

Long term post-fire dynamics of *Pinus halepensis* forests of Central Greece: plant community patterns

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ABSTRACT: Long-term post-fire dynamics of mediterranean pine communities were followed in terms of changes in species richness, species abundance and vegetation cover. Three different chronosequences that represented the major types of *Pinus halepensis* forests of Central Greece. In all cases, the dominant species of the mature stand were found to regenerate after fire, thus participating to the structure of vegetation from the initial point. Differences in the patterns of vegetation dynamics recorded between the studied chronosequences are related to differences in the initial structure of the woody vegetation component.

1 INTRODUCTION

Almost 16% of the forested areas around the Mediterranean Basin are pine forests that grow under the influence of the mediterranean climate and, consequently, under the frequent influence of fire (Barbero et al., 1998). *Pinus halepensis*, *P. brutia* and *P. pinaster* are the main tree species that dominate those forested ecosystems. In Greece, *Pinus halepensis* forests cover almost 9% of the total forested area, but account for more than 48% of the burned forested area, over a period of 25 years (1965-1989) (Kailidis, 1992). Although during the last decade, a lot of data on the post-fire recovery of those ecosystems have become available, there was a significant lack in our knowledge concerning long-term dynamics of those forests. This is due to both the complex structure of those mediterranean ecosystems and the long time required for them to reach maturity.

After a first attempt to record the long-term plant community dynamics of those ecosystems with the application of a chronosequence approach (Kazanis & Arianoutsou, 1996), strong evidence was produced that the overall diversity pattern differs from what has been reported for mediterranean shrublands (Hanes, 1971; Arianoutsou-Faraggitaki, 1984; Trabaud, 1987). In order to widen our knowledge on the changes occurring along the maturation of the *P. halepensis* communities, we have chosen to combine the application of the diachronic and synchronic approaches, in such a way so as to diminish the shortcomings, while exploiting the advantages of each approach.

2 STUDY SITES

Twenty-one (21) *Pinus halepensis* communities were selected for sampling in the Attica region and the neighboring island of Euboia. Criteria for the selection of the communities in question were the availability of data on fire history for the burned communities, the inclusion of as many age classes as possible, the inclusion of sites with different environmental characteristics (altitude, aspect, soil type) so as to test their influence on post-fire dynamics, and the low influence of any human activities. The characteristics of the studied communities are summarized in Table 1.

Table 1. Characteristics of the sampled communities.

Site Code	Post-fire Age	Parent-rock Material	Altitude (m)	Aspect (°)
Pis	1-2	Tertiary Deposits	180	200
Pim	1-2	Tertiary Deposits	180	200
Mav	1-3	Schists	420	280
Dis	1, 3-4	Limestone	350	310
Dim	1, 3-4	Limestone	350	240
Ags	2-4	Tertiary Deposits	310	10
Stb	5-8	Schists	405	20
Avl	6-7	Limestone	360	40
Fys	8-9	Schists	410	230
Fyl	8-9	Limestone	410	270
Lav	12-13	Schists	170	40
Dir	14-15	Limestone	330	280
Dio	13-16	Schists	460	50
Bel	13-16	Limestone	590	180
Pib	17	Tertiary Deposits	190	120
Bah	17-18	Schists	660	80
TAT	~40	Limestone	560	160
PIK	~40	Tertiary Deposits	180	200
STA	~55	Schists	420	40
SOU	~55	Schists	180	340
AGM	~65	Schists	580	240

The five last communities in Table 1, the age of which is approximated, refer to mature forests. Since there were no data available concerning the last fire event in these cases, the stand age was estimated with the measurement of pine trees annual growth rings.

3 METHODS

Within each selected community three 50-m-long transects have been established. Three times per year (late autumn, late winter and late spring), all plants growing along the transects were recorded. Thus, data on species presence/absence and species abundance (in terms of linear density, Brower et. al, 1990) have been acquired. In addition, vegetation cover, in terms of the relative contribution of herbs, shrubs and pines was mapped and measured in 10 plots per transect, of 1x1m² size, all established adjacent to each transect. Data sampling was repeated with the same annual frequency for up to four consecutive years.

Data on plant species presence and abundance were analyzed with the use of CANOCOTM 4.0 for windows software. Direct gradient analysis was performed so as to evaluate whether post-fire age is an influential variable and furthermore to identify other possible influential variables.

4 RESULTS - DISCUSSION

After performing indirect gradient analysis (CA) on the matrix of the vegetation composition data, two well-defined groups of communities were produced (Fig. 1). Each group consists of a chronosequence with early, medium and late post-fire stages.

