ISRAEL JOURNAL OF ECOLOGY & EVOLUTION, Vol. 58, 2012, pp. 137–149
10.1560/IJEE.58.2-3.137

SOIL ARTHROPOD COMMUNITIES AND POPULATION DYNAMICS FOLLOWING WILDFIRES IN PINE FORESTS OF THE MEDITERRANEAN BASIN: A REVIEW

Canella Radea* and Margarita Arianoutsou
Department of Ecology and Systematics, Faculty of Biology, School of Sciences, National and Kapodistrian University of Athens, 15784 Panepistimiopolis, Greece

ABSTRACT

The Mediterranean pine species of low-and mid-elevations, namely *Pinus halepensis* Mill., *Pinus brutia* Ten., *Pinus pinea* L. and *Pinus pinaster* Ait., constitute an important component of forest vegetation in Mediterranean-type ecosystems around the Mediterranean basin. These forests are strongly influenced by wildfires, which have occurred for millennia in Mediterranean regions. In burned Mediterranean pine forests, the community composition and the population dynamics of soil arthropods are determined by their life history traits and the wildfire regime. In these ecosystems, the effects of fire regime on soil arthropods at the taxonomical level of order are similar to those recorded in other Mediterranean-type ecosystems. Severe wildfires cause a simplification of the structure of the soil community due to both the immediate mortality of soil animals and the structural alteration of the soil organic horizon. Frequent wildfires influence the soil arthropods indirectly, preventing the recovery processes of the vegetation and, consequently, of the organic horizon. Wildfires do not influence the phenology of soil arthropods, at least at the taxonomical level of order, and the seasonality of the Mediterranean climate remains the principal environmental factor controlling the dynamics of soil arthropod populations. The recovery patterns of soil arthropods vary in relation to species, fire regime, and the environmental characteristics of the forest under consideration.

Keywords: Mediterranean ecosystems, pine forests, fire regime, soil arthropods, post-fire recovery

INTRODUCTION

Pine forests constitute one of the dominant Mediterranean-type ecosystems (MTEs) in the regions around the Mediterranean basin (Quézel, 1980). These forests consist of low- to mid-elevation pine species, namely *Pinus halepensis* Mill., *Pinus brutia* Ten., *Pinus pinea* L., and *Pinus pinaster* Ait., and occupy the thermo- to supra-Mediterranean bioclimatic zone (Quézel, 1980; Barbéro et al., 1998). The first two species alone account for about 25% of the forested area (Quézel, 2000), the others being of secondary

*Author to whom correspondence should be addressed. E-mail: kradea@biol.uoa.gr
Received 15 September 2011; accepted in revised form 5 March 2012.

importance (Quézel, 1980). *P. halepensis* is the most abundant pine in the Mediterranean basin, covering more than 2.5 million ha (Pausas et al., 2008).

The Mediterranean pine forests (MPF) are characterized by high litter production, low to moderate decomposition rate of accumulated dead organic matter (Rapp, 1967; Dannaoui, 1981; Radea, 1989), and high flammability because live and dead plant tis- sues of the Mediterranean vegetation usually contain large amounts of essential oils and resins (Attiwill, 1994; Trabaud, 2000).

Mature pine and mixed forests with pines, oaks, and shrubs represent the most important biosphere landscapes acting as the last refuges for Mediterranean plants and animals (Naveh, 2000; Fattorini, 2010).

Fire is considered an integral part of the dynamic of various ecosystems including the Mediterranean ones (Pausas and Vallejo, 1999; Bengtsson, 2002). Around the Mediterranean basin, fire has been a predominant environmental factor shaping the landscape for millennia (Pausas et al., 2008). Fire incidents are very common in the Mediterranean regions and, in recent decades, both the number of fires and the burned surface area have increased (Moreira et al., 2011).

In the Mediterranean basin, the most fire-sensitive ecosystems are the pine woodlands, especially the lowland ones, because their ability to persist after fire is threatened by increased fire recurrence and burn severity (Pausas et al., 2008).

Arthropods are ubiquitous components of forest soils and they participate actively in all kinds of soil processes influencing soil structure, biological functions, and nutrient cycling (e.g., Wallwork, 1970; Petersen and Luxton, 1982). The effects of fire on soil arthropods have been studied extensively in various ecosystems globally, such as evergreen, deciduous, and mixed forests, maquis, phrygana, savannas, and grasslands (e.g., Athias-Binche, 1976; Lussenhop, 1976; Prodon et al., 1987; Sgardelis et al., 1995; Broza and Izhaki, 1997; Coleman and Rieske, 2006; Moretti et al., 2006; Mordkovich et al., 2008; Radea et al., 2010).

A qualitative review of the available information concerning wildfire effects on the soil arthropod communities and populations' dynamics in MPF is attempted here. All the study cases, the timing of burning, the monitoring period after the fire event, the sampling methods, as well as the taxonomical level of studied soil arthropods, are presented in Table 1.

