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GENETIC CONSEQUENCES OF FIRE TO NATURAL POPULATIONS

Ofer Steinitz,[a,b,*] D. Shohami,[b] R. Ben-Shlomo,[a] and R. Nathan[b]
[a]*Department of Biology, University of Haifa–Oranim, Kiryat Tiv'on 36006, Israel*
[b]*Movement Ecology Lab, Department of Ecology, Evolution, and Behavior, The Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Jerusalem 91904, Israel*

ABSTRACT

Fire plays an important role in many ecosystems worldwide. The implications of fire on population and community dynamics in natural ecosystems have been studied extensively. Nevertheless, the impact of fire on genetic diversity, a crucial component of biodiversity, remains largely under-investigated. We summarize the theoretical expectations on how ecological effects of fire can be translated into genetic impact in natural populations. We formulate predictions on the effect of fire on genetic variance between and within populations, on the change in allelic frequencies and on the spatial genetic structure within populations. We review the empirical evidence for the effect of fire on genetic characteristics of natural populations. Thus far, research on the genetic consequences of fire has been limited to plant populations with a few exceptions of reptile populations. Because the genetic impact of fire is diverse and complex, consideration of simultaneous ecological effects of fire, controlled analyses of pre-/post-fire in the same study site, and comparison of species differing in their ecological response to fire is crucial for disentangling the mechanisms by which fire affects genetic characteristics of natural populations. The expected increase in fire frequency and extent in natural ecosystems as a result of global climate change stresses the importance of understanding the genetic impact of fire. As more and more genetic data on natural populations in fire-prone habitats accumulate, this challenge will be advanced.

Keywords: fire, genetic impact, genetic diversity, gene flow, spatial geneticc structure

THE EFFECT OF FIRE ON NATURAL POPULATIONS

Fire, either natural or anthropogenic, has diverse effects on populations, communities and ecosystems around the world (Whelan, 1995; Bond and Van Wilgen, 1996). Although fire effects on ecosystems have been studied in detail, the effect of fire on genetic variation of natural populations remains largely under-investigated. While the genetic variation within a species is the least apparent component of biodiversity, it is the raw

*Author to whom correspondence should be sent. E-mail: ofer.steinitz@mail.huji.ac.il
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material for evolution and adaptation to environmental changes (Templeton et al., 2001). Here, we summarize predictions on the short-term genetic consequences of fire and review empirical studies that have examined the effect of fire on genetic characteristics of natural populations. Fire has additional important long-term genetic consequences as a selective force promoting fire-resistance traits, such as post-fire persistence in seed banks (Lamont et al. 1991; Goubitz et al., 2004; Bond and Keeley, 2005; Verdú and Pausas, 2007), that are not covered in this review. Since most of the research on this topic was carried out on plant populations, this review is focused on plants. However, we also include the few studies on the genetic impact of fire on populations of animals, which are currently confined to reptiles.

THEORETICAL EXPECTATIONS ON GENETIC CONSEQUENCES OF FIRE

To understand the genetic consequences of fire, one must consider its ecological impact on plants and animals. Plants are the major fuel for wildfire. Thus, fire directly affects plant survival, growth and reproduction. Fire is a discrete event "opening up space" at multiple scales, up to more than 1 million ha, at intervals up to 1000 years (Bond and van Wilgen, 1996). Fire can kill and injure portions of animal populations, but its indirect effects on animals, e.g., altering habitat conditions, can be even more dramatic (Whelan, 1995).

The effect of fire on both plants and animals is complex. Reproduction of many plant species is stimulated by fire, through enhanced flowering, seed germination, and seedling recruitment (Bond and van Wilgen, 1996), while many animal species are attracted to burned areas due to increased availability of food resources (Whelan, 1995). In fire-prone communities, in which recurring fire is an integral part of the ecosystem, fire suppression can have immense ecological consequences for the community (Templeton, et al., 2001; Nowacki and Abrams, 2008).