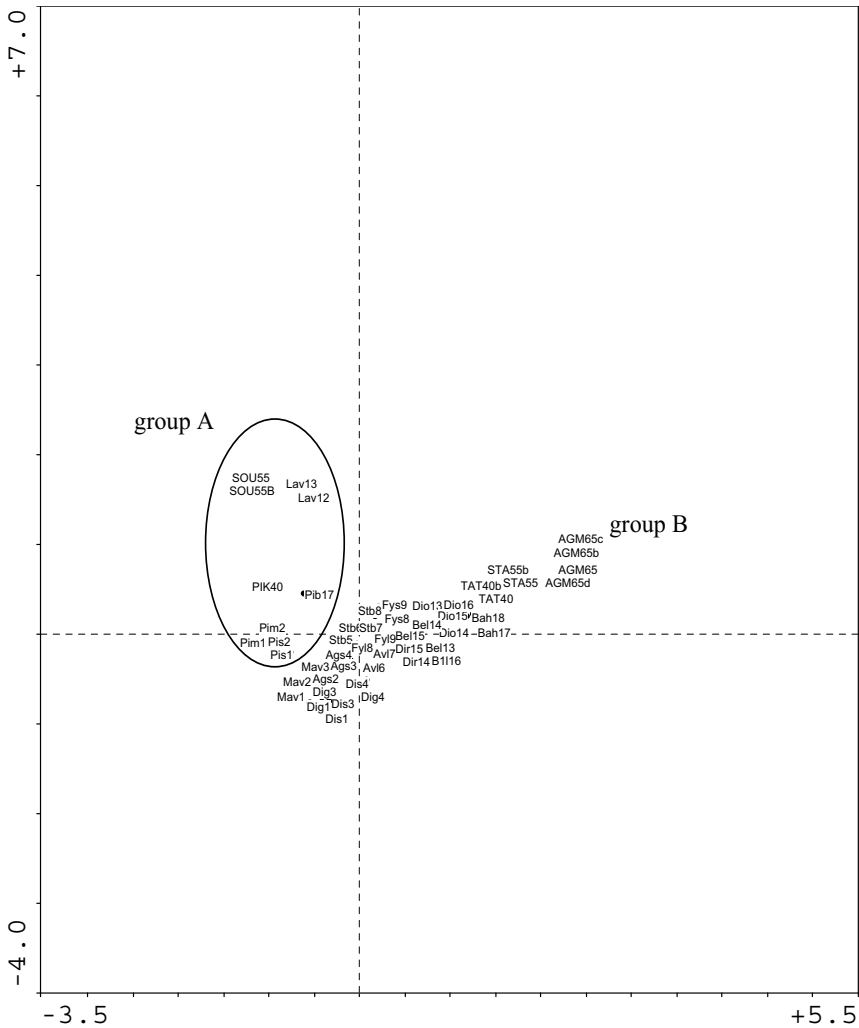


Figure 1. Ordination of the study sites after performing indirect gradient analysis (CA) on vegetation composition data.

The first group of communities (A in Fig.1) refers to *P. halepensis* communities of low altitude (less than 300 m.a.s.l). These communities are found at the southeastern part of the region of Atica, where conditions are drier than those prevailing at the other sites. This must be the main reason

why the understorey woody component in the mature stands of this group is sparse. On the contrary, the other group (B in Fig.1) refers to *P. halepensis* communities of higher altitudes (more than 300 m.a.s.l), where the woody component of the understorey of the mature stands is dense. As shown in Table 2, the main difference in the structure of the pine forests of these two groups lies in the presence and the abundance of several evergreen sclerophyllous woody species, such as *Quercus coccifera*, *Pistacia terebinthus*, *Phillyrea latifolia* and *Arbutus andrachne*.

Table 2. Mean cover of the understorey of the mature pine forests of higher and lower altitudes studied in the context of this chronosequence.

Forest type	Understorey cover	Woody component	Herbaceous component	Evergreen sclerophyllous shrubs
Low altitude, sparse understorey	61.67 ± 6.11	29.45 ± 7.21	32.67 ± 3.06	15.66 ± 3.89
High altitude, dense understorey	94.12 ± 8.53	78.53 ± 6.61	14.13 ± 3.56	69.56 ± 3.46

The role played by the variable “altitude” in the ordination of the communities is even more evident after performing direct gradient analysis (CCA, Fig. 3). The distinction of the two groups of communities is better presented, while, within each group, communities are ordinated with increasing post-fire age.