THE EFFECTS OF FIRE ON SOIL ARTHROPOD COMMUNITY

Fire influences the composition of soil arthropod fauna and the relative abundances of feeding guilds either directly, through instant mortality and quick colonization by fire-favored species, or indirectly, through habitat alteration (Wikars and Schimmel, 2001; Ferrenberg et al., 2006).

In Mediterranean regions, some soil arthropod species are protected under conditions of environmental stress, such as the wildfires, by life history traits, especially by the coexistence of conservative (e.g., long lasting adulthood and reduced adult mortality) and conformist (e.g., relatively high reproductive rate and rapid development of juve-

Table 1
Data concerning all the reviewed case studies of Mediterranean pine forests

Authors	Country	Pine species	Month of fire event	Monitoring time since the fire	Sampling and extraction methods	Identification level of soil arthropods
Broza et al. (1993)	Israel	*P. halepensis*	September	2nd–3rd year	Soil samples Berlese-Tullgern apparatus	Order Family
Broza et al. (1995)	Israel	*P. halepensis*	September	2nd–3rd year	Soil samples Berlese-Tullgern apparatus	Genus Order
Broza and Izhaki (1997)	Israel	*P. halepensis*	September	2nd–5th year	Soil samples Berlese-Tullgern apparatus	Order
Broza (2000)	Israel	*P. halepensis*	September	2nd–5th year	Soil samples Berlese-Tullgern apparatus	Order
Radea and Arianoutsou (2000)	Greece	*P. halepensis*	July	3–16 months	Soil samples Berlese-Tullgern apparatus	Order
Fernádez Fernádez, Saldago Costas (2002)	Spain	*P. pinaster*	June	10–15 months	Pitfall traps	Species
Santalla et al. (2002)	Spain	*P. pinaster*	June	10–15 months	Pitfall traps	Species
Fernádez Fernádez, Saldago Costas (2004)	Spain	*P. pinaster*	June	10–15 months	Pitfall traps	Species
Pitzalis et al. (2005)	Italy	*P. pinea*	July	9–21 months	Pitfall traps	Species
Antunes et al. (2009)	Portugal	*P. pinaster*	August	3–8 months	Pitfall traps	Family
Fattorini (2010)	Italy	*P. pinea*	July	9–21 months	Pitfall traps	Species
Pitzalis et al. (2010)	Italy	*P. pinea*	July	9v21 months	Pitfall traps	Species
Radea et al. (2010)	Greece	*P. halepensis*	July	2nd–3rd year	In situ using pincer & aspirator	Order

niles into adults) characteristics (Stamou et al., 2004). Additionally, some soil arthropod groups are protected from fire by body characteristics, such as a thick chitinized cuticle, and behavioral adaptations, such as vertical migrations within soil profile (Di Castri and Vitali-Di Castri, 1981; Wikars and Schimmel, 2001; Coleman and Rieske, 2006). These arthropods can benefit following fire because of (i) potential reductions in competitors and predators (Coleman and Rieske, 2006), (ii) increases in dead prey, for saprophagous species feeding on dead animals (Coleman and Rieske, 2006; Antunes et al., 2009), (iii) increased suitability for predators of hunting area due to its structural simplification (Antunes et al., 2009) and, finally, (iv) more favorable environmental conditions for xerophilic species preferring open habitats (Fattorini, 2010).

Differences in species composition and the abundance of soil arthropods in burned versus unburned stands have been recorded in many MTEs, such as phrygana in Greece (Sgardelis and Margaris, 1993; Sgardelis et al., 1995), cork–holm oak forests in France (Prodon et al., 1987), and jarrah forests in Australia (Springett, 1979).

In burned MPF, the composition of soil arthropod communities is considerably difsferent from that recorded in unburned ones (Broza et al., 1993; Broza and Izhaki, 1997; Radea and Arianoutsou, 2000; Antunes et al., 2009; Radea et al., 2011). Fire have detrimental effects on some groups of soil arthropods, such as Collembola, Acarina Cryptostigmata, larvae of Diptera, Araneae, Pseudoscorpionida, Lithobiomorpha, Diplopoda, at least the first years after the fire event (Broza et al., 1993; Broza and Izhaki, 1997; Radea and Arianoutsou, 2000).

In addition, the dominance by some taxa is stronger overall in the burned than in the unburned pine forests (Antunes, et al., 2009). For instance, the Tenebrionidae beetle *Tentyria grossa*, which is one of the rarest species of soil fauna in unburned *P. pinea* woodland in Italy, becomes the dominant species after fire due to both its increased post-fire abundance and the decreased abundance of almost all the other tenebrionid species. Fattorini (2010) attributes the dominance of *T. grossa* after fire to the transformation of vegetation type from woodland into a garrigue-like habitat, the latter being favorable for this species. Broza et al. (1995) found a remarkable increase in the abundance of *Rhizoecus* sp. (Coccoidea, Homoptera) in the soil of a burned *P. halepensis* forest, two years after fire. Antunes et al. (2009) found higher abundance of predatory and saprophagous Coleoptera (Staphylinidae and Silphidae and Lathridiidae respectively) as well as of some pyrophilous species of Araneae in a burned *P. pinaster* forest in Portugal. Similarly, Fernádez Fernádez and Saldago Costas (2002), Santalla et al. (2002), and Fernádez Fernádez and Saldago Costas (2004) observed a greater specific richness of Coleoptera fauna in total, and a greater abundance of Carabidae in particular, in a burned *P. pinaster* forest due to the arrival of opportunistic species after the wildfire.

