

Factors determining low Mediterranean ecosystems resilience to fire: the case of *Pinus halepensis* forests

D. Kazanis & M. Arianoutsou

Department of Ecology and Systematics, Faculty of Biology, School of Sciences, National and Kapodistrian University of Athens, 15784 Athens, Greece
dkazanis@biol.uoa.gr

Keywords: species richness, functional groups, legumes, vegetation cover, fire interval, regeneration, slope effect, limestone outcrops

ABSTRACT: Factors acting as drivers of low resilience to fire in *Pinus halepensis* ecosystems are being examined. The commonest factor seems to be fire interval. From the several time windows examined, that of, the shortest one ever reported in this type of communities (3 years only) seemed to be the most crucial. From the plant species previously existing on the site woody and herbaceous obligate seeders are mainly affected by this factor. Other factors, affecting mainly pine regeneration, are the abundance of *Quercus coccifera* individuals in the regenerating community and the high percentage of limestone outcrops. As an example of a landscape approach to the problem of evaluating resilience to fire, the case of Sounion Peninsula National Park is presented.

1 INTRODUCTION

Fire is a major natural disturbance in pine forest ecosystems throughout the world (Richardson and Rundel 1998). The fire regime of these ecosystems ranges from short-interval and low-intensity to long-interval and high-intensity fire events (Agee 1998), depending on the combined effects of the prevailing climatic conditions and the vegetation structure of the forest. In the Mediterranean Europe, two, ecologically and phylogenetically distinguished groups of pines are found (Barbero et al. 1998). The species of the first group form extended forests in areas of high altitude, with cold winters and wet, mild summers, whereas the species of the second group account for the vast majority of forested land in areas of lower altitude, usually near the sea. The climate of those areas is typical mediterranean, i.e. with dry, hot summers and mild, wet winters. Consequently, the fire regime in the forests of these two groups of pines is expected to be quite different.

Pinus halepensis Mill. belongs to the second, the mediterranean group of pines. The importance of fire for the maintenance of the structure and the biodiversity of *P. halepensis* forests has been recognized (Naveh 1994). The typical fire regime of these ecosystems is characterized by high intensity fire events (Agee 1998), with a fire interval of approximately 30 to 50 years (Arianoutsou 2001).

Similarly to mediterranean-type shrublands, *P. halepensis* forests are resilient to fire (Trabaud 2000, Arianoutsou and Ne'eman 2000, Kazanis and Arianoutsou 2002). Resilience, an important ecosystem function, was initially described as the system capacity to absorb the effects of disturbance and to maintain its structure (Holling 1973). Later, Westman (1986) has broadened the concept by not only emphasizing on the final outcome but also on the processes and pathways that act towards return of the system to its pre-disturbance situation. Accordingly, the vast majority of plant

species inhabiting those ecosystems have evolved under the influence of the respective fire regime and their life traits include all the necessary mechanisms that enable them either to avoid fire or to establish successfully in the post-fire environment (Naveh 1975, Keeley 1986, Arianoutsou 1998).

P. halepensis forests are not homogeneous across a forested landscape, since differences in site characteristics are reflected to differences in the composition and the structure of the understorey (Trabaud et al. 1985). Similarly, resilience to fire may differ among the various patches of the forested landscape, since the ability of several key plant species to regenerate after fire maybe different, given the specific biotic and abiotic interactions developed within the various patches (Hobbs et al. 1984). Differences in fire and land use history increase this diverse response to fire (Arianoutsou et al 2002, Lloret and Vila 2003).

During the last decade, large fire events are commonly affecting thousands of hectares of *P. halepensis* forests and woodlands in countries of the northern Mediterranean Basin (primarily Spain, France and Greece). As a result, there was an increased public demand for effective post-fire ecosystem management. Given the above-mentioned heterogeneity in ecosystem resilience across large burned areas and the limitations in personnel and financial support, it is essential for the Forestry Department Officials to be able to identify patches with low resilience to fire, so as to apply management practices only to those parts that actually required them. Towards this direction, this paper aims to highlight factors, which seem to determine low ecosystem resilience, and to propose biological indicators that could help the land managers to evaluate the actual post-fire situation.

2 CHOOSING THE RIGHT CRITERIA AND INDICATORS

In the summer of years 1998 and 2000 large fires swept areas covered by *P. halepensis* ecosystems on the mountains surrounding Athens metropolitan area. In spring 2002, preliminary measurements across the burned areas were performed, so as to identify patches of low resilience. The first critical step was the selection of criteria that would allow us to 'classify' a community as of low resilience. The selected communities were surveyed according to specific protocols (developed within SPREAD, an EU-funded scientific project) so as to elaborate proper biological indicators of low resilience and to relate them with the respective factor (or factors) that determine low resilience in each case.

