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# Drivers of *Pinus halepensis* Plant Community Structure across a Post-Fire Chronosequence

**Dimitris Kazanis** [1] , **Sofie Spatharis** [2] , **Giorgos D. Kokkoris** [3,*] , **Panayiotis G. Dimitrakopoulos** [4] and **Margarita Arianoutsou** [1]

1   Department of Biology, Section of Ecology and Systematics, National and Kapodistrian University of Athens, Panepistimiopolis, 15784 Athens, Greece; dkazanis@biol.uoa.gr (D.K.); marianou@biol.uoa.gr (M.A.)
2   School of Biodiversity, One Health and Veterinary Medicine, University of Glasgow, Glasgow G12 8QQ, UK; sofie.spatharis@glasgow.ac.uk
3   Department of Marine Sciences, School of Environment, University of the Aegean, 81132 Mytilene, Greece
4   Department of Environment, University of the Aegean, 81132 Mytilene, Greece; pdimi@aegean.gr
*   Correspondence: gkok@aegean.gr; Tel.: +30-2251036833

**Abstract:** The *Pinus halepensis* (Aleppo pine) forests prevailing in the western part of the Mediterranean Basin are amongst the most severely affected by fire due to their inherent flammability. Our understanding of the environmental factors driving post-fire community dynamics is currently limited by the lack of time-series data at temporal scales. In this present study, we analyzed a chronosequence of Greek Aleppo pine forests spanning a post-fire period of 65 years. Our goal is to explore the role of post-fire age, altitude, exposure, slope level, parent-rock material, rock cover, and cover of evergreen sclerophyllous shrubs (maquis) on plant assemblage diversity (species richness and Menhinick's diversity index) and composition. Post-fire age had a significant effect on taxonomic distinctness and community turnover but not on species richness. Taxonomic distinctness increased with post-fire age due to a higher prevalence of the families Fabaceae, Asteraceae, and Poaceae during the early post-fire period. Maquis cover was significantly associated with Menhinick's diversity index, taxonomic distinctness, and community turnover. Exposure and slope influenced only Menhinick's diversity index. The turnover in species composition was primarily driven by the geographical proximity of the forests and secondarily by post-fire age and the maquis cover. This highlights the importance of the initial floristic composition in the process of autosuccession after a fire in Mediterranean-climate ecosystems.

**Keywords:** Aleppo pine forests; plant species composition; taxonomic distinctness; habitat characteristics; autosuccession

## 1. Introduction

Fire is an ancient, recurrent natural disturbance worldwide and occurs in the Mediterranean biome in particular [1]. The Mediterranean-type climate is ideal for the ignition and spreading of fires due to its long, hot and dry summers, short and mild winters, and seasonal hot and dry wind gusts. Fires have been an integral component of the Mediterranean Basin environment, at least since the Miocene, and probably even more so after the Mediterranean's seasonality intensified during the Pliocene [2]. Nowadays, fires are common throughout the Mediterranean region, and many burn pine forests and woodlands. About 65,000 fires occur every year in Europe, burning 0.5 million ha of forested areas, 85% of which are in the Mediterranean region [3]. Recently, fire events in Mediterranean Europe have become a more serious problem, burning over larger areas [3] as a consequence of climate shifts [4,5] or land use changes [6]. Studying the post-fire community structure contributes to understanding how these changes affect ecosystem dynamics, developing adaptive management strategies that can mitigate the effects of altered fire regimes, and

guiding conservation priorities and restoration practices. However, although understanding the environmental drivers of post-fire dynamics of the Mediterranean communities' structures and compositions is critical for forest management decisions following fire events as well as for fire prevention, it is eliminated due to a lack of time-series data across relevant temporal scales for post-fire forest species growth and forest stand development.

Pine forests and woodlands are a major component of the extant vegetation in the Mediterranean region [7]. Out of the total area covered by forests, the proportion occupied by coniferous forests varies among countries: in more mesic countries, broad-leaved forests are dominant, while in drier countries, nearly half of the forested areas may be coniferous [7]. Most coniferous forests comprise species of *Pinus*, with Turkey leading the area covered by these species. Pine species growing in each country vary from west to east. For example, *P. pinaster* Ait. is abundant in the west, *P. halepensis* Mill. is widespread throughout the region, and *P. brutia* Ten. is in the east; the latter two form the majority of pines across the region [8]. *Pinus halepensis* (Aleppo pine) forests are estimated to cover from $2.5 \times 10^6$ ha [9] to about $3.5 \times 10^6$ ha [10] in the Mediterranean Basin. The Aleppo pine forests of Greece (which cover 371,984 ha, 8.72% of the total forested area) grow in more arid conditions than those of the western Mediterranean [11], and they are found in altitudes of up to 800 m a.s.l. [12].

Post-fire regeneration of Aleppo pine plant communities is a rather straightforward process, provided that they are subjected to a normal fire regime and especially to a fire frequency that allows the regenerating pines to reach a maturity level varying from 11–15 years [13]. Aleppo pine communities consist of the dominant tree species, the seeder *Pinus halepensis,* with an understory of resprouting and seeding shrubby and herbaceous species [14–16]. Post-fire vegetation succession follows the pattern of autosuccession; that is, plant species that were growing in the affected area recover after the fire successfully, either through resprouting or through seed germination [15–17]. The regeneration of post-fire Aleppo pine forests in the Mediterranean Basin is relatively well described. A relatively high initial density of pine seedlings after a fire, followed by a decrease during the following years, is typical of the eastern Mediterranean Basin [12,18,19]. *Cistus* spp. and legume seedlings are also abundant in the first post-fire years, originating from the fire-activated soil seed bank [20–22], while other herbaceous species also occur in the early post-fire years. Post-fire plant species richness shows an initial increase followed by a gradual decrease until the richness typical to unburned forests is reached [12,15]. No classical succession, namely species replacement, occurs during the post-fire regeneration of the burned Aleppo pine communities, as species typical to unburned mature forests are present already in the first post-fire year. The major changes are in species abundance (density and cover) [12].

