Fire variability, as well as frequency, can explain coexistence between seeder and resprouter life histories

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Summary

1. Studies in fire-prone Mediterranean ecosystems have repeatedly shown that the mean values of fire regimes (particularly frequency, but also size and intensity) are important for managing sensitive species and maintaining diversity. However, recent studies suggest that invariant fire regimes – that is, those with no variation about the mean value – may not be sufficient to maintain the coexistence mechanisms which could help explain the high levels of species diversity. However, there has been a little examination of the potential mechanisms by which variability in fire regimes might foster coexistence.

2. In these species-diverse ecosystems, fluctuations in fire regimes promote the coexistence of competitively unequal species, thus providing a potential mechanism of coexistence. We examine the role of variability in the length of the interfire interval and ask whether this variability can allow a fluctuation-dependent mechanism, namely the storage effect, to promote the coexistence of species. We focus on dominant trade-offs in fire regeneration strategies (i.e. obligate resprouting vs. obligate seeding) common among Mediterranean plant species and use simulations to explore the inter-relationship between variability in the time between fires and the coexistence of species.

3. Several empirical studies have found that variability in the length of the interfire interval improved diversity – our simulations suggested one mechanism that could explain this result. Variability can greatly increase the regions over which coexistence between two species – a fire obligate seeder and a resprouter – occurs.

4. *Synthesis and applications.* Mediterranean ecosystems tend to have high plant diversity, and yet the mechanisms maintaining this diversity are often incompletely understood, and thus management actions that aim to promote coexistence may be relying on imprecise information. In general, fire events drive the evolution and maintenance of diversity and are an important management tool. It is high likely that fluctuations or variability in fire are also important, and this suggests that invariant regimes of prescribed burning or fire suppression could be detrimental to the mechanisms that play a role in the maintenance of diversity in these Mediterranean ecosystems. As a result, attention should be paid to historical fire regimes and the variation in fire return times they displayed when developing prescribed burning regimes.

Key-words: diversity, fire regimes, Mediterranean ecosystems, prescribed burning, storage effect, temporal heterogeneity

Introduction

Fire-dominated landscapes include some of the most diverse ecosystems on the planet, with the fire-prone semi-arid shrublands in South Africa, California, Southwest Australia and the Mediterranean basin being recognized as globally important biodiversity hotspots, due to the combination of high concentrations of endemic species and high habitat loss (Myers *et al.* 2000). In some of these regions, fire regimes are actively managed to reduce fuel load and to control the frequency and size of natural

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wildfires using prescribed burning (Wade & Lunsford 1989; Fernandes & Botelho 2003). However, prescribed burning may also be applied to achieve management goals that extend beyond hazard reduction to include ecosystem management goals such as diversity maintenance (Bradstock, Keith & Auld 1995; Richards, Possingham & Tizard 1999; Haines, Busby & Cleaves 2001). However, the use of prescribed burning in ecosystem management is controversial (e.g. Morrison *et al.* 1996; Clarke 2008; Reinhardt *et al.* 2008), and evidence suggests that fire management and prescribed burns may not have the desired effects on community diversity and composition compared with natural fire regimes (Bond & van Wilgen 1996). For example, attempts to protect the rare fynbos shrub *Orothamnus zeyheri* by suppressing fires resulted in near extirpation of populations, as the shrub was an obligate fire recruiter. Fortunately, controlled burns were instituted before the species' seed banks disappeared (Boucher 1981).

The different aspects of the fire regime – including fuel type, temporal nature and spatial pattern (Bond & Keeley 2005) – affect diversity and coexistence, population size and persistence, the likelihood of invasion, and ecosystem structure and services in Mediterranean-type and other ecosystems (e.g. Boucher 1981; Richardson & van Wilgen 1992; Cary & Morrison 1995; Bradstock & Kenny 2003; Brooks *et al.* 2004; Pausas *et al.* 2004; Bowman *et al.* 2009). Determining targets related to fire frequency, intensity, or season, for managed fire regimes in Mediterranean ecosystems (Gill 1975) is the focus of much research (for example, Gill 1977; Gill & Bradstock 1997; Richards, Possingham & Tizard 1999; McCarthy, Possingham & Gill 2001). This research focuses on the length of the time between fires (the interfire interval) and its relationship to important life-history events among plant species including maturation, seed bank accumulation and senescence. In the case of Mediterranean shrub species, when fires burn too frequently, species may not have time to mature and produce seed, leading to population extirpation (Gill & Groves 1981; Gill & Bradstock 1995; Pausas 2001). When fires occur too infrequently, seed banks of species that require fire-related cues for germination may be lost (Pausas 2001), thereby limiting population recruitment.

Variation in the interfire interval may also be important in determining the outcome of fire regimes, but the effect of variation is much less understood (Cary & Morrison 1995; Bradstock *et al.* 1996). Work from fire-prone heathlands in Australia suggests that invariant timing of fire events can be harmful to overall diversity (Keith & Bradstock 1994; Morrison *et al.* 1995; but see Wittkuhn *et al.* 2011), possibly because some mechanisms of coexistence rely on fluctuations in fire occurrence. However, theoretical work explicitly considering the mechanisms that relate variation in the fire interval and species diversity is still generally lacking, making it difficult to determine how much variation should be incorporated into a fire regime to maintain diversity in an ecosystem (Gill & McCarthy 1998).

The characteristics of present day fire regimes in Mediterranean ecosystems are important because species' life histories are adaptations to historical fire regimes, the result of which is that the timing and nature of fires determine species' presences and abundances (Bond, LeRoux & Erntzen 1990; Bond & van Wilgen 1996; Bond & Midgley 2003; Bond & Keeley 2005). Across different Mediterranean shrublands, convergent evolution has repeatedly produced woody, evergreen, sclerophyllous shrub species (Mooney & Dunn 1970). Crown-fires in these shrublands consume the majority of above-ground biomass, leading to a well-documented trade-off in postfire regeneration strategies among shrub species: species either rely on fire-stimulated germination or postfire resprouting behaviour (Mooney & Dunn 1970; Bond & Midgley 2003).

