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One-year effects of stand age, pre-fire treatments, and hillslope aspect on recovery of plant diversity and soil properties in a Mediterranean forest burnt by a severe wildfire

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ABSTRACT

Although several management options are adopted to redirect post-fire forest ecosystems towards less vulnerable and more resilient and functional communities, little is known about the interactions among tree stand age, pre-fire forest management, and slope aspects, and their consequences for plant species and soil properties recovery immediately after severe wildfires. To address this knowledge need, this study evaluates the post-fire changes in species richness and diversity (with a specific focus on regeneration mechanisms and life forms) of regenerating plants as well as the main physico-chemical and biological properties of burned soils with the reciprocal relations. Plant cover and diversity, and many soil properties have been monitored in forests of southeast Spain with mature, middle and young stands, presence of pre-fire treatments or not, and north and south hillslopes about one year after the fire. To this aim, the reciprocal relationships among soil properties and plants were evaluated adopting a combination of statistical techniques

(PERMANOVA, Non-metric Multi-Dimensional Scaling, Distance-based Linear Modelling, Distance-based Redundancy Analysis, and Spearman correlation analysis). The damage to soil and vegetation was so high that both plants and pre-fire soil properties slowly recovered. Only a few life forms of vegetation (geophytes and herbaceous chamaephytes) were influenced by the stand age. If combined with soil aspect, stand age resulted in significantly lower germinating species in mature stands and lower resprouters in young stands, both on south hillslopes. Plant diversity was high, and the post-fire regeneration did not change the species richness and evenness. The post-fire changes in soil properties were limited, and only slight small differences in pH and betaglucosidase among stands of different age were found. No evident associations between soil properties and plant diversity were revealed by the low correlation coefficient. The low variance in plant cover and diversity, as well as in soil properties, resulted in a low accuracy of the dbRDA model to reproduce its variability among sites with different pre-fire characteristics.

Keywords: stand maturity; plant cover; enzymatic activities; organic matter; species richness; evenness; post-fire recruitment.

1. INTRODUCTION

Severe wildfires frequently impact forest ecosystems by removing almost all vegetation (trees, shrubs, herbs and litter) with high losses of biodiversity (Stinca et al., 2020; Lucas-Borja et al., 2022), and strongly altering several soil properties, such as the contents of organic matter and nutrients, stability of aggregates, electrical conductivity, and level of soil hydrophobicity (DeBano, 1981; Certini, 2005; Zavala et al., 2014). In addition to fire disturbance, also topography and forest management generate spatial and temporal variations in the burned landscapes. This variability affects plant and soil characteristics, which produce a biological and environmental heterogeneity at the local scale (He et al., 2019). More specifically, forest management can intentionally alter stand structure and plant biomass density, thus catalysing the behaviour and impact of wildfires. Moreover, it is important to note the key influence of the hillslope aspect, since plant survival and growth of most regenerating species are largely controlled by climatic conditions and morphological factors (Pigliucci, 2001). Depending on these factors, plants may respond differently to climatic and pedologic constraints (e.g., sunlight or soil water content) that limit the success of soil and plant recovery after wildfires (Su et al., 2019; De Frenne et al., 2021).

The impacts of fire, climate, topography and management can lead to severe alterations in many ecosystem functions of forests associated to plant diversity and soil characteristics (Stavi, 2019;

Nelson et al., 2022). Alteration of soil properties after severe wildfires plays an essential role in degradation rates of forests. For instance, organic matter is a key property to support the equilibrium between chemical and biological properties (Entry and Emmingham, 1998; Bastida et al., 2007). Vegetation diversity increases the heterogeneity of forest resources, such as litter composition and root exudates (Lucas-Borja and Delgado-Baquerizo, 2019). In this regard, composition of tree and herbaceous species regulates the accumulation and consumption of organic matter and the cycles of nutrients in forest soils (Entry and Emmingham, 1998; Byrnes et al., 2014). Moreover, plant composition significantly influences the enzymatic activities that are related to the cycles of nitrogen, phosphorus, carbon, and sulphur (Bastida et al., 2008; Hedo et al., 2015), as well as the growth and activity of microbial communities (i.e., dehydrogenase activity and soil respiration). Post-fire vegetation regeneration is supported by the plant capacity to resprout (resprouting species) or by fire stimulation of their recruitment (seeders or germinating species) (Bodí et al., 2012).

The literature related to the wildfire impacts on forest ecosystems is wide and eminent (e.g., Gouveia et al., 2010; Zituni et al., 2019; Nolan et al., 2021), but the majority of these studies have separately analysed post-fire soil property dynamics and vegetation regeneration (e.g., soils: Zavala et al., 2009; Carmona-Yáñez et al., 2023; biodiversity: Reilly et al., 2006; Burkle et al., 2015; Miller and Safford, 2020). In contrast, the studies that have jointly explored the post-fire dynamics of soil properties and vegetation regeneration are much less existing (Garrido-Ruíz et al., 2022; Granged et al., 2011; Spanos et al., 2005). In this context, there is the need to better understand the recovery capacity of the forest ecosystem after severe wildfires focusing on three important drivers, such as the wildfire-affected stand age, presence of pre-fire silvicultural treatments and the hillslope aspect. Since the most severe changes in vegetation and soil processes occur a few months after fire occurrence, and a prompt management action may enhance a balanced recovery of both soil properties and plant diversity. However, very scarce studies have adopted a comprehensive approach that explores the effects of the aforementioned factors on post-fire changes in soil properties and plant diversity, as well as the relationships between these components of forest ecosystems. In this regard, only Capitanio and Carcaillet (2008), who investigated the effects of silvicultural works on differences in Aleppo pine recruitment after a wildfire, found that species diversity is not related to time since the last fire, but to site location with a progressive transition from initial, through transitional, to mature vegetation stages, each one characterized by different species density. In spite of this isolated experience, there is the need to explore how some key natural or human-induced factors, such as stand age, pre-fire treatments, and hillslope aspect, influence post-fire recovery of plant diversity and restoration of soil properties in semi-arid forests.