The objective of the current paper is to explore the role of post-fire age, geographical proximity, altitude, aspect, slope, rock, and maquis cover on the Aleppo pine plant community structure and composition. Our hypotheses were that (a) richness and evenness would decrease with post-fire age, as woody species will become more abundant than the early appearing pioneer herbaceous species; (b) taxonomic distinctness would increase with post-fire age, as the numerous closely related taxa of herbaceous vegetation will decrease in numbers when progressing to more mature communities; and (c) post-fire age will drive the species composition but not independently of the geographic location, as the role of initial floristic composition is the basis for autosuccession taking place in Mediterranean climate ecosystems, such as the *Pinus halepensis* forests.

## 2. Materials and Methods

### 2.1. Study Sites

Our study sites are located in the prefecture of Attica as well as one of them at the nearby island of Euboia (Central Greece) (Figure 1). The prefecture of Attica, where the Athens metropolitan area is located, is the largest urbanized area in the country. Until the last decade of the 20th century, Aleppo pine was the dominant forest tree both in Attica and Euboia [23], forming forested areas both at lowland and mountainous sites, up to

600–800 m a.s.l. [12]. Since the mid-70s, an increasing number of forest fires have been encountered across the areas covered by this forest type, primarily due to demographic changes and other economic causes [24,25]. For the period 1977–2023, 45% of the area burned corresponded to *P. halepensis* forests.
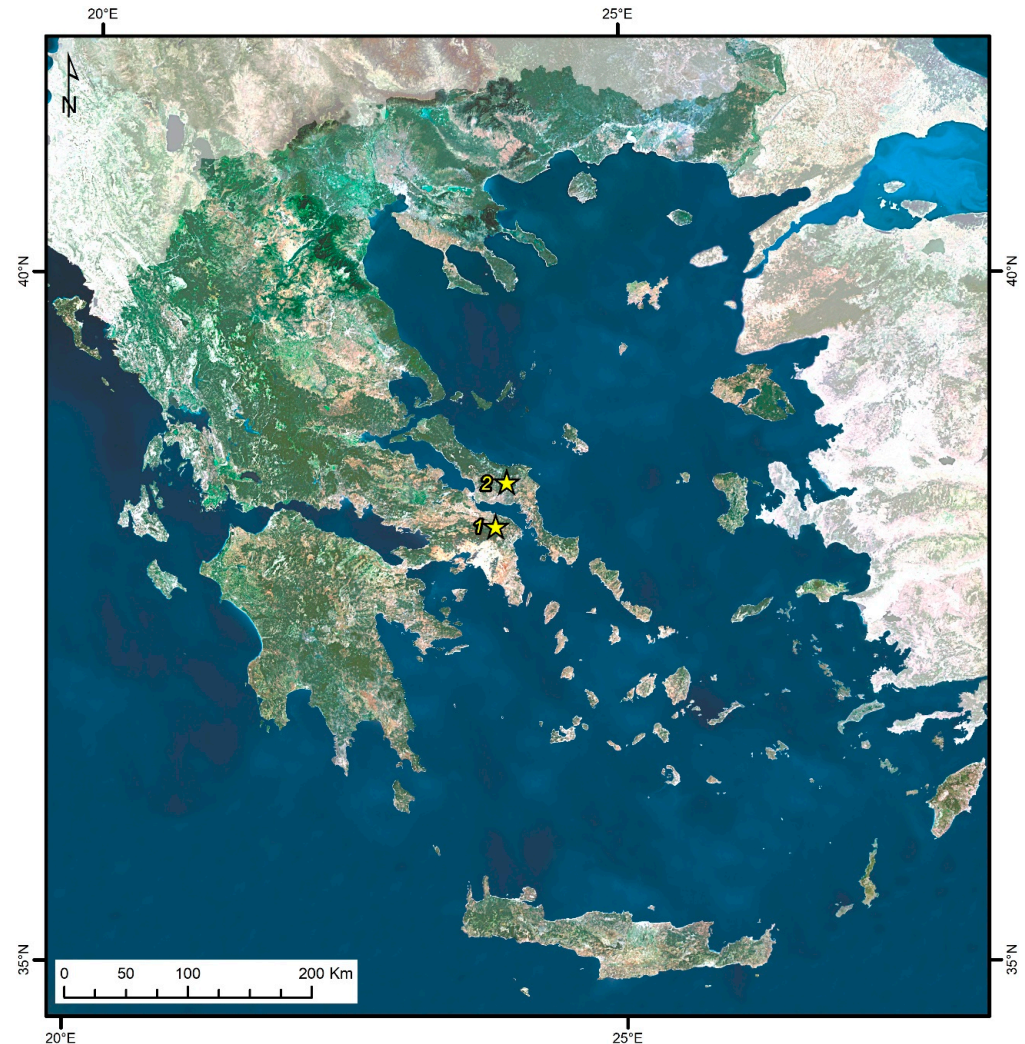


**Figure 1.** Map of Greece with the regions studied (with stars) in Attica (1) and Euboia (2).

To study the long-term post-fire dynamics of Aleppo pine forest plant communities, a chronosequence initializing from recently burned communities until mature forest communities was considered for the sampling (Table 1). The criteria for the selection of these communities were the availability of data on the fire event, the minimum possible post-fire human intervention, the inclusion of as many post-fire age classes as possible, and last but not least, the inclusion of sites with different environmental characteristics (altitude, aspect, and soil type) so as to test their influence on post-fire dynamics. From the local forest departments, we were able to identify the fourteen (14) cases shown in Table 1, with the post-fire age ranging from 1 to 18. The effort to include several pine communities burned in the past in the chronosequence is lessened by the fact that they have been re-burned since the first time. For the mature, unburned pine communities, the age of the forest stand was estimated by measuring tree rings with the use of an increment borer. Field sampling was repeated for 4 consecutive years at the Agios Merkourios unburned community and for two years at the Pontos, Markati, and Tatoi communities, whereas at the Pikermi unburned community, it took place for only one year since it was burned afterward (PikM and Pik, Table 1).