We hypothesize that variability in the length of the interfire interval may be one mechanism by which fire promotes coexistence among species. In particular, we provide an example of a possible mechanism – a temporal storage effect – through which variability in the length of the interfire interval could promote species coexistence between an obligate resprouter and obligate seeder. The storage effect (Chesson & Huntley 1997; Chesson 2000; Adler & Drake 2008) is a form of temporal partitioning in which competing species show differential recruitment in response to environmental conditions. There are several conditions required for the storage effect to act (Chesson & Huntley 1997): (1) species must have differential responses to environmental conditions including disturbances; (2) there must be covariance between competition and these environmental conditions, which occurs when one species is favoured over another by particular conditions; and (3) there must be a mechanism for buffered population growth, allowing species to persist through unfavourable conditions when interspecific competition is high, by 'storing' fitness from past times when conditions were more favourable. Storage could be a result of long-lived life-history stages such as seed banks or long-lived perennials (Chesson 2000). Although the focus is usually on fluctuations in the abiotic environment, variability in fire events can also create a storage effect (e.g. Miller & Chesson 2009). Given that shrub species in Mediterranean systems fulfil the requirements for the storage effect, we develop a model to show that varying the length of the interfire interval could alter the effect of fire regimes on seeder and resprouter species in Mediterranean ecosystems.

Materials and methods

LOTTERY MODEL

We model the storage effect using a simple version of the lottery model (Chesson & Warner 1981). A lottery model considers the division of available sites among species as being in proportion to their representation in the available pool of recruits (Sale 1977, 1978). Such a model is useful for space-limited systems, where

there are more recruits than there are available sites for establishment, or to represent stochastic recruitment in systems, where species appear similar in form and function (Hubbell 2001). A simple formulation of the lottery model represents the proportion of sites occupied by species i as:

$$P_i(t+1) = \frac{\beta_i(t)P_i(t)}{(\sum_{j=1}\beta_j(t)P_j(t))} \qquad \text{eqn 1}$$

where $\beta_i(t)$ represents the net per capita reproduction species i at time (t) and $P(t)$ represents the proportion of sites occupied by species i at time (t). Evidence from similar models developed for both plants and animals suggest that in general, when there are overlapping generations and environmental variation, an inferior and superior competitor can coexist (Fagerstrom & Agren 1979; Chesson & Warner 1981).

The lottery model has been used to represent recruitment in Mediterranean shrublands, where species are often very similar in structure, phenology and other ecological characteristics usually associated with niche differentiation (Cowling 1987; Lamont, Connell & Bergl 1991; Bond, Cowling & Richards 1992; Laurie & Cowling 1994), but given the apparent lack of niches, diversity is perplexingly high. We are considering Mediterranean systems with obligate resprouters and obligate seeders, which differ from the traditional formulation of the lottery model. Recruitment and mortality are strongly tied to fire events, particularly for fire obligate seeders, where all recruitment and total mortality can be assumed to occur following each fire (Keeley 1986). Because the recruitment of seeds from obligate seeders occurs immediately following the most recent fire event, and seeder and resprouter recruitment functions represent a build-up of seeds that depend on the length of the interval between fires, we treat each time step in the model as a fire event with some associated interfire interval length (f). Each step then ends with a fire leading to recruitment of the next generation of individuals. The recruitment function represents the number of seeds available for recruitment at a given interfire interval: this is ultimately a function of both species longevity and seed bank longevity, as it represents the accumulation of the year's seed production and all surviving seeds in the seed bank. For obligate seeder species, recruitment comes from the seed bank formed during the interval between fires. For the purposes of our model, we will assume that this is a soil-based seed bank, which means that seeds can survive in the seed bank after the adult plant has died. For the obligate resprouter species, the recruitment function represents seed production during a given year only: these species do not form seed banks and seeds tend to be short-lived and disperse away from the site (Keeley 1986). For simplicity, we consider sites to be saturated immediately following fire events, so that recruitment of both resprouting species (from seeds produced during the previous year) and seeding species (from the seed bank accumulated over the time between fires) only occurs during the postfire period when mortality makes sites available. Here seeds in the seed bank are considered to be in the soil and so survive past the death of the plant. As resprouters survive fire events, we treat this as a situation when one species (resprouters) have overlapping generations, while the other (seeders) does not.

This model shows the proportion of sites occupied by species i with adult population size $N_i(f)$ at a given fire (f):

$$P_i(f+1) = (1-\delta_i(f))P_i(f) + \left[\sum_{j=1}\delta_i(f)P_j(f)\right]\left[\frac{\beta_i(f)P_i(f)}{\sum_{j=1}\beta_j(f)P_j(f))}\right] \qquad \text{eqn 2}$$

where $\beta_i(f)$ represents the seed bank accumulated by species i over the current interval and $P(f)$ represents the proportion of sites occupied by species i at the end of the fire interval. Henceforth, we will use the subscript Sp to represent the resprouter species and the subscript Se to represent the seeder species. δ represents mortality caused by a fire event: for the resprouter species this can take a range of values between 0 and 1, ranging from no mortality, to total mortality of adult resprouters. This value can be a function of the interfire interval, or may be represented as a constant value. For the seeder species, δ is set to 1, representing the total mortality of seeders following a fire event.

For the seeder species, $\beta_{Se}(f)$ represents the seed bank accumulated during the interfire period, which we represent as a Gaussian function of the length of the interfire interval. The seeder species is most common when fire intervals are intermediate, as recruitment is low when fire intervals are too short to allow time for establishment and reproduction, or too long, causing seed bank exhaustion (Keeley 1986; Bond & van Wilgen 1996; Schwilk, Keeley & Bond 1997; Pausas 2001).

$$\beta_{Se}(f) = c * e^{\frac{-(f-\mu)^2}{2\sigma^2}} \qquad \text{eqn 3}$$

where μ represents the length of the interfire period giving the seeder the highest number of seeds, f is the length of the interfire period, σ corresponds to the width of the function and c is a constant representing the maximum seed production. σ represents the degree of tolerance to the length of the interfire interval a species' recruitment shows – larger values would represent longer-lived seeder species and/or longer-lasting seed banks. This allows the model to be extended to species with differing life spans or seed bank longevity.

