Rekindling an old flame: A haploid model for the evolution and impact of flammability in resprouting plants

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ABSTRACT

Using a two-locus diallelic population genetic model, we studied the evolution and impact of flammable traits in resprouting plants. A 'flammability locus' determines the flammable character of a plant and the frequency of alleles at this locus affects the probability that any plant in the population will burn. A linked 'disturbance locus' determines how a plant fares in the presence or absence of fire. Thus, the frequencies of alleles at the flammability locus influence evolution at the disturbance locus. The evolution of flammability-enhancing alleles is influenced by asymmetries in the genotypic fitnesses as well as by the base flammability of the population and the genetic structure of the system (with tighter linkage increasing the possibility that the population becomes more flammable). We demonstrate that stable polymorphisms of plants differing in flammability alleles are possible. The magnitude of the organism's impact on the flammable character of the environment influences where such polymorphisms are expected. Furthermore, predictions concerning the evolution of alleles at the disturbance locus based solely on fitness asymmetries may fail due to the influence of plants on their environment. Unusual population dynamics, including stable and unstable cycles of genotypes, are also presented. The relation of this model to the Mutch hypothesis and the recently developed theories of 'niche construction' and 'ecosystem engineering' is discussed.

Keywords: ecosystem engineering, fire, flammability, frequency-dependent selection, Mutch hypothesis, niche construction, plant population genetics, resprouting plants, stable cycles, two-locus theory, unstable cycles.

INTRODUCTION

Fire is inextinguishably tied to life. Fire enhances, multiplies, stimulates, recycles, and animates, a plural not a singular process, massaging a varied, subtle biota. It is above all vital – at times awesome but also playful. Always it is associated with life. Life made fire possible – and fire, in return, dramatized … life. (Pyne, 1991, p. 11)

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As Darwin (1859, p. 108) was in the process of presenting the concept of Natural Selection to the public, he made the following observation: 'Let it be borne in mind how infinitely complex and close-fitting are the *mutual* relations of all organic beings to each other and to their physical conditions of life; and consequently what infinitely varied diversities of structure might be of use to each being under changing conditions of life' (emphasis added). In one sentence, Darwin expressed the idea that individuals are not only affected by other organisms and the environment, but they also *affect* both the environment and other individuals. Furthermore, he suggested that this intricate network of mutual interactions is an essential consideration in the understanding of evolution by natural selection. An evolving population may change in ways that have drastic effects on other organisms or the environment, thereby, in the end, changing the selective pressures that the population itself experiences.

   A dramatic example of the interaction between organisms and their environment concerns the ecology of plants in fire-prone regions. Fire has been recognized as a substantial force in shaping plant communities in grassland environments (Vogl, 1974), the Australian eucalypt forest (Pyne, 1991), Mediterranean shrublands (Papio and Trabaud, 1991), the North American boreal forest (Johnson, 1992), the Eurasian boreal forest (Goldammer and Furyaev, 1996), the Californian chaparral (Biswell, 1974; Zedler *et al.*, 1983; Keeley, 1991), the South African fynbos (Kruger, 1977; Bond *et al.*, 1984; Schwilk *et al.*, 1997) and the heathlands of Great Britain (Hobbs and Gimingham, 1987).

   Many ecologists have noted morphological and reproductive adaptations of the flora to fire in fire-prone regions. Thick bark (Uhl and Kaufmann, 1990; Whelan, 1995) and tree architecture where the canopy rests atop long bare trunks (Bond and van Wilgen, 1996) are structural barriers to the destructive power of fire. Many woody species are able to resprout after being burnt, either from epicormic buds above ground or from large subterranean storage organs called 'lignotubers' (Gill, 1981a,b; Zedler *et al.*, 1983; Whelan, 1995; Bond and van Wilgen, 1996). Finally, fire can play an important role in completing the reproductive cycle of some plants in fire-prone regions. Fire-stimulated flowering, seed release and seed germination have been noted in several species (Gill, 1981a,b; Bond and van Wilgen, 1996). For example, many species in sclerophyllous vegetation and coniferous forests have serotinous seed-bearing structures, which are retained in closed form on the plant until heat-stimulated opening allows for seed release (Givnish, 1981; Muir and Lotan, 1985; Lamont *et al.*, 1991). In addition, many researchers have also found that charred wood or smoke may play a role in seed germination (Wicklow, 1977; Keeley, 1991, 1993; Keeley and Fotheringham, 1997; Roche *et al.*, 1998). The above evidence suggests that selection induced by the fire-prone environment has affected the flora in many ways. But do the plants affect the environment?

   In 1970, Robert Mutch offered a hypothesis that subsequently became quite influential: 'If species have developed reproductive and anatomical mechanisms to survive periodic fires, then fire-dependent plants might also possess characteristics obtained through natural selection that actually enhance the flammability of these communities' (p. 1047). This hypothesis revised the idea that plants simply respond to fire. Rather, the flora are seen as active agents influencing the flammable character of their own environment (and the environment of their offspring). There is no shortage of empirical evidence, which, on the surface, coincides with Mutch's hypothesis. The existence of volatile compounds (Philpot, 1977; Rundel, 1981), low silica-free mineral content (Philpot, 1970), high surface area to volume ratios (Rundel, 1981; Papio and Trabaud, 1991), relatively flammable bark or leaf

litter (Mutch, 1970; Gill 1981a; Williamson and Black, 1981; Rebertus *et al.*, 1989) and the retention of dead branches (Papio and Trabaud, 1991) are traits found in several fire-prone species which increase fire frequency or intensity. The idea is that traits leading to pyrogenesis are selected when the plants already possess traits to persist in the face of fire. Several authors have posited that flammable traits function to exclude less fire-tolerant competitive species (Mutch, 1970; Williamson and Black, 1981; Buckley, 1984).

A fair amount of criticism has been levied against Mutch's hypothesis. Snyder (1984) suggested that increased flammability may be a secondary effect of selection for other traits – there may be no selection for flammability *per se*. For instance, the flammability-enhancing compounds in pyrophytes may have been selected for herbivore defence (Snyder, 1984). The hypothesis has also been criticized on the grounds that selection is perceived as operating at the group level (Troumbis and Trabaud, 1989). Many studies have emphasized an interspecific argument with regard to the evolution of flammability (e.g. Mutch, 1970; Philpot, 1977; Williamson and Black, 1981; Buckley, 1984), with flammability viewed as a characteristic of all members of the group. The contention is that it is difficult to see how a trait that makes an individual more flammable than neighbouring conspecifics would spread through a population (Snyder, 1984). Bond and Midgley (1995) took up this issue in a clever simulation model that investigated the evolution of flammability at the level of the individual. Using a cellular automata model, they monitored the frequency of plants possessing fire-enhancing characteristics (*torches*) following introduction and 'ignition' on the margins of a population of less flammable conspecifics (*damps*). They found that the flammable trait would increase if fire spreads from torches to neighbouring plants and the torches carry additional fitness benefits. In their model, the trait affecting flammability also controls the plant's response to fire (fitness in the fire-cleared gap).

In this paper, we study the evolution of flammability using a haploid genetic model that separates traits affecting flammability from traits influencing how a plant fares in the presence or absence of the fire environment. Our goal is to uncover the role that genetic recombination, plant/environment parameters and fitness asymmetries play with regard to the evolution of flammability. We also investigate the influence of an environment (altered by any change in its flammable residents) on other plant traits. Specifically, if alleles promoting flammability alter the impact of fire in the environment, how do changes in their frequency influence evolution at other genetic loci whose fitnesses depend on the presence or absence of fire? This system introduces some of the theoretical considerations that surround the *mutual* relations between organisms and their environment.

THE MODEL

We consider a haploid model with two genetic loci, the first of which is responsible for the flammable quality of the plant. The alleles of this 'flammability locus' are T and D. Plants possessing the T allele are labelled *torches*, while those with the D allele are designated *damps* (terminology taken from Bond and Midgley, 1995). As the labels imply, torch plants burn more readily or with greater intensity than damps. Furthermore, if fire spreads, the frequency of torches in the population influences the probability that any plant (of arbitrary genotype) will burn. This flammability locus is linked to a second 'disturbance locus', which has two alleles G and N. Plants possessing the G allele are dubbed *gap* plants and fare better (i.e. have higher fitness) in an open gap than the *non-gap* plants, which contain the N allele. If the two varieties are growing through a stand of established plants

(essentially a 'non-gap' environment), non-gap plants have an advantage over gap plants. For example, the disturbance gene might control the starch investment in a lignotuber or underground storage organ. In this case, gap plants would invest heavily and resprout vigorously after fire, while non-gap plants would shift investment into shoot growth and reproductive structures. Several researchers have reported a significant reduction in growth rate, shoot : root ratios, inflorescence size and number, fruit production and/or seed output in sprouting species compared with non-sprouting (but fire-recruiting) species (Carpenter and Recher, 1979; Keeley and Keeley, 1977; Pate *et al.*, 1990; Hansen *et al.*, 1991). Thus, in our case, non-gap plants outcompete conspecific gap plants in a stand, whereas the gap plants display superior resprouting recovery in a fire-cleared gap. Although we model resprouting plants, a gap plant might be envisioned, alternatively, as a plant with higher seedling recruitment or growth in a fire-cleared gap (characteristics possessed by some fire-adapted *non-sprouting* species) with little alteration in the model's predictions.

Table 1 lists the four haploid genotypes with associated fitnesses. The variables x_1, x_2, x_3 and x_4 represent the frequencies of the genotypes *DG*, *DN*, *TG* and *TN* respectively. There are two arrays of fitnesses, one pertaining to a gap environment (e.g. a post-fire clearing) and the other pertaining to a non-gap environment (e.g. a stand of established plants). The fact that a *DG* individual has an advantage over a *DN* individual in a gap environment, and that the situation is reversed in a non-gap environment, is reflected in the constraints on the fitnesses. Specifically, a (the gap fitness of *DN*) must be less than 1 (the gap fitness of *DG*), while Γ (the non-gap fitness of *DN*) is greater than Φ (the non-gap fitness of *DG*). Similar inequalities constrain the fitnesses of *TG* and *TN*: $\beta > \kappa$ and $\Lambda < \Omega$. Fitness asymmetries within genotypes express our assumption that gap plants are expected to fare better in a gap environment, whereas non-gap plants prosper in a non-gap environment – thus, $\Phi < 1$, $a < \Gamma$, $\Lambda < \beta$ and $\kappa < \Omega$.

