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Predicting the post-fire regeneration and resilience of Mediterranean plant communities

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ABSTRACT: Human intervention on the Mediterranean ecosystems since the second world war has changed both in its intensity and its extent of practice. This has greatly affected land cover patterns and fire regimes. Under these conditions the prediction of post-fire regeneration potential and resilience becomes crucial. Ecological models based on the exploitation of species vital attributes can be a promising tool. A brief review of such most recent ecological models is attempted in this contribution.

1 INTRODUCTION

The climatic conditions prevailing in the Mediterranean environments induce specific morphological, phenological, physiological and ecological strategies in the plant species occurring in these systems (Rundel 1981, Arianoutsou 1998a). The climatic conditions and the adaptive strategies of these plant species may induce and support fires.

Mediterranean ecosystems have been evolved under the periodic influence of fire almost since their establishment (Naveh 1975, Rundel 1998). Human intervention to the Mediterranean ecosystems is dated back to their establishment as well (Le Houerou 1981). However, the intensification of human influence on the Mediterranean ecosystems changed critically the land cover patterns and the fire regime after the Second World War (Grove and Rackham 1991, Arianoutsou 2001, Arianoutsou et al 2002).

Under these conditions, prediction of post-fire regeneration dynamics becomes crucial. To this direction, the use of ecological models has become a useful tool not only for the shake of the prediction itself, but also for supporting the right decision of post-fire management of the burned landscapes. The level of precision of these models is very much based upon the rules they are derived from and the information used for their parameterisation. On the basis of all these models there exists the knowledge of plant regeneration mechanisms and the routes they follow in building up their communities.

2 PLANT ADAPTIVE STRATEGIES

Plants of Mediterranean environments have been subjected to the action of recurrent fires for thousands of years, thus they have developed specific adaptation mechanisms, which enable them not only to survive fire's action but also to regenerate and quickly recover. These adaptation mechanisms are mainly the vegetative resprouting of the same burned individuals and the establishment of new individuals through seed germination.

Most phryganic shrubs i.e. *Sarcopoterium spinosum*, *Phlomis fruticosa* as well as shrubs of evergreen sclerophyllous maquis (*Quercus coccifera, Pistacia lentiscus*, *Arbutus unedo*, *Phillyrea* spp.), regenerate through resprouting. This is performed through the dormant buds, which are located at the root crown, and they protected by the soil. Species forming lignotubers such as *Erica arborea*, *Euphorbia acanthothamnos* or having subterranean bulbs (e.g. *Cyclamen* spp., *Muscari commosum* and many others) regenerate through resprouting too. Resprouting usually starts shortly after fire in the evergreen sclerophyllous shrubs, while in the phryganic ones may be delayed till the autumn rains. This difference has been attributed to the different rooting depth of the two types of species. Leaves developing on the resprouts are larger and much richer in chlorophyll content as compared to those of the unburned plants (Arianoutsou and Margaris 1981a), having also a higher photosynthetic rate (Oechel, pers. comm.). The recovering plants appear to have accelerated their reproductive developmental phases too: they flower and they produce fruits and seeds even from the 1st year of their recovery (Arianoutsou and Margaris 1981a).

The second mechanism of post-fire plant regeneration is seed germination. Seedlings appear on the burned ground after the first autumn rains. Their origin could be either the soil seed bank or the canopy seed bank. Cistaceae and Leguminosae are families with members of the former type, while Pinaceae, Proteaceae belong to the second. Seeds of the soil seed bank are mostly hard-coated, the dormancy of which breaks as a result of the action of temperature released by fire (Arianoutsou and Margaris 1981b, Thanos nad Georghiou 1988 among others). Canopy seed bank is related to the existence of hard cones or other type of fruits, the opening of which is induced by the heat released during fire. The number of seedlings appearing on the burned ground is usually very high, but shortly it is self thinned (especially after the first summer period), (Arianoutsou and Margaris 1981a, Papavassiliou and Arianoutsou 1997, Daskalakou and Thanos 1997, Skourou and Arianoutsou 1998, Skourou 2003, Kazanis and Arianoutsou unpublished data). Seedlings growth is also very quick, especially in the herbaceous and low shrubby species. Soon the young individuals reach maturity and produce new seeds, which are either deposited in the ground (Papavassiliou and Arianoutsou 1997, Skourou and Arianoutsou 2004) or in the canopy of the trees (Thanos et al. 1998, pers. observ.).