Plants may be divided into two categories based on their vegetative response to fire: resprouters survive fire and regenerate from buds, while non-resprouters are eradicated by fire and regenerate from seed banks (Bond and van Wilgen, 1996). These strategies apparently have different impacts on the genetic characteristics of the post-fire generation compared to the pre-fire population, and on the spatial genetic structure (tendency of like genotypes to cluster) of post-fire populations. Adult individuals of post-fire resprouting species have a high probability of surviving fires; consequently, fire probably has little impact on their allelic frequencies or spatial genetic structure. In contrast, adult plants of post-fire obligate seeding species die during fires, and a new seedling generation is recruited after a fire (Bond and van Wilgen, 1996). In such plants, seed banks (in soil or in canopy-stored fire-resistant cones) serve as genetic reservoirs harboring and replenishing the lost genetic variation of the adults (Lamont et al., 1991; del Castillo, 1994; Barrett et al., 2005; Ayre et al., 2010; Ottewell et al., 2011).

The degree of fire-resistance and behavioral response of animals to fire varies between species (Whelan, 1995; Webb and Shine, 2008). Thus, the demographic effect of fire on animal populations depends on fire severity and species characteristics, such as dispersal ability and the ability to re-colonize burnt areas (Whelan, 1995). Some of the traits that determine the demographic outcome following fire evolved in response to the species' past fire regime (Ne'eman et al., 2004; Bond and Keeley, 2005; Verdú and Pausas, 2007). Thus, the evolutionary history of the species may shape their demographic response.

Table 1 summarizes the ecological processes associated with fire and their major predicted consequences on different genetic attributes, further discussed below. Some of these predictions are only valid under specific conditions, so that contrasting predictions apply for different groups of species and systems. These predictions apply for species that suffer from direct or indirect reduction in population size following fire. However, in fire-maintained communities subject to frequent fires, fire may result in rise in population size of many species (Gerber and Templeton, 1996; Templeton et al., 2011) and increase in the connectivity between populations (Templeton et al., 2001; Schrey et al., 2011a). In accordance with the ecological effect predicted for these species, the genetic consequences following fire are basically the opposite of those presented in Table 1 and for simplicity are not included in the table.

A common direct and indirect effect of fire is reduction in population size (Whelan, 1995; Bond and van Wilgen, 1996), which may lead to a genetic bottleneck and genetic drift. Only a sample of the original individuals and their genes survive, and therefore a

Table 1
Ecological effects of fire and their predicted genetic impact[a]

Ecological effect of fire	Genetic impact				
	Genetic variation within population	Inbreeding level	Genetic variation between populations	Change in allelic frequencies	Spatial genetic structure
Reduction in population size	–	+	+	+	
Fragmentation and decreased dispersal levels	–	+	+	+	+
Sink effect	+	–	–	+	–
Increased dispersal levels	+/–	–	–		+/–
Habitat heterogeneity				+	+
Higher density		–			+/–
Lower density		+			+/–
Decrease in sexual reproduction (in resprouters)	–		+	–	+
Even-aged population (in non-resprouters)	–			+	+/–

[a] Predicted genetic impact for different ecological effects of fire are marked by a positive or a negative sign, whereas empty cell signify cases of no significant impact. Cases where the same ecological effect is predicted to have either positive or negative impact on a genetic characteristic through different mechanisms are marked by +/–.

decline in genetic variance within a population is expected. Small isolated populations also exhibit a higher chance of mating between relatives and may thus suffer from inbreeding depression, lower individual fitness, and, consequently, low population persistence (Young et al., 1996; Bacles and Jump, 2011).