Figure 1 is a schematic representation of one generation cycle. To start, we envision a large population of resprouters. Each generation experiences a fire, which burns some fraction of the population (step 1 of Fig. 1). In the absence of torches, there is some base fraction of plants that burn, which we call π. Then, as the frequency of torches ($x_3 + x_4$) increases, the fraction of the population burnt (written $F(x_3, x_4)$) grows proportionally. While torch frequency affects the fraction of the population burnt, the genotype distribution within the burnt patches is assumed to mirror the population-wide distribution. In step 2 of Fig. 1, gap selection is applied to plants that resprout vegetatively in the fire-cleared patches (gap fitnesses 1, a, β and κ multiply the gap terms in the recursions; see below). Meanwhile, plants that did not burn reproduce. We assume random mating between

Table 1. Gap and non-gap fitnesses for the haploid genotypes

Genotype	Description	Frequency	Gap fitness	Non-gap fitness
DG	Damp/gap plant	x_1	1	Φ
DN	Damp/non-gap plant	x_2	a	Γ
TG	Torch/gap plant	x_3	β	Λ
TN	Torch/non-gap plant	x_4	κ	Ω

$a < 1; \kappa < \beta; \Gamma > \Phi; \Omega > \Lambda$
$\Phi < 1; a < \Gamma; \Lambda < \beta; \kappa < \Omega$
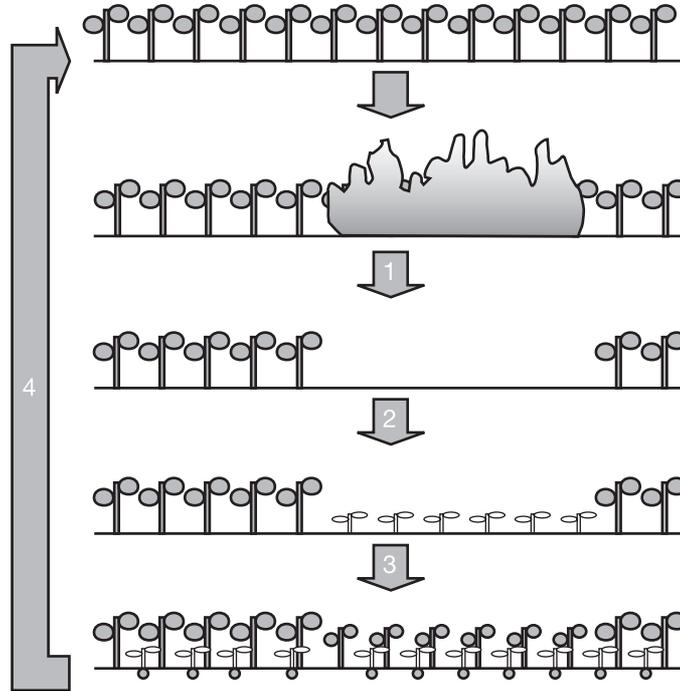
Fig. 1. A schematic representation of one generation in the model. (1) Fire burns a fraction (which increases linearly with torch frequency) of the population. (2) 'Gap' selection is applied to resprouting plants in the gaps left by fire. Meanwhile, random mating occurs in non-burnt plants. (3) Seeds are dispersed randomly and germinate. Subsequently, 'non-gap' selection is applied to the seedlings growing up through a stand of plants. (4) Non-burnt parents die and a new generation is born.

these plants. In step 3, there is a brief diploid phase, during which recombination occurs (at a rate r) and the resulting haploid seeds are randomly dispersed. Subsequently, non-gap selection is applied to the germinated seedlings as they grow through a stand of resprouted and parental individuals (non-gap fitnesses Φ, Γ, Λ and Ω multiply the non-gap terms of the recursions; see below). In the final step 4 of Fig. 1, the non-burnt parental plants die and we have the next generation. This description of the life-cycle generates the following recursions for the genotype frequencies:

$$Wx_1' = F(x_3, x_4)x_1 + (1 - F(x_3, x_4))\Phi[x_1 - r\mathfrak{D}] \tag{1}$$

$$Wx_2' = F(x_3, x_4)ax_2 + (1 - F(x_3, x_4))\Gamma[x_2 + r\mathfrak{D}] \tag{2}$$

$$Wx_3' = F(x_3, x_4)\beta x_3 + (1 - F(x_3, x_4))\Lambda[x_3 + r\mathfrak{D}] \tag{3}$$

$$Wx_4' = F(x_3, x_4)\kappa x_4 + (1 - F(x_3, x_4))\Omega[x_4 - r\mathfrak{D}] \tag{4}$$

On the right-hand side of each recursion there are two terms, the first representing the gap contribution and the second giving the non-gap contribution to the next generation. The function giving the fraction of the population that burns is $F(x_3, x_4) = \pi + \delta(x_3 + x_4)$. Thus, with no torches present in the population ($x_3 = x_4 = 0$) there is some base fraction of

the population that burns, namely π. The fraction that burns then increases linearly with x_3 or x_4 (i.e. as torch frequency grows, the fraction that burns grows proportionally). We assume that $\pi > 0$, $\delta > 0$ and $0 < \pi + \delta \leq 1$. $\mathfrak{D}$ is the linkage disequilibrium ($\mathfrak{D} = x_1 x_4 - x_2 x_3$). Lastly, W is a normalizing factor, namely, the sum of the right-hand sides of (1)–(4). Genotype notation, fitnesses and constraints on the fitness parameters are listed in Table 1. Table 2 describes the remaining system parameters.

Since gap and non-gap plants are assumed to differ in their survival rates in a clearing and a stand, the fitnesses in Table 1 are viability fitnesses. An additional model, currently under investigation, considers the impact of flammability on the evolution of serotiny. Since serotinous structures potentially affect reproductive output of plants in a fire-cleared gap and a stand, the fitnesses, in this case, are fecundity fitnesses.

ANALYTICAL RESULTS

In two-locus diallelic models, the frequencies of the four genotypes are usually visualized as a point inside or on a tetrahedron with each of the vertices labelled with one of the four genotypes, as in Fig. 2. The frequency of a specific genotype is found by connecting the relevant vertex through the point to the face opposite the vertex. The distance (after normalizing) of the line segment from the point to the opposite face yields that genotype frequency. Thus, if the point is located on the tetrahedron edge connecting vertices DG and DN, then the population has no torches ($x_3 = x_4 = 0$). If the point is located, for instance, at the DG vertex, then the population is fixed on genotype DG ($x_1 = 1$).

DG/DN edge considerations

We start with an investigation of a population without any torches; that is, somewhere on the *DG/DN* edge of the tetrahedron. The first result is that no equilibria exist in the interior of this edge. With only DG and DN present, the population will fix on either DG or DN (with the exception of a trivial neutrally stable case). Which fixation occurs is independent of initial genotype frequencies and depends on the parameters as follows:

$$\pi > \frac{\Gamma - \Phi}{\Gamma - \Phi + 1 - a} \Rightarrow DG \text{ fixes} \tag{5}$$

$$\pi < \frac{\Gamma - \Phi}{\Gamma - \Phi + 1 - a} \Rightarrow DN \text{ fixes} \tag{6}$$

Table 2. Notation for system parameters

Parameter	Description
r	Recombination rate
π	Base fraction of the population that burns
δ	Coefficient measuring the impact of torches on the fraction burnt
$\mathfrak{D}$	Linkage disequilibrium
W	Normalizing factor

$0 \leq r \leq 0.5$; $\pi > 0$; $\delta > 0$; $0 < \pi + \delta \leq 1$
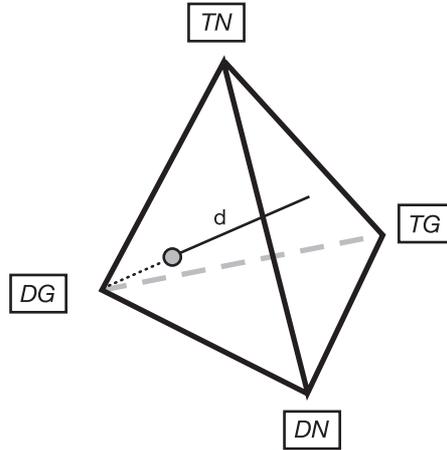
Fig. 2. Visualizing the four genotype frequencies using a tetrahedron. A point inside or on the tetrahedron carries all the information needed to specify genotype frequencies. To find any specific genotype frequency, connect the labelled vertex through the point to the face opposite the vertex. The distance (marked 'd' in the case shown for *DG*) from the point to the opposite face (once normalized) is the frequency.

$$\pi = \frac{\Gamma - \Phi}{\Gamma - \Phi + 1 - a} \Rightarrow \text{neutral stability} \tag{7}$$

When π is greater than $(\Gamma - \Phi)/(\Gamma - \Phi + 1 - a)$, the environment has become sufficiently 'gap-like' to favour the fixation of *DG*. When π drops below $(\Gamma - \Phi)/(\Gamma - \Phi + 1 - a)$, enough plants experience a non-gap environment and consequently *DN* fixes.

Qualitative understanding of (5)–(7) is facilitated by writing the critical fraction $(\Gamma - \Phi)/(\Gamma - \Phi + 1 - a)$ as $(s_{\Gamma\Phi})/(s_{\Gamma\Phi} + s_{1a})$. Here, the *s* coefficients are fitness differentials: $s_{\Gamma\Phi} = \Gamma - \Phi$ and $s_{1a} = 1 - a$. If $s_{\Gamma\Phi}$ is large in comparison to s_{1a} (the fitness boost to *DN* over *DG* in a non-gap overwhelms the fitness cost to *DN* in the gap), then $(s_{\Gamma\Phi})/(s_{\Gamma\Phi} + s_{1a})$ will be close to 1 and most likely $\pi < (s_{\Gamma\Phi})/(s_{\Gamma\Phi} + s_{1a})$, in which case *DN* will fix. On the other hand, if s_{1a} is large in comparison to $s_{\Gamma\Phi}$ (the fitness cost to *DN* with respect to *DG* in a gap overrides the fitness boost to *DN* in the non-gap), then $(s_{\Gamma\Phi})/(s_{\Gamma\Phi} + s_{1a})$ will be close to zero. In this case, it is most likely that $\pi > (s_{\Gamma\Phi})/(s_{\Gamma\Phi} + s_{1a})$ and *DG* will fix. Conditions (5)–(7) can be restated as follows:

$$s_{\Gamma\Phi} < \frac{\pi}{1 - \pi}(s_{1a}) \Rightarrow DG \text{ fixes} \tag{8}$$

$$s_{\Gamma\Phi} > \frac{\pi}{1 - \pi}(s_{1a}) \Rightarrow DN \text{ fixes} \tag{9}$$

$$s_{\Gamma\Phi} = \frac{\pi}{1 - \pi}(s_{1a}) \Rightarrow \text{neutral stability} \tag{10}$$

Thus, while high values of π generally favour fixation of *DG* and low values of π generally favour fixation of *DN*, in most cases very high $s_{\Gamma\Phi}/s_{1a}$ ratios favour *DN* and very low $s_{\Gamma\Phi}/s_{1a}$ ratios favour *DG*.

