EFFECTS OF FIRE HISTORY UPON SOIL MACROARTHROPOD COMMUNITIES IN *PINUS HALEPENSIS* STANDS IN ATTICA, GREECE

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ABSTRACT

The composition of the soil macroarthropod community was studied in three forest stands which constitute a gradient of increased fire frequency. All stands were adjacent to each other, on the foothills of Mt. Penteli, Attica, Greece, and they shared similar physiography, climate, altitude, while their original pre-fire vegetation was a well-developed Pinus halepensis forest. The stands were severely burned by a large fire early in summer 1995. Two of them had been burned previously: the first in 1978 and the second in 1978 and 1987. Sampling was carried out during the 2nd year after the last fire event. Although the phenology of soil macroarthropods was not altered in frequently burned stands, the number of taxa collected, as well as their population size, was extremely low. Canonical Correspondence Analysis showed that fire frequency does not directly affect soil arthropod communities, but influences them through increased abundance of specific plant groups, i.e., phrygana vegetation and legumes. Seasonality of climate seemed to be another significant factor controlling the structure of macroarthropod communities in the stands studied.

Keywords: Mediterranean ecosystems, fire regime, soil macroarthropods, Aleppo pine forests, Greece

INTRODUCTION

Soil arthropods participate actively in soil physical, chemical, and biological processes (e.g., McBrayer and Reichle, 1971; McBrayer et al., 1977; Tian et al., 1997) and they contribute to the creation and maintenance of a good soil quality (Anderson, 1988; Schrader et al., 1997; Knoepp et al., 2000). The community of soil arthropods is highly sensitive to any soil disturbance since the soil sub-system is its habitat and the source of all supplies required by the animals (Lavelle et al., 2006). Consequently, soil arthropods could be placed among the best potential bio-indicators of ecosystem health and balance (e.g., Hogervorst et al., 1993; Kay et al., 1999; Radea and Arianoutsou, 2002).

Fire is considered as the predominant natural disturbance that has shaped landscapes and ecosystems across low elevation areas around the Mediterranean Basin. The ef-

*Author to whom correspondence should be addressed. E-mail: marianou@biol.uoa.gr Received August 11, 2010; accepted December 21, 2010. fects of fire on soil invertebrates have been investigated in various ecosystems such as coniferous and deciduous forests, shrublands, and grasslands. Results of these studies show that fire regime, i.e., fire intensity (Springett, 1979; Radea and Arianoutsou, 2000; Antunes et al., 2009), fire frequency (Springett, 1976; Abbott et al., 1984; Cook and Holt, 2006; Moretti et al., 2006), and season of burning (Sgardelis et al., 1995; Radea and Arianoutsou, 2000) constitute the factors affecting both arthropod abundance and community composition in the soil subsystem after a fire event. Fire may exert an effect on soil fauna either directly, through mortality, or indirectly by changing plant community composition and foliar characteristics, reducing or eliminating organic horizon, and modifying soil moisture and temperature (e.g., Springett, 1976; Athias-Binche et al., 1987; Prodon et al., 1987; Greenberg et al., 2010).

Pinus halepensis forests are the forest ecosystems in the European Mediterranean Basin most affected by fire (Arianoutsou, 2001; Pausas and Keeley, 2009). However, our knowledge of how recurrent natural fires in Aleppo pine forests influence the soil arthropod fauna is for the most part unknown. The aim of this study was to examine the effects of fire on the composition of soil macroarthropod communities across a gradient of *Pinus halepensis* stands recovering after recurrent fire events. It was hypothesized that (1) recurrent fires decrease the number of taxa and the density of soil macroarthropods, (2) there is a prominent role of vegetation upon the composition of soil arthropod communities in frequently burned stands, and (3) seasonality of climate (that is, the succession of wet and dry seasons of the year) influences strongly the soil arthropod communities in all burned stands.

MATERIALS AND METHODS

The study stands are located in the Pikermi area, 20 km NE of Athens, on the foothills of Mt. Penteli (1204 m a.s.l.). The climate of the area is typical Mediterranean. The highest mean monthly temperature in summer reaches 26 °C. Annual precipitation is 434 mm, 87% of which is concentrated in the wet period. Until the early 1970s, the largest part of the mountain was covered by *Pinus halepensis* forests, while in the lowland peripheral zone shrublands and agricultural lands were encountered. Land use patterns changed when urbanization pressure started in the surroundings of Athens. At the same time a number of fires burned over in several areas of the mountain, creating thus a mosaic of patches with different fire history (Arianoutsou et al., 2002).

