

Genetic niche-hiking: an alternative explanation for the evolution of flammability

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In fire-prone ecosystems, many plants possess traits that enhance their relative flammability and ecologists have suggested increased flammability could result from natural selection. To date, theoretical models addressing the evolution of flammable characteristics assume that flammable plants realize some direct fitness advantage. In this paper, we explore the idea that enhanced flammability can increase in frequency in a population without any direct fitness benefit to the flammable type. In our model, flammability evolves due to an association between an allele that promotes flammability and alleles at unlinked loci that give high fitness. In analogy to genetic hitchhiking, in which a deleterious allele can invade due to a genetic linkage, we call this process “genetic niche-hiking,” because the association results from localized niche construction. Specifically, flammable plants sacrifice themselves and their neighbors to produce local fire-cleared gaps (the constructed niche) in which their offspring are able to continually track an ever-changing environment. Niche-hiking requires that mating, dispersal and niche construction all occur locally (i.e. the population is spatially structured), such that offspring are likely to experience the niches their parents construct. Using a spatially-explicit lattice-based simulation, we find that increased flammability can evolve despite the “self-killing” cost of such a trait. Genetic niche-hiking may also be applicable to the evolution of other traits in spatially structured ecological systems such as plant disease susceptibility and forest tree characteristics that influence gap production.

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Wildfire is a recurring event in many ecosystems – from savannas to Mediterranean shrublands to boreal forests – and ecologists have long been intrigued by the striking and presumably adaptive responses of plants to fire. These responses include mechanisms to survive fire, such as resprouting from underground storage organs and thick insulating bark (Keeley 1992, Lopez-Soria and Castell 1992, Haidinger and Keeley 1993, Moreno and Oechel 1993, Bell and Pate 1996, Enright and Goldblum 1999, Jackson et al. 1999, Bellingham 2000). Other responses, such as fire-stimulated seed germination, fire-stimulated flowering, and serotiny, cue reproduction to the fire event (Went et al. 1952, Christiansen and Muller 1975, Keeley et al. 1985, Keeley 1991, Lamont et al. 1991, Baldwin et al. 1994, Keeley and

Bond 1997, Keeley and Fotheringham 1997, Keeley and Zedler 1998, Roche et al. 1998). Species unable to survive fire but possessing fire-cued reproduction may, in fact, require fire to persist. Such evidence suggests that the historical interaction with fire has influenced plant characteristics. Plants, however, are not only affected by fire, but as fuel, also may influence the nature of this disturbance.

The occurrence and character of wildfire is determined not only by climate, but also by characteristics of the vegetation. Different vegetation types can behave quite differently as fuels (Rothermel 1972, Philpot 1977, Rundel 1981, Williamson and Black 1981, van Wilgen et al. 1990, Papio and Trabaud 1991); thus it is possible in Mediterranean-climate California to have the highly

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flammable chaparral occurring adjacent to much less flammable oak woodland, which experiences a less severe fire regime. Traits such as the retention of dead branches, fine thin branching patterns that influence the air/fuel mix, and the presence of volatile oils have all been cited as potential flammability-enhancing traits. Evidence from the genus *Pinus* suggests that such flammability-enhancing traits may exhibit an evolutionary correlation with fire-dependent seedling recruitment (Schwilk and Ackerly 2001).

Observing that some plants depend upon fire for their continued persistence and that many of these plants are relatively flammable prompted Mutch (1970) to suggest that if plants possess reproductive or anatomical mechanisms to persist through fire events, then there may be selection for characteristics that enhance flammability in these plants. Mutch suggested that flammability in fire-adapted vegetation would prevent invasion by less flammable, fire-sensitive species. The Mutch hypothesis, however, has received a good deal of criticism. One line of criticism was that the hypothesis was framed at the level of competing vegetation types (Snyder 1984, Troumbis and Trabaud 1989). Critics argue that it is difficult to imagine how a more flammable mutant would spread in a population of less flammable conspecifics. In direct response to this line of criticism, two individual-based models have been put forward (Bond and Midgley 1995, Kerr et al. 1999) that attempt to describe the conditions under which flammable types can invade a population.

A second criticism of the Mutch hypothesis states that so-called flammability traits are more likely to be secondary results of selection on other traits (Snyder 1984). For instance, there may be selection for plants with volatile compounds if such compounds deter herbivores, and it is only incidental that such traits also increase the flammable character of the plant – in such a case, there is no direct selection for flammability. Even if flammability is a true side-effect of selection for other traits, however, a more flammable vegetation will create new selective pressures. Kerr et al. (1999) have demonstrated that the presence of flammability-enhancing traits can actually redirect the evolution of other traits. Such feedback effects may lead to “Mutch’s converse,” where, for instance, the evolution of fire-response traits such as enhanced resprouting capability or smoke-stimulated seed germination could be influenced strongly by selection for any trait that changes the probability or intensity of burning.

In the population genetic model of Kerr et al. (1999) genes interact through the effects that alleles have on the flammable character of the environment. In general, the process whereby organisms modify their environment through their life-activities has been labeled “niche construction” (Lewontin 1983, Laland et al. 1996, Odling-Smee et al. 1996, Laland et al. 1999). These environmental modifications can feedback to

shape the selective pressures experienced by the original organisms. Flammability provides a dramatic example of a niche-constructing trait and of the ways in which genes may interact through environmental intermediaries.

Although the individual-based models of Bond and Midgley (1995) and Kerr et al. (1999) for the invasion of flammability revealed interesting niche construction possibilities, they both required that the flammability trait provide some additional fitness benefit in order for it to invade (this benefit can be interpreted as the higher fitness of a trait that only secondarily makes the plant more flammable). It is therefore natural to ask the following question: Must there be explicit fitness benefits to traits that enhance the flammable character of the plant in order for flammability to invade? In this paper, we propose a new hypothesis for the evolution of flammability which suggests the answer to this question is “no.” Our hypothesis lays out conditions by which flammability-enhancing traits might increase within a population despite the obvious fitness disadvantage caused by increased probability of death. We emphasize that, in this hypothesis, no explicit fitness advantage is given to flammable types in order to counter the “self-killing” disadvantage.

How might a trait without a direct fitness benefit invade a population? Within the context of population genetics, the phenomenon of genetic hitchhiking provides one possible answer. If a neutral or slightly deleterious allele is tightly linked to another strongly beneficial allele, then the former allele can increase in frequency by “free-riding” or “hitchhiking” on the success of its associated chromosome resident. It is the association itself that is important and such associations do not necessarily depend upon physical linkage on a chromosome. Indeed, the association might take a more subtle form. In this paper we suggest a process by which spatial structure leads to a genetic association and allows an otherwise deleterious allele to increase in frequency.

The hypothesis

In a changing environment where mating, dispersal and fire-spread are local processes, plants with traits that enhance flammability (probability of igniting and spreading fire) may increase in frequency without any direct fitness benefit of the flammable trait.