Since a population without torches will fix on *DG* or *DN*, we next investigate the stability of these fixations to invasion by the *T* allele.

Stability of the *DG* and *DN* corners

If only *DG* (or only *DN*) is present so that $x_1 = 1$ (or $x_2 = 1$), is the population stable to invasion by the other genotypes? Again, employing the tetrahedron, this question boils down to the following: If the point representing genotype frequencies is given an epsilon push off the *DG* (or *DN*) corner towards the centre of the tetrahedron, will it move back to that corner (stability to invasion) or further into the interior of the tetrahedron (instability to invasion)? Since we are interested in the evolution of flammability here, we pay particular attention to the conditions under which genotypes *TG* and *TN* invade the population.

Appendix 1 describes the stability analyses for the *DG* and *DN* corners. The tighter the linkage between the flammability locus and the disturbance locus, the greater the chance of invasion by the torch allele at either damp corner. Thus, invasion of a population near *DG* fixation by the *TN* genotype, as well as invasion of a population near *DN* fixation by the *TG* genotype, is facilitated by lower values of *r*. As the base fraction of plants that burn (π) increases, the potential for stability of the *DG* population to *TN* invasion is improved (see Appendix 1). Specifically, as π increases, there is a transition to a gap environment in which the chance of invasion by *TN* (a non-gap plant) is reduced. Near *DN* fixation, as the base fraction of plants that burn increases, the potential for stability to *TG* invasion declines. In this case, the chance of invasion by *TG* (a gap plant) is increased as the transition to a gap environment occurs. These results demonstrate the importance of the genetic structure (*r*) and environmental/plant parameters (π) in the conditions for torch invasion and thus for the evolution of flammable traits in plants.

Timing of *T* introduction

Are there parameter settings at which torches can invade at one vertex of the tetrahedron (*DG* or *DN*) but not the other? The answer is 'yes'. For instance, with $r = 0.5$, $\pi = 0.5$, $\delta = 0.1$, $\alpha = 0.5$, $\beta = 1$, $\kappa = 0.6$, $\Phi = 0.85$, $\Gamma = 0.9$, $\Lambda = 0.8$ and $\Omega = 1.2$, torches can invade at the *DN* vertex but not the *DG* vertex. Numerous parameter settings will produce the same sorts of stability asymmetry. The point is that if a population is moving from *DG* to *DN* or vice versa, the timing of the introduction of *T* (that is, the frequencies of *DG* and *DN* when *T* is introduced) may be important in the evolution of flammability.

DG/TG edge considerations

The unique interior equilibrium on the *DG/TG* edge is given by:

$$\hat{x}_1 = 1 - \frac{\pi(\beta - 1) + (1 - \pi)(\Lambda - \Phi)}{\delta(1 - \beta + \Lambda - \Phi)} \qquad \hat{x}_3 = \frac{\pi(\beta - 1) + (1 - \pi)(\Lambda - \Phi)}{\delta(1 - \beta + \Lambda - \Phi)} \tag{11}$$

provided that one of the following two scenarios holds:

Scenario 1

$$\pi(\beta - 1) + (1 - \pi)(\Lambda - \Phi) > 0 \tag{12}$$

$$1 - \beta + \Lambda - \Phi > 0 \tag{13}$$

$$\delta(1 - \beta + \Lambda - \Phi) > \pi(\beta - 1) + (1 - \pi)(\Lambda - \Phi) \tag{14}$$

Scenario 2

$$\pi(\beta - 1) + (1 - \pi)(\Lambda - \Phi) < 0 \tag{15}$$

$$1 - \beta + \Lambda - \Phi < 0 \tag{16}$$

$$\delta(1 - \beta + \Lambda - \Phi) < \pi(\beta - 1) + (1 - \pi)(\Lambda - \Phi) \tag{17}$$

Appendix 1 shows that (11) is a stable edge polymorphism under the conditions of scenario 1, whereas it is unstable under scenario 2. In Appendix 1, we consider the stability of a population near the equilibrium of (11) under scenario 1 (to invasion by non-gap plants). It is possible that recombination can influence stability. If it does, then larger values of r increase the likelihood of stability while complete linkage may result in instability. Again the theme of tighter linkage facilitating invasion, this time by non-gap plants, is echoed on the *DG/TG* edge.

DN/TN edge considerations

The analysis on this edge mirrors that of the previous section. Expressions (11)–(17) are virtually identical here, simply with the gap and non-gap fitnesses of *DG* and *TG* inter-changed with those of *DN* and *TN*. Thus, a stable polymorphism of damps and torches is possible in a population fixed for *N*. Furthermore, as on the *DG/TG* edge, tighter linkage assists the invasion of gap plants into a population near the stable interior equilibrium on the non-gap edge.

TG/TN edge considerations

There are no stable equilibria in the interior of the *TG/TN* edge. Assuming $0 < (\pi + \delta) < 1$, the conditions leading to fixations are:

$$t_{\Omega\Lambda} < \frac{(\pi + \delta)}{(1 - (\pi + \delta))} t_{\beta\kappa} \Rightarrow TG \text{ fixes} \tag{18}$$

$$t_{\Omega\Lambda} > \frac{(\pi + \delta)}{(1 - (\pi + \delta))} t_{\beta\kappa} \Rightarrow TN \text{ fixes} \tag{19}$$

$$t_{\Omega\Lambda} = \frac{(\pi + \delta)}{(1 - (\pi + \delta))} t_{\beta\kappa} \Rightarrow \text{neutral stability} \tag{20}$$

The above equations are very similar in form to equations (8)–(10). The t coefficients are again fitness differentials – they measure deviation of the fitnesses of *TN* from the fitnesses of *TG*. Specifically, $t_{\Omega\Lambda} = \Omega - \Lambda$ and $t_{\beta\kappa} = \beta - \kappa$. Also, the role of π in (8)–(10) is played by $\pi + \delta$ in inequalities (18)–(20). The significance of the last remark is that even if the fitness differences between *DG* and *DN* are identical to those between *TG* and *TN* ($t_{\Omega\Lambda} = s_{\Gamma\Phi}$ and $t_{\beta\kappa} = s_{1a}$), then due to the increased flammability of torches ($\delta > 0$), in the absence of *T* the

population can fix on N while in the absence of D it fixes on G. As δ increases, the above scenario becomes more likely. For instance, with $t_{\Omega\Lambda} = s_{\Gamma\Phi} = 0.2$, $t_{\beta\kappa} = s_{1\alpha} = 0.4$, $\pi = 0.3$ and $\delta = 0.1$, inequalities (9) and (18) simultaneously hold. Thus, the presence of torches in the environment can lead to gap plant fixation where otherwise non-gap plants would dominate (see Fig. 3). This is an example of the way in which the frequencies of alleles at the flammability locus may have a drastic effect on evolution at the disturbance locus.
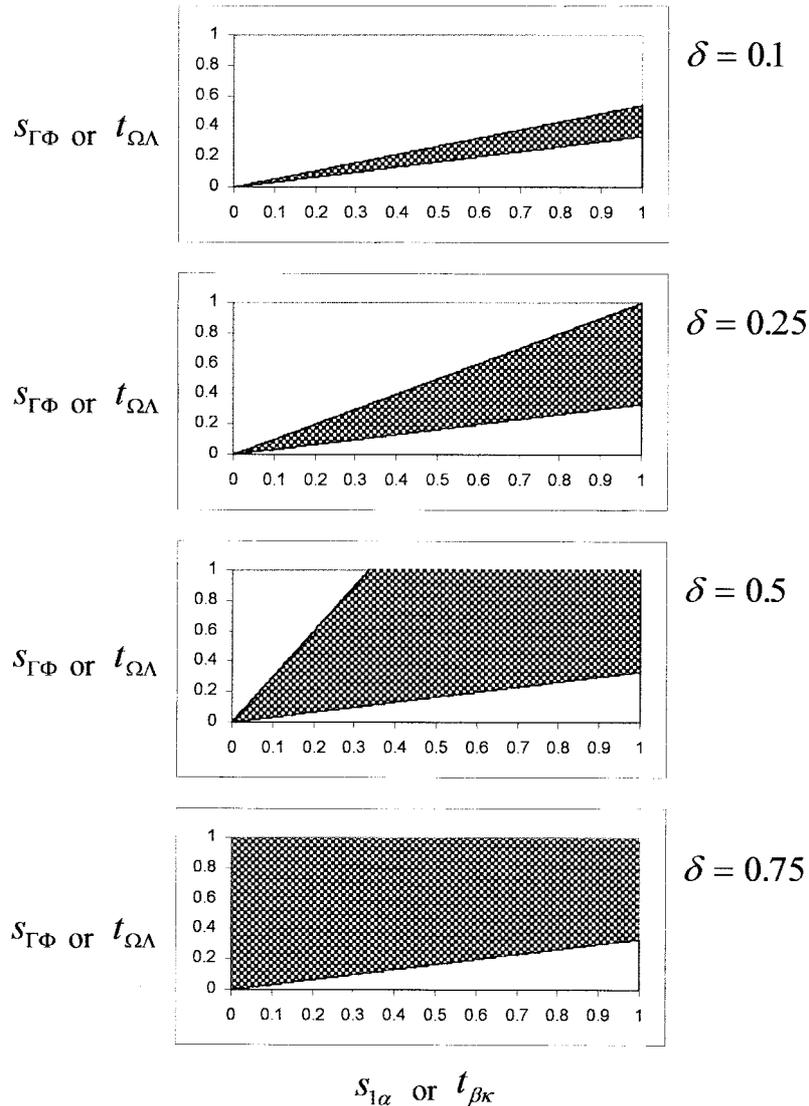
Fig. 3. The effect of δ in gap versus non-gap fixation on the *DG/DN* and *TG/TN* edges. We assume here that $s_{1\alpha} = t_{\beta\kappa}$ is on the x-axis and $s_{\Gamma\Phi} = t_{\Omega\Lambda}$ is on the y-axis. The shaded regions are the fitness differential pairs ($(s_{1\alpha}, s_{\Gamma\Phi})$ or $(t_{\beta\kappa}, t_{\Omega\Lambda})$), where N fixes on the *DG/DN* edge but G fixes on the *TG/TN* edge. As δ is increased, the shaded region grows (note $\pi = 0.25$).

