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FIRE IN THE MEDITERRANEAN—FROM GENES TO ECOSYSTEMS

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INTRODUCTION

The "Carmel 2010 Fire" was the largest in Israel's history and involved 2,000 policemen, 650 fire-fighters from several countries, and 58 airplanes. These fire-fighters battled flames under severe winds and high temperatures for 3 days until the flammable materials were reduced in amount, the weather changed, and control was gained. The fire burned 2,500 hectares of forest, destroyed 81 homes and damaged 173 more, and sadly took the lives of 44 victims. Because of its heartbreaking results, the Israel State Comptroller conducted an independent investigation, and in June, 2012, published a comprehensive report that points to many long-term faults of all involved authorities and ministries. The detailed report (Israel State Comptroller, 2012) addressed the actions of the police, fire brigades, Ministry of the Interior, Finance Ministry, Ministry of Environmental Protection and the involved municipalities, as well as the Nature and Parks Authority (NPA) and the Forestry Department of the Jewish National Fund (KKL–JNF) for their lack of fire preventive management measures in forests, national parks, nature reserves, roadsides, and around human settlements and campsites.

There is no doubt that the Carmel 2010 Fire was extraordinary in its scale and effect on humans and nature, but can these results be explained simply by extraordinary weather conditions at the time of the fire? The specific weather conditions during the Carmel 2010 Fire and the preceding weeks were indeed exceptional: a long dry spell of over 8 months, extremely high temperatures with exceptionally low relative humidity, and the intense easterly winds that are normal for that season, caused the very rapid propagation of this disastrous fire (Kutiel, 2012). At the end, when the wind shifted from easterly to westerly, the fire-fighters' headquarters declared that the fire was under control. Energy budget analysis confirms that all available suppression equipment, including the support of international airplanes, were insufficient under the specific situation (Kutiel, 2012).

According to climatic models, most of the Mediterranean ecosystems will be exposed to a pronounced increase in drought by the end of the 21st century. Therefore, together

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with the increasing trend in this region to replace cultivated areas with forests (Lloret et al., 2002) and reducing grazing, the Mediterranean Basin is potentially expected to face a more intensive fire regime. Hence, the burned areas in the Mediterranean Basin are expected to increase 3–5 fold at the end of this century (Dury et al., 2011). Therefore, although Mediterranean ecosystems have a long history of wildfires and are assumed to be fire-resilient, this expected change in fire regime will potentially alter the resilience of the flora and fauna, and their composition.

Following the Carmel Fire, this special issue of the *Israel Journal of Ecology & Evolution* on the topic of "Fire in the Mediterranean—from genes to ecosystems" provides a broad and updated scope of the effect of wildfires on natural ecosystems and forest plantations. This compendium presents updated mini-reviews and case studies on various aspects of fire ecology, focusing on Mediterranean ecosystems. The articles range from a global comparison of the five Mediterranean-Type Climate (MTC) regions (Mediterranean Basin, California, South Africa, Western and South Australia, and central Chile), large scale weather and regional landscape studies (climate, fire models, and soil), fire effects on specific vegetation types (pine forest and maquis), various organism groups (plants, invertebrates, and vertebrates), and biotic interactions (pollination and dispersal), down to the effect of fire on plant population genetics. Finally, to bridge the gap between science and practice, taking into account the various effects of fire, we present a review of postfire management in the Mediterranean region, which aims at reducing the negative effects of fire on human properties, forests, and natural ecosystems by enhancing natural regeneration and succession.