Fire can turn large areas into barriers for dispersal and subdivide continuous populations into isolated subpopulations. Genetic drift in isolated small populations is expected to increase genetic differentiation between populations (Slatkin, 1987). Fragmented isolated populations also have higher rates of mating between relatives and selfing (Robledo-Arnuncio et al., 2004; Jamieson et al., 2007; Steinitz et al., 2011), and are therefore expected to show higher inbreeding levels and higher spatial genetic structure (De-Lucas et al., 2009). In general, fragmentation is expected to reduce gene flow between populations and further increase genetic differentiation between them (Slatkin, 1987; Young et al., 1996), although empirical evidence, mainly from tree species, shows a rather mixed picture (White et al., 2002; Dick et al., 2003; Bacles et al., 2004, 2006; Jump and Peñuelas, 2006; Bacles and Jump, 2011). For species that favor burned habitats, fire may increase population size and connectivity between populations, counteracting the genetic effects of population size reduction and fragmentation (Templeton et al., 2001; Schrey et al., 2011a).

Opening of the landscape or canopy following fire should facilitate wind-driven pollen and seed dispersal for longer distances, owing to reduction of obstacles for movement (Nathan et al., 2008) and stronger winds with increased vertical eddy motion (Nathan and Katul, 2005), leading to increased gene flow (He et al., 2004). In addition, if some plants survive the fire either in small patches or as isolated individuals, they will be in a much sparser population, resulting in increased pollen dispersal distances (for both animal- and wind-pollinated plants) because the distance to the nearest conspecifics has increased and the strength of local dilution effects has reduced. Elevated seed and pollen dispersal distances are expected to reduce spatial genetic structure at least in the first seed cohort pollinated after the fire (Shohami, 2012).

Fire can also influence source/sink dynamics (Schrey et al., 2011a). A reduction in population size or suppressed reproduction in a surviving post-fire population may reduce competition with locally-produced progeny, thus promoting establishment of individuals from neighboring populations, increasing incoming gene flow. The increased gene flow into a local population is expected to change the local allelic frequencies and to increase its genetic similarity to other source populations (Schrey et al., 2011a). The sink effect could increase genetic diversity in the post-fire population and reduce inbreeding levels (Schrey et al., 2011a), but, on the other hand, may also cause loss of genetic variation unique to the local population by gene "swamping" (Lenormand, 2002). If the burned population has a high pre-fire genetic diversity compared to neighboring unburned populations (as in a case of a natural population surrounded by conspecific agricultural fields), higher incoming gene flow induced by fire will reduce the genetic variance within the burned population.

The consequences of increased gene flow on fine-scale spatial genetic structure are context- and scale-dependent. Increased gene flow from neighboring populations is expected to break down spatial genetic structure as the high stochasticity typical for long-distance dispersal (Nathan, 2006) prevents clustering of similar genotypes. However, in some cases where incoming gene flow is spatially structured, for example, due to genetic differentiation between neighboring populations and directionality in dispersal (Steinitz et al., 2011), spatial genetic structure in relevant scales is expected to strengthen.

Fire may also affect the mode of reproduction. For resprouting plants, fire induces vegetative reproduction at the expense of sexual reproduction, resulting in less genetic recombination compared to fire-free population. This may reduce genetic diversity, increase genetic load (Lamont and Wiens, 2003), and lower the chance of a change in allelic frequencies between generations. Since pollen and seed are considered more efficient dispersal units (in terms of distance) than vegetative dispersal units (Winkler and Fischer, 2001), the lower amount of sexual reproduction entails reduction in gene flow and is expected to increase genetic differentiation between populations and spatial genetic structure.