Apart from altitude and post-fire age, three other environmental variables were found to play important role in the ordination of the communities (parent rock material, aspect and rock cover) with the canonical eigenvalues reaching 35% of all unconstrained eigenvalues (Table 3).

Table 3. Summary of the direct gradient analysis (Canonical Correspondence Analysis).

Axes	1	2	3	4	Total inertia
Eigenvalues	0.309	0.231	0.208	0.162	3.318
Species-environment correlations	0.978	0.970	0.966	0.976	
Cumulative percentage variance					
of species data	9.3	16.3	22.5	27.4	
of species-environment relations	26.8	46.7	64.7	78.7	
Sum of all unconstrained eigenvalues					3.318
Sum of all canonical eigenvalues					1.156

The ordination shows that *Pinus halepensis* communities preserve their main floristic identity (which is a result of several environmental factors, such as altitude and parent-rock material) throughout the post-fire succession. If this was not the case, then communities would have been mainly ordinated according to their post-fire age (Espirito-Santo et al., 1993). This is a first indication that, as already reported from other mediterranean-type ecosystems, the post-fire dynamics of *Pinus halepensis* forests is not characterized by a replacement of different communities over time (as it is the case in the post-fire dynamics of temperate pine forests, where there is a true secondary succession). According to our data, the post-fire dynamics of those mediterranean pine forests fits more to what Hanes (1971) described as “autosuccession”, meaning that the majority of the taxa that grow in the mature stands are already present from the initial stages and the overall dynamics follows the “initial floristics” pattern (Egler 1954).

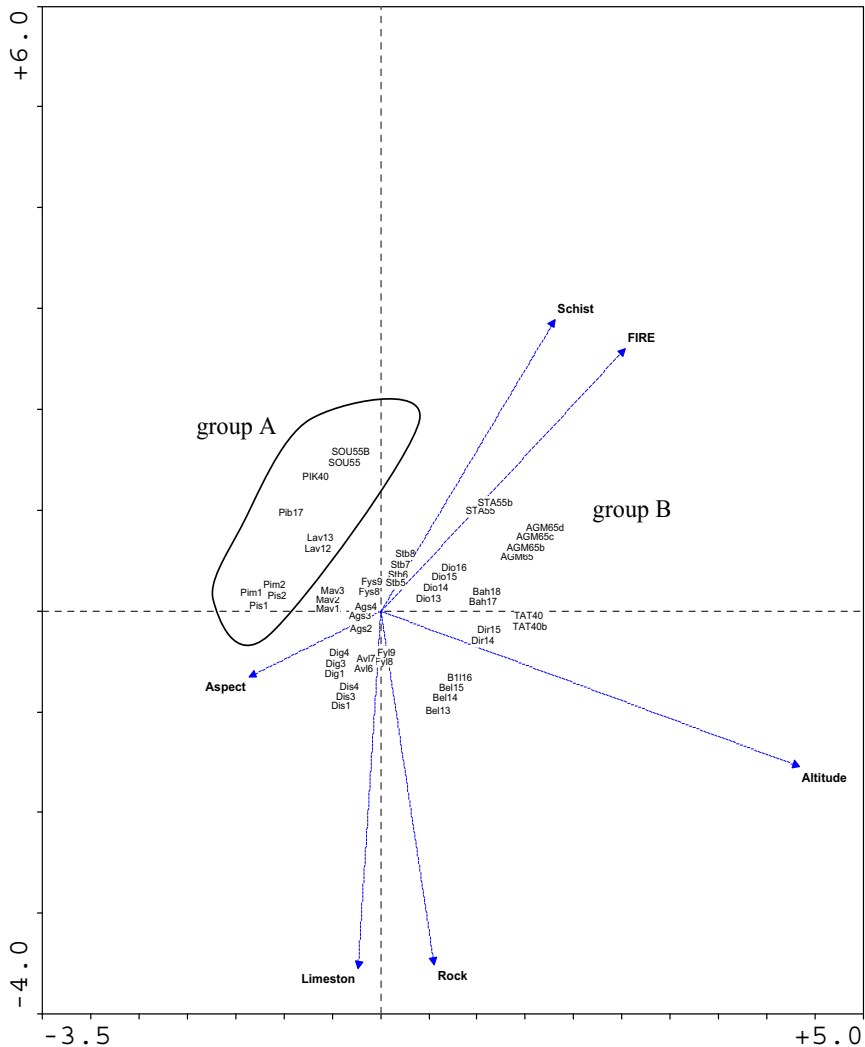


Figure 2. Ordination of the study sites after performing direct gradient analysis (CCA) on vegetation composition data.