It can be, therefore, hypothesised that these post-fire drivers of forest ecosystem evolution (i.e., stand age, pre-fire treatments and hillslope aspect) play a noticeable influence on life forms and regeneration mechanisms of vegetation as well as on physico-chemical and biochemical properties (with a particular reference to organic carbon, enzymatic activities and basal respiration) of soil.

To fill this literature gap and address this hypothesis, this study analyses the short-term effects of stand age, pre-fire treatments (tree biomass reduction) and hillslope aspect on recovery of plant diversity and soil properties in a Mediterranean forest burnt by a severe wildfire. In more detail, the post-fire changes in species richness and diversity (with a specific focus on regeneration mechanisms and life forms) of regenerating plants, as well as in a large set of physico-chemical and biological properties of burned soils, have been evaluated in forest sites of Vall d'Ebo (Alicante, South East Spain) with three different stand ages (mature, middle and young), the presence of pre-fire treatments or not, and north and south aspects of hillslopes. In spite of the short monitoring time of the study and the lack of further analysis on key soil health indicators (e.g., microbial biomass), information about the relationships among those forest features, and soil and vegetation characteristics is essential for forest managers, as it may support the most effective actions aimed at a quick recovery of the burned ecosystems in the Mediterranean area with similar characteristics as the study area.

2. MATERIAL AND METHODS

2.1 Study area

The study area is located in the north-east of the Province of Alicante, in Comunidad Valenciana (Southern Spain) (Figure 1). The altitude ranges between 200 and 1165 metres. The climate is semi-arid, Csa type according to the Koppen’s classification (Kottek et al., 2006), with mean annual values for precipitation and air temperature of 1220 mm and 18 °C, respectively (Figure 1). Forest is one of the main types of land use, with *Pinus halepensis* Mill. that have stand ages ranging from 10 to 80 years. Shrub vegetation mainly consists of *Chamaerops humilis* L*., Quercus coccifera* L*., Juniperus oxycedrus* L*., Rhamnus alaternus* L*., Daphne gnidium* L*., Cistus albidus* L*., Ulex parviflorus* Pourr*., Rosmarinus officinalis* L., and herbaceous layers include *Brachypodium retusum* (Pers.) Beauv., and sometimes in the wetter and deeper soils *Brachypodium phoenicoides* (L.) Roem. & Schult. The soil, mainly shallow and chalky with mean contents of 20 ± 5% of sand, 30 ± 7% of silt and 50 ± 7% of clay, can be classified as limestone and loamy soil (Nachtergaele, 2001; Soil Survey Staff, 2014).

In August 2022, a large wildfire burned a total area of 11604 ha (named “Vall d’Ebo wildfire”). The 41% of the area burned has been reforested mainly with *Pinus halepensis*. These reforestations had variable success and when the area was burned only 26% of the total area burned was covered by forest (Figure 1). The wildfire severity was variable depending on different ecosystem factors, such as vegetation or soil type. The wildfire resulted in soil severe burning, according to the visual classification proposed by Vega et al. (2013), which is based on qualitative indicators, e.g., vegetation burning level, charring, ground colour), as described by Parson et al. (2010).