According to Westman's concept, resilience is a multi-dimensional function. This is the reason why resilience evaluation depends on the person who performs it (Grubb and Hopkins 1986). For a soil scientist, for example, the key function is vegetation cover, since it is of primary importance for preventing soil erosion, whereas an ornithologist will be more interested in the shrubs and trees to re-build their pre-fire architecture, so as to present a variety of nesting and feeding habitat alternatives to avifauna. For the vegetation scientist, any attempt to study and evaluate the resilience of ecosystems implies either the existence of a sequence of different species dominance and replacement (typical secondary succession), or of a sequence of change in species relative abundance along the "autosuccessional" model (Fox and Fox 1986). The later is the case for mediterranean-type shrublands and forests (Hanes 1971, Arianoutsou-Faraggitaki 1984, Trabaud 2000, Arianoutsou and Ne'eman 2000, among many others). Therefore, the resilience potential of any mediterranean-type plant community is evident even from the first post-fire years, given that the pre-fire species composition and abundance is known. Since we are referring to wildfires, this is seldom the case. As a result, the preliminary criteria should be chosen in such a way so as to have global application throughout the burned area, regardless the specific structural and compositional characteristics of each patch. Two such criteria could be applied: mean vegetation cover and pine regeneration.

Apart from the first year, post-fire regenerating *P. halepensis* plant communities are characterized by high soil vegetation cover, due to complexity in vegetation structure (consisting of a variety of plant groups) (Kazanis and Arianoutsou 2002, Kazanis and Arianoutsou in press). Consequently, low vegetation cover would strongly indicate negative fire effect on one or more plant groups. Sufficient pine regeneration is essential for the resilience of those ecosystems. Therefore, low pine re-

generation was another criterion for including a patch in “target group of patches”. Both mean vegetation cover and pine regeneration were variables that could be visually (thus non-time consuming) estimated in the field. Similar to pine regeneration, the regeneration of other dominant woody species, whenever there was available evidence of their dominance in the pre-fire situation, was taken into account as criterion for taking patches into consideration.

The next step was to decide what other indicators, apart from vegetation cover and pine regeneration, would be looked for in order to evaluate the resilience capacity of the plant community. As already mention, the ideal would be to know exactly what was there before the fire event and examine whether it has regenerated or not. This was applicable only in three cases where the necessary data were available (see below). In all the other cases, we were able to overcome this unavailability of data through a simulation based on the composition of the expected functional groups.

Identification of functional groups in regard to disturbance has been recognized as a promising tool towards the understanding and prediction of species composition change risk due to changes in disturbance regime (Pausas and Lavorel 2003). We have, recently, proposed a functional group classification system that is based on species long-term post-fire performance and have applied it in *P. halepensis* ecosystems of Greece (Kazanis and Arianoutsou, in press). This application allowed us to recognize the diversity of different life traits combinations shared by species of the ecosystems in question (Table 1) and, furthermore, to follow the long-term post-fire richness and abundance pattern for each functional group. Consequently, deviations from the expected community composition in terms of functional groups, on a given autosuccessional stage or phase, were regarded as potential indicators of low resilience.

Table 1. Biological attributes that characterize the species classified in each functional group. Different groups are named after a typical species.

Functional Group (Symbol)	Growth form	Regeneration mode	Mode of Persistence	Dispersal Agent	Specific competitive advantage
<i>Pinus halepensis</i> group (Phal)	Tree	Obligate seeder	Long life span	Wind	None
<i>Crataegus monogyna</i> group (Cmon)	Tree	Obligate resprouter	Long life span	Animals	None
<i>Quercus coccifera</i> group (Qcoc)	Tall shrub	Obligate resprouter	Long life span	Animals	None
<i>Calicotome villosa</i> group (Cvil)	Tall shrub	Facultative resprouter	Long life span	None	Nitrogen Fixation
<i>Juniperus phoenicea</i> group (Jpho)	Tall shrub	Colonizer	Long dispersal mode	Animals	None
<i>Smilax aspera</i> group (Sasp)	Woody liana	Obligate resprouter	Long life span	Animals	None
<i>Asparagus acutifolius</i> group (Aacu)	Short shrub	Obligate resprouter	Long life span	Animals	None
<i>Erica manipuliflora</i> group (Eman)	Short shrub	Facultative resprouter	Long life span	Wind	None
<i>Hypericum empetrifolium</i> group (Hemp)	Short shrub	Facultative resprouter	Secondary establishment Long dispersal mode	Wind	None
<i>Genista acanthoclada</i> group (Gaca)	Short shrub	Obligate seeder	Long life span Soil seed bank	None	Nitrogen Fixation
<i>Dorycnium hirsutum</i> group (Dhir)	Short shrub	Obligate seeder	Secondary establishment Soil seed bank	None	Nitrogen Fixation
<i>Cistus salvifolius</i> group (Csal)	Short shrub	Obligate seeder	Secondary establishment Soil seed bank	None	None
<i>Coridothymus capitatus</i> group (Ccap)	Short shrub	Delayed seeder	Secondary establishment	None	None