In non-resprouter plants, fire often eradicates many or all mature individuals and causes a synchronous mass-recruitment of new seedlings, frequently several orders of magnitude higher than fire-free recruitment (Nathan and Ne'eman, 2004) either from the few surviving adults or from soil- or canopy-stored seed banks, resulting in an even-aged population (Lamont et al., 1991; Parker et al., 2001; Premoli and Kitzberger, 2005). Because of temporal variability in allelic frequencies of pollen and seed pool, even-aged populations are expected to have lower within-population genetic diversity and a greater change in allelic frequencies before and after a fire event compared to fire-free populations. However, if a seed bank results from the accumulation of reproductive output over several years, this homogenizing effect may be attenuated. Genetic differentiation among tree cohorts was suggested as a mechanism promoting spatial genetic structure in populations with continuous recruitment (uneven-aged), compared with synchronously recruiting populations (Perry and Knowles, 1991). On the other hand, synchronous mass-recruitment caused by fire is expected to result in highly dense populations (Boyle et al., 1990; Uchiyama et al., 2009), leading to higher overlap in seed shadows that is expected to weaken spatial genetic structure in the following cohort (Hamrick et al., 1993). In contrast, when fire has a fine-scale heterogeneous nature (e.g., a subset of individuals are killed by the fire), it can result in a lower-density population with less overlap in seed shadows, and, consequently, stronger spatial genetic structure in recruiting offspring (Hamrick et al., 1993).

Since selection to fine-scale environmental conditions promotes clustering of similar genotypes (Epperson, 1992), spatially non-uniform fire intensity may create patchiness in habitat conditions and contribute to spatial genetic structure. Ayre et al. (2009) suggested that non-uniform fire intensity is expected to shift allelic frequencies in populations with strong spatial genetic structure.

EMPIRICAL EVIDENCE FOR GENETIC EFFECTS OF FIRE

Studies on genetic consequences of fire follow two main approaches: 1) comparisons of sites with different fire history, and 2) pre/post fire comparisons in the same site. The first approach, although more frequently used, can be misleading because of potential pre-fire spatial heterogeneity in genetic characters due to underlying heterogeneity in environmental and historical conditions unrelated to fire history (Johnson and Miyanishi, 2008; Jump et al., 2009). We summarize empirical studies that used the first approach (Table 2) and highlight the few studies carried out using the second approach (Table 3).

COMPARISONS OF SITES WITH DIFFERENT FIRE HISTORY

Genetic variation within population and inbreeding levels

Several studies on plant populations support the prediction of negative effect of fire on genetic diversity (Boyle et al., 1990; Truesdale and McClenaghan, 1998; Premoli and Kitzberger, 2005; Kettle et al., 2007). Analyses of allozyme diversity in 17 subpopulations with different fire history from four populations of the serotinous obligate seeder, Tecate cypress (*Cupressus forbesii*), revealed that observed and expected heterozygosity increased significantly with time since the last fire but were not significantly associated with fire return interval. Mean number of alleles per locus increased significantly as a function of mean interval between fires and time since last fire (Truesdale and McClenaghan, 1998). In the critically endangered *Araucaria nemorosa*, a loss of rare alleles and elevated levels of inbreeding in the juvenile cohort, relative to the adult cohort, were attributed to habitat degradation as a result of frequent fires, among other factors. Similar genetic changes between cohorts were not observed in populations of the locally common sister species, *Araucaria columnaris*, that did not suffer from habitat degradation and had similar genetic characteristics as the adult cohort of *Araucaria nemorosa* (Kettle et al., 2007). A black spruce (*Picea mariana*) population, assumed to establish after fire, had a lower number of alleles and higher inbreeding level compared to a fire-free population (Boyle et al., 1990).

Other studies did not support the prediction of negative effect of fire on genetic diversity (Parker et al., 2001; Céspedes et al., 2003; Uchiyama et al., 2006). For example, in the tree *Betula maximowicziana*, post-fire stands and mixed conifer–hardwood stands did not differ in within-population genetic variation evaluated with 11 microsatellite markers in both adults and seeds (Uchiyama et al., 2006). This result was explained by the high wind-mediated seed and pollen dispersal ability of the species and its persistent soil seed bank.