The niche-hiking process

Consider a single species of non-sprouting plants in a fire-prone ecosystem. For simplicity, we consider a haploid plant in which the alleles at a single

“flammability locus” determine how likely the plant is to ignite and spread fire. We propose that a flammability allele can increase from a low frequency within this population if the following conditions are satisfied

- (1) Fire spreads from flammable types to their neighbors (flammable and non-flammable).
- (2) Pollen and seed dispersal are local.
- (3) Fire-cleared gaps are colonized by seeds produced before the fire.
- (4) Mortality unrelated to fire (background mortality) is low.
- (5) Seeding fitness is determined by how well alleles at other loci (unlinked to the flammability locus) match a changing optimum.

Note that we do not assume that seedlings with a flammability allele possess any advantage in becoming established in the gap, nor do we assume that there are differences in non-fire-related adult mortality due to the alleles at the flammability locus. Thus, the only direct effect of the flammability allele on the individual possessing it is greatly enhanced mortality due to fire. We label this process of invasion “genetic niche-hiking.” In this case, a seemingly deleterious allele (the flammability allele) invades due to its association with a gap, where seedlings (which have a good chance of carrying the allele) can track a changing environment. This hypothesis combines aspects of both genetic hitchhiking and niche construction. As in cases of hitchhiking, the flammability-enhancing allele invades due to an association (in this case between the presence of the allele and an opportunity to track a changing environment). However, plants with the flammability-enhancing allele demonstrate niche construction in that they are responsible for creating this association by producing the gap.

The simulation model

Consider a species in a fire-prone community with a regular fire-return interval, seedling establishment limited to gaps, and where mortality is highest during seedling recruitment. These assumptions correspond well to many fire-prone shrubland species as well as some serotinous pines and are the primary assumptions of the Bond and Midgley (1995) model. We simplify this system to a model that consists of a population of haploid organisms occupying a spatial square lattice of 150 by 150 cells with toroid geometry. Each cell always contains a single haploid plant that is characterized by two types of genetic information: a single flammability locus with two possible alleles, *T* or *D*, denoting a “torch” or “damp” plant (Bond and Midgley 1995), and a set of fitness loci represented by an array of 25 bits. The fitness of an individual plant will be given by

how well its values in this fitness array match some optimal genotype sequence, that is, a 25 bit target sequence.

Each time step of the simulation begins with the lattice filled with adult plants. The following sequence of events occurs each time step:

- (1) Background mortality occurs randomly.
- (2) Fire occurs.
- (3) Candidate seedlings fill all gaps left by background and fire-induced mortality.
- (4) Viability selection occurs among candidates.

In step (1), each plant is killed with probability d , regardless of genotype, thereby forming a gap. In step (2), both living and dead torches (plants with the *T* allele) combust and burn all neighbors in their burn neighborhood (a square with sides of length $2s_b + 1$ cells centered on the burning torch).

In step (3), four candidate seedlings are created for each gap (gaps produced by background mortality and fire). Both parents are chosen from the population living before the gaps were produced. For each seedling, a mother is first chosen randomly from within the seed dispersal neighborhood of the gap (a square with sides of length $2s_s + 1$ centered on the empty cell), then a father is chosen from within the pollen dispersal neighborhood of the mother (a square with sides of length $2s_p + 1$ centered on the mother cell). We disallow selfing.

A seedling genotype is created by assembling a new genotype from the father and mother genotypes. Assembly begins by choosing a parent at random. The chosen parent’s alleles are copied sequentially until a recombination event occurs, after which the other parent’s alleles are copied until another recombination event occurs, and so on. After copying each parental allele, a recombination event occurs between adjacent loci with probability r (Table 1), giving an effective recombination rate

$$r_e(x) = \frac{\{1 - (1 - 2r)^{x+1}\}}{2}$$

between any two fitness loci with x bits between them (Appendix A). Recombination events are independent of one another. In all simulation runs presented here, the flammability locus is unlinked to the fitness bit array. Only fitness loci mutate, and this is achieved by flipping the bit at a fitness locus (i.e. $0 \rightarrow 1$ or $1 \rightarrow 0$) with probability μ ; this is done as each bit is copied from a parent to its offspring (Table 1).

In step (4), after four candidate seedlings are created, the seedling whose genotype best matches the current optimal genotype sequence (has the lowest Hamming distance, Woodcock and Higgs 1996) is selected as a replacement plant for this cell. Thus, selection in our

Table 1. Model parameters. The “Values explored” column gives the range of parameter values explored. The “Constant value used” column gives the value which was used in all runs in which that parameter was held constant while other parameters were explored.

Symbol	Parameter description	Values explored	Constant value used
r	Recombination rate between adjacent bits	0–0.1, step 0.01 and 0–0.007, step 0.001	0.05
μ	Mutation rate per locus	10^{-8} , 10^{-7} , 10^{-6} , 10^{-5} , 10^{-4}	0.0001
d	Mortality rate per time step	0–0.9 step 0.1	0.1
s_p	Pollen neighborhood	1–4	1
s_s	Seed neighborhood	1–4	1
s_b	Burn neighborhood	1–4	1
E	Environmental change period	1–4	8

model is viability selection on the seedlings. After all replacements are chosen, the empty cells are repopulated synchronously.

The optimal genotype sequence changes over time. This change occurs periodically at a frequency determined by the environmental change period, E . Every E time steps, one randomly chosen bit is flipped in the target sequence.

We explored how the parameters affected the invasion of torches by running replicate sets of simulations. Each simulation started with a population of 22 500 damps (individuals with allele D) with randomly assigned fitness genotypes. This population was allowed to evolve under the set environmental change regime until the mean fitness of the population was relatively stable (less than 1 percent change in mean fitness over 3 consecutive 10-cycle averages). At this point, 0.5 percent of the plants were chosen at random and their flammability allele was changed from D to T . The

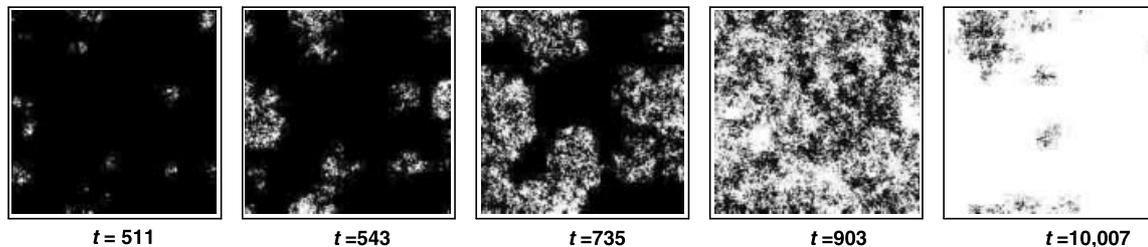
simulation was then continued until the torches either went extinct or a stop criterion was met (less than 1 percent change in relative torch frequency over 3 consecutive 10-cycle averages). Each result section described below is based on 20–50 independent replicate simulation runs for each combination of parameter values. The simulation model was coded in C++ and the code is available from <http://www.schwilk.org/research/data.html>.