FIRE IN MEDITERRANEAN-TYPE CLIMATE REGIONS

The Mediterranean Basin has a globally unique Mediterranean-Type Climate (MTC) with hot, dry summers commonly lasting four to six months, and a wet winter. The other four MTC regions—California, South Africa, Western and South Australia, and central Chile—share a similar MTC, which stands as one of the classic examples of convergent evolution (see, for example, Cody and Mooney, 1978; Keeley et al., 2012). One major selective agent of this global convergence, fire, has been largely absent from earlier comparative studies, but recently was raised as an important factor affecting plant evolution in all MTC regions (Keeley et al., 2012). However, differences in current fire regimes and, mainly, in the geological history of the various MTC regions, affected the general convergent evolution of plant traits and resulted in differences in the fire-related traits that promote the postfire regeneration of vegetation. Higher soil fertility and consequently greater competition among plants in the postfire environments in California and the Mediterranean Basin has probably resulted in more intensive selection for postfire vegetative resprouting and fire-independent recruitment. Consistent with this hypothesis is the observation that, in both these regions, postfire seeding species are abundant at the arid end of the moisture gradient. In South Africa and Western Australia, where soils are geologically older, acidic, and nutrient poor, postfire resprouters do not pose a highly competitive challenge to seedlings and thus postfire seeding is more widespread (Keeley, 2012).

FIRE, SOIL, AND LANDSCAPE

During severe wildfires much of the aboveground biomass is consumed, producing high temperatures (300–1,000 ºC), and leaving exposed soil and ash layers. This drastic change in the landscape commonly increases runoff and soil erosion (Shakesby, 2011) and export by wind and water of the nutrients that were part of the plants' biomass and turned to ashes (Trabaud, 1987). The fire also affects physical, chemical, and biological soil properties (organic matter, deterioration of structure and porosity, loss of nutrients), and exposes bare soil to erosion (Neary et al., 1999). The extent of these processes determines postfire regeneration of soil-dwelling animals (Radea and Arianoutsou, 2012) as well as plants (Malkinson et al., 2011). During the first postfire year, soil loss after the Carmel Fire exceeded natural renewal rates at a very localized scale, but on larger scales the data are inconsistent, owing to greater spatial heterogeneity and difficulties in assessing field variability (Wittenberg, 2012). The rate of postfire soil recovery may last up to a couple of decades, while in the meantime nutrients are mineralized and soil is exposed to increased erosion. The data on the effects of fire on soil properties and dynamics are important and need to be considered for postfire management decisions (Wittenberg, 2012).

Habitat heterogeneity is a major factor affecting biodiversity (Atauri and de Lucio, 2001); thus, fires that consume the vegetation leave relatively homogeneous bare soil that might negatively affect biodiversity in the regenerating forests and other plant formations. Fire intensity affects post-fire soil properties and erosion (Shakesby, 2011), and consequently also post-fire regeneration (Moritz et al., 2005). Therefore, studying the factors affecting spatial heterogeneity of fire intensity is important for predicting the expected heterogeneity of the regenerating forests and their biodiversity. Three main natural factors affecting wildfire scale and intensity: vegetation properties, weather conditions, and topographical relief (Moritz et al., 2005); an additional factor is the spatial aspects of preventive fire-control measures. The interaction among these factors also determines the heterogeneity of the post-fire landscape. Using post-fire aerial photographs of Mount Carmel (December, 2010) and fire spread simulation models, post-fire spatial heterogeneity was studied (Malkinson, 2012). Broadleaved oak-dominated communities were less flammable than pine forests, and flame heights in those communities were lower. Wildfire was more sensitive to wind speed than to foliar moisture content. Consequently, it is suggested that extreme conditions generated higher severity damage with a lower heterogeneity in the landscape (Malkinson, 2012).

FIRE AND PLANTS

In spite of the convergent evolution among MTC regions (Keeley, 2012), when examining fire-related traits of the Mediterranean Basin flora at a finer scale we recognize several characteristics that differ from other MTC regions (Ne'eman et al., 2012). The relative number of species with lignotubers, which are underground storage organs that produce abundant post-fire regeneration buds, and plants with serotinous cones or fruits, which open and disperse seeds mainly after fire, are both lower in the Mediterranean

Basin flora than in most other MTC regions (except central Chile). However, serotinous plants are much more prominent in the Mediterranean Basin than in Californian landscapes. Many Mediterranean Basin species have physically dormant seeds that are cued to germinate after fire by heat shock, while the effect of smoke on seed germination in the Mediterranean Basin flora is less common than in other MTC regions. Geophytes expressing massive postfire flowering in the Mediterranean Basin are opportunistic and not obligate fire-stimulated flowering species (Ne'eman et al., 2012). It is proposed that differences in current, historical, and geological fire regimes could account for the differences among MTEs in plants' fire-related traits (Keeley, 2012; Ne'eman et al., 2012).