Early in summer 1995, an area of nearly 7,000 ha covering the southeastern parts of the mountain was severely burned (Ntouros, 1995). The burned landscape consisted of patches of mature (>50-yr-old) pine forest (3100 ha) co-existing with younger pine forest of different post-fire age (875 ha).

Within the periphery of the burned mature forest, at the Pikermi locality, an area of 90 ha (Pik50) was selected. Two adjacent pine communities that had been re-burned in 1978 (Pik17) and in 1978 and 1987 (Pik8), covering an area of 110 and 40 ha, respectively were also selected. The selection of the specific stands was based on the degree

of similarity in their characteristics, i.e., they overlie on tertiary deposits and are located on south-facing slopes at an altitudinal zone of 180–200 meters a.s.l.

Given the fact that all environmental parameters (climate, geology, aspect, elevation) were similar among the studied stands, the role of vegetation upon the structure of soil arthropod communities could be prominent.

Plant community analysis was performed in autumn, spring, and summer of the 2nd year after the last fire event by applying the line transect sampling method, which is more advantageous over the traditional plot sampling method since it allows the survey of a wider part of the community within a minimum time (Brower et al., 1990). Accordingly, three 50-m-long line transects were randomly established in each of the three study stands, keeping a minimum distance of 200 m between them. All plants, growing at or intercepting transects were recorded. Based on these records, species abundance was evaluated for each stand.

Since the effect of vegetation upon soil biota operates mainly through the litter produced (see for example di Castri and Vitali-di Castri, 1981; David et al., 1999), plant taxa recorded in the stands were grouped according to their leaf litter characteristics. Four groups were identified for woody plant species, i.e., pines, evergreen sclerophyllous shrubs (maquis), seasonal dimorphic shrubs (phrygana), and dwarf shrubs. The "pines" group consists of Pinus halepensis, with needle-leaf litter. The "maquis" group encompasses tall sclerophyllous shrubs such as Pistacia lentiscus and Quercus coccifera, which form litter with tough leathery leaves. The "phrygana" group, being the richest in terms of species number and including primarily Cistaceae (e.g., Cistus spp.), shrubby Leguminosae (e.g., Genista acanthoclada, Anthyllis hermanniae), and Labiateae (e.g., Satureja spp., Teucrium spp.), produces litter with soft leaves. Finally, the group of "dwarf shrubs" comprises all other short woody species (e.g., Asparagus spp., Osyris alba, etc.) with narrow or needle-like leaf litter. Herbaceous plant species were classified into three groups, i.e., legumes, grasses, and forbs, as proposed by other authors in relevant studies (e.g., Siemann et al., 1998; Symstad et al., 2000; Whiles and Charlton, 2006).

Soil macroarthropods were collected from randomly chosen quadrates located along the 50-m-long transects. In each stand, 5 quadrates of 50×50 cm (with a minimum distance of 50 m from each other) per transect and sampling period were carefully surveyed between 9.00 and 11.00 am using a pincer and an aspirator (see Sgardelis, 1995).

The specimens were preserved in 75% ethanol solution with 5% glycerine; they were identified to the level of order and counted under a stereomicroscope (Zeiss Stemi 2000-C). Sampling took place in three periods of the year (spring, summer, autumn) during the second post-fire year (1997) in all studied stands.

Canonical Correspondence Analysis (CCA) was performed for the ordination of studied stands based on the response of soil macroarthropods to nine environmental variables: fire frequency (values in nominal scale), plant group abundance [i.e., maquis, phrygana, pines, dwarfs, legumes, grasses and forbs (values in ordinal scale)] and season of the year [wet and dry season (values in nominal scale)], using the statistical program CANOCOTM 4.5 for Windows (Ter Braak, 1996).

RESULTS

Nine (9) soil macroarthropod taxa were identified for Pik50, seven for Pik17, and six for Pik8. A slight variation in the total mean annual density was recorded among Pik50, Pik17, and Pik8, that is, 0.68, 0.79, and 0.20 ind/m² respectively. A list of macro-arthropod taxa and their relative abundance (%) in the soil community is provided per sampling period in Fig. 1.

The ordinal-level composition of the soil macroarthropod fauna differed at the three stands studied. Specimens of Pseudoscorpionida, Coleoptera (both adults and larvae), and Phalangida were exclusively found in the mature stand (at the time of burning) Pik50; specimens of Lithobiomorpha, Iulida, and Dermaptera in the young stand (at the time of burning) Pik17; while Dictyoptera were collected from Pik17 and Pik 8, the very young stand at the time of burning.

