Supporting Information

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SI Text

Simulation Description and Sensitivity Analysis

Model Description. The central structure of the model was a modification of the Ricker model, a discrete-time density-dependent population model (1). At each annual time step, the model tracked three state variables: the density of serotinous ($n_{s,t}$) and nonserotinous ($n_{n,t}$) individuals (and, by extension, the total population size: $N_t \equiv n_{s,t} + n_{n,t}$), and the current stand age (a_t). Serotinous individuals produced and accumulated seeds, with dispersal allowed only immediately following a fire, whereas nonserotinous individuals dispersed seeds during each time step. We assumed that both phenotypes had identical mortality and seed production rates. We modeled serotiny as a single-locus haploid trait. Although this is certainly an unrealistic assumption (2, 3), we chose this method for simplicity and computational efficiency. For deterministic scenarios, we analyzed the relative fitness of serotiny after a single generation of selection. For stochastic scenarios, we present the means of 1,000 model runs (of 2,000 model-years each) at each parameter combination. Because the frequency of serotiny varies with stand age (as nonserotinous trees fill in gaps and adult trees die), we analyzed the frequency of serotiny at a constant stand age of 100 y. A complete list of state variables and parameters, along with the results of parameterization, is available in Table S2.

Population Dynamics. Population dynamics varied depending on whether a stand was mature (i.e., stands where self-thinning had ceased; $a_t < a_{mature}$, the age at maturity, estimated at 200 y from ref. 4) or immature. For immature stands, we modified the Ricker model:

$$n_{s,t+1} = n_{s,t}e^{\rho\left(1 - \frac{N_t}{K(a_t)}\right)}; \quad 0 < a_t < a_{mature}, \quad \text{[S1]}$$

where ρ is the population growth rate and K is the self-thinning function, representing the carrying capacity for a given stand age. We used an identical corresponding equation for nonserotinous individuals ($N_{n,t+1}$). We lacked specific literature values for ρ. Therefore, we used preliminary model runs to tune this parameter, using infilling time as a relatively independent criterion for tuning. Literature estimates suggest that stands that are sparse at initiation reach high density in ~50 y (5, 6). We selected $\rho = 0.05$ as a value that replicated this behavior (stands achieved >60% of maximal density in 50 y). We discuss the implications of this tuning further in the section on sensitivity analysis. Finally, empirical data show that lodgepole pine continues to establish for several decades following fires (5, 6), and some of this establishment is likely due to seeds released from immature trees that are genetically serotinous but produce open cones at a young age (2, 7). Lotan and Perry (8) speculated that cone opening by immature serotinous trees is an adaptive trait that allows serotinous trees to contribute to ongoing postfire recovery in stands where initial recovery was sparse. Therefore, for stands younger than 30 y old, we assumed infill trees were serotinous or nonserotinous in proportion to the existing population. Once the stand aged beyond 30 y, we assumed serotinous trees produced closed cones and all infilling trees were from nonserotinous parents.

Carrying capacity was determined using a self-thinning curve where maximum stand density declined as a function of age using a power rule (9):

$$\log K(a) = \beta_0 + \beta_1 \log a, \quad \text{[S2]}$$

where β_0 and β_1 are parameters fit from empirical data. For self-thinning, density is generally predicted as a function of tree size; here, for simplicity we assumed that individual size increases with stand age, and modeled density directly as a function of stand age. We fit the parameters of this model directly using empirical data (10) ($n = 4$, stands ranging from 12 to 250 y old, $R^2 = 0.997$). Our empirically estimated slope of -1.39 is similar to the -1.5 slope of Yoda's law (9), suggesting that the assumption that size scales with age is plausible.

For mature stands, we assumed the population was stable (i.e., all dead individuals were immediately replaced), with an annual deterministic mortality rate μ. We assumed annual turnover of 0.5% based on mortality rates for conifers in the region (11). Because we lacked information on the variance in mortality rates, and mortality rates in *Pinus* may be as high as 2% (11), we varied this parameter from 0.5% to 2% during sensitivity analysis.

Fire and Postfire Recovery. We used both deterministic and stochastic processes to govern fire occurrence. In both cases, fire occurrence was controlled by a single parameter F, the fire return interval in years. We used deterministic simulations to examine the relative fitness of serotiny under varying fire and predation rates (e.g., Fig. 2 in main text). For these simulations, a fire was initiated every F years. We used stochastic simulations to examine how model predictions about the frequency of serotiny compared with empirical results (Figs. 3 and 4 in main text). For these simulations, fires were initiated randomly with an annual probability of $1/F$. For all simulations, fires killed all individuals, triggered the release of stored serotinous seeds, and initiated the postfire recovery phase of the model. Fire was allowed in all stands exceeding 100 y old (12). We varied F from 100 to 400 y in simulations, based on published estimates of 135–185 y for low elevations and 280–310 y for high elevations within the Greater Yellowstone Ecosystem (GYE) (13).

