$ and $g = 0.025$ - 0.05 . When $e_L > 0$, both f_p and $f_{0.1}$ decline rapidly with β_I regardless of the magnitude of e_L . This qualitative relationship holds for the observed range of g values. There is a quantitative difference between two measures of fire frequency such that $f_p < f_{0.1}$. Panel (c) and (d) depict this discrepancy when $e_L = 0.00001$ for $g = 0.025$ [panel (c)] and $g = 0.05$ [panel (d)]. Panels (e) and (f) depict the discrepancy when $e_L = 0.1$ for $g = 0.025$ [panel (e)] and $g = 0.05$ [panel (f)]. The difference between f_p and $f_{0.1}$ is greatest when $e_L \rightarrow 0$ and decreases at higher values of e_L .

Figure 3 gives the minimum fire frequency required for population persistence (f_p) as a function of β_I and e_L . When seed bank longevity is essentially infinite (i.e., $e_L \rightarrow 0$), the persistence criterion simplifies to $\beta_I f_p > 0$, suggesting that when colonization rate is non-zero, even very low fire frequencies can ensure persistence [Figs. 3(a), (c) and (d)]. When the seed bank has finite longevity ($e_L \rightarrow 0$) but the colonization rate is low (i.e., below 0.001), f_p increases by an order of magnitude or more [Figs 3(e) and (f)]. However, as β_I increases f_p declines rapidly, regardless of the magnitude of e_L .

The minimum fire frequency required for 10% habitat occupancy ($f_{0.1}$) exhibits a qualitatively similar relationship with β_I and e_L [Fig. 3(b)]. When $e_L > 0$, $f_{0.1}$ declines rapidly with β_I . As with f_p , this relationship is not affected by finite values of the seed bank longevity [Figs 3(e) and (f)]. When $e_L \rightarrow 0$, long-term habitat occupancy requires $f_x > I_2^*g/(1-I_2^*)$. This means that if the seed bank is very long-lived, $f_{0.1} > g/9$ is sufficient to guarantee 10% habitat occupancy [Figs 3(c) and (d)].

Although both f_p and $f_{0.1}$ exhibit the same qualitative relationship with colonization rate and seed bank longevity, there is a quantitative difference. For all values of β_I and e_L , fire frequency needed for 10% habitat occupancy is greater than that required for non-zero habitat occupancy. This is to be expected since the former is a more stringent requirement for persistence than the latter. This discrepancy is illustrated in Figs. 3(c-f) for the two cases, $e_L \rightarrow 0$ and $e_L > 0$. The difference between f_p and $f_{0.1}$ appears to be greater when the seed bank is relatively long-lived (i.e., $e_L \rightarrow 0$). For example, when e_L is small the fire frequency may need to be an order of magnitude higher for 10% occupancy compared to non-zero occupancy.

As can be seen from the above analyses, the fire frequency required for long-term persistence declines rapidly with increasing rates of colonization. Seed bank longevity does not affect the qualitative nature of this relationship. It does however have a strong quantitative effect on fire frequency when colonization rates are very small (i.e., below $\frac{1}{1000}$ generations). Management for a prescribed level of habitat occupancy $f_{0.1}$ requires greater fire frequency than that required for non-zero occupancy (f_p), but provides for a more realistic management criterion.

Discussion

We have presented a model that combines elements of both metapopulation and patch dynamics. We have analysed the model using the epidemiological framework. The model leads to predictions about equilibrium patch occupancy as a function of both the species' biology as well as extrinsic processes such as disturbance and succession.

This approach of combining the dynamics of patch suitability with extinction-colonization dynamics is important for several reasons. First, persistence of many species cannot be understood within a simple metapopulation framework that defines patches solely in terms of occupancy. For example, for most herbivorous insects a habitat patch consists of a particular host plant or a patch of host plants. If the host plant is an annual or a short-lived perennial, then the dynamics of patch turnover have to be considered in concert with the extinction-colonization dynamics of the herbivore.