Studies on reptiles demonstrate that the effect of fire on genetic diversity depends on the habitat preferences of the species. A study of Florida sand skink (*Plestiodon reynoldsi*) populations in the Florida scrub with a controlled fire regime, revealed that expected heterozygosity and abundance were positively correlated with time since the last fire, corresponding with the species' preference for long unburned habitat. However, other genetic indices were not correlated with time since last fire (Schrey et al., 2011b). A comparative study of this species with two lizard species that prefer open habitat revealed a variable response of genetic diversity to time since last fire (Schrey et al., 2011a). As for the Florida sand skink, the genetic diversity of the six-lined racerunner (*Aspidoscelis* *sexlineata*) increased with longer time since fire, whereas the genetic diversity of the Florida scrub lizard (*Sceloporus woodi*) decreased. The genetic diversity was higher in the preferred habitat of the species for the Florida sand skink (long unburned area) and for the Florida scrub lizard (recently burned area). Nonetheless, a different trend, though weaker, was shown for the six-lined racerunner, which had lower genetic diversity in its preferred habitat (recently burned area). The opposing trends may be explained by the dispersal ability of the species: the six-lined racerunner has very good dispersal ability compared to the other two dispersal-limited lizards, suggesting that the genetic diversity levels measured for the six-lined racerunner in the study sites were not determined by local fire history (Schrey et al., 2011a).

Genetic variation between populations

Support for the prediction that fire increases genetic differentiation, comes from a study on the tree *Betula maximowicziana*. Post-fire stands had a higher differentiation level ($F_{ST} = 0.016$ for 4 adult populations) than mixed conifer-hardwood stands ($F_{ST} = 0.008$ for 6 adult populations), despite the fact that the average of geographic distances between stands was shorter in post-fire stands (4.8 km) than in mixed stands (7.3 km). This result is consistent with the higher support for genetic bottleneck in the post-fire populations as compared to the fire-free populations, as revealed in the same study (Uchiyama et al., 2006).

Spatial genetic structure

Contrasting results for the response of spatial genetic structure to fire exist in the literature. Spatial genetic structure was measured in the conifer tree *Pinus clausa* var. *clausa* using 12 allozyme loci, in pairs of populations with different fire history from three locations. Spatial genetic structure was detected in the three young populations that experienced a relatively recent fire (1956–1970), but not in any of the neighboring old populations (last burned in ~1920–1930). Genetic structure was less evident in populations of another variety of the species, *Pinus clausa* var. *immuginata*, distributed in areas that are not fire-prone with uneven age distribution (Parker et al., 2001). In the Mediterranean maritime pine (*Pinus pinaster*), stronger spatial genetic structure was found in a fragmented population subject to recurrent fires in the last centuries compared with two continuous populations. Since density did not differ between the populations, the result was attributed to limited effective seed dispersal and increased mating between relatives, and to selfing in the fragmented population (De-Lucas et al., 2009).

In contrast to the above results, a black spruce (*Picea mariana*) population assumed to establish after fire had no spatial genetic structure, whereas a fire-free population 2 km away had significant spatial genetic structure (Boyle et al., 1990). The authors suggested that the spatial genetic structure developed in the fire-free population because close-stand conditions limit seed dispersal, whereas in post-fire conditions, seed dispersal is more efficient. Comparisons between neighboring burned (characterized by high density and even age) and unburned (characterized by low density and uneven age) populations of the obligate seeder forest tree *Nothofagus dombeyi*, revealed significant spatial genetic structure only in unburned stands (Premoli and Kitzberger, 2005). In contrast,

Table 2
Empirical results of studies examining the genetic consequences of fire in plant and animal populations by comparing sites with different fire history. TSF = Time since last fire.

