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Abstract Wildfire frequency and intensity in the Mediterranean region are predicted to increase with climate and anthropogenic changes in the following decades. Pines species often posses fire-embracing and fire-avoiding strategies that increase the probability of persistence and performance in fire-prone habitats. One such strategy is serotiny, i.e., the capacity to retain seeds in long-closed cones within the plant canopy; serotinous cones release seeds only when either a fire or a heat shock occurs. In this work, we used a simulation approach and *Pinus pinaster* populations as a model system to investigate how (i) an increased frequency of fire, (ii) genetic characteristics of serotiny, and (iii) observed differences in life histories interact to determine (a) risk of local population extinction and (b) temporal changes in the prevalence of serotiny in the modeled population. In addition, we tested whether the contemporary evolution of serotiny in the face of increased probability of occurrence of fires increased the probability of population persistence with respect to a scenario in which serotiny was not allowed to evolve. Our simulations showed that over the 300 years of simulated time, the evolution of serotiny did not substantially contribute to the persistence of populations. Extinction risk increased with the increasing probability of occurrence of fire and slightly decreased with (i) higher gene flow from outside the modeled population, and (ii) higher prevalence of serotiny at the beginning of the simulation. The prevalence of serotiny at the end of simulation time was difficult to predict and mostly driven by stochasticity.

Keywords Adaptation · Climate change · Extinction risk · Extreme events · Gene flow · Population dynamics

Introduction

Both the frequency and intensity of extreme events, such as fire, floods, extreme temperatures, rainfall, or droughts, are expected to increase with climate change (IPCC 2007, 2012; Jentsch et al. 2007). The effects of extreme events may result in population extinctions

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(Frederiksen et al. 2008; Piessens et al. 2009; Tryjanowski et al. 2009), genetic bottlenecks (Shama et al. 2011), species invasion (Diez et al. 2012; Greenville et al. 2012), changes in community structure, and ecosystem function (Gutschick and BassiriRad 2003; Thibault and Brown 2008; Wernberg et al. 2012; Milner et al. 2012; Thompson et al. 2013), and shifts in the timing of life-cycle events of plant and animal species (Jentsch et al. 2009).

The air temperature in the Mediterranean region is expected to increase over the twenty first century, while precipitation is predicted to decrease in autumn and increase in winter (IPCC 2007). Those two effects of climate change will profoundly affect fire activity (Pinol et al. 1998; Pausas 2004), and a clear pattern of increasing fire activity at least partially to be ascribed to the increasing mean annual and summer temperatures has been already shown for the Mediterranean region (Pausas 2004). Regions experiencing severer droughts are also predicted to be affected by an increase of wildfire frequency and intensity (Dury et al. 2011). There is widespread support for the hypothesis that the fire regime is a strong selective agent that can shape the intraspecific variability of multiple traits in some plant species, such as early flowering, the presence of serotinous cones, bark thickness, self-pruning, longevity, and flammability (Keeley et al. 2011b; Pausas et al. 2012; Keeley 2012). However, the ever-increasing fire frequencies might overwhelm the potential fire protection or post-fire adaptation provided by those traits (Pausas et al. 2008). A different fire regime (fuel consumption and fire spread patterns, intensity, severity, frequency, and seasonality) induced by climate change and anthropogenic changes to the environment (Alvarez et al. 2012) will cause fire events that should be considered as extreme climatic events (Smith 2011), that is, events including "extremeness" in both the driver (climate, weather) and the response at different levels of biological organization (i.e., genes, populations, communities, etc.).

Serotiny is defined as the capacity to retain seeds in long-closed cones within the plant canopy (Gauthier et al. 1996). More operationally, serotiny of a tree can be measured as the proportion of serotinous cones, i.e., mature cones in the tree canopy that remain closed until seed release is triggered by high temperatures (usually >45 °C), such as those associated with fires. Serotiny is prevalent in Australia, South Africa, the Mediterranean basins, and areas of California, North Africa, and the Middle East occupied by coniferous forests (Tapias et al. 2004). Serotiny is a trait expressed in at least 22 different species across the genus *Pinus* and appears to have evolved independently multiple times since the mid-Cretaceous period (Grotkopp et al. 2004; He et al. 2012).

Large differences in serotiny have been observed among populations of maritime pine (*Pinus pinaster* Aiton) as well as in other pine species (Tapias et al. 2001; Goubitz et al. 2004; Hernández-Serrano et al. 2013), with geographically closed, genetically similar populations in which serotiny is either fixed (i.e., all cones are serotinous), completely absent, or at intermediate levels (Tapias et al. 2004). The intensity, frequency, size, and spatial distribution of fires have been frequently indicated as the main factors driving the observed high variability in the degree of serotiny among populations (Gauthier et al. 1996; Radeloff et al. 2004; Hernández-Serrano et al. 2013), although other agents of selection such as seed predation might also be important (Saracino et al. 1997; Benkman and Siepielski 2004). It has been suggested that recurrent fires occurring within the average life span of a species are conditions favoring an increased prevalence of serotiny (Lamont et al. 1991; Enright et al. 1998). At the population level, serotiny is indeed higher in *P. pinaster* and *P. halepensis* populations from areas affected by frequent forest fires (Hernández-Serrano et al. 2013). Nonetheless, some exceptions to this general pattern (i.e., low serotiny in fire-prone habitats and viceversa) have been documented (Tapias et al. 2004).

Although explicit measures of fitness advantages of serotinous trees are lacking, in the case of an heritable trait large and intense fires should favor highly serotinous trees in fire-prone environments because regeneration will almost completely result from serotinous progenitors (Tinker et al. 1994), thus potentially maintaining a higher level of serotiny in the resulting population. On the other hand, when either fire recurrence intervals exceed the average life span of trees or fires are of low intensity, non-serotinous or low-serotinous individuals should be favored (Johnson and Gutsell 1993).

However, predictions on the evolution of serotiny depend on assumptions regarding the genetic architecture of the trait as well as its reaction norms, with faster response being expected in the case of a Mendelian trait. The fast selection for serotiny that was observed in different pine species immediately after the occurrence of fires (Teich 1970; Muir and Lotan 1985; Goubitz et al. 2004) led to the hypothesis of a simple genetic control (one locus with two alleles) for serotiny (Hartl 1979; Perry and Lotan 1979). More recently, Parchman et al. (2012) found through a genome-wide association study that genetic variation across 11 loci explained 50 % of the phenotypic variation in serotiny in lodgepole pine, while Budde et al. (2014) found through an in situ genetic association study that 17 loci explained ~29 % of the phenotypic variation among natural eastern Iberian populations of *P. pinaster*. These recent results point towards serotiny as a polygenic quantitative trait, with a narrow-sense heritability (h^2, the fraction of phenotypic variance explained by additive genetic variance, Falconer and Mackay 1996) ranging from 0.2 to 0.67 (Budde et al. 2014).