For the obligate resprouter, no seed bank is formed, and recruitment is assumed to include only those seeds produced in the last year of the interfire interval. This number of seeds is assumed to be a linear function of the length of the interfire interval, as resprouter size and seed production are correlated (Higgins, Flores & Schurr 2008). (Although resprouting ability may be reduced as the interfire intervals decrease (Bond & Midgley 2001)).

$$\beta_{Sp}(f) = f * a, \qquad \text{eqn 4}$$

where the length of the interfire period (f) and a constant level of seed production (a) determine resprouter seed production. The assumption is that the resprouting species live at least as long as the longest interfire interval (40 years).

A DISTURBANCE-BASED STORAGE EFFECT

The necessary components of the storage effect have been identified as (Chesson 2003): differences in species' responses between environments; storage (persistence) through unfavourable periods; and covariance between environment and competition. We develop a version of the storage model to account for differences

in seeder and resprouter ecology, in particular, differences in their responses to the length of the interfire interval. Variation in environment is represented here by variability in the timing of fire events and accordingly in the length of the interfire interval – that is, the number of years between fires. We model this as a normally distributed random variable:

$$f = N(\text{mean, variation}). \qquad \text{eqn 5}$$

Differences in seeder and resprouter responses to the length of the interfire interval are driven by differences in their life histories. In Mediterranean ecosystems, resprouters are often observed to have lower seed recruitment than seeder species and being outcompeted by seeders (Keeley 1986; Burgman & Lamont 1992; Pausas 2001). While there is variation among Mediterranean ecosystems in seeder and resprouter life histories and in fire regimes, we follow a general model where seeders dominate at intermediate interfire intervals and resprouter at low and high interfire intervals (Burgman & Lamont 1992; Pausas 2001).

Finally, both the seeder and resprouter species can buffer their fitness, either through fire tolerance and survival of resprouters or seed bank formation by seeders. Competition among seeder and resprouter species occurs primarily during the recruitment of seedlings (Yeaton & Bond 1991; Laurie & Cowling 1994), and once established, adult resprouters may persist for multiple fire cycles. Hence, resprouters that establish during favourable periods can maintain their populations by persisting through unfavourable periods. Seeds produced by seeder species are either stored in serotinous seed banks or, particularly in the South Africa and Australia, cached underground by ants. Comprehensive data on the longevity of these buried seeds are lacking, but at least some buried seeds from seeder species may remain viable for longer periods of time and this confers some buffering of fitness (Holmes & Cowling 1997; Auld, Keith & Bradstock 2000; Holmes & Newton 2004; Willis & Read 2007). As stated earlier, we assume soil-based seed banks in this analysis.

For simplicity's sake, we model a generic obligate resprouter and obligate seeder species with a soil-based seed bank in an ecosystem with similar fire regimes as those found in the Cape Floristic Region of South Africa (CapeNature & SANBI 2008). Although this is necessarily a simplification of the actual relationship between seeders and resprouters and fire (and it ignores species-specific differences), it is sufficient to highlight how fluctuations in fire occurrences could promote long-term persistence of these life histories.

NUMERICAL SIMULATIONS

We chose to simulate a co-occurring obligate seeder and obligate resprouter species in a system where the mean length of the interfire interval ranged between 0–40 years and varied by between 0–15 years (see Appendix S1, Supporting Information for R code). This represents a realistic range of values for the Cape Floristic Region of South Africa (CapeNature & SANBI 2008), but the specific values are less important than the necessity that the requirements of the storage effect be met, and any Mediterranean ecosystem could have been modelled provided the life histories of species and their relationship to historical fire regimes were understood. The total number of available sites in a community was set to 1000, and initial starting populations were set in accordance to invasion analysis: that is, the invading species had a starting population of one individual and the resident a starting population of 999. The invader was considered the species with the fewer seeds available for recruitment for each length of the interfire interval, when variability in length of the interfire interval is zero, given the parameter values used for a and c (see below).

We repeated the simulations 1000 times at each combination of interfire interval (for lengths between 0 and 40 years) and variation (from 0 to 15 years), a total of 600 000 simulations. It should be noted that regimes with short periods between fires and high variability are unlikely to be observed in nature. For each simulation, we recorded the proportion of the community occupied by resprouters and seeders after 1000 time steps. We calculated the probability of coexistence at each combination of interfire length and variability as the number of runs per 1000 in which seeders and resprouters persisted together after 1000 time steps. Persistence was defined as occupying at least one site in the community after the 1000 time steps. Throughout the results, where we refer to 'coexistence', we imply this definition of long-term persistence, rather than analytical coexistence.

PARAMETER VALUE SELECTION

The numbers of seeds available for recruitment at time each fire event were set to $c = 8000$ (equation 3) for seeders and $a = 50$ (equation 4) for resprouters. c is equivalent to the accumulated seed bank available for recruitment for seeders; this seed bank is modelled to be largest when the fire return interval (μ) is 20 years (Fig. 1), which is equivalent to saying that the combination of seeder life span and seed bank longevity results in the greatest number of seeds at 20 years. We examine the effects of changing the seeder seed recruitment function, to account for different species life spans or seed bank longevity: however, the results of our simulation do not fundamentally change (Fig. S1, Supporting information). Resprouters are likely to have far fewer seeds available for recruitment (Bond & Midgley 2001) (one record from the CFR found that resprouters produced between 9·7% to 88·0% of the number of cones produced by seeder species (Higgins, Flores & Schurr 2008)), and resprouters do not form a lasting seed bank (Keeley 1986). Given these parameter values, resprouters are invaders for sites with fire frequencies less than ~33 years. Resprouters were invaders for sites with frequencies between those values. Resprouter fire mortality (δ_{Sp}) was set to 0·25 (i.e. 75% survival). We examine the sensitivity of our model to the difference in the number of seeds available for recruitment between seeders and resprouters (see below).