**Table 1.** Study site characteristics forming the Aleppo pine post-fire chronosequence. [Classes of slope inclination: 0, very low (0–5%); 1, low (5–20%); 2, moderate (20–40%)].

| Site Name | Site Code | Region | Fire Year | Post-Fire Age (Years Since Fire) | Altitude (m a.s.l) | Parent-Rock Material | Slope Inclination | Slope Aspect (Degrees) |
|---|---|---|---|---|---|---|---|---|
| Mavrinora | Mav | Mt Penteli | 1995 | 1–3 | 420 | Schist | 2 | 280 |
| Pikermi | Pik | Mt Penteli | 1995 | 1–2 | 180 | Tertiary deposits | 0 | 200 |
| Loutsa | Lou | Evoia, Mt Dirfy | 1994 | 1–4 | 350 | Limestone | 2 | 310 |
| Agios Stefanos | Ags | Mt Penteli | 1993 | 2–5 | 310 | Schist | 1 | 10 |
| Stamata | Sta | Mt Penteli | 1990 | 5–8 | 405 | Schist | 1 | 20 |
| Avlona | Avl | Mt Parnitha | 1991 | 6–7 | 360 | Limestone | 2 | 40 |
| Fili | Fyl | Mt Parnitha | 1989 | 8–9 | 410 | Limestone | 1 | 270 |
| Fili | Fys | Mt Parnitha | 1989 | 8–9 | 410 | Schist | 1 | 230 |
| Kamariza | Kam | Sounion National Park | 1985 | 12–13 | 170 | Limestone | 1 | 40 |
| Kamariza | Kas | Sounion National Park | 1985 | 12–13 | 170 | Schist | 1 | 40 |
| Beletsi | Bel | Mt Parnitha | 1982 | 13–16 | 590 | Limestone | 0 | 180 |
| Dionisos | Dio | Mt Penteli | 1982 | 13–16 | 460 | Schist | 0 | 50 |
| Bahounia | Bah | Mt Parnitha | 1980 | 17–18 | 660 | Limestone | 0 | 80 |
| Pikermi | PikY | Mt Penteli | 1977 | 17 | 180 | Tertiary deposits | 0 | 200 |
| Pikermi | PikM | Mt Penteli | No fire | 40 | 180 | Tertiary deposits | 0 | 200 |
| Tatoi | Tat | Mt Parnitha | No fire | 40 | 560 | Limestone | 1 | 160 |
| Pontos | Pon | Mt Penteli | No fire | 55 | 420 | Schist | 0 | 40 |
| Markati | Sou | Sounion National Park | No fire | 55 | 180 | Schist | 0 | 340 |
| Agios Merkourios | Agm | Mt Parnitha | No fire | 65 | 580 | Schist | 0 | 240 |

### 2.2. Field Sampling

The plant community's qualitative and quantitative composition was sampled with the application of the line transect method, which is more advantageous than the traditional plot sampling method since it allows the survey of a larger part of the community at a minimum time [26]. Three 50 m long line permanent transects were established in each community. The initial point of each transect was randomly selected. The three transects had different directions and were located at least 25 m apart so as to sample the maximum of the community in question. All plants, either growing along the transects or having their canopy intercepted by them, were recorded. Data recording was performed three times per year (in late autumn, late winter, and late spring) so as to include the autumnal and winter species whose non-dormancy period is very short, from the autumn of the year 1994 to the spring of the year 1998.

Thus, the data on species presence/absence and species abundance (in terms of the linear density, Ref. [26]) were acquired. Data sampling was repeated with the same annual frequency for up to four consecutive years per site. For most of the herbaceous species that had different values of linear density among the autumnal, winter, and spring samplings, the maximum values were taken into consideration as their representative values.

At the beginning of the field campaign, several environmental variables at each of the study sites were recorded, i.e., the altitude, the parent-rock material, the slope inclination (0, very low; 1, low; 2, moderate), and the slope aspect (in degrees) (Table 1). Furthermore, two additional factors related to the regeneration of Aleppo pine and the community in general, i.e., rock cover and the cover of evergreen sclerophyllous shrubs (maquis shrubs) [27], were taken into consideration. For them, the variables were recorded once per year within ten 1 × 1 m² quadrats that were established along the transects, and the % of

rock and the % of maquis cover were recorded by visual estimations. This sampling was performed in spring.

### 2.3. Data Analysis

Community diversity was expressed using five indices (species richness, Menhinick's index, evenness (according to Pielou), Berger and Parker dominance, and the average taxonomic distinctness). Species richness is the number of species (S). Menhinick's diversity index (I) [28] is calculated by the following formula:

$$I = \frac{S}{\sqrt{N}}$$

where $N$ is the total transect abundance or the number of individuals in the transect considered, and the advantage of this diversity index is that it normalizes species richness by the community size expressed by its total abundance $N$.

Evenness was expressed by Pielou's evenness index $J'$ [29], which is the Shannon index divided by the maximum possible values of Shannon index $H'$ given the species richness ($S$) of the transect considered. This maximum value is the natural logarithm of the species richness ($S$) in the transect.

$$J' = \frac{H'}{H'_{max}}$$

where $H' = -\sum_{i=1}^{S} \left(\frac{N_i}{N}\right) ln\left(\frac{N_i}{N}\right)$ and $H'_{max} = lnS$, $N_i$ are the abundance of the $i$th species present in the transect. Evenness in this formulation is expressed as a number between 0 and 1, where 1—the ideal state—implies that all species are represented with the same number of individuals.

Evenness was also expressed by the Berger–Parker dominance index [30], which is the ratio of the most abundant species in the transect divided by the total abundance of all species in the transect. Its formula is given below:

$$d = \frac{N_{i,max}}{N}$$

Average taxonomic distinctness was calculated for each of the 144 transects as the average taxonomic distance of all pairwise combinations of plant species in that transect [31]. Its formula is given below:

$$\Delta^+ = \frac{\sum\sum_{i,j} \omega_{ij}}{S(S-1)/2}$$

where $S$ is the number of species present in the transect, and for the double summation, $i$ and $j$ range over these S species; $\omega_{ij}$ is the 'distinctness weight' given to the path length linking species $i$ and $j$ in the hierarchical classification.