We modeled postfire seedling density as a function of the prefire size of the canopy seed bank, s_t, given immigration rate (γ_0) and seedling density (γ_1) parameters (13–16):

$$\begin{aligned} \log n_{n,t} &= \gamma_0, \\ \log n_{s,t} &= \gamma_1 s_{t-1}, \end{aligned} \quad a_t = 0. \quad \text{[S3]}$$

Because we lacked data on necessary processes (e.g., seed production, dispersal, and germination rates), we treated s_t as a latent variable determined by population density ($n_{s,t}$, $n_{n,t}$) and the seed predation rate (see below). This allowed us to parameterize the relationship using available data.

Seed Predation. We modeled seed predation as a proportional reduction in the size of the canopy seed bank (for serotinous individuals) or a reduction in the rate of infilling (for nonserotinous individuals). Empirical data show that the size of the canopy seed bank (represented by the prefire frequency of serotiny) strongly predicts postfire stand density (16, 17). Our model assumes that rates of seed predation measured for individual trees translates to a stand-level reduction in the canopy seed bank. Thus:

$$s_t = (1 - \pi_s)s_{max}\frac{n_s}{K(a_t)}, \quad \text{[S4]}$$

where π_s is the predation rate of cones on serotinous trees, s_{max} is the maximal size of the accumulated seed bank (i.e., when the

population is saturated and nonpredation seed losses are balanced by seed production), and $n_{s,t}/K(a_t)$ is the ratio of the current serotinous population size to the maximal population size (thus normalizing the seed bank to the number of individuals available to produce seeds). Because we lacked the data to express s_t and s_{max} in terms of individual seeds, we instead abstracted away processes of germination and seed dispersal, and expressed these quantities in terms of seedlings. We were then able to parameterize this relationship using data relating postfire seedling density to the frequency of serotiny [i.e., $n_{s,t}/K(a_t)$ assuming the population is at carrying capacity]. We built a regression model using data from refs. 16 and 17 to parameterize Eq. S3 using the relationship in Eq. S4, assuming the intercept (i.e., the number of seedlings predicted when no trees were serotinous) represented immigration of nonserotinous seeds dispersed from outside the focal (burned) stand. Because the sites for the source data were chosen without regard to squirrel density or seed predation (16, 17), we set π_s to the median predation rate observed in the present study for the purposes of parameterization, recognizing that this results in unexplained variance (due to predation rates varying among sites) but that the mean predictions will be unbiased assuming sites were selected without bias in the original study. Finally, we used the data in the main text of this paper to relate the predation rates (π_s, π_n) to squirrel density, and then varied squirrel density systematically across a range of realistic values for the GYE (18) to determine the effects of predation on selection on serotiny.

Seed Dispersal and Recruitment. The number of seeds dispersed and the contribution to the new class of seedlings in each model year depended on stand age, frequency of serotiny, and whether a fire occurred. In nonfire years, all seeds produced and not eaten by squirrels either entered the canopy seed bank or were immediately dispersed. For young stands (see *Population Dynamics* above), both serotinous and nonserotinous seeds were dispersed, whereas in all other stands all serotinous seeds entered the canopy seed bank. In fire years, seeds were dispersed as in nonfire years, but in addition all seeds in the canopy seed bank were also dispersed. Finally, dispersed seeds were converted into new individuals based on the number of new individuals predicted by the population model, with serotinous and nonserotinous individuals recruiting in proportion to their representation in the dispersed seed cohort. All extra seeds not recruited were lost (i.e., there was no soil seed bank).

Model Evaluation. We first ran the model with deterministic parameters to directly assess how variation in fire frequency and squirrel density affected the fitness of serotinous trees. To do this, we calculated the per-generation population growth rate for both genotypes (λ_s and λ_n for serotinous and nonserotinous trees, respectively), and then calculated the relative fitness of serotinous trees as λ_s/λ_n. To assess how these fitness differences might translate to observed frequencies of serotiny in real stands, where average fire regimes are known but exact fire intervals are variable, we used stochastic disturbances and varied fire probability and squirrel density. We ran 1,000 simulations at each parameter combination, and report the observed frequency of serotiny in 100-y-old stands (chosen to provide a fixed point for comparison of all model runs) after 2,000 y of simulation. For validation, we compared the model predictions with empirical results from our previous work (18).