Fully interior equilibria

Analytical determination of equilibria of (1)–(4) in the interior of the tetrahedron was not tractable. Therefore, we numerically iterated these recursions to survey the dynamic behaviour of the system. The parameter values used were as follows (written *parameter*[*low value, step size, high value*]): r[0, 0.1, 0.5], π[0.2, 0.2, 0.8], δ[0.2, 0.2, 0.8], a[0.7, 0.1, 0.9], β[0.9, 0.1, 1.2], κ[0.8, 0.1, 1.1], Φ[0.7, 0.1, 0.9], Γ[0.9, 0.1, 1.1], Λ[0.8, 0.1, 1.1] and Ω[0.9, 0.1, 1.2] for a total of 663,552 runs. Those not satisfying the conditions in Tables 1 and 2 were omitted. For each parameter set, we started the population at 11 different positions in the tetrahedron (four near the corner equilibria, four near the edges and three interior positions). Each run continued until the maximum of the differences $|x_i' - x_i|$, for $i \in \{1, 2, 3, 4\}$, was less than 10^{-12} over 800 consecutive iterations of the recursions. We found globally stable interior equilibria, simultaneous stability of fixations and polymorphisms, stable cycles and evidence for unstable cycles (see below).

Stable interior equilibria

For a given parameter set, if from all starting positions there is convergence to the same fully interior position, a globally stable interior equilibrium exists. We found numerous parameter sets that led to stable interior equilibria. For instance, with $r = 0.1$, $\pi = 0.4$, $\delta = 0.4$, $a = 0.7$, $\beta = 1$, $\kappa = 0.9$, $\Phi = 0.9$, $\Gamma = 1$, $\Lambda = 0.8$ and $\Omega = 1.1$, all starting positions converge to the final frequencies $x_1 \approx 0.262$, $x_2 \approx 0.026$, $x_3 \approx 0.191$, $x_4 \approx 0.521$ – a globally stable interior equilibrium.

If the largest eigenvalue for each edge and corner equilibrium is greater than unity, there is a protected polymorphism (see Appendix 3 for details). All parameter sets that produced globally stable interior equilibria satisfied the conditions for protected polymorphism (Appendix 3). When $r > 0$, as the value of r was increased, fewer stable interior equilibria were discovered. This result coincides with the analytical results above that higher r values promote boundary stability.

Simultaneous fixed points

With several parameter sets we found two locally stable fixed points, with the initial population position determining the final population position. For instance, with $r = 0.2$, $\pi = 0.4$, $\delta = 0.4$, $a = 0.8$, $\beta = 0.9$, $\kappa = 0.8$, $\Phi = 0.8$, $\Gamma = 0.9$, $\Lambda = 0.8$ and $\Omega = 1.1$, a population with all genotypes initially present either fixes for the *DG* genotype ($x_1 = 1$, $x_2 = x_3 = x_4 = 0$) or approaches a stable interior point ($x_1 \approx 0.504$, $x_2 \approx 0.138$, $x_3 \approx 0.148$, $x_4 \approx 0.210$). Figure 4 provides a two-dimensional representation of the regions inside the tetrahedron from which each equilibrium is approached in this case. While the *DG* corner is locally stable to invasion (its leading eigenvalue is less than unity), *DG* may not fix if enough non-gap plants are present in the initial population.

Stable cycles

Several parameter sets produced stable cycles of the genotype frequencies. Figure 5a illustrates this behaviour using the two-dimensional representation of the tetrahedron. Figure 5b gives a specific cycle path for the parameter set: $r = 0.5$, $\pi = 0.4$, $\delta = 0.6$, $a = 0.8$, $\beta = 1.0$, $\kappa = 0.9$, $\Phi = 0.9$, $\Gamma = 1.1$, $\Lambda = 0.8$ and $\Omega = 1.1$. Finally, Fig. 5c shows the initiation of
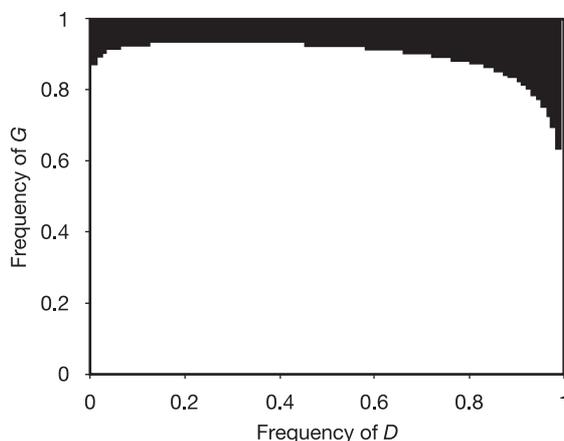
Fig. 4. Under the parameter set $r = 0.2$, $\pi = 0.4$, $\delta = 0.4$, $a = 0.8$, $\beta = 0.9$, $\kappa = 0.8$, $\Phi = 0.8$, $\Gamma = 0.9$, $\Lambda = 0.8$, $\Omega = 1.1$, two locally stable equilibria occur. If the population starts with genotype frequencies in the black region, the DG genotype fixes. If the population starts in the white region, a fully interior equilibrium is attained at $x_1 \approx 0.504$, $x_2 \approx 0.138$, $x_3 \approx 0.148$ and $x_4 \approx 0.210$. The region was determined by separately incrementing the starting frequencies of the D and G alleles by 0.01 across the ranges: $0.01 \leqslant \mathrm{fr}(D) \leqslant 0.99$ and $0.01 \leqslant \mathrm{fr}(G) \leqslant 0.99$.

the cycle for the DG genotype under the above parameter set starting with all genotypes at equal initial frequency.

Unstable cycles

We found evidence for unstable cycles as well. With certain parameter sets ($r = 0.5$, $\pi = 0.2$, $\delta = 0.6$, $a = 0.8$, $\beta = 1.0$, $\kappa = 0.9$, $\Phi = 0.9$, $\Gamma = 1.0$, $\Lambda = 0.8$ and $\Omega = 1.1$ is the example used here), there appears to be a separatrix within the tetrahedron. Inside the separatrix the population cycles into a stable isolated equilibrium ($x_1 \approx 0.109$, $x_2 \approx 0.032$, $x_3 \approx 0.519$, $x_4 \approx 0.340$ for the given parameter set). Outside the separatrix the population cycles outward, moving closer to the surface of the tetrahedron with each turn. This behaviour is summarized in Fig. 6a. Figure 6b provides a two-dimensional representation of the separatrix for the above parameter set with the white spot serving as the stable equilibrium. The behaviour of the system when the initial position lies outside the separatrix is illustrated in Fig. 6c. The population approaches each vertex in the order $DG \rightarrow DN \rightarrow TN \rightarrow TG \rightarrow DG \rightarrow \ldots$ This behaviour seems to reflect the values of the eigenvalues of each corner (see Table 3). Specifically, each corner is unstable *only* to the corner next in the sequence. That is, each corner eigenvalue corresponding to the direction of the 'next' corner is greater than unity. (For this parameter set, there are no stable edge equilibria.) As the population cycles out from the separatrix, the amount of time spent near each vertex increases (see Fig. 6c). Thus, in a finite population subject to genetic drift and with these fitness parameters, fixation might occur on any chromosome by chance!

The specific roles played by recombination, π, δ and fitness asymmetries in the unusual interior dynamics described above are under investigation.
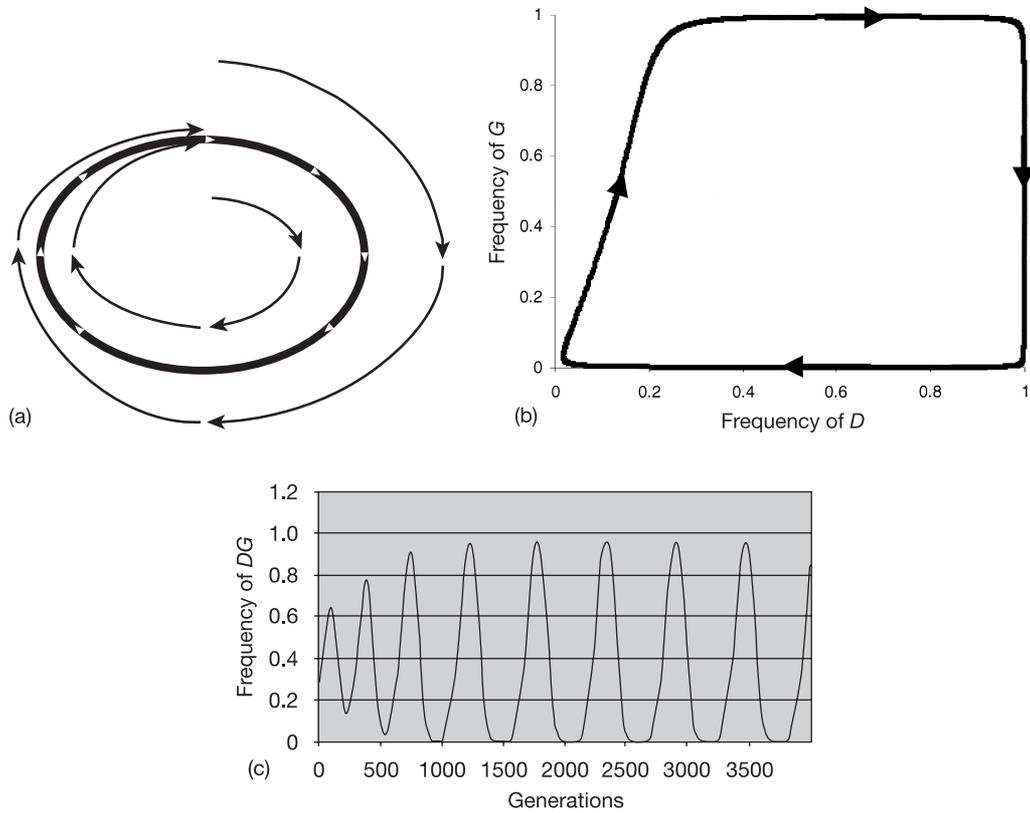
Fig. 5. (a) A general schematic showing stable cycles. Some path exists in the tetrahedron space (thick black line with open arrows) which is approached if the population starts off the path. (b) A specific stable cycle path for the parameter set $r = 0.5$, $\pi = 0.4$, $\delta = 0.6$, $a = 0.8$, $\beta = 1.0$, $\kappa = 0.9$, $\Phi = 0.9$, $\Gamma = 1.1$, $\Lambda = 0.8$, $\Omega = 1.1$. The arrows indicate the direction of 'flow' along the path. (c) The fluctuations in the frequency of the genotype DG showing approach to a stable cycle (all genotypes were started at equal frequency). The other genotypes demonstrated a similar approach to stable cycles.

