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The Fire and Flammability Niches in Plant Communities

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We construct a model of a multispecies forest that is often affected by major fires and explicitly incorporates life-history attributes of trees that are related to fire—flammability and susceptibility to fire. The model is used to explore coexistence mechanisms in forests; two fire-dependent coexistence mechanisms were identified. The first allows coexistence along a temporal axis since the last fire; this niche axis is well documented in the literature. The second coexistence mechanism relies on the influence of tree flammability on the incidence of fires and/or tree reproductive success. This "flammability niche" is explored in detail, with particular reference to eucalypt forests in Australia and Tasmania. Using the technique of linearized stability analysis about a positive equilibrium, we explored the local stability of assemblages with randomly generated life-history attributes. A robust and testable prediction of the model is that two species of fire-adapted tree are likely to coexist with a late-successional species if their flammabilities are very different, and if the most flammable species is more susceptible to fire but less likely to die as a result of non-fire causes. Our results have implications for managing fire-dependent ecosystems to maintain biodiversity. Although the motivation for this paper is observations on Australian eucalypt forests, the principles of coexistence that we discuss apply to all fire-prone forest and woodland ecosystems.

1. Introduction

Explaining how different tree species coexist in environmentally homogeneous sites is a topical issue in ecology (Loucks, 1970; Horn, 1974; Connell, 1978; Woods, 1979; Huston, 1979; Denslow, 1980; Finegan, 1984; Comins & Noble, 1985; Warner & Chesson, 1985; Chesson & Huntly, 1988). In this paper we address the specific question of whether or not more than one fire-adapted species can coexist with a species that is not adapted to recruit after fire. This question is prompted by observations on eucalypt forest and woodland communities in South-Eastern Australia. In these forests two or more fire-adapted tree species coexist in apparently homogeneous sites, with or without the presence of a species that is not adapted to fire (Pryor, 1976; Rogers & Westman, 1979; Margules *et al*., 1987; personal observation). No mechanism has been suggested to explain this coexistence, however first we will consider the coexistence of early and late successional species.

Many plant species appear to owe their existence to the frequent occurrence of fires which prevent their replacement by "late successional" plant species that dominate in the absence of fire. The coexistence of early-successional and late-successional species depends on the superior ability of each type of species to colonise space following different forms of disturbance (Grubb, 1977; West *et al*., 1981; Pickett & White, 1985; Runkle, 1985; Crawley & May, 1987; Huston & Smith, 1987; Chesson & Huntly, 1988; Rees & Long, 1992). In communities that are subject to severe fires species tend to fall into two groups, those that recruit soon after fires and species that recruit in the absence of fire, often as a consequence of senescence of fire-adapted species.

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Henceforth we will refer to the species that is not adapted to recruit in the absence of fire as a rainforest species because, in Australia, many rainforest species display this sort of life-history strategy. Many rainforest species regenerate poorly after fire but tolerate low light levels and colonise sites left vacant as a result of non-fire causes in Australia (Baur, 1957; Cremer, 1960; Webb, 1968) and Tasmania (Gilbert, 1959; Jackson, 1968; Henderson & Wilkins, 1975; Wilkins, 1976; Bowman & Jackson, 1981; Hill, 1982; Hill & Read, 1984). Despite this terminology, the late-successional species in a particular locality may be a late-successional eucalypt species, a tree fern, or a species of native pine *Callitris* sp. (Clayton-Greene, 1981).

Similarly, we will refer to the fire-adapted species as eucalypts. Eucalypt forests are frequently burnt, and the eucalypt genus is believed to have evolved many features in response to the high frequency of fire (Mount, 1964; Mutch, 1970; Gill, 1975; Bowman & Kirkpatrick, 1986; Noble, 1989). These features include fire-resistant bark (Gill & Ashton, 1968; McArthur, 1968), lignotuberous seedlings (Noble, 1984), serotiny (Webb, 1966; Gill, 1981) and flammability (Mutch, 1970). In our search for a coexistence mechanism we focus our attention on the fire-adapted life-history attributes of the eucalypts.

Although the motivation for this paper is observations on Australian eucalypt forests, the principles of coexistence that we discuss apply to fire-prone ecosystems around the world, particularly North America (Hough & Forbes, 1943; Heinselman, 1973; Viereck, 1973; Williamson & Black, 1981; Franklin & Hemstrom, 1981; Cwynar, 1987; Veblen & Lorenz, 1987) see Table 1.

We begin by describing a mathematical model that elucidates the conditions under which the coexistence of more than one eucalypt species is possible. The stability of combinations of coexisting species are examined to determine the attributes of the most stable assemblages. Given a stable assemblage, we explore the consequences of slow changes in fire frequency on community stability. We postulate that two fire-related life-history attributes of eucalypts play a key role in determining the conditions for coexistence: the flammability of the species, and the susceptibility of the species to fire. The flammability of trees in a forest is assumed to influence the frequency of severe fires. We define the susceptibility of an individual as the probability that the individual dies when burnt. We also incorporate the possibility that high individual flammability may confer a local seed advantage. Neighbours of a highly flammable individual are more likely to be burnt which increases the relative availability, to a more flammable individual, of sites suitable for colonization.