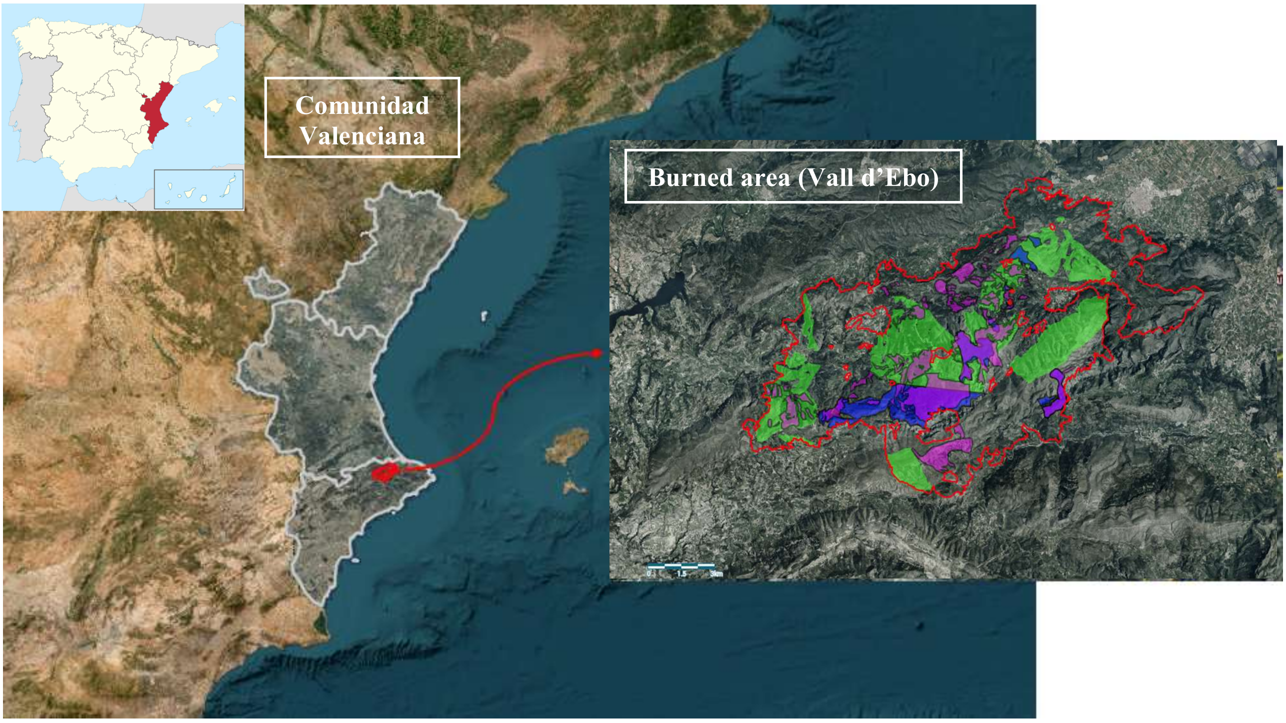


Figure 1 – Geographical location and map of the three large groups of reforested stands (green: before 1970; blue: between 1970 and 1990; purple: after 1990) in the Vall d’Ebo wildfire (Comunidad Valenciana, Spain).

2.2 Experimental design

The focus of this study was ascertaining the impacts of forest management and hillslope aspect on sites burned by severe wildfires. Therefore, the study area was identified in a severely burned site. Here, three forest stands planted on different dates were identified inside the burned area (Figure 1): (i) a mature stand (planted between 1955 and 1960 using manpower with slight device); (ii) a middle-age stand (planted between 1985 and 1990 using slight machinery and manpower); (iii) a young stand (planted between 2005-2010 using both manual work and machinery). In each stand, two pairs of sites were identified, one site was subjected in the past to forest management actions (tree biomass reduction), while the other site was undisturbed by any management. Both sites were at altitudes between 600 and 800 m a.s.l. Forest management was carried out at each stand approximately 20 years after reforestation. For each of these two pairs of sites, two single hillslopes were selected, one with north aspect, and the other exposed to south.

In each hillslope/site/stand, three square plots (each of 10 x 10 m, covering 100 m^2) were randomly delimited, where soil sampling and vegetation surveys were carried out. The plots were located at a reciprocal distance not lower than 500 m to reduce the problems associated to possible pseudo-replications, and therefore statistically dependent observations or correlations of measurements in time or space. Since the altitude range of plots in the study area was narrow, elevation was not considered as an environmental driver, such as aspect of hillslopes or age of forest stand, and therefore not included as statistical factor.

Overall, the experimental design consisted of three forest stand age (mature, middle and young), two soil condition (pre-fire treatment or no action) and two hillslope aspect (north and south) with three replicated plots for each factor, totalling 36 plots.

2.3 Data collection

2.3.1 Soil sampling and analysis

In May 2023, after removing litter, soil was manually collected in the 0 to 5 cm depth layer in the experimental plots with a hoe. Three samples (each of ca. 200 g) per plot were collected at as many randomly selected points, and then mixed to obtain a composite sample. The composite samples were immediately transported to the laboratory and dried for 48 hours at room temperature. After sieving (2-mm diameter), the samples were kept at 4 °C for 15 days until analysis. The following physico-chemical properties were analysed: (i) pH and electrical conductivity (EC, in distilled water, at a soil solution ratio of 1:2.5 and 1:5, respectively, using a digital pHmeter (LAQUA PH1100, HORIBA, Tokio, Japan) and conductivimeter (Crison 522, Barcelona, Spain); (ii) Total Organic Carbon (TOC, by Walkley and Black, 1934), modified by Mingorance et al. (2007), and measured in a spectrophotometer (Spectronic Helios Gamma UV-Vis, Thermo Fisher Scientific, Massachusetts, USA); (iii) Available plant water (AW), by measuring the wilting point (WP) at -1500 and the field capacity (FC) at -33 kPa by Richards' method (Richards, 1947); (iv) soil water content (SWC), using a VG400 (Vegetronix, Utah, USA) device placed on the soil surface and connected to a data logger (Onset HOBO, Massachusetts, USA).

Moreover, the following biological properties were determined: (i) Basal soil respiration (BSR, expressed as mg C-CO_2 kg^{-1} day^{-1} of dry soil, and c-BSR expressed as cumulative mg C-CO_2 kg^{-1} values for 32 days of measurement), using an infrared CO_2 sensor (IRGA S151, Qubit Systems Inc., Canada) on soils held at the same water holding capacity; (ii) Dehydrogenase activity (DHA, expressed as μmol INTF $hour^{-1}$ g^{-1} of dry soil), by reduction of p-iodonitrotetrazolium chloride (INT) to p-iodonitrotetrazolium formazan (INTF) following García et al. (1997); (iii) Urease activity (UA, expressed as μmol N-NH_4^+ $hour^{-1}$ g^{-1} of dry soil), using urea as a substrate and a borate buffer at pH = 10 (Kandeler and Gerber, 1988) ; (iv) Alkaline phosphatase (PA) and β-glucosidase (BGA) (both expressed as μmol pNP g^{-1} of dry soil), using the methods of Tabatabai and Bremner (1969) and Eivazi and Tabatabai (1988), respectively.