Sensitivity Analysis. Model sensitivity was assessed by altering parameters one at a time and inspecting the effect of these perturbations on the relationship between the predicted frequency of serotiny and both fire frequency and the seed predation rate for stochastic scenarios. We evaluated sensitivity under two conditions: variable fire probability (ranging from 0.0025 to 0.01

and corresponding to expected intervals of 100–400 y, as in the main model runs) with no seed predation (i.e., squirrel density = 0), and variable squirrel density (range: 0–2.1 individuals per ha) with fire probability held constant at 0.00625 [i.e., expected 160-y intervals, approximating fire frequency at low elevations in the GYE (13)]. Under each of these conditions, we altered parameter values one at a time. For parameters lacking SE estimates (population growth rate and mortality rate), we chose four to five values from the ranges given in Table S2. For all other parameters, we chose values ranging from −2 to +2 SEs relative to the mean in increments of one-half the SE. Each combination was evaluated over 1,000 separate model runs as in the main analysis.

SI Results

Population Growth Rate. The model was sensitive to the population growth rate r, but only when the growth rate was very low (Fig. S2). When the growth rate was 0.01, serotiny was much more strongly favored than under the default, even at low fire frequency. Further exploration of low values of ρ ($0.01 \leq \rho \leq 0.1$) revealed a threshold of approximately $\rho = 0.03$; below this value, serotiny is favored at increasing rates. However, growth rates this slow also produced unrealistic estimates of infilling rates (e.g., >100 y to reach mature densities), suggesting that these values are not plausible (5, 6). At values higher than the default, population growth rate had little effect on the frequency of serotiny, with no change in the model predictions when $\rho \geq 0.11$.

Low growth rates favoring serotiny is unsurprising given the structure of our model. This parameter controls the rate at which nonserotinous seedlings fill in stands with sparse postfire recovery. Very low growth rates result in incomplete infilling, resulting in less competition for serotinous seedlings that established immediately after a fire and ultimately resulting in higher frequencies of serotiny in mature stands. The lack of sensitivity at high growth rates is likely the result of complete saturation of sparse stands with nonserotinous seedlings; beyond this saturation point, increasing the growth rate has no effect on postfire stand composition. However, our default value of $\rho = 0.05$ is close to a threshold, below which the model becomes highly sensitive to growth rate. If actual growth rates in lodgepole pine are lower than what we have used, then the predictions of our model may be poor. MacDonald and Cwynar (19) reported on doubling times in lodgepole pine populations undergoing postglacial expansion; the fastest-expanding population in their study had a population growth rate of 0.009, and the mean of all populations was 0.001, substantially lower than our default. However, our model simulates a burned stand in a connected forest, where competition is minimal, the climate is suitable, soil is mature (i.e., not postglacial), and seed sources from surviving trees and nearby stands are present. It is likely that growth rates under these conditions will be significantly greater than at the leading edge of population expansion that likely would be slowed by dispersal limitation, suboptimal climatic conditions, poorly developed soil, and competition with existing vegetation types.

Self-Thinning. The model showed little sensitivity to the self-thinning curve (β_0 and β_1). In the absence of seed predation, neither parameter had an effect on model predictions. When squirrel densities were varied, we observed some sensitivity to the self thinning curve at low to moderate squirrel densities (~0.7–1.5 individuals per ha for β_0, 0.0–0.5 individuals per ha for β_1). At these densities, a large increase (2 SEs) in either the intercept (indicating higher densities at stand initiation) or the slope (indicating slower thinning over time) resulted in a decrease of as much as 30% in the predicted frequency of serotiny (Figs. S3 and S4).

Mortality Rate. Mortality rates above the rate of 0.005 used as our model default resulted in large decreases in the predicted frequency of serotiny (Fig. S5). The effect was greatest when examining the relationship between seed predation rate and the frequency of serotiny; a doubling of the mortality rate from 0.005 to 0.01 resulted in very low (<20%) serotiny at all squirrel densities. Increased mortality in adult stands results in increased turnover, allowing nonserotinous trees to replace dead trees more rapidly and resulting in unfavorable conditions for serotiny. We used mortality rates from ref. 11, which reported an increase in mortality rates for the genus *Pinus* in western North America since 1960 from ~0.0025 to 0.02. It is likely that contemporary patterns in serotiny reflect more the historical mortality rate than rates that have increased over the past several decades. Thus, our default value may somewhat underestimate the relative fitness of serotinous trees in historical stands. However, if increased mortality rates in mature stands are the new norm in lodgepole pine forests, serotiny may become increasingly disfavored, and mortality rates (or, more generally, nonfire disturbance rates) may be an underappreciated factor influencing the evolutionary dynamics of serotiny.