<i>Phagnalon graecum</i> group (Pgra)	Short shrub	Colonizer	Long dispersal mode	Wind	None
<i>Cyclamen graecum</i> group (Cgra)	Perennial herb	Obligate resprouter	Long life span	Various	Subterr. re- source organs
<i>Brachypodium pinnatum</i> group (Bpin)	Perennial herb	Obligate resprouter	Long life span	Various	Vivid lateral growth
<i>Centaurea mixta</i> group (Cmix)	Perennial herb	Obligate resprouter	Long life span	Wind	None
<i>Convolvulus elegantissimus</i> group (Cele)	Perennial herb	Facultative resprouter	Long life span Soil seed bank	None	None
<i>Bituminaria bituminosa</i> group (Bbit)	Perennial herb	Obligate seeder	Secondary establishment Soil seed bank	Animals	Nitrogen Fixation
<i>Ajuga chamaepitys</i> group (Acha)	Perennial herb	Obligate seeder	Secondary establishment Soil seed bank	None	None
<i>Stachys cretica</i> group (Scre)	Perennial herb	Delayed seeder	Secondary establishment	None	None
<i>Scilla autumnalis</i> group (Saut)	Perennial Herb	Colonizer?	Long life span? Long dispersal mode?	Unclear	Subterr. re- source organs
<i>Scabioza columbaria</i> group (Scol)	Perennial Herb	Colonizer	Long dispersal mode	Various	None
<i>Cytinus hypocistis</i> group (Chyp)	Perennial herb	Colonizer?	Long life span	Unclear	Parasite
<i>Lathyrus cicera</i> group (Lcic)	Annual herb	Obligate seeder	Secondary establishment Soil seed bank	Animals	Nitrogen Fixation
<i>Tuberaria guttata</i> group (Tgut)	Annual herb	Obligate seeder	Secondary establishment Soil seed bank	None	None
<i>Hypochoeris achyrophorus</i> group (Hach)	Annual herb	Obligate seeder	Secondary establishment	Various	None
<i>Biscutella didyma</i> group (Bdid)	Annual herb	Delayed seeder	Secondary establishment	None	None
<i>Aira elegantissima</i> group (Aele)	Annual herb	Colonizer	Long dispersal mode	Various	None
<i>Cuscuta epithymum</i> group (Cepi)	Annual Herb	Colonizer	Long dispersal mode	Animals	Parasite

3 FACTORS RELATED TO LOW ECOSYSTEM RESILIENCE

3.1 Fire Interval

Fire regime changes include risks of changes in the floristic composition of vegetation, since the regeneration modes of species may prove inadequate under the new conditions (Bond and van Wilgen 1996, Arianoutsou 2001). During the last twenty years, there is a continuous risk of change due to a decrease in the average fire interval (Arianoutsou et al. 2002, Diaz-Delgado et al. 2002). Similarly to what has been reported from other parts of the world (Gill and Williams 1996), socio-economic and land-use changes are the main driving force for this change (Trabaud and Galtie 1996, Pausas et al. 1999, Vazquez and Moreno 2001, Arianoutsou 2001). This tendency may become even more dramatic in the future, under the global scenario of climate change (Mouillot et al 2002).

Within the area burned in the summer of 1998, there were three young pine stands of increasing post-fire age. These stands were of great importance to us, since data on their vegetation composition and structure until just before the fire were available in detail. All three communities had been sampled diachronically in the context of a previous study (Kazanis and Arianoutsou 2002, Kazanis

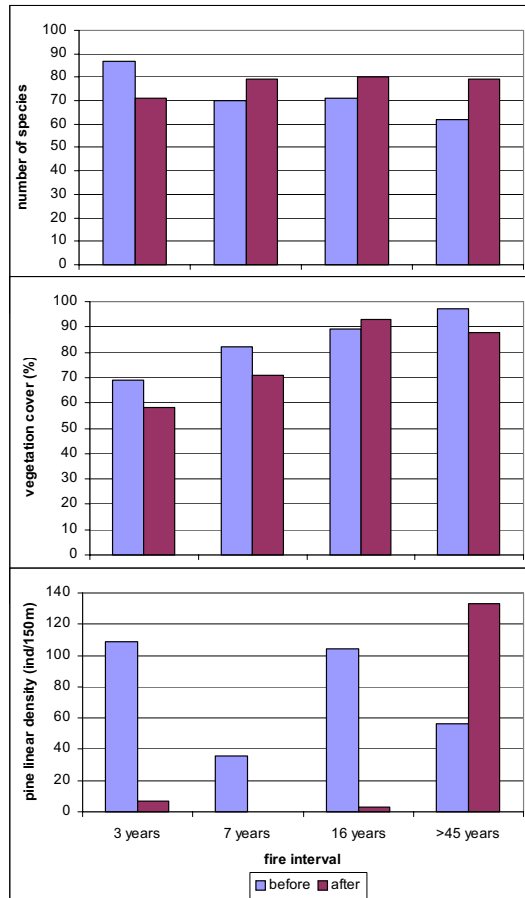


Figure 1. Species richness, vegetation cover and pine density in four burned pine stands forming a chronosequence of increasing fire interval. Data referring as “before” fire were sampled the year just before the second fire event, whereas data referring as “after” fire were produced from re-sampling in the 4th post-fire year.

and Arianoutsou in press). Four years later, in spring of 2002, these stands were re-sampled in order to encounter the role of fire interval. As a control, the case of a mature pine forest (>45 years old) that had been sampled before a 1995 fire event and, diachronically since this event for 4 years.