DISCUSSION

Through their activity, physiology and development, individuals can alter their environment. This idea of organisms defining, shaping, creating and destroying aspects of their niches has recently been labelled 'niche construction' (Laland *et al.*, 1996; Odling-Smee *et al.*, 1996) or 'ecosystem engineering' (Jones *et al.*, 1994; Lawton and Jones, 1995; Gurney and Lawton, 1996). For example, earthworms, through their burrowing activity and feeding habits, affect soil structure and chemistry. The nest-building behaviour of many birds, social insects and burrowing mammals changes the form of their environment. Allelopathy, masting and flammability are features within plant populations that can have strong effects on the community and surroundings (Lawton and Jones, 1995; Odling-Smee *et al.*, 1996).

By affecting their environment, organisms may change the nature of selection to which they and their descendents are exposed (Lewontin, 1983). These altered selective pressures may be viewed as a 'returning boomerang' – set in motion by the original biotic effect on the
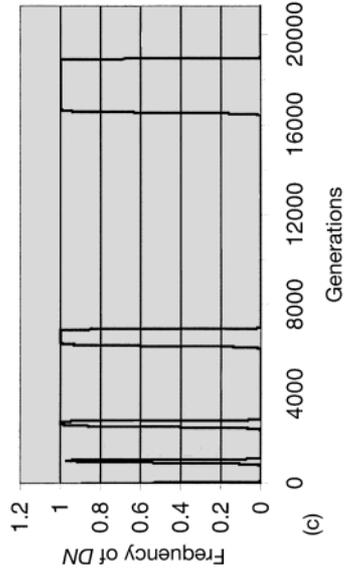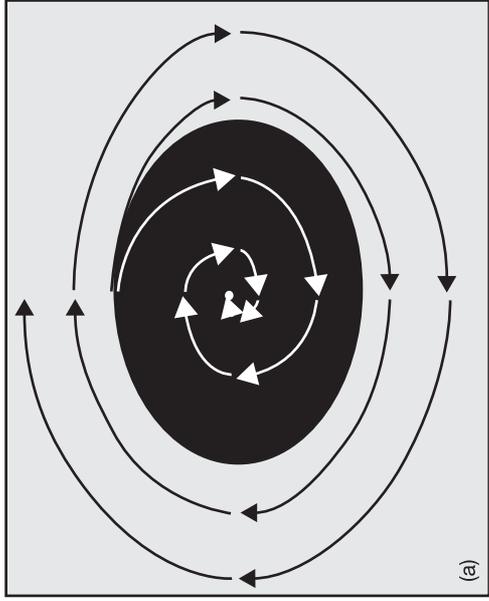
Fig. 6. (a) A general schematic showing unstable cycles. Some separatrix exists in the tetrahedron space (interface between the black and grey region). If the population starts to the inside of the separatrix, it spins into a stable equilibrium (i.e. follows the white arrows). If the population starts on the outside of the separatrix, it spins outward towards the surface of the tetrahedron (i.e. follows the black arrows). (b) A specific unstable cycle for the parameter set $r = 0.5$, $\pi = 0.2$, $\delta = 0.6$, $\alpha = 0.8$, $\beta = 1.0$, $\kappa = 0.9$, $\Phi = 0.9$, $\Gamma = 1.0$, $\Lambda = 0.8$, $\Omega = 1.1$. If the population is started in the black region, it spins into a stable node at $x_1 \approx 0.109$, $x_2 \approx 0.032$, $x_3 \approx 0.519$, $x_4 \approx 0.340$ (the white spot in the diagram). If the population starts in the grey region, it spins outward, visiting each of the vertices in turn. Although not visible in the diagram, there are continuous narrow corridors of grey region to the top and left of the black region (such that the grey region completely surrounds the black region). (c) The population is started outside the separatrix at $x_1 = 0.01$, $x_2 = 0.97$, $x_3 = 0.01$, $x_4 = 0.01$. The genotypes are visited in the order $DG \rightarrow DN \rightarrow TN \rightarrow TG \rightarrow DG \rightarrow \ldots$. All genotype frequency plots look similar to the one shown for DN (with the TN plot hitting its peaks after the DN peaks, TG hitting its peaks after TN, etc.). The frequency plot shows how the population spends more time near each vertex over successive cycles. Note that the maximum frequency at any one peak is strictly less than 1 (and the minimum at any trough is strictly greater than zero). However, the maximum frequency at any peak is greater than the maximum at any previous peak for any given genotype.
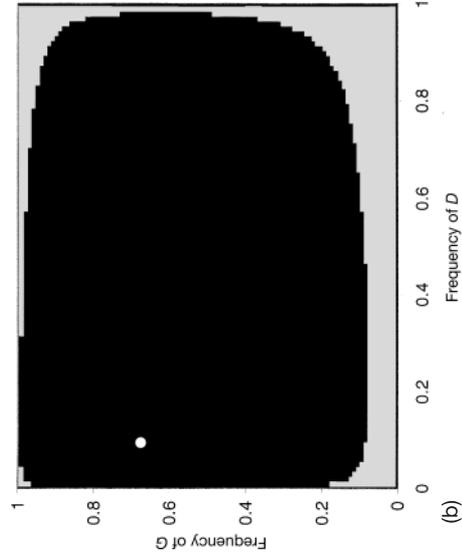
Table 3. The corner eigenvalues under the parameter set: $r = 0.5$, $\pi = 0.2$, $\delta = 0.6$, $a = 0.8$, $\beta = 1.0$, $\kappa = 0.9$, $\Phi = 0.9$, $\Gamma = 1.0$, $\Lambda = 0.8$, $\Omega = 1.1$

| Corner | Eigenvalues in directions of other corners | | | |
	λ_{DG}	λ_{DN}	λ_{TN}	λ_{TG}
DG		1.043	0.674	0.913
DN	0.958		1.104	0.542
TN	0.947	0.894		1.021
TG	1.021	0.771	0.979	

Note that one eigenvalue at each corner is greater than unity; specifically, the eigenvalue in the direction of the 'next' vertex in the sequence $DG \rightarrow DN \rightarrow TN \rightarrow TG \rightarrow DG \ldots$ For instance, focusing on DN, the population is attracted to DN from the directions of DG ($\lambda_{DG} = 0.958$) and $TG(\lambda_{TG} = 0.542)$; however, it is repulsed from DN in the direction of $TN(\lambda_{TN} = 1.104)$. A similar scenario occurs at each vertex. If the population begins in the grey region of Fig. 6, this leads to cycles where the population moves from vertex to vertex, attracted and then repulsed (according to the sequence above), each time moving closer to the surface of the tetrahedron (see Fig. 6c).

environment. How niche construction feeds back to alter selection at other genetic loci is an area of evolutionary biology that has not received much attention (but see Laland *et al.*, 1996). Our work here is an attempt to investigate some of this feedback by modelling the evolution and impact of flammability in resprouting plants.

We considered a haploid model, but a diploid model where the heterozygotes assume intermediate fitnesses is expected to give qualitatively similar results (Crow and Kimura, 1970). A simulation of a diploid version of the identical two-locus system is under investigation (D.W. Schwilk, unpublished). This diploid model includes spatial effects, which may be important in such considerations as seed shadow shape, pollen dispersal distances, and the potential of *neighbouring* plants specifically to spread fire. It may also be important to consider more than one competing species (each possessing genetically variable responses to fire) to explore community effects on the evolution of flammability. While such extensions promise to be informative, our work here shows that interesting results are realized even in the absence of such spatial and community effects.

We have investigated a simple genetic system where alleles at one locus (the flammability locus) have the potential to influence the environment experienced by an entire population. Thus, the flammable plant is viewed as an 'autogenic engineer' (Jones *et al.*, 1994; Lawton and Jones, 1995), as the physical characteristics of the plant are responsible for environmental modulation. The fate of alleles at the second locus (the disturbance locus) depends ultimately on the state of the environment and thus indirectly on the genetic constitution at the flammability locus. In our model, only the previous generation affects the flammable character of the environment (i.e. what fraction of the population burns). However, a more realistic view would take into account the influence of multiple past generations. Thus, as leaf or bark litter (not to mention dead organisms) accumulates over *multiple* generations in unburned areas, the fraction of the population expected to burn will change.

Laland *et al.* (1996) considered a diallelic two-locus model where multiple generations of niche construction could have an effect on the quantity of a resource (which in turn

affected genotype fitnesses). They found many interesting results, including evolutionary momentum and inertia, fixation of deleterious alleles, the elimination of expected stable polymorphisms and the creation of unexpected stable polymorphisms. Within a multiple generation framework, organism-independent processes of depletion may be important for our plant system as well (for instance, the degradation of litter due to decomposition). Such depletion would affect the fuel load and consequently the fraction of plants expected to burn. In an extended model, however, Laland *et al.* (in press) found that niche construction is still a potent evolutionary force even with independent depletion (or renewal) of a resource. Such theoretical extensions to our model are under consideration.

One criticism of the body of work surrounding the evolution of flammable traits is that flammability is just a by-product of selection for other functions (Snyder, 1984). For instance, the volatile compounds that make some fire-prone species flammable may have been selected for the function of herbivore defence or relatively flammable scleromorphic leaves might have resulted from selection for drought tolerance. We contend, however, that even if flammable traits are by-products, they still act as a source of selection on other genetic loci. That is, whatever may cause the appearance and maintenance of flammable traits, the environment is affected by their presence and loci responsive to the altered aspect of the environment may realize dramatic new courses of evolution (as Snyder suggests). Thus, volatile compounds or scleromorphic leaves may indirectly select for investment in improved resprouting mechanisms (in a fire-cleared gap) or fire-triggered serotinous structures (to complete the reproductive cycle), to name but a few possibilities. Below we discuss the effect that fitness asymmetries, the base flammability of the population (π), torch impact (δ) and genetic structure (r) have on both the evolution of flammability and the evolution of other traits responsive to the flammable character of the environment.

In the complete absence of torches, the disturbance locus will fix on G (gap plants) or N (non-gap plants). Which allele fixes depends on the magnitude of the base fraction of plants burnt – with large values of π favouring G and smaller values favouring N. Conceivably, π could oscillate. For instance, after large fires, values of π might be lower than pre-fire values due to litter consumption. However, over generations of smaller burns, π might grow again due to litter accumulation in unburned fractions of the population. If such a scenario occurs, then both alleles might persist, waxing and waning in cycles. With π constant and in the absence of damps (on the *TG/TN* edge of the tetrahedron), the disturbance locus will again fix on G or N. Predictions of which allele will fix based solely on fitnesses may fail due to the impact of torches (δ) on the environment. Thus, even if *TG* and *TN* mirror the fitness differences of *DG* and *DN*, the population of torches may fix on G, while the population of damps fixes on N if δ is sufficiently high. This echoes the results of Laland *et al.* (1996), who reported that otherwise deleterious alleles can fix in the presence of niche construction.