Our analysis predicts that, in homogeneous sites, two fire-adapted eucalypt species can coexist with a non-fire adapted rainforest species. Coexistence of the eucalypt species depends on the existence of flammability effects on fire frequency and/or reproduction. Where two eucalypt species coexist with a rainforest species we make testable predictions about the characteristics of those eucalypt species. The most stable combination of species includes a eucalypt species that is much more flammable, more susceptible to fire, and less likely to die of non-fire causes, than the other eucalypt species. We find that equilibrium communities are very sensitive to changes in fire frequency, and changes in fire frequency may produce community changes that are counter-intuitive. These results have implications for the management of ecosystems in which fire is an important disturbance event.

2. Model and Results

Consider a community that may contain one rainforest species, and *N* eucalypt species. Assume that the environment is made up of a large number of identical sites, each of which is dominated by a single species. We envisage that these sites are roughly equal to the area occupied by a mature tree. When a species loses a site in the absence fire it is colonised by the rainforest species, but when a site is burnt all the eucalypt species compete for the vacant site. Throughout the development of the model we assume that the pattern of species presence has no spatial structure: that is, each individual tree is assumed to be surrounded by a representative sample of trees in the forest.

The equations describing the dynamics of the system are

$$\frac{\mathrm{d}n_0(t)}{\mathrm{d}t}=\sum_{i=1}^{N}\mu_i n_i(t)-l_0 n_0(t) \tag{1a}$$

$$\frac{\mathrm{d}n_i(t)}{\mathrm{d}t}=\frac{An_i(t)s_i}{\bar{s}}-l_i n_i(t)-\mu_i n_i(t) \qquad \text{for } i=1,\dots,N, \tag{1b}$$

where

- $n_0(t)$ is the proportion of sites occupied by the rainforest species at time t;
- $n_i(t)$ is the proportion of sites occupied by eucalypt species i at time t;
- μ_i is the non-fire death rate of eucalypt species i;

- l_i is the rate at which individuals of species i lose their site as a consequence of fire;
- s_i is the relative ability of species i to colonize and establish itself by seed in recently burnt sites;
- $$\bar{s}=\sum_{i=1}^{N} s_i n_i(t)$$

  is the mean ability of all eucalypts in the forest to colonize recently vacated sites; hence the probability that species i colonizes a recently burnt site is $s_i n_i(t)/\bar{s}$; and
- A is the rate at which sites are vacated as a result of fire and become available for seed competition amongst the fire-adapted species,

  $$A=\sum_{i=0}^{N} l_i n_i(t).$$

Because all sites are occupied

$$\sum_{i=0}^{N} n_i(t)=1$$

at all times.

Equations (1a) and (1b) can be interpreted as follows. New sites are occupied by the rainforest species at the rate at which eucalypts die from non-fire causes, minus the rate at which rainforest sites are lost as a result of fire [eqn (1a)]. Note that we assume rainforest sites cannot be lost in the absence of fire. Eucalypt species i gains new sites at a rate determined by the rate at which new sites become available as a result of fire, A, multiplied by the probability that species i claims a site $n_i(t)s_i/\bar{s}$, minus the rate at which species i loses sites as a result of non-fire mortality and fire [eqn (1b)].

It is important to carefully define the rate at which an individual of species i loses its site as a consequence of fire. This rate, l_i, is equal to the average rate at which fires, above a certain intensity, pass through a site, multiplied by the susceptibility of an individual of species i to a fire above a certain intensity. Let $l_i = Fl_i^*$ where F is the frequency of fires above a certain intensity and l_i^* is the susceptibility of an individual of species i. There are a variety of factors that influence the susceptibility of a species. Many eucalypt species possess thick bark which increases the resistance of the tree to fire (Vines, 1968), while other species resprout from their trunk, branches or root stock thereby forming lignotuberous resprouts (Chattaway, 1958).

So far, we have introduced no flammability effects and the different flammabilities of the species in the forest are assumed to have no influence on the population dynamic equations. These effects will be introduced later.

CASE 1: A RAINFOREST SPECIES AND ONE EUCALYPT SPECIES

The equations for this case are:

$$\frac{dn_0(t)}{dt}=\mu_1 n_1(t)-l_0 n_0(t) \qquad (2a)$$

$$\frac{dn_1(t)}{dt}=l_0 n_0(t)-\mu_1 n_1(t) \qquad (2b)$$

The solution to this system of equations is well known,

$$n_1(t)=\hat{n}_1(1-\exp[-(l_0+\mu_1)t]) + n_1(0)\exp[-(l_0+\mu_1)t],$$

where the equilibrium proportion of sites occupied by the eucalypt species is

$$\hat{n}_1=\frac{l_0}{l_0+\mu_1}.$$

The rate at which the system returns to equilibrium following a small perturbation (which is a measure of the local stability of the equilibrium) is determined by the sum $l_0+\mu_1$. The larger the value of this sum the greater the stability of the coexistence. In this case a stable coexistence is possible if $l_0>0$ and $\mu_1>0$. Note that species 1 can invade when rare if $l_0>0$, while species 0 can invade when rare if $\mu_1>0$. This result merely confirms our intuition that both sources of mortality must occur if a stable equilibrium is to occur. Increasing the frequency of fires increases the stability of the equilibrium; however, if either μ_1 or l_0 is significantly greater than the other then one species will be very rare.

