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ORIGINAL PAPER

The role of succession in the evolution of flammability

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Abstract

Fire-prone ecosystems contain plants that are both fire-adapted and flammable. It has been hypothesized that these plants were under selection to become more flammable, but it is unclear whether this could be adaptive for an individual plant. We propose arrested succession as a robust mechanism that supports the evolution of flammability in surface fire ecosystems without the need to invoke group selection or additional fitness benefits. We used the natural history of lodgepole pine (*Pinus ponderosa*) forests, longleaf pine (*Pinus palustris*) forests, and tall grass prairies to create a general mathematical model of surface fire ecosystems and solved for the evolutionarily stable strategy (ESS) level of flammability. In our model, fires always kill understory plants and only sometimes kill overstory plants. Thus, more flammable plants suffer increased mortality due to fires, but also more frequently arrest succession by clearing their understory of late successional competitors. Increased flammability was selected for when the probability of an overstory plant dying from an individual fire was below a maximum threshold and the rate of succession relative to fires was above a minimum threshold. Future studies can test our model predictions and help resolve whether or not plants have been selected to be more flammable.

Keywords Arrested succession · ESS · Evolution · Flammability · Mutch Hypothesis

Introduction

Fire is a widespread disturbance that has shaped global biome distribution and the evolution of plants (Bond and Keeley 2005; Bond et al. 2005). An estimated 40% of the Earth is covered by fire-prone ecosystems and plants in these communities often have specific adaptations to cope with regular fires (Chapin et al. 2002; Keeley et al. 2011). Several studies have shown that highly flammable and fire-adapted plants could lead to alternative stable states of either frequently burned or rarely burned vegetation (Beckage and Ellingwood 2008; Kitzberger et al. 2012; Staver and Levin 2012; Schertzer et al. 2014). It is possible that ecosystems including savannas, rain forests, temperate forest, and shrub-dominated vegetation could all be structured by these plant-fire feedbacks (Jackson 1968; Nowacki and Abrams 2008; Warman and Moles 2009; Odion et al. 2010; Murphy and Bowman 2012; Wood and Bowman 2012; Dantas et al. 2013; Ratajczak et al. 2014a, b; Pausas 2015).

In 1970, Robert Mutch proposed that plants with fire adaptations are selected to be more flammable, making observed plant-fire feedbacks an outcome of natural selection (Mutch 1970). This idea, now called the Mutch Hypothesis, is an example of niche construction, the process by which organisms actively increase their fitness by modifying their environment (Wilson and Agnew 1992). Mutch reasoned that fire-adapted species have a competitive advantage over species without fire adaptations in the presence of fires, making it advantageous for fire-adapted species to increase the probability of a fire. His hypothesis suggests that fire-prone ecosystems are not simply the result of environmental factors, but have been actively constructed by plants. The Mutch Hypothesis has since served as an evolutionary rationale for the high flammability of fire-adapted communities and the existence of pyrophytes—fire-adapted niche constructing plant species that have increased fitness in the presence of fires. However, the Mutch Hypothesis has been controversial because it is hard to prove that flammability is a trait under selection (Bowman et al. 2014; Keeley et al. 2011). The Mutch Hypothesis was also criticized on theoretical grounds because Mutch originally relied on a group selection

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mechanism (Snyder 1984; Troumbis and Trabaud 1989). Even though fire-adapted communities could suppress non-fire-adapted communities by becoming more flammable, increased flammability in an individual fire-adapted plant would increase its fire mortality rate relative to less flammable fire-adapted plants. This makes Mutch's original mechanism susceptible to "cheater" pyrophytes that decrease in flammability and are consequently favored due to their lower mortality rates relative to conspecifics. For pyrophytes to evolve, there would need to be an individual benefit to increased flammability relative to conspecifics that more than offsets the costs of increased fire mortality. Without a plausible mechanism for the Mutch Hypothesis, there is no theoretical grounding to claims that flammability is an evolved trait.

Following these criticisms, the Mutch Hypothesis has been an ongoing topic of debate (Bradshaw et al. 2011a, 2011b; Keeley et al. 2011; Pausas and Moreira 2012; Midgley 2013; Bowman et al. 2014), with promising new research suggesting mechanisms that do not rely on group selection (Bond and Midgley 1995; Schwilk and Kerr 2002; Gagnon et al. 2010). Although the two new theoretical models used to support the Mutch Hypothesis present dramatic improvements over Mutch's original formulation (Bond and Midgley 1995; Schwilk and Kerr 2002), they also include unrealistic dispersal, fire spread, and fitness assumptions (Midgley 2013). In the model proposed by Bond and Midgley (Bond and Midgley 1995), pyrophytes only consistently outcompete non-pyrophytes when they are given additional fitness benefits in the form of higher fire survival or increased seed production. While the modifications that Schwilk and Kerr (Schwilk and Kerr 2002) made to the Bond and Midgley model allowed pyrophytes to invade non-pyrophytes without additional fitness benefits, their model is based on an environmental niche tracking mechanism. This mechanism allows the higher mortality rate of pyrophytes to translate into shorter generation times and thus an increased ability to track a stochastic environment. However, the Schwilk and Kerr model relies on an unrealistically strong stochastic environmental selective pressure as well as the original dispersal and fire spread assumptions of the Bond and Midgley model. Although both models present alternative mechanisms to Mutch's group fitness mechanism, these models do not provide empirical evidence to support their assumptions and were not based on real pyrophyte ecosystems. Consequently, there is currently no strong modeling evidence that increased flammability can be adaptive.

We develop a new analytically tractable mathematical model to explore the theoretical plausibility of the Mutch Hypothesis in surface fire ecosystems. Although there is a diversity of fire-prone ecosystems, we restrict our model to surface fire ecosystems to keep the model tractable and to allow us to focus on a single mechanism. Unlike previous models, this model is inspired by three specific ecosystems with frequent surface fires and incorporates the important ecological process of succession. Incorporating succession into the Mutch Hypothesis highlights the fact that early successional plants not only compete with each other, they also compete with late successional plants in their understories. If an early successional individual could decrease the fitness costs arising from competition with late successional competitors, it would have a competitive advantage over other early successional individuals. This is comparable to how, all else equal, prey individuals with a genotype that makes them better at avoiding predation would have a higher fitness than their more heavily predated conspecifics and we would expect that individuals with this genotype would outcompete their less fit conspecifics. Similarly, if an early successional genotype could reduce death due to competition with late successional species, individuals with that genotype would be favored when in competition with conspecifics.