Even though long-term post-fire dynamics of these ecosystems does not consist of true sequential stages, studying the pattern of vegetation composition change with post-fire age enables us to identify different phases that are characterized by the interaction of vegetation development and composition. The number of species recorded in the communities of each one of the chronosequences identified by the ordination is shown in Fig. 3.

As it can be seen in Figure 3, in both cases the number of species recorded in the first years after the fire is higher than in the mature stand (i.e. before the fire). An important difference in the species richness pattern that is produced for low and high altitude communities lies in the change of species number from the intermediate to the late communities of the chronosequence. In the for-

mer case, vegetation composition was found to increase with the maturation of the community, while the opposite stands for the latter case. We shall discuss this result further on.

High standard deviation values of species richness for the intermediate age communities included in the high altitude chronosequence (Fig. 3b) imply that there is certain variability among the communities of the same age. This is true. The high altitude pine communities that we have studied can be furthermore divided in two groups. The first group develops usually on limestones (calicolous, rocky soils) with the understorey been dominated by *Quercus coccifera*. The second group develops usually on siliceous soils (schists) and the understorey, apart from *Quercus coccifera*, is characterized by the presence of a wide variety of other shrubs, such as *Arbutus* spp., *Erica* spp., *Pistacia* spp. and *Cistus* spp. As it was mentioned before, these two groups of the high altitude pine communities preserve their floristic identity as expressed by differences in the species composition pattern through time.

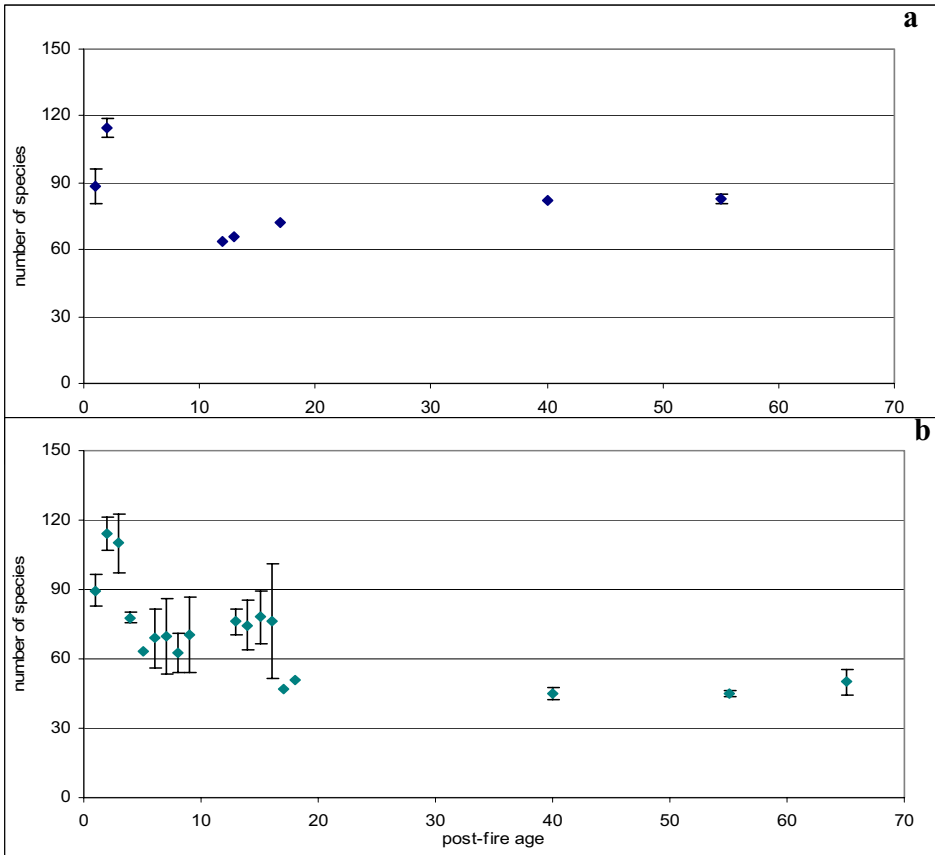


Figure 3. Species richness in the communities of the low (a) and the high (b) altitude chronosequences.

Thus, from that point onwards, we will analyse our data separately for each one of the groups of communities identified, namely the “lowland group”(low elevation pine communities), the “siliceous group” (high elevation pine communities, usually on schists) and the “calicolous group” (high elevation pine communities on limestone) of communities.