Reference	Kingdom	Species	Fire history or fire return interval	Ecological effect of fire
Boyle et al., 1990	Plants	*Picea mariana*	Unspecified	High density, even-aged population
Truesdale and McClenaghan, 1998	Plants	*Cupressus forbesii*	Fire interval 23–115 years	Fragmentation, reduction in population size
Parker et al., 2001	Plants	*Pinus clausa* var. *clausa*	Fire interval 30–60 years	Even-aged population
Cespedes et al. 2003	Plants	*Swietenia macrophylla*	Multiple fires over the last 50 years	Unknown or unspecified
Premoli and Kitzberger, 2005	Plants	*Nothofagus dombeyi*	TSF—80, 60, and 50 years	High density, even-aged population
Uchiyama et al., 2006	Plants	*Betula maximowicziana*	TSF—90 years	High density population; presumed drastic reduction in population size
Kettle et al., 2007	Plants	*Araucaria nemorosa*	Much of disturbance attributed to last 150 years	Habitat degradation, lower density of adult population
Premoli and Steinke, 2008	Plants	*Nothofagus antarctica*	TSF—8–154 years	Unknown or unspecified
Uchiyama et al., 2009	Plants	*Betula maximowicziana*	TSF—90 years	High density population; presumed drastic reduction in population size
De-Lucas et al., 2009	Plants	*Pinus pinaster*	Recurrent forest fires throughout centuries	Fragmentation
Schrey et al., 2011a	Animals	*Aspidoscelis sexlineata*	TSF—3–21 years. Habitat-dependent fire interval 15–20 or 15–100 years	Sparser vegetation; unspecified effect on studied species
Schrey et al., 2011a	Animals	*Sceloporus woodi*	TSF—3–21 years. Habitat-dependent fire interval 5–20 or 15–100 years	Sparser vegetation; unspecified effect on studied species
Schrey et al., 2011b	Animals	*Plestiodon reynoldsi*	TSF—3–6, 8–14, 18–39 years. Habitat-dependent fire interval 5–20 or 15–100 years	Sparser vegetation; unspecified effect on studied species

Genetic variation within population	Inbreeding level	Genetic variation between populations	Spatial genetic structure
Burned<unburned	Burned>unburned	Unaffected by fire	Significant only in unburned population
Increase with TSF and fire return interval			
No effect of TSF			Weakens with TSF
Decrease in number of alleles with TSF but not in effective number of alleles, no change in heterozygosity			
Burned<unburned not in all indices			Significant only in unburned populations
No effect in adults and seeds		After>before fire	No effect in adult trees
Young cohort<adults	Young cohort>adults	Unaffected by fire	
			Significant in post-fire populations
			Significant in pollen pool only in post-fire populations; significant cant in seeds only in fire-free populations
			Stronger in sites subject to recurrent fires
Increase with TSF			
Decrease with TSF			
Increase in expected heterozygosity with TSF			

Table 3
Empirical results of studies examining the genetic consequences of fire in plant and animal populations using pre-/post- fire comparisons in the same site. TSF = Time since last fire.

Reference	Kingdom	Species	Fire history or fire return interval	Ecological effect of fire
Dolan et al., 2008	Plants	*Hypericum cumulicola*	Fire-prone habitat, TSF—1,2,3 years	Nearly all plants killed, followed by rapid increase in population size
Ayre et al., 2009	Plants	*Persoonia mollis* ssp. *nectens*	TSF—0.5 and 3.5 years	Complete population eradication in 1st fire; complete eradication of all emergent seedlings in 2nd fire
Ottewell et al., 2011	Plants	*Acacia pinguifolia*	TSF—0.5 to 1.5 years	All adults but one killed in fire
Hutchison and Templeton, 1999; Templeton et al., 2001; Neuwald, 2008	Animals	*Crotaphytus collaris collaris*	Fire-maintained community. Fire return interval—once every 5 years in historically natural settings (and also after initialization of prescribed burnings)	Higher dispersal levels and increased population size; lower density of plants

post-fire populations of the resprouter sister species *Nothofagus antarctica* showed a significant spatial genetic structure (Premoli and Steinke, 2008).