SENSITIVITY OF THE MODEL TO PARAMETER VALUES

One essential question is how important is the difference in the seeds available for recruitment for seeders and resprouters. We examined how altering the number of seeder and resprouter seeds available changed the likelihood of coexistence at different interfire intervals. We expect that there should be a relationship between the amount of variation that allows coexistence, the differences in seeds available for recruitment and the amount of storage that the species have (Chesson 2000). To explore this relationship, we simulated all combinations of parameters of length
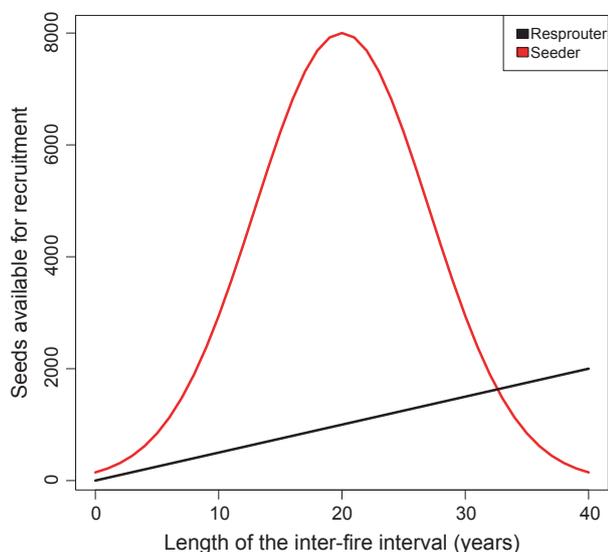
Fig. 1. Conceptual model showing the number of seeds available for recruitment (β_i, equation 2) as a function of the length of the interfire interval (f) for a generic seeder (red) and resprouter (black) species. $c = 8000$ and $a = 50$. See Materials and methods for further details on parameterization.

of interfire period variation ($f \in [0, 40]$), buffering ($\delta_{Sp} \in [0\cdot1, 0\cdot9]$) and the difference in the number of seeds available for recruitment between seeder and resprouter ($c \in [3000, 10\,000]$, $a \in [10\,300]$) and recorded the corresponding minimum variation in length of interfire period required for coexistence at each combination of these.

An important point is that the storage effect should not function in the absence of some form of storage or buffering that allows species to maintain their populations through unfavourably short or long interfire intervals. For example, if the resprouter species are no longer able to survive fire events, variability in the length of the interfire period should not promote coexistence of the seeder and resprouter species. We removed buffering of resprouter fitness by setting δ_{Sp} to 0, so that no adult resprouters survive fire events. We then repeated the simulations 1000 times at each combination of length of interfire period (for fire frequencies between 0 and 40 years) and variation (for values ranging from 0 to 15 years). For each simulation, we recorded the proportion of the community occupied by resprouters and seeders after 1000 time steps.

Results

COEXISTENCE WITH NONVARIABLE FIRE RETURN

When there is no variability in the length of the interval between fires, there is a small range of fire frequencies where the seeder and resprouter species are expected persist (Fig. 2a, greyed regions 2, 4). These regions reflect the length of the interfire period that minimize the difference in recruitment between seeders and resprouters and allow persistence under the lottery model. However, for the majority of fire frequencies, only one of the two species is predicted to persist when variability is set to 0 (Fig. 2b, regions 1, 3, 5).

COEXISTENCE WITH VARIABLE FIRE RETURN

When variability in the length of the interfire period is incorporated, persistence of seeders and resprouters can occur in regions where exclusion occurred in the absence of variation (Fig. 2b, 1–5). For example, in region 3 (Fig. 2b-3) where the seeder species excluded the resprouter species when variability is zero, increased variation means that the resprouter species periodically has high recruitment, which, combined with buffered population growth, allows its population to coexist with the seeder species. In contrast, higher variability can decrease the ability of the seeder to persist (region 4), by increasing the number of unfavourably long interfire intervals. Ultimately, the likelihood that the seeder and resprouter species coexist is determined by the interaction between the length of the interfire interval (and implicitly, its relationship with the number of seeder and resprouter seeds available for recruitment) and the variability in this length, which interacts with buffering ability (Fig. 3). When variation in the length of interfire period is 0 in this plot, the red regions of coexistence are equivalent to the grey areas in Fig. 2a. There is a high probability of coexistence of the seeder and resprouter species across the widest range of fire frequencies when the variability is ~8·5 years. In fact, when variation is this high, the resprouter and seeder species coexist across nearly all interfire intervals below 30 years.

When adult mortality of the resprouter species was set to 1, so that there was no storage of fitness between generations for that species, variability in length of interfire period did not increase the region over which resprouters and seeders could coexist (Fig. 4).

INFLUENCE OF PARAMETER VALUES ON COEXISTENCE

The values of a and c that we chose appear to be less important for the outcome of our model than the overall difference in the number of seeds available for recruitment between seeders and sprouters. Figure 5 suggests that there is a relationship between the size of this difference in seed number and the mortality resprouters experience during fire events and the corresponding amount of variation necessary for coexistence. When seeders have more seeds available for recruitment, greater variability in the interfire interval is necessary for the resprouters to coexist. When resprouter mortality is low, resprouters are able to maintain sites and more effectively compete, so less variability is required for their coexistence with seeders. When resprouter mortality is higher, greater variability is required for coexistence. The initial choice of parameter values (a and c) for the resprouter and seeder species is not as important as having the essential components of the storage effect present, that is variation in length of interfire period and buffering of fitness.