LOWLAND GROUP

This group consists of six communities (Pis, Pim, Lav, Pib, Pik & SOU), with the post-fire age ranging from 1 to ~55 years (Table 1). One hundred eighty two (182) taxa were collected and identified from the communities of that group, the 35 of which are woody and the rest herbaceous. In the context of this study and for the purposes of the floristic analysis, plant taxa have been classified into four groups, two for woody species and two for the herbaceous.

Woody species were classified according to their participation in the formation of the vegetation layers. Accordingly, two groups were identified, namely the group of tall woody taxa, that includes tree species and species of tall shrubs (mainly evergreen sclerophyllous) and the group of short shrubs, that includes woody legumes, *Cistus* spp., other seasonal dimorphic shrubs and some dwarf shrubs. (A third group of woody taxa, that of the climbers, was omitted from this analysis due to the very low number of species (2 to 4)). Herbaceous species were classified according to their life span, so the groups produced were that of perennial and that of annual herbs.

The higher number of species (Fig. 4a) together with the higher overall abundance of plants (Fig. 4b) was recorded during the first post-fire years. This is attributed mainly to annual species, which are abundant after fire. This is due to either the availability of seeds that germinate only after a fire event (this is the case of annual species of the Leguminosae family) or the ability to take advantage of the favorable post-fire conditions (the case of several annual species of the Compositae and Gramineae families). Overall, any change in the species number and the overall abundance of plants that was recorded within this group of communities reflected relative changes in the group of annual herbs, since the other three groups remained almost stable throughout the chronosequence.

In all cases but for the first post-fire year, the dominating element in terms of vegetation cover was the pine (Fig. 4c). Thus, not surprisingly at all, it is the availability of space regulated by this species that controls the establishment of annual species. Between the 10th and 20th post-fire years, the young pines have green branches up to the ground level. Being the dominant element of the mono-layered vegetation, there is very little space available for the establishment of herbaceous plants. This is the reason why, a decrease in the cover of pines in this period is reflected at an increase in herbaceous vegetation cover, species richness and abundance (Fig. 4). Furthermore, there is evidence that as the community reaches maturity, the space availability increases beneath the tree canopy (given the fact that the woody understorey is sparse), which results to the establishment of annual taxa. These taxa are adopted for long dispersal (anemochorous, zoochorous, etc.). Still, it is interesting that the increase in species number during maturation is not followed by increase in the population of the established taxa.

SILICEOUS GROUP

This group consists of eight communities (Mav, Ags, Stb, Fys, Dio, Bah, STA, AGM), with the post-fire age ranging from 1 to ~65 years (Table 1). Two hundred twenty five (225) taxa were collected and identified from the communities of that group, the 53 of which are woody and the rest herbaceous. Once more, the higher number of species and the higher overall abundance of plants were recorded in the first post-fire years (Fig. 5a,b). The herbaceous component dominates during the first 2 or 3 years after fire but then it is reduced because of competition with the growing individuals of *Cistus* species. *Cistus* species are obligate seeders, which germinate massively after the fire and form abundant populations (Arianoutsou & Neeman, 2000). As soon as the senescence of *Cistus* populations starts, space becomes available for annual species establishment (Fig. 5c). Still, this second peak in the diversity of the community lasts for a rather short period, since it coincides with the time that pine growth rate increases.

CALCICOLOUS GROUP

This group consists of seven communities (Dis, Dim, Avl, Fyl, Dir, Bel, TAT), with the post-fire age ranging from 1 to ~40 years (Table 1). Two hundred thirty (230) taxa were collected and identified from the communities of that group, the 48 of which are woody and the rest herbaceous. The "calcicolous groups" of communities forms the weakest chronosequence of our study. This is the case because of the high dissimilarity of the chosen communities both in terms of vegetation structure (i.e. degree of *Q. coccifera* dominance) and site characteristics (even local changes in rocky outcrops percentage, degrees of slope, slope aspect and altitude seem to affect more the community structure than in the case of the communities on siliceous soils). Still, there are some general conclusions that can be produced from our study.

A first conclusion could be that pine regeneration seems to be less successful on limestone than on schists and tertiary deposits. A second conclusion is that species richness remains relatively high during the first 15 post-fire years, since *Cistus* and *Pinus* populations are rather sparse to play a limiting role for space availability. Members of the Leguminosae family continue to contribute to the composition of the vegetation, though in smaller populations than right after the fire. Striking is the high percentage of bulbous perennial taxa in the flora of those communities (some of which might be of importance for biodiversity conservation reasons, - rare, endemics, orchids etc.).