Invasive plants can threaten biological diversity by reducing genetic variation and eroding gene pools, through the extinction of endemic species, and by altering habitat and ecosystem functioning (Vilà et al., 2010). However, in some cases they can add to biodiversity if they occupy less populated habitats or support many insect species and their predators (Tepedino et al., 2008). The early post-fire environment is open for competition among heliophylous, fast-growing plants, characteristics typical of many alien invasive species. In addition, some plant invaders can significantly alter fire regimes by changing plant fuel properties through the replacement of existing fire-sensitive plant communities by more flammable but fire-resistant invasive species (Brooks et al., 2004). In the Mediterranean Basin, research on post-fire biological invasions is rather limited compared to other MTC regions of the world (Arianoutsou and Vilà, 2012). Dry and fire-prone habitats of the Mediterranean Basin seem to be less susceptible to alien plant invasions relative to other MTC regions. However, the expansion of perennial grasses over shrubs in frequently burned areas in Spain has been reported as a critical issue related to plant invasions. In areas of southern Europe with more humid climates (northern and central Portugal), woody invasive species such as *Acacia* spp. and *Eucalyptus* spp. seem to have become a problem (Arianoutsou and Vilà, 2012).

The genetic structure of populations reflects the evolutionary history of the species, but is also shaped by the current ecological conditions via their effect on population size and connectivity (Loveless and Hamrick, 1984; Hartl and Clark, 2007). Although fire has dramatic ecological effects on the populations of all organisms living in the burned area, and the implications of fire on population and community dynamics in MTC ecosystems have been extensively studied (Keeley et al., 2012), fire impact on genetic diversity is largely under-investigated. Plants have different post-fire regeneration strategies (Steinitz et al., 2012). Post-fire resprouters survive fires, and fire probably has little impact on their allelic frequencies or spatial genetic structure; in contrast, obligate seeding species regenerate from canopy or soil seed banks and thus are more exposed to the effects of fire. The demographic effect of fire on animal populations depends on fire severity and species characteristics, such as escape ability and the ability to re-colonize burnt areas. Thus, the genetic response to fire is species-, season-, location-, and event-specific. Fire may commonly affect breeding systems by increasing inbreeding in isolated populations. In wind-pollinated and wind-dispersed plants, fire may increase potential pollen and seed dispersal distances by opening up the landscape. Increased gene flow from neighboring populations, post fire, is expected to break down spatial

genetic structure. However, where incoming gene flow is spatially structured, genetic structure at relevant scales is expected to strengthen. Several studies on plant populations support the prediction of a negative effect of fire on genetic diversity, while others do not. Contrasting results for the response of plant spatial genetic structure to fire exist in the literature (see references in Steinitz et al., 2012).

FIRE AND ANIMALS

Studies on reptiles demonstrate that the effect of fire on genetic diversity depends on habitat preferences of the species. The expected increase in fire frequency and extent in natural and forested Mediterranean ecosystems as a result of global climate change, stresses the importance of understanding the genetic impact of fire (Steinitz et al., 2012).