Investigating how plant species will respond to novel and challenging extreme fire events is of primary importance in order to predict the evolution of vegetation systems, as well as to implement appropriate management and conservation plans. The recent evidence pointing toward serotiny as a polygenic trait with moderate-to-high heritability has yet to be included in models describing and predicting population dynamics of plant species living in fire-prone environments, as well as testing the potential contemporary evolution of serotiny within populations exposed to an increasing frequency of fires. In addition, it remains to be tested whether a fast selection for serotiny after fire can be solely explained by polygenic inheritance of the trait and the reproductive advantage of serotinous trees when fires occur.

In this work, we used *P. pinaster* populations as a model system to investigate how (i) an increased frequency of fire, (ii) genetic characteristics of the trait, and (iii) different life histories interact to determine (a) risk of local population extinction, and (b) temporal changes in the prevalence of serotiny in the modeled population. In addition, we tested whether the evolution of serotiny in response to an increase in probability of occurrence of fires increased the probability of population persistence with respect to a scenario in which serotiny was not allowed to evolve. Since the model is analytically intractable, we used extensive numerical simulations along with statistical analyses on simulation results to explore its behavior. Simulations last for 300 years. The model combines aspect of fire dynamics, aspects of individual and population dynamics, and hypothesis on the genetic architecture of the trait.

Materials and methods

Overview of the model

We consider a maritime pine population living in a habitat population ceiling of which is K, here intended as the maximum number of individuals that can be supported (Mangel and Tier 1993). We chose a moderate K in order to represent a scenario of a population at the risk of extinction with an increased probability of occurrence of fires.

Reproduction is discrete in time, and the population is composed of $N(t,x)$ individuals of different ages x at time t (years). Each individual is characterized by a single quantitative trait a corresponding to its breeding value for a phenotypic trait z (i.e., serotiny). After an initial period with no fires occurring, the habitat is then characterized by the occurrence of fires causing a non-selective (i.e., all individual share the same risk independent of their breeding value for the trait z) age-dependent increase in mortality in the population.

Serotiny

The phenotype z of an individual i, z_i, is commonly modeled as the sum of its genotypic (also called breeding) value a_{i} and an environmental effect e_{i} (Lynch and Walsh 1998):

$$z_i = a_i + e_i \tag{1}$$

At the population level, breeding values are theoretically normally distributed $N(\mu_{\mathrm{G}},\sigma^2_{\mathrm{G}})$, while e_i is a statistically independent random environmental effect from $N(\mu_{\mathrm{E}}, \sigma^2_{\mathrm{E}})$. The narrow-sense heritability of the trait h^2 is given by $\sigma^2_{\mathrm{G}}/\sigma^2_{\mathrm{Z}}$, where σ^2_{G} is the additive genetic variance for the trait and σ^2_{Z} is the phenotypic variance.

In our model, z_i corresponds to the proportion of serotinous cones (i.e., cones that release seeds only after the occurrence of a fire) in the sexually mature plant i, while $(1 - z_i)$ is the proportion of non-serotinous cones, i.e., cones that release seeds independent of fire.

Due to a lack of more detailed information on the genetic architecture of the trait, we did not model either dominance or epistatic variation. Environmental variance includes all variation of non-genetic origin, i.e., variation due to external environmental conditions (e.g., nutrition, climate, disease) and internal conditions such as developmental noise.

Inheritance of serotiny

To model the inheritance of serotiny, we used the infinitesimal model of quantitative genetics (Lynch and Walsh 1998). With this theoretical model, genetic variances remain constant during the natural selection processes. With inheritance rules based on the infinitesimal model, each seedling's value for a polygenic trait z is drawn from a normal distribution centered on the arithmetic mean of the two parental values (a_{p1} and a_{p2}), while the variance of this distribution is equal to half the total additive genetic variance for the trait at the population level ($\sigma^2_{A,S}/2$). With this formulation, both the within-family additive variance and the total additive genetic variance for the trait at the population level remain constant across generations (Bulmer 1971; Lynch and Walsh 1998).

Monte Carlo simulations

We use Monte Carlo simulations to study population dynamics and the evolution of serotiny in maritime pine populations. Since this study focuses on the short-term effects of climate change, simulations last for 300 years. Trees settle on a squared grid of dimension $k \times k$, where $k^2 = K$, i.e., the population ceiling. Since maximum density of mature stands of maritime pine is ~1,000 trees per hectare (De-Lucas et al. 2008), each tree occupies an area of ~10 m^2. When a plant dies, either due to natural causes or the occurrence of fire, one new seedling can establish in the empty spot. In the absence of fire, trees survive with annual probability, e^{-m}.

Fires in pine forests may be categorized as surface fires, in which fire does not reach the canopy; and crown fires, in which fire also burns the canopy of pines (Gill and Allan 2008; Keeley 2012). Although surface and crown fires exert different selective pressures on the evolution of plant traits (Keeley and Zedler 1998; Keeley et al. 2011a), we did not explicitly differentiate between them. However, as described further below, scenarios with higher probability of survival of pines after a fire may represent environments characterized by surface fires, while scenarios with low survival of pines after fire may refer to environments characterized mostly by crown fires. In case of fire—which occurs with annual probability p_f—survival probability σ_f is a sigmoidal function of pine age x:

$$\sigma_f = \alpha/(2 + e^{-\beta(-20+x)}), \qquad (2)$$

where $\alpha/2$ is the maximum survival for a pine of age x_{max}, and β is a parameter defining the shape of the function. Tree mortality can directly arise from fire-caused injury to crown, vascular, or root tissues, either solely or in combination. Larger trees (therefore, usually older trees within a population) should be able to survive intense fires (at least surface fires) with higher probability (Fernandes et al. 2008) mainly because of thicker bark and higher position of the foliage.

In the absence of fires, when an individual dies, a new seedling grows in the newly found empty spot. As mean dispersal distance is estimated as ~10 m in maritime pine (González-Martínez et al. 2006), we assumed that sexually mature pines for the female function within three cells in every direction from the dead pine (including the dead pine) contribute to the seed bank according to their proportion of non-serotinous cones, assuming 20 cones produced by each plant. A single seed was randomly drawn from the seed bank and grew in the spot left empty. As older, larger trees are likely to produce either more cones/seeds or seeds of higher quality or both (González-Martínez et al. 2006), the "weight" of seeds in the random drawing procedure increased with tree's age (i.e., seeds of trees younger than 10 years old had a weight of 1, and trees older than 40 years old had a weight of 5). Seeds were either fertilized by local pollen (i.e., from trees in the $k \times k$ grid) or from outside the population (i.e., from trees not in the $k \times k$ grid). The parameter g_F, which is bounded between 0 and 1, indicates the magnitude of gene flow. For example, when $g_F = 0.5$, 50 % of seeds were fertilized by external pollen. We assumed that the distribution of breeding values for serotiny of external pollen was constant through simulation time and equal to the breeding distribution of serotiny at $t = 1$ for the modeled population (μ_S). For local pollen, we assumed that each tree in the $k \times k$ grid was equally