From our results it is evident that, in contrary to what is reported from other mediterranean type ecosystems, as well as from *Pinus halepensis* woodlands in Western Mediterranean (Trabaud 2000), change of vegetation composition does not follow a simple, gradually decreasing pattern that can be described by a power function. Perhaps that is the case in the stands where *Quercus coccifera* overdominates the understorey (calcicolous chronosequence). In most cases, the complexity of the understorey as expressed by the participation of species with different life attributes and characteristics regulates space availability and consequently species richness in a not monotonous, towards post-fire age, way. From the Eastern Mediterranean, Kutiel (2000) reports a secondary peak in species richness, 30 years after the fire, a pattern similar to the "lowland chronosequence".

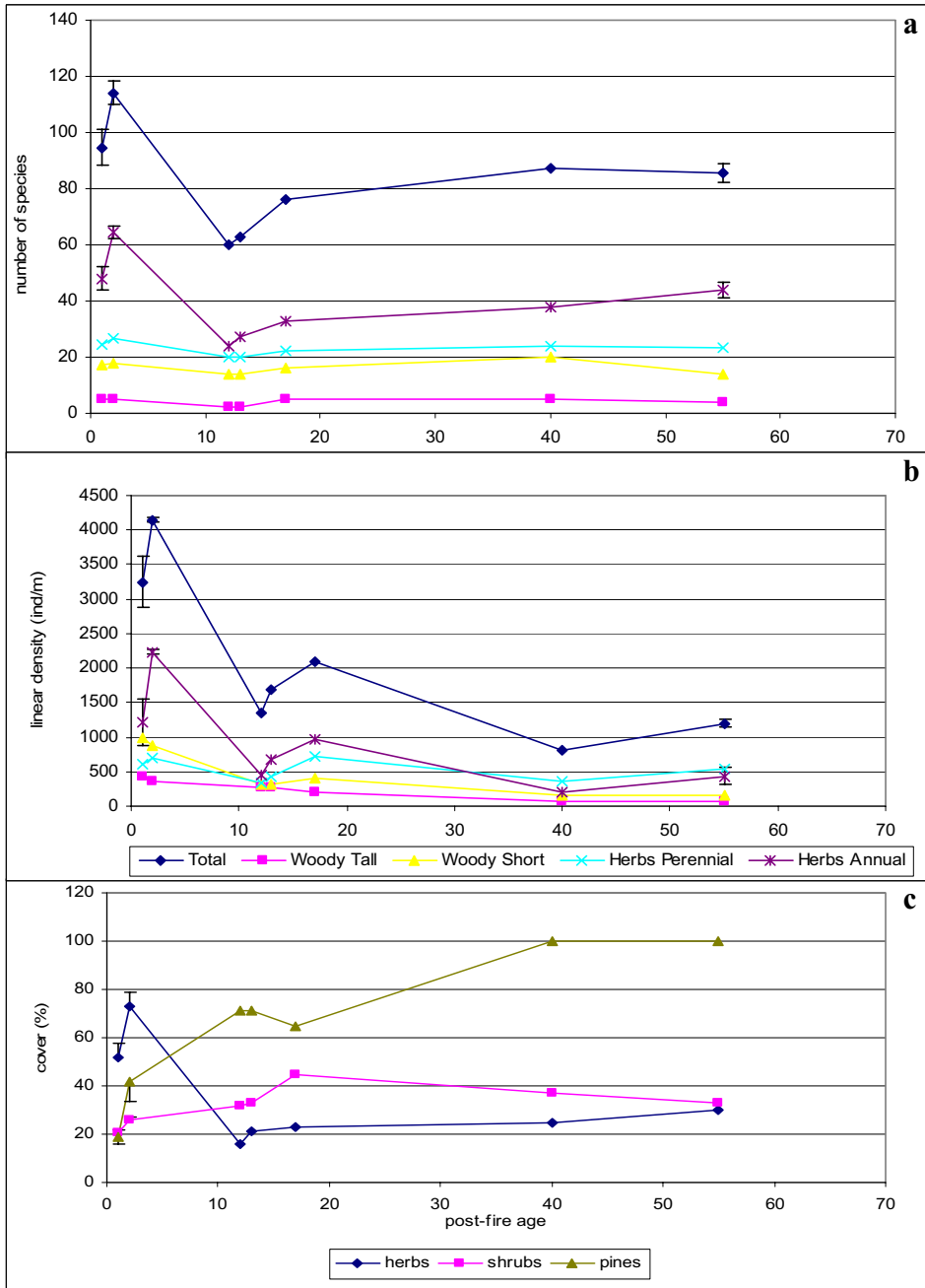


Figure 4. Change of species richness (a), species abundance (b) and vegetation cover (c) along the “lowland group” of communities