(a) Without variation in the inter-fire interval

(b) 5 Regions with variation in the inter-fire interval
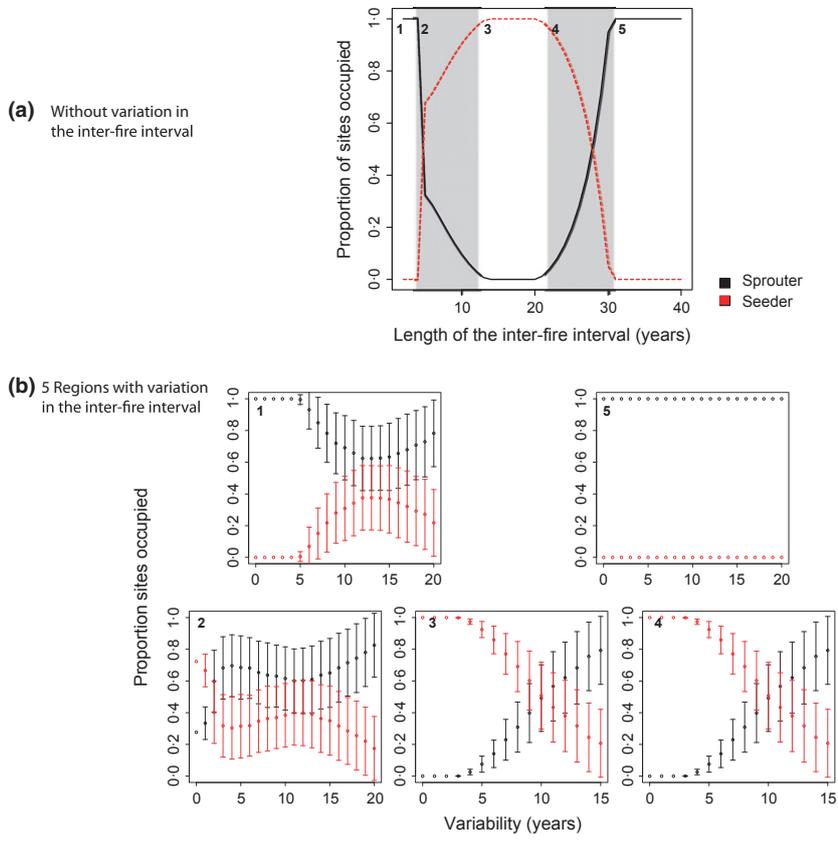
Fig. 2. (a) Mean interfire intervals for which coexistence or exclusion between seeder and resprouter species is expected, when the length of the interfire interval is invariant. $c = 8000$ and $a = 50$. Five regions of interfire intervals are highlighted; grey regions indicate where long-term persistence is predicted. (b) 1–5: Relationship between variability in the length of the interfire interval and coexistence for the five regions from (a). Points represent the average proportion of sites in a community occupied by the seeder (red) and resprouter (black) species at a site, calculated from 1000 replications for each value of fire variability. Error bars represent the standard deviation.
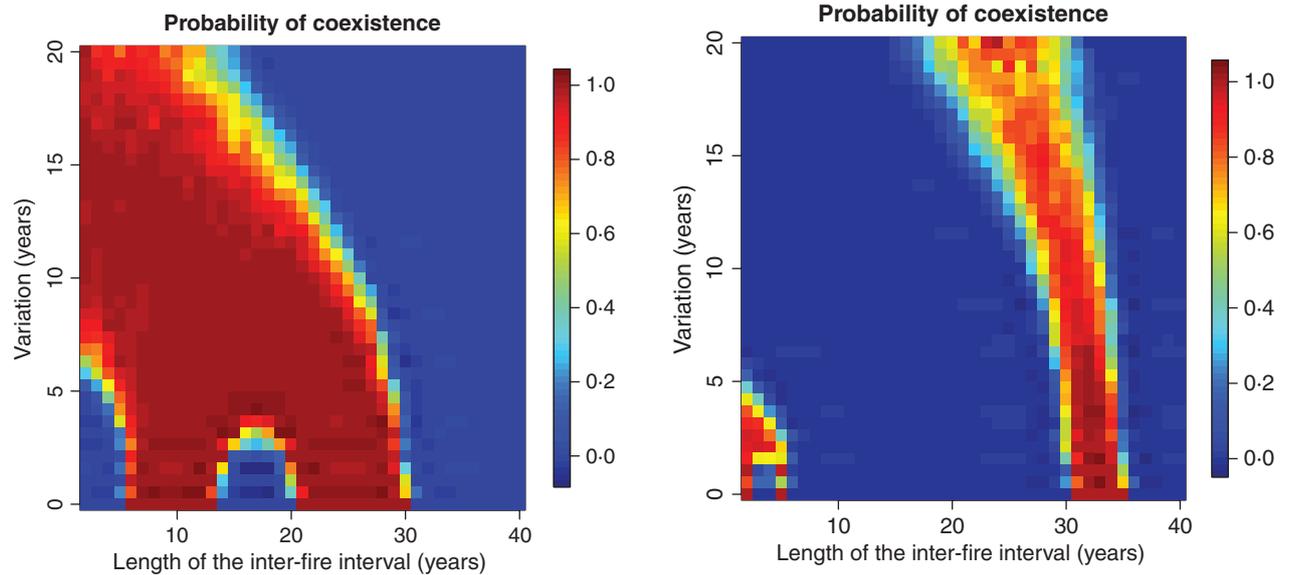
Fig. 3. The probability of coexistence between the seeder and resprouter species, as a function of both the length of the interfire interval and variation in the fire return interval. Cells are colour-coded in a gradient from blue to red, representing the probability of coexistence (from 0 to 1) occurring at a given combination of fire return interval and variation. $c = 8000$ and $a = 50$; see Materials and methods for details on the calculation.

Fig. 4. The probability of coexistence between seeders and resprouters when there is no storage for the resprouter species (i.e. $\delta = 1$), as a function of the length of the interfire interval and variation in the length of the interfire interval. Cells are colour-coded in a gradient from blue to red, representing the probability of coexistence (from 0 to 1) occurring at a given combination of fire return interval and variation.