For example, a transect only comprising species of the family Fabaceae would have a lower value than a transect comprising species belonging to the families Asteraceae and Lamiaceae. The explanatory variables included the post-fire period (an ordinal factor with 3 levels: 1–7, 8–18, and 40–65 years post-fire), slope (an ordinal factor with three levels: 0, 1, and 2), substrate (a factor with 3 levels: lime, schist, and tertiary), degrees of northness and eastness, which express the slope aspects of the pine forest (respectively, calculated as the cosine and sine of the slope aspect in degrees after conversion into radians), altitude (in m), rocks (% cover), and maquis (% cover). The variable "Site" (a factor with 19 levels) was included as a random effect.

To test the effect of the explanatory variables on species richness, we fitted a negative binomial generalized mixed-effects model (GLMM) to account for overdispersion in the initial Poisson model. Menhinick's diversity index and the taxonomic distinctness index were fitted with a Gaussian GLMM, whereas the evenness and Berger–Parker dominance

were both fitted with a beta distribution GLMM suitable for data ranging between 0 and 1. The site was included in all models as a random effect (19 levels). Collinearity was assessed using the "performance" package [32], and the variable "substrate" was omitted from the model due to significant variance inflation. Thereafter, statistical inference was tested using likelihood ratio tests via the drop1 function.

Multivariate analysis was carried out to assess the beta diversity patterns in the plant assemblage composition (i.e., non-transformed, species-abundance data). To achieve this, the Bray–Curtis index [33] was used to assess the similarity of all pairwise combinations of the 144 transects, and the resulting triangular plant community similarity matrix was expressed visually using multidimensional scaling ordination (nMDS). General dissimilarity models [34] were subsequently employed to explain the compositional similarity patterns based on the similarity patterns in the environmental covariates (post-fire age, slope, degrees of northness and eastness, altitude, rocks, and maquis). The beta diversity patterns due to geographical proximity were accounted for prior to their association with environmental covariates. The geographical proximity was calculated using Euclidean distance between the transects using latitude and longitude data expressed in the UTM format. Prior to applying the GDMs, a backward-selection procedure was used to eliminate the covariates that did not contribute significantly to the explanation of the observed compositional turnover. A variable was eliminated by calculating the difference in deviance between the two models, with and without the variable. The observed difference in deviance was then compared to a null distribution of the differences in deviance obtained by fitting the two models using a number (e.g., 500) of random permutations of the order of sites in the response variable (compositional dissimilarity matrix). If no significant difference was found in the deviance between the two models, then the removed variable was not a significant predictor of compositional dissimilarity and could be eliminated from the model. From our covariates, the variable "Eastness" was eliminated at a 5% significance level. More details on the GDM methodology are provided in the Supplementary Materials.

All analyses were performed using R (v. 4.1.1) statistical software [35]. The normality of the residuals and overdispersion in the Poisson model was checked using the package DHARMa (v. 0.4.6) [36]. Multivariate analyses of the community data were carried out using the "vegan" (v. 2.6-6) package [37], and general dissimilarity models were fitted using the package "gdm" (v. 1.6.0) [38]. Mixed-effects models were fitted using the "lme4" (v. 1.1-34) package [39]. All graphs were plotted using "ggplot2" (v. 3.5.1) [40]. The beta distribution GLMM was fitted with the "glmmTMB" (v. 1.1.9) package [41].

## 3. Results

### 3.1. Effects of Post-Fire Stage on Aleppo Pine Forests' Plant Community Diversity

The Menhinick index of diversity (I) presented the same trend as species richness (S) but was overall more sensitive in responding to the effects of the environmental variables. Menhinick's index of diversity (I) was significantly affected by the degree of exposure to the north and east, by the maquis cover, and by the slope level (Table 2). Specifically, it decreased when moving from west to east and was also higher in the south-facing forests than in the north-facing ones (Figure 2). Species richness was also higher in the forests with more steep slopes. Taxonomic distinctness (delta plus) was positively affected by an increasing cover of rock and maquis as well as the post-fire period (Table 1, Figure 2). None of the environmental variables had an effect on the evenness and dominance of plant assemblages (Table 1).