Results

Example simulation run

Figure 1 shows the simulation grid at a series of time points during torch invasion. The expanding white patches (Fig. 1a) are the radiating clusters of individuals carrying the T allele. Figure 1b shows the spatial

(a) Spatial distribution of genotypes



(b) Spatial distribution of fitness

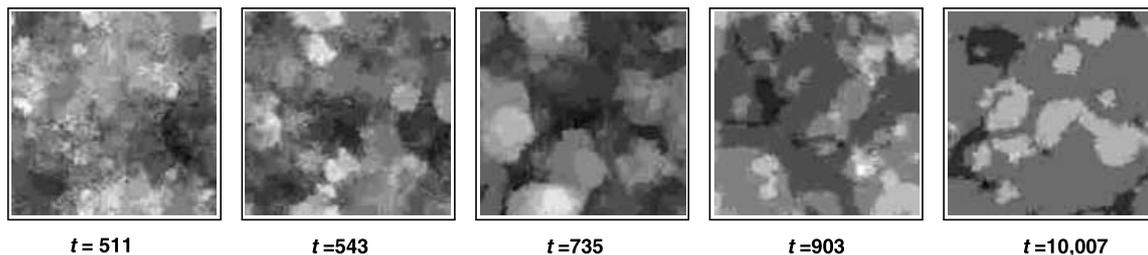
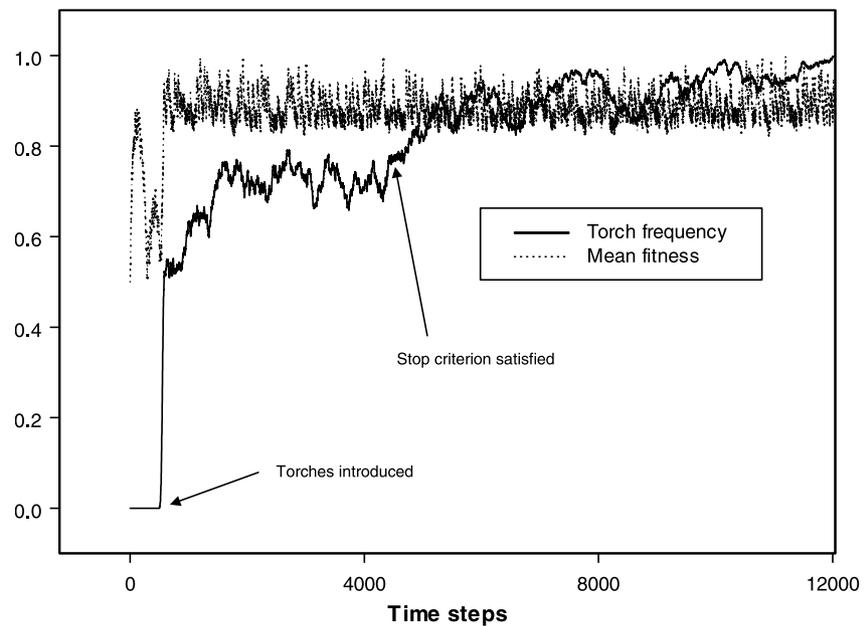


Fig. 1. Figure 1–3 describe the simulation landscape during an example run in which the torches invade. Parameters used for this run were as given in the “constant values used” column of Table 1. Series a shows the distribution of the T allele at four time points during the simulation run. The white squares are torches, dark squares are damps. Series b shows the relative fitness of plants on the simulation landscape at the same set of time steps. Lighter squares have relatively higher fitness. This example was allowed to run beyond the stop criterion used in runs exploring parameter values.

Fig. 2. Torch frequency and mean population fitness over the example simulation run displayed in Fig. 1. An arrow marks the point at which the stop criterion was met.



pattern of plant fitness with lighter shades indicating relatively higher fitness. The first time point ($t = 511$) is soon after the T allele is introduced. Note how torches are clustered and how these torch patches expand over time. At each time point, patches that are predominantly torches also have relatively higher fitness (Fig. 1b).

Figure 2 and 3 show a time series of statistics for this same simulation run. This run was allowed to

continue past the stop criterion used in all later runs. The basic periodicity in the oscillating mean fitness (dotted line) is produced by the change period, E . Throughout the run following T allele introduction, the mean fitness of torches is higher than the mean fitness of damps (Fig. 3). The difference between these mean fitnesses decreases as torch frequency increases, but is maintained over even the final 1000 time steps.

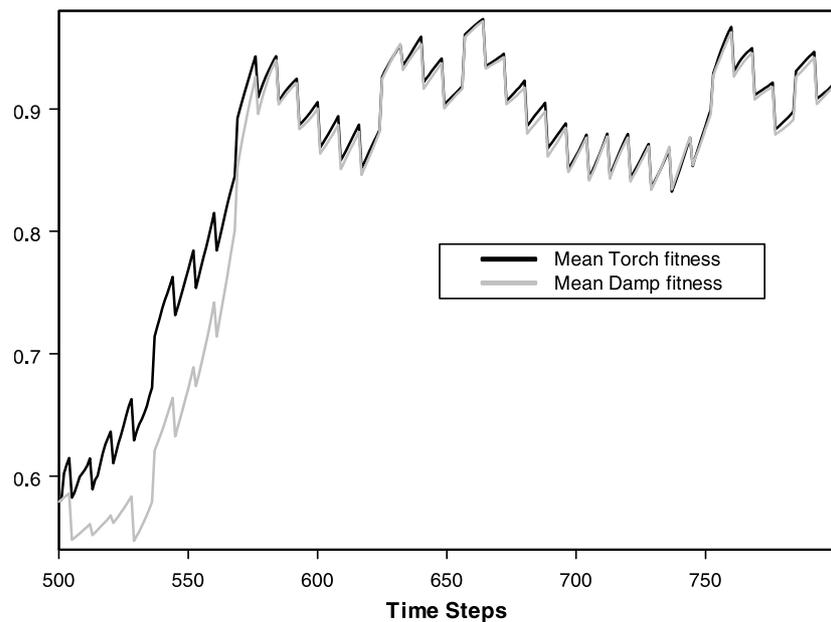


Fig. 3. Mean fitness of torches and damps during the initial period after introduction of the T allele for the example run displayed in Fig. 1 and 2. The slight fitness advantage of torches is maintained throughout the simulation run.

Effect of spatial parameters

Invasion of the *T* allele is highly dependent upon spatial parameters. As seed and pollen dispersal become less local (increasing s_p or s_s), invasion of flammability becomes less likely (Fig. 4). As the burn neighborhood (s_b) increases (Fig. 4a–c), however, the niche construction effect of the flammability allele increases. Although invasion becomes possible over a wider range of pollen and seed dispersal parameters, the frequency of torches when the stop criterion is met decreases with increasing burn neighborhood of each torch (Fig. 4).