DIRECT EFFECTS OF FIRE

The direct effect of fire on soil arthropods, that is, the mortality due to burning, occurs in the immediate period (hours during and after fire) (Swengel, 2001).

No qualitative or quantitative data exist concerning the direct effect of fire on soil arthropods in MPF.

INDIRECT EFFECTS OF FIRE

The indirect effects of fire on soil arthropod community appear to be driven by fire-induced habitat changes, namely the consumption of vegetation and organic horizon as well as the microclimate changes in the soil (Athias-Binche et al., 1987; Sgardelis and Margaris, 1993; York, 1999). These effects can be short-term (0 to 1–2 months after fire), intermediate-term (1–2 to 12 months after fire) and long-term (more than 12 months after fire) (Swengel, 2001).

In MPF, fire consuming the soil organic matter (i) alters the structure of the organic horizon, (ii) changes its physicochemical properties, (iii) decreases the microbial biomass and the available quantity of soil organic matter (Sevink et al., 1989; Hernández et al., 1997), and, thus, it reduces the food resources for saprophagous and saprophagous–microphytophagous arthropods.

Arthropods depending on structural complexity of organic horizon, such as Araneae (Bultman and Uetz, 1984) and hygrophilous groups, such as Pseudoscorpionida, Julida, Collembola, and larvae of Diptera, whose density are strongly related to the moisture content of the organic horizon in unburned *P. halepensis* forest (Radea, 1989), show low abundance in a burned *P. halepensis* forest (Radea and Arianoutsou, 2000). This fact can be attributed to the creation of a less heterogeneous habitat with modified microclimate in the soil sub-system after fire (Athias-Binche et al., 1987; Antunes et al., 2009) and it has also been observed in various other MTEs, such as phrygana and maquis (Prodon et al., 1987; Sgardelis and Margaris, 1993; Sgardelis et al. 1995).

Three months after a summer wildfire, the number of soil arthropod taxa and their density in a burned *P. halepensis* forest in Greece were lower than levels recorded in the unburned ones (Radea and Arianoutsou, 2000). In addition, Antunes et al. (2009) found reduced diversity of edaphic arthropods three months after a summer wildfire in a *P. pinaster* forest in Portugal, while Broza and Izhaki (1997) reported long-term fire effects (during the period from 2nd to 5th post-fire years) on the soil arthropod community in stands dominated by *P. halepensis* burned during autumn.

THE EFFECTS OF FIRE REGIME ON SOIL ARTHROPOD COMMUNITY

Fire regime encompasses several parameters, including fire severity, fire frequency, and season of burning. These parameters play an important role for soil fauna, and their impact on the composition of soil arthropod community and the patterns of survival, colonization, and recovery has been studied in many types of forest ecosystems, such as coniferous, deciduous, and mixed oak–pine forests (e.g., Wikars and Schimmel, 2001; Coleman and Rieske, 2006; Moretti et al., 2006), jarrah forests (e.g., Springett, 1979; York, 1999) and Mediterranean pine and mixed pine-oak forests (Broza et al., 1993; Broza and Izhaki, 1997; Broza, 2000; Radea and Arianoutsou, 2000; Antunes et al., 2009; Radea et al., 2010).

Natural fire regime is difficult define in the Mediterranean basin because of the long history of human intervention with the landscape. However, as already mentioned for the lowland Mediterranean pine woodlands, increased fire recurrence and burn severity have been observed during the last decades (Pausas et al., 2008;, Moreira et al., 2011).

FIRE SEVERITY

Fire produces a spectrum of severities that depends on the interactions of fire intensity and duration, fuel loading, combustion type and degree of oxidation, vegetation type, fire climate, slope, topography, soil texture and moisture, soil organic matter content, time since last burning, and area burned (Neary et al., 1999). The higher the severity of fire, the greater the modifications induced in the soil and, consequently, in the arthropod community (Springett, 1976, 1979; Abbott et al., 1984; Mallström, 2010). In unburned MPF, the accumulation of large quantities of slowly decomposing flammable dead material forming a rather thick organic horizon (Radea, 1989; García-Plé et al., 1995), in combination with the high temperatures and low moisture during summer, provides the conditions for summer fires of high severity.

In severely burned *P. halepensis* forest in Greece and Israel the qualitative composition of soil arthropod community, at the order level, differ from those in the unburned forests, and the abundances of the various groups are generally lower (Broza et al., 1993; Broza and Izhaki, 1997; Radea and Arianoutsou, 2000). In a severely burned stand of *P. pinea* in central Italy, Isopoda show reduced abundance while the abundance of Collembola is surprisingly higher in this stand (Pitzalis et al., 2005).