By incorporating succession into a model of the evolution of flammability, we can ask if it is possible that the benefits of increased flammability can outweigh the costs of increased flammability. Although high flammability in early successional individuals increases their risk of dying from a fire, it also increases the chance that fires kill late successional competitors in their understories, thereby arresting succession. This provides a potential selective pressure favoring increased flammability and a possible explanation for why pyrophytes are early successional species that are replaced by less flammable late successional species in the absence of fire (Clements 1936; Odum 1969; Frelich and Reich 1999; Nowacki and Abrams 2008; Warman and Moles 2009; Odion et al. 2010; Staver and Levin 2012; Wood and Bowman 2012; Ratajczak et al. 2014a, b). If this mechanism is viable, it could lead to the counterintuitive result that early successional individuals that increase their own flammability, and therefore their own risk of dying from fires, are more fit than less flammable early successional individuals.

In this study, we develop a simple mathematical model of surface fire ecosystems to test whether arrested succession can create a selective pressure for increased flammability. In Mutch's original mechanism, a group of fire-adapted species competed against a group of non-fire-adapted species. In this model, we compete two genotypes of a fire-adapted early successional species that differ only in their flammability. Both early successional genotypes are also in competition with a late successional species that will replace them unless fires arrest succession. Using this mathematical model, we find the optimal flammability of an early successional individual. Selection for increased flammability in early successional species would provide evidence for arrested succession as a novel mechanism that could drive the evolution of pyrophytes.

Model

Empirical case studies

We consider three different ecosystems with fire regimes characterized by frequent low mortality surface fires to build the assumptions for a new mathematical model of the evolution of flammability. The first example system is ponderosa pine (*Pinus ponderosa*) dominated forests in the western USA. Ponderosa pine is a shade-intolerant and drought-tolerant tree with a large range, including distribution in savannas and mesic forests. In mesic forests, ponderosa pine is replaced by more shade-tolerant evergreens like firs (*Abies* spp.) and Douglas fir (*Pseudotsuga menziesii*) in the absence of fire (Thomas and Agee 1986; Graham and Jain 2005). Frequent low to moderate severity surface fires are common in ponderosa pine forests with return intervals ranging as low as 4–7 years (Agee 1998; Shepperd and Battaglia 2002; Graham and Jain 2005). Low severity surface fires cause low mortality to adult ponderosa pines due to their thick insulating bark (Graham and Jain 2005). Late successional trees are less fire resistant and suffer considerable mortality from surface fires when in the understory (Thomas and Agee 1986). Thus, frequent fires arrest succession by killing late successional understory species before they can outcompete ponderosa pines. This allows ponderosa pine to remain dominant until occasional long fire-free intervals allow late successional species to develop sufficiently thick bark to survive fires (Keane et al. 1990; Hagmann et al. 2013). Fire suppression from human activities has reduced the frequency of fire in areas with ponderosa pine and has led to the replacement of ponderosa pine with late successional evergreens (Graham and Jain 2005).

The second system is longleaf pine (*Pinus palustris*) forests in the southeastern USA. The fire regime in these areas is characterized by frequent low severity surface fires that may occur every 1–5 years (Platt et al. 1988; Agee 1998). Longleaf pine has an unusual juvenile grass stage characterized by a thick bunch of needles at ground level that protect the apical bud and the growth of a long taproot. This grass stage makes longleaf pines resistant to low severity surface fires. After the initial 3–5 years in the grass stage, the tree rapidly grows in height and bark thickness, protecting it from future surface fires (Agee 1998). Frequent fires suppress resprouting understory hardwoods, allowing the shade-intolerant longleaf pines to dominate (Platt et al. 1988; Van Lear et al. 2005). After long fire-free intervals, shade-tolerant hardwoods like oaks (*Quercus* spp.) and hickories (*Carya* spp.) can become too large to be top-killed by fires, allowing them to eventually replace longleaf pines (Gilliam and Platt 1999; Van Lear et al. 2005; Loudermilk et al. 2011). Recent fire suppression has allowed succession to proceed uninterrupted, contributing to the loss of longleaf pine forests (Van Lear et al. 2005).

The final case system is the tall grass prairie in central North America. These systems are dominated by flammable C4 grasses, including big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), and Indiangrass (*Sorghastrum nutans*). Tall grass prairies span a range of climactic and edaphic conditions and support deciduous forest along rivers. Historically, low severity fires and grazing by bison (*Bison bison*) have been major disturbances in tall grass prairies. The pre-European fire return interval in tall grass prairie may have been as short as 1 year (Bragg and Hulbert 1976), but grasses are able to survive these frequent fires by resprouting from insulated buds (Benson and Hartnett 2006; Choczynska and Johnson 2009). Unlike grasses, the seedlings of woody plants are vulnerable to fire, allowing frequent fires to suppress woody plants. Given longer fire return intervals, shrubs such as smooth sumac (*Rhus glabra*), roughleaf dogwood (*Cornus drummondii*), and coralberry (*Symphoricarpos orbiculatus*) can survive fires by resprouting. This allows shrubs to replace grasses if the fire return interval is long enough for shrubs to escape the vulnerable seedling stage (Bragg and Hulbert 1976; Briggs et al. 2005; Ratajczak et al. 2014a). Further increases in fire return interval allow for the establishment of trees like eastern redcedar (*Juniperus virginiana*), which can only resist fires when large (Briggs et al. 2005; Ratajczak et al. 2014b). Due to their shade intolerance, grasses and shrubs are eventually excluded by trees (Ratajczak et al. 2014b). Fire suppression causes tall grass prairie to transition into stable shrubland and forests (Briggs et al. 2005; Ratajczak et al. 2014b).

These three empirical systems show some of the diversity and commonalities within surface fire ecosystems. Each system has a unique abiotic and biotic composition, natural history, and fire regime. However, ponderosa pine forests, longleaf pine forests, and tall grass prairies also share similar characteristics that can be incorporated into a general model of surface fire systems. In all three systems, pyrophytes have adaptations that increase their chances of surviving surface fires, such as thick bark and resprouting, and juvenile pyrophytes survive to adulthood in sufficient numbers that adult pyrophytes can dominate the landscape. In contrast, fires suppress late successional species growing in the understory and this arresting of succession limits the dominance of late successional species. In the absence of fires, late successional species replace early successional species and can become more resistant to fires due to increased size. Thus, even though all three systems have their own idiosyncrasies, they share three important qualities: pyrophytes are early successional species that are eventually replaced by late successional species in their understory, all adult plants have the ability to survive fires, and understory late successional plants are easily suppressed by fires due to their small size, resulting in an arresting of succession. These characteristics provide the basis for arrested succession as a potential mechanism for the evolution of flammability. If individual pyrophytes can increase their flammability, they may increase the time that succession is arrested and therefore increase their lifetime reproduction even though increased flammability will also increase the chance that they die from fires. We construct a simple mathematical model of surface fire ecosystems based on the shared natural history of these three ecosystems to determine the conditions under which arrested succession could lead to the evolution of flammability.