2.3.2 Plant diversity analysis

During soil sampling, plant species were surveyed at the experimental plots. Three transects 20-m long were delimited along the longitudinal profile of each of the 36 plots, i.e. 108 transects. One transect was setup in the middle part, and the two others on the plot sides. In each transect, plant cover and species were identified using the line intercept method (Canfield, 1941), together with their regeneration mechanism (seeders or resprouters) and their life forms (therophytes, hemicryptophytes, geophytes, phanerophytes, woody chamaephytes, and herbaceous chamaephytes) by field observations. More specifically, a tape was extended along the transect, and the observer identified and recorded plants intercepted by the tape. From these surveys, two plant diversity indices were calculated in each plot: (i) the species richness (S, the total number of the different species); (ii) and the Shannon index (Shannon, 1948). Shannon's index (H) indicates the relative abundance of the different species in a site, and was calculated by the following formula:

$$H = -\sum_{i=1}^{S} p_i \ln p_i \qquad (1)$$

where $p_i = \frac{n_i}{N}$ is the frequency of "n_i" plants of the "i-th" species compared to the total number of plants "N" in the transect. H varies in the range 0 to ln N; a H is equal to 0 indicates no plant diversity (i.e., only one species in the site), while, when H is maximum, all species have the same number of individuals (i.e., perfect evenness). Finally, the values of the S and H indexes were averaged among the three transects in each plot.

2.4 Statistical analysis

The reciprocal relationships among the soil properties and plants were evaluated adopting a combination of statistical techniques.

First, the statistical differences in measurements were determined by the multivariate permutational analysis of variance (PERMANOVA, Anderson, 2005), using the tree factors (stand age, presence of forest treatments, slope aspect) as factors. Stand age, and slope were chosen as fixed factors, whereas pre-fire forest treatments were fixed and nested in stand age factor). The PERMANOVA tests allow the statistical analysis of a simultaneous response of various variables to one or more factors in an experimental design based on any resemblance matrix, using permutation method. Before PERMANOVA, the matrices with soil properties and plant species cover were square root transformed; the similarity matrix was built using the Euclidean and Bray Curtis distance for the soil properties and plant species cover data, respectively. The sums of squares type were type III (partial) and each factor (or interactions among factors) was a fixed effect. The permutation method used was the unrestricted permutation of raw data and the number of permutations was 999.

Second, the Non-metric Multi-Dimensional Scaling (NMDS) and the Kruskal stress formula (minimum stress: 0.01) were applied to plant diversity, to evaluate the similarity level in the individual cases of the dataset.

Third, a DISTLM function (distance-based linear modelling) was developed, to determine the relative importance of any soil properties on plant diversity. For the DISTLM function, we developed "marginal" tests of the relationship between the plant diversity and individual variables (soil property), to identify the independent variables that explain the variations in the soil samples. Following the marginal tests, "sequential" tests of individual variables were performed to assess whether adding an individual variable contributes significantly to the explained variation of the response variable.

Fourth, distance-based redundancy analysis (dbRDA) was applied to build a regression model against two new response variables ("axis" 1 and "axis" 2), built on the soil properties and covers. The AICc (Akaike, 1974) criterion was adopted to select the best model, and the step-wise procedure was followed to build the model.

Finally, a Spearman correlation heatmap including the correlation coefficients between soil properties (EC, pH, TOC, AW, SWC, DHA, BGA, PA, UA, and c-BSR) and plant diversity (S, PI, MDS1 and MDS2, the latter being the axes of the multidimensional scaling analyses of plant diversity) was calculated, in order to explore the relationships between soil and plant diversity.

For statistical analyses, PRIMER V7® with PERMANOVA add-on (Anderson, 2005) and Statgraphics Centurion XVI® (StatPoint Technologies, Inc., Warrenton, VA, USA) were used. A significance level of 0.05 was used, unless otherwise indicated.

3. RESULTS

3.1 Variability of plant cover

According to PERMANOVA, the only factor generating significant differences in plant cover was the interaction age and aspect for seeder plants ($p < 0.05$), while the other factors were not influent. In more detail, the maximum percentage of ground cover by seeders (59.3%) was surveyed in treated stands with young age exposed to south (Figure 2). Differences in ground cover for resprouting plants were never significant (Table 1.SI).