Coleoptera adults (28.7%), Hemiptera (28.1%), Coleoptera larvae and Geophilomorpha (both with 11.2%) in Pik50; Iulida (32.6%), Araneae (27.7%), and Dermaptera (16.3%) in Pik17; and Araneae (54.9%), Dictyoptera (26.1%), and Geophilomorpha (13.1%) in Pik8 were the taxa showing the highest relative abundance annually.

Canonical Correspondence Analysis (CCA) was performed using the abundance of soil arthropod groups as dependent variables and the environmental variables mentioned above as independent variables. Results of CCA revealed that a high percentage of the variance of taxa abundance (61.2%) can be explained by the first three canonical axes (Table 1). The ordination of groups of sites and of the arthropod taxa is depicted in planes of the first three significant axes of CCA (Figs. 2a,b). Due to the high mutual correlation between the abundance of phrygana and herbaceous legumes (Table 2), intraset correlation coefficients were used for interpreting canonical axes (Ter Braak, 1996). Intraset correlation coefficients are presented in Table 3.

A Monte Carlo permutation test was used for the evaluation of the relationship between macroarthropod taxa and the whole set of environmental variables. Most significant relationships were found with the abundance of phrygana (F = 2.744, p = 0.0005), season of the year (F = 2.038, p = 0.0285), and herbaceous legumes (F = 2.016, p = 0.0460).

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	Axis 1	Axis 2	Axis 3	Total inertia
Eigenvalues	0.672	0.417	0.295	2.239
Species-environment correlations	0.941	0.973	0.950	
Cumulative percentage variance				
of species data	30.0	48.6	61.8	
of species-environment relationship	48.6	78.7	100.0	
Sum of all eigenvalues				2.239
Sum of all canonical eigenvalues				1.383

 Table 1

 Results of Canonical Correspondence Analysis for the first three most significant axes



Fig. 1. Mean (±SE) density of macroarthopod groups per site and sampling season. Pik50—site burned 50 years before 1995, Pik17—site re-burned 17 years before 1995; Pik8—site re-burned 8 years before 1995.



Fig. 2. Canonical Correspondence Analysis triplot of macroarthropod taxa, sites and environmental variables. a (above): Axis 1 (horizontal) and Axis 2 (vertical), b (opposite): Axis 1 (horizontal) and Axis 3 (vertical). Aran—Araneae, Pseud—Pseuscorpionida, Lithob—Lithobiomorpha, Geoph—Geophilomorpha, Isop—Isopoda, Thysan—Thysanura, Coleopt—Coleoptera, Dictyopt—Dictyoptera, Hemipt—Hemiptera, L. Coleopt.—Larvae of Coleoptera, Phalang—Phalangida, Derm—Dermaptera, Iul: Iulida. Pik50—site burned 50 years before 1995, Pik17—site reburned 17 years before 1995, Pik8—site re-burned 8 years before 1995. S—Summer, Sp—Spring, F—Fall.



Axis 1 accounted for 30.0% of total variance in macroarthropod abundance and was mainly correlated (negatively) with the abundance of phrygana (Table 3). Therefore Axis 1 was a gradient of decreasing phrygana abundance that separated all samples collected from Pik17 as well as those from Pik8 during summer from all other samples. It also separated Lithobiomorpha, Araneae, Isopoda, Iulida, Dermaptera, and Dictyoptera, which were mainly found in samples from stands and periods characterized by high phrygana abundance.

Canonical Axis 2 accounted for 18.6% of total variance in abundance data. It was correlated with the season of the year (Table 3), displaying a gradient from wet to dry periods of the year. It is remarkable that all samples collected from the very young forest stand at the time of burning, Pik8, even those collected during spring and fall, were projected on the positive part of Axis 2 indicating the dry period of the year. This axis also separated Lithobiomorpha, Araneae, Thysanura, Pseudoscorpionida, Phalangida, and adult Coleoptera, which were mainly collected during the dry period of the year.

Canonical Axis 3 accounted for 13.2% of total variance in abundance data and was negatively correlated with the abundance of herbaceous legumes (Table 3). Axis 3 separated Thysanura, Geophilomorpha, Dermaptera and Dictyoptera, which were poorly associated with herbaceous legumes, from all other taxa.