Pitzalis et al. (2010) conclude that the community organization of Isopoda and Collembola was affected by the fire event. Indeed, the community structure was non-random at the unburned sites and random in the severely burned ones. The increased abundance of Collembola observed by the above authors after fire could be a result of collection technique, that is, pitfall trapping, and may simply reflect the increased locomotor activity of these taxa after burning of vegetation and dense leaf-litter. It should be mentioned that pitfall trapping is a semi-quantitative method estimating primarily locomotory activity on the soil surface and, indirectly, the species abundance (e.g., Greenslade, 1964; York, 1999).

So far, there is no other published work comparing the arthropod community in severely versus less-severely burned MPF except that in a *P. halepensis* forest in Greece (Radea and Arianoutsou, 2000). The results derived from this work show that both the number of taxa and the density of their populations are clearly lower in the severely burned site.

FIRE FREQUENCY

In general, high fire frequency, meaning short intervals between recurrent fires, is primarily associated with prescribed burning and low-severity fire events (Romme, 1982; Halofsky et al., 2011). Abbott et al. (1984) found that periodic non-severe fires have few permanent effects on most of the invertebrate taxa present in the organic horizon of the jarrah forests. In contrast, York (1999) found a persistent reduction in richness and abundance of many soil arthropod taxa in Australia's coastal forests frequently burned by non-severe fires for a period of twenty years.

In *P. halepensis* stands, fire frequency does not directly affect soil arthropods but influences them through the alteration of vegetation structure (Radea et al., 2010). This can be easily explained by the regeneration process of vegetation, which in turn influences the organic horizon formation and soil microclimate: in the case of relatively short intervals between wildfires in *P. halepensis* forests, the vegetation shows low resilience (Arianoutsou et al., 2002) and the organic horizon barely recover to the conditions before the first fire event (Eugenio et al., 2006).

SEASON OF BURNING

In Mediterranean ecosystems, most wildfires occur during the hot and dry period of the year lasting from May until to the end of October. Since the depth of burning of organic layers depends partly on their moisture content, which in turn is linked to the weather history for several weeks prior to fire (Van Wagner, 1983), the consumption of soil organic horizon in Mediterranean ecosystems is expected to be almost complete. However, the combustible organic matter, and therefore the depth of burning, may vary strongly in these ecosystems depending on the type of organic horizon and the former management, if any, on the area (Sevink et al., 1989).

It seems that the fires during the hot and dry period of the year are less detrimental for soil arthropods than fires occurring in spring or early summer because most soil taxa found during summer in the upper layers of organic horizon have already been prepared to tolerate or to avoid the unfavorable microclimatic conditions of this period. For instance, various taxa collected in pine forests undergone estival fires (Radea and Arianoutsou, 2000; Antunes et al., 2009; Radea et al., 2010) are able to escape from fire either because they are fast-moving animals (e.g., Araneae, Phalangida, Geophilomorpha, Lithobiomorpha, and Dictyoptera), or because they are able to burrow (Julida, Geophilomorpha) or to use small soil crevices (e.g., Polyxenida) and move down during summer (Geophilomorpha), or, finally, they have a thick chitinized cuticle (e.g., Julida, Coleoptera, Carabidae, and Tenebrionidae), which protects them from desiccation (Wallwork, 1970; Athias-Binche et al., 1987). However, the low abundance of Coleoptera, Araneae, Psocoptera, and Polyxenida after fire in a *P. halepensis* forest of Greece indicates that, despite their adaptations to Mediterranean climate and their ability to escape from burning, the populations of these xerophilous–mesophilous animal groups suffer large losses attributed to the direct effect of burning (Radea and Arianoutsou, 2000).

EFFECTS OF FIRE ON THE PHENOLOGY OF SOIL ARTHROPOD POPULATIONS

Fire no doubt interacts with phenology for many invertebrates (Smith, 2000). In some Mediterranean ecosystems the monthly fluctuations of post-fire abundance of soil arthropods seems to have been influenced by the fire. For instance, Sgardelis et al. (1995) found that the phenology of some macroarthopod taxa in a phryganic ecosystem of Greece is affected by fire, and they attributed this alteration to microclimatic changes caused by fire. Athias-Binche et al. (1987) recorded also an impact of fire on the phenology of an Uropodina group in a burned cork-oak stand.

However, no impact of fire on the phenology of soil arthropods was detected by Broza and Izhaki (1997) in a mixed forest dominated by *P. halepensis* in Israel, or by Radea and Arianoutsou (2000) and Radea et al. (2011) in a *P. halepensis* forest in Greece.

Nevertheless, all the above authors have demonstrated that, even after fire, the seasonality of Mediterranean climate is the principal environmental factor controlling the phenology of soil fauna, at least at the taxonomical level of order.