Table 1 Parameters of the model

Parameters	Values	Description
K	400	Population ceiling
h^2	0.3, 0.4, 0.5, 0.6	Heritability of serotiny
$T_{\max}$	300	Simulation time
α_M	5	Age of sexual maturation for the male function
α_F	7	Age of sexual maturation for the female function
g_F	0.2, 0.5, 0.7, 0.9	Pollen gene flow from outside the population
μ_S	0.1, 0.3, 0.5, 0.7	Mean breeding value for serotiny at $t = 1$
β	0.2	Parameter determining shape of the sigmoid function of fire-induced mortality
p_f	0.02, 0.05, 0.10	Annual probability of fire occurrence
μ_E	0	Mean environmental effect
σ_E^2	0.01	Variance of the environmental effect
m_E	−0.03	Mortality rate for natural causes
$\alpha/2$	0.3, 0.5, 0.7, 0.9	Maximum survival in case of fire

We report values of the parameters or range in case of multiple scenarios investigated. Given heritability of serotiny h^2 and variance of the environmental effect σ_E^2, additive genetic variance for serotiny $\sigma_{A,S}^2$ is computed as $\sigma_{A,S}^2 = h^2\sigma_E^2/(1 - h^2)$. Simulation with $K > 400$ did not change simulation results

likely to fertilize the seed, and we allowed self-fertilization. Preliminary simulations with probability of fertilization as function of distance from the target tree considerably slowed down simulations without altering any of the results. In case of fire, we applied the same procedure described above for the establishment of new seedlings, but this time sexually mature pines produced seeds according to their proportion of serotinous cones.

At each time step t, simulations proceeded as follows: (1) We computed the total number of individuals alive $N(t,x)$ and checked the distribution of trait z in the population. A population was considered extinct if at any time during the simulation no trees or seeds were alive/viable in the population. (2) We determined the survival of individuals using Bernoulli trials, where the annual survival probability was e^{-m}. (3) When a tree died, a new seedling established in the empty spot if neighbouring trees could reach the empty spot by seed dispersal. The number of seeds produced by a tree increased with $(1 - \mu_S)$. (4) The breeding value of the newly established seedling was randomly drawn from a normal distribution with the mean centred on the mean of the breeding values of the parents (seed—a_{p1} and pollen—a_{p2}) and variance being equal to $\sigma_{A,S}^2/2$. (5) In case of fire, steps (2)–(4) were repeated, but in this case the number of seeds produced by a tree increased with its degree of serotiny.

Our simulation model had the following parameters: annual probability of occurrence of a fire p_f, heritability of serotiny h^2, parameters of the survival function in case of fire α and β, environmental variance σ_E^2, additive genetic variance for serotiny $\sigma_{A,S}^2$, age at sexual maturity for the male function α_M and for the female function α_F (Santos-del-Blanco et al. 2012) (Table 1).

The parameter space is rich, and its full exploration is beyond the scope of the present work. We fixed most of the parameters, and we performed simulations for combinations of pollen gene flow g_F, maximum survival in case of fire σ_f, probability of occurrence of a fire p_f, heritability of serotiny h^2, and mean breeding value of serotiny at $t = 1$ μ_S (Table 1). In order to test whether the evolution of serotiny increased the probability of persistence of the population, we also modeled a scenario in which serotiny did not evolve after the first part of the simulation, as explained below. The parameter space for simulations includes combination of traits and processes that can be observed in nature. For example, when simulating a relatively high survival of pines after a fire, high frequency of fires and high gene flow, we may refer to a scenario of frequently occurring surface fires affecting a population genetically well connected to surrounding stands. On the other hand, low survival of pines after a fire, high frequency of fires, and low gene flow may refer to a scenario of frequently occurring crown fires affecting an isolated population.

We started each simulation replicate with K trees (population at maximum capacity) with breeding values of serotiny $a_1, \ldots, a_{k^2}$ randomly drawn from $N(\mu_S, \sigma_{A,S}^2)$, where μ_S is the mean breeding value of serotiny and $\sigma_{A,S}^2$ is its additive genetic variance, which remained constant throughout the simulation time. Then, the proportion of serotinous cones of each

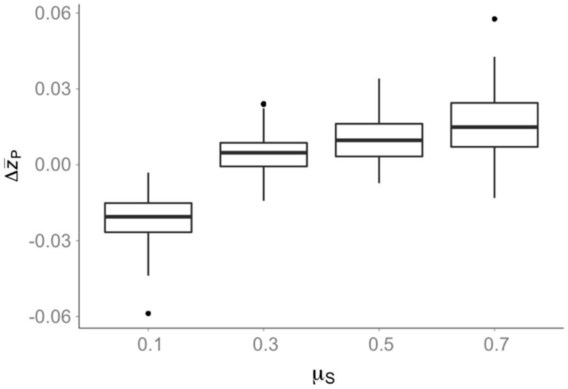

Fig. 1 Boxplot of change in mean serotiny from $t = 1$ to $t = 100$ ($\Delta\bar{z}_{\mathrm{P}}$) for initial mean values of serotiny μ_{S} used in the simulations

tree (i.e., its phenotype) was obtained by randomly drawing a value of ε from $N(\mu_{\mathrm{E}}, \sigma_{\mathrm{E}}^2)$ [Eq. (1)]. When the resulting phenotype was either <0 or >1, we constrained the phenotype to be equal to 0 or 1, respectively. At the start of simulations, the age of a tree was randomly drawn from a uniform distribution between 4 and 50. For each simulation replicate, we first let the population evolve for the first 100 years in an environment in which no fires occurred, which allowed populations to achieve a quasi-stable degree of serotiny (Fig. 1). Then, for the remaining 200 years of simulation, time fires occurred with annual probability p_{f}. In the case of no evolution of serotiny after the first 100 years, we assigned phenotypic values to seedlings for $t > 100$ by randomly drawing from the distribution of serotiny at time $t = 100$. This way, the long-term mean value and the variance of serotiny were equal to those at $t = 100$.

We carried out five replicates for each combination of parameters, and we treated the 7,680 replicates as independent realizations. At the level of single replicates, to characterize the behavior of the simulated populations we (a) recorded whether the population was extinct or still persisting at the end of the simulation time (0 for persistence and 1 for extinction); and (b) tracked the distribution of the trait z in the population as a function of time and, in particular, the difference between its mean value $\bar{z}$ at the end of the simulation time when the population did not go extinct and the mean value before the occurrence of fires (i.e., at year 100), $\Delta\bar{z}$. To avoid the transient effects caused by fires occurring shortly before the end of simulation time, we averaged mean z in the last 10 years of the simulation and during the years 90–100.

Statistical analysis

We used simulation results as pseudo-empirical data and proceeded to analyze them with standard statistical techniques. For all models, we standardized the predictors in order to compare their importance (Schielzeth 2010), and we treated all predictors as continuous variables. As we use realistic variable ranges representing the variability observed (or likely to be observed in the future) in nature, the estimated parameters can be compared in terms of effect on a standardized scale, where the estimates of regression parameters corresponds to the effect of one standard deviation of variation of the predictor on the response variable.