DISCUSSION

The macroarthropods collected in Pikermi are fast-moving animals (Araneae, Phalangida, Dictyoptera, Lithobiomorpha), they have the capacity to burrow or to make use of small soil crevices (Iulida, Geophilomorpha), they tolerate the dryness of Mediterranean ecosystems (Araneae, Phalangida, Dictyoptera), they are able to move down during summer (Geophilomorpha), they have a thick cuticle (Iulida, Coleoptera adults) (see Wallwork, 1970; Petersen and Luxton, 1982; Athias-Binche et al., 1987). These adaptations could increase the chance of these animals to survive both fire events and post-fire

1.0000 Phrygana Herbaceous legumes -0.62201.0000 Season of the year -0.0307 0.0442 1.0000 'Phrygana' Herbaceous legumes Season of the year Table 3 Intraset correlation coefficients for the first three axes of Canonical Correspondence Analysis Phrygana -0.9344 -0.2294-0.2727 Herbaceous legumes 0.8308 -0.0111-0.5564Season 0.1615 -0.9268 0.3391 ENVI AX3 ENVI AX1 ENVIAX2

Table 2
Mutual correlation of environmental variables used in Canonical Correspondence Analysis

conditions, showing their adaptation to fire (Wikars and Schimmel, 2001; Hartley et al., 2007). Despite the above adaptations, the number of taxa collected, as well as the density of their populations in the studied stands (0.20–0.79 ind/m²), was extremely low compared to four unburned mature Aleppo pine forests of central Greece (78.4–962.4 ind/m²) (see Table 4 for details) (Legakis, 1986; Radea, 1989; Karamaouna, 1990; Marmari, 1991). Broza and Izhaki (1997) have found similar results in comparing the structure of soil macroarthopod communities in burned and unburned Aleppo pine forest of Israel during the 2nd and 3rd year after fire. The decline of densities in burned sites during the 2nd and 3rd year after fire has been reported to be more pronounced for some taxa such as Geophilomorpha (Athias-Binche et al., 1987). Additionally, tenebrionids Coleoptera are also reported to be sensitive indicators of habitat transformations caused by fire in a *P. pinea* plantation, showing important changes in community structure between woodlands and burned open habitats (Fattorini, 2010). It is well-known that soil arthropods depend on structural and microclimatic features of organic horizons and,

Table 4
Soil macroarthropods, in ind/m ² , in the studied stands and four unburned Pinus halepensis forests o
central Greece. ⁽¹⁾ Radea (1989), ⁽²⁾ Marmari (1991), ⁽³⁾ Karamaouna (1990), ⁽⁴⁾ Legakis (1986)

Taxa Pikermi				Scopelos ⁽¹⁾ Euboea ⁽²⁾		Sophico ⁽³⁾	Hymettus ⁽⁴⁾	
	Pik50	Pik17	Pik8	_			East slope	West slope
Araneae	3.3	11.3	5.6	52.4	38.3	39.0	14.4	4.8
Pseudoscorpionida	0.3	0.0	0.0	95.3	30.1	68.8	14.4	20.8
Phalangida	0.7	0.0	0.0	0.5	0.0	1.4	No data	No data
Lithobiomorpha	0.0	0.8	0.0	26.5	0.0	18.3*	8.0*	20.8*
Geophilomorpha	4.0	4.1	1.3	6.1	10.8			
Iulida	0.0	13.3	0.0	15.6	10.0			
Polydesmida	0.0	0.0	0.0	4.2	0.0	39.0**	9.6**	4.8**
Polyxenida	0.0	0.0	0.0	80.2	34.3			
Isopoda	0.2	2.0	0.3	15.2	0.0	5.7	No data	No data
Hemiptera	10.0	0.0	0.1	25.0	71.9	8.4	16.0	19.2
Psocoptera	0.0	0.0	0.0	141.0	106.6	No data	No data	No data
Thysanoptera	0.0	0.0	0.0	85.5	324.5	No data	No data	No data
Diptera (mature)	0.0	0.0	0.0	24.9	23.5	No data	No data	No data
Coleoptera(mature)	10.2	0.0	0.0	20.0	12.9	25.6	0.0	16.0
Diptera (larvae)	0.0	0.0	0.0	350.6	31.3	224.0***	0.0	8.0
Coleoptera (larvae)	4.0	0.0	0.0	14.8	99.6		16.0	0.0
Thysanura	2.9	0.0	0.1	0.5	0.0	1.8	0.0	0.0
Dictyoptera (Blatoidea)	0.0	2.7	2.7	1.6	0.0	9.7	0.0	4.8
Embioptera	0.0	0.0	0.0	2.5	0.0	0.6	0.0	0.0
Dermaptera	0.0	6.7	0.0			No data		

*Chilopoda, **Diplopoda, ***Holometabolan larvae.

therefore, may be sensitive to fuel reduction that alters this habitat (Greenberg et al., 2010). These alterations are obviously more profound in severely burned areas, where the consumption of the organic horizon (depth of burning) is high or complete (Ahlgren, 1974; Springett, 1979, Radea and Arianoutsou, 2000; Wikars and Schimmel, 2001) as in the case of Pikermi stands, which were all severely burned.