POST-FIRE RECOVERY OF SOIL ARTHROPOD POPULATIONS

Forest soil communities are dynamic and their re-organization after a disturbance, such as wildfire, may take a long time since different taxa re-establish at different rates, and the dynamics of trees and organic matter constrain the dynamics of soil species and communities (Bengtsson, 2002).

The recovery of soil arthropod populations to the pre-fire stage depends on: (i) their resistance and resilience to fire (Moretti et al., 2006), (ii) the biological features and requirements of each taxon, e.g., the trophic level (Prodon et al., 1987), (iii) the possibility of recolonization from adjacent unburned areas or even from unburned or lightly burned patches inside the burned area (Bengtsson, 2002), (iv) the post-fire environmental conditions (Ahlgen, 1974), and (v) the recovery of soil organic horizon, which in turn depends on the recovery of vegetation (Athias-Binche et al., 1987; Sgardelis and Margaris, 1993; Sgardelis et al., 1995) and, consequently, on fire regime (York, 1999; Gill and Alan, 2008).

The recovery of soil arthropods after fire has been studied in several MTEs. In *Eucalyptus marginata* and *E. diversicolor* forests in Australia, soil fauna seems to be permanent simplified and to not recover after prescribed non-severe fires on a five to seven year rotation for forty years (Springett, 1976). In a phryganic ecosystem in Greece, where the recovery of organic horizon is a rather quick process (Arianoutsou-Faraggitaki, 1984), the recovery time for microarthropod groups is estimated to be less than 3-4 years (Sgardelis and Margaris, 1993) whereas Julida show significant reduction of their abundance and no recovery one year and a half after fire (Sgardelis et al., 1995).

In MPF the recovery patterns vary in relation to taxa, the fire regime, and the environmental characteristics of the forest under consideration. In a *P. pinaster* forest in Spain, a greater specific richness of Coleoptera is observed in the burned area ten months after fire (Fernádez Fernádez and Saldago Costa, 2002). In the same forest, a greater abundance of Carabidae is recorded in the burned site, whereas the diversity of this family is similar in the unburned and the burned site. However, the composition of Carabidae fauna differs greatly between burned and unburned sites, because mesophilous and xerophilous species adapted to open areas, as well as pyrophilous species, are recorded in the burned site, and hygrophilous species adapted to forest and grasslands in the unburned one (Fernádez Fernádez and Saldago Costa, 2004).

In a mixed forest dominated by *P. halepensis* on Mt. Carmel, Israel, soil macroarthropod populations had not recovered five years after a severe fire event (Broza and Izhaki, 1997). In the same area, the populations of soil microarthropods showed a sharp decline during the second post-fire year (Broza et al., 1993) and the complete recovery of soil arthropods was evident only 22–38 years after fire (Broza, 2000).

The soil arthropod population seems to recover gradually even in the severely burned site of a *P. halepensis* forest in Greece. In this forest, an increase in the number of taxa and the abundance of their populations were recorded during the second post-fire year (Radea and Arianoutsou, 2000).

SYNOPSIS

Over the last decades, much information has been produced about the effects of fire on the soil sub-system and soil arthropods in MPF. These effects can be highly variable depending on climate, fire regime, and life history traits of soil arthropods. Additionally, a great variation exists among the relative papers in experimental design and sampling procedure, time of beginning and duration of field work after fire, the taxonomic level of soil arthropods, and the analyses based on all these factors. The foregoing can explain the differences recorded in some papers concerning the response showing by the same taxa to fire disturbance.

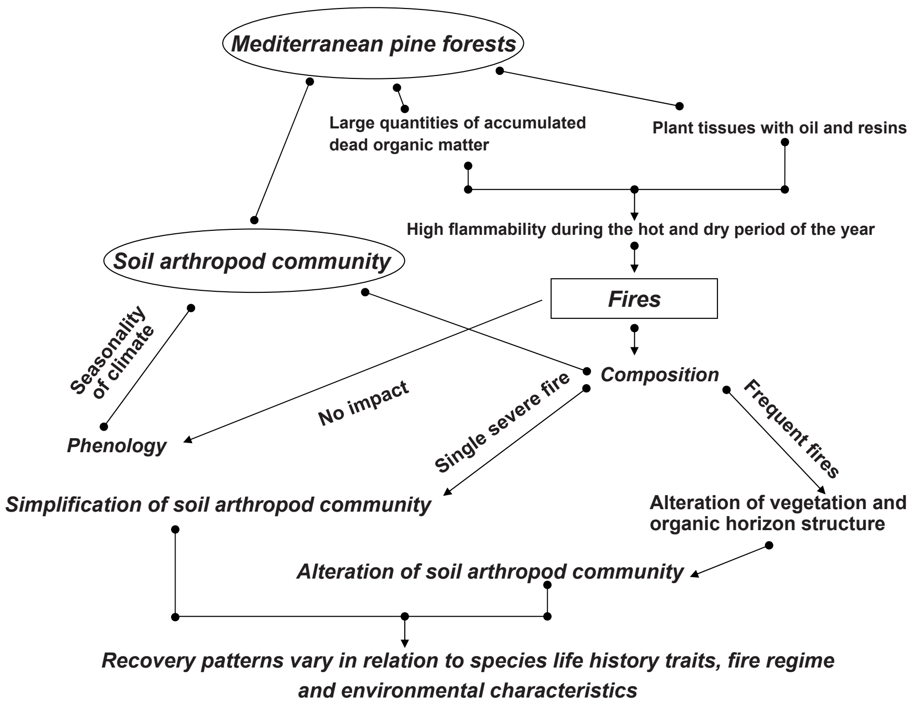

Fig. 1. Schematic overview of the effects of wildfires on community composition and dynamics of soil arthropod fauna in Mediterranean pine forests.