Mathematical model

This model aims to test whether flammability could be adaptive in surface fire ecosystems using a simple mathematical model. We develop a continuous-time model of succession that allows us to solve for the evolutionarily stable strategy (ESS) level of flammability for an early successional species. In this model, two different genotypes of an early successional species compete with each other and the only way that they differ is in their flammability. To solve for the ESS level of flammability, we test whether a rare invading genotype will increase in population size when introduced to a community of residents with another genotype. This invader represents an early successional individual with a mutation that changes its flammability. Early successional individuals that have the ESS flammability cannot be successfully invaded by any other early successional genotype that has a different flammability. Also, the genotype with the ESS flammability can invade any other genotype with a different flammability as long as they are otherwise identical (Maynard Smith 1982). Thus, the ESS flammability represents the flammability of the early successional genotype that can outcompete all other early successional genotypes with a different flammability. By solving for the ESS level of flammability, we are solving for the evolutionarily most competitive level of flammability.

This mathematical model incorporates the shared dynamics from the empirical case studies. By focusing on these dynamics, we create a general model designed to specifically test whether increased flammability can be adaptive due to arrested succession in surface fire ecosystems, not a model that produces specific results for a particular system. Recall that the three major dynamics that this model must capture are the following: early successional plants that are replaced by late successional plants growing in their understory, adaptations that allow adult plants to survive some fires, and understory late successional plants with a high vulnerability to fires. For simplicity, we assume that early successional species grow quickly enough that the time it takes for them to reach adulthood and acquire resistance to fires is negligible, allowing us to treat all early successional plants as reproducing plants with a resistance to fire.

In this model, fires always kill late successional understory plants, but only sometimes kill adult plants. We assume that understory plants are more vulnerable to fires than overstory plants due to their small size. When plants reach the overstory, we assume they have developed some resistance to fires through survival mechanisms like thick bark or resprouting that allow them to survive a proportion of fires. Thus, we only consider fires of sufficient severity to kill late successional understory individuals because we assume that fires that do not harm understory individuals will also have no effect on adult plants and can therefore be ignored. To test the plausibility of the Mutch Hypothesis, we assume that flammability is a selectable trait that allows plants to affect their local fire severity or fire return interval by modifying fuel or microclimate, but for simplicity, we do not treat fires as spatially explicit phenomena.

In this model, space is divided into an infinite number of patches, with the state variables representing the fraction of patches occupied by a particular type of plant. The fraction of patches not occupied by plants is called free space, F. The proportion of patches occupied by early successional plants is denoted by E. We expect the number of seeds produced by early successional plants to be proportional to the proportion of early successional patches, E, and assume all early successional plants have the same fecundity and probability of successful establishment in free space, F. To determine the number of early successional seeds that establish in free space, we assume that seeds collide with free space following basic mass action. This means that early successional plants, E, colonize free space at a rate given by the product of the fraction of patches occupied by early successional plants, the fraction of free space, and some constant c denoting fecundity and seedling establishment (Fig. 1 and Table 1). Late successional species, L, are by definition assumed to be poor colonizers of free space relative to early successional species. We explore parameter space in which the fraction of patches colonized by late successional species is sufficiently small that these terms can be ignored (Fig. 1 and Table 1).

Succession is represented by late successional establishment in the understory of early successional plants, with late successional woody plants technically in the understory of herbaceous species like grasses. We divide early successional patches into those without a late successional understory, E_1, and those with late successional establishment, E_2. Following the same basic assumptions used for the early successional colonization of free space, the rate at which L colonize E_1 patches and transition them to E_2 patches is equal to $\omega L E_1$, where ω represents late successional fecundity and establishment. E_2 patches then transition to L at some constant rate, s, as the late successional species replace early successional species through overtopping (Fig. 1 and Table 1). This aspect of the model reflects the observation that pyrophytes are early successional species that can be eventually outcompeted by late successional species growing in their understories.

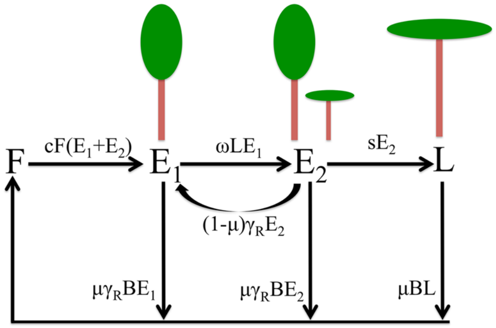

Fig. 1 A diagram of the resident model with rates shown next to transitions. *F* represents free space, which is colonized by early successional individuals in E_1 and E_2. Late successional individuals can establish under early successional canopies, causing E_1 to transition to E_2. E_2 then transition to *L* as late successional individuals replace early successional individuals. Plants create free space when they die in fires, which occur at rate *B*, but full-grown plants only have a probability μ of dying from an individual fire. If the early successional plant in E_2 survives a fire, it transitions back to E_1. γ_R represents increased flammability as part of a pyroflora strategy. This system is then invaded by a mutant species, *P*, with a flammability of γ_I. This diagram shows the resident model before rescaling by *B*

Occupied patches are converted to free space at rate μB, where *B* represents the intrinsic fire frequency and μ represents the proportion of burned overstory plants that die in the fire. The parameter μ ecologically corresponds to the severity of fires relative to the ability of plants to survive fire through thick bark, resprouting, or other fire survival adaptations. We make the conservative assumption that overstory *E* and *L* plants have the same probability of surviving a fire, μ, but the key difference is that all understory late successional individuals die in fires. Thus, if an E_2 patch burns, there is a $(1 - \mu)$ probability that the understory late successional plant dies, but the early successional plant survives and the patch is therefore converted back into an E_1 patch (Fig. 1 and Table 1). As μ decreases, early successional plants are able to survive a higher proportion of fires due to a combination of lower fire severity and an increase in fire adaptations that prevent mortality. This leads to a high proportion of E_2 patches converting back into E_1 patches, which results in an increase in the arresting of succession (Fig. 1 and Table 1). This part of the model represents two key dynamics found in our case studies—adult plants have a probability of surviving fires $(1 - \mu)$ and differential mortality between overstory and understory plants allows fires to arrest succession.