As stated in the Introduction, many eucalypt species have characteristics that enhance their flammability and the susceptibility of their near neighbours. These characteristics include: high levels of oil in the leaves (King & Vines, 1969), ribbony bark, and the production of large quantities of leaf litter that decays slowly and increases the fuel load on the ground (Raison *et al.*, 1986). Here, we assume that each eucalypt species has a certain flammability, f_i, that reflects these attributes.

Let the frequency of fires above a certain intensity (this intensity will determine the susceptibility of the species to fire) depend on the average flammability of trees in the forest according to the equation

$$F=F_0(1+c\bar{f})$$

where $\bar{f}$ is the mean flammability of the forest,

$$\bar{f}=\sum_{i=0}^{N} f_i n_i(t),$$

c is a parameter that determines the influence of mean flammability on fire frequency, and F_0 is the frequency of fires in the absence of any flammability effect, i.e. when all the trees in the forest have zero flammability. Henceforth we refer to F_0 as the community-independent fire frequency, and F as the community-dependent fire-frequency because it reflects the influence of the plant community on the frequency of fires above a certain intensity.

The coexistence of a rainforest species and one eucalypt species is not surprising and the coexistence mechanism described above is well known in the literature (Abugov, 1982; Armstrong, 1989). It is presented here as a point of departure for understanding the coexistence of more than one eucalypt species.

Case 1b: Forest flammability affects fire frequency

If $c \neq 0$ many of the conclusions of the previous case hold, although it is worth noting that introducing a flammability effect on fire frequency increases the local stability of the equilibrium if eucalypt forest is more common than rainforest at equilibrium, but decreases local stability if the rainforest species is more common than the eucalypt (see Appendix A).

To conclude case 1, a system with one eucalypt species and one rainforest species is stable. There are two regeneration niches, the fire niche and the non-fire niche. Both species will persist as long as some sites become available as a result of both kinds of disturbance. This result is well known, and the formulation presented here serves to lay the foundations for the more interesting three species case.

The effects of flammability

Before we address the question of whether three species may coexist, we introduce an advantage of high flammability. We assume that individuals gain a reproductive advantage that is in direct proportion to the difference between their flammability and the average flammability of the forest,

$$s_i=s_i'(1+a(f_i-\bar{f})),$$

where s'_i reflects the reproductive ability of species i in the absence of a flammability advantage and a is a constant of proportionality. This reproductive advantage is intended to reflect the relatively greater number of sites that become available adjacent to a highly flammable tree, including the site occupied by the tree. Henceforth we refer to this aspect of the model as the "flammability effect on reproduction", while the influence of mean forest flammability on the frequency of fires will be referred to as the "flammability effect on fire".

CASE 2: RAINFOREST AND TWO EUCALYPT SPECIES

The equations for this system are (dropping the time variable)

$$\frac{dn_0}{dt}=\mu_1 n_1+\mu_2 n_2-l_0 n_0 \tag{3a}$$

$$\frac{dn_1}{dt}=\frac{An_1 s_1}{\bar{s}}-l_1 n_1-\mu_1 n_1 \tag{3b}$$

$$\frac{dn_2}{dt}=\frac{An_2 s_2}{\bar{s}}-l_2 n_2-\mu_2 n_2. \tag{3c}$$

Before carrying out a linearized stability analysis of this model, we will find the conditions for which each fire-adapted species will invade an equilibrium community of the other two species when rare. This will help us to understand later results. Eucalypt species i invades when rare if

$$\frac{s_i(\bar{f})}{l_i(\bar{f})+\mu_i}>\frac{s_j(\bar{f})}{l_j(\bar{f})+\mu_j}\quad \text{for } i=1,\ j=2 \text{ and } i=2,\ j=1, \tag{4}$$

where $n_i=0$ and the other species are at equilibrium. Because the invasion of each species depends on the mean flammability of the forest, which in turn depends on the equilibrium forest composition, it is possible that inequality (4) is true for both $i=1$ and $i=2$ and both species can invade when rare.

Case 2a: No flammability effects, $c=0$ and $a=0$

In this case the mean flammability of the forest does not influence fire frequency and there is no reproductive advantage to a highly flammable tree. The terms s_i and l_i in the invastion inequality (4) are independent of the composition of the forest, consequently both inequalities cannot be true simultaneously and only one fire-adapted species exists at a constant equilibrium. This conclusion follows directly from the "competitive exclusion principle" that two or more species cannot stably coexist on a single resource at fixed densities (Armstrong & McGehee, 1980).

Case 2b. A flammability effect on fire frequency: $c>0$ and $a=0$

In this case there is no flammability effect on reproduction but the flammability of the forest as a whole does influence the frequency of fires. With the parameters chosen we found that it is possible for the forest composition to change the frequency of fires three-fold (see Appendix B). Because l_i depends on the mean flammability of the forest, it is possible for both invasion inequalities (4) to be true.

The protocol for carrying out the linearized stability analysis is as follows: a positive equilibrium point is first found by choosing $\hat{n}_2$ and $\hat{n}_2$ and then finding the parameters μ_1, μ_2 and s_1/s_2 that allow this particular equilibrium (see Appendix B). We then carry out a linearized stability analysis about the equilibrium from which the real part of largest eigenvalue, γ, is extracted (May 1973). The size of the real part of the largest eigenvalue determines the stability of the system. If $\gamma < 0$ then the system is stable. The value $1/|\gamma|$ is a measure of the time it takes for the system to approach equilibrium, the characteristic return time. The greater the value of $|\gamma|$ the more stable the system. We chose parameters so that the rates in the equations are expressed in unit per 100 years: for example if $\mu_1 = 1.0$ then the probability that an individual of species 1 dies each year as a result of non-fire mortality is about 0.01. Similarly, if $\lambda = -0.1$ the characteristic return time is 1000 years.