Before discussing the results, there should be a short description of the average, long-term, post-fire pattern of these *P. halepensis* communities under the typical fire interval. This autosuccessional pattern consists of different successive phases, named after their main physiognomic characteristics (Kazanis and Arianoutsou 2002, Kazanis and Arianoutsou in press). Accordingly, the initial herbaceous phase (lasting until the 3rd to 4th year) is been followed by a shrub layer dominance phase (with varied length, related to the life span and abundance of the dominant shrub groups, but never exceeding the 15th year). After the shrub dominance phase, there is the phase of the young pines, when pines are forming their own stratum and their presence is dominant in the physiognomy of the community. This phase ends with the last phase of the mature pine forest (more than 30 years since fire). Species richness pattern follows the pattern of the vegetation structure, pre-

Table 2. Species number per functional group before and after a fire incidence that burned four *P. halepensis* communities. The four communities differed among each other in the fire interval between this last fire event and the previous one. Each community was sampled just before this last fire incidence and re-sampled in the 4th post-fire year.

Functional Groups	Fire interval							
	3 years		7 years		16 years		>45 years	
	before	after	before	after	before	After	before	after
Phal	1	1	1	0	1	1	1	1
Cmon	-	-	-	-	2	2	-	-
Qcoc	4	4	9	9	5	5	4	4
Cvil	1	1	2	2	3	3	1	1
Sasp	2	2	3	3	3	3	0	0
Aacu	1	1	3	3	1	1	1	1
Eman	1	2	0	0	2	2	2	2
Hemp	1	1	1	1	1	1	2	2
Gaca	2	2	2	2	2	2	2	2
Dhir	1	0	0	0	0	1	0	0
Csal	5	4	4	4	4	5	3	4
Ccap	3	5	0	1	3	3	3	1
Pgra	0	1	1	1	3	0	3	2
Cgra	8	8	7	7	9	9	9	11
Bpin	4	4	3	3	3	3	3	3
Crap	2	2	5	5	2	3	2	4
Cele	2	1	1	2	1	2	3	3
Acha	1	1	-	-	0	1	-	-
Bbit	2	2	3	3	4	4	0	3
Scol	1	1	-	-	1	1	2	2
Chyp	1	0	-	-	-	-	0	1
Lcic	14	6	14	6	7	11	4	13
Tgut	7	5	0	5	4	1	2	5
Hach	3	3	1	3	3	3	7	6
Bdid	6	6	2	2	2	4	2	1
Aele	14	11	7	16	2	9	10	5
woody species	22	24	26	26	30	29	22	20
herbaceous species	65	51	44	53	41	51	47	59

senting a maximum in the first phase and a secondary peak during the transition from the shrub to the pine dominance phase.

From the above, it is evident that the studied chronosequence includes one burned representative from each post-fire phase. In Fig. 1, the fire effect on species richness, vegetation cover and pine density for the different fire intervals is presented. The 3-yr-old burned community was the only one that showed decreasing species number when re-sampled. Three years as a fire interval is very rare and extreme for these types of ecosystems, and, as far as we know, has never been reported in the past, at least in Greece. Reduced species number is linked with limited representation of several herbaceous groups, primarily these of obligate seeders (Lcic, Tgut) (Table 2). This apparent low regeneration of the species in question can be attributed to low fire severity (due to low fuel load), that did not induce the breaking of seed dormancy. A comparison of annual legumes richness and abundance in two burned patches of pine forest with different fuel load supports this idea (Andriopoulos and Arianoutsou unpubl data). Another explanation could be that the seeds re-

leased from plants within the first four years have not yet been incorporated in deeper soil layers, being, thus, exposed to the direct effect of fire. The low regeneration of annual legumes (recognized as the most abundant group in the first post-fire years, (Kazanis and Arianoutsou 2002, Kazanis and Arianoutsou in press) observed also in the 7-yr-old burned community, but not in the other two, apart from being an indicator of low resilience, has direct effects on the nitrogen balance of these ecosystems (Papavassiliou 2001) Apart from the herbaceous obligate seeders, two woody species sharing the same regeneration mode, did not regenerate, *Cistus monspeliensis* (Cistaceae, Csal group) and *Dorycnium hirsutum* (Leguminosae, Dhir group). Both species are rare in the mature stands, and appear massively after the fire (as in the example of the control stand).

Pine regeneration was very low to zero in all the communities of short fire interval. *Pinus halepensis* individuals may produce their first mature cones after the 6th year, but the age when half of the population becomes reproductive varies between 7 and 15 years (Thanos and Daskalaku 2000). The few pine saplings recorded in the community of the shortest fire interval were originated from seeds arrived at the sites from neighboring unburned pine trees. This is the case of landscape level effect on resilience that will be discussed later. On the contrary, the few saplings encountered in the 16-yr-old burned stand were produced by seeds from cones that had been produced in the same stand.

Finally, vegetation cover follows a pattern proportional to fire interval, with the highest erosion risk in the community of the shortest fire interval.