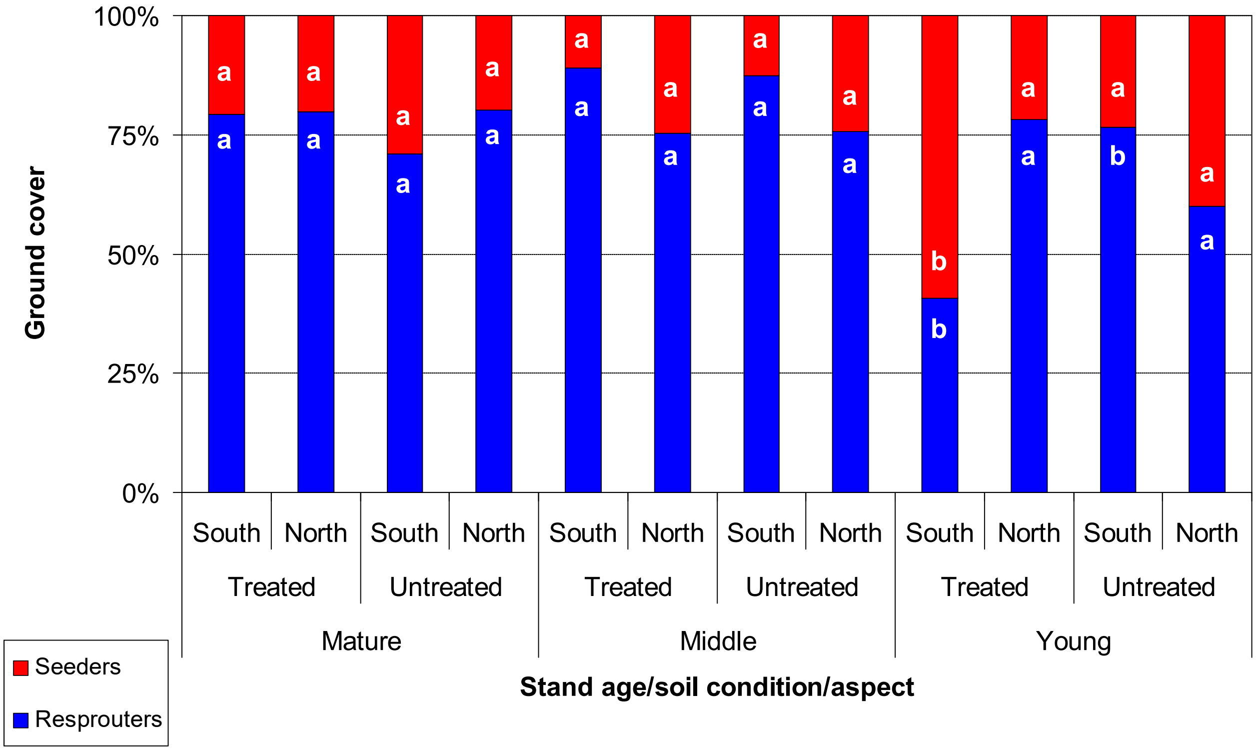


Figure 2 – Percent distribution of plant cover according to the regeneration strategy in forests with different stand age (mature, middle, young), soil condition (with or without treatment) and aspect (South or North) in the study area (Vall d'Ebo, Comunidad Valenciana, Spain). Different letters indicate significant differences in pairwise comparisons after PERMANOVA.

As shown by the results of PERMANOVA, the similarity among stands of different age and aspect was high in terms of regeneration strategy, except for resprouters, which were significantly different on hillslopes exposed to south between young and mid-age stands, and seeders, for which the differences were significant between mature stands on one side, and mid-age and young stands on the other side, in all cases with south aspect (Table 2.SI).

The PERMANOVA showed significant differences in life forms of the surveyed species geophytes, which were different with stand age. Phanerophytes and herbaceous chamaephytes showed differences between stands with different age and aspect (Table 3.SI). The rest of life forms did not show any effect of the analysed factors, Despite of this relatively low significance of the differences, a prevalence of therophytes (54.3% of the total ground cover) was detected in young stands and of herbaceous chamaephytes (69.7%) in stands with middle age, both treated and exposed to south. In contrast, the soil covered by geophytes and woody chamaephytes was generally small in all treatments (less than 8%) (Figure 3).