Soil-dwelling arthropods make up an almost undetected group that has an extremely important function in forest ecosystems. Many of them live on detritus that accumulates on the forest floor, breaking it down and increasing the surface-to-mass ratio, which enhances further chemical degradation by fungi and microbes (Lavelle et al., 1997). Community composition and population dynamics of soil arthropods in burned Mediterranean pine forests are determined by their life history traits and fire regime (Radea and Arianoutsou, 2012). Severe wildfires cause a simplification of soil arthropod community structure due to immediate mortality of soil animals and alterations in content and structure of soil organic horizon. Frequent wildfires indirectly influence soil arthropods by impeding recovery of the vegetation and the organic soil horizon. However, at least at the taxonomic level, wildfires don't change the phenology of soil arthropods, and the unique seasonality of the Mediterranean climate remains the principal factor controlling the dynamics of soil arthropod populations. Post-fire recovery of soil arthropods varies with species and fire regime, and is dependent on characteristics of the post-fire forest regeneration (Radea and Arianoutsou, 2012).

Most of the ecological fire research has been performed in connection to plants, as fuel or as a response group, while the study of fire ecology of animals is relatively rare, as can be seen in textbooks (for example, Trabaud, 1987; Whelan, 1995; Bond and van Wilgen, 1996; Keeley et al., 2012). Wildfires impose drastic habitat and landscape modifications that govern vertebrate dynamics and structure at the population and community levels. At the population level, burned areas support species of open- and edge-habitat, whereas in unburned woody areas forest-dwelling species are abundant (Izhaki, 2012). Wildfires reduce habitat availability for forest animals, but their overall impact on biodiversity conservation can be positive since they increase landscape heterogeneity. The effect of fires in the Mediterranean Basin on biodiversity is highly variable and dependent upon the extent, severity, and frequency of fires, the initial state of the ecosystem, and the spatial arrangement and isolation of the postfire burned and unburned patches. Management of the landscape as a mosaic of habitats and areas with different fire histories is vital for the preservation of high vertebrate biodiversity in the Mediterranean region (Izhaki, 2012).

Pollination and seed dispersal by animals represent two critical points in plant life

history where mutual relations with different kind of animals are involved. Plants affect the populations of their pollinators and dispersers by supplying them food; in return the sexual reproduction, seed dispersal, and population genetic structure of the plants, all critical for their survival or expansion, are affected by the populations of pollinators and seed dispersers (Loveless and Hamrick, 1984). Postfire plant communities change in their composition, structure, floral resources, as well as seed and fruit resources (Dafni et al. 2012). Fire directly affects communities of pollinators, seed dispersers, and seed predators mainly by mortality, and indirectly through changes in the quality and quantity of food and nesting resources. Pollinators, seed-dispersers, and seed predators depend on plant community composition and on the flower, seed, and fruit resources they produce. As a consequence, their community composition, structure, and function are expected to vary in response to post-fire temporal and spatial changes in plant communities, which in turn depend on fire severity, frequency, scale, and the distance from fire-edge, as well as their foraging range. In return, the changes resulting from fire in pollinator, seed-disperser, and seed predator communities may affect plant fecundity and plant community composition (Dafni et al., 2012).

MANAGEMENT

If we are to enhance natural post-fire processes in a way that conserves nature and its biodiversity, we need to investigate and understand not just the scientific issues but also the impact of forest fire prevention management as well as post-fire restoration actions. The traditional restoration approach to large forest fires in the late 1970s, when forest fire frequency in pine plantations and natural vegetation in the Mediterranean Basin began to increase, involved planting pines and building check dams where soil erosion was expected (Vallejo and Alloza, 2012). In the last two decades, post-fire restoration practices have increasingly diversified in both number of plant species used in plantations and the type of restoration actions taken. In an attempt to provide a comprehensive post-fire restoration strategy, new protocols that include scientific knowledge provided by fire and restoration ecology are currently being developed and tested. Using a GIS-based approach, fire-vulnerable forests and shrublands are identified. Vegetation resilience is assessed on the basis of fire regeneration strategies of dominant plant species. Vulnerable areas meriting emergency actions are those predicted to have a low plant cover regeneration rate and a high erosion risk. Mid- and long-term actions are planned according to the specific management objectives for burned areas, and the prediction of long-term ecosystem recovery. These actions may include assisted natural regeneration, (re)introduction of tree or shrubby species, and fire-prevention measures (Vallejo and Alloza, 2012).