3.2 Understorey structure

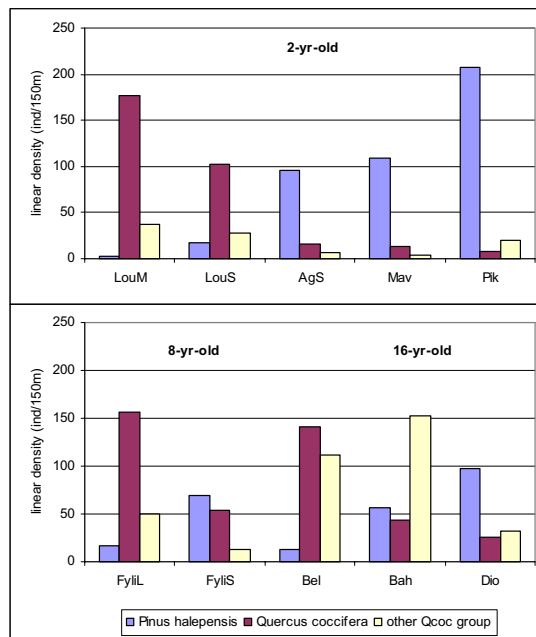


Figure 2. Linear density of *P. halepensis*, *Q. coccifera* and other members of the Qcoc functional group. Presented data are produced from vegetation analysis, with the linear transect method, from six, two and three communities of 2-yr-old (LouM, LouS, AgS, Mav and Pk), 8-yr-old (FyLiL, FyLiS) and 16-yr-old (Bel, Bah, Dio) post-fire age, respectively.

The composition and the abundance of the woody species that participate in the formation of the understorey can be reflected in the ecosystem resilience. Two such cases have been encountered. The first is the case of pine stands with high abundance of *Juniperus phoenicea* in the understorey. In this case, the regeneration of all species and functional groups is satisfactory but for this species, which is known to be unable to regenerate vegetatively and doesn't form seed banks (Martinez-Sanchez et al. 1997, Kazanis unpubl. data). The highest the abundance of this species is in the understorey of the unburned pine forest, the lowest the resilience capacity of the system is evaluated. The second is the case of stands with high abundance of *Quercus coccifera* in the understorey. Species of the *Q. coccifera* functional group are characterized by vigorous resprouting even from the first few days after the fire event (Konstantinidis and Tsiourlis 2002, Kazanis and Arianoutsou, unpubl. data). Among those species, *Q. coccifera* is the one with the most vivid lateral growth.

As a consequence, although it is not the species with the highest rate of sprout elongation among the species of the same group, it is the species with the highest rate of horizontal expansion (Kazanis and Arianoutsou 1997). As a consequence, there seems to be a negative relation between *Q. coccifera* and *P. halepensis* abundance after the fire (Fig. 2). This negative relation is not always the case when the abundance of the other members of the Qcoc group is considered. It is worth mentioning, that in both cases the criterion of low vegetation cover had no application.

3.3 Site characteristics

Pine regeneration depends on the availability of soil surface not covered by stones or rocks, for the released seeds to deposit and germinate after the first autumnal rainfalls. Whenever there is no available bare soil, there is a high risk of low pine regeneration. This is the case of patches developed on limestone, in sites with high rocky outcrops and stone cover. These sites are usually characteristic of the upper zone (around the peak) of low-altitude, mediterranean-climate mountains.

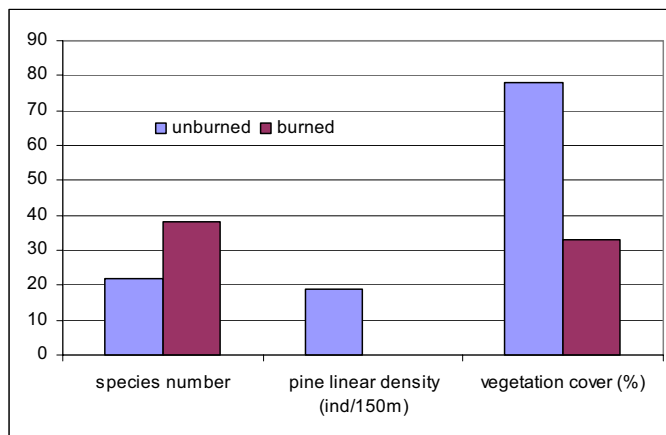


Figure 3. Species richness, pine density and vegetation cover in one burned and the adjacent unburned stand of *P. halepensis* forests developed on a location with high limestone outcrops cover. The age of the burned stand was 4-yr-old.

Pine stands on these locations have poorly developed understorey, with sparse, cushion-like individuals of *Q. coccifera*. In Fig. 3, data from one, 4-yr-old, burned and the adjacent unburned stand, developed on such a location, are presented. No pine regeneration has been encountered in the burned stand. Pine density of the unburned stand is lower than the mean density of a typical pine stand (Kazanis and Arianoutsou in press). Vegetation cover is much lower in the burned stand,

Table 3. Species number per functional group in one burned and the adjacent unburned stand of *P. halepensis* forests developed on a limestone site with high rocky outcrops cover. The age of the burned stand was 4-yr-old.