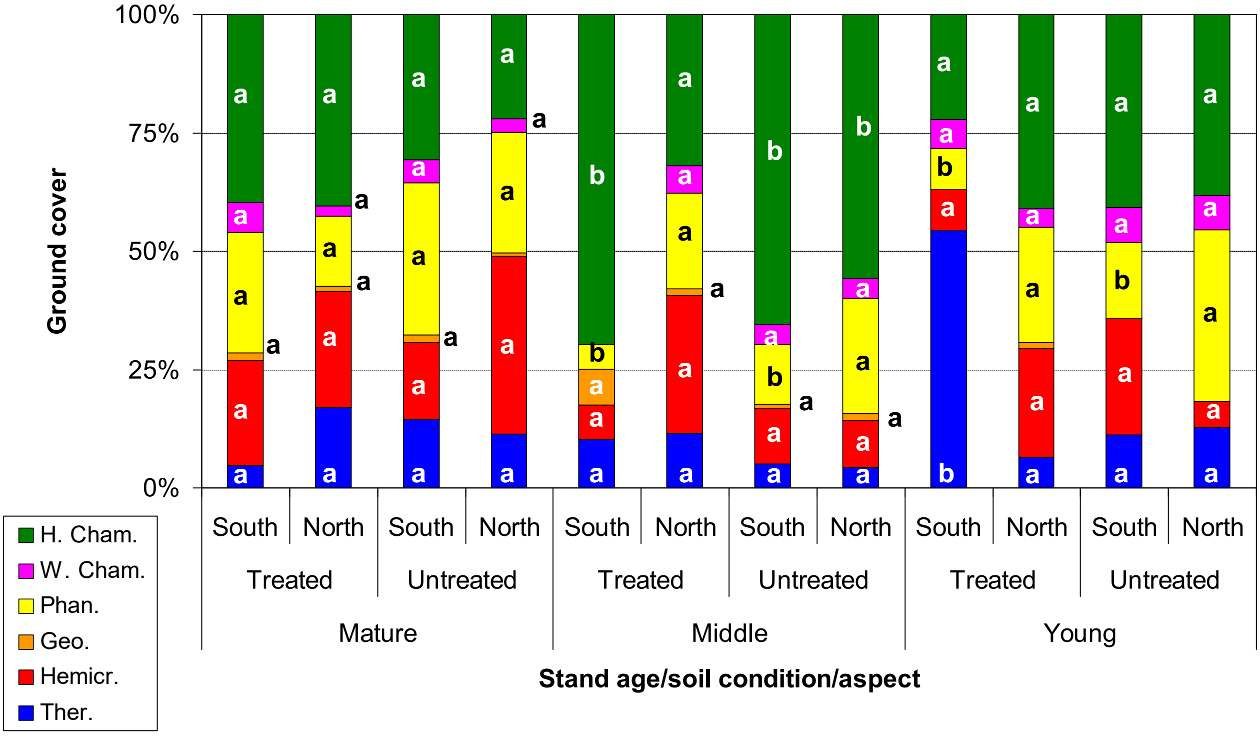


Figure 3 – Percent distribution of plant cover according to the life form (Ther. = Therophytes; Hemicr. = Hemicryptophytes; Geo. = Geophytes; Phan. = Phanerophytes; W. Cham. = Woody Chamaephytes; H. Cham. = Herbaceous Chamaephytes) in forests with different stand age (mature, middle, young), soil condition (with or without treatment) and aspect (South or North) in the study area (Vall d'Ebo, Comunidad Valenciana, Spain). Different letters indicate significant differences in pairwise comparisons after PERMANOVA.

All stands with different age were similar regardless of the aspect in terms of life form, except for the herbaceous chamaephytes exposed to south, which was significantly different between young stands and stands of middle age (Table 4.SI).

Regarding multidimensional scaling analyses, the NMDS does not show evident clusters of sites according to the factors “stand age” and “aspect” for plant diversity (Figure 4).