From over 1000 sets of randomly selected parameters, we chose combinations of life-history characteristics of the two eucalypt species that gave the most stable three species equilibrium assemblages. We discovered that the most stable communities contained one highly flammable eucalypt species (species A) and one less flammable eucalypt species (species B) with the following associated life-history traits:

Species A: high flammability, high susceptibility, low non-fire mortality

Species B: low flammability, low susceptibility, high non-fire mortality.

A typical set of model parameters illustrating coexistence under these circumstances is shown in Table 2. The assemblage stability (of those combinations which were stable) was positively correlated with (i) the difference between the flammabilities of the eucalypt species, and (ii) the community-dependent fire frequency.

The stability mechanism, at first sight, appears to be simple. An increase in the frequency of the highly flammable species, species A, reduces its competitive ability relative to that of species B, because it increases the frequency of fires which, in turn, disadvantages species A because of its higher susceptibility. There are, however, some more insights which can be unravelled by considering the ratio of the site loss rate of species A, to the site loss rate of species B,

$$R = (l_A(\bar{f}) + \mu_A)/(l_B(\bar{f}) + \mu_B), \tag{5}$$

which represents the flammability-dependent part of the invasion inequality (4) when $a = 0$. The way in which R behaves as the frequencies of the species changes only depends on the way in which R varies with $\bar{f}$. The partial differential of R with respect to $\bar{f}$ is negative if

$$\mu_A l'_B < \mu_B l'_A. \tag{6}$$

If inequality (6) is true then an increase in the mean flammability of the forest will decrease the relative competitive ability of species A. Coexistence is possible if inequality (6) is true and an increase in the abundance of species A causes $\bar{f}$ to increase which decreases the relative ability of species A. An increase in $\bar{f}$ can be caused by an increase in the abundance of species A in

TABLE 1

Dominant tree species of fire-prone forests

Region	Fire-sensitive and/or shade tolerant	Fire-adapted and/or shade intolerant	Source reference
Pennsylvania	*Pinus sp.*	*Tsug canadensis*	Hough & Forbes (1943)
Minnesota	*Abies balsamea* *Picea glauca* *Betula papyrifera*	*Pinus contorta*	Heinselman (1973)
Alaska	*Picea glauca* *Populus* sp.	*Betula sp.*	Viereck (1973)
Florida	*Quercus laevis* *Quercus geminata*	*Pinus palustris*	Williamson & Black (1981)
Pacific Northwest	*Tsuga heterophylla* *Abies amabilis*	*Pseudogat menziesii* *Pseudogata menzeisii* *Abies procera*	Franklin & Hemstrom (1981) Franklin & Hemstrom (1981)
Cascade Range	*Tsuga heterophylla* *Alnus rubra*	*Pseudogata menziesii*	Cwynar (1987)
Patagonia	*Austrocedus chilensis*	*Nothofagus dombeyi*	Veblen & Lorenz (1987)

TABLE 2

Parameter value of stable three species combinations (rates expressed per 100 *years)*

	Flamability	Susceptibility	Reproduction	Non-fire mortality
In all cases				
Rainforest	0.20	0.20	—	—
Case 2b	$c=2$, $F_0=1.9$, $F=5.2$, $\lambda=-0.20$			
	f_i	l_i	s_i	μ_i
Eucalypt A	1.47	0.33	0.05	0.34
Eucalypt B	0.71	0.21	0.07	1.82
Case 2b	*Approximately equal mortality rates:* $c=2$, $F_0=2.4$, $F=3.3$, $\lambda=-0.05$			
Eucalypt A	0.72	0.30	0.75	0.69
Eucalypt B	0.01	0.04	0.36	0.65
Case 2b	*Equal susceptibility:* $c=2$, $F_0=1.3$, $F=4.2$, $\lambda=-0.15$			
Eucalypt A	1.91	0.25	0.47	0.25
Eucalypt B	1.32	0.25	1.00	1.72
Case 2b	*Equal flammability:* $\mathbf{c}=2$, $F_0=1.4$, $F=3.6$, $\lambda=-0.18$			
Eucalypt A	2.0	0.26	0.28	0.65
Eucalypt B	2.0	0.05	0.59	3.67
Case 2b	*Equal flammability and susceptibility:* $c=2$, $F_0=1.8$, $F=5.3$, $\lambda=-0.28$			
Eucalypt A	2.00	0.25	0.09	0.27
Eucalypt B	2.00	0.25	0.27	3.71
Case 2c	$a=2$, $F_0=8.5$, $F=8.5$, $\lambda=-0.015$			
Eucalypt A	0.99	0.25	0.32	3.38
Eucalypt B	0.84	0.24	0.18	0.51
Case 2d	$a=4$, $c=2$, $F_0=1.2$, $F=2.1$, $\lambda=-0.032$			
Eucalypt A	1.42	0.24	5.18	2.60
Eucalypt B	1.16	0.03	0.79	0.28

two ways. One mechanism is independent of the presence of rainforest, the other operates through changes in rainforest frequency.