CONCLUSIONS

Fires are commonly regarded by laymen as "force majeure", meaning that humans cannot predict or control them. However, a rapid look at the Mount Carmel's fire-history

reveals that during 1944–1982 the frequencyof large fires was ca. once every 6 years, whereas during 1983–2010 it increased to about one large fire every 3 years (Wittenberg and Malkinson, 2009). The anticipated climatic changes in the region may cause repetitions of such weather conditions as during the Carmel 2012 Fire (Kutiel, 2012). This means that fires are predictable and even expected to increase in frequency because of global climate change and socioeconomic processes. Thus, we need to learn how to live with fires while minimizing their damages to mankind and nature.

The large body of knowledge presented in this *Israel Journal of Ecology & Evolution* special issue is far from inclusive of all scientific and applied aspects of fire in the Mediterranean Basin. The scientific importance of this special issue is mainly in that it presents recent advances in the various research fields. However, from the applied point of view, the highly variable responses to fire across scales (plot to landscape), organization levels (genes, individuals, population, and communities), taxonomic groups, life forms, and trophic levels, as well as the unknown effect on other organisms that have not been studied yet, makes it practically impossible to draw sufficient management conclusion that may minimize the negative effects of fires on all categories. Nevertheless, two general conclusions can be drawn: (1) Due to the huge difficulty to suppress wildfires under extreme weather conditions, which are expected to become more frequent in the future, we must change the national policy of forest fire fighting away from just suppressing fires to pre-fire application of forest management techniques and prevention measures that will decrease fire risk and increase the success of fire fighting. (2) Application of different postfire restoration regimes in relatively small areas will create a "mosaic pattern" at all possible landscape scales will enhance biodiversity and potentially improve ecosystem functions on postfire landscapes, while minimizing negative effects of any single management treatment.

REFERENCES

Arianoutsou, M., Vilà, M. 2012. Fire and invasive plant species in the Mediterranean Basin. Isr. J. Ecol. Evol. 58: 195–203 (in this issue).

Atauri, J.A., de Lucio, J.V. 2001. The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. Landscape Ecol. 16: 147–159.

Bond, W.J., van Wilgen, B.W. 1996. Fire and plants. Chapman & Hall, London, 263 pp.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., DiTomaso, J.M., Grace, J.B., Hobbs, R.J., Keeley, J.E., Pellant, M., Pyke, D. 2004. Effects of invasive alien plants on fire regimes. Bioscience 54: 677–688.

Cody, M.L., Mooney, H.A. 1978. Convergence versus nonconvergence in mediterranean-climate ecosystems. Annu. Rev. Ecol. Syst. 9: 265–321.

Dafni, A., Izhaki, I., Ne'eman, G. 2012. The effect of fire on biotic interactions in Mediterranean basin ecosystems: pollination and seed dispersal. Isr. J. Ecol. Evol. 58: 235–250 (in this issue).

Dury, M., Hambuckers, A., Warnant, P., Henrot, A., Favre, E., Ouberdous, M., Francois, L. 2011. Responses of European forest ecosystems to 21st century climate: assessing changes in interannual variability and fire intensity. Forest-Biogeosciences and Forestry 4: 82–99.

Hartl, D.H., Clark, A.G. 2007. Principles of population genetics, 4th Ed. Sinauer Associates, Sunderland, MA.

Israel State Comptroller. 2012. The December 2110 Carmel Fire report. Cat # 2012 004, ISSN 0334-9713 Jerusalem, 544 p.

Izhaki, I. 2012. The impact of fire on vertebrates in the Mediterranean Basin: an overview. Isr. J. Ecol. Evol. 58: 221–233 (in this issue).

Keeley, J.E. 2012. Fire in Mediterranean climate ecosystems—a comparative overview. Isr. J. Ecol. Evol. 58: 123–135 (in this issue).