We estimated parameters of Generalized Linear Models with logit link function or Ordinary Least-Square regression models using as response variable either (i) extinction(1)/persistence(0), and (ii) $\Delta\bar{z}$ for the populations that did not go extinct and only for the scenario with evolution of serotiny also for $t > 100$. In order to test for nonlinear effects, we also estimated parameters of generalized additive models (GAMs) for (i) and (ii), using smooth (i.e., non-linear) terms for the gene flow g_{F}, the heritability of serotiny h^2, and the initial mean breeding value for serotiny μ_{S}. After preliminary analyses, we decided not to include interactions among predictors in order to improve the interpretability of results (along with the little explanatory power of interactions). We visually checked residuals for variation to model assumptions. Although we report p values, our considerations on the relative importances of the various predictors are not based on statistical significance, but rather on effect sizes and sign of the estimated parameters (White et al. 2013).

Code and data are available at http://dx.doi.org/10.6084/m9.figshare.935573.

Results

In the first 100 years of simulation (i.e., before the occurrence of fires), mean serotiny slightly decreased for mean breeding value at $t = 1$ for μ_S equal to 0, slightly increased for $\mu_{\mathrm{S}} = 0.7$; and remained constant

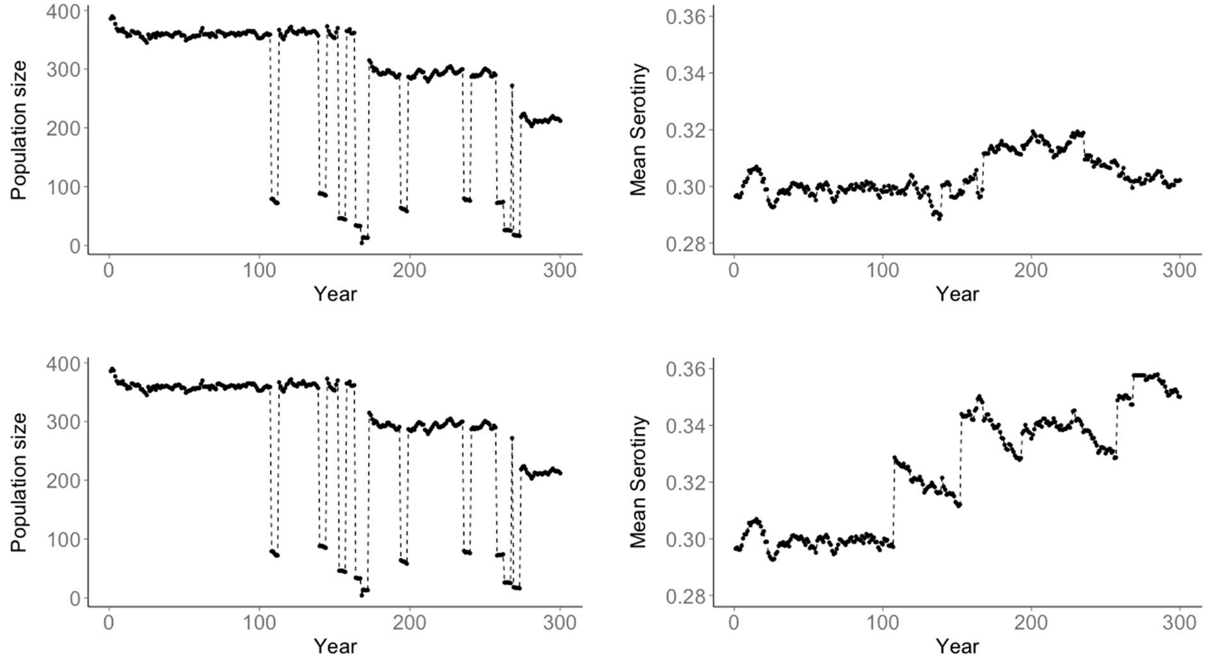

Fig. 2 Examples of simulations without (*top row*) and with (*bottom row*) evolution of serotiny for $t > 100$. Both replicates were run with the same sequence of random numbers. Fires caused a strong decrease in population size (here as number of trees older than 5 years). When serotiny was allowed to evolve for $t > 100$ there was often an increase in mean serotiny in the years following a fire

(on average) for $\mu_S = 0.3$ and $= 0.5$ (Fig. 1). In the scenario with evolution of serotiny, we often observed a slight, but noticeable, increase in mean serotiny in the population after fires (Fig. 2).

Extinction risk

The logistic regression model provided a good description of the risk of extinction in the modeled populations (Table 2). Different scenarios of frequency of fires determined large differences in extinction risk. Pollen gene flow from outside the population decreased the risk of extinction, along with maximum survival in case of fire and initial mean breeding value of serotiny μ_S. The evolution of the trait after the first phase with no occurrence of fire (i.e., for $t > 100$) did not increase the probability of persistence of the population. The heritability of serotiny had no role in determining the extinction risk of the population.

The GAM model found non-linear effects of gene flow and mean breeding value for serotiny at $t = 1$ (Fig. 3). However, for gene flow, the effects were substantially linear over the entire range of g_F values, while for mean breeding value, we observed a decreased risk of extinction with increasing μ_S, although effects were plateauing for higher values of μ_S (Fig. 3).

Shifts of serotiny

The linear model described only a small part the observed variability in the difference between mean serotiny at the end of simulation time and mean serotiny before the occurrence of fire, $\Delta\bar{z}$ (Table 2). Maximum survival in case of fire had no effect on $\Delta\bar{z}$, while all other variables had a positive, albeit very slight, effect on $\Delta\bar{z}$. The only exception was pollen gene flow, which tended to decrease $\Delta\bar{z}$.

The GAM model for $\Delta\bar{z}$ found non-linear effects for gene flow, heritability, and initial mean breeding value of serotiny (Fig. 4). However, the effects were of very small magnitude, and the contributions of gene flow, heritability, and mean breeding value at $t = 1$ can be considered to be quasi-linear over the range of values we considered.

We observed a greater mean $\Delta\bar{z}$ for small values of μ_S, while for higher values of μ_S, the mean values of $\Delta\bar{z}$ across all replicates were very close to 0 (Fig. 5).