Effect of background mortality and environmental change

The frequency of environmental change (determined by E) and the background mortality rate (d) are also important parameters influencing the invasion of the *T* allele (Fig. 5). As background mortality rate increases, torch invasion is possible over a smaller range of environmental change periods. Similarly, as E increases (lower rates of environmental change), torch invasion is possible over a smaller range of background mortality

rates. Thus, more frequent environmental change and lower background mortality promote torch invasion and success.

Effect of mutation and recombination rates

Extremely low mutation rates at the fitness loci or low recombination rates between fitness loci do seem to hamper torch invasion: mutation rate displayed a step effect with invasion only possible at mutation rates above 10^{-6} (unpubl.). Beyond this apparent transition point, increasing mutation rate had a slightly beneficial effect on final frequency of the *T* allele (with other parameters fixed). The effect of recombination rate was less strong with a slight decrease in final torch proportion at a recombination rate of zero. Since all other parameter explorations took place with $r = 0.01$ and $\mu = 10^{-4}$, the results represent runs under relatively high mutation rates, where variation is not limited by mutation or recombination. Although we did not explore population size, the effect of mutation rate is likely dependent upon the number of plants in the simulation and spatial population structure since the relative advantage of younger individuals depends upon

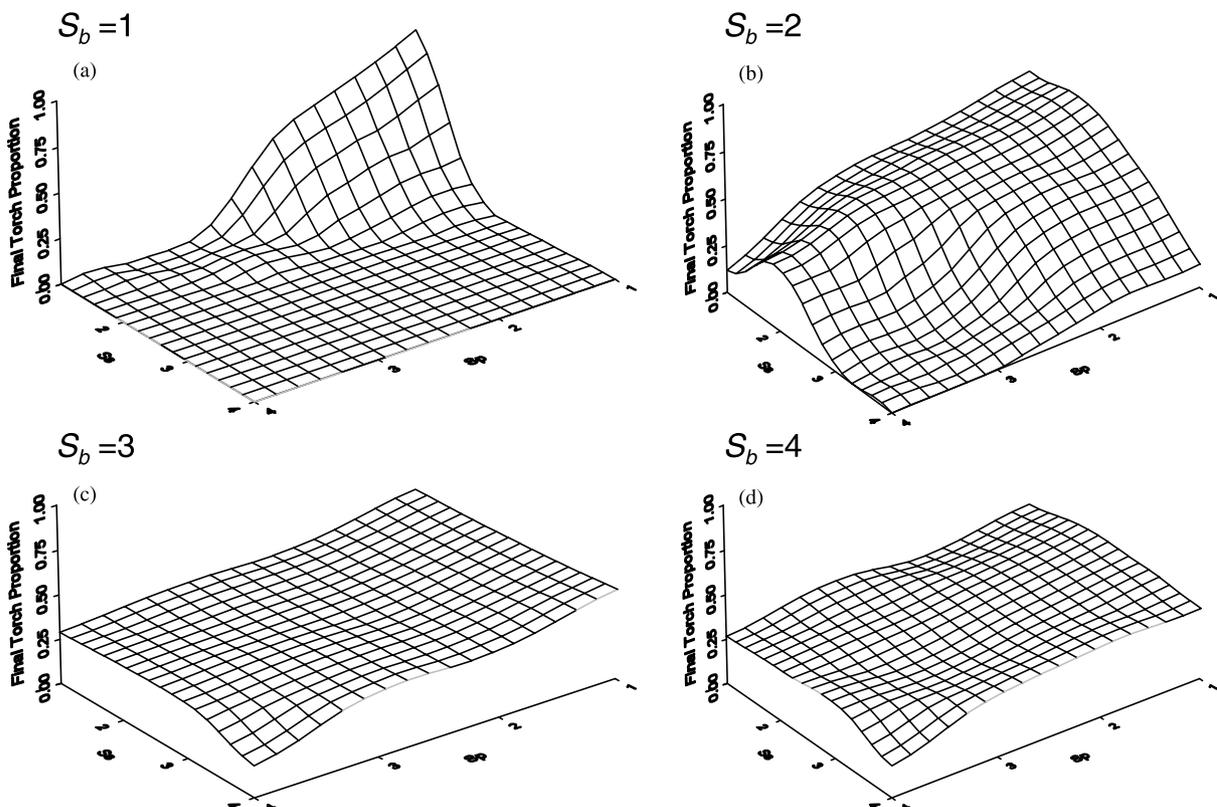
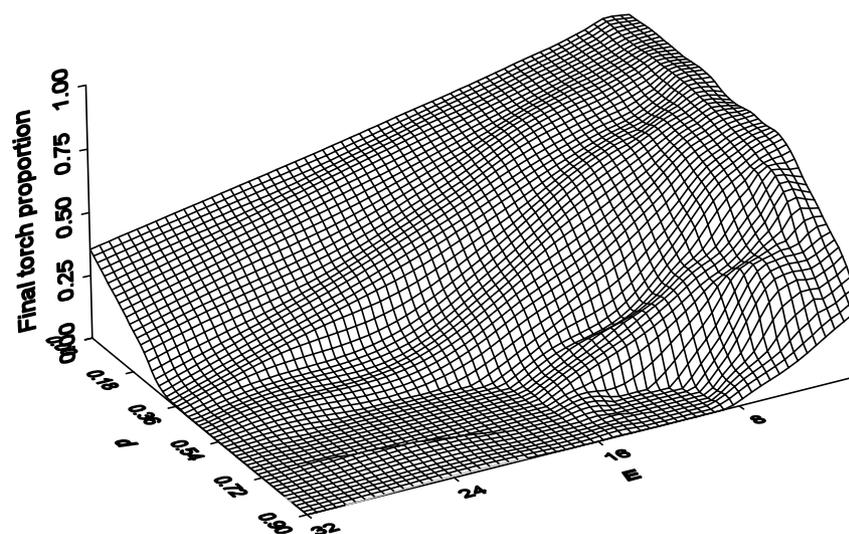


Fig. 4. Spatial parameters. This series of graphs shows the effects of seed (s_s) and pollen (s_p) neighborhoods on the invasion of the torch allele. The z-axis indicates the final proportion of the torch allele. The series of panels shows the effect of increasing the burn neighborhood (s_b). The surfaces result from 15–20 replicate runs for each combination of spatial parameters.

Fig. 5. Exploration of the change period (E) and mortality rate (d) parameters. The x and y-axes are the change period and mortality rate; the z-axis shows the frequency of the torch allele when the stop criterion was satisfied. The surface results from 50 replicate runs for each set of parameter value (5400 runs total).



the availability of novel genotypes as well as recombination.

Effect of temporal autocorrelation in changing environment

The simulation runs described above investigated different change periods E , but in all cases, the environment changed in a positive autocorrelated manner with only one bit in the optimal genotype flipping every E cycles. In another set of simulation runs, the number of bits changed at random was varied along with the change period. A new variable, n , was introduced for this set of runs. Each change period, n bits were chosen at random in the target sequence and were assigned as zero or one with equal probability. This differs from previous runs where a single bit was selected at random and flipped. This allowed us to investigate more thoroughly the importance of the nature of environmental change. When change was frequent (low E), the probability of torch invasion decreased with increasing number of loci changed each period. However, at longer change intervals, n had the opposite affect, with torch invasion becoming more likely and final torch proportions higher when more loci were changed each period (i.e. n increases).