The early post-fire communities had a lower taxonomic distinctness than the late post-fire communities (Figure 2). This is because, in the early post-fire period, species in their majority belonged to the family Fabaceae, followed by the families Asteraceae and Poaceae (Figure 3). This increased taxonomic relatedness led to decreased values of average taxonomic distinctness (Figure 3, lower right figure). In contrast, in the late post-fire communities, the number of species was much more evenly distributed among the 16 different plant families observed, resulting in a higher taxonomic distinctness.
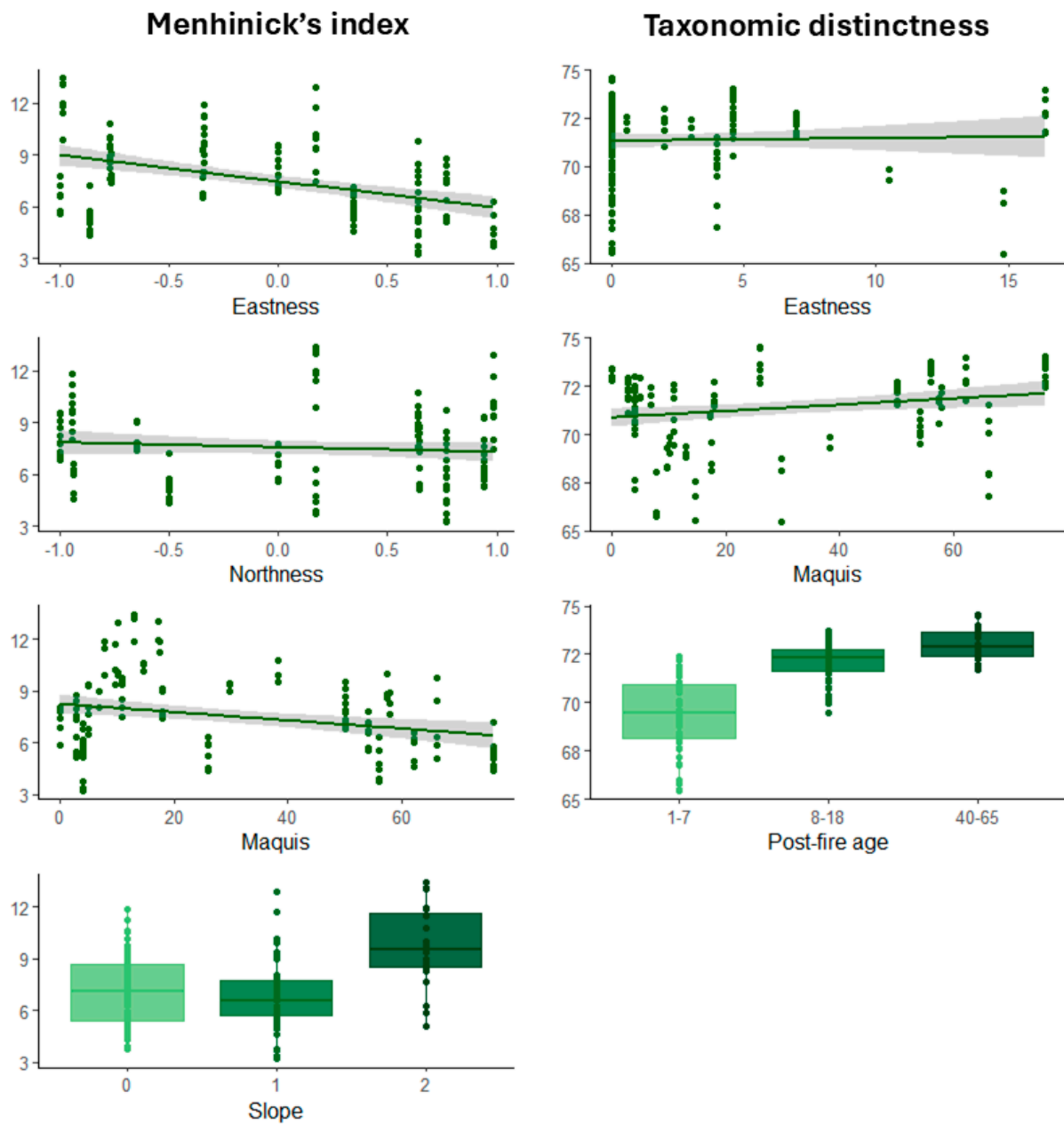
## Menhinick's index

## Taxonomic distinctness



**Figure 2.** The left plots show the relationship of Menhinick's diversity index with eastness (slope = $-1.15$, $p < 0.05$), northness (slope = $-0.93$, $p < 0.05$), maquis cover (slope = $-0.04$, $p < 0.05$), and slope level. The right plots show the relationship of the taxonomic distinctness index with rock cover (slope = $0.83$, $p < 0.05$), maquis cover (slope = $0.07$, $p < 0.05$), and post-fire age.

**Table 2.** Effect on five diversity response variables of seven explanatory variables, namely rock cover, exposure to the north and east, altitude, maquis cover, slope level, and post-fire age (1–7, 8–18, and 40–65 years post-fire). The inference is based on the fitting of GLMMs with the site as a random effect, and the results show the $\chi^2$ value, explained degrees of freedom, and $p$-values from the likelihood ratio test.

| Explanatory Variables | Response Variables | | | | |
| --- | --- | --- | --- | --- | --- |
| | **Species Richness** | **Menhinick's Index** | **Taxonomic Distinctness** | **Pielou Evenness** | **Dominance Berger–Parker** |
| **Rock cover** | 0.25, 1 $p = 0.62$ | 0.35, 1 $p = 0.55$ | 12.41, 1 $p < 0.001$ *** | 2.35, 1 $p > 0.05$ | 2.04, 1 $p > 0.05$ |

**Table 2.** *Cont.*

| Explanatory Variables | Response Variables | | | | |
|---|---|---|---|---|---|
| | Species Richness | Menhinick's Index | Taxonomic Distinctness | Pielou Evenness | Dominance Berger–Parker |
| Northness | 1.55, 1 $p = 0.21$ | 3.93, 1 $p = 0.04$ * | 0.11, 1 $p = 0.74$ | 0.91, 31 $p > 0.05$ | 0.00, 1 $p > 0.05$ |
| Eastness | 4.08, 1 $p = 0.043$ * | 5.04, 1 $p = 0.02$ * | 2.85, 1 $p = 0.91$ | 0.35, 1 $p > 0.05$ | 1.27, 1 $p > 0.05$ |
| Altitude | 0.16, 1 $p = 0.69$ | 0.01, 1 $p = 0.91$ | 0.04, 1 $p = 0.84$ | 0.46, 1 $p > 0.05$ | 0.86, 1 $p > 0.05$ |
| Maquis cover | 3.45, 1 $p = 0.06$ | 8.07, 1 $p < 0.01$ ** | 8.72, 1 $p < 0.01$ ** | 0.00, 1 $p > 0.05$ | 0.77, 1 $p > 0.05$ |
| Slope | 4.71, 2 $p = 0.09$ | 8.25, 2 $p = 0.05$ * | 1.35, 2 $p = 0.51$ | 3.9, 2 $p > 0.05$ | 1.86, 2 $p > 0.05$ |
| Post-fire period | 1.62, 2 $p = 0.44$ | 1.66, 2 $p = 0.43$ | 8.37, 2 $p = 0.01$ * | 1.03, 2 $p > 0.05$ | 0.28, 2 $p > 0.05$ |