Table 2 Results of statistical analyses on simulation results used as pseudo-empirical data when response variable is either extinction/persistence (binomial GAM and binomial GLM), or difference between mean phenotype $\bar{z}$ at the end of simulation time ($t = 300$) and $\bar{z}$ at $t = 100$ (Gaussian GAM and ordinary least-square regression model, OLS)

	Extinction			$\Delta\bar{z}$		
	GLM $R^2 = 0.66$	GAM $R^2 = 0.53$	edf	OLS $R^2 = 0.36$	GAM $R^2 = 0.36$	edf
Intercept	−4.98 (0.15)**	−5.00 (0.05)**	–	0.03 (0.00)**	0.03 (0.00)**	–
Evol	0.02 (0.11)	0.02 (0.11)	–	–	–	–
g_F	−0.41 (0.05)**	–	1.49**	−0.01 (0.00)**	–	1.72**
$\alpha/2$	−2.48 (0.10)**	1.78 (0.03)**	–	0.00 (0.00)	0.00 (0.00)	–
p_f	2.47 (0.10)**	2.48 (0.10)**	–	0.01 (0.00)**	0.47 (0.002)**	–
h^2	−0.04 (0.05)	–	1.00	0.01 (0.00)**	–	1.93**
μ_S	−0.32 (0.05)**	–	1.87**	0.01 (0.00)**	–	1.00**

edf are the estimated degrees of freedom. Evol = 1 is for the scenario with evolution of serotiny, Evol = 0 is for scenario without evolution of serotiny for $t > 100$. All terms with * are statistically significant at the 0.05 level, with ** at the 0.01 level. We report R^2 when response variable is either continuous or binary for GAMs and for OLSs. We report Nagelkerke's R^2 for GLMs

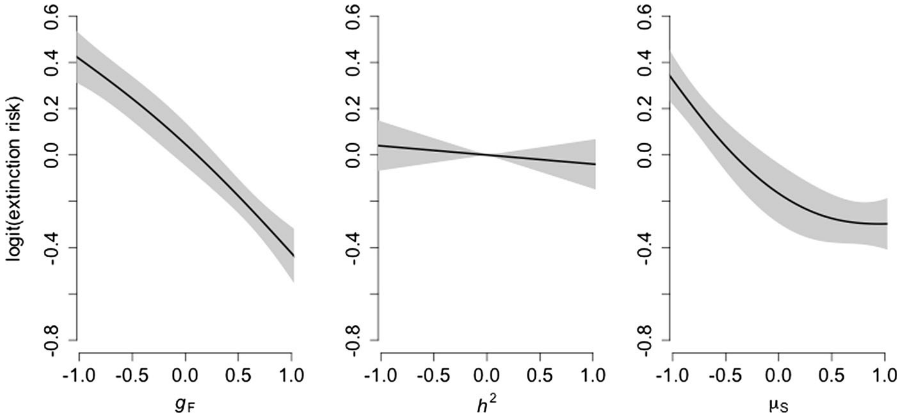

Fig. 3 Smooth components of Generalized Additive Model with extinction (1)/persistence (0) of populations as binary response variable. Predictors are on a standardized scale. g_F Gene flow, h^2 heritability of serotiny, μ_S mean breeding value for serotiny at $t = 1$. *Bands* indicate 95 % confidence intervals

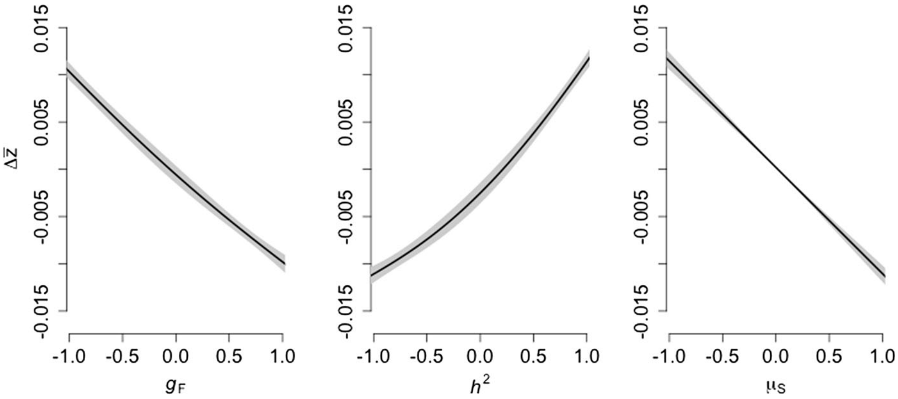

Fig. 4 Smooth components of Generalized Additive Model with $\Delta\bar{z}$ as response variable. Predictors are on a standardized scale. g_F Gene flow, h^2 heritability of serotiny, μ_S mean breeding value for serotiny at $t = 1$. *Bands* indicate 95 % confidence intervals

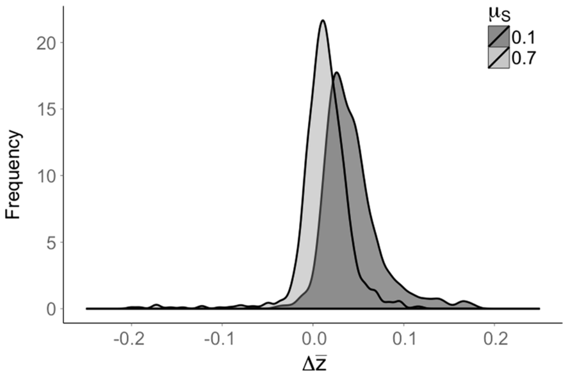

Fig. 5 Distribution of $\Delta\bar{z}$ over all replicates with mean breeding value for serotiny at $t = 1$ μ_S equal to 0.1 and 0.7

Discussion

The management of maritime pine in fire-prone habitats is a challenging task, and the ability to predict population responses to the predicted increase in the probability of fires will be valuable for conservation efforts. In addition to exploring simulation results, we believe that understanding the potential effects of climate- or human-induced modifications of the habitat is best approached by combining theoretical expectations, modeling hypothesis, and empirical observations, in which the empirical work guides the theoretical constructs, and the modeling results identify key pieces of (missing) empirical information.

The parameter space of our simulations allowed us to model realistic combinations of traits and processes that can be observed in nature. Although some simplifications were necessary in order to facilitate the interpretation of results (for instance, probability of occurrence of a crown fire is likely to increase with time after fire (Alvarez et al. 2012), while in our simulations, the probability of fire occurrence was constant within a replicate), our results provided clear insights into the risk of local population's extinction and temporal changes of the prevalence of serotiny in fire-prone environments.

We have shown that the evolution of serotiny does not increase the short-term probability of persistence of maritime pine stands; however, probability of persistence increases with higher starting mean serotiny of the population. Since we modeled serotiny as a polygenic trait with moderate-to-high heritability, we did not expect a substantial increase in serotiny in response to the occurrence of fires, and our simulation results confirmed our intuition. Thus, the fast selection for increased serotiny often observed in the first generations after the occurrence of fire cannot be explained solely by the reproductive advantage of highly serotinous trees in the case of fire; reaction norms or plastic responses induced by post-fire environmental cues may be partially driving the observed fast increases of serotiny after fire (Teich 1970; Muir and Lotan 1985; Goubitz et al. 2004).

We discuss in detail the effects of fire frequency on the extinction risk of pine populations, the evolution of the prevalence of serotiny, and the role of gene flow in shaping the genetic structure of pine forests in fire-prone environments.

Effect of fire frequency on extinction risk

In the Mediterranean, fires occur with a frequency of 10–40 years (Pausas 1999) and act as a major driver in the population dynamics of pine forests (Hernández-Serrano et al. 2013). However, the number and extension of fires have markedly increased since the late 1970s in the Mediterranean basin as well as in other European regions (Moreno et al. 1998; Pinol et al. 1998; Pausas 2004). The increase in fire frequency and extent is related to both human and climatic factors (Moreno et al. 1998; Pausas and Fernández-Muñoz 2011). For instance, the risk of crown fires (usually causing very high tree mortalities) is increasing as a consequence of the suppression of most fires by firefighters and the reduction of thinning caused by the depopulation of rural areas (Alvarez et al. 2012).