The Mutch hypothesis (Mutch, 1970) suggests that flammability evolves when plants already possess adaptations to persist in the fire-prone environment. Our analysis shows that the converse of Mutch's hypothesis may hold. That is, anatomical and reproductive traits used to persist in fire-prone ecosystems may evolve when plants possess traits that enhance their flammability. For instance, consider a population of damps where *DN* always fixes (thus, inequality (9) holds). However, assume that the *TN* genotype can invade the *DN* population and eventually fix. This can either happen if $\kappa > \alpha$ and $\Omega > \Gamma$ or if $\kappa > \alpha$, $\Omega < \Gamma$, δ is large and there is pronounced population substructure (see below). Since torches increase the fraction of the population burnt, it is now possible for gap plants (in the form of *TG*) to invade and fix. This happens if inequality (18) holds, which becomes more likely
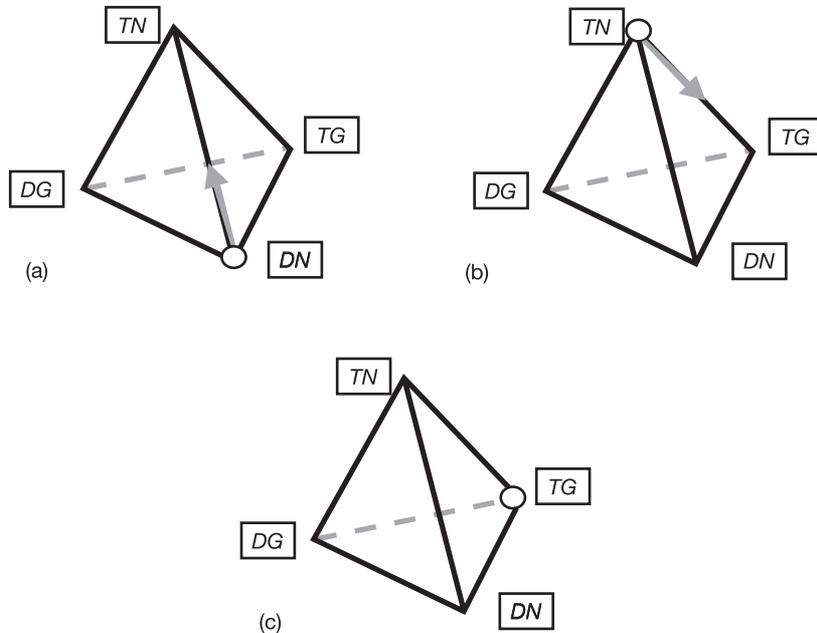
Fig. 7. An environment inhospitable to the *G* allele is altered through niche construction to favour the fixation of *G*. (a) A population originally fixed on *DN* (and stable to invasion by *DG*) is invaded by *TN*. (b) *TN* fixes and, in the more flammable environment, *TG* invades and (c) fixes.

as δ is increased (see Fig. 3). Figure 7 shows this scenario using the tetrahedron. Niche construction through enhanced flammability transforms an environment originally inhospitable to the *G* allele to an environment where its fixation occurs. As the impact of niche construction is intensified (i.e. as δ increases), the potential for Mutch's converse to hold also increases. Thus, an environment made more flammable by its flora could select for fire-adapted traits (in this case the *G* allele).

Mutch's converse does not eliminate the possibility that flammable traits may be less constrained in their evolution if plants already possess some fire-adapted traits. Indeed, flammable traits (even if useful to the plant for other reasons) may be unsuccessful if the plant is not reproductively or morphologically equipped to deal with the enhanced presence/intensity of fire (this issue is not addressed in our model). Some capacity to resprout is considered an ancestral trait in woody species (Whelan, 1995; Bond and van Wilgen, 1996) and might be best viewed as a preadaptation to fire. We certainly do not rule out a scheme by which flammability and fire-adapted traits co-evolve over small time steps. That is, the flora may become slightly more flammable, thereby intensifying a selective pressure for fire-adapted traits. The evolution of persistence in the face of fire may then allow for more leeway with regards to the further evolution of flammable traits. The significance of Mutch's converse lies in the claim that the plant itself may act as a co-author in its own evolution.

The above argument may reconcile another criticism of the Mutch hypothesis. The contention is that if flammability evolves in fire-adapted vegetation for the purpose of fending off fire-sensitive competitors, one might expect nearly *all* fire-adapted species in the

fire-prone community to be flammable (Whelan, 1995). After all, the more flammable the community, the more competitive protection afforded its inhabitants. However, not all species in the fire-prone environment possess characteristics that enhance their flammability (Snyder, 1984; Whelan, 1995). While the Mutch hypothesis is at odds with the observation that only a portion of the fire-adapted flora in some communities is flammable, Mutch's converse remains entirely consistent with this information. That is, if flammability evolves in only a few species and the environment is consequently altered, then populations of *all* species in the region could potentially be subjected to selection for traits to cope with the enhanced presence of fire. Thus, the niche-constructing traits of a single species may influence not only its own evolutionary path, but also the evolutionary trajectories in other species. Flammability may, in this way, extend its reach beyond the confines of the flammable species.

Several factors are important with regard to the invasion by torches into a population of damps. If torches possess higher fitnesses than damps in both gap and non-gap environments, then torch fixation is inevitable (see Appendix 1). For instance, if compounds that make a plant more flammable also function in herbivore defence or allelopathy, torches could potentially have higher fitnesses than damps in both a gap and non-gap. Tighter linkage between the disturbance locus and flammability locus increases the likelihood of torch invasion. This result is reflected in the simulated diploid version of this system, where tighter linkage corresponds to a greater fraction of runs in which torches invade successfully (D.W. Schwilk, unpublished). The base fraction of plants that burn (π) affects the evolution of flammability as well. Lastly, the frequency of alleles at the disturbance locus (the position on the *DG/DN* edge of the tetrahedron) influences the chances of invasion by the *T* allele – and thus the evolution of flammability.

Given certain fitness asymmetries, torch–damp polymorphisms exist (on the *DG/TG* and *DN/TN* edges of the tetrahedron). The frequencies of torches and damps at equilibrium depend on the impact of torches on the environment (δ). Higher values of δ lead to lower torch frequency at equilibrium (see (11)). If torches do better in a fire-cleared gap and damps do better in an established stand, then an unstable edge equilibrium results (i.e. $\beta > 1$ and $\Phi > \Lambda$ could potentially satisfy (15)–(17)). Raising δ will, in essence, lower the threshold torch frequency (above which torches will fix). With higher values of δ, a little torch goes a long way in promoting a gap environment – specifically, less torches are needed to exceed the threshold. Population substructure may facilitate torch invasion as well. Although we assume random mating here, if plants were to mate exclusively with near neighbours and seeds were deposited close to the parent plant, a torch frequency under the above threshold in a randomly mating population could exceed the threshold in such locally mating populations – thus leading to (first local, then population-wide) torch fixation. Such population substructure is likely to be important given the low seed-dispersal distances of many plants in fire-prone systems (Bond and van Wilgen, 1996).

On the other hand, if damps do better in a gap and torches do better in a stand, a stable mixed population of torches and damps is possible ($1 > \beta$ and $\Lambda > \Phi$ could potentially satisfy (12)–(14)) on the *DG/TG* edge. Here, raising δ means that torches are more forcibly promoting an environment in which they do poorer – thus a lower torch frequency at the stable equilibrium is realized. The population substructure in this case would be expected to have the opposite effect to that described for the unstable equilibrium above. Specifically, a population-wide torch frequency below the stable equilibrium, might exceed the equilibrium in smaller locally interbreeding subpopulations. Thus, the frequency of torches

would be pushed lower and, possibly, depending on the degree of population substructure, reach zero. Here, by reproducing with near neighbours and dumping its seeds close to the parent plant, the torch is 'digging its own grave', since the environment promoted by its presence discriminates against torches.

With complete linkage, invasion by non-gap plants into a population of gap plants (the stable interior equilibrium on the *DG/TG* edge) or invasion by gap plants into a population of non-gap plants (the stable interior equilibrium of the *DN/TN* edge) depends only on the fitnesses of the haploid genotypes (see Appendix 1). However, more frequent recombination may prevent this invasion. This reflects the general result that higher recombination values promote boundary stability in diallelic two-locus systems (Karlin and Feldman, 1970).

Lastly, with all genotypes present, unusual population dynamics can occur. Specifically, genotypes may converge to a single globally stable equilibrium or converge to one of two locally stable equilibria. Under certain parameter sets, the genotypes experience stable cycles, while under other parameter sets, the genotypes will either cycle into a stable point or outward towards the corners of the tetrahedron. Thus, starting conditions may be quite important in determining the final position of the population. Furthermore, small changes in parameters can have drastic effects (note that the examples given for unstable and stable cycles above differ only in two parameters: π and Γ). Such dynamics expand the list of unusual evolutionary phenomena that can occur in a niche-constructing population (Laland *et al.*, 1996).

The above analysis shows that genetic structure and environmental conditions, as well as fitness asymmetries, may be important in the evolution of flammability. Furthermore, the evolution of flammable traits and the magnitude of the organism's impact on the environment may drastically affect evolution at other genetic loci, leading to results that differ from expectation. Theoretical treatments of the effects of niche construction or ecosystem engineering may help describe some of the intricacies involved in the mutual relations between organisms and their environment.