Stars indicate the usual levels of statistical significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.
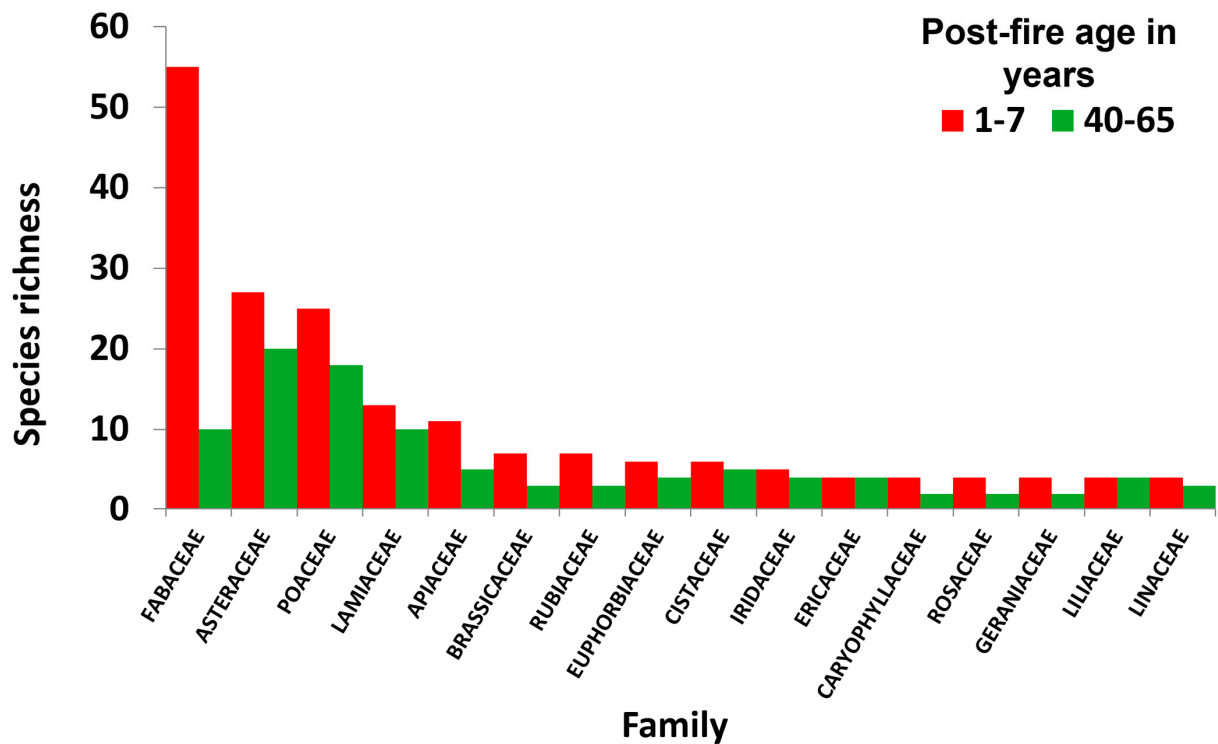


**Figure 3.** Barplot comparing the number of plant species across the different families at the early post-fire period (1–7 years) and at the late post-fire period (40–65 years). Taxonomic distinctness is much higher early after fire as the majority of the species appearing belong to fewer families. This condition changes as we move towards the mature Aleppo pine communities (see also Figure 4).
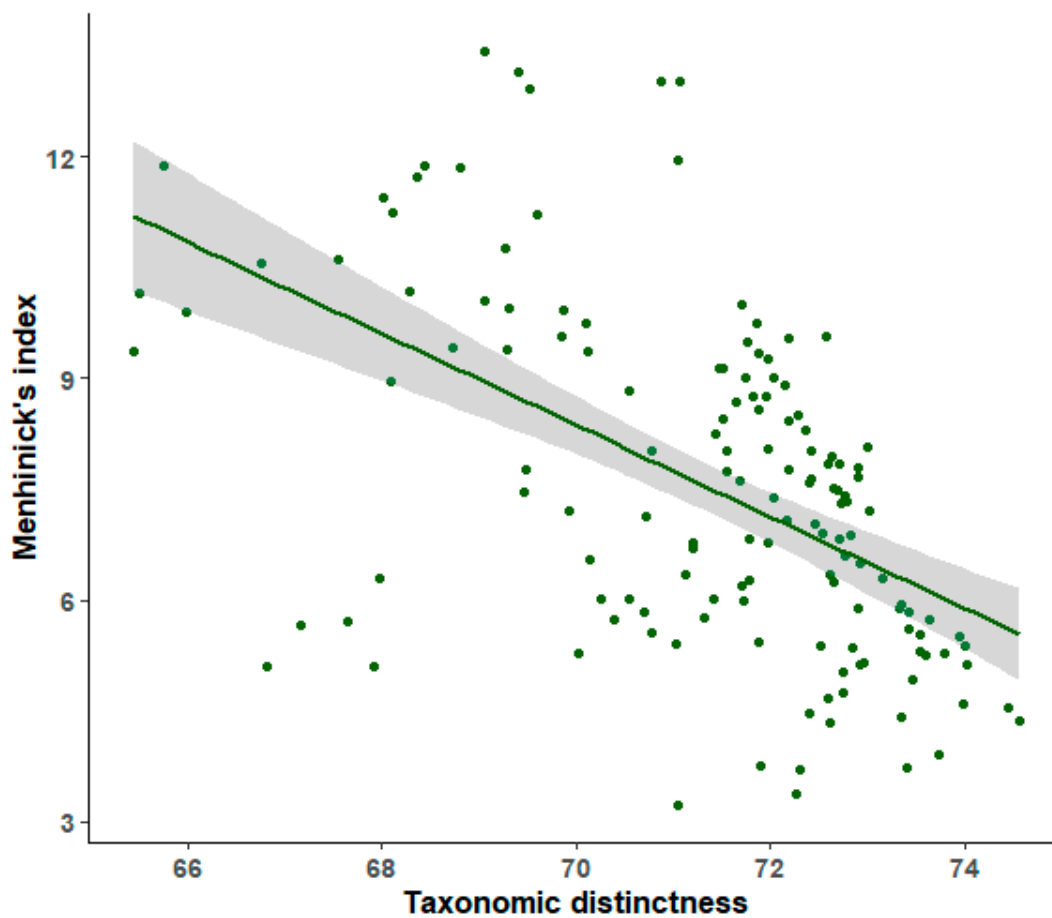
**Figure 4.** Relationship between Menhinick's diversity index and taxonomic distinctness index in the plant communities studied.