Frequently occurring fires may not allow natural stands to persist by overwhelming their recovery capacity. Postfire populations of seeder species may have the same density of the prefire population only when fire intervals are long enough to allow a critical seed store for self-replacement (Enright et al. 1998).

Across replicates, we found that by increasing the annual probability of fire occurrence from $p_f = 0.02$ to $p_f = 0.10$ (from a fire every 50 years to a fire every 10 years, on average), the extinction risk increased from 0 to 31 %. For Mediterranean pines, it has been found that natural stands may not be able to persist when time intervals between fires are shorter than the time required to accumulate a sufficient seed bank (Kazanis and Arianotsou 2004; Màrcia et al. 2006), determining the so-called immaturity risk (Zedler

1995). In *P. halepensis*, a complete replenishment of the aerial seed bank after a destructive fire generally does not occur before 10–20 years (Pausas et al. 2008), and a similar time frame should be expected for *P. pinaster*. In addition, the probability of surface fire occurrence increases after a fire, since the burning of trees creates a shrubland-like structure characterized by high flammability (Moreira et al. 2001). Our results show that a further increase in fire frequency ($p_\mathrm{f} > 0.10$) would lead to high extinction risk, in particular for populations characterized by a low degree of serotiny and low genetic connectivity with surrounding stands, as in the case of highly isolated populations.

Evolution of serotiny as a polygenic trait

There have been relatively few attempts to study the evolution of serotiny in response to fires and the optimal degree of serotiny in plant species living in fire-prone habitats, intended as the degree of serotiny maximizing population growth rate. However, those models were either answering questions different from ours (Enright et al. 1998; Lamont and Enright 2000; Tonnabel et al. 2012), or faced limitations derived by a poor understanding of the genetic architecture of the trait (Hartl 1979; Perry and Lotan 1979). Models with a simple genetic control for serotiny (one locus, two alleles) predicted strong selection for the serotinous-coned trees within a few post-fire generations (Hartl 1979; Perry and Lotan 1979), while optimality models found that the mean and variability of recurrence interval of fires strongly determined the optimal degree of serotiny (Enright et al. 1998; Lamont and Enright 2000; Tonnabel et al. 2012).

We modeled serotiny as the proportion of cones opening up and releasing seeds only after the occurrence of a fire; the seed production of a pine after the occurrence of fire was proportional to its degree of serotiny. Thus, low-serotinous pines also contributed to the aerial seed bank and their genes had the chance to be represented in the post-fire generation (and, vice-versa, highly serotinous pines had the chance to be represented in the next generation in the absence of fires). This did not allow for a fast response of serotiny to the occurrence of fire(s), although the initial mean value of serotiny had a positive effect on the probability of persistence of the population. It remains to be tested whether on longer time scales (e.g., millennia) more substantial shifts of serotiny may be observed. A substantial increase of serotiny in response to a very high frequency of fires is unlikely in the absence of evolution of age of maturity toward younger ages. Thus, on one hand, serotiny evolves little over contemporary time scales, and the evolution of serotiny does not offer an advantage in terms of population persistence; on the other hand, the persistence chances of the population increase with the average degree of serotiny characterizing a population, which confirms the findings of other studies (Enright et al. 1998; Lamont and Enright 2000; Tonnabel et al. 2012).

Serotiny is tied to crown-fire regimes, and its higher prevalence is potentially adaptive in these environments. Recently, Bradshaw et al. (2011) advanced the hypothesis that a number of traits usually associated with fire (serotiny, resprouting, physical dormancy, smoke-induced germination, and flammability) might be "exaptations" (or pre-adaptations, Gould and Vrba 1982), i.e., traits enhancing fitness in a given environment (e.g., fire-prone habitat) that have not evolved through the action of natural selection in the same environment (e.g. those traits are adaptive in arid and nutrient-impoverished soils). However, there is convincing evidence for serotiny as a trait that evolved in response to fire (Keeley et al. 2011b; He et al. 2012; Hernández-Serrano et al. 2013), but how fast this trait can evolve and whether reaction norms or plastic responses induced by early cues (nutrients, soil, temperature, etc.) are involved is still unclear.

Gene flow

Pollen gene flow from a background population characterized by a mean breeding value of serotiny equal to that of the modeled pine population at $t = 1$ moderately lowered the risk of population extinction, but had very little effect on the shift in mean serotiny through simulation time. The slight positive effect of gene flow that was observed in terms of extinction risk was related to its buffering effect against the loss of serotiny in periods without fires.

In our model, we maintained both pollen gene flow from outside and local seed dispersal constant over simulation time, but recent evidence points toward an increase of gene flow after a marked reduction of population size in the context of fire-induced habitat disturbance (Shohami and Nathan 2014). Human-induced and natural fires are among the main causes of catastrophic changes in Mediterranean forests. Population genetics theory predicts reduced gene flow as well as higher within-population inbreeding and among-population genetic differentiations after habitat fragmentation determined by large fires. Contrary to these theoretical expectations, Shohami and Nathan (2014) found an increased pollen immigration in a *P. halepensis* natural stand after a fire that cleared 96 % of the adult population, possibly due to either the limited post-disturbance local pollen production or stronger winds that were allowed by a more sparse forest. They concluded that gene flow could be enhanced by habitat fragmentation as long as the scale of dispersal is greater than the scale of isolation. It has also been shown that *P. pinaster*'s long-distance seed-dispersal capability might not be so limited as previously thought (Juez et al. 2014), thus enabling a rapid colonization of new habitats. The increasing availability of data from gene flow experiments will allow us to refine the simulation of gene flow patterns in highly dynamic environments affected by fire.

Future work

In our work, we did not introduce correlation between (putatively) fire-adaptive traits, which existence and strength may depend on the fire regime (Keeley and Zedler 1998; Schwilk and Ackerly 2001). One trait that may show a strong correlation with degree of serotiny is age at sexual maturity. Maritime pines reach maturity and begin producing cones at the age of 7–8 years (Santos-del-Blanco et al. 2012). However, as also predicted by life-history theory (Stearns 1992; Roff 2002), populations that experience frequent fires can produce cones at as early as 4 years old (Tapias et al. 2001), and this might select for higher degrees of serotiny over contemporary time scales.

Highly skewed fecundity and/or reproductive success accompanied by regeneration failure at sites facing severe drought (Juez et al. 2014) may also contribute to the evolution of serotiny. The scarcely studied issues of changes in serotiny related to tree size/age (Ne'eman et al. 2004), different performance of seeds from serotinous cones in early life stages on burned soils (De Las Heras et al. 2012), and possible plastic responses (e.g., influence of the peculiar post-fire soil characteristics on the degree of serotiny in newly established seedlings) should also be investigated.