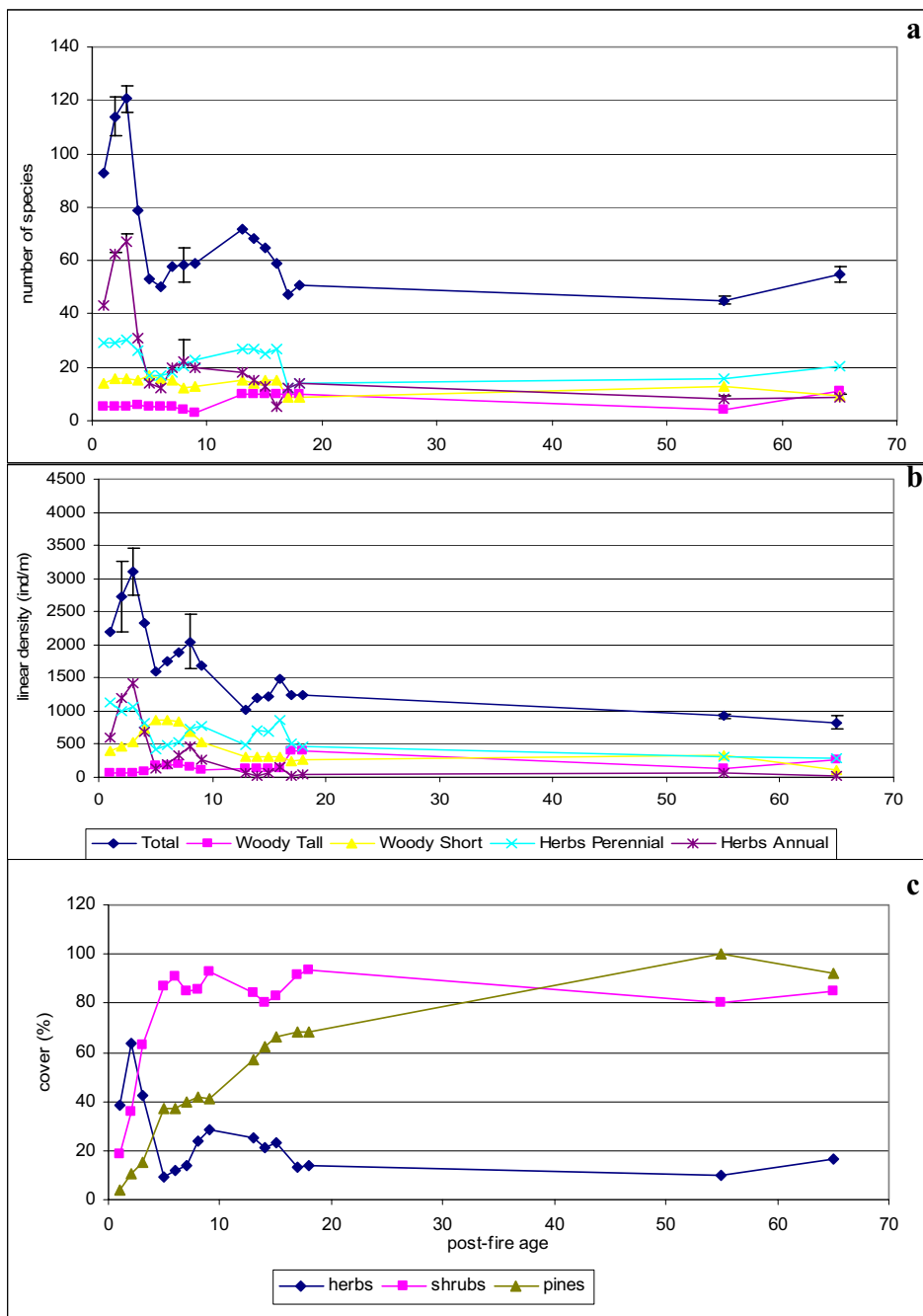


Figure 5. Change of species richness (a), species abundance (b) and vegetation cover (c) along the “siliceous group” of communities