Study on the tree *Betula maximowicziana* shows that the effect of fire on spatial genetic structure may differ between life stages. For adult trees, no significant genetic structure was detected in both low density fire-free stands and high density post-fire stands (Uchiyama et al., 2006). No significant genetic structure was detected in the pollen pools in low density fire-free stands, as opposed to significant genetic structure in post-fire high density stands, implying an enhanced pollen flow between adults in low density stands (Uchiyama et al., 2009). However, significant genetic structure among dispersed seeds was detected in the low density fire-free stands, but not in the high density post-fire stands (Uchiyama et al., 2009), as expected due to higher overlap in seed shadow in populations with higher density.

PRE/POST FIRE COMPARISONS IN THE SAME SITE

In a study by Ayre et al. (2009), unique circumstances in a fire-prone habitat enabled the analysis of the genetic consequences of multiple fire disturbances in the same study site for a population of a fire-sensitive obligate seeder shrub, *Persoonia mollis* ssp.

Genetic variation within population	Genetic variation between populations	Change in allelic frequencies	Spatial genetic structure
Increases after fire	Unaffected by fire	Significant change in allelic frequencies; addition of new alleles	
No change between adults and seedlings emerged after 1st and 2nd fire		No change in allelic frequencies between adults and seedlings that emerged after 1st and 2nd fire	Significant only in post-fire seedlings, stronger after 2nd fire
No change between adults and post-fire seedlings			
Decreases prior to fire, increases after fire	Increases before fire, stabilizes after fire		

nectens. Its relatively low overall allozyme diversity in this population was attributed to frequent local extinctions and recolonizations following fire (Krauss, 1997). In 1997, all adult plants in the studied population were killed in a wildfire. In 2001, a second wildfire eradicated all seedlings that emerged from the soil-stored seed bank following the 1997 fire (before they reached the reproductive stage). The second fire stimulated the germination of a second cohort of seedlings. DNA samples of the adults and seedlings from the two fire-induced cohorts were genetically analyzed using six microsatellite loci. There was no significant change in allelic frequencies or in genetic diversity (number of alleles and levels of heterozygosity) between the adults and the two post-fire seedling cohorts following the repeated wildfires. Ayre et al. (2009) concluded that the large and resilient soil-stored seed bank is a bet-hedging strategy shaped as an evolutionary response to frequent fires, which provides a genetic buffer against the effects of repeated fires, preventing erosion of genetic diversity. While no spatial genetic structure was detected in the adults, perhaps due to the much smaller sample size, significant spatial genetic structure was detected in both post-fire seedling cohorts, and it was much stronger after the second fire (Ayre et al., 2009).

Similarly, the seed bank of the endangered Australian obligate seeding shrub *Acacia* *pinguifolia* also acted as a genetic buffer in two sites exposed to prescribed burning, in which the relatively few seedlings that recruited after the fire (an equivalent number to that of pre-fire adults) had non-significantly higher expected heterozygosity than the pre-fire adults (Ottewell et al., 2011).

Another pre-/post-fire comparison within the same site was conducted by Dolan et al. (2008), for the short-lived perennial herb *Hypericum cumulicola*, in two neighboring sites (6 km apart) in the Florida scrub. Analyses of allozyme markers were performed for complete censuses conducted before a fire that burnt almost all the aboveground plants, and during three consecutive years after it. Population size and expected heterozygosity increased in both sites. Most seedlings probably recruited from persistent seed bank, since seed dispersal is extremely limited (average distance <1 m). In spite of significant changes in allele frequencies, and addition of new alleles following fire in each of the two sites, genetic differentiation between the two sites did not change after the fire (Dolan et al., 2008).