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APPENDIX 1: STABILITY ANALYSES

DG corner stability

Standard local stability analysis produces the following linear approximation to the system (1)–(4) near $x_1 = 1$:

$$\begin{pmatrix} \varepsilon_2' \\ \varepsilon_3' \\ \varepsilon_4' \end{pmatrix} = \frac{1}{(\pi + (1-\pi)\Phi)} \begin{bmatrix} \pi a + (1-\pi)\Gamma & 0 & r(1-\pi)\Gamma \\ 0 & \pi\beta + (1-\pi)\Lambda & r(1-\pi)\Lambda \\ 0 & 0 & \pi\kappa + (1-r)(1-\pi)\Omega \end{bmatrix} \begin{pmatrix} \varepsilon_2 \\ \varepsilon_3 \\ \varepsilon_4 \end{pmatrix} \quad \text{(A1)}$$

Here the eigenvalues of the matrix determine whether the initially small frequencies of *DN*, *TG* and *TN* (ε_2, ε_3 and ε_4, respectively) grow or decay. Specifically, if the largest eigenvalue is less than unity, then the *DG* corner is stable to invasion (and the allele *T* promoting increased flammability will not invade). Since this is a triangular matrix, the eigenvalues line the diagonal and the conditions for stability are:

$$\frac{\pi a + (1 - \pi)\Gamma}{\pi + (1 - \pi)\Phi} < 1 \qquad (A2)$$

$$\frac{\pi \beta + (1 - \pi)\Lambda}{\pi + (1 - \pi)\Phi} < 1 \qquad (A3)$$

$$\frac{\pi \kappa + (1 - r)(1 - \pi)\Omega}{\pi + (1 - \pi)\Phi} < 1 \qquad (A4)$$

Here (A2) (the same as (5)) is the condition under which fixation on *DG* is stable to invasion by *DN*, while (A3) is the analogous condition for stability to invasion by *TG*. If both (A2) and (A3) hold, then whether or not invasion by alleles *T* and *N* occurs is governed by (A4). Equation (A4) can be rewritten as follows (note $\pi \neq 1$):

$$\Omega < \left(\frac{-\pi}{(1 - \pi)(1 - r)}\right)\kappa + \frac{\pi + (1 - \pi)\Phi}{(1 - \pi)(1 - r)} \qquad (A5)$$

The striped region in Fig. 8 gives all (κ, Ω) pairs leading to stability at the *DG* corner. Note that the striped region is bounded below by the line $\Omega = \kappa$ and above by the line $\Omega = (-\pi/((1 - \pi)(1 - r)))\kappa + (\pi + (1 - \pi)\Phi)/((1 - \pi)(1 - r))$, since inequality (A5) implies stability near $x_1 = 1$. The stippled region represents all (κ, Ω) pairs leading to invasion at the *DG* corner by *TN* (where $\Omega > \kappa$ and (A5) is not satisfied). The triangular area within the 'section of stability' (A_s) is given by:
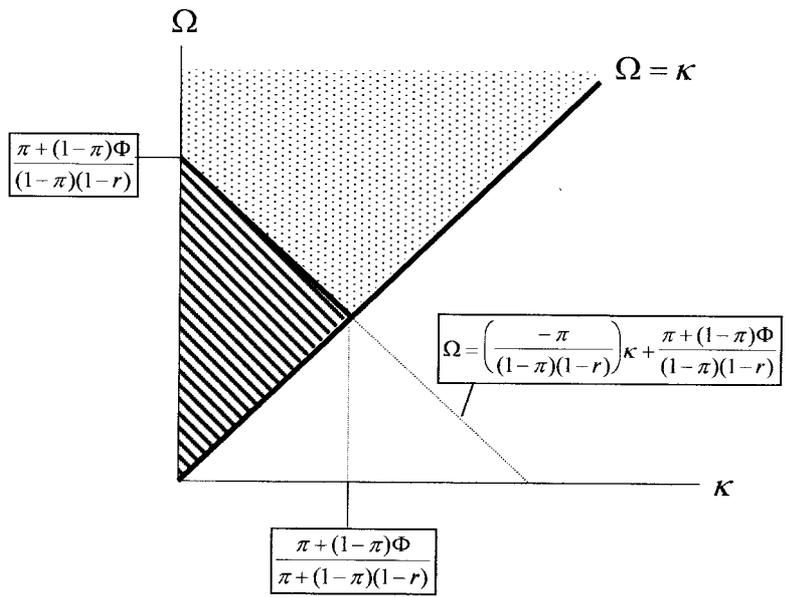
Fig. 8. The striped region describes where *DG* is stable to invasion by *TN*. The boundaries result from the inequality (A5) and the fitness constraint $\Omega > \kappa$. The stippled region is where *TN* invades. See Appendix 1 for a discussion of the parameter effects on the area of this 'section of stability'.

$$A_s = \frac{(\pi + (1-\pi)\Phi)^2}{2(\pi + (1-\pi)(1-r))((1-\pi)(1-r))} \tag{A6}$$

Note that, as r increases, A_s also increases. Thus, higher values of r lead to a greater possibility of stability. We deduce the effect of π by taking the derivative:

$$\frac{\partial A_s}{\partial \pi} = \frac{(\pi(1-\Phi) + \Phi)((1-\Phi)(1-\pi) + 1 - 2r(1-\pi))}{2(1-r)(1+r(\pi-1))^2(1-\pi)^2} \tag{A7}$$

The right-hand side of (A7) is positive (since $0 < \Phi < 1$, $0 \le r \le 0.5$ and $0 < \pi < 1$). Thus, as π increases, so too does the potential for stability.

DN corner stability

Local linear stability analysis near $x_2 = 1$ gives the following system:

$$\begin{pmatrix} \varepsilon_1' \\ \varepsilon_3' \\ \varepsilon_4' \end{pmatrix} = \frac{1}{(\pi a + (1-\pi)\Gamma)} \begin{bmatrix} \pi + (1-\pi)\Phi & r(1-\pi)\Phi & 0 \\ 0 & \pi\beta + (1-r)(1-\pi)\Lambda & 0 \\ 0 & r(1-\pi)\Omega & \pi\kappa + (1-\pi)\Omega \end{bmatrix} \begin{pmatrix} \varepsilon_1 \\ \varepsilon_3 \\ \varepsilon_4 \end{pmatrix} \tag{A8}$$

Here ε_1, ε_3 and ε_4 represent the initial small frequencies of DG, TG and TN, respectively, near fixation of DN. The eigenvalues again line the diagonal of the matrix and the following conditions for stability are easily deduced:

$$\frac{\pi + (1-\pi)\Phi}{\pi a + (1-\pi)\Gamma} < 1 \tag{A9}$$

$$\frac{\pi\beta + (1-r)(1-\pi)\Lambda}{\pi a + (1-\pi)\Gamma} < 1 \tag{A10}$$

$$\frac{\pi\kappa + (1-\pi)\Omega}{\pi a + (1-\pi)\Gamma} < 1 \tag{A11}$$

Here (A9) (identical to (6)) gives the condition for stability of the population fixed on DN to invasion by DG, while (A11) gives the analogous condition for stability to invasion by TN. If both (A9) and (A11) hold, then invasion by alleles T and G is determined by inequality (A10). If (A10) holds for $r = 0$, it holds for all r (since the left-hand side of (A10) is a decreasing function in r). Furthermore, using an argument identical to that used for the DG corner above, it can be shown that, as r increases, the potential for stability increases (the same effect as with the DG corner above). And as π is raised, the potential for stability drops (the opposite effect of that above).

DG/TG edge stability considerations

Here we consider the fate of chromosomes carrying N introduced near this edge. First, we address the dynamics on the edge itself.

Corner stability

With the population fixed on DG ($x_1 = 1$), the condition for stability to invasion by TG along the DG/TG edge is:

$$\pi(\beta - 1) + (1 - \pi)(\Lambda - \Phi) < 0 \tag{A12}$$

which is identical to (15) and (A3).

At the other vertex of the edge (*TG* fixed, $x_3 = 1$), the condition for stability to invasion by *DG* is given by:

$$\pi(\beta - 1) + (1 - \pi)(\Lambda - \Phi) + \delta(\beta - 1 + \Phi - \Lambda) > 0 \tag{A13}$$

If $\beta < 1$ and $\Lambda < \Phi$, then (A12) holds while (A13) does not. In this case, *DG* will fix as long as, initially, $x_1 \neq 0$. If $\beta < 1$ and $\Lambda < \Phi$, then *TG* has both a lower gap and non-gap fitness than *DG*, and it is not surprising that *DG* fixes in this case. Such constraints are sufficient but not necessary conditions under which *DG* fixes.

If $\beta > 1$ and $\Lambda > \Phi$, then (A13) holds while (A12) does not. In this case, *TG* fixes if, initially, $x_3 \neq 0$. Here, since *TG* has both a higher gap and non-gap fitness than *DG* (possessing an advantage in both environments), it is expected to fix.

Interior DG/TG edge equilibrium

Under scenario 1 ((12)–(14)), fixation on both *DG* and *TG* is unstable, as can be seen from (A12) and (A13). In fact, if the conditions in scenario 1 hold, then the equilibrium (11) is globally stable in the *DG/TG* edge.

Inequalities (15)–(17) together imply that both vertices are stable. It is then easy to show that, under scenario 2, if the frequency of *DG* is greater than its equilibrium value in (11), it fixes, and if it is lower, *DG* is lost. Thus, scenario 2 corresponds to an unstable edge equilibrium.

Stability to invasion by non-gap plants

We can address this by asking when an initially small fraction of *N*, introduced near the equilibrium (11) where *G* is fixed, increases over time. Local stability analysis yields the following linear system in ε_2 and ε_4, the initial small frequencies of *DN* and *TN*, respectively, near the *DG/TG* edge equilibrium (11) under scenario 1:

$$\begin{pmatrix} \varepsilon_2' \\ \varepsilon_4' \end{pmatrix} = \begin{bmatrix} Y - r\Gamma\hat{x}_3 H & r\Gamma\hat{x}_1 H \\ r\Omega\hat{x}_3 H & Z - r\Omega\hat{x}_1 H \end{bmatrix} \begin{pmatrix} \varepsilon_2 \\ \varepsilon_4 \end{pmatrix} \tag{A14}$$

with:

$$\hat{W} = \frac{\Lambda - \Phi\beta}{1 - \beta + \Lambda - \Phi}$$

$$H = \frac{1 - (\pi + \delta\hat{x}_3)}{\hat{W}}$$

$$Y = \frac{\Gamma + (\pi + \delta\hat{x}_3)(a - \Gamma)}{\hat{W}}$$

$$Z = \frac{\Omega + (\pi + \delta\hat{x}_3)(\kappa - \Omega)}{\hat{W}}$$

If $\beta < 1$ and $\Lambda > \Phi$, all the entries of the matrix in (A14) are positive (see Appendix 2). The Perron-Frobenius theorem for positive matrices guarantees that the largest eigenvalue is real and positive – thus, the other eigenvalue must also be real. The eigenvalues are the roots of the characteristic quadratic $f(\lambda)$, where:

$$f(\lambda) = \lambda^2 - (Y - r\Gamma\hat{x}_3 H + Z - r\Omega\hat{x}_1 H)\lambda + (YZ - Yr\Omega\hat{x}_1 H - Zr\Gamma\hat{x}_3 H) \tag{A15}$$

The parabola $f(\lambda)$ is characterized by the position of its two roots with respect to $\lambda = 1$. If the larger positive root is less than unity, then the interior equilibrium on the DG/TG edge is stable to invasion by non-gap plants. Otherwise, N invades. If the signs of $f(1)$ and $f'(1)$ are known, the stability can be deduced. We have:

$$f(1) = (1 - Y)(1 - Z) + r((1 - Y)\Omega\hat{x}_1 H + (1 - Z)\Gamma\hat{x}_3 H) \tag{A16}$$

$$f'(1) = 2 - Y - Z + r(\Omega\hat{x}_1 H + \Gamma\hat{x}_3 H) \tag{A17}$$

both of which are linear functions of r. If $f(1) > 0$ and $f'(1) > 0$, then both eigenvalues are less than unity. If $f(1) < 0$, then one eigenvalue is greater than 1. If $f(1) > 0$ and $f'(1) < 0$, then both eigenvalues are greater than unity. Can recombination influence the stability of the DG/TG interior edge equilibrium? For instance, is it possible under the same parameter settings that N could not invade at $r = 0$, but could for some larger r value? Or could N invade with complete linkage, but not with $r > 0$?