3 COMMUNITY RECOVERY

Post-fire community recovery is a process of autosuccession (Arianoutsou 1979, 1998a, Trabaud 1994, Kazanis and Arianoutsou 1996, Kazanis and Arianoutsou 1998, Arianoutsou 1998a, Arianoutsou and Ne'eman 2000), which is based on the initial floristic composition principle (Egler 1954, Kazanis and Arianoutsou in press) or the *inhibition model* described by Conell and Slatyer (1977): all prefire species are present immediately after fire, even if later the relative abundance or frequency of individuals changes. In other words, there is no real succession, or floristic relays, or different communities on the same site, as is the main characteristic of the secondary succession, but an autosuccession process leading to a recovery of the prefire communities (Trabaud 1994, Kazanis and Arianoutsou 1998, Arianoutsou and Ne'eman 2000). In this process, provided that no secondary disturbance takes place, the burned community retains its floristic identity in time even though it looks different for a certain time. The most important stages of this process are described in Arianoutsou (1998a).

4 VEGETATION DEMOGRAPHY

Recovery of plant species that regenerate vegetatively is a rather straight forward process which depends on the meteorological conditions prevailing on the site, the productivity of the site (available nutrients in the soil), competition between recovering plants and external factors such as grazing. Populations of these species generally consist of one age cohort, that of the initially regenerated plants. The situation is different with the seeding species, as their recovery is strongly dependent on the specific life histories of the plants, that is whether they are short living plants, such as the annual herbaceous legumes, or relatively short living plants, such as the rockroses or long living plants, such as the pines.

From the few demographic studies in post-fire communities it is shown that a decrease in seedling density of seeding shrubs occurs in the 1st post-fire year (Naveh 1974, Papanastasis 1977, Arianoutsou and Margaris 1981b, Skourou 2003, Kazanis and Arianoutsou in prepar.). No evidence of remarkable seed germination exists so far for these woody species during the second post-fire year. On the contrary, several herbaceous legumes exhibit massive seed germination during the second and even the third post-fire year (Papavassiliou and Arianoutsou in Arianoutsou and Ne'eman 2000).

The juvenile phase for most of the woody seeding species, such as the rockroses, lasts for only two years that is, they reach maturity and consequently reproductive age quite soon. Skourou (2003) has found that there is a secondary seedling recruitment in these species, which coincides with the maximum of the initial population decline, approximately 15 years after fire.

As an example of the canopy seed storage strategy *Pinus halepensis* (Aleppo pine) and *Pinus brutia* (East Mediterranean pine), the two most important Mediterranean pines are referred. This seed bank is composed of bradychorous (serotinous) cones and the seeds they enclose. Serotiny is impressively obvious in the newly formed cones on the young pine treelets of Aleppo pine although their seeds exhibit normal germinability (Thanos et al. 1998). The juvenile phase of the tree seeders, the Mediterranean pines last longer than in the shrubs. It has been found by Thanos et al. (1998) that the juvenile phase lasts for 4 years in Aleppo pine forest, while it is slightly longer in the East Mediterranean pine. However, at the population level this characteristic is very much affected by the conditions prevailing on the site (meteorological and soil). Based on personal observations on a series of sites forming a post-fire chronosequence of *Pinus halepensis* forests, it is after the 15th – 20th year that a pine population is at reproductive maturity.