A fascinating example of studying the genetic consequences of fire under controlled experimental conditions comes from a long-term research on collared lizards (*Crotaphytus collaris collaris*) of the Missouri Ozarks (Hutchison and Templeton, 1999; Templeton et al., 2001). These lizards avoid close vegetation, and are restricted to glade habitats maintained by fire. Suppression of fire caused fragmentation of the glade habitat, low within-glade genetic diversity, and extremely high genetic differentiation between glades. In the same area, managed forest fires facilitated less woody and more open vegetation, increasing dispersal, colonization and population sizes of the collared lizard (Hutchison and Templeton, 1999; Templeton et al., 2001). Reintroduced populations of the species with known initial genetic characteristics were monitored for ten years under habitat fragmentation due to fire suppression, followed by another ten years of habitat restoration due to prescribed fires. Genetic analyses of six microsatellites revealed that prior to the initiation of prescribed burning, genetic diversity decreased within glades and population differentiation increased among glades. For the years following these burns, genetic diversity within glades increased, and population differentiation among glades stabilized (Neuwald, 2008).

Finally, Shohami (2012) examined gene flow via pollen dispersal in an Aleppo pine (*Pinus halepensis*) population inhabiting a fire-prone Mediterranean habitat in Israel. This tree is a wind-pollinated obligate seeder and "fire embracer" (Ne'eman et al., 2004), with a canopy-stored seed bank in serotinous cones that open and release their seeds in response to fire. A fire in 1998 reduced the studied Aleppo pine population by 96%. Thirteen trees survived the fire, and seven of these trees still had a few pre-fire serotinous cones that remained closed despite the fire, providing a unique opportunity to compare pre-fire and post-fire pollen dispersal on the same trees. Seeds were collected from the surviving trees from three cone cohorts—before the fire, immediately after the fire, and 10 years after the fire—and the pollen gametes sampled by these seeds were genetically analyzed using microsatellite markers. The study found that the pollen pool before the fire was highly spatially structured, and the bulk of the pollen most likely originated from within the population and from few, or highly similar, pollen donors.

After the fire, pollen dispersal was far less restricted, with a decrease in spatial genetic structure, increased arrival of pollen from outside the population, and a five-fold jump in the effective number of pollen donors, leading to an overall increase in incoming gene flow. The study attributed the results to the drastic drop in population size and density caused by the fire, leading to both a reduction in local (within-population) pollen production and ensuing dilution effect, and to increased winds in the sparse post-fire landscape (Shohami, 2012).

CONCLUSIONS

Fire has complex genetic implications that strongly depend on the temporal and spatial scales of the fire, and on the evolutionary history of the studied species that shaped their fire-response ecology. Studies of the genetic consequences of fire must consider the demographic outcome of the fire and its effect on movement patterns of genes and individuals. Many studies on this topic lack important information on the intensity of the fire, and its ecological effects on the studied populations (Tables 2, 3). Examining the genetic effects on several species (e.g., Schrey et al., 2011a) is a promising approach for linking species ecology to the genetic consequences of fire. The initial, pre-fire spatial distribution of genetic variation among individuals and populations can mold the genetic impact of fire. Therefore, inference of genetic consequences of fire from comparison of genetic characteristics between burned and unburned sites or in different locations is of limited value. Including control populations not affected by fire is essential for differentiating between fire and other temporal effects. As can be seen in Table 1, a genetic outcome might not be exclusive for one ecological effect of fire, and the same ecological effect might have contrasting genetic impacts. Thus, drawing conclusions on the mechanism for the genetic impact of fire from empirical results is a difficult task.

Disentangling the mechanisms explaining the genetic effects of fire remains an important challenge for future studies. Achieving this goal requires consideration of simultaneous ecological effects of fire and knowledge of the ecology of the study species and its response to fire. Because the genetic consequences of fire are diverse, more research on this topic is needed to better understand the genetic processes induced by fire. With the increasing availability of molecular tools, genetic data on more natural populations will accumulate. Data of this kind, collected in habitats likely to be affected by fire, should provide future research with more opportunities for pre- and post-fire comparisons and improve our understanding of the genetic impact of fire. This topic has important implications for biodiversity conservation and forest management, especially due to the incorporation of prescribed burning as an ecosystem and population management tool (Ottewell et al., 2011), and to the role of global warming in changing fire regime in natural ecosystems (McKenzie et al., 2004; Bowman et al., 2011).

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