Discussion

Our results demonstrate that a seemingly deleterious allele may invade because of its association with recruitment opportunity in which a changing environment can be tracked. The T allele confers no immediate fitness benefit; on the contrary, its owners die every time step. However, this death is a subversive form of

niche construction. The niche produced by the torch is a localized gap. If the environment is changing, the new occupant of a gap (selected from the entering offspring) will tend to be fitter than the rest of the surviving adult population. Given that torches produce gaps and given that mating and seed dispersal are local processes, individuals filling newly produced gaps in the population have a reasonable chance of possessing the T allele, even when torches are at very low frequencies. Specifically, these new individuals may be the offspring produced by torches before their death. Thus, niche construction allows the torch subpopulation to stay both young and fit. In a changing environment where most fit offspring are likely to come from the youngest parents, torches in effect trade longevity for relative offspring advantage.

We emphasize that the T allele in our model is genetically unlinked to the fitness loci. However, given the above assumptions, it will tend to be associated with the currently fitter genotypes. This occurs due to its enduring association with tracking opportunities, an association for which it is responsible. While genetic hitchhikers rely on chromosomal associations, our genetic niche-hiker simply requires niche construction in a spatially structured population. The primary threats to a would-be genetic hitchhiker are (1) chromosomal recombination, which leads to disruption of the association between the hitchhiker and the beneficial allele and (2) a decrease in the value of the allele associated with the hitchhiker. The analogous threats to our genetic niche-hiker involve (1) either expansion of the distances involved in the processes of mating, dispersal and niche construction, or an increase in non-fire related mortality, each of which disrupts the association between the T allele and the tracking opportunity and (2) an unfavorable pattern of environmental change (which certainly includes environmental stasis). In both cases,

either (1) the association is disrupted or (2) the association is devalued. Thus, our hypothesis of genetic niche-hiking rests on several assumptions. Here, we discuss these assumptions in light of the results of our simulation model as well as the biology of plants in fire-prone regions.

The importance of spatial structure: assumptions 1 and 2

Spatial parameters are important in this niche construction system (Fig. 4). In order for genetic niche-hiking to occur, offspring must have a high probability of experiencing the environment created by their parents. In this case, the environment created is a gap. Plants with the *T* allele provide an opportunity to track the changing environment by producing gaps. If gap production occurs locally (i.e. close to the torch) and if the processes of pollination and seed dispersal are also local, an association will develop between the *T* allele and genotypes better adapted for the continually changing environment. Figure 1 illustrates this association. At times $t = 511, 543$ and 735 , the clusters of torches (Fig. 1a) contain more fit genotypes (Fig. 1b). It is this association that is critical to the *T* allele's success as an invader. Space is very important for the maintenance of this association: in a spatially structured population torches both construct niches and benefit from niche construction.

How reasonable are assumptions 1 and 2 for actual fire-prone vegetation? Assumption 1 states that torches produce gaps locally. Whether plants that seem to possess flammability-enhancing traits do indeed have such local effects is still an open question. We return to this issue below. Assumption 2 states that mating and seed dispersal are local. Gravity dispersed seeds are common in many fire-prone systems. Such seeds have dispersal distributions with modes near the parent plant (Keeley 1991, Whelan et al. 1998). Wind dispersal of seeds or pollen can widen these distributions, but seeds are still likely to be relatively narrowly dispersed around the parent plant (Anderson 1991, Benkman 1995).

The importance of reproductive timing: assumption 3

The assumption that plants produce seeds before fire events is certainly critical. Although we did not explicitly explore violations of this assumption within our model, it is intuitive that if torches burned before reaching reproductive maturity, the *T* allele would become extinct (note that we do not consider mutation-selection balance at this locus). In most fire-prone ecosystems, the period between fires allows plants am-

ple time to either contribute to a soil seedbank or retain seeds on the plant (e.g. serotinous cones in pines). In many cases, the fire event is critical in the germination (e.g. smoke-induced germination for some soil stored seeds) or release (e.g. physical ejection of seeds from serotinous pine cones due to the melting of resin binding the scales of the cone) of seeds produced before the fire. Although it is possible in natural systems for fire to occur before the youngest plants have reached reproductive maturity, our model does not allow this and only considers a minimum time step which restricts fire return intervals to the time needed for plants to produce their first seeds.

The importance of low background mortality: assumption 4

As background (non-fire-related) mortality increases to high levels, recruitment opportunities will occur at many locations in the population. In which case, gaps are no longer concentrated around locales containing the *T* allele. Thus, environmental tracking becomes a cosmopolitan activity, rather than one that exclusively occurs in regions rich with torches. As shown in Fig. 5, torch invasion depends upon the rate of mortality unrelated to fire. As non-fire related recruitment opportunities become more frequent, the relative advantage of possessing the gap-forming *T* allele decays.

In several fire-prone systems, the rate of non-fire related mortality, or stand thinning, does indeed seem to be low among established plants. Our model represents a species in which recruitment is limited to gaps and viability selection takes place during the establishment stage. It is in the gaps where a winning genotype is chosen from a group of contenders. This selection process involves the deaths of the losing seeds/seedlings. However, once a plant has won the space (i.e. established itself) its probability of death is taken to be low despite its genotype. One characteristic of species that inhabit such fire-prone systems is the relative weight of selection during seedling establishment and first-year survival. For many species in fire-prone Mediterranean climate shrublands, for example, most selection takes place during the first summer drought following germination. This is true of California chaparral (Mills 1983, Tyler and D'Antonio 1995, Tyler 1996), South African fynbos (Bond and Stock 1989, Maze and Bond 1996), and Australian *Banksia* woodlands (Lamont and Witowski 1995, Roche et al. 1998).

The importance of the pattern of environmental change: assumption 5

Torch invasion depends upon a relative advantage in tracking the changing environment. High background

mortality can weaken this advantage, as can an environment that is either impossible to track or unnecessary to track. Too rapid a rate of environmental change (large values of n in the “Effect of temporal autocorrelation” section) can inhibit invasion. When change is infrequent and small (E is large, n is small), torches do not invade. Under these parameters, the population of damps can track the environment through recruitment into non-fire gaps during periods between target sequence changes. In this situation, there is no relative advantage to opening local gaps frequently. When change is frequent and large (E is small and n is large), neither damps nor torches can successfully track environmental change and torches experience little relative benefit to compensate for the self-killing disadvantage. In the trivial case at the extreme, when every locus can change every time step, there is no environmental autocorrelation at all and past and present fitness are unrelated.