In general, the effects of wildfire regime on soil arthropods in MPF are similar to those recorded in other MTEs, and they are depicted in Fig. 1.

In the Mediterranean pine forests reviewed:

- Soil arthropods, having adaptations to cope with the microclimatic conditions during the warm and dry period, suffer no devastating losses during summer fires.
- The seasonality of climate remains the principal environmental factor controlling the phenology of soil arthropods at the order level, even after fire.
- The recovery patterns of soil arthropods vary in relation to species, fire regime, and the environmental characteristics of the forest under consideration.

It is important to note that although most soil arthropods at the order level show rather similar response to wildfire in the pine forests examined, there may have been remarkable dissimilarities in species-level responses. Therefore, a species-level analysis is indispensable to elucidate the composition and dynamic of the soil arthropod community in MPF after wildfires.

ACKNOWLEDGMENTS

We thank three anonymous reviewers whose comments greatly improved this manuscript. Dr. Penny Marinou (Litterae) is acknowledged for her support in the linguistic improvement of the manuscript.

REFERENCES

Abbott, I., Van Heurk, P., Wong, L. 1984. Responses to long-term fire exclusion: physical, chemical and faunal features of litter and soil in a Western Australian Forest. Austral. Forest 47: 237–242.

Ahlgren, I.F., 1974. The effect of fire on soil organisms, In: Kozlowski, T.T., Ahlgren, C.E., eds. Fire and ecosystems. Academic Press, New York, pp. 47–71.

Antunes, S.C., Curado, N., Castro, B.B., Concalves, F. 2009. Short-term recovery of soil functional parameters and edaphic macro-arthropod community after a forest fire. J. Soil Sedim. 9: 267–278.

Arianoutsou, M., D. Kazanis, D., Kokkoris, Y., Skourou, P. 2002. Land-use interactions with fire in Mediterranean *Pinus halepensis* landscapes of Greece: patterns of biodiversity. In: Viegas, D.X., ed. IV International Forest Fire Research Conference, Millpress, electronic edition.

Arianoutsou-Faraggitaki, M. 1984. Post-fire successional recovery of a phryganic (East-Mediterranean) ecosystem. Oecol. Plant. 5: 387–394.

Athias-Binche, F. 1976. Recherche sur les microarthropodes du sol de la savane de Lamto (Cote d'Ivoire). Anal. Univ. Abidjan (Ecol.) 7: 191–271.

Athias-Binche, F., Briard, J., Fons, R., Sommer, F. 1987. Study of ecological influence of fire on fauna in Mediterranean ecosystems (soil and above-ground layer). Patterns of post-fire recovery. Ecol. Medit. 13: 135–154.

Attiwill, P.M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. For. Ecol. Manage. 63: 247–300.

Barbéro, M., Loisel, R., Quézel, P., Richardson, D.M, Romane, F. 1998. Pines of the Mediterranean basin. In: Richardson, D.M. ed. Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge, UK, pp. 153–170.

Bengtsson, J. 2002. Disturbance and resilience in soil animal communities. Eur. J. Soil Biol. 38: 119–125.

Broza, M., 2000. Soil arthropods in east Mediterranean *Pinus halepensis* forests. In: Ne'eman, G., Trabaud, L., eds. Ecology, biogeography and management of *Pinus halepensis* and *P. brutia* forest ecosystems in the Mediterranean basin. Backhuys, Leiden, pp. 203–216.

Broza, M., Izhaki, I., 1997. Post-fire arthropod assemblages in Mediterranean forest soils in Israel. Int. J. Wild. Fire 7: 317–325.

Broza, M., Poliakov, D., Weber, S., Izhaki, I.– 1993. Soil microarthropods on post-fire pine forest on Mount Carmel, Israel. Wat. Sci. Tech. 27: 533–538.

Broza, M., Weber, S., Poliakov, D., Ben-Dov, Y. 1995. Populations of *Rhizoecus* sp. (Pseudococcidae) in post-fire soil of pine forest at Mount Carmel, Israel. Isr. J. Entomol. 29: 149–152.

Bultman, T.L., Uetz, G.W. 1984. Effect of the structure and nutritional quality of litter on abundance of litter-dwelling arthropods. Am. Midl. Nat. 111: 165–172.

Coleman, T.W., Rieske, L.K. 2006. Arthropod response to prescription burning at the soil–litter interface in oak–pine forests. For. Ecol. Manage. 233: 52–60.