Discussion

We found that variability in the length of time between fires can greatly increase the likelihood of coexistence between species with obligate seeder and obligate resprouter life histories. This trade-off (between seeder and resprouter life histories) is common in Mediterranean ecosystems. In many ecosystems, recurrent fires are
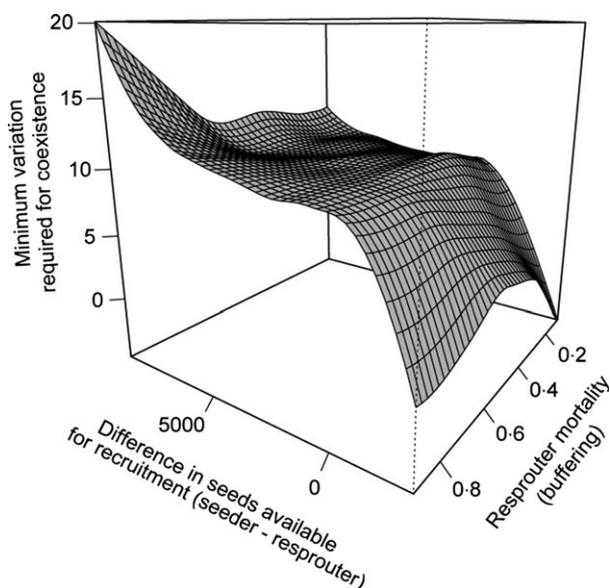
Fig. 5. The interaction between the number of seeds available for recruitment and resprouter mortality (δ) and their effect on the minimum amount of variation in the interfire interval necessary for coexistence. Recruitment is calculated as a function of the length of the interfire interval, as in equations (3) and (4), with $f \in [0, 40]$, buffering ($p_2 \in [0.1, 0.9]$), and $c \in [3000, 10\,000]$, $a \in [10\ 300]$.

necessary to maintain community composition and diversity (Cowling & Campbell 1980; Keeley 1986), in part because disturbance creates opportunities for temporal niche differentiation (Bonis, Lepart & Grillas 1995; Buckling *et al.* 2000). In such situations, invariant fire return intervals would be likely to reduce diversity by removing temporal niches for differentiation among species. However, achieving a balance between risk reduction through fire management and diversity maintenance may be difficult, especially when it is unclear which aspects of natural fire regimes must be retained for diversity maintenance. For example, maintaining an appropriate mean return interval between fires but neglecting variability in the return interval could lead to a reduction in diversity, if coexistence depends on temporal fluctuations in fire events.

Historically, fire regimes were both spatially and temporally variable. Fire regimes in Mediterranean ecosystems were initiated by lightning strikes (prior to human habitation) and initiation was probabilistic, dependent on the combination of suitable weather and fuel conditions in addition to the initial spark (Keeley *et al.* 1989; Keeley & Fotheringham 2003). In fact, most aspects of fires were likely much more variable in the past (Keeley, Fotheringham & Baer-Keeley 2005). Plant species in Mediterranean ecosystems show clear adaptations that allow postfire regeneration (seed banks, resprouting ability) and can provide a buffering mechanism against some variability in fire return intervals. It may be that managed fire regimes should account for the historical variability in fire return

in a region and the life-history traits of species present that have evolved in response to it. Although there have been few empirical studies looking at the relationship between variability in the length of the interfire interval and diversity, Morrison *et al.* (1995) found that variability in the length of the interfire interval is associated with increased diversity of both fire-sensitive and fire-tolerant species, similar to the expectation of a storage effect. Although we did not explore the effect of variability over multiple spatial scales, both temporal variability and spatial variability in the length of the interfire period could be important in these regions. The combination of both temporal rescue of populations via storage and spatial rescue via seed dispersal could concurrently act to maintain diversity in fire-prone ecosystems (Miller & Chesson 2009). While our results show that the coexistence of resprouter and seeder species may even be possible in the absence of variability, in situations with multiple (>2) species, variability may be an important coexistence mechanism.

The exact shape of the relationship between resprouter and seeder seed recruitment and the length of fire return interval in different Mediterranean regions will differ from our model (Bellingham & Sparrow 2004), as different fire regimes have different selective effects on the relationship between seeder or resprouter fitness and the fire return interval (for example, in the Californian chaparral, some obligate seeders may re-establish even after 100 + years between fires (Keeley 1986)). However, the seed recruitment curves implicitly encompass a number of life-history traits, including seed bank longevity and species life span, making them flexible across different species and ecosystems where these traits may vary in complex ways. Our model is also flexible in terms of parameter values (degree of buffering, shape of the relationship between seeder and resprouter fitness and fire) and only requires that the components of the storage effect be present. It is of particular importance that buffering must be present, as systems where species show little ability to tolerate unfavourable conditions will do poorly when variation is increased. Further, the storage effect, modelled here to explain a two species interaction, could explain the coexistence of multiple seeder and resprouter species, if these species are differentiated along additional axes relating to fire conditions (intensity) and/or specialized within the seeder or resprouter response, or even partitioned along other aspects of the biotic and abiotic environment.

MANAGEMENT IMPLICATIONS

For high-diversity Mediterranean regions, the specific mechanisms by which disturbance can contribute to and promote coexistence have important management implications. In most fire-prone systems, species have evolved to historical fire regimes and it is highly probable that historical fire regimes were variable. In these systems, even if

there is an absence of species-specific information about fire responses, it should be assumed that fire is an important aspect of species coexistence. In these cases, we argue management programs need to consider the variability, as well as frequency, in fire events. The storage effect may be a fundamentally important coexistence mechanism in these systems, and management activities that remove variability in fire occurrence could ultimately result in population declines and extinctions. Thus, it is increasingly important to develop mechanistic models of the relationship between diversity maintenance and fire in these species-rich, fire-prone systems. However, the value of variability in managed fire regimes must be balanced against the higher fuel loads that result from longer than average interfire intervals, and the increased risk of large, high-intensity fires which put human communities and property at risk. It will remain important to optimize risk management against the ecological gains of incorporating variability into fire regimes in Mediterranean ecosystems.

Acknowledgements

References

Adler, P.B. & Drake, J.A. (2008) Environmental variation, stochastic extinction, and competitive coexistence. *The American Naturalist*, **172**, E186–E195.

Auld, T.D., Keith, D.A. & Bradstock, R.A. (2000) Patterns in longevity of soil seedbanks in fire-prone communities of south-eastern Australia. *Australian Journal of Botany*, **48**, 539–548.