5 FIRE REGIME

5.1 *Fire frequency*

For the long term survival of the plants it is essential to know not only their adaptive traits towards a 'normally' occurring fire event, but also how they are affected by the fire regime, i.e. frequency, intensity, season, spatial extent. In this contribution we will refer only to fire frequency, fire intensity and fire spatial extent, as in the Mediterranean region wildfires occur only in summer. On the other hand, arson also occurs in summer. Spatial extent of a fire may be important, as it will define the possibilities of propagule dispersal from unburned areas, susceptibility to grazing etc.

All fires in the mediterranean climate regions of the world burn areas that have also been burned in the past. Consequently, the vegetation is really a mosaic of fire histories, with some parts having had more fires than others, over a given period of time.

Plants that are killed by fire and reproduce through seed germination rely on this seed germination in order to persist at the specific location. For these plants, there must be sufficient time between successive fires for the seedlings to mature and produce seeds and hence to add seeds to the seed bank. This time will vary between species (see above), from species that flower within the 1st year after fire (such as the herbaceous legumes), to species that flower within 1-2 years after fire (such as the rockroses) to those that may take 6-8 years to reach maturity (the pines). If another fire occurs before these plants have matured, dramatic changes in the vegetation composition and physiognomy might occur. Recent evidence from field observations in moderately burned sites support the existence of positive relationship between seed germination of hard-coated seeds lying in the soil seed banks and severe fires.

5.2 *Fire intensity*

Fire intensity is expressed as the amount of heat released during its passage. This is due to several factors among which the most important ones are the amount of the fuel, the moisture of the fuel, its distribution etc. Plants experience fire intensity through the amount of the heat released and the duration of the heating. Intense fires usually kill the stems of the resprouters, but it seems that their regeneration is not generally affected, as it is relied upon the available carbohydrates of the underground parts, being protected by the soil. Seeds lying in the soil seed banks seem also not to be negatively influenced by intense fires. On the contrary, there are several references in the literature about heat induced seed germination after fire (Arianoutsou and Margaris 1981b, Thanos and Georgiou 1988, Keeley 1991).

6 PREDICTING VEGETATION REGENERATION AND RESILIENCE

6.1 *The functional groups approach*

One of the most recent and promising approaches is the use of plant functional types as suitable for modelling based on responses to disturbance, such as fire and grazing (Pausas 1999, Lavorel et al. 1997, Pausas and Lavorel 2003). These models can predict the possible population dynamic trends for the 4 functional types that can be distinguished in the Mediterranean plants (Fig. 1 and Table 1).

Table 1. Relation between different life history traits and the four functional types distinguished in the Mediterranean vegetation in relation to the regenerative response after fire (after Pausas 1999).

Life history traits	Functional types			
Resprouting ability	Yes (high)	Yes (moderate)	No	No
Fire stimulated recruitment	No	Yes	Yes	No
Life Span	Long	Long/intermediate	Short	Short
Growth rate	Low	Intermediate	High	High/interm.
Dispersal units	Big, fleshy or acorns, non refractory	Small, light, refractory	Small, light, hard, refractory	Small, light, non refractory
Number of dispersal units	Few	Intermediate	Many	Many
Dispersal agent	Animals	Variable	Wind	Wind
Seed bank	No	Variable	Yes (soil or canopy)	Variable?
Seed viability	Short	Short/variable	Long	Short
Seedling establishment	Low	Intermediate	High	High
Susceptibility to disturbance	Low	Intermediate	High	High
Examples	*Quercus ilex* *Q. coccifera* *Arbutus unedo* *Pistacia lentiscus* *Phillyrea* spp.	*Anthyllis cytisoides* *Bituminaria bituminosa* *Genista scorpius* *Piptatherum* sp.	*Cistus* spp. *P. halepensis* *P. brutia* *Ulex parviflorus*	*Taraxacum* spp. *Chenopodium* *Juniperus phoenicea*