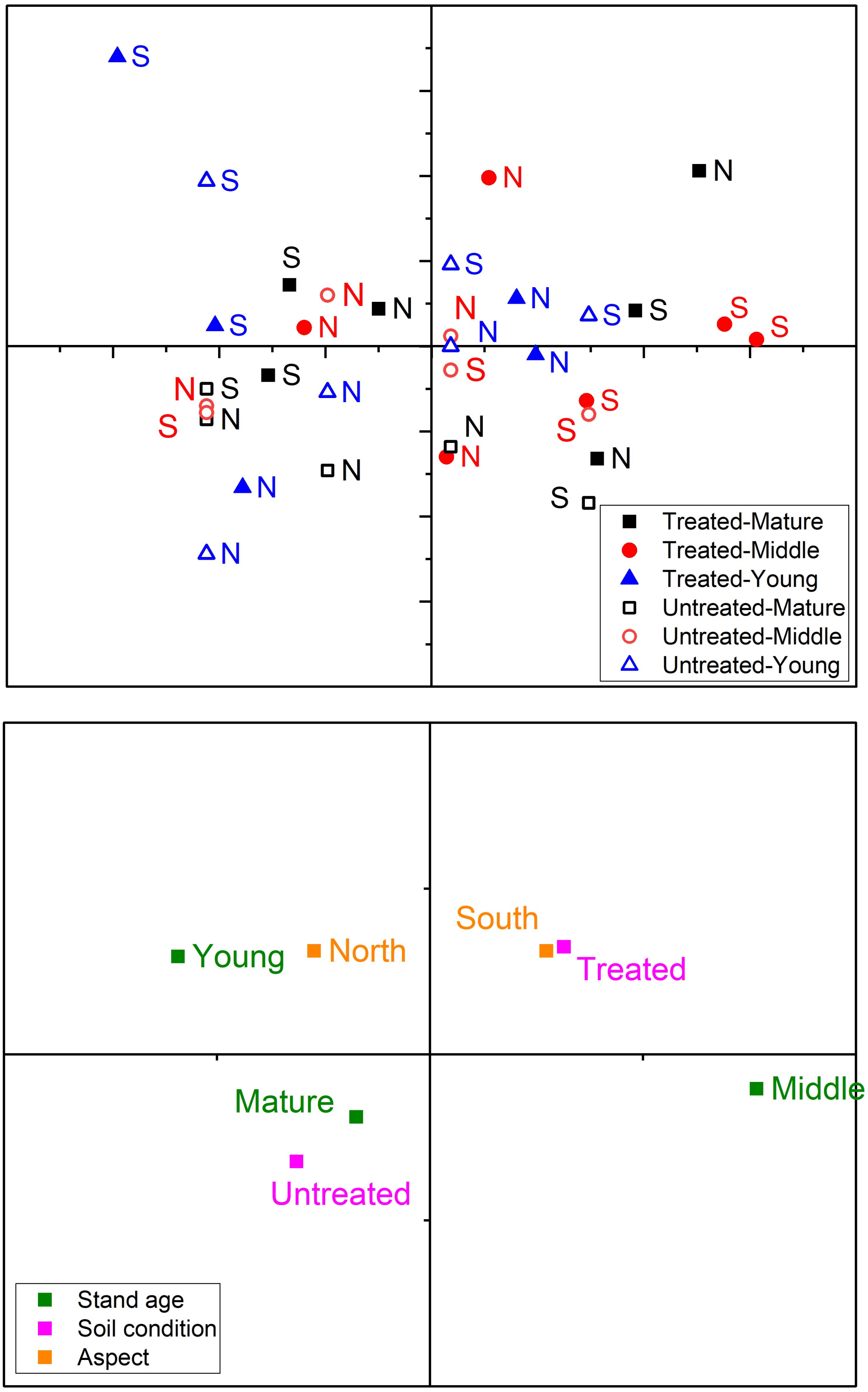


Figure 4 - Results of nonmetric multidimensional scaling (NMDS) routine applied to plant diversity in forests with different stand age (mature, middle, young), soil condition (treated or untreated) and soil aspect (south or north) in the study area (Comunidad Valenciana, Spain) – lower panel reports the centroids of each group of clusters. Legend: S = south aspect; N = north aspect.

3.2 Variability of plant diversity

PERMANOVA did not show any significant difference either in species richness or evenness (measured by Shannon index) among the factors (Table 5.SI). In general, the number of species was in the range 6.33 ± 2.40 (young treated stands exposed to south) to 16 ± 0.88 (mature treated stands exposed to north), while their distribution varied between 1.21 ± 0.49 (treated and young stands exposed to south) and 2.23 ± 0.34 (untreated and mature stands exposed to north).
A similarity in plant diversity as found only between mid-aged and young stands with south aspect (Table 6.SI).
Brachypodium retusum, Cistus albidus, and *Ulex parviflorus* were the species that most contributed to the overall similarity among the forest stands, as shown by Table 7.SI, but also *Pinus halepensis* was found mainly in young stands, and secondarily in mid-age plots regardless of soil condition and aspect. Species such as *Euphorbia segetalis* and *Avena sterilis* appear in stands with middle age, but not in stands with younger or older maturity.

3.3 Variability of soil properties

None of the analysed physical-chemical properties of soil showed significant differences among the stands of different age, soil condition, and aspect (Table 8.SI). In more detail, among the chemical properties, pH varied in a narrow range (7.65-8), but the changes between young stands (7.90 ± 0.11) and stands with older age (7.72 ± 0.05, mature, and 7.75 ± 0.63) were significant. In contrast, the variability of TOC was from 7.93 ± 2.82% (untreated young stands exposed to north) to 13.9 ± 3.99% (treated young stands exposed to south), whereas EC varied from 0.397 ± 0.061 mS/cm (again measured untreated young stands exposed to north) to 1.31 ± 0.77 mS/cm (in treated young stands exposed to north). Regarding the physical properties, also SWC was even affected by a high variability, as shown by the higher changes measured (from 12.5 ± 6.42% of untreated young stands exposed to north to 33.4 ± 4.05% of untreated stands with middle age exposed to north for AW), while the variability of SWC was much lower (in the range of 4.05% to 5.85%) (Figure 5).