In our model, flammability acts as an ecologically-mediated generation time modifier. Ecologists studying the distribution of sprouting and non-sprouting taxa have suggested that the shorter generation time of nonsprouters might lead to faster rates of evolution (Wells 1969, Raven 1973). Some results from modifier theory suggest that a changing environment can be important in the evolution of alleles that affect genetic processes such as recombination and mutation. Because recombination and mutation events occur only with recruitment into gaps, the torch subpopulation experiences higher frequencies of these events. Thus the T allele may be viewed as an indirect modifier of these genetic processes. In analogy to our results, models investigating direct modifiers of recombination have shown that a recombination-increasing modifier allele can invade given an ever-changing optimal target at other loci (Maynard Smith 1980, 1988).

Fire ignition and spread

The very simple method of fire ignition and spread we employed in this model is probably unrealistic for many fire-prone systems. For systems such as coniferous forests with distinct crown and ground fire regimes, however, this “spontaneous combustion” ignition may apply to the canopy species that experience crown fire (Bond and Midgley 1995). In such a system, ground fire may occur with some regularity, represented by our time step/minimum maturation time. Although ground fire may occur regularly based on the accumulation of grass and shrub fuels, canopy fire may depend upon some trees having branches that extend into the ground-fire fuel layer. In our model, the ignition of torches can represent the spread from ground to canopy and the ignition of damp from torch represents the spread of fire through the canopy.

The results presented here do not entirely depend upon the arbitrary and highly artificial method of fire spread employed in these simulations. We explored a series of runs in which this spontaneous combustion fire spread method was replaced by a more realistic model and the results are nearly identical. In this alternative model, fire spreads from random ignition sources and then percolates through the population with damps only burning if they are adjacent to a burning torch. Torches burn if they are adjacent to a burning torch or a burning damp. This requires an additional parameter, the per time step ignition probability, but for a wide range of values the results mirror those of the simpler model.

Spatial niche construction

Over the past decade, there has been a growing trend to investigate the effect of spatial structure on population dynamics. Several authors have utilized either lattice-based or continuous-space computer simulations to probe the effects of space. More recently, analytic approximation techniques borrowed from statistical physics have been used for ecological models. These techniques include pair approximation (Iwasa 2000, Sato and Iwasa 2000) and continuous-space moment closure (Levin and Pacala 1997, Bolker et al. 2000, Law and Dieckmann 2000). One reason that spatial structure has been so interesting to theoretical ecologists is that system behavior can dramatically change upon moving from a well-mixed system to a structured system. For instance, spatial structure has been shown to be important to invasion ability of rare types (Iwasa et al. 1998) and coexistence of different types within the system (Durrett and Levin 1997). There has even been empirical demonstration of the importance of structure in microbial systems (Chao and Levin 1981, Rainey and Travisano 1998, Kerr et al. 2002).

Most of the spatially explicit models have explored ecological systems, where the properties of the types tracked do not change over time. However, allowing for evolutionary change within these models can also turn up some interesting results. One such result is the phenomenon of genetic niche-hiking, where the effects of niche construction are disproportionately experienced due to the spatial structure within an evolving population. Such spatial structure places the niche constructing allele near the effects of the construction. Our model explores the hypothesis that flammable traits in fire-prone vegetation are niche-hikers.

Fire ecologists have long been interested in the spatial heterogeneity of fire's effects. This interest has largely been focused on the differential behavior of vegetation types as for use in modeling the fire hazard of different communities (Philpot 1977). One potential criticism of our model is that flammability is best

construed as an emergent property of an entire community (Troumbis and Trabaud 1989) with individual plant traits having little local effect. However, post-fire community patterns have been attributed to spatial variation in fire-intensity (Rice 1993, Schwilk et al. 1997, Odion and Davis 2000). Local fire characteristics can produce differing post-fire microhabitats. The extent to which the traits of individual plants influence this heterogeneity is still an open question. In our model, traits that enhance flammability can niche-hike if their effects are local. Many fire-prone systems contain species with traits that may influence fire behavior (such as retention of dead branches, possession of volatile compounds, high surface area to volume ratios). Ongoing experimental work (Schwilk, unpubl.) examines the influence of individual plant traits on fire intensity to determine if these traits do, in fact, have effects at local scales.

Genetic niche-hiking: predictions and generalizations

Comparative tests of distinct lineages may provide one way to test some of the predictions of this model. The genetic niche-hiking process depends upon spatial population structure and would therefore predict increased flammability as more likely among species with limited dispersal and gene flow.

The environmental change period, E , is the parameter most difficult to relate to empirically measured values. If this changing environment is climate change, for example, then the evolutionary meaningful parameter is the rate of change in fitness caused by a change in an environmental variable such as temperature. Population migration in response to climate change will complicate the relationship between climate change and changing fitness, however. A difficult but conceivable test of the niche-hiking process would be a comparative analysis of flammability in relation to predicted past rates of climate change among geographical distinct lineages.

The genetic niche-hiking process may apply to ecological scenarios other than the evolution of flammability. Consider a trait that causes death of its possessor after reproduction but simultaneously results in the death of neighbors. Given a changing environment and spatial population structure, this seemingly deleterious trait can increase through niche-hiking. Genetic niche-hiking seems especially applicable to plants given their sessile nature as well as occurrence of seed storage which enables recruitment after the parent's death. For example, traits potentially subject to niche-hiking may include disease susceptibility and plant characteristics leading to tree-fall gaps.

Plant-pathogen interactions can exhibit strong spatial patterns (Real and McElhany 1996) and genetic vari-

ability in resistance traits is well documented (Parker 1986, Burdon and Jarosz 1988, Jarosz and Burdon 1988, Heath 1991). If dose or vector density is important to pathogen spread and host mortality, then the evolution of susceptibility may be subject to a niche-hiking process similar to that proposed for plant flammability. Similarly, forest gap-dynamics may create conditions for genetic niche-hiking. Among tree species that require forest gaps for recruitment, both gap producing and non-gap producing species exist (Shugart 1997). If tree-fall causes the mortality of neighboring trees, then it is conceivable that niche-hiking effects may influence the evolution of gap-producing traits. Similarly, if palatable grasses attract herbivores which increase mortality of the palatable types and their neighbors, selection for increased palatability is analogous to selection for increased flammability through this "niche-hiking" process.

Flammability in this model is an instance of altruism. Previous empirical and theoretical investigations have emphasized the importance of spatial population structure for the invasion of traits similar to flammability (e.g. colicinogeny in *E. coli*, Chao and Levin 1981, Iwasa et al. 1998). Our model for the evolution of flammability depends upon the indirect benefit to the flammability-increasing T allele provided by more rapid tracking of environmental change. The benefit provided by the altruistic type, however, may be more direct. In general, the term "genetic niche-hiking" may be a useful description of systems in which spatial population structure facilitates the invasion of an altruistic niche-construction trait.