First, if the death rates of both eucalypt species are equal then increasing the frequency of species A does not alter the frequency of the rainforest species. Under these circumstances the increase in species A causes the mean flammability to rise simply because it has a greater flammability than species B. As the death rates are equal, this leads to the simplest coexistence case:

Species A: high flammability, high susceptibility.
Species B: low flammability, low susceptibility.

The greater the difference in the flammabilities and the susceptibilities, the more stable the equilibrium. A set of parameters which yields coexistence for approximately equal non-fire death rates is shown in Table 2.

Second, if both eucalypt species have equal flammability an increase in the frequency of species A may still cause an increase in the flammability of the forest through changes in the frequency of rainforest. In general, rainforest trees are much less flammable than eucalypts. If species A has a relatively low death rate, an increase in species A decreases the frequency of the rainforest species which, in turn, increases the frequency of fires and stabilises the coexisting pair of eucalypt species. In this case the coexisting eucalypts have the following properties:

Species A: low death rate, high susceptibility,
Species B: high death rate, low susceptibility.

Finally it is worth noting that the two species need not have different susceptibilities to fire. In this case the coexisting species will have the following traits:

Species A: high flammability, low non-fire mortality,
Species B: low flammability, high non-fire mortality.

All of these results were confirmed by stability analysis and a stable parameter set for each case is shown in Table 2. If the flammabilities of all species (including the rainforest species) are equal then coexistence is not possible because the mean flammability of the forest is independent of the composition of the forest. This confirms our intuition that the cause of stable coexistence is the influence of forest composition on fire frequency. Throughout history, and especially recently, the frequency at which fires are initiated has changed dramatically. Consequently it is of interest to determine the effect of changing F_0 on the stability of three species assemblages. Figures 1, 2 and 3 illustrate several interesting properties of the equilibrium community which are consistent for all the examples tested.

(i) As community-independent fire frequency increases the equilibrium abundance of the more flammable species decreases and the equilibrium abundance of the less flammable species increases.

(ii) The stability of the equilibrium has a maximum at a particular fire frequency; on either side of that maximum, stability decreases until the three species equilibrium becomes unstable.

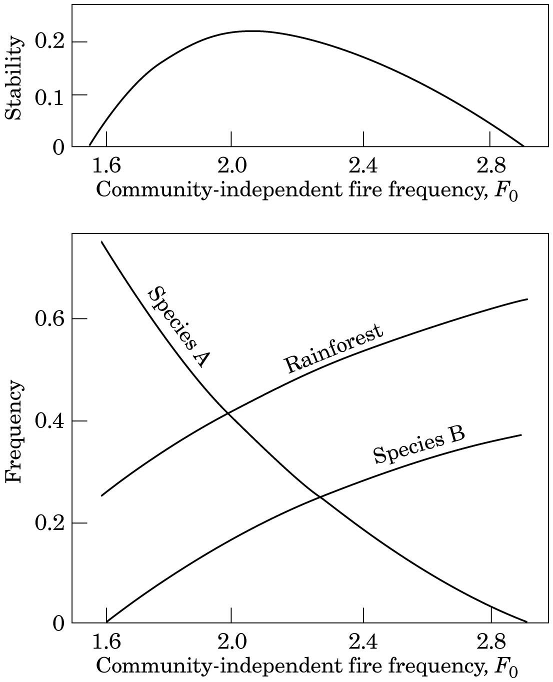

FIG. 1. The effect of changing community-independent fire frequency on the local stability, and composition, of three-species tree assemblages with randomly generated life-history properties when there is no flammability effect on reproduction, but tree flammability does affect the frequency of fires. Local stability is measured by the absolute value of the largest negative eigenvalue found by solving a linearized form of equation (3) about a positive equilibrium point. The species parameters are:

	f_i	l_i	s_i	μ_i
Eucalypt A	1.47	0.33	0.05	0.34
Eucalypt B	0.71	0.21	0.07	1.82

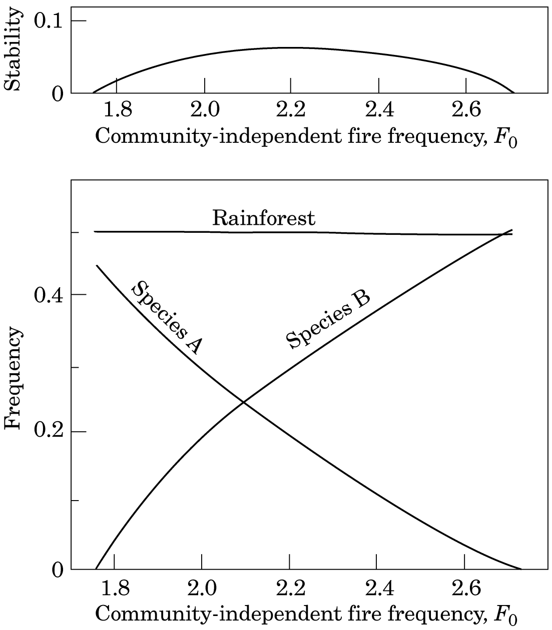

FIG. 2. As for Fig. 1 with approximately equal non-fire mortality rates. The species parameters are:

	f_i	l_i	s_i	μ_i
Eucalypt A	0.72	0.30	0.75	0.69
Eucalypt B	0.01	0.04	0.36	0.65

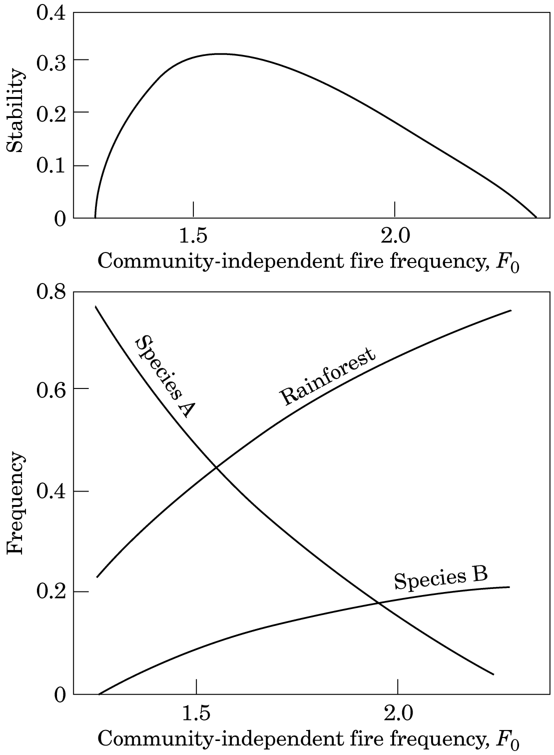

FIG. 3. As for Fig. 1 with the two eucalypt species having equal flammabilities and susceptibilities. The species parameters are:

	f_i	l_i	s_i	μ_i
Eucalypt A	2.00	0.25	0.09	0.27
Eucalypt B	2.00	0.25	0.27	3.71

(iii) The community-dependent frequency of fires, F, remains unchanged as community-independent fire frequency changes because of the response of the community composition. This remarkable property of the assemblage occurs because, at equilibrium, eqn (4) is an equality,

$$\frac{s_1}{l_1' F+\mu_1}=\frac{s_2}{l_2' F+\mu_2},$$

and hence community-dependent frequency is constant at equilibrium. This occurs because the flammability of the community changes to compensate for changes in community-independent fire frequency. Given this is an equilibrium result, the change in community composition may lag well behind long-term changes in fire frequency.

(iv) There are two mechanisms which enhance stability in three species assemblages, one of which involves alterations in the frequency of the rainforest species because of differences in the death rates of the eucalypts. It is precisely this mechanism which causes the apparently counter-intuitive result: *increasing community-independent fire frequency increases the equilibrium frequency of the rainforest species*. An increase in fire frequency favours the species with the lower fire susceptibility, which is the species that invariably has a higher non-fire death rate. This effect increases the total eucalypt non-fire death rate so rainforest frequency increases. This result is not true when stable assemblages exist in the absence of non-fire mortality differences between the eucalypts, but always occurred in the most stable assemblages (see Fig. 2).

Case 2*c*: $c=0$, $a>0$. *Flammability affects reproductive ability but not fire frequency*

In this case the flammability of the forest has no influence on the frequency of fires, but individuals gain a reproductive advantage by being flammable. Under these circumstances coexistence between two species of eucalypt is possible. We know that coexistence may occur because changes in the mean flammability of the forest can cause changes in the relative fitness of the two species (as in the previous case). By carrying out linearized stability analyses about randomly chosen equilibrium assemblages we found that the most stable pairs of coexisting eucalypts invariably showed the following properties:

Species A:	slightly higher flammability, high non-fire death rate, high reproductive ability.
Species B:	slightly lower flammability, low non-fire death rate, low reproductive ability.

In contrast to the previous case, there was no correlation between community stability and either community-independent fire frequency, or the magnitude of the difference in flammabilities of the two eucalypt species. Indeed, the most stable combinations occurred when the difference in flammability was small but not negligible. In this case it was much harder to find species combinations which were stable, and no realistic combinations had return times less than 1000 years (in contrast to the previous case where return times could be as low as 200 years with reasonable parameters).

To understand these results consider the relative reproductive abilities of the two species, s_A/s_B, which is influenced by the global variable, mean forest flammability. The ratio of the reproductive abilities represents the only part of the invasion inequality (4) that changes as species composition changes. Differentiating s_A/s_B with respect to $\bar{f}$ yields an expression which is negative if $f_A<f_B$. This means that an increase in the mean flammability of the forest increases the competitive advantage of species A if the flammability of species A is greater than the flammability of species B. As $f_A>f_B$, then increasing the frequency of species A is likely to increase the flammability of the forest which, in turn, increases the competitive advantage of species A. The introduction of a flammability advantage effect appears to be destabilizing. The system can only be stable if an increase in the abundance of the most flammable species causes a decrease in the mean flammability of the forest, which at first sight appears to be impossible. However this may be possible if the flammability of the rainforest species is low compared to the flammabilities of both eucalypt species, and the more flammable species has a comparatively high non-fire death rate. Under these circumstances an increase in the most flammable species may decrease the flammability of the forest by causing an increase in the abundance of the non-flammable late-successional community. The differences in susceptibility and reproductive rates between the two species merely reflects compensation for the large difference in non-fire mortality rates (see Table 2).