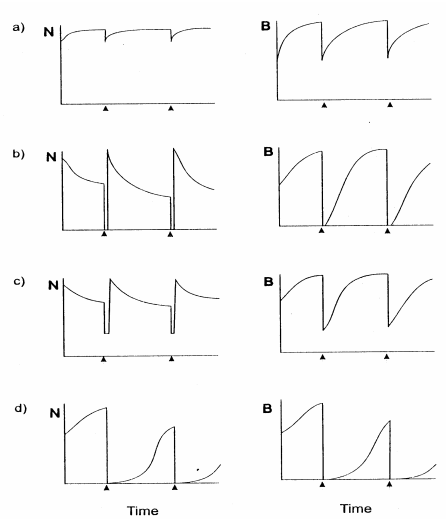

Figure 1. Possible population dynamics for the 4 functional types. (N: population size, B: Biomass-including below ground). Arrows indicate fires. (a): resprouting species, (b): non-resprouting but seed germinating species, (c): resprouting species with seed germination stimulated by fire, (d): non-resprouting species with recruitment non- stimulated by fire (after Pausas 1999).

Recently, Kazanis and Arianoutsou (in press) have suggested an analogous scheme for predicting either the sensitivity or the post-fire resilience of a plant community. The basic idea of this approach is that this property is depended on the sensitivity / resilience of individual species. As it is impossible to deal with all individual species separately, the organization of species in functional groups is the solution. In consequence, the dominance of different functional plant groups will define correspondingly the expected patterns of community resilience. In this scheme, the plant attributes used for the categorization of species in the proposed functional groups are shown in Table 2.

Table 2. Plant attributes selected for the formation of functional groups (after Kazanis and Arianoutsou in press).

Growth form	Regeneration Mode	Mode of persistence	Long distance dispersal mode	Specific competitive advantages
Tree				
Tall shrub	Obligate resprouter	Long life span	Anemochorous	Nitrogen Fixation
Short shrub	Obligate seeder	Secondary seedling establishment	Zoochorous	Subterranean storage organs
Woody liana	Facultative seeder	Soil seed bank	None	Vivid lateral growth
Perennial herb	Colonizer	Long dispersal		Parasite
Annual herb				None

The novelty of this approach is the inclusion of those parameters, which do not deal only with the initial (though quite critical) stage of regeneration mode but with all those attributes which enable the species to persist in time. In order to be able to suggest such a scheme, one must have information from long-term studies, which reveal the patterns of all these attributes. In our case, this became feasible through a field study, which was designed in such a way so as to provide diachronic and synchronic data. The application of this suggested scheme in post-fire *Pinus halepensis* communities of Central Greece has produced 29 functional groups (14 for the woody species and 15 for the herbaceous) each one named after one characteristic species. The prediction of the resilience level of a given *P. halepensis* community will thus be based upon the relative representation of each of the above functional groups. Detailed representative examples of this model application can be found in Kazanis and Arianoutsou (2004).

6.2 *The PROMETHEUS system approach*

The PROMETHEUS system is consisted of 6 different modules each one concerning various aspects of pre- and post-fire issues as well as the fire behaviour itself. The module interested us in this contribution concerns regeneration and resilience. Full description of system approach and analysis can be found in Arianoutsou (1998b) and in Arianoutsou et al (in press). Parameters used in the module are chosen between those which are critical for defining vegetation regeneration and hence its resilience and have been parameterized for *Pinus halepensis* forests and maquis ecosystems (Fig. 2).