The parameter γ modifies the intrinsic fire frequency, *B*, for early successional plants and represents increased flammability as part of a pyrophyte strategy. Our model assumes that there is at least one trait that can be under selection, such as the characteristics of litter or traits that affect local microclimates that can affect flammability (Moreira et al. 2014; Ripley et al. 2015; Pausas et al. 2016; Simpson et al. 2016). A high γ can be interpreted as an increase in the probability of a fire of sufficient severity to kill understory plants. This could be caused by both an increase in the local fire severity that makes previously harmless fires lethal to understory individuals and an increase in the probability that a patch catches fire from direct ignition or neighboring patches. Therefore, a high γ leads to a higher early successional death rate due to fire, but also an increased ability to delay death due to succession (Fig. 1 and Table 1). In this model, the evolution of pyrophytes occurs when the ESS value of γ is greater than one, as this shows that increased flammability is adaptive. We assume that μ is controlled by preexisting fire survival adaptations that evolved in response to frequent fires driven by climate and that these adaptations may then drive selection for increased flammability, γ. It would be more realistic to model plant

Table 1 A list of state variables and parameters as well as a description of the variable and the range of values it can take

List of variables		
State variables	Description	Values
E_1	Proportion of patches occupied by resident early successional species with no understory	$0 < E_1 < 1$
E_2	Proportion of patches occupied by resident early successional species with a late successional understory	$0 < E_2 < 1$
P_1	Proportion of patches occupied by invader early successional species with no understory	$0 < P_1 < 1$
P_2	Proportion of patches occupied by invader early successional species with a late successional understory	$0 < P_2 < 1$
L	Proportion of patches occupied by adult late successional species	$0 < L < 1$
F	Proportion of patches occupied by free space	$0 < F < 1$
Parameters		
c	Number of seeds produced by an early successional patch that can successfully establish in free space	$c > 0$
B	Intrinsic fire frequency	$B > 0$
γ	Scaling parameter that increases the intrinsic fire frequency as part of the pyrophyte strategy	$\gamma \geq 1$
μ	Probability of an overstory plant dying in a fire	$0 < \mu < 1$
ω	Number of seeds produced by a late successional patch that can successfully establish in an early successional patch	$\omega > 0$
s	Rate at which late successional understory plants outcompete early successional plants, transitioning them to late successional patches	$s > 0$

investment in μ as a dynamic variable that must be traded off with other parameters, such as c, s, or ω. The ESS would then be an investment strategy that results in optimal values for γ, μ, and the parameter that trades off with μ. To keep the system analytically tractable, we assume that μ is static and solve for the ESS level of flammability as a function of μ.

To solve for the ESS level of flammability, we include a mutant early successional genotype, P, which competes with E. The only difference between the two types is that they have different levels of flammability. E_1 and E_2 have flammability γ_R, denoting the fact that they are the resident population, and P_1 and P_2 have flammability γ_I, denoting the fact that they are the invader population. Note that E, P, and L all compete for limited space because $F + E_1 + E_2 + P_1 + P_2 + L = 1$. Intraspecific competition between E and P is represented by their competition for free space, F, via seed production and establishment. Interspecific competition between L and both E and P is represented by the conversion of E_1 and P_1 into E_2 and P_2 respectively, and their subsequent conversion to L. The full system of equations (Eq. 1) is as follows:

$$
\begin{aligned}
\frac{dE_1}{dt} &= cF(E_1 + E_2) - E_1(\mu\gamma_R B + \omega L) + (1-\mu)\gamma_R B E_2 \\
\frac{dE_2}{dt} &= \omega L E_1 - E_2(\gamma_R B + s) \\
\frac{dL}{dt} &= s(E_2 + P_2) - \mu B L \\
\frac{dP_1}{dt} &= cF(P_1 + P_2) - P_1(\mu\gamma_I B + \omega L) + (1-\mu)\gamma_I B P_2 \\
\frac{dP_2}{dt} &= \omega L P_1 - P_2(\gamma_I B + s) \\
\frac{dF}{dt} &= \mu B(\gamma_R(E_1 + E_2) + \gamma_I(P_1 + P_2) + L) - cF(E_1 + E_2 + P_1 + P_2) \\
F &= 1 - E_1 - E_2 - P_1 - P_2 - L
\end{aligned}
$$

We note that a high γ increases the fire mortality term, $\mu\gamma B$, for both E and P. However, it also increases the rates at which E_2 and P_2 patches are converted back into E_1 and P_1 patches, respectively. This is seen in the arrested succession term $(1-\mu)\gamma B$ for both E and P and represents late successional individuals being removed from the understory of early successional patches. This arresting of succession can increase the fitness of E and P because it increases their lifetime reproduction. Since E and P only differ in their flammability, γ, we can determine if and when a higher γ allows P to invade E communities. Note that in the absence of succession, a $\gamma > 1$ is always unfavorable because its only effect is increasing fire mortality, which has a purely negative impact on fitness. Hence, in a reduced system without succession, the ESS $\gamma = 1$ because minimizing γ is always the most competitive strategy (Appendix: Methods).

To make the full system easier to analyze, we can rescale the equations by dividing them all by B and changing the timescale to $d\tau = dtB$. This produces equations identical to those above, but t, c, ω, and s scale in units of B—$\tau = t/B$, $c^* = c/B$, $\omega^* = \omega/B$, and $s^* = s/B$ (Appendix: Methods; Eq. 3). We assume that $c^* > 0$, $\omega^* > 0$, $s^* > 0$, $0 < \mu < 1$, $\gamma \geq 1$, and that state variables cannot take on negative values. To solve for the ESS level of flammability, we conduct an invasion analysis and determine the value of γ_R that cannot be invaded by any γ_I.

Results

Increased flammability is selected for over a range of parameter values. The invasion analysis allows us to analytically solve for the ESS level of flammability, γ_{opt} (Appendix: Methods; Eq. 2; Fig. 2):

$$
\gamma_{\text{opt}} = \frac{(\mu + s)\sqrt{\mu(\mu + 4s^*\omega^*)} - \mu(\mu + s^*(2(s^* + \omega^*) + 1))}{2\mu s^*}
$$

Increased flammability is adaptive in the parameter space where $\gamma_{\text{opt}} > 1$. From this invasion criterion and Eq. 2, we derive three important results. First, pyrophytes can only invade if the probability of dying from a fire, μ, is below a threshold value, μ_{crit} (Eq. 12; Appendix: Methods). This threshold increases with the rate at which late successional species replace early successional species relative to fire, s^*, and has a maximum value of 0.25. As μ decreases, the rate at which early successional patches clear their understory increases and the costs of increased fire frequency decrease. This increases the adaptive value of a high γ.