Eugenio, M., Lloret, F., Alcañiz, J.M. 2006. Regional patterns of fire recurrence effects on calcareous soils of Mediterranean *Pinus halepensis* communities. For. Ecol. Manage. 221: 313–318.

Dannaoui, S. 1981. Production de litière et restitution au sol d'éléments biogènes dans des peuplements méditerranéens de *Pinus pinea* L. et *Pinus brutia* Ten. Ecol. Medit. 7: 13–25.

Di Castri, F., Vitali-di Castri, V. 1981. Soil fauna of Mediterranean-climate regions. In: di Castri, F., Goodall, F., Specht, R.L., eds. Ecosystems of the world. II. Mediterranean shrublands. Elsevier, Amsterdam, pp. 445–478.

Fattorini, S. 2010. Effects of on tenebrionid communities of a *Pinus pinea* plantation: a case study in a Mediterranean site. Biodivers. Conserv. 19: 1237–1250.

Fernádez Fernádez, M., Saldago Costas, J.M. 2002. Recolonization of a burnt pine forest (*Pinus pinaster*) by edaphic Coleoptera. Entomol. Gener. 26: 17–28.

Fernádez Fernádez, M., Saldago Costas, J.M. 2004. Recolonization of a burnt pine forest (*Pinus pinaster*) by Coleoptera (Carabidae). Eur. J. Soil Biol. 40: 47–53.

Ferrenberg, S.M., Schwilk, D.W., Knapp, E.E., Groth, E., Keeley, J.E. 2006. Fire decreases arthrowpod abundance but increases diversity: early and late season prescribed fire effects in a Sierra Nevada mixed-conifer forest. Fire Ecol. 2: 79–102.

García-Plé, C., Vanrell, P., Morey M. 1995. Litter fall and decomposition in a *Pinus halepensis* forest on Mallorca. J. Veg. Sci. 6: 17–22.

Gill, A.M., Allan, G. 2008. Large fires, fire effects and the fire regime concept. Int. J. Wild. Fire 17: 688–695.

Greenslade, P.J.M., 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). J. Anim. Ecol. 33: 301–310.

Halofsky, J.E., Donato, D.C., Hibbs, D.E., Campbell, J.L., Donaghy Cannon, M., Fontaine, J.B., Thompson, J.R., Anthony, R.G., Bormann, B.T., Kayes, L.J., Law, B.E., Peterson, D.L., Spies, T.A. 2011. Mixed-severity fire regimes: lessons and hypotheses from the Klamath–Siskiyou Ecoregion. Ecosphere 2: 1–19.

Hernández, T., García, C., Reinhardt, I. 1997. Short-term effect of wildfire on the chemical, biochemical and microbiological properties of Mediterranean pine forest soils. Biol. Fertil. Soils 25: 109–116.

Lussenhop, J. 1976. Soil arthropod response to prairie burning. Ecology 57: 88–98.

Mallström, A. 2010. The importance of measuring of fire severity—evidence from microarthropods studies. For. Ecol. Manage. 260: 62–70.

Mordkovich, V.G., Berezina, O.G., Lyubechanskii, I.I., Andrievskii, V.S., Marchenko, I.I. 2008. Soil Arthropoda of post-fire successions in Northern Taiga of West Siberia. Cont. Probl. Ecol. 1: 96–103.

Moreira, F., Viedma, O., Arianoutsou, M., Curt, Th., Koutsias, N., Rigolot, E., Barbati, A., Corona, P., Vaz, P., Xanthopoulos, G., Mouillot, F., Bilgili, E. 2011. Landscape–wildfire interactions in southern Europe: implications for landscape management. J. Env. Management 92: 2389–2402.

Moretti, M., Duelli, P., Obrist, M.K. 2006. Biodiversity and resilience of arthropod communities after fire disturbance in temperate forests. Oecologia 149: 312–327.

Naveh, Z. 2000. Mediterranean pine forests facing the challenges of multiple stresses. In: Ne'eman, G., Trabaud, L., eds. Ecology, biogeography and management of *Pinus halepensis* and *P. brutia* forest ecosystems in the Mediterranean basin. Backhuys Publisher, Leiden, pp. ix–xii.

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

Pausas, J.G., Vallejo, V.R. 1999. The role of fire in European Mediterranean ecosystems. In: Chuevico, E., ed. Remote sensing of large wildfires in the European Mediterranean basin. Springer-Verlag, Berlin, pp. 3–16.

Pausas, J.G., Llovet, J., Rodrigo, A., Vallejo, R. 2008. Are wildfires a disaster in the Mediterranean basin? – a review. Int. J. Wildl. Fire 17: 713–723.

Petersen, H., Luxton, M. 1982. A comparative analysis of soil arthropod population and their role in decomposition processes. Oikos 39: 288–388.

Pitzalis, M., Fattorini, S., Trucchi, E., Bologna, M.A. 2005. Comparative analysis of species diversity of Isopoda Oniscidea and Collembola communities in burnt and unburnt habitats in central Italy. Ital. J. Zool. 72: 127–140.