Bellingham, P.J. & Sparrow, A.D. (2004) Resprouting as a life history strategy in woody plant communities. *Oikos*, **89**, 409–416.

Bond, W.J., Cowling, R.M. & Richards, M.B. (1992) Competition and coexistence in proteoid shrubs. *The Ecology of Fynbos: Fire, Nutrients, and Diversity* (ed. R.M. Cowling), pp. 206–225. Oxford University Press, Cape Town.

Bond, W.J. & Keeley, J.E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution*, **20**, 387–394.

Bond, W.J., LeRoux, D. & Erntzen, R. (1990) Fire intensity and regeneration of myrmecochorous Proteaceae. *South African Journal of Botany*, **56**, 326–330.

Bond, W.J. & Midgley, G.F. (2001) Ecology of sprouting woody plants: the persistence niche. *Trends in Ecology and Evolution*, **16**, 45–51.

Bond, W.J. & Midgley, J.J. (2003) The evolutionary ecology of sprouting in woody plants. *International Journal of Plant Sciences*, **164**, S103–S114.

Bond, W.J. & van Wilgen, B.W. (1996) *Fire and Plants*. Chapman & Hall, London.

Bonis, A., Lepart, J. & Grillas, P. (1995) Seed bank dynamics and coexistence of annual macrophytes in a temporary and variable habitat. *Oikos*, **74**, 81–92.

Boucher, C. (1981) Autoecological and population studies of Orothamnus zeyheri in the Cape of South Africa. *The Biological Aspects of Rare Plant Conservation* (ed. H. Synge), pp. 343–353. Wiley, Chichester, UK.

Bowman, M.J.S., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A., D'Antonio, C.M., DeFries, R.S., Doyle, J.C., Harrison, S.P., Johnston, F.H., Keeley, J.E., Krawchuk, M.A., Kull, C.A., Marston, J.B., Moritz, M.A., Prentice, I.C., Roos, C.I., Scott, A.C., Swetnam, T.W., van der Werf, G.R. & Pyne, S.J. (2009) Fire in the earth system. *Science*, **324**, 481–484.

Bradstock, R.A., Keith, D.A. & Auld, T.D. (1995) Fire and conservation: imperatives and constraints on managing diversity. *Conserving Biodiversity: Threats and Solutions* (eds R.A. Bradstock, T.D. Auld, D.A. Keith, R.T. Kingsford, D. Lunney & D.P. Sivertsen), pp. 323–333, Surrey Beatty & Sons in association with NSW National Parks and Wildlife Service, New South Wales.

Bradstock, R.A. & Kenny, B.J. (2003) Application of plant functional types to fire management. *Journal of Vegetation Science*, **14**, 345–354.

Bradstock, R.A., Bedward, M., Scott, J. & Keith, D.A. (1996) Simulation of the effect of spatial and temporal variation in fire regimes on the population viability of a *Banksia* species. *Conservation Biology*, **10**, 776–784.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M. & Pyke, D. (2004) Effects of invasive alien plants on fire regimes. *BioScience*, **54**, 677–688.

Buckling, A., Kassen, R., Bell, G. & Rainey, P.B. (2000) Disturbance and diversity in experimental microcosms. *Nature*, **408**, 961–964.

Burgman, M.A. & Lamont, B.B. (1992) A stochastic model for the viability of *Banksia cuneata* populations: environmental, demographic and genetic effects. *Journal of Applied Ecology*, **29**, 719–727.

CapeNature & SANBI (2008) GIS Metadata – all_fires_07_08.shp. (ed. C. Tucker). Cape Town.

Cary, G.J. & Morrison, D.A. (1995) Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: Combinations of inter-fire intervals. *Australian Journal of Ecology*, **20**, 418–426.

Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, **31**, 343–366.

Chesson, P. (2003) Quantifying and testing coexistence mechanisms arising from recruitment fluctuations. *Theoretical Population Biology*, **4**, 345–357.

Chesson, P. & Huntley, N. (1997) The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *The American Naturalist*, **150**, 519–553.

Chesson, P. & Warner, R.R. (1981) Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist*, **117**, 923–943.

Clarke, M.F. (2008) Catering for the needs of fauna in fire management: science or just wishful thinking? *Wildlife Research*, **35**, 385–394.

Cowling, R.M. (1987) Fire and its role in coexistence and speciation in Gondwanan shrublands. *South African Journal of Science*, **83**, 106–112.

Cowling, R.M. & Campbell, B.M. (1980) Convergence in the vegetation structure in the mediterranean communities of California, Chile, and South Africa. *Plant Ecology*, **43**, 191–197.

Fagerstrom, T. & Agren, G.I. (1979) Theory for coexistence of species differing in regeneration properties. *Oikos*, **33**, 1–10.

Fernandes, P.M. & Botelho, H.S. (2003) A review of prescribed burning effectiveness in fire hazard reduction. *International Journal of Wildland Fire*, **12**, 117–128.

Gill, A.M. (1975) Fire and the Australian flora: a review. *Australian Forestry*, **38**, 4–28.

Gill, A.M. (1977) Management of fire-prone vegetation for plant species conservation in Australia. *Journal of the Australian and New Zealand Association for the Advancement of Science*, **8**, 20–26.

Gill, A.M. & Bradstock, R.A. (1995) Extinction of biota by fires. *Conserving Biodiversity: Threats and Solutions* (eds R.A. Bradstock, T.D. Auld, D.A. Keith, R.T. Kingsford, D. Lunney & D.P. Sivertson), pp. 309–322. Surrey Beatty and Sons, Sydney, Australia.

Gill, A.M. & Bradstock, R.A. (1997) Prescribed burning: patterns and strategies. *13th International Conference on Fire and Forest Meteorology*. Victoria, Australia.

Gill, A.M. & Groves, R.H. (1981) Fire regimes in heathlands and their plant-ecological effects. *Ecosystems of the World, 9B, Heathlands and Related Shrublands* (ed. R.L. Specht), pp. 61–84. Elsevier, Amsterdam.