Although the fauna of each studied stand has its own characteristics, some similarities are observed in the relative abundance of Araneae and Dictyoptera. The comparison of stands as regards these fast moving epigeic taxa suggests that the sequence of increasing relative abundance is Pik50 < Pik17 < Pik8. Araneae (a predatory taxon) seem to be resistant to frequent mild fires (Moretti et al., 2006), while the abundance of scavengers feeding on plant and animal remains (like Dictyoptera) has been found to be high in burned areas (Antunes et al., 2009). Araneae and Dictyoptera may have taken advantage of the abundant food in the post-fire mosaic of soil habitats (Moretti et al., 2004). Taking into account that most relevant studies on these taxa concern frequent mild fires or a single severe fire, a better taxonomic resolution of Araneae and Dictyoptera collected is probably required for explaining the above sequence and for understanding the response of these taxa to frequent and severe fires.

On the contrary Geophilomorpha, a humicolous taxon, at least during the dry summer period of the year when the fire event occurred, show quite similar relative abundances in the three stands. They were found under stones where they seek refuge failing a wellformed organic horizon. It seems that the deep organic horizon layers, where this taxon thrives, protect it from the impact of frequent summer fires. This finding corroborates the conclusions of Prodon et al. (1987) and Moretti et al. (2006).

It is interesting to note that Pseudoscorpionida and Coleoptera (both adults and larvae), as well as Lithobiomorpha, Iulida, and Dermaptera which were exclusively found in Pik50 and Pik17 respectively, took shelter under stones like Geophilomorpha. Apart from adult Coleoptera (Tenebrionidae) having thick cuticles all the other orders consist mainly of hygrophilous taxa thriving in loose litter, under the bark of fallen decaying trees and in rock crevices (Wallwork, 1970) in unburned ecosystems.

The results derived from Canonical Correspondence Analysis denote that the abundance of herbaceous legumes and phrygana and the seasonality of climate have the most profound effects on the qualitative and quantitative composition of the soil macroarthropod community.

The significance of herbaceous legumes and the phrygana group for soil fauna is explained by the leaf litter they produce. During the early stages of the post-fire recovery process, resprouters and seeders such as maquis species and pines, respectively, do not shed leaves as massively as the annual herbaceous legumes do (Kazanis and Arianout-sou, 1996). The leaf life-span of *P. halepensis*, *Q. coccifera*, and *P. lentiscus* is 35.5, 15.6, and 30 months respectively (Gratani and Bombelli, 2001; Mediavilla et al., 2008). Therefore, the litter of herbaceous legumes would serve as the major input of high-quality organic matter to the soil (Radea and Arianoutsou, 2004). Additionally, the phrygana group, which consists mainly of summer semi-deciduous shrubs, shed a high quantity of relatively large size soft leaves just before summer drought (Arianoutsou and Margaris,

1981; Fioretto et al., 2003). Obviously, herbaceous legumes and phrygana contribute greatly to the formation of an organic horizon that is rudimentary, but indispensable for soil fauna during the first years after fire.

The post-fire abundance of macroarthropod taxa in Pikermi shows fluctuations during the sampling period. This dynamics might be due to both demographic processes and seasonality of climate. In fact, the succession of the wet and dry periods of the year was found to be a very significant environmental factor controlling the abundance of soil macroarthropods in Pikermi stands. The phenology of soil macroarthropods has not been altered even after the frequent fires in Pik17 and Pik8, although fire may cause changes in the phenology of some taxa according to Sgardelis et al. (1995). The highest number of taxa and individuals in Pikermi was recorded during the wet period of the year. This temporal pattern has also been observed in unburned Aleppo pine forests of Greece (Radea, 1989; Marmari, 1991) and in burned and unburned Aleppo pine forests of Israel (Broza and Izhaki, 1997), as well as in burned phryganic ecosystems of Greece (Sgardelis et al., 1995). According to the latter authors the seasonality of the Mediterranean climate imposes greater variations of arthropod abundance than those caused by fire.