Under complete linkage

When $r = 0$, equations (A16) and (A17) become:

$$f(1)|_{r=0} = (1 - Y)(1 - Z) \tag{A18}$$

$$f'(1)|_{r=0} = 2 - Y - Z \tag{A19}$$

If both $Y < 1$ and $Z < 1$, then $f(1)|_{r=0} > 0$ and $f'(1)|_{r=0} > 0$ and the equilibrium is stable to invasion. If we assume that $\beta < 1$, then we can restate the conditions ($Y < 1$ and $Z < 1$) for stability as:

$$\frac{s_{\Gamma\Phi}}{s_{1a}} < \frac{s_{\Lambda\Phi}}{s_{1\beta}} \tag{A20}$$

$$\frac{s_{\Omega\Phi}}{s_{1\kappa}} < \frac{s_{\Lambda\Phi}}{s_{1\beta}} \tag{A21}$$

Here the s coefficients are fitness differentials with $s_{\Gamma\Phi} = \Gamma - \Phi$, $s_{1a} = 1 - a$, $s_{\Lambda\Phi} = \Lambda - \Phi$, $s_{1\beta} = 1 - \beta$, $s_{\Omega\Phi} = \Omega - \Phi$ and $s_{1\kappa} = 1 - \kappa$. If DN has a very slight non-gap fitness advantage over DG ($s_{\Gamma\Phi}$ small compared to $s_{\Lambda\Phi}$), or if DN or TN have very severe gap fitness disadvantages with respect to DG (s_{1a} and $s_{1\kappa}$ both large compared to $s_{1\beta}$), then conditions (A20) and (A21) become easier to satisfy. Thus, the gap plant population would be more likely to resist invasion by the non-gaps. On the other hand, if TN and DN receive either large non-gap fitness boosts or very slight gap fitness drops, then non-gap plant invasion becomes more likely.

Stability when $r > 0$

If $Y < 1$ and $Z < 1$, then equation (A18) guarantees $f(1)|_{r=0} > 0$, and from (A16), $f(1)$ is an increasing linear function of r. $f(1)$ does not change sign and there is no way, by increasing r, to move from the stability at $r = 0$, where both eigenvalues are less than 1, to a situation where an eigenvalue is greater than 1. For this to happen, $f(1)$ would have to change sign from positive to negative, which is impossible. Indeed, the equilibrium becomes more stable as r increases (the dominant eigenvalue decreases). Therefore, if the interior equilibrium on the DG/TG edge is stable to non-gap invasion at $r = 0$, it is stable *for all r*.

If $Y > 1$ and $Z > 1$, $f(1)|_{r=0} > 0$ and $f'(1)|_{r=0} < 0$ and both eigenvalues are greater than unity at $r = 0$. From (A16), if $Y > 1$ and $Z > 1$, then $f(1)$ is a decreasing linear function of r. Thus, for $0 \le r \le 0.5$, the value of the characteristic at $\lambda = 1$ could change from positive to negative but there can be, at most,

only one sign change. Thus, one eigenvalue will remain greater than 1 and, if $Y > 1$ and $Z > 1$, the interior edge equilibrium is unstable for all r.

In the two previous cases, recombination does not qualitatively affect the stability of the interior edge equilibrium; however, if $Y > 1$ and $Z < 1$ or if $Y < 1$ and $Z > 1$, recombination may influence stability. Here $f(1)|_{r=0} < 0$ and $f'(1)|_{r=0}$ can be positive, negative or zero. If the coefficient of r in (A16) is positive, then the value of the characteristic equation at $\lambda = 1$ may change from negative to positive once. Such a change occurs if:

$$(1 - Y)(1 - Z) + \tfrac{1}{2}((1 - Y)\Omega\hat{x}_1 H + (1 - Z)\Gamma\hat{x}_3 H) > 0 \tag{A22}$$

Since $f'(1)$ is an increasing (linear) function in r, if (A22) holds, a transition to a state with both eigenvalues less than unity occurs as r is increased from 0 to 0.5.

DN/TN edge stability considerations

The analysis here is identical to that worked out for the *DG/TG* edge above. Thus, higher values of r can promote stability to invasion by the G allele at a stable edge equilibrium on the *DN/TN* edge as well.

APPENDIX 2

Here we show that all the entries of the matrix in (A14) are positive. First we show that the normalizing factor $[(\Lambda - \Phi\beta)/(1 - \beta + \Lambda - \Phi)]$ is positive. The denominator of the normalizing factor $(1 - \beta + \Lambda - \Phi)$ is positive since we are investigating a *stable* interior edge equilibrium – thus, inequality (13) of scenario 1 holds. If $\beta < 1$ and $\Lambda > \Phi$, then the numerator $\Lambda - \Phi\beta$ is certainly positive as well.

It is a trivial matter to show H, Y and Z (from expression (A14)) to be positive. Thus the off-diagonal entries in the matrix (A14) are certainly positive. The diagonal entries are:

$$Y - r\Gamma\hat{x}_3 H = \frac{\Gamma + (\pi + \delta\hat{x}_3)(a - \Gamma) - r\Gamma\hat{x}_3 + r\Gamma\hat{x}_3(\pi + \delta\hat{x}_3)}{\hat{W}} = \frac{a(\pi + \delta\hat{x}_3) + \Gamma(1 - r\hat{x}_3)(1 - (\pi + \delta\hat{x}_3))}{\hat{W}}$$

$$Z - r\Omega\hat{x}_1 H = \frac{\Omega + (\pi + \delta\hat{x}_3)(\kappa - \Omega) - r\Omega\hat{x}_1 + r\Omega\hat{x}_1(\pi + \delta\hat{x}_3)}{\hat{W}} = \frac{\kappa(\pi + \delta\hat{x}_3) + \Omega(1 - r\hat{x}_1)(1 - (\pi + \delta\hat{x}_3))}{\hat{W}}$$

Clearly, both fractions are positive – thus, all the entries in the matrix in (A14) are positive and the Perron-Frobenius theorem applies.

APPENDIX 3: PROTECTED POLYMORPHISM REQUIREMENTS

Below are the requirements for a protected polymorphism assuming $\pi \neq (\Gamma - \Phi)/(\Gamma - \Phi + 1 - a)$, $(\pi + \delta) \neq (\Omega - \Lambda)/(\Omega - \Lambda + \beta - \kappa)$, scenario 1 ((12)–(14)) holds, and an equivalent set of inequalities to that of scenario 1 holds on the *DN/TN* edge of the tetrahedron (simply replace the gap and non-gap fitnesses of *DG* and *TG* in scenario 1 with those of *DN* and *TN*, respectively). We list the corner or edge equilibrium and then the requirements for its instability.

- *DG corner*: for the *DG* corner to be unstable, the opposite of at least one of the inequalities (A2)–(A4) must hold.
- *DN corner*: for the *DN* corner to be unstable, the opposite of at least one of the inequalities (A9)–(A11) must hold.
- *TG corner*: for the *TG* corner to be unstable, at least one of the following inequalities must hold:

$$\frac{(\pi + \delta) + (1 - (\pi + \delta))\Phi}{(\pi + \delta)\beta + (1 - (\pi + \delta))\Lambda} > 1 \tag{A23}$$

$$\frac{(\pi + \delta)a + (1 - (\pi + \delta))(1 - r)\Gamma}{(\pi + \delta)\beta + (1 - (\pi + \delta))\Lambda} > 1 \tag{A24}$$

$$\frac{(\pi + \delta)\kappa + (1 - (\pi + \delta))\Omega}{(\pi + \delta)\beta + (1 - (\pi + \delta))\Lambda} > 1 \tag{A25}$$

- *TN corner*: for the *TN* corner to be unstable, at least one of the following inequalities must hold:

$$\frac{(\pi + \delta) + (1 - (\pi + \delta))(1 - r)\Phi}{(\pi + \delta)\kappa + (1 - (\pi + \delta))\Omega} > 1 \tag{A26}$$

$$\frac{(\pi + \delta)a + (1 - (\pi + \delta))\Gamma}{(\pi + \delta)\kappa + (1 - (\pi + \delta))\Omega} > 1 \tag{A27}$$

$$\frac{(\pi + \delta)\beta + (1 - (\pi + \delta))\Lambda}{(\pi + \delta)\kappa + (1 - (\pi + \delta))\Omega} > 1 \tag{A28}$$

- *DG/TG edge*: assuming scenario 1 holds ((12)–(14)), if the dominant eigenvalue of matrix (A14) is greater than unity, then this edge equilibrium is unstable to (non-gap) invasion. Thus, the sufficient condition for instability is:

$$\tfrac{1}{2}(Y - r\Gamma\hat{x}_3 H + Z - r\Omega\hat{x}_1 H + \sqrt{(Y - r\Gamma\hat{x}_3 H + Z - r\Omega\hat{x}_1 H)^2 - 4(YZ - Yr\Omega\hat{x}_1 H - Zr\Gamma\hat{x}_3 H)}) > 1 \tag{A29}$$

H, Y and Z are defined in Appendix 1.

- *DN/TN edge*: assuming a stable interior edge equilibrium exists (that is, conditions similar to scenario 1 apply on the non-gap edge), the following is sufficient for instability to gap invasion:

$$\tfrac{1}{2}(A - r\Phi\hat{x}_4 J + B - r\Lambda\hat{x}_2 J + \sqrt{(A - r\Phi\hat{x}_4 J + B - r\Lambda\hat{x}_2 J)^2 - 4(AB - Ar\Lambda\hat{x}_2 J - Br\Phi\hat{x}_4 J)}) > 1 \tag{A30}$$

with

$$\hat{W}^* = \frac{\Omega a - \Gamma\kappa}{a - \kappa + \Omega - \Gamma}$$

$$J = \frac{1 - (\pi + \delta\hat{x}_4)}{\hat{W}^*}$$

$$A = \frac{\Phi + (\pi + \delta\hat{x}_4)(1 - \Phi)}{\hat{W}^*}$$

$$B = \frac{\Lambda + (\pi + \delta\hat{x}_4)(\beta - \Lambda)}{\hat{W}^*}$$

and

$$\hat{x}_2 = 1 - \frac{\pi(\kappa - a) + (1 - \pi)(\Omega - \Gamma)}{\delta(a - \kappa + \Omega - \Gamma)}$$

$$\hat{x}_4 = \frac{\pi(\kappa - a) + (1 - \pi)(\Omega - \Gamma)}{\delta(a - \kappa + \Omega - \Gamma)}$$