Functional groups	Unburned	Burned	Functional groups	Unburned	Burned
Phal	1	0	Cgra	3	2
Qcoc	1	1	Bpin	3	3
Sasp	1	1	Crap	3	3
Csal	0	2	Bbit	0	3
Ccap	1	1	Scol	1	1
Pgra	0	1	Lcic	0	3
			Tgut	1	2
			Hach	1	3
			Bdid	0	3
			Aele	6	9
Woody species	4	6	Herbaceous species	18	32

due to the removal of the tree layer. Species richness is increased in the burned stand due to the establishment of annuals species (Table 3). The absence of any herbaceous leguminous species is characteristic in the unburned stand, whereas three perennial and three annual species are present in the burned stand. Their number could be higher during the first three years after fire. Similarly, no representatives of the obligate seeders Csal functional group were encountered in the unburned stand.

4 HETEROGENEOUS LANDSCAPES: A COMBINATION OF FACTORS

In all the cases that have, briefly, been examined so far, there is a predominant causal factor. Still, communities are not isolated entities. They interact with each other across a landscape. Therefore, shifting from the community to the landscape level may reveal the interaction of different factors, having as a result either the intensification of low resilience or the opposite effect. Such an example has already been reported from the 3-year-fire interval burned community, where some young pine saplings were recorded, establishing by seeds produced by unburned neighboring patches (resilience by migration, sensu Grubb and Hopkins 1986).

Aiming at evaluating whether soil type and slope deteriorates resilience in a burned landscape, where the vast majority of the area had been covered by 15-yr-old young *P. halepensis* communities, all different available combinations were considered for sampling. The landscape in question is found on the south-eastern part of Attica region, Central Greece. It is a hilly area that used to be covered by dense, old growth *P. halepensis* forests, the extend and the beauty of which made the authorities to declare the site as a National Park in 1974. In the summer of 1985 a forest fire burned most of the forest, but pine regeneration was quite vigorous and abundant. The area was reburned in the summer of year 2000, with a fire interval of fifteen years.

The area in question is one of the most diverse, in terms of geological substrata, in continental Greece, but two types of rock are the most frequent, allowing us to have an adequate number of replicates, that of limestone and schist. Limestone is always found on the medium and upper altitudinal zones of the hills, while schist is expanding in all altitudinal zones. This explains the inexistence of limestone sites with low slope (plains). Consequently, five groups of communities have been sampled within the limits of the area affected by fire both in 1985 and 2000. These groups refer to patches on limestone, with moderate (15_Lime_m) and high ((15_Lime_h) slopes, and patches on schist, with low (15_Sch_l), moderate (15_Sch_m) and high (15_Sch_h) slope (Fig. 4). For control, the only mature forest stand that was burned in the same, 2000 fire was considered

for sampling. It had been developed on schists and it consisted of two parts, the one with moderate (50_Sch_m) and the other with high (50_Sch_h) slopes (Fig. 4).

In the spring of the second post fire year, communities of the “15_Lime_h” group presented the lowest vegetation cover, both in terms of total and woody cover (Fig. 4). Surprisingly, from the schist group communities developed on locations with low slope showed the minimum vegetation cover. Pine regeneration was low to zero throughout the twice burned area (Fig. 4). Low densities of young pine samplings were recorded in the “15_Sch_l” communities, explained by the neighboring presence of unburned, mature trees. These trees escaped both fire events by being next to dirt roads (present in all the plain sites of the area) that ensure quick arrival of fire fighters.

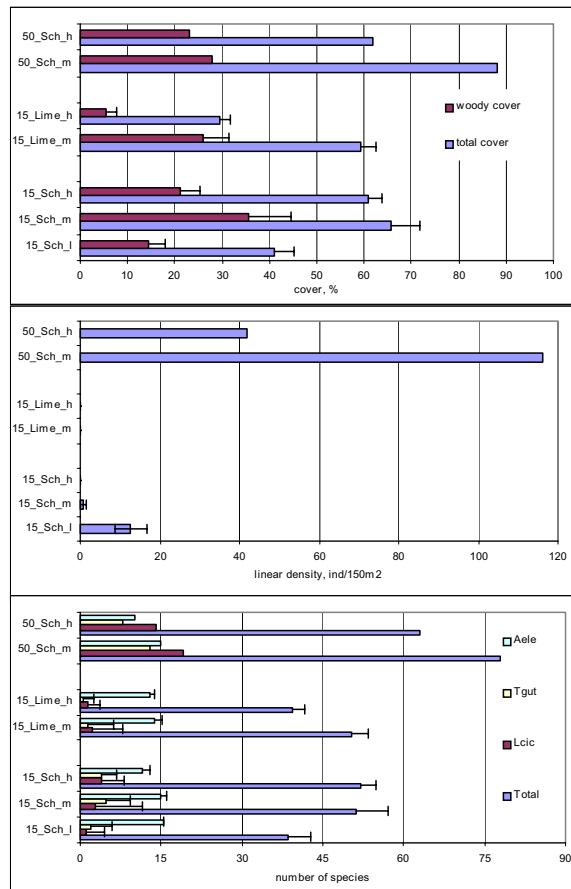


Figure 4. Average vegetation cover, pine density and species richness in the various groups of communities sampled in the burned area of the Sounion Peninsula National Park. All data refer to the 2nd post-fire year.