The effect of fire frequency on the communities of soil macroarthropods is indirectly depicted through the changes that occurred in vegetation structure.

In the case of *P. halepensis* forests, fire frequency is known to cause many changes in vegetation structure because it defines the ability of several plant groups to regenerate (Kazanis and Arianoutsou, 2004; Eugenio et al., 2006; Kazanis et al., 2007). It is wellknown that vegetation controls soil biota mainly through the quantity and quality of litter, the main input to the soil organic horizon, and the physical effects of vegetation cover on soil microclimate and surface protection (e.g., Swift and Anderson, 1994; David et al., 1999; Chikoski et al., 2006). Especially in Mediterranean ecosystems, vegetation cover and quantity of soil organic matter constitute key factors controlling community structure and population dynamics of soil fauna (di Castri and Vitali-di Castri, 1981; Swift and Anderson, 1994; Radea and Arianoutsou, 2002). Considering that the populations of soil fauna aggregate gradually following the post-fire building of organic horizon (Athias-Binche et al., 1987), and that repeated fires with short intervals between successive events decrease the amount of soil organic horizon (Moretti et al., 2004; Eugenio et al., 2006), the role of plant abundance and litter production after the last fire event appears to be crucial. The significance of phrygana and herbaceous legume abundance for soil macroarthropods in burned areas becomes more obvious when the timing of the litterfall is taken into account. Litterfall from these plant groups takes place in summer, and the accumulated organic matter contributes to the improvement of soil microclimate and maintenance of soil community structure and function during this harsh period. Thus in Pik8, where the abundance of phrygana and legumes was low and the organic horizon was almost completely absent, the abundance of macroarthropods sampled during fall and spring was quite similar to that of the unfavorable dry summer period.

Our work shows that although soil biota of Mediterranean forests are adapted to fire, fire frequency is crucial in defining structure and abundance of soil arthropod communities.

There is strong evidence that the wildfire regime across the Mediterranean Basin tends to change under the influence of both socioeconomic factors and climate change (Arianoutsou, 2004, 2007). Although the resilience of an ecosystem (its capacity to recover after a perturbation) has been related mainly to its plant community, soil biota may also play a critical role in this ecosystem property, given that soil biota perform organic matter comminution, decomposition, and mineralization. In this perspective, our findings constitute strong evidence of increased soil biological system destruction and hence support the idea of using soil biota as an additional indicator of ecosystem vulnerability (Van Straalen, 1998; Dauber et al., 2005; Marra and Edmonds, 2005).

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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. 47–72.
- Anderson, J.M., 1988. Spatiotemporal effects of invertebrates on soil processes. Biol. Fertil. of Soils 6(3): 216–231.
- 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. 2001. Landscape changes in Mediterranean ecosystems of Greece: implications for fire and biodiversity issues. J. Medit. Ecol. 2: 165–178.
- Arianoutsou, M. 2004. Predicting the post fire regeneration and resilience of Mediterranean plant communities. In: Arianoutsou, M., Papanastasis, V.P. eds. Ecology, conservation and management of Mediterranean climate ecosystems. Millpress (electronic edition), http://www. iospress.nl/loadtop/load.php?isbn = millpress.
- Arianoutsou, M. 2007. Resilience of Mediterranean vegetation to fire: issues under the global change scenarios. In: Rokich, D.,Wardell-Johnson, G., Yates, C., Stevens, J., Dixon, K.R., McLellan, R., Moss, G., eds. Proceedings of the MEDECOS XI Conference, Perth, Australia. Kings Park and Botanic Garden, Perth, pp. 5–7.
- Arianoutsou, M., 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, http://www.iospress.nl/loadtop/load.php?isbn = millpress).
- Arianoutsou, M., Margaris, N.S. 1981. Producers and the life cycle in a phryganic ecosystem. In: Margaris, N.S., Mooney, H.A., eds. Composition of productivity of Mediterranean-climate regions—

basic and applied aspects. Dr W. Junk Publishers, The Hague, Boston, London, pp. 181-190.