*3.2. Effects of Post-Fire Stage on Aleppo Pine Forests' Plant Community Composition*

The plant taxa composition along the 144 transects of the chronosequence presents a strong spatial pattern, with transects within the same site or of adjacent sites within the same region being grouped more closely together than sites that belonged to different regions (Figure 5). This was confirmed by the general dissimilarity models, which showed that the degree of geographic proximity explains most of the beta diversity patterns in the plant species-abundance compositions (Figure 6). After the geographical proximity had been accounted for, post-fire age and maquis cover were the two most important variables associated with the patterns in species composition and, to a lesser degree, altitude. Rock cover, slope, and northness had very small contributions, whereas eastness was completely eliminated at a prior stage, as explained in the data analysis section of the methods.
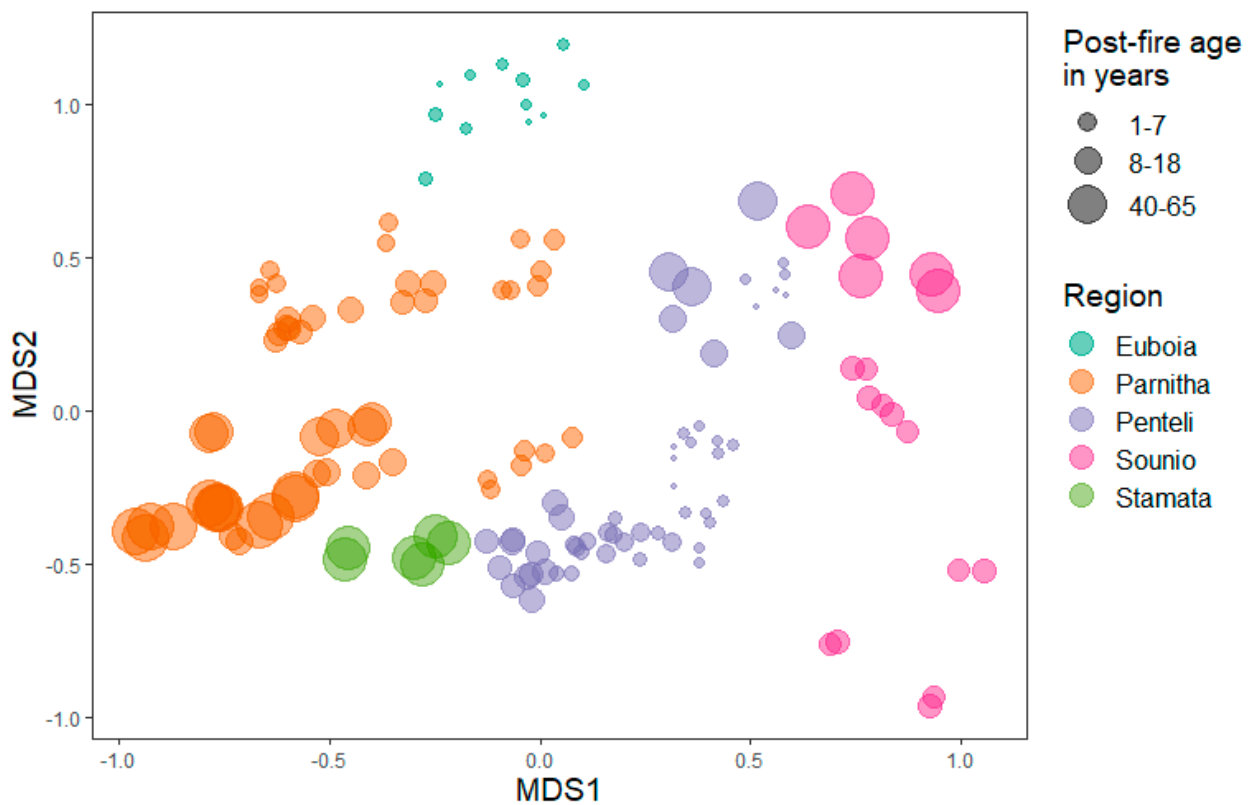
**Figure 5.** Relative similarities between the 144 transects sampled across 19 forest sites from 5 regions in Greece for up to 4 consecutive years. Increasing bubble size reflects a transition from early post-fire communities (1–7 years) to late post-fire communities (40–65 years). Similarities are based on the Bray–Curtis similarity index calculated on non-transformed plant species-abundance data.
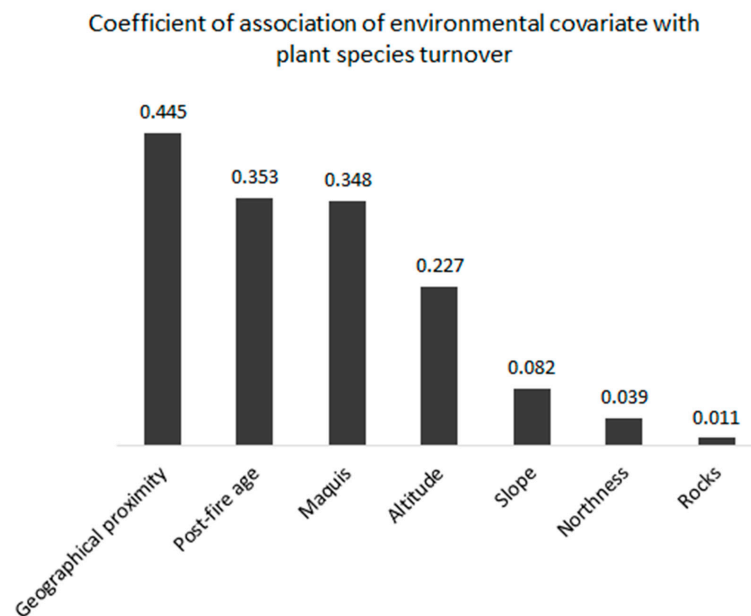


**Figure 6.** Contribution of environmental covariates (post-fire age, maquis cover, altitude, slope, degree of northness, and rock cover) to the community's beta diversity after accounting for the contribution of geographical proximity. Beta diversity (i.e., the dissimilarity between transects) was calculated with the Bray–Curtis similarity index on non-transformed plant species-abundance data. The degrees of eastness were removed from this analysis due to backward elimination at a 5% significance level.