As far as species richness and composition is concerned, the overall species number is lower in the twice-burned communities, with its minimum in the “15_Sch_l” and the “15_Lime_h” communities. The two groups of annual obligate seeders (Lcic and Tgut groups) are always under-represented, which is not the case for the annual colonizers (Aele group) (Fig. 4). In conclusion, low resilience is the case throughout the twice-burned area, but it is deteriorated under the combi-

nation of certain factors (limestone – high slope, schist – low slope). On the other hand, pine resilience is enhanced in plain areas, near unburned, mature trees.

5 CONCLUSIONS

Producing biological indicators for low ecosystem resilience is not an easy task. It, primarily, requires a detailed knowledge on the ecosystems response and performance under the absence of such factors as those described in this paper. Functional group diversity is a very promising tool, since it is recognized as a link between ecosystem structure and function. (Diaz and Cabido, 2001). According to our results, no species indicators have been identified, since none of them fulfilled the criteria that have been proposed for the objective selection of an indicator taxon (Noss 1990).

Mouillot et al (2002) have run a simulation model with fire frequency and Mediterranean-type vegetation dynamics scenarios under the climate change context. They have found a replacement of forest-dominated by shrub-dominated landscapes. This trend seems to be the case in *Pinus halepensis* forested landscapes, if fire interval becomes shorter than the required time for pine to form an adequate canopy seed bank. A lot of experimental and field research is needed towards the clarification of the causal mechanisms that link the various factors with low resilience.

ACKNOWLEDGEMENTS

This paper reports on part of the research work performed under the context of an EU-funded scientific project, SPREAD (EVGT-CT2001-00043).

REFERENCES

- Agee, J.K. 1998. Fire and pine ecosystems. In: Richardson, D.M. (ed). *Ecology and biogeography of Pinus*. Cambridge University Press, New York., pp. 193-218.
- Arianoutsou, M. 1998. Aspects of demography in post-fire plant communities of Greece. In: Rundel, P.W., Montenegro, G. & Jaksic, F (eds). *Landscape Degradation and Biodiversity in Mediterranean Type Ecosystems*. Ecological Studies 136. Springer-Verlag, Berlin, Heidelberg, pp. 273-295.
- Arianoutsou, M. 2001. Landscape changes in Mediterranean Ecosystems of Greece: implications for Fire and Biodiversity issues. *Journal of Mediterranean Ecology* 2: 165-178.
- Arianoutsou, M. & Ne'eman, G. 2000. Post-fire regeneration of natural *Pinus halepensis* forests in the East Mediterranean Basin. In: Ne'eman, G. & Trabaud, L (eds). *Ecology, Biogeography and Management of Mediterranean Pine Forest*. Backhuys Publishers, pp. 269-290.
- 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). *Proceedings of the IV International Forest Fire Research Conference, Millpress, The Netherlands, Electronic Edition*.
- Arianoutsou-Faraggitaki, M. 1984. Post-fire successional recovery of a phryganic (East Mediterranean) ecosystem. *Acta Oecologica (Oecologica Plantarum)* 5(19):287-394.
- Barbero, M., Loisel, R., Quezel, 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, New York. pp. 153-170.
- Bond. W.J. & van Wilgen. B.W. 1996. *Fire and Plants*. Chapman and Hall Publishers, London.
- Diaz, S. & Cabido, M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* 16:646-655.
- Diaz-Delgado, R., Lloret, F., Pons, X. & Terradas, J. 2002. Satellite evidence of decreasing resilience in Mediterranean plant communities after recurrent wildfires. *Ecology* 83(8):2293-2303.
- Fox, B.J. & Fox, M.D. 1986. Resilience of animal and plant communities to human disturbance. In: Dell, B., Hopkins, A.J.M. & Lamont, B.B. (eds). *Resilience in mediterranean-type ecosystems*, Dr. W. Junk Publishers, Dordrecht, pp. 39-64.