The positive relationship between the upper bound of the probability of dying from a fire, μ_{crit}, and the relative rate of succession and fire, s^*, suggests that increased flammability could be adaptive in a range of fire regimes. If low values of the rate of succession relative to fire correspond to a fire regime of frequent low intensity surface fires, a lower probability of dying from a fire for overstory plants is plausible because surviving low intensity fires

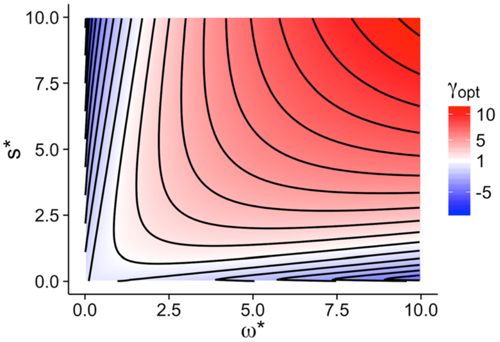

Fig. 2 γ_{opt}, the evolutionary stable strategy (ESS) value of flammability, is highest for high and nearly equal values of ω^* and s^*. Red areas denote parameter space that leads to the evolution of pyrophytes ($\gamma_{\text{opt}} > 1$). We do not allow plants to become less flammable, so regions of parameter space where $\gamma_{\text{opt}} < 1$, denoted in blue, are simply areas where pyrophytes cannot evolve. In this figure, $\mu = 0.1$, but results are qualitatively similar for all $\mu < \mu_{\text{crit}}$. Note that γ_{opt} is not a function of c^*

would require more modest fire adaptations. Conversely, if high values of the rate of succession relative to fire correspond to a fire regime of less frequent but moderate intensity surface fires, a higher allowable probability of dying from fire partly offsets the increased mortality expected from the more intense fires. The fact that the upper bound of the probability of dying from a fire increases for fire regimes expected to have higher mortality makes it conceptually reasonable that pyrophytes could invade in both high frequency and moderate frequency fire regimes.

The second result is that increased flammability sacrifices increased deaths due to fire for decreased deaths due to succession. Thus, as the threat of dying due to succession relative to fires increases (high ω^* and s^*), the ESS level of flammability increases (Appendix: Methods). Finally, γ_{opt} is maximized when ω^* and s^* are nearly equal (Appendix: Methods). This is because our model represents arrested succession by the additional time a patch spends as E_1 due to fires that convert E_2 patches back to E_1. If ω^*, the rate at which late successional species establish in early successional patches relative to fire, is high relative to s^*, E_1 patches are almost immediately converted to E_2 patches. Consequently, a high γ results in a higher death rate due to fires, but offers very little benefit because the short time spent as an E_1 patch hardly delays succession. Similarly, when s^* is high relative to ω^*, E_2 patches are almost immediately converted to L. This leaves few E_2 patches and thus little opportunity to convert E_2 back to E_1, decreasing the potential for arrested succession.

A fully age structured model would represent arrested succession more realistically than our use of three discrete successional categories. Our omission of a juvenile early successional category would make the model more realistic, as juvenile early successional species can be killed by fire before becoming resistant. Nevertheless, the fact that a sufficient number of early successional individuals establish in the overstory to dominate surface fire ecosystems suggests that the effect of juvenile mortality would not affect the qualitative results of the model. Furthermore, our simple representation of succession retains the key dynamic that, by definition, early successional individuals reach the overstory much faster than late successional species and it takes longer for late successional plants to replace early successional plants following fires. Therefore, even if we expect large differences between the relative rates of late successional establishment and succession (ω^* and s^*) in real systems, the qualitative results of our model should hold as long as fires delay succession (e.g., by killing, damaging, or slowing the growth of late successional plants) and overstory plants can survive a sufficiently high proportion of fires. This is because as long as increased flammability can decrease deaths due to succession, we expect there to be parameter space in which increased flammability is adaptive.

Discussion

Our simple model shows the counterintuitive result that increased flammability can benefit early successional individuals in surface fire regimes. Even though increased flammability increases early successional mortality due to fire, it also increases the probability that understory late successional species will be killed by fire before they can outcompete early successional individuals. We show that pyrophytes are selected for when adults plants have a relatively low probability of dying from individual fires, there is differential fire mortality between overstory and understory plants, and early successional plants are replaced by late successional species at a high rate. These assumptions were all chosen because they were supported by empirical evidence in ponderosa pine forests, longleaf pine forests, and tall grass prairie. Although our model cannot capture every aspect of our example systems, it provides a general model of surface fire ecosystems that captures the dynamics necessary for the evolution of flammability. This provides a theoretical mechanism for increased flammability being adaptive for plants that can be tested empirically in future investigations.

In our model, the probability of a pyrophyte dying in a fire, μ, must be less than 25% for flammability to be adaptive. Fire mortality below this upper threshold is found in all three of our empirical case studies, with some pyrophytes rarely dying of fire (Thomas and Agee 1986; Boyer 1990; Swezy and Agee 1990; Glitzenstein et al. 1995; Benson and Hartnett 2006; Varner et al. 2007; Choczynska and Johnson 2009; Hammond et al. 2016). Similarly, low fire mortality is found in many ecosystems dominated by pyrophytes such as Australian dry sclerophyll forest (Knox and Clarke 2006), Australian savanna (Ondei et al. 2015), South American grasslands (Hermann et al. 2012), and California black oak (*Quercus kelloggii*) forest (Cocking et al. 2014). The differential mortality of understory and overstory plants is reasonable when low crown height and small size make species more vulnerable to fire, a result found in our example systems as well as other fire-prone ecosystems (Stephens and Finney 2002; McHugh and Kolb 2003; Gurvich et al. 2005; Ordóñez et al. 2005; Van Lear et al. 2005; Knox and Clarke 2006; Sah et al. 2010; Brando et al. 2012; Ratajczak et al. 2014b). The successional pressure (ω* and s*) in our case systems as well as other fire-prone ecosystems is evident in the successional replacement of pyrophytes if fire is suppressed, but it is unclear if the pressure is strong enough to favor the evolution of flammability (Clements 1936; Jackson 1968; Odum 1969; Frelich and Reich 1999; Briggs et al. 2005; Graham and Jain 2005; Van Lear et al. 2005; Nowacki and Abrams 2008; Warman and Moles 2009; Odion et al. 2010; Staver and Levin 2012; Wood and Bowman 2012; Ratajczak et al. 2014a, b). Given that our simple model assumes a constant intrinsic fire frequency, B, and the fact that it would be difficult to separate the observed fire frequency in a pyrophyte system, γB, from the intrinsic fire frequency, our parameters ω^* and s^* are difficult to compare quantitatively to field observations. Although this model was inspired by three specific systems, we expect that arrested succession is a potential mechanism for the Mutch Hypothesis in any system where our assumptions are valid.