Postfire Stand Density. The curve relating prefire serotiny to postfire stand density has two parameters: the immigration rate γ_0 and the slope γ_1. The model was moderately sensitive to immigration rate, with an increase of 1 SE resulting in a decline in serotiny of ~15% (Fig. S6). Because the model assumes that immigration is only from nonserotinous trees, it is expected that increasing this rate will favor nonserotinous trees. In actual stands, pollen dispersal in nonfire years, quantitative inheritance and incomplete heritability (3), and postfire dispersal of serotinous seeds from surrounding stands are likely to contribute serotinous individuals as well. Incorporating these dynamics into the model would likely decrease the sensitivity of the model to immigration rate. The model was less sensitive to changes in the slope of the postfire stand density curve (Fig. S7), with changes in the frequency of serotiny of less than 5% per SE.

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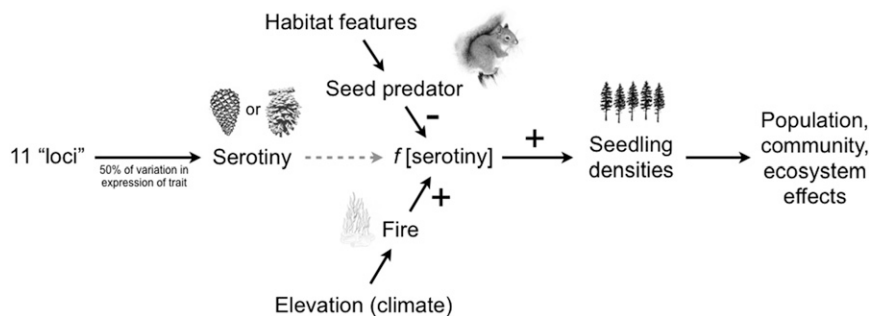
Fig. S1. Conceptual diagram of the interrelationships between genetic variation, selective agents, and ecosystem structure and function in lodgepole pine.

Fig. S2. The effect of altering the population growth rate, ρ, on model predictions for (*A*) variable fire frequency with no seed predation, and (*B*) variable seed predation under relatively high fire frequencies (160 y).

Fig. S3. The effect of altering the intercept of the self-thinning curve, β_0, on model predictions for (*A*) variable fire frequency with no seed predation, and (*B*) variable seed predation under relatively high fire frequencies (160 y).

Fig. S4. The effect of altering the slope of the self-thinning curve, β_1, on model predictions for (*A*) variable fire frequency with no seed predation, and (*B*) variable seed predation under relatively high fire frequencies (160 y).

Fig. S5. The effect of altering the mortality rate, μ, on model predictions for (*A*) variable fire frequency with no seed predation, and (*B*) variable seed predation under relatively high fire frequencies (160 y).

Fig. S6. The effect of altering the immigration rate, γ_0, on model predictions for (*A*) variable fire frequency with no seed predation, and (*B*) variable seed predation under relatively high fire frequencies (160 y).

Fig. S7. The effect of altering the slope of the postfire density curve, γ_1, on model predictions for (*A*) variable fire frequency with no seed predation, and (*B*) variable seed predation under relatively high fire frequencies (160 y).

Table S1. Fixed effects from the generalized linear mixed model for cone survival

Parameter	Estimate*	SE*	z	P
Intercept	1.90	0.59	3.20	0.001
Cone type: serotinous (green)	−0.42[†]	0.074	−5.71	<0.001
Cone type: serotinous (brown)	1.48[†]	0.11	13.79	<0.001
Distance from midden	0.27	0.29	0.92	0.36
Distance × serotinous (green)	0.19	0.086	2.19	0.028
Distance × serotinous (brown)	0.51	0.14	3.78	<0.001
DBH[‡]	0.21	0.032	6.67	<0.001

*Estimates and SEs are presented on the logit scale, standardized to mean = 0 and unit variance for numeric predictors.
[†]Parameters for cone type are relative to nonserotinous cones (i.e., the intercept).
[‡]Diameter at breast height, in centimeters.

Table S2. List of parameters and state variables

Description	Symbol	Default	Range	SE	Source, ref.
State variables					
Serotinous population size	n_s				
Nonserotinous population size	n_n				
Stand age	a				
Selection parameters					
Fire return interval	F	n/a	100–400		1
Squirrel density	S	n/a	0–2.10		2
Other parameters					
Population growth rate	ρ	0.05	0.01–0.21	*	3, 4
Self-thinning: intercept	β_0	14.64		0.24	5
Self-thinning: slope	β_1	−1.39		0.055	5
Adult mortality rate	μ	0.005	0.005–0.02	*	6
Immigration rate	γ_0	6.56		0.21	7, 8
Seedling density slope	γ_1	8.87		0.37	7, 8

*No SE was available for these parameters, so the ranges were used for sensitivity analysis.

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8. Benkman CW, Siepielski AM, Parchman TL (2008) The local introduction of strongly interacting species and the loss of geographic variation in species and species interactions. *Mol Ecol* 17(1):395–404.

Other Supporting Information Files

Dataset S1 (CSV)