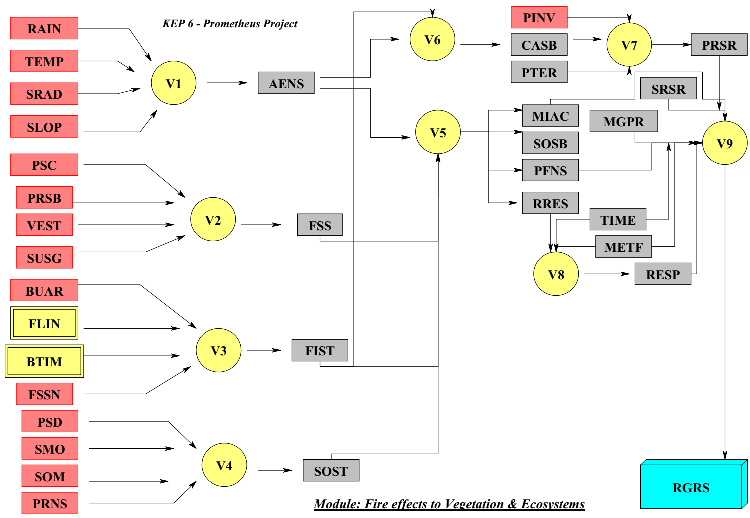

Figure 2. Functional diagram of the KEP "Fire effects to vegetation and ecosystem

The final product of all reasonable relationships between the defined parameters is the expected output which reveals the impacts of the selected fire regime upon the vegetation and its resilience. Although the type of rules followed is qualitative, they do represent valuable ecological information (Salles et al. 1996). This rule-based modelling approach enables us to capture a considerable amount of information that it is usually too broad and detailed and incorporate it into a predictive model. These kinds of models also have the advantage that they are simple for the user, the land manager in this case, to understand, to modify and to apply (Legg et al. 1997).

The final product of the work described above was the development of a knowledge- based software module. The software through a friendly user interface (Pressman 1992) provides the opportunity to perform a decision making process according to predefined scenaria of fire conditions, to examine and understand how fire behaviour is related to prevention planning, fuel management and effects and even to check and validate the knowledge, but also to find out the parts in this knowledge that could be improved (Eftichidis et al. 1998).

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Further development of the PROMETHEUS system was made through its geographical applications supported by the GIS part of the system, which permits a spatial reasoning process for geographic areas with heterogeneous conditions in terms of topography, vegetation and meteorology. (Eftichidis et al. 1998). A component of the spatial analysis procedure was the development and estimation of a quantitative factor defined as “PROMETHEUS code” which expresses numerically the fire impact and fire severity against the management objectives. PROMETHEUS code is actually a quantification of the spatial information resulting from the GIS raster analysis and permits the easy and comprehensive comparison between different fires and between different fire management objectives.

A pilot case concerning the geographical area of Penteli Mountain in Attica, Greece will be briefly presented here. Vegetation patches were transformed to fuel types according to PROMETHEUS rules and a map of fuel load (Fig. 3) was produced. The DTM for the studied site was also available. Over these two maps 2 different fire scenarios were applied (Fig. 4), based on the parameter of the fire line intensity (critical parameter developed in the fire behavior module). The PROMETHEUS system predicted two different outputs in the expected Regeneration and Resilience (Fig. 5).

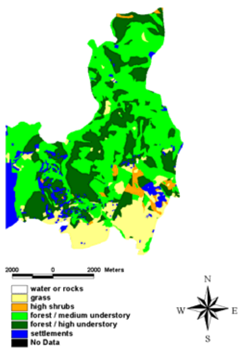

Figure 3. Fuel map of Penteli Mt. study sites

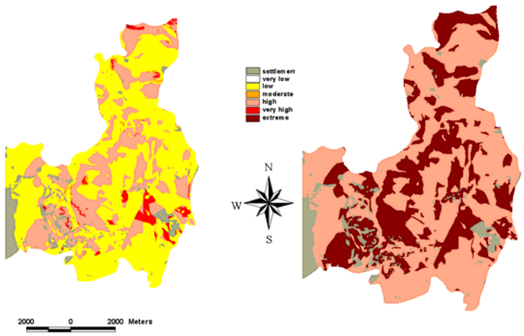

Figure 4. Fire line intensity scenarios tested: (left): air temperature = 25 ^{0}C, air humidity = 40%, wind speed = 2m/s, wind direction NE; (right): air temperature = 30 ^{0}C, air humidity = 30%, wind speed = 8 m/s, wind direction NE.