In contrast to previous models of the evolution of flammability, this model produces an analytical result that unambiguously shows the conditions under which pyrophytes could evolve. Furthermore, this model does not assume any differences between pyrophyte and non-pyrophyte early successional species except their flammability. Instead, the vulnerability of understory late successional individuals to fire leads to selection for increased flammability in otherwise identical early successional individuals. The mechanism proposed by Bond and Midgley effectively treats pyrophytes as a pathogen that locally kills non-pyrophytes and itself and then disperses its seeds into the resulting gaps (Bond and Midgley 1995). When the pyrophytes can on average recolonize more than one of these patches, they are expected to spread. This assumes that a single pyrophyte can consistently affect the fire conditions experienced by surrounding plants and concentrate seed dispersal into its fire neighborhood. While local seed dispersal may be an additional mechanism that supports the Mutch Hypothesis either alone or in conjunction with arrested succession, our model assumes that seeds disperse randomly and that an adult plant can only affect the fire conditions that it and its understory experience. This mean-field treatment of space keeps the model simple, but also prohibits a more spatially realistic treatment of fire spread and seed dispersal. Our model is also independent of the environmental niche tracking mechanism in the Schwilk and Kerr model (Schwilk and Kerr 2002), instead relying on fire mortality as the only consequence of increased flammability. We believe that the conservative and empirically supported assumptions used in this model make it the most robust theoretical evidence in support of the Mutch Hypothesis.

This model was developed to reflect the dynamics in ecosystems with a surface fire regime. In crown fire regimes, mortality is high and post-fire recruitment strategies like serotinous seeds are common (Keeley and Zedler 1998; Paula and Pausas 2008; Clarke et al. 2010). Although the results of our model are not meant to be extended outside of surface fire ecosystems, it is interesting to note that arrested succession could still produce a selective pressure in favor of high flammability in crown fire ecosystems. The general result of the model is that the increased mortality due to increased flammability can be offset if it also decreases the probability that a plant will die from successional replacement. In the current model, early successional species can lower their fire mortality through survival adaptations alone. However, if our model were applied to a crown fire ecosystem, fire survival could be considered the probability of an adult surviving the fire or an offspring recapturing the parent's original patch. This would make the model applicable to systems with predictable crown fires such as pitch pine (*Pinus rigida*) forests in the eastern USA, jack pine (*Pinus banksiana*) forests in boreal North America, and Mediterranean fire systems such as California chaparral and South African fynbos. By combining arrested succession with the local seed dispersal mechanism in the Bond and Midgley model, it is possible that a qualitatively similar result would emerge, but this would have to be verified by an additional model.

Our simple mathematical model of surface fire ecosystems serves as a proof of concept that arrested succession is a plausible mechanism for the evolution of flammability. Empirical evidence is necessary to test whether arrested succession is a sufficiently strong selective pressure to lead to the evolution of pyrophytes. It is not yet established whether flammability is a selectable trait, but there is some evidence that it is (Moreira et al. 2014; Ripley et al. 2015; Pausas et al. 2016; Simpson et al. 2016). Within the case study systems, there is some support for ponderosa pine and longleaf pine litter being particularly flammable compared to other pines, but it is inherently difficult to prove whether this is because flammability is under selection (Fonda 2001). The benefit of our theoretical model is that it presents a falsifiable hypothesis regarding the evolution of flammability. If pyrophytes that were experimentally manipulated to become less flammable did not decrease in fitness due to increased competition with late successional species, arrested succession could be falsified as a mechanism. Ideally, an experimental test would manipulate flammability in the field and then measure the effects on both early and late successional species.

The closest example of experimental evidence of arrested succession potentially increasing the fitness of pyrophytes is from extensive work on longleaf pine forests (Williamson and Black 1981; Rebertus et al. 1989; Ellair and Platt 2013; Platt et al. 2016). A study by Williamson and Black showed that experimental fires under longleaf pine trees had a higher maximum temperature than those under oaks (Williamson and Black 1981). A later study using experimental fires found that proximity to longleaf pine trees increased the risk of crown mortality in turkey oaks (*Quercus laevis*) and decreased the probability that crown-killed oaks would resprout (Rebertus et al. 1989). Ellair and Platt experimentally manipulated the leaf litter underneath understory hickories and found that longleaf pine needles increased fire temperatures and duration relative to herbaceous fuels, while hickory leaves had no effect on fire characteristics relative to herbaceous controls (Ellair and Platt 2013). Furthermore, they found that although all hickories survived the prescribed fires by resprouting, the height of the resprouting decreased in the presence of pine needles, forcing the hickories to resprout from underground root crowns rather than along the stem (Ellair and Platt 2013).

A recent study also manipulated longleaf pine litter and found that pine needles increased the temperature and duration of heating in prescribed fires and that these pine needles delayed oak resprouting after fire (Platt et al. 2016). All of these studies also suggest that longleaf pines may promote their own dominance by suppressing understory hardwoods through pyrogenic litter (Williamson and Black 1981; Rebertus et al. 1989; Ellair and Platt 2013; Platt et al. 2016). This evidence supports arrested succession as a mechanism that can lead to the evolution of flammability through litter effects on fire severity, but these studies have not been able to determine if longleaf pines or their ancestors have increased in flammability due to natural selection for flammability. Other experiments in different systems did not find evidence for flammability as an adaptive trait (Clarke et al. 2014) and further studies that directly test the fitness effects of flammability are necessary to conclusively determine in which systems, if any, flammability is adaptive.

This model provides an evolutionary rationale for the development of proposed fire-mediated alternative stable states (Beckage and Ellingwood 2008; Kitzberger et al. 2012; Staver and Levin 2012; Schertzer et al. 2014). There is overwhelming evidence that communities undergo successional change when fires are suppressed (Clements 1936; Jackson 1968; Odum 1969; Frelich and Reich 1999; Briggs et al. 2005; Graham and Jain 2005; Van Lear et al. 2005; Nowacki and Abrams 2008; Warman and Moles 2009; Odion et al. 2010; Staver and Levin 2012; Wood and Bowman 2012; Ratajczak et al. 2014a, b). Although pyrophytes are not always regarded as early successional species, they meet the formal definition because they both dominate after fire disturbance and are outcompeted by non-pyrophytes unless subsequent fires come quickly enough to reset succession. Thus, increased flammability can provide an individual benefit to pyrophytes when in competition with other less flammable early successional individuals by allowing them to increasingly arrest succession. When succession is arrested indefinitely, it effectively creates alternative stable states, which only transition when there is a sufficiently long period without fire. During long fire-free intervals, late successional species that suppress fire frequency have the time necessary to replace pyrophytes and persist in a non-flammable stable state until the next fire. If this plant-fire feedback is a result of the evolution of flammability, our model provides a potential explanation for the emergence of these systems.