Gill, A.M. & McCarthy, M.A. (1998) Intervals between prescribed fires in Australia: what intrinsic variation should apply? *Biological Conservation*, **85**, 161–169.

Haines, T.K., Busby, R.L. & Cleaves, D.A. (2001) Prescribed burning in the South: trends, purpose, and barriers. *Southern Journal of Applied Forestry*, **25**, 149–153.

Higgins, S.I., Flores, O. & Schurr, F.M. (2008) Costs of persistence and the spread of competing seeders and sprouters. *Journal of Ecology*, **96**, 679–686.

Holmes, P.M. & Cowling, R.M. (1997) Diversity, composition and guild structure relationships between soil-stored seed banks and mature vegetation in alien plant-invaded South African fynbos shrublands. *Plant Ecology*, **133**, 107–122.

Holmes, P.M. & Newton, R.J. (2004) Patterns of seed persistence in South African Fynbos. *Plant Ecology*, **172**, 143–158.

Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press.

Keeley, J.E. (1986) Resilience of mediterranean shrub communities to fire. *Resilience in Mediterranean-Type Ecosystems* (eds B. Dell, A.J.M. Hopkins & B.B. Lamont). Dr. W. Junk Publishers, Dordrecht.

Keeley, J.E. & Fotheringham, C.J. (2003) Impact of past, present, and future fire regimes on North American mediterranean shrublands. *Ecological Studies*, **160**, 218–262.

Keeley, J.E., Fotheringham, C.J. & Baer-Keeley, M. (2005) Factors affecting plant diversity during post-fire recovery and succession of mediterranean-climate shrublands in California, USA. *Diversity and Distributions*, **11**, 525–537.

Keeley, J.E., Zedler, P.H., Zammit, C.A. & Stohlgren, T.J. (1989) Fire and demography. *The California Chaparral. Paradigms Reexamined.* (ed. S.C. Keeley), pp. 151–153. N.H.M.o.L.A. County, Los Angeles.

Keith, D.A. & Bradstock, R.A. (1994) Fire and competition in Australian heath: a conceptual model and field investigation. *Journal of Vegetation Science*, **5**, 347–354.

Lamont, B.B., Connell, S.W. & Bergl, S.M. (1991) Seed bank and population dynamics of *Banksia cuneata:* the role of time, fire, and moisture. *Botanical Gazette*, **152**, 114–122.

Laurie, H. & Cowling, R.M. (1994) Lottery coexistence models extended to plants with disjoint generations. *Journal of Vegetation Science*, **5**, 161–168.

McCarthy, M.A., Possingham, H.P. & Gill, A.M. (2001) Using stochastic dynamic programming to determine optimal fire management for Banksia ornata. *Journal of Applied Ecology*, **38**, 585–592.

Miller, A.D. & Chesson, P. (2009) Coexistence in disturbance-prone communities: how a resistance-resilience trade-off generates coexistence via the storage effect. *The American Naturalist*, **173**, E30–E43.

Mooney, H.A. & Dunn, E.L. (1970) Convergent evolution of Mediterranean-Climate Evergreen Sclerophyll Shrubs. *Evolution*, **24**, 292–303.

Morrison, D.A., Cary, G.J., Pengelly, S.M., Ross, D.G., Mullins, B.J., Thomas, C.R. & Anderson, T.S. (1995) Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: inter-fire interval and time-since-fire. *Australian Journal of Ecology*, **20**, 239–247.

Morrison, D.A., Buckney, R.T., Bewick, B.J. & Cary, G.J. (1996) Conservation conflicts over burning bush in south-eastern Australia. *Biological Conservation*, **76**, 175.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Pausas, J.G. (2001) Resprouting vs seeding: a mediterranean perspective. *Oikos*, **94**, 193–194.

Pausas, J.G., Bradstock, R.A., Keith, D.A. & Keeley, E.R. (2004) Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology*, **85**, 1085–1100.

Reinhardt, E.D., Keane, R.E., Calkin, D.E. & Cohen, J.D. (2008) Objectives and considerations for wildland fuel treatment in forested ecosystems of the interior western United States. *United States Forest Ecology and Management*, **256**, 1997–2006.

Richards, S.A., Possingham, H.P. & Tizard, J. (1999) Optimal fire management for maintaining community diversity. *Ecological Applications*, **9**, 880–892.

Richardson, D.M. & van Wilgen, B.W. (1992) Ecosystem, community and species response to fire in mountain fynbos: conclusions from the Swartboskloof experiment. *Ecological Studies: Analysis and Synthesis*, **93**, 273–284.

Sale, P.F. (1977) Maintenance of high diversity in coral reef communities. *The American Naturalist*, **111**, 337–359.

Sale, P.F. (1978) Coexistence of coral reef fishes–a lottery for living space. *Environmental Biology of Fishes*, **3**, 85–102.

Schwilk, D.W., Keeley, J.E. & Bond, W.J. (1997) The intermediate disturbance hypothesis does not explain fire and diversity pattern in fynbos. *Plant Ecology*, **132**, 77–84.

Wade, D. & Lunsford, J.D. (1989) A guide for prescribed fire in Southern forests. Technical Publication R8-TP-US Department of Agriculture, Forest Service, Southern Region. Atlanta, GA.

Willis, T.J. & Read, J. (2007) Soil seed bank dynamics in post-fire heathland succession in south-eastern Australia. *Plant Ecology*, **190**, 1–12.

Wittkuhn, R.S., McCaw, L., Wills, A.J., Robinson, R., Anderson, A.N., Van Heurck, P., Farr, J., Liddelow, G. & Cranfield, R. (2011) Variation in fire interval sequences has minimal effects on species richness and composition in fire-prone landscapes of south-west Western Australia. *Forest Ecology and Management*, **261**, 965–978.

Yeaton, R.I. & Bond, W.J. (1991) Competition between two shrub species: dispersal differences and fire promote coexistence. *The American Naturalist*, **138**, 328–341.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. R code for disturbance-based storage model.

Figure S1. Coexistence in relation to variability when seeder life span (μ) is 10 years.