- Gill, A.M. & Williams, J.E. 1996. Fire regimes and biodiversity: the effects of fragmentation of southeastern Australian forests by urbanization, agriculture and pine plantations. *Forest Ecology and Management* 85:261-278.
- Grubb, P.J. & Hopkins, A.J.M. 1986. Resilience at the level of the plant community. In: Dell, B., Hopkins, A.J.M. & Lamont, B.B. (eds). *Resilience in mediterranean-type ecosystems*, Dr. W. Junk Publishers, Dordrecht. pp. 21-37.
- Hanes, T.L. 1971. Succession after fire in the chaparral of southern California. *Ecological Monographs* 41(1):27-52.
- Hobbs, R.J., Mallik, A.U. & Gimingham, C.H. 1984. Studies on fire in Scottish heathland communities. III. Vital attributes of the species. *Journal of Ecology* 72:963-976.
- Holling, C.S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4:1-23.
- Kazanis, D. & Arianoutsou, M. 1997. Growth patterns of obligate seeders and obligate resprouters along a post-fire chronosequence of Aleppo pine forests of Attica, Greece. In: Trabaud L (ed.), *Book of Abstracts of the International Workshop on Fire, Landscape and Dynamics in the Mediterranean Area*, Banyuls, France, p 47.
- Kazanis, D. & Arianoutsou, M. 2002. Long term post-fire dynamics of *Pinus halepensis* forests of Central Greece: plant community patterns. In: Viegas, D.X. (ed). *Proceedings of the 4th International Conference of Forest Fire Research*, Millpress, The Netherlands, Electronic Edition.
- Kazanis, D. & Arianoutsou, M. in press. Long-term post-fire vegetation dynamics in *Pinus halepensis* forests of central Greece: a functional-group approach, *Plant Ecology*.
- Keeley, J.E. 1986. Resilience of mediterranean shrub communities to fires. In: Dell, B., Hopkins, A.J.M. & Lamont, B.B. (eds). *Resilience in mediterranean-type ecosystems*, Dr. W. Junk Publishers, Dordrecht, pp. 95-112.
- Konstantinidis, P. & Tsiourlis, G. 2002. Preliminary results of the post-fire resprouting growth of typical Mediterranean maquis species (Sithonia Peninsula, N. Greece). In: Viegas, D.X. (ed). *Proceedings of the 4th International Conference of Forest Fire Research*. Millpress, The Netherlands, Electronic edition.
- Lloret, F. & Vila, M. 2003. Diversity patterns of plant functional types in relation to fire regime and previous land use in Mediterranean woodlands. *Journal of Vegetation Science* 14(3):387-398.
- Martinez-Sanchez, J.J., Herranz, J.M., Guerra, J. & Trabaud, L. 1997. Influence of fire on plant regeneration in a *Stipa tenacissima* L. community in the Sierra Larga mountain range (SE Spain). *Israel Journal of Plant Sciences* 45(4):309-316.
- Mouillot, F, Rambal, S. & Joffer, R. 2002. Simulating climate change impacts on fire frequency and vegetation dynamics in a Mediterranean-type ecosystem. *Global Change Biology* 8(5):423-437.
- Naveh, N. 1975. Effects of fire in the Mediterranean region. In: Kozlowski, T.T. & Ahlgren, C.E. (eds). *Fire and Ecosystems*, Academic Press, pp. 401-434.
- Naveh, Z. 1994. The role of fire and its management in the conservation of mediterranean ecosystems and landscapes. In: Moreno, J.M. & Oechel, W.C. (eds). *The role of fire in Mediterranean-type ecosystems*, Springer-Verlag Publishing, London, pp.163-185.
- Noss, R. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4:355-364.
- Papavassiliou, S. 2001. *The role of legumes in post-fire regeneration of Mediterranean forest ecosystems*. Ph.D Thesis. University of Athens.(in Greek with an English summary).
- Pausas, J.G. and Lavorel, S. 2003. A hierarchical deductive approach for functional types in disturbed ecosystems. *Journal of Vegetation Science*, 14:409-416.
- Pausas, J.G., Carbo, E., Caturla, R.N., Gil, J.M. & Vallejo, R. 1999. Post-fire regeneration patterns in the eastern Iberian Peninsula. *Acta Oecologica* 20(5):499-508
- Richardson, D.M. & Rundel, P.W. 1998. Ecology and biogeography of *Pinus*: an introduction. In: Richardson, D.M. (ed.). *Ecology and biogeography of Pinus*. Cambridge University Press, New York. pp. 3-46
- Thanos, C.A. & Daskalidou, N.E. 2000. Reproduction in *Pinus halepensis* and *Pinus brutia*. In: Ne'eman, G. & Trabaud, L. (eds). *Ecology, biogeography and Management of Pinus halepensis and Pinus brutia forest ecosystems in the Mediterranean Basin*, Backhuys Publishers, Leiden, The Netherlands, pp. 79-90.
- 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 Pinus brutia forest ecosystems in the Mediterranean Basin*, Backhuys Publishers, Leiden, The Netherlands, pp. 257-268.
- Trabaud, L. & Galtie, J.F. 1996. Effects of fire frequency on plant communities and landscape pattern in the Massif des Aspres (southern France). *Landscape Ecology* 4:215-224.

- Trabaud, L, Grosman, J. & Walter, T. 1985. Recovery of burned *Pinus halepensis* forests I. Understorey and litter phytomass development after wildfire. *Forest Ecology and Management* 12:269-277.
- Vazquez, A. and Moreno, J.M. 2001 Spatial distribution of forest fires in Sierra de Gredos (Central Spain). *Forest Ecology and Management* 147(1):55-65
- Westman, W.E. 1986. Resilience: concepts and measures. In: Dell, B., Hopkins, A.J.M. & Lamont, B.B. (eds.). *Resilience in mediterranean-type ecosystems*. Dr. W. Junk Publishers, Dordrecht. pp. 5-19.