- 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(4): 135–154.
- Brower, J.E., Zar, J.H., von Ende, C.N. 1990. Field and Laboratory Methods for General Ecology, 3rd Edition. Brown, W.C. Publishers, Dubuque, 237 p.
- Broza, M., Izhaki, I. 1997. Post-fire arthropod assemblages in Mediterranean forest soils in Israel. Int. J. Wild. Fire 7: 317–325.
- Chikoski, J.M., Ferguson, S.H., Meyer, L. 2006. Effects of water addition on soil arthropods and soil characteristics in a precipitation-limited environment. Acta Oecol. 30: 203–213.
- Cook, W.M., Holt, R.D. 2006. Fire frequency and mosaic burning effects on a tallgrass prairie ground beetle assemblage. Biodiv. Conserv. 15: 2301–2323.
- Dauber, J., Purtauf, T., Allspach, A., Frisch, J., Voigtländer, K., Wolters, V. 2005. Local vs. landscape controls on diversity: a test using surface-dwelling soil macroinvertebrates of differing mobility. Global Ecol. Biogeogr. 14: 213–221.
- David, J.F., Devernay, S., Lougougary, G., Le Floc'h, E. 1999. Belowground biodiversity in a Mediterranean landscape: relations between saprophagous macroarthropod communities and vegetation structure. Biodiv. Conserv. 8: 753–767.
- 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.
- Eugenio, M., Lloret, F., Alcaniz, J.M. 2006. Regional patterns of fire recurrence effects on calcareous soils of Mediterranean *Pinus halepensis* communities. For. Ecol. Manage. 221: 313–318.
- Fattorini, S. 2010. Effects of fire on tenebrionid communities of a *Pinus pinea* plantation: a case study in a Mediterranean site. Biodivers Conserv. 19: 1237–1250.
- Fioretto, A., Papa, S., Fuggi, A. 2003. Litter-fall and litter decomposition in a low Mediterranean shrubland. Biol. Fertil. Soils 39: 37–44.
- Greenberg, C.H., Forrest, T.G., Waldrop, Th. 2010. Short-term response of ground-dwelling arthropods to prescribed fire and mechanical fuel reduction in southen Appalachian upland hardwood forest. Forest Sci. 56(1): 112–121.
- Gratani, L., Bombelli, A. 2001. Differences in leaf traits among Mediterranean broad-leaved evergreen shrubs. Ann. Bot. Fennici 38: 15–24.
- Hartley, M.K., Rogers, W.E., Siemann, E., Grace, J. 2007. Responses of prairie arthropod communities to fire and fertilizer: balancing plant and arthropod conservation. Am. Midl. Nat. 157: 92–105.
- Hogervorst, R.F., Verhoef, H.A., Straalen, N.M. 1993. Five-year trends in soil arthropod densities in pine forests with various levels of vitality. Biol. Fertil. Soils 15: 189–195.
- Karamaouna, M., 1990. On the ecology of the soil macroarthropod community of a Mediterranean pine forest (Sophico, Peloponnese, Greece). Bull. Ecol. 21: 33–42.
- Kay, F.R., Sobhy, H.M., Whitford, W.G. 1999. Soil microarthropods as indicators of exposure to environmental stress in Chihuahuam Desert rangelands. Biol. Fertil. Soils 28: 121–128.
- Kazanis, D., Arianoutsou, M. 1996. Vegetation composition in a post-fire successional gradient of *Pinus halepensis* forests in Attica, Greece. Int. J. Wild. Fire 6(2): 83–91.
- Kazanis, D., Arianoutsou, M. 2004. Factors determining low Mediterranean ecosystems resilience to fire: The case of *Pinus halepensis* forests. In: Arianoutsou, M., Papanastasis, V.P., eds. Ecology, Conservation and Management of Mediterranean Climate Ecosystems. Millpress (electronic edition). http://www.iospress.nl/loadtop/load.php?isbn = millpress).