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References

- Anderson, M. 1991. Mechanistic models for the seed shadows of wind-dispersed plants. – *Am. Nat.* 137: 476–497.
- Baldwin, I., Stasak-Kozinski, L. and Davidson, R. 1994. Up in smoke. I. Smoke-derived germination cues for postfire annual *Nicotiana attenuata* Torr. ex. Watson. – *J. Chem. Ecol.* 20: 2303–2345.
- Bell, T. L. and Pate, J. S. 1996. Growth and fire response of selected Epacridaceae of south-western Australia. – *Aust. J. Bot.* 44: 509–526.
- Bellingham, P. J. 2000. Resprouting as a life history strategy in woody plant communities. – *Oikos* 89: 409–416.
- Benkman, C. W. 1995. Wind dispersal capacity of pine seeds and the evolution of different seed dispersal modes in pines. – *Oikos* 73: 221–224.
- Bolker, B. M., Pacala, S. W. and Levin, S. A. 2000. Moment methods for ecological processes in continuous space. – In: Dieckmann, U., Law, R. and Metz, J. A. (eds), *The geometry of ecological interactions: simplifying spatial complexity*. Cambridge Univ. Press, pp. 388–410.

- Bond, W. J. and Midgley, J. J. 1995. Kill thy neighbour: an individualistic argument for the evolution of flammability. – *Oikos* 73: 79–85.
- Bond, W. J. and Stock, W. D. 1989. The costs of leaving home: ants disperse myrmecochorous seeds to low nutrient sites. – *Oecologia* (Heidelberg) 81: 412–417.
- Burdon, J. J. and Jarosz, A. M. 1988. The ecological genetics of plant pathogen interactions in natural communities. – *Philos. Trans. R. Soc. Lond. Ser. B – Biol. Sci.* 321: 349–363.
- Chao, L. and Levin, B. R. 1981. Structured habitats and the evolution of anticompensator toxins in bacteria. – *Proc. Nat. Acad. Sci. USA – Biol. Sci.* 78: 6324–6328.
- Christiansen, N. L. and Muller, C. H. 1975. Relative importance of factors controlling germination and seedling survival in *Adenostoma* chaparral. – *Am. Midl. Nat.* 93: 71–78.
- Durrett, R. and Levin, S. 1997. Allelopathy in spatially distributed populations. – *J. Theoret. Biol.* 185: 165–171.
- Enright, N. J. and Goldblum, D. 1999. Demography of a non-sprouting and resprouting *Hakea* species (Proteaceae) in fire-prone *Eucalyptus* woodlands of southeastern Australia in relation to stand age; drought and disease. – *Plant Ecol.* 144: 71–82.
- Haidinger, T. L. and Keeley, J. E. 1993. Role of high fire frequency in destruction of mixed chaparral. – *Madroo* 40: 141–147.
- Heath, M. C. 1991. Evolution of resistance to fungal parasitism in natural ecosystems. – *New Phytol.* 119: 331–343.
- Iwasa, Y. 2000. Lattice models and pair approximation in ecology. – In: Dieckmann, U., Law, R. and Metz, J. A. (eds), *The geometry of ecological interactions: simplifying spatial complexity*. Cambridge Univ. Press, pp. 227–251.
- Iwasa, Y., Nakamaru, M. and Levin, S. A. 1998. Allelopathy of bacteria in a lattice population: competition between colicin-sensitive and colicin-producing strains. – *Evol. Ecol.* 12: 785–802.
- Jackson, J. F., Adams, D. C. and Jackson, U. B. 1999. Allometry of constitutive defense: a model and a comparative test with tree bark and fire regime. – *Am. Nat.* 153: 614–632.
- Jarosz, A. M. and Burdon, J. J. 1988. The effect of small-scale environmental-changes on disease incidence and severity in a natural plant-pathogen interaction. – *Oecologia* 75: 278–281.
- Keeley, J., Morton, B., Pedrosa, A. and Trotter, P. 1985. Role of allelopathy, heat and charred wood in the germination of chaparral herbs and suffrutescents. – *J. Ecol.* 73: 445–458.
- Keeley, J. E. 1991. Seed germination and life history syndromes in the California chaparral. – *Bot. Rev.* 57: 81–116.
- Keeley, J. E. 1992. Demographic structure of California chaparral in the long-term absence of fire. – *J. Veg. Sci.* 3: 79–90.
- Keeley, J. E. and Bond, W. J. 1997. Convergent seed germination in South African fynbos and Californian chaparral. – *Plant Ecol.* 133: 153–167.
- Keeley, J. E. and Fotheringham, C. 1997. Trace gas emissions and smoke-induced seed germination. – *Science* 276: 1248–1250.
- Keeley, J. E. and Zedler, P. H. 1998. Evolution of life histories in pines. – In: Richardson, D. and Cowling, R. (eds), *Ecology and biogeography of Pinus*. Cambridge Univ. Press, pp. 220–248.
- Kerr, B., Schwilk, D. W., Bergman, A. and Feldman, M. W. 1999. Rekindling an old flame: a haploid model for the evolution and impact of flammability in resprouting plants. – *Evol. Ecol. Res.* 1: 807–833.
- Kerr, B., Riley, M. A., Feldman, M. W. and Bohannan, B. 2002. Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. – *Nature* 418: 171–174.
- Laland, K. N., Odling-Smee, F. J. and Feldman, M. W. 1996. The evolutionary consequences of niche construction: a theoretical investigation using two-locus theory. – *J. Evol. Biol.* 9: 293–316.
- Laland, K. N., Odling-Smee, F. J. and Feldman, M. W. 1999. Evolutionary consequences of niche construction and their implications for ecology. – *Proc. Nat. Acad. Sci. USA* 96: 10242–10247.
- Lamont, B. B., Maitre, D. L., Cowling, R. and Enright, N. 1991. Canopy seed storage in woody plants. – *Bot. Rev.* 57: 277–317.
- Lamont, B. B. and Witowski, E. T. F. 1995. A test for lottery recruitment among four *Banksia* species based on their demography and biological attributes. – *Oecologia* 101: 299–308.
- Law, R. and Dieckmann, U. 2000. Moment approximations of individual-based models. – In: Dieckmann, U., Law, R. and Metz, J. A. (eds), *The geometry of ecological interactions: simplifying spatial complexity*. Cambridge Univ. Press, pp. 252–270.
- Levin, S. A. and Pacala, S. W. 1997. Theories of simplification and scaling of spatially distributed processes. – In: Tilman, D. and Kareiva, P. (eds), *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton Univ. Press, pp. 271–295.
- Lewontin, R. C. 1983. The organism as the subject and object of evolution. – *Scientia* 118: 65–82.
- Lopez-Soria, L. and Castell, C. 1992. Comparative genet survival after fire in woody Mediterranean species. – *Oecologia* 91: 493–499.
- Maynard Smith, J. 1980. Selection for recombination in a polygenic model. – *Genet. Res.* 35: 269–277.
- Maynard Smith, J. 1988. Selection for recombination in a polygenic model: the mechanism. – *Genet. Res.* 51: 59–63.
- Maze, K. E. and Bond, W. J. 1996. Are *Protea* populations seed limited? Implications for wildflower harvesting in Cape fynbos. – *Aust. J. Ecol.* 21: 96–105.
- Mills, J. N. 1983. Herbivory and seedling establishment in post-fire California chaparral. – *Oecologia* 60: 267–270.
- Moreno, J. M. and Oechel, W. C. 1993. Demography of *Adenostoma fasciculatum* after fires of different intensities in southern California chaparral. – *Oecologia* 96: 95–101.
- Mutch, R. W. 1970. Wildland fires and ecosystems – a hypothesis. – *Ecology* 51: 1046–1051.
- Odion, D. C. and Davis, F. W. 2000. Fire, soil heating, and the formation of vegetation patterns in chaparral. – *Ecol. Monogr.* 70: 149–169.
- Odling-Smee, F. J., Laland, K. N. and Feldman, M. W. 1996. Niche construction. – *Am. Nat.* 147: 641–648.
- Papio, C. and Trabaud, L. 1991. Comparative study of the arial structure of five shrubs of Mediterranean shrublands. – *For. Sci.* 37: 146–159.
- Parker, M. A. 1986. Individual variation in pathogen attack and differential reproductive success in the annual legume; *Amphicarpaea bracteata*. – *Oecologia* 69: 253–259.
- Philpot, C. 1977. Vegetative features as determinants of fire frequency and intensity. – In: Mooney, H. and Conrad, C. (eds), *Proc. Symp. Environ. Consequences of Fire and Fuel Manage. in Mediterranean Ecosystems*. USDA Forest Service Technical Report WO-3.
- Rainey, P. B. and Travisano, M. 1998. Adaptive radiation in a heterogeneous environment. – *Nature* 394: 69–72.
- Raven, P. 1973. The evolution of the mediterranean floras. – In: diCasti, F. and Mooney, H. (eds), *Mediterranean-type ecosystems: origin and structure*, volume 7 of *Ecological Studies*. Springer-Verlag, pp. 213–224.
- Real, L. A. and McElhany, P. 1996. Spatial pattern and process in plant–pathogen interactions. – *Ecology* 77: 1011–1025.
- Rice, S. K. 1993. Vegetation establishment in postfire *Adenostoma* chaparral in relation to fine-scale pattern in fire intensity and soil nutrients. – *J. Veg. Sci.* 4: 115–124.