Keeley, J.E., Bond, W.J., Bradstock, R.A., Pausas, J.G., Rundel, P.W. 2012. Fire in Mediterranean Climate ecosystems: ecology, evolution and management. Univ. of Cambridge Press, Cambridge, UK, 515 pp.

Kutiel, H. 2012. Weather conditions, forest fire propagation, and climatic changes. Isr. J. Ecol. Evol. 58: 113–122 (in this issue).

Lavelle, P., Bignell, D., Lepage, M., Wolters, W., Roger, P., Inespon, P., Heal, O.W., Dhillson, N. S. 1997. Soil function in a changing world: the role of invertebrate ecosystem engineers. J. Soil Biol. 33: 159–193.

Lloret, F., Calvo, E., Pons, X., Diaz-Delgado, R. 2002. Wildfires and landscape patterns in the Eastern Iberian Peninsula. Landscape Ecol. 17: 745–759.

Loveless, M.D., Hamrick, J.L. 1984. Ecological determinants of genetic structure in plant populations. Annu. Rev. Ecol. Sys. 15: 65–95.

Malkinson, D. 2012. Wildfire heterogeneity: empirical vs. simulated observations—the Carmel 2010 wildfire as a case study. Isr. J. Ecol. Evol. 58: 165–176 (in this issue).

Malkinson, D., Wittenberg, L., Beeri, O., Barzilai, R. 2011. Effects of repeated fires on the structure, composition, and dynamics of Mediterranean maquis: Short- and long-term perspectives. Ecosystems 14: 578–488.

Moritz, M.A., Morais, M.E., Summerell, L.A., Carlson, J.M., Doyle, J. 2005. Wildfires, complexity, and highly optimized tolerance. Proc. Natl. Acad. Sci. USA 102:17912-917.

Ne'eman, G., Lev-Yadun, S., Arianoutsou, M. 2012. Fire-related traits in Mediterranean basin plants. Isr. J. Ecol. Evol. 58: 177–194 (in this issue).

Neary, D.G., Klopatek, C.C., DeBano, L.F., Ffolliott, P.F. 1999. Fire effects on belowground sustainability: a review and synthesis. Forest Ecol. Manage. 122: 51–71.

Radea, C., Arianoutsou, M. 2012. Soil arthropod communities and population dynamics following wildfires in pine forests of the Mediterranean Basin: a review. Isr. J. Ecol. Evol. 58: 137–149 (in this issue).

Shakesby, R.A. 2011. Post-wildfire soil erosion in the Mediterranean: review and future research directions. Earth-Sci. Rev. 105: 71–100.

Steinitz, O., Shohami, D., Ben-Shlomo, R., Nathan, R. 2012. Genetic consequences of fire to natural populations. Isr. J. Ecol. Evol. 58: 205–220 (in this issue).

Tepedino V.J., Bradley, B.A., Griswold, T.L. 2008. Might flowers of invasive plants increase native bee carrying capacity? Intimations from Capitol Reef National Park, Utah. Nat. Areas J. 28: 44–50.

Trabaud, L. 1987. The role of fire in ecological systems. SPB Academic Publishing, The Hague.

Vallejo, V.R., Alloza, J.A. 2012. Post-fire management in the Mediterranean Basin. Isr. J. Ecol. Evol. 58: 251–264 (in this issue).

Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A., Roy, D., Hulme, P.E., DAISIE partners, 2010. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Front.

Ecol. Environ. 8: 135–144.
Whelan, R.J. 1995. The ecology of fire. Cambridge Univ. Press, Cambridge, New York, 346 pp.
Wittenberg, L., Malkinson, D. 2009. Spatio-temporal perspectives of forest fire regimes in a maturing Mediterranean mixed pine landscape. Eur. J. For. Res. 128: 297–304.
Wittenberg. L. 2012. Post-fire soil ecology: properties and erosion dynamics. Isr. J. Ecol. Evol. 58: 151–164 (in this issue).