- Kazanis, D., Gimeno, T., Pausas, J.G., Vallejo, R., Arianoutsou, M. 2007. Characterization of fire vulnerable *Pinus halepensis* ecosystems in Spain and Greece. Options Medit. 75: 131–143.
- Knoepp, J.D., Coleman, D.C., Crossley, D.A. Jr., Clark, J.S., 2000. Biological indices of soil quality; an ecosystem case study of their use. For. Ecol. Manage. 138: 357–368.
- Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., Rossi, J.-P. 2006. Soil invertebrates and ecosystem services. Eur. J. Soil Biol. 42: 3–15.
- Legakis, A. 1986. Comparative studies of the soil arthropods of three ecosystems on mount Hymettos (Attica, Greece). Biol. Gallo-Hellenica 12: 371–375.
- Marmari, A. 1991. Effects of human activities on soil arthropods in a *Pinus halepensis* Mill. ecosystem of N. Euboea (Greece). Ph.D. Thesis, University of Athens, Athens, 221 pp.
- Marra, J.L., Edmonds, R.L. 2005. Soil arthropod responses to different patch types in a mixedconifer forest of the Sierra Nevada. For. Sci. 3: 255–265.
- McBrayer, J., Reichle, E. 1971. Trophic structure and feeding rates of forest soil invertebrate populations. Oikos 22: 381–388.
- McBrayer, J.F., Ferris, J.M., Metz, L.J., Gist, C.S., Cornaby, B.W., Kitazawa, Y., Kitazawa, T., Wernz, J.G., Krantz, G.W., Jessen, H. 1977. Decomposer invertebrate populations in U.S. forest biomes. Pedobiologia 17: 89–96.
- Mediavilla, S. Garcia-Ciudad, A., Garcia-Criado, B., Escudero, A. 2008. Testing the correlations between leaf life span and leaf structural reinforcement in 13 species of European Mediterranean woody plants. Funct. Ecol. 22: 787–793.
- Moretti, M., Obrist, M.K., Duelli, P. 2004. Arthropod biodiversity after forest fires: winners and losers in the winter fire regime of the Southern Alps. Ecography 27: 173–186.
- Moretti, M., Duelli, P., Obrist, M.K. 2006. Biodiversity and resilience of arthropod communities after fire disturbance in temperate forests. Oecologia 149: 312–327.
- Ntouros, G. 1995. Reforestation study of the SE area of Penteli mountain. Attica Directorate of Reforestations, Athens, pp. 44.
- Pausas, J.G., Keeley, J.E. 2009. A burning story: the role of fire in the history of life. Bioscience 59: 593–601.
- Petersen, H., Luxton, M. 1982. A comparative analysis of soil arthropod population and their role in decomposition processes. Oikos 39: 288–388.
- 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 ecological systems. SPB Academic Publishing, The Hague, pp. 121–157.
- 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 the insular Greece. Ph.D. Thesis, University of Athens, Athens, pp. 256.
- 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., Arianoutsou, M. 2002. Environmental responses of soil arthropod communities along an altitudinal–climatic gradient of Western Crete in Greece. J. Medit. Ecol. 3: 38–48.
- Radea, C., Arianoutsou, M. 2004. Decomposition rates of legumes and cellulose in a *Pinus halepensis* Mill. forest of Greece after a wildfire. In: Arianoutsou, M., Papanastasis, V.P. eds. Ecology, conservation and management of Mediterranean climate ecosystems. Millpress (electronic edition), http://www.iospress.nl/loadtop/load.php?isbn = millpress.
- Schrader, S., Langmaack, M., Helming, K. 1997. Impact of Collembola and Enchytraeidae on soil surface roughness and properties. Biol. Fertil. Soils 25: 396–400.
- Sgardelis, S.P., Pantis, J.D., Argyropoulou, M.D., Stamou, G.P. 1995. Effects of fire on soil mac-

roinvertebrates in a Mediterranean phryganic ecosystem. Int. J. Wild. Fire 5: 113–121.

- Siemann, E., Tilman, D., Haarstad, J., Ritchie, M. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. Amer. Natur. 152: 738–750.
- 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.
- Swift, M.J., Anderson, J.M. 1994. Biodiversity and ecosystem function in agricultural systems. In: Schultze, E.-D., Mooney, H.A. eds. Biodiversity and ecosystem function. Springer-Verlag, Berlin, pp. 13–41.
- Symstad, A.J., Siemann, E., Haarstad, J. 2000. An experimental test of the effect of plant functional group diversity on arthropod diversity. Oikos 89: 243–253.
- Ter Braak, C.J.F. 1996. Unimodal models to relate species to environment. DLO-Agricultural Mathematics Group, Wageningen, pp. 266.
- Tian, G., Brussaard, L., Kang, B.T., Swift, M.J. 1997. Soil fauna-mediated decomposition of plant residues under constrained environmental and residue quality conditions. In: Cadish, G., Giller, K.E., eds. Driven by nature. Plant litter quality and decomposition. Oxon CAB International, pp. 125–135.
- Van Straalen, N.M. 1998. Evaluation of bioindicator systems derived from soil arthropod communities. App. Soil Ecol. 9: 429–437.
- Wallwork, J.A. 1970. Ecology of soil animals. Mc Graw Hill, London,
- Whiles, M.R., Charlton, R.E. 2006. The ecological significance of tallgrass prairie arthropods. Ann. Rev. Entomol. 51: 387–412.
- 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.