## 4. Discussion

In this paper, we explored the relative influence of post-fire age, environmental factors, and geographical proximity on the Aleppo pine forest's community diversity and composition (i.e., structure). Given the inherent difficulty of following burned Aleppo pine communities' recoveries until they become mature, we circumvented this limitation by using multiple sites of different post-fire ages in a synchronic study—an approach adopted in other cases in the eastern as well as the western Mediterranean [42,43], respectively. Still, in the case of other studies, the chronosequences studied consisted of a low number of communities. The unique dataset of the current study enabled us to assess the post-fire succession of Aleppo pine communities up to the age of 65 years. We found that diversity (expressed both as species richness and Menhinick's index), as well as evenness (expressed both as Pielou's index and Berger–Parker dominance), were not influenced by the post-fire age. Instead, Menhinick's diversity index was more influenced by environmental factors, such as exposure to the east, level of inclination, and maquis cover. Taxonomic distinctness increased with post-fire age, while post-fire age was less important in driving the Aleppo pine community composition than geographical proximity, although this was more important than other environmental factors (e.g., altitude, maquis, aspect, slope, and rocks).

Diversity (expressed both as species richness and Menhinick's index) was not influenced by the post-fire age, contrary to our original hypothesis. This is not an uncommon pattern, as it has been observed, for example, in the first 70 years of a chronosequence after the last fire in Mediterranean forests transitioning from *P. halepensis* to *Quercus* spp. [44]. In our study, this pattern highlights that species composition in post-fire Aleppo pine forests is strongly determined by the species used to compose their initial floristic composition [45]. The initial floristic composition model (in contrast to the 'relay floristic composition' [46] that viewed succession as a directed replacement of vegetation types, with each type creating favorable conditions for its successor) predicts that all plant species that were found in the mature Aleppo pine communities per transect and geographical area were also present in the initial stages after the fire. Therefore, species richness will be at its highest level immediately after a fire event, providing little compliance to the so-called intermediate disturbance hypothesis [47]. Similar findings are reported in other studies in Mediterranean climate ecosystems (e.g., [16,48–52]).

Plant species richness (S) seems to be less sensitive in capturing environmental changes than the Menhinick diversity index [53]. The Menhinick diversity index (I) was significantly affected by the degree of exposure to the north and east, as well as the maquis cover and slope level (Table 1). Specifically, it decreased when moving from west to east and was also higher in the south-facing communities than in the north-facing ones (Figure 2). The Menhinick diversity index was also higher in communities with steeper slopes. Generally, it has been reported that north-facing slopes are more favorable for plant growth as compared to south-facing ones because the latter concentrate higher amounts of temperature and are less moist, but they receive a higher amount of solar radiation [54]. On the other hand, several studies note the importance of steep slopes for plant occurrence, especially for the endemic ones [55,56]. Last but not least, it should be noted that both slope inclination and aspect play a role in fire intensity and post-fire recovery patterns of plant communities [57].

A strong negative linear relationship was found between the Menhinick diversity index and the taxonomic distinctness index (Figure 4). More diverse transects appear to contain species that are taxonomically related, belonging to very few different families. Taxonomic distinctness, which is not a diversity index per se but estimates the taxonomic variation in each transect, is determined by maquis and rock cover as well as the post-fire period for each community studied. The relative contribution of evergreen sclerophyllous shrubs of Aleppo pine understory (maquis cover) is reasonable for defining taxonomic distinctness, as the thicker the understory is, the less space remains free for other species to be present [2]. The presence of rocky outcrops acts in a similar way, leaving also little space for fewer plants to exist, especially those that are adapted to such relatively harsh habitats.

Finally, beta diversity, that is, the species composition, depends on several factors and, most critically, on post-fire age, maquis cover, and altitude. Plant communities in the post-fire chronosequence are grouped together regarding the species composition (Figures 5 and 6) when they are close geographically, but also when they are of the same age. This is another piece of evidence reflecting the initial floristic composition model's functioning, as it has also been shown by other scientists (e.g., [58]). Fire is a recurrent disturbance in landscapes across Mediterranean-climate regions [59] and has strongly influenced plant species composition and diversity [60]. In most cases where post-fire successional plant dynamics are discussed in Mediterranean climate ecosystems, research outputs support the initial floristic composition model of succession, e.g., heathlands in Australia and South Africa, and shrublands and forests in California and the Mediterranean [14,15,61,62].

## 5. Conclusions

Our dataset enabled us to demonstrate that plant diversity, as well as evenness, were not influenced by the post-fire age in the post-fire site chronosequences studied. Instead, Menhinick's diversity index was more influenced by environmental factors. Taxonomic distinctness increased with post-fire age, while post-fire age was less important in driving Aleppo pines' community composition than geographical proximity, although this was more important than other environmental factors.

This current paper reconfirms the significant role of initial floristic composition in the process of autosuccession after a fire in the thermo-Mediterranean *Pinus halepensis* forests, which overcomes other habitat characteristics and even post-fire age. This is important when decisions on post-fire management practices are made, especially in sites that have been burned multiple times. If natural regeneration is halted because of frequent fires, then artificial restoration should be applied, and this should definitely consider the initial floristic composition of the sites burned so as to contribute to its actual restoration.

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