Given the widespread distribution of pyrophytes and their ecological importance, it is important to understand the evolutionary origin of flammability. When Mutch first proposed that flammability could be adaptive, he did not present a rigorous mechanism. Here, we present arrested succession as a robust mechanism for surface fire ecosystems that could allow for the evolution of flammability as part of an individual-based ESS. We do not propose that this model validates the Mutch Hypothesis or captures the full ecology of surface fire ecosystems, but we believe that succession should be considered as a potentially important mechanism that would allow for the evolution of flammability. This model makes predictions that can be tested empirically and we look forward to future research that directly tests the fitness benefits associated with flammability. It is clear that the selective pressure of fire has shaped plants in fire-prone ecosystems, but it is unclear to what extent plants have played an active role in creating these ecosystems (Keeley et al. 2011). If Mutch was correct and plants have evolved to alter their local fire regimes, then it is possible that many ecosystems and their distributions are a repercussion of the evolution of flammability.

Appendix: Methods

Invasion analysis of system without succession

Removing the late successional species yields the following system of equations (Eq. 3):

$$\begin{aligned}
\frac{dE}{dt} &= cFE - E\mu\gamma_R B \\
\frac{dP}{dt} &= cFP - P\mu\gamma_I B \\
\frac{dF}{dt} &= \mu B(\gamma_R E + \gamma_I P) - cF(E+P) \\
F &= 1 - E - P
\end{aligned}$$

To find the ESS level of flammability, we conduct an invasion analysis by testing the stability of the boundary equilibrium in which $\hat{P} = 0$. Unlike in the full system, the reduced system is simple enough that we do not need to assume that $\hat{F} \approx 0$ and we do not rescale the equations by B. The internal equilibrium values for the resident community are (Eq. 4):

$$\begin{aligned}
\hat{E} &= \frac{c - \mu\gamma_R B}{c} \\
\hat{F} &= \frac{\mu\gamma_R B}{c}
\end{aligned}$$

Evaluated at the internal boundary equilibrium, the Jacobian of Eq. 3 reduces to (Eq. 5):

$$A = \begin{bmatrix} \mu B(\gamma_R - \gamma_I) & 0 & 0 \\ 0 & 0 & c - \mu\gamma_R B \\ \mu B(\gamma_I - \gamma_R) & 0 & \mu\gamma_R B - c \end{bmatrix}$$

We note that the boundary condition reduces to a one-dimensional system because $E + F = 1$. It is straightforward to show that the resident internal equilibrium is stable and that the necessary and sufficient condition for invasion to succeed is (Eq. 6):

$$\gamma_R > \gamma_I$$

Thus, in the absence of succession, an invader can only succeed by having a lower γ than the resident. Since we set the minimum value of γ to one, a resident must have a γ_R equal to one to always resist invasion and only an invader with a γ_I equal to one can invade all residents with a different γ. Thus, $\gamma_{\text{opt}} = 1$ and a high flammability is always detrimental to an early successional species because it only increases mortality. This is in direct contrast to the result of the model that includes succession, as there is parameter space in which $\gamma_{\text{opt}} > 1$. By including succession, high flammability has the added benefit of arresting succession and can potentially offset the losses from increased fire mortality through decreased mortality due to succession.

Invasion analysis of rescaled system

The rescaled system of equations is (Eq. 7):

$$\begin{aligned}
\frac{dE_1}{d\tau} &= c^* F(E_1 + E_2) - E_1\left(\mu\gamma_R + \omega^* L\right) + (1-\mu)\gamma_R E_2 \\
\frac{dE_2}{d\tau} &= \omega^* L E_1 - E_2\left(\gamma_R + s^*\right) \\
\frac{dP_1}{d\tau} &= c^* F(P_1 + P_2) - P_1\left(\mu\gamma_I + \omega^* L\right) + (1-\mu)\gamma_I P_2 \\
\frac{dP_2}{d\tau} &= \omega^* L P_1 - P_2\left(\gamma_I + s^*\right) \\
\frac{dL}{d\tau} &= s^*(E_2 + P_2) - \mu L \\
\frac{dF}{d\tau} &= \mu(\gamma_R(E_1 + E_2) + \gamma_I(P_1 + P_2) + L) - c^* F(E_1 + E_2 + P_1 + P_2) \\
F &= 1 - E_1 - E_2 - P_1 - P_2 - L
\end{aligned}$$

To determine when the invaders, P_1 and P_2, can invade the residents, E_1 and E_2, we test the stability of the boundary equilibrium in which $\hat{P}_1 = 0$ and $\hat{P}_2 = 0$. We assume that $\hat{F} \approx 0$ and consequently that $\hat{E}_1 + \hat{E}_2 + \hat{L} \approx 1$ to solve for the equilibrium values of the residents at the boundary equilibrium. This assumption holds for high values of c^* and is ecologically reasonable in areas where there is very little space open to colonization. The equilibrium values of the resident community (Eq. 8) are:

$$\begin{aligned}
\hat{\hat{E}}_1 &= \frac{\mu(\gamma_R + s^*)}{\omega^* s^*} \\
\hat{\hat{E}}_2 &= \frac{\mu(\omega^* s^* - \mu(\gamma_R + s^*))}{\omega^* s^*(\mu + s)} \\
\hat{L} &= \frac{(\omega^* s^* - \mu(\gamma_R + s^*))}{\omega^*(\mu + s)} \\
c^* \hat{F} &= \frac{\omega^*(\gamma_R\mu + s^*) + \mu(\gamma_R - 1)(\gamma_R + s^*)}{\gamma_R + s^* + \omega^*}
\end{aligned}$$

The Jacobian for Eq. 8 can be arranged in upper triangular block form. The eigenvalues, λ, of this matrix are the eigenvalues of the resident community matrix in the absence of invaders and the eigenvalues of the invader community matrix when the invader is rare. It is straightforward to show that in the absence of invaders, the internal equilibrium of the resident community is stable. Thus, the eigenvalues of the resident community matrix are always less than zero. Evaluated at the resident internal equilibrium, the invader matrix (Eq. 9) is:

$$A = \begin{bmatrix} c^* \hat{F} - \gamma_I\mu - \omega^* \hat{L} & c^* \hat{F} + \gamma_I(1-\mu) \\ \omega\hat{L} & -\left(\gamma_I + s^*\right) \end{bmatrix}$$