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References

Alvarez A, Gracia M, Vayreda J, Retana J (2012) Patterns of fuel types and crown fire potential in *Pinus halepensis* forests in the Western Mediterranean Basin. For Ecol Manag 270:282–290. doi:10.1016/j.foreco.2011.01.039

Benkman CW, Siepielski AM (2004) A keystone selective agent? Pine squirrels and the frequency of serotiny in lodgepole pine. Ecology 85:2082–2087. doi:10.1890/04-0177

Bradshaw SD, Dixon KW, Hopper SD et al (2011) Little evidence for fire-adapted plant traits in Mediterranean climate regions. Trends Plant Sci 16:69–76. doi:10.1016/j.tplants.2010.10.007

Budde KB, Heuertz M, Hernández-Serrano A et al (2014) In situ genetic association for serotiny, a fire-related trait, in Mediterranean maritime pine (*Pinus pinaster*). New Phytol 201:230–241. doi:10.1111/nph.12483

Bulmer MG (1971) The effect of selection on genetic variability. Am Nat 105:201–211

De Las Heras J, Moya D, Vega JA, Al E (2012) Chapter 6: Post-fire management of serotinous Pine forests. In: Moreira F, Arianoutsou M, Corona P, De las Heras J (eds) Post-fire management and restoration of southern European forests. Springer, New York, pp 121–150

De-Lucas AI, Robledo-Arnuncio JJ, Hidalgo E, González-Martínez SC (2008) Mating system and pollen gene flow in Mediterranean maritime pine. Heredity (Edinb) 100:390–399. doi:10.1038/sj.hdy.6801090

Diez JM, D'Antonio CM, Dukes JS et al (2012) Will extreme climatic events facilitate biological invasions? Front Ecol Environ 10:249–257. doi:10.1890/110137

Dury M, Hambuckers A, Warnant P et al (2011) Responses of European forest ecosystems to 21st century climate: assessing changes in interannual variability and fire intensity. iForest 4:82–99. doi:10.3832/ifor0572-004

Enright NJ, Marsula R, Lamont BB, Wissel C (1998) The ecological significance of canopy seed storage in fire-prone environments: a model for non-sprouting shrubs. J Ecol 86:946–959

Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics. Prentice Hall, Harlow, p 464

Fernandes PM, Vega JA, Jiménez E, Rigolot E (2008) Fire resistance of European pines. For Ecol Manag 256:246–255. doi:10.1016/j.foreco.2008.04.032

Frederiksen M, Daunt F, Harris MP, Wanless S (2008) The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. J Anim Ecol 77:1020–1029. doi:10.1111/j.1365-2656.2008.01422.x

Gauthier S, Bergeron Y, Simon J-P (1996) Effects of fire regime on the serotiny level of jack pine. J Ecol 84:539–548

Gill AM, Allan G (2008) Large fires, fire effects and the fire-regime concept. Int J Wildl Fire 17:688. doi:10.1071/WF07145

González-Martínez SC, Burczyk J, Nathan R et al (2006) Effective gene dispersal and female reproductive success in Mediterranean maritime pine (*Pinus pinaster* Aiton). Mol Ecol 15:4577–4588. doi:10.1111/j.1365-294X.2006.03118.x

Goubitz S, Nathan R, Roitemberg R et al (2004) Canopy seed bank structure in relation to: fire, tree size and density. Plant Ecol 173:191–201. doi:10.1023/B:VEGE.0000029324.40801.74

Gould SJ, Vrba ES (1982) Exaptation—a missing term in the science of form. Paleobiology 8:4–15

Greenville AC, Wardle GM, Dickman CR (2012) Extreme climatic events drive mammal irruptions: regression analysis of 100-year trends in desert rainfall and temperature. Ecol Evol 2:2645–2658. doi:10.1002/ece3.377

Grotkopp E, Rejmánek M, Sanderson MJ, Rost TL (2004) Evolution of genome size in pines (*Pinus*) and its life-history correlates: supertree analyses. Evolution 58:1705–1729

Gutschick VP, BassiriRad H (2003) Extreme events as shaping physiology, ecology, and evolution of plants: toward a unified definition and evaluation of their consequences. New Phytol 160:21–42. doi:10.1046/j.1469-8137.2003.00866.x

Hartl DL (1979) Selection for serotiny in lodgepole pine: mathematical analysis of the model of Perry and Lotan. Evolution (NY) 33:969–972

He T, Pausas JG, Belcher CM et al (2012) Fire-adapted traits of *Pinus arose* in the fiery Cretaceous. New Phytol 194:751–759. doi:10.1111/j.1469-8137.2012.04079.x

Hernández-Serrano A, Verdú M, González-Martínez SC, Pausas JG (2013) Fire structures pine serotiny at different scales. Am J Bot 100:2349–2356. doi:10.3732/ajb.1300182

IPCC (2007) Climate change 2007. Synthesis report. Contribution of Working Groups I, II & III to the fourth assessment report of the Intergovernmental Panel on Climate Change. IPCC, Geneva

IPCC (2012) Summary for policymakers. In: Field CB, Barros V, Stocker TF, Dahe Q (eds) Managing the risks of extreme events and disasters to advance climate change adaptation. Cambridge University Press, Cambridge, pp 1–19

Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate change experiments: events, not trends. Front Ecol Environ 6:315–324

Jentsch A, Kreyling J, Boettcher-Treschkow J, Beierkuhnlein C (2009) Beyond gradual warming: extreme weather events alter flower phenology of European grassland and heath species. Glob Chang Biol 15:837–849. doi:10.1111/j.1365-2486.2008.01690.x

Johnson EA, Gutsell SL (1993) Heat budget and fire behaviour associated with the opening of serotinous cones in two. J Veg Sci 4:745–750

Juez L, González-Martínez SC, Nanos N et al (2014) Can seed production and restricted dispersal limit recruitment in *Pinus pinaster* Aiton from the Spanish Northern Plateau? For Ecol Manag 313:329–339. doi:10.1016/j.foreco.2013.10.033

Kazanis D, Arianotsou M (2004) Factors determining low Mediterranean ecosystems resilience to fire: the case of *Pinus halepensis* forests. In: Proceedings of 10th MEDECOS conference

Keeley JE (2012) Ecology and evolution of pine life histories. Ann For Sci 69:445–453. doi:10.1007/s13595-012-0201-8

Keeley JE, Zedler PH (1998) Evolution of life histories in Pinus. In: Richardson DM (ed) Ecology and biogeography of Pines. Cambridge University Press, Cambridge, p 219

Keeley JE, Bond WJ, Bradstock RA et al (2011a) Fire in mediterranean ecosystems: ecology, evolution and management. Landsc Ecol 28:571–572

Keeley JE, Pausas JG, Rundel PW et al (2011b) Fire as an evolutionary pressure shaping plant traits. Trends Plant Sci 16:406–411. doi:10.1016/j.tplants.2011.04.002

Lamont BB, Enright NJ (2000) Adaptive advantages of aerial seed banks. Plant Species Biol 15:157–166. doi:10.1046/j.1442-1984.2000.00036.x

Lamont BB, Maitre DC, Cowling RM, Enright NJ (1991) Canopy seed storage in woody plants. Bot Rev 57:277–317. doi:10.1007/BF02858770