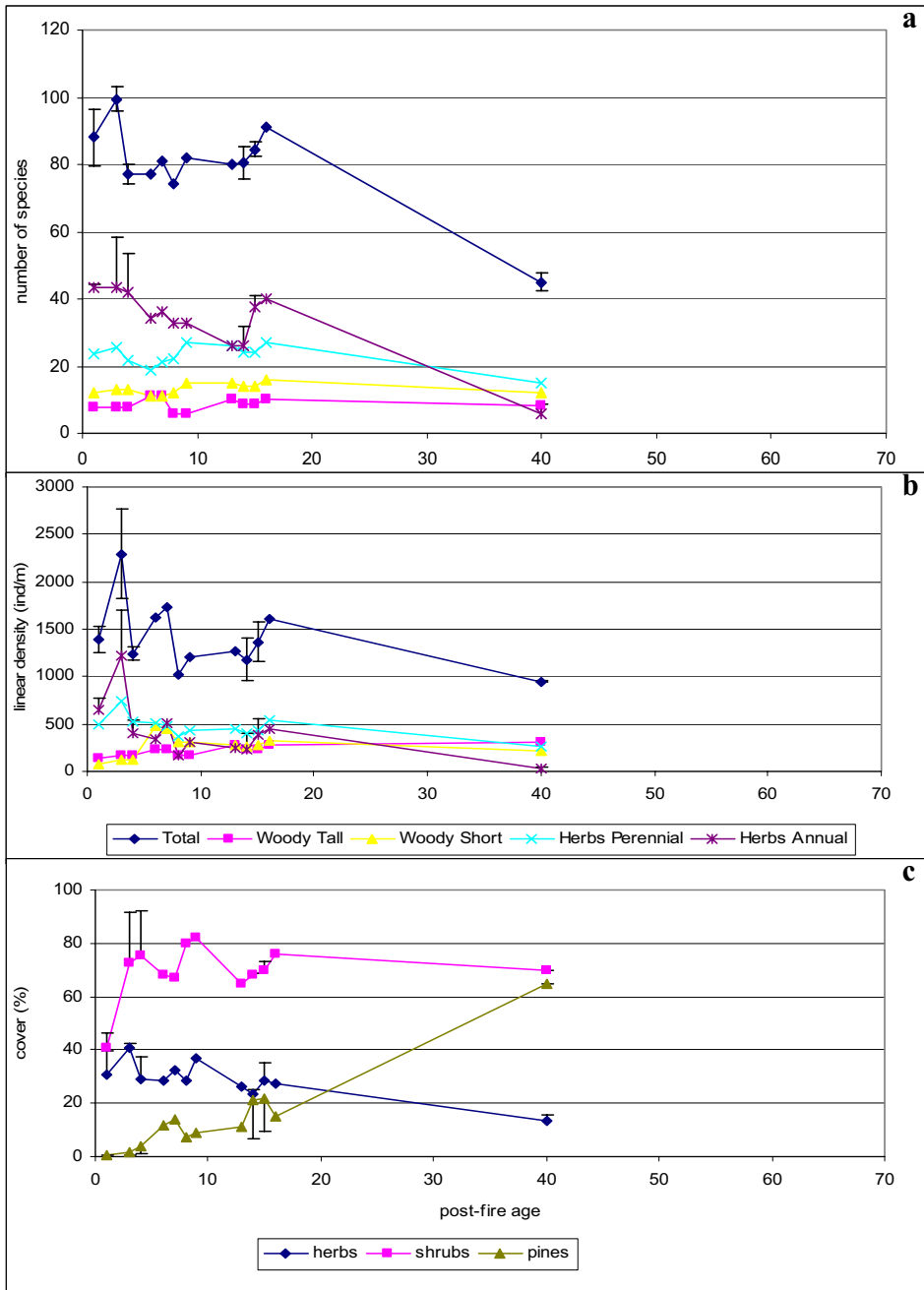


Figure 6. Change of species richness (a), species abundance (b) and vegetation cover (c) along the “calicolous group” of communities

5 CONCLUSIONS

Data on long-term post-fire dynamics of *Pinus halepensis* forests establish for these mediterranean ecosystems the model of “autosuccession”, since there hasn’t been noted any replacement of different communities. Any change in vegetation composition is driven by the development of vegetation structure, which, in turn, is regulated by either the growth rate of the long-lived woody species, or the life span of the short-lived ones. Thus, differences in the overall pattern of vegetation dynamics might differ from case to case, dependent on the initial relative abundance of species with different life attributes. Thus, it is necessary to create a species classification system related to their life attributes, in order to have the necessary tools to predict the development of vegetation given the initial composition of the community (Kazanis & Arianoutsou 2002).

Knowing the patterns and the mechanisms that define post-fire vegetation dynamics of those pine communities not only widens our understanding on their function, but, also, provides us with the reference material, in order to detect and evaluate those cases where, due to several driving forces there is a risk of failure to the regeneration of the systems (Arianoutsou 2001, Arianoutsou et al. 2002).

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