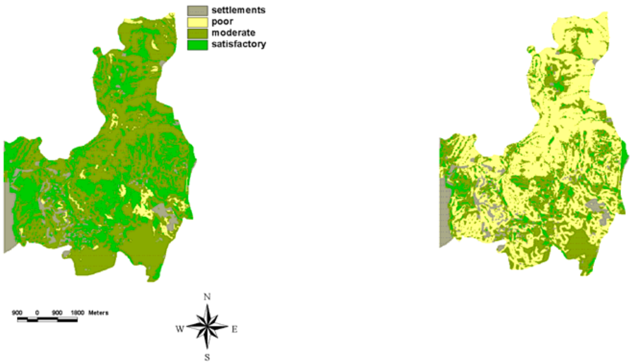

Figure 5. Regeneration and resilience of the vegetation types of the study sites predicted after the application of the two-fire scenarios: fire case 1 (left – less severe fire) and fire case 2 (right – more severe fire).

Further development of the PROMETHEUS system can provide us with predictions on specific questions related to regeneration and resilience, e.g. the risk of changing the vegetation physiognomy (Arianoutsou et al 2000). Following is a pilot application in *P. halepensis* forests of Mt Penteli, Attica Greece. The area was covered by *P. halepensis* forest in various forms and it was burned in 1995. Part of the area was reburned 3 years later. The parameter used was the density of Aleppo pine saplings. Based on the existing knowledge, 3 classes of density have been identified: low, when fewer than 0.5 individuals per m^2 are encountered, medium for the density values between 0.5-1 ind./ m^2 and high for the densities higher than 1 ind./ m^2. The acquired knowledge was transformed in knowledge rules of the form if {condition 1} and {condition 2} then {result} and subsequently applied in every geographical unit (map cell) of the area of interest. GIS raster overlay analysis was then performed and a map with the required output was produced (Fig. 6).

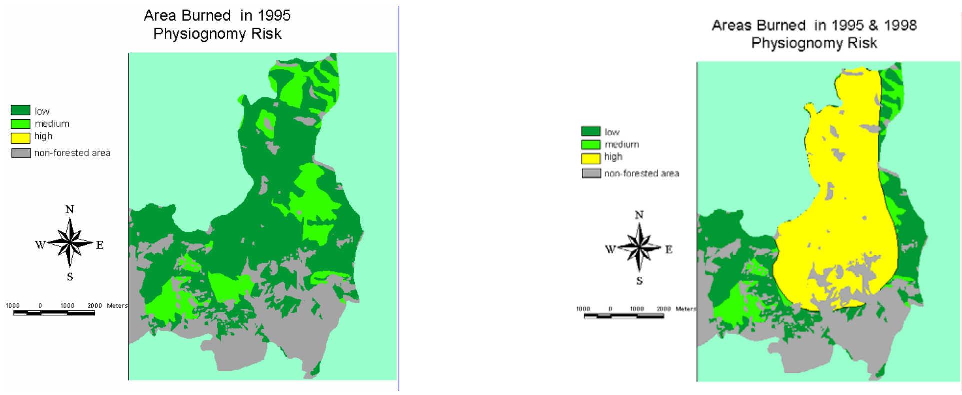

Figure 6. Prediction of the risk of change in the physiognomy of the vegetation under changing fire regime; left: one fire event; right: two fire events with 3 years interval.

7 CONCLUSIONS

Because fire regime is changing nowadays, the prediction of post-fire regeneration and resilience of plant communities becomes very crucial. Since fire acts as a community-level filter, the predictions of post-fire community resilience can be facilitated if species are grouped in functional types The ecological indicators of post-fire resilience to be selected must be reliable, preferably each one corresponding to fundamental features of the plant community structure and function. In the light of global change, ruled-based modelling is becoming a promising tool given the availability of increasing ecological knowledge.

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