A framework that considers both patch dynamics and extinction-colonization dynamics is essential to understanding how diversity is maintained in successional habitats or those subject to frequent disturbance. In classical metapopulation theory, disturbances are considered only in terms of their impact on the extinction rates of local populations (e.g., Hastings, 1980). Our approach allows one to separate the role of disturbances (e.g., fires, droughts, earthquakes) on species' extinction rates from that due to life history characteristics (e.g., longevity). It also provides a straightforward way of incorporating dormant life cycle stages into the patch occupancy framework. There is little or no theory that investigates successional dynamics (but see Caswell & Cohen, 1991; Pacala & Rees, 1998). The epidemiological approach allows us to explore the interaction between seed accumulation (colonization) and seed dormancy (treated as

equivalent to the occupation of a latent host), an issue that is central to the dynamics of early plant succession. It also allows us to make predictions about how extrinsic processes such as disturbances scale with life history characteristics such as longevity, dormancy and dispersal ability.

The model has the potential to provide broad management guidelines for species that live in disturbance-prone habitats. Model predictions may be particularly useful in fire management, and the analytical theory developed here provides a benchmark for more detailed spatially explicit modelling. One result that is particularly relevant is the asymptotic relationship between the disturbance to colonization ratio (f/β_i) and the equilibrium patch occupancy. This relationship allows one to determine a cost-effective fire management strategy by knowing only three parameters: colonization rate of the focal species, successional or maturation rate of the habitat (e.g., the rate at which early successional species are replaced by late successional species), and the natural disturbance frequency. Since the qualitative nature of the predictions involving these three parameters are not altered by how the extinction rate scales with the colonization rate, the management implications may be applicable to species with widely differing life-history strategies.

One natural community that these predictions are likely to apply to is the Florida scrub ecosystem discussed previously. The fire frequency is sufficiently low that the dominant shrubs can invade and displace herbaceous local endemics such as *E. cuneifolium* from open patches. Burning of sites on a more frequent basis has been suggested as a management strategy for *E. cuneifolium* (Menges & Kimmich, 1996). We used the model to predict the critical fire frequency required to maintain *E. cuneifolium* populations at or around 10% occupancy. A sensitivity analysis of the model to the two unknown parameters, colonization rate and seed bank longevity, suggests the former may have a greater influence on persistence than the latter. For instance, seed bank longevity has a strong effect on fire frequency when colonization rate is below 0.001 per year, but no discernible effect when colonization is in the range 0.001–1 per year. If *E. cuneifolium* has an intrinsically low rate of seed (or pollen) dispersal, or if the distance between occupied and vacant patches is too large relative to the species' colonization ability, then seed bank longevity should be taken into account. Otherwise, the rate at which *E. cuneifolium* colonizes empty patches is likely to be the information most relevant for management. It should be noted that the model is spatially implicit and does not consider such factors as patch size and configuration, and spatial scale of disturbance (local as opposed to global). An important future direction is to examine the robustness of model predictions when these aspects of spatial structure are taken into account. The analytical theory developed here provides the basis for interpreting results from a more detailed spatially explicit model.

Interestingly, the sensitivity analysis of the parameterized model for *E. cuneifolium* suggests an overwhelming role for colonization in persistence. Similar results have been obtained for patch occupancy models in which species coexist via a trade-off between competition and dispersal (Tilman et al., 1994, 1997). These parallels beg an important question: is this result an artifact of the patch occupancy models themselves or is there an underlying ecological phenomenon?

Patch occupancy models, by definition, put an overwhelming emphasis on extinction-colonization dynamics. Hence it is possible that the important role of

colonization in persistence is a direct consequence of model structure and assumptions. However, there is some biological justification for the role of colonization in species persistence and coexistence (Hanski et al., 1994; Tilman et al., 1994, 1997; Lei & Hanski, 1998). Fugitive species in general, and early successional species in particular, are able to persist because they can preempt superior competitors in time or space (Harper, 1961; Bazzaz, 1979; Paine, 1979; Brown, 1982; Silander & Antonovics, 1982). A seed bank may allow in situ recolonization of a previously occupied site, but the species will nevertheless be displaced once a superior competitor arrives. The key to persistence lies in the ability to colonize more sites, and faster, than superior competitors. Clearly, the fugitive lifestyle puts a high premium on colonization ability.

This approach of combining patch dynamics and metapopulation dynamics using the epidemiological framework could be extended to other types of species interactions. For example, the four-patch framework can be interpreted as a mutualistic interaction between an obligate (e.g., a plant that requires animal pollination or seed dispersal) and a facultative mutualist (a generalist pollinator or seed disperser). If the obligate mutualist has a density-independent colonization rate and the facultative mutualist has a density-dependent colonization rate, then the criterion for the persistence of both species can be derived with a slight modification of parameters. We will present a detailed analysis of the mutualism model in a subsequent paper.

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