Lynch M, Walsh B (1998) Genetic and analysis of quantitative traits. Sinauer Associates, Sunderland

Mangel M, Tier C (1993) A simple direct method for finding persistence times of populations and application to conservation problems. Proc Natl Acad Sci USA 90:1083–1086

Màrcia E, Iraima V, Francisco L, Josep Maria E (2006) Recruitment and growth decline in *Pinus halepensis* populations after recurrent wildfires in Catalonia (NE Iberian Peninsula). For Ecol Manag 231:47–54. doi:10.1016/j.foreco.2006.05.007

Milner AM, Robertson AL, McDermott MJ et al (2012) Major flood disturbance alters river ecosystem evolution. Nat Clim Chang 3:137–141. doi:10.1038/nclimate1665

Moreira F, Rego FC, Ferreira PG (2001) Temporal (1958–1995) Pattern of change in a cultural landscape of northwestern Portugal: implications for fire occurrence. Landsc Ecol 2:557–567

Moreno JM, Vazquez A, Velez R (1998) Recent history of forest fires in Spain. In: Moreno JM (ed) Large forest fires. Backhuys Publishers, Leiden, pp 159–186

Muir PS, Lotan JE (1985) Disturbance history and serotiny of *Pinus contorta* in Western Montana. Ecology 66:1658–1668

Ne'eman G, Goubitz S, Nathan R (2004) Reproductive traits of *Pinus halepensis* in the light of fire—a critical review. Plant Ecol 171:69–79

Parchman TL, Gompert Z, Mudge J et al (2012) Genome-wide association genetics of an adaptive trait in lodgepole pine. Mol Ecol 21:2991–3005. doi:10.1111/j.1365-294X.2012.05513.x

Pausas JG (1999) Response of plant functional types to changes in the fire regime in Mediterranean ecosystems: a simulation approach. J Veg Sci 10:717–722

Pausas JG (2004) Changes in fire and climate in the Eastern Iberian Peninsula (Mediterranean Basin). Clim Change 63:337–350

Pausas JG, Fernández-Muñoz S (2011) Fire regime changes in the Western Mediterranean Basin: from fuel-limited to drought-driven fire regime. Clim Change 110:215–226. doi:10.1007/s10584-011-0060-6

Pausas JG, Llovet J, Rodrigo A, Vallejo R (2008) Are wildfires a disaster in the Mediterranean basin?—A review. Int J Wildl Fire 17:713. doi:10.1071/WF07151

Pausas JG, Alessio GA, Moreira B, Corcobado G (2012) Fires enhance flammability in *Ulex parviflorus*. New Phytol 193:18–23

Perry DA, Lotan JE (1979) A model of fire selection for serotiny in lodgepole pine. Evolution (NY) 33:958–968

Piessens K, Adriaens D, Jacquemyn H, Honnay O (2009) Synergistic effects of an extreme weather event and habitat fragmentation on a specialised insect herbivore. Oecologia 159:117–126. doi:10.1007/s00442-008-1204-x

Pinol J, Terradas J, Lloret F (1998) Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain. Clim Change 38:345–357

Radeloff VC, Mladenoff DJ, Guries RP, Boyce MS (2004) Spatial patterns of cone serotiny in *Pinus banksiana* in relation to fire disturbance. For Ecol Manag 189:133–141. doi:10.1016/j.foreco.2003.07.040

Roff D (2002) Life history evolution. Sinauer Associates, Sunderland

Santos-del-Blanco L, Climent J, González-Martínez SC, Pannell JR (2012) Genetic differentiation for size at first reproduction through male versus female functions in the widespread Mediterranean tree *Pinus pinaster*. Ann Bot 110:1449–1460. doi:10.1093/aob/mcs210

Saracino A, Pacella R, Leone V et al (1997) Seed dispersal and changing seed characteristics in a *Pinus halepensis* Mill. forest after fire. Plant Ecol 130:13–19

Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. Methods Ecol Evol 1:103–113. doi:10.1111/j.2041-210X.2010.00012.x

Schwilk DW, Ackerly DD (2001) Flammability and serotiny as strategies: correlated evolution in pines. Oikos 2:326–336

Shama LNS, Kubow KB, Jokela J, Robinson CT (2011) Bottlenecks drive temporal and spatial genetic changes in alpine caddisfly metapopulations. BMC Evol Biol 11:278. doi:10.1186/1471-2148-11-278

Shohami D, Nathan R (2014) Fire-induced population reduction and landscape opening increases gene flow via pollen dispersal in *Pinus halepensis*. Mol Ecol 23:70–81. doi:10.1111/mec.12506

Smith MD (2011) An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. J Ecol 99:656–663. doi:10.1111/j.1365-2745.2011.01798.x

Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

Tapias R, Gil L, Fuentes-Utrilla P, Pardos JA (2001) Canopy seed banks in Mediterranean pines of south-eastern Spain: a comparison between *Pinus halepensis* Mill., *P. pinaster* Ait., *P. nigra* Arn. and *P. pinea* L. J Ecol 89:629–638. doi:10.1046/j.1365-2745.2001.00575.x

Tapias R, Climent J, Pardos JA, Gil L (2004) Life histories of Mediterranean pines. Plant Ecol 171:53–68. doi:10.1023/B:VEGE.0000029383.72609.f0

Teich AH (1970) Cone serotiny and inbreeding in natural populations of *Pinus banksiana* and *Pinus contorta*. Can J Bot 48:1805–1809

Thibault KM, Brown JH (2008) Impact of an extreme climatic event on community assembly. Proc Natl Acad Sci USA 105:3410–3415

Thompson RM, Beardall J, Beringer J et al (2013) Means and extremes: building variability into community-level climate change experiments. Ecol Lett 16:799–806. doi:10.1111/ele.12095

Tinker DB, Romme WH, Hargrove WW et al (1994) Landscape-heterogeneity in lodgepole pine serotiny. Can J For Res 24:897–903

Tonnabel J, Van Dooren TJM, Midgley J et al (2012) Optimal resource allocation in a serotinous non-resprouting plant species under different fire regimes. J Ecol 100:1464–1474. doi:10.1111/j.1365-2745.2012.02023.x

Tryjanowski P, Sparks TH, Profus P (2009) Severe flooding causes a crash in production of white stork (*Ciconia ciconia*) chicks across Central and Eastern Europe. Basic Appl Ecol 10:387–392. doi:10.1016/j.baae.2008.08.002

Wernberg T, Smale DA, Tuya F et al (2012) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nat Clim Chang 5:1–5. doi:10.1038/nclimate1627

White WJ, Rassweiler A, Samhouri JF et al (2013) Ecologists should not use statistical significance tests to interpret simulation model results. Oikos. doi:10.1111/j.1600-0706.2013.01073.x

Zedler PH (1995) Fire frequency in southern California shrublands: biological effects and management options. In: Keeley JE, Scott T (eds) Brushfires in California wildlands: ecology and resource management. International Association of Wildland Fire, Fairfield, pp 101–112