It is straightforward to show the eigenvalues of the invader matrix are always real. Consequently, for invasion to succeed the dominant eigenvalue of the invader community matrix must be greater than zero. We solve for the boundary surface that separates parameter space into regions of invasion and non-invasion by setting the dominant eigenvalue to zero. This is equivalent to setting the determinant of the invader matrix to zero because the determinant being less than zero is a necessary and sufficient condition for invasion. We solve $\det(A) = 0$, which yields a quadratic function of γ_I with roots (Eq. 10):

$$\begin{aligned}
\gamma_I &= \gamma_R \\
\gamma_I = \gamma_b &= \frac{\dfrac{s^*(\mu(1-s^*) + s^*)}{\mu}\gamma_R\mu - s^*\omega^* - \dfrac{(\gamma_R + s^*)(\mu + s^*)^2}{\mu(\gamma_R + s^* + \omega^*)}}{\mu + s^*}
\end{aligned}$$

These roots are the values of γ_I that make $\det(A) = 0$ and therefore the dominant eigenvalue exactly zero. When $\gamma_I = \gamma_R$, the invaders and residents are identical, while γ_b represents the value of γ_I that just balances the costs and benefits of γ_I relative to γ_R. Thus, invasion can only occur for the values of γ_I between γ_R and γ_b (Fig. 3). When $\gamma_R = \gamma_b$, there is no value of γ_I that allows invasion and the maximum eigenvalue of zero occurs when $\gamma_I = \gamma_R$. Solving for γ_R when $\gamma_R = \gamma_b$ thus gives the ESS value of γ, called γ_{opt} (Eq. 11; Figs. 2 and 3):

$$\gamma_{\text{opt}} = \frac{(\mu + s)\sqrt{\mu(\mu + 4s^*\omega^*)} - \mu(\mu + s^*(2(s^* + \omega^*) + 1))}{2\mu s^*}$$

For all cases examined, γ_{opt} is a fitness maximum. Solving for the conditions under which $\gamma_{\text{opt}} > 1$ gives the conditions for invasion of pyrophytes (Eq. 12):

$$\begin{aligned}
&\mu < \mu_{\text{crit}}, \text{ where } \mu_{\text{crit}} = \frac{s^*}{4 + 4s^*} \\
&\omega^* > \frac{-2\mu s^* - \mu + s^*}{2\mu} - \frac{1}{2}\sqrt{\frac{-4\mu^3(1 + s^*) - 8\mu^2 s^{*2} - 7\mu^2 s^* - 4\mu s^{*3} - 2\mu s^{*2} + s^{*3}}{\mu^2 s^*}} \\
&\omega^* < \frac{-2\mu s^* - \mu + s^*}{2\mu} + \frac{1}{2}\sqrt{\frac{-4\mu^3(1 + s^*) - 8\mu^2 s^{*2} - 7\mu^2 s^* - 4\mu s^{*3} - 2\mu s^{*2} + s^{*3}}{\mu^2 s^*}}
\end{aligned}$$

The maximum value of μ that allows pyrophytes invasion, called μ_{crit}, approaches 0.25 as s^* becomes large, creating an upper bound on invasion. The range of ω^* that allows invasion

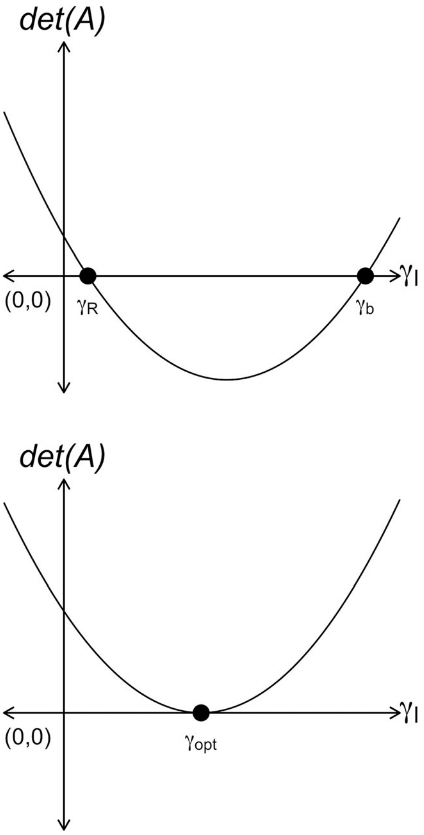

Fig. 3 A necessary and sufficient condition for the dominant eigenvalue to be greater than zero is det(A) < 0. The det(A) = 0 exactly when γ_I equals γ_R or γ_b. In the region between γ_R and γ_b, the det(A) < 0 and invasion is possible. When $\gamma_R = \gamma_b$, there is no value of γ_I that allows for invasion and the best possible invader is the resident. Solving for this value yields the ESS level of flammability, γ_{opt}

decreases with μ and increases with s^*. The relationship between ω^* and s^* becomes more clear when we analyze γ_{opt} in new axes corresponding to $x = \omega^* + s^*$ and $y = \omega^* - s^*$. We solve $\frac{\partial \gamma_{opt}}{\partial y} = 0$ for the function $y(x)$ that tracks the value of y that maximizes γ_{opt}. As x becomes large, the value of y that maximizes γ_{opt} approaches a small finite value (Eq. 13; Fig. 4):

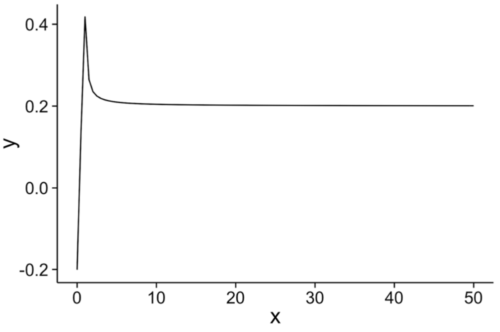

Fig. 4 The value of y (the difference between ω^* and s^*) that maximizes γ_{opt} approaches the value of 2μ as x (the sum of ω^* and s^*) increases. In this figure, $\mu = 0.1$

$$\lim_{x \to \infty} y(x) = 2\mu$$

As $x \to \infty$, the rate of succession increases and γ_{opt} is maximized when there is a small finite difference between ω^* and s^*. Thus, γ_{opt} is maximized when ω^* and s^* have a roughly 1:1 ratio, with departures from this ratio decreasing γ_{opt} and eventually prohibiting invasion by pyrophytes.

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