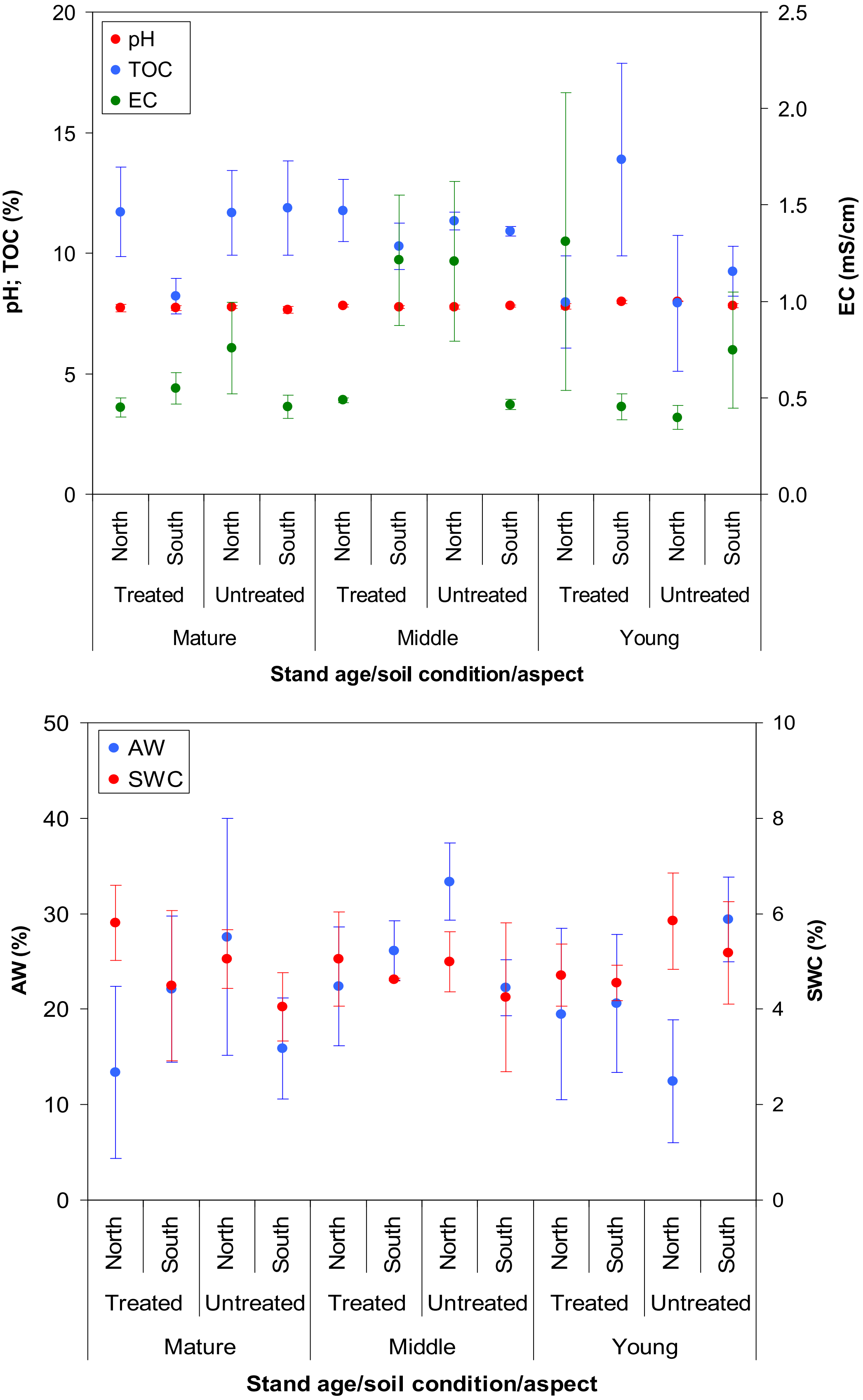
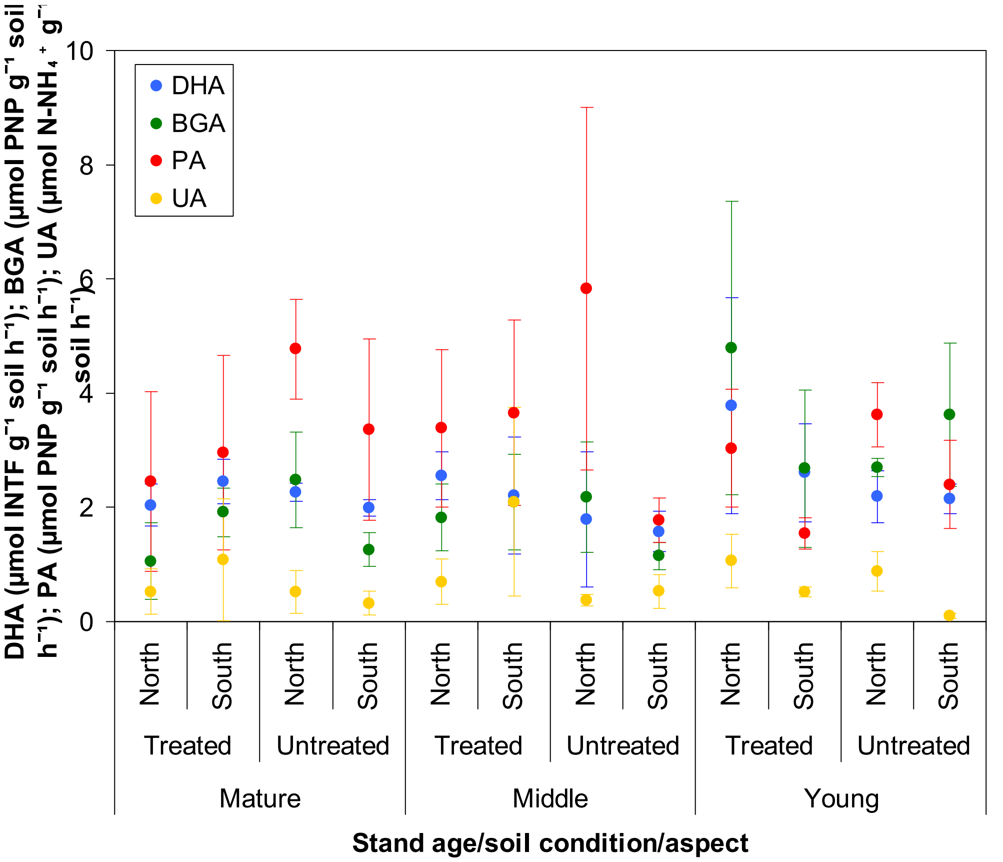


Figure 5 – Mean ± standard error (n = 3) of the main physico-chemical properties of soils (EC = electrical conductivity; TOC = total organic carbon; AW = available water; SWC = soil water

content) sampled in forests with different stand age (mature, middle, young), soil condition (with or without treatment) and aspect (South or North) in the study area (Vall d'Ebo, Comunidad Valenciana, Spain).

Among the biochemical properties, only BGA was significantly different but only among stands of different age (Table 9.SI). For the other biochemical properties tested, the differences were not significant. More specifically, BGA of young stands (3.45 ± 0.89 µmol PNF g^{-1} soil h^{-1}) was significantly higher compared to mature stands (1.68 ± 1 µmol PNF g^{-1} soil h^{-1}) and stands with middle age (1.81 ± 1.67 µmol PNF g^{-1} soil h^{-1}). DHA, PA and UA were variable between 1.58 and 3.78 µmol INTF g^{-1} soil h^{-1}, 1.55 and 5