In summary, a flammability effect on reproduction may allow two species of eucalypt (fire-adapted tree) to coexist with a rainforest species (late-successional species) in the following special circumstances. The two eucalypt species must have slightly different flammabilities, the most flammable species must have a significantly higher non-fire death rate, and the rainforest species must be far less flammable than the two eucalypts. We do not believe that this mechanism is likely to allow two eucalypt species to coexist because the two species must have enormously different non-fire mortality rates. It may be a plausible

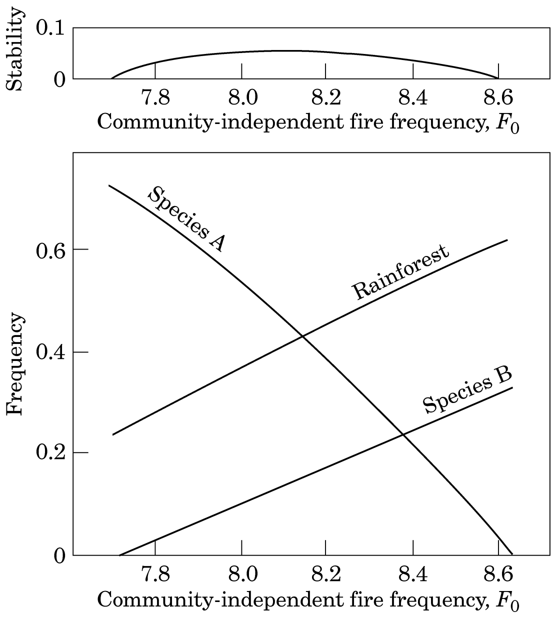

FIG. 4. As for Fig. 1 without a flammability effect on fire frequency, but with a flammability effect on reproduction. The species parameters are:

	f_i	l_i	s_i	μ_i
Eucalypt A	0.99	0.25	0.32	3.38
Eucalypt B	0.84	0.24	0.18	0.51

explanation for the coexistence of eucalypts with a species in a different genus, for example acacias in Australia. Acacias have comparatively short life spans, high flammabilities and high reproductive rates (Farrell & Ashton, 1978). An acacia with a flammability that is slightly higher than a eucalypt, a very high non-fire death rate, and a high reproductive rate, may be able to coexist with a eucalypt as a consequence of the mechanism outlined in this section.

As before, we are interested in determining the influence of changes in fire frequency on ecosystem stability. Figure 4 shows an example of changes in the properties of an equilibrium community as community-independent fire frequency changes. Few generalizations could be made about these systems, however one property was consistently true: stability reached a peak at a finite value of community-independent fire frequency. As with the previous example, large changes in community-independent fire frequency are likely to cause the assemblages to break down.

Case 2d: $c>0$, $a>0$. *Flammability influences fire frequency and reproductive ability*

In this case both flammability effects are incorporated into the model. Results from 2000 experiments with randomly selected species attributes indicate that the stable assemblages fall into two groups, each group corresponds to one of the two patterns described in the previous two sections. In general, the stable assemblages were not as stable as when there was a flammability effect on fire frequency, but not on reproduction (case 2b), because the two stability mechanisms tend to counteract each other. One stability mechanism is strongest when the eucalypts have very different flammabilities, the other when there is a small difference in flammabilities. When there is a flammability effect on fire frequency the more flammable eucalypt species has a smaller non-fire death rate in stable assemblages, but when there is a flammability effect on reproduction the more flammable species must have a greater non-fire death rate for stable coexistence.

CASE 3: THREE EUCALYPT SPECIES COEXISTING WITH RAINFOREST

As there is only one global variable, mean flammability, that influences the interaction between the eucalypts, there is no possibility for the coexistence of three species. This observation was confirmed by linearized stability analysis on eqn (1) with three fire-adapted species. We also considered the possibility that incorporating a simple age structure into the model may allow coexistence between three eucalypt species and rainforest. However the conclusion that only two fire-adapted species is robust with regard to this extension.

3. Discussion

In our model we have introduced the possibility that the influence of tree flammability on fire frequency and/or reproduction allows two species of fire-adapted eucalypt species to coexist in what we call the "flammability niche". In the remainder of this paper we summarize our conclusions, explicitly state testable hypotheses regarding the properties of coexisting trees in communities that are frequently burnt, and point out some of the limitations of our work. Throughout it is important to note that our predictions are qualitative; the problems of space and scale mean that the model is not capable of making quantitative predictions about forest composition.

Before discussing our conclusions it is worth noting the following limitations of the work we present here. Undoubtedly the most significant simplification is the absence of spatial structure. This simplification manifests itself in the assumption that all individuals are surrounded by a suite of tree species which are in direct proportion to their presence in the forest. This problem with the model could be solved by simulating the forest on a grid. The introduction of spatial structure enables other coexistence mechanisms (Pacala, 1986; Pacala & Tilman, 1994); however, there is no reason to expect that the mechanism described will cease to operate with the addition of an explicit spatial structure.

Another limitation is that the population dynamic processes in the model assume no evolution among the competing species. The time scale is consequently shorter than that required for significant life-history evolution by the eucalypts. The question of the evolution of fire-adapted traits is addressed in a companion paper (Possingham *et al*., in preparation). Also, the model does not address short-term changes in forest composition, for example annual changes. The changes in forest composition with which we are concerned occur over periods of hundreds or thousands of years.