Pitzalis, M., Luiselli, L., Bologna, M.A. 2010. Co-occurrence analyses show that non-random community structure is disrupted by fire in two groups of soil arthropods (Isopoda Oniscidea and Collembola). Acta Oecol. 36: 100–106.

Prodon, R., Fons, R., Athias-Binche, F. 1987. The impact of fire on animal communities in Mediterranean patch. In: Trabaud, L., ed. The role of fire in ecologicalsystems. SPB Academic Publishing, The Hague, pp. 121–157.

Quézel, P., 1980. Biogéographie et écologie des conifères sur le pourtour méditerranéen. In: Pesł son, P., ed. Actualitès d' ´Ecologie Forestière. Gauthiers-Villars, Paris, pp. 205–256.

Quézel, P., 2000. Taxonomy and biogeography of Mediterranean pines (*Pinus halepensis* and *P. brutia*). In: Ne'eman, G., Trabaud, L., eds. Ecology, biogeography and management of *Pinus halepensis* and *P. brutia* forest ecosystems in the Mediterranean basin. Backhuys Publisher, Leiden, pp. 1–12.

Radea, C. 1989. Study on the litter production, the decomposition rate of organic matter and the arthropod community in ecosystems with *Pinus halepensis* Mill. of insular Greece. Ph.D. Thesis, University of Athens, Athens, 256 pp.

Radea, C., Arianoutsou, M. 2000. Cellulose decomposition rates and soil arthropod community in a *Pinus halepensis* Mill. forest of Greece after a wildfire. Eur. J. Soil Biol. 36: 57–64.

Radea, C., Kazanis, D., Arianoutsou, M., 2010. Effects of fire history upon soil macroarthropod communities in *Pinus halepensis* stands in Attica, Greece. Isr. J. Ecol. Evol. 56: 165–179.

Rapp, M. 1967. Production de litière et apport au sol d'éléments minéraux et d'azote dans un bois de pin d' Alep (*Pinus halepensis* Mill.). Oecol. Plant. 2: 325–338.

Romme, W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecol. Monogr. 52: 199–221.

Santalla, S., Salgado, J.M, Calvo, L.M. 2002. Changes in the Carabidae community after a large fire in a *Pinus pinaster* stand. In: Trabaud, L., Prodon, R., eds. Fire and biological processes. Backhuys Publisher, Leiden, pp. 215–231.

Sevink, J., Imeson, A.C., Verstraten, J.M. 1989. Humus form development and hillslope runoff, and the effects of fire and management under Mediterranean forest in NE-Spain. Catena 16: 461–475.

Sgardelis, S.P., Margaris, N.S. 1993. Effects of fire on soil microarthropods of a phryganic ecosystem. Pedobiologia 37: 83–94.

Sgardelis, S.P., Pantis, J.D., Argyropoulou, M.D., Stamou, G.P. 1995. Effects of fire on soil macroinvertebrates in a Mediterranean phryganic ecosystem. Int. J. Wild. Fire 5: 113–121.

Smith, J.K. 2000. Wildland fire in ecosystems: effects of fire on fauna. Gen. Tech. Rep. RMRS-GTR-42-1. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 83 pp.

Springett, J.A. 1976. The effect of prescribed burning on the soil fauna and on litter decomposition in Western Australian forests. Austr. J. Ecol. 1: 77–82.

Springett, J.A. 1979. The effects of a single hot summer fire on soil fauna and on litter decomposition in jarrah (*Eucalyptus marginata*) forest in Western Australia. Austr. J. Ecol. 4: 279–291.

Stamou, G.P., Stamou, G.V., Papatheodorou, E.M., Argyropoulou, M.D., Tzafestas, S.G. 2004. Population dynamics and life history tactics of arthropods from Mediterranean-type ecosystems. Oikos 104: 98–108.

Swengel, A. 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. Biodivers. Conserv. 10: 1141–1169.

Trabaud, L. 2000. Post-fire regeneration of *Pinus halepensis* forests in the West Mediterranean, In: Ne'eman, G., Trabaud, L., eds. Ecology, biogeography and management of *Pinus halepensis* and *P. brutia* forest ecosystems in the Mediterranean basin. Backhuys, Leiden, pp. 257–268.

Van Wagner, C.E., 1983. Fire behaviour in northern conifer forests and shrublands. In: Wein, R.W., McLean, D.A., eds. The role of fire in northern circumpolar ecosystems. Wiley, New York, pp. 65–80.

Wallwork, J.A., 1970. Ecology of soil animals. Mc Graw Hill, London.

Wikars, L.O., Schimmel, J., 2001. Immediate effects of fire-severity on soil invertebrates in cut and uncut pine forests. For. Ecol. Manage. 141: 189–200.

York, A., 1999. Long-term effects of frequent low-intensity burning on the abundance of litter-dwelling invertebrates in coastal blackbutt forests of southeastern Australia. J. Insect Conserv. 3: 191–199.