- Roche, S., Dixon, K. W. and Pate, J. S. 1998. For everything a season: smoke-induced seed-germination and seedling recruitment in a Western Australian *Banksia* woodland. – *Aust. J. Ecol.* 23: 111–120.
- Rothermel, R. 1972. A mathematical model for predicting fire spread in wildland fuels. For. Serv. Res. Paper INT-115, USDA.
- Rundel, P. 1981. Structural and chemical components of flammability. – In: Mooney, H., Bonnicksen, T., Christensen, K. et al. (eds), Proc. Conf. Fire Regimes and Ecosystem Properties. USDA For. Serv. General Tech. Rep. WO-86, pp. 183–207.
- Sato, K. and Iwasa, Y. 2000. Pair approximations for lattice-based ecological models. – In: Dieckmann, U., Law, R. and Metz, J. A. (eds), The geometry of ecological interactions: simplifying spatial complexity. Cambridge Univ. Press, pp. 341–358.
- Schwilk, D. W. and Ackerly, D. D. 2001. Flammability and serotiny as strategies: correlated evolution in pines. – *Oikos* 94: 326–336.
- Schwilk, D. W., Keeley, J. E. and Bond, W. J. 1997. The intermediate disturbance hypothesis does not explain fire and diversity pattern in fynbos. – *Plant Ecol.* 132: 77–84.
- Shugart, H. 1997. Plant and ecosystem functional types. – In: Smith, T., Shugart, H. and Woodward, F. (eds), Plant functional types: their relevance to ecosystem properties and global change. Cambridge Univ. Press, pp. 20–43.
- Snyder, J. R. 1984. The role of fire: mutch ado about nothing? – *Oikos* 43: 404–405.
- Troumbis, A. S. and Trabaud, L. 1989. Some questions about flammability in fire ecology. – *Acta Oecologica – Oecologia Plant.* 10: 167–175.
- Tyler, C. M. 1996. Relative importance of factors contributing to postfire seedling establishment in maritime chaparral. – *Ecology* 77: 2182–2195.
- Tyler, C. M. and D'Antonio, C. M. 1995. The effects of neighbors on the growth and survival of shrub seedlings following fire. – *Oecologia* 102: 255–264.
- van Wilgen, B. W., Higgins, K. and Bellstedt, D. 1990. The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. – *J. Ecol.* 78: 210–222.
- Wells, P. V. 1969. The relation between mode of regeneration and extent of speciation in woody genera of the California chaparral. – *Evolution* 23: 264–267.
- Went, F. W., Juhren, G. and Juhren, M. 1952. Fire and biotic factors affecting germination. – *Ecology* 33: 351–364.
- Whelan, R. J., Dejong, N. H. and Vonderburg, S. 1998. Variation in bradyspory and seedling recruitment without fire among populations of *Banksia serrata* (Proteaceae). – *Aust. J. Ecol.* 23: 121–128.
- Williamson, G. and Black, E. 1981. High temperature of forest fires under pines as a selective advantage over oaks. – *Nature* 293: 643–644.
- Woodcock, G. and Higgs, P. G. 1996. Population evolution on a multiplicative single-peak fitness landscape. – *J. Theoret. Biol.* 179: 61–73.

Appendix A

Effective rate of recombination

Our fitness array was comprised of 25 bits in sequence. Here we label this array as follows: $L_1, L_2, L_3, \dots, L_{25}$. In this appendix, we derive the effective rate of recombination between any two fitness loci, say L_i and L_j , given that the probability of recombination between any two adjacent loci is r ($0 \leq r \leq 0.5$). If L_i and L_j have x loci in between them ($x \geq 0$), then there are $x + 1$ positions in which a crossover event may occur. A crossover event occurs with probability r at each position. A recombination event occurs if there are an odd number of crossovers in the $x + 1$ positions between them. Assuming that crossovers at different positions occur independently, the probability of a recombination event between L_i and L_j is given as follows:

$$r_e(x) = \begin{cases} \sum_{k=1}^{(x/2)+1} \binom{x+1}{2k-1} r^{2k-1} (1-r)^{x+2-2k} & \text{if } x \text{ even} \\ \sum_{k=1}^{(x+1)/2} \binom{x+1}{2k-1} r^{2k-1} (1-r)^{x+2-2k} & \text{if } x \text{ odd} \end{cases}$$

The sums on the right-hand sides are the odd terms of the binomial expansion of

$$(r + (1-r))^{x+1}$$

Another way to write the above is

$$r_e(x) = 1 - \frac{(r + (1-r))^{x+1} + (-r + (1-r))^{x+1}}{2} = \frac{1 - (1-2r)^{x+1}}{2}$$

If $x = 0$, then $r_e(x) = r$. That is, if there are no loci in between L_i and L_j ($j = i + 1$), then the probability of recombination between these adjacent loci is just r . And we have

$$0 \leq r_e(x) \leq 0.5 \text{ for all } x \geq 0.$$