To test empirically the various hypotheses set forth in this paper we suggest the following protocol. First determine the identity of the dominant tree species in a large (of the order of 100 square kilometres) and environmentally homogenous site, or in several nearby sites which have the same environment but are not necessarily contiguous. If there are more than four dominant tree species then the theory presented here cannot adequately explain the diversity and other coexistence mechanisms may be operating contemporaneously. In this case two or more of the species may be lumped into a one functional group if their life-history characteristics are sufficiently similar.

Second, look for a late-successional species (or community). This species should have the following properties: poor regeneration after fire, persistence in the understorey as suppressed individuals, and good recruitment following tree-fall. If there is no late-successional species then we predict that, if there are two fire-adapted species then the species with the greater flammability will be more susceptible to fire and there is a flammability effect on fire frequency, but if there is only one fire-adapted species present then its high flammability and high resistance to fire excludes other species. If a late-successional species is present in the community then there are three possible coexistence mechanisms.

(i) If there is a strong flammability effect on reproduction then there may be two fire-adapted species with the slightly more flammable species having a much greater (probably an order of magnitude) non-fire mortality rate. This strong flammability effect on reproduction will manifest itself by enhanced individual recruitment in and around a recently burnt site, and increased probability of site loss adjacent to more flammable trees.

(ii) If there is a strong flammability effect on fire frequency then there may be two fire-adapted species with the more flammable species being more susceptible and/or having a greater non-fire death rate.

(iii) If there is a flammability effect on fire frequency but the two fire-adapted species show no difference in flammability then the species with the lowest non-fire death rate must be more susceptible, and the late-successional community must be much less flammable than either of the fire-adapted species. If the late-successional community is more flammable than either fire-adapted species then the species with the lowest non-fire death rate must be less susceptible.

The most likely coexistence mechanism relies on community effects on fire frequency. The same sort of argument may apply to other disturbance types in which the community composition influences the disturbance rate. This may be true for large wind-fall gaps (Foster, 1988).

The most probable stable systems in which two fire-adapted species coexist are those in which the coexisting fire-adapted species display large differences in flammabilities, death rates and susceptibilities, there is a high community-independent frequency of fires F_0, and a large flammability effect on fire frequency, c. In forests with no late-successional species we predict that a coexisting pair of fire-adapted species will have the following attributes: one will be highly flammable and very susceptible to fire the other will be less flammable and less susceptible to fire. In forests with a late-successional species or community the situation is more complex, with differences in non-fire mortality playing a crucial role. In the presence of a late-successional community that has a low flammability, very stable coexisting species assemblages are more likely than in the absence of a late-successional community, with the more flammable fire-adapted species being more susceptible to fire but less likely to die in the absence of fire.

In communities with two or more fire-adapted species, the stability of the community is very sensitive to changes in fire frequency. This has implications for the management of ecosystems that are frequently burnt. Changes in fire-frequency may result in the local extinction of one or more of the dominant tree species. As so many other organisms are dependent on the presence of particular tree species the loss of dominant tree species may have catastrophic effects. This is particularly true when the fire-adapted tree species provide very different resources for other organisms: for example, a pine and an oak, or a rough-barked and a smooth-barked eucalypt.

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APPENDIX A

Local Stability Analysis for Two-species Equilibrium where there is a Flammability Effect on Fire Frequency

The equation for the dynamics of the eucalypt species is

$$\frac{\mathrm{d}n_1}{\mathrm{d}t} = Fl'_0(1+cf_1n_1)(1-n_1)-\mu_1n_1. \qquad (\text{A.1})$$

Using local stability analysis, the equilibrium is locally stable if

$$-\mu_1 - Fl'_0 + Fl'_0cf_1(1-2\hat{n}_1) < 0. \qquad (\text{A.2})$$

The stability of the linearized system will be reduced if both $c>0$ and $1-2\hat{n}_1>0$. Consequently, if the eucalypt species is rare at equilibrium ($\hat{n}_1$ small), and the presence of eucalypts increases the frequency of fires significantly, then the local equilibrium will be less stable that in the absence of a flammability effect on fire frequency.

APPENDIX B

Methods used for Randomized Parameter Selection and Linearized Stability Analysis

In all cases the following rainforest life-history parameters were fixed: $f_0=0.2$, $l'_0=0.8$. The eucalypt life-history parameters were chosen randomly within the following bounds:

$$0<1'_1<1,\ 0<f'_i<2, \text{ for } i=12.$$

Where there was a flammability effect on either fire frequency or reproduction $c=2$ and $a=2$. The community-independent fire frequency was chosen within the bounds $0<F_0<5$. To guarantee positive equilibrium frequency we randomly chose the positive equilibrium frequency for each of the two eucalypt species and then evaluated the appropriate values of μ_1, μ_2 and s_1/s_2 to fit these positive equilibria. The non-fire mortality rates were constrained within the range $0.2<\mu_1<5$ (i.e. from 0.2% to 5% annual site loss rates).

Whenever an appropriate set of parameters was found we carried out a local stability analysis about the equilibrium. The largest negative eigenvalue determines the stability of the species assemblage (see Roughgarden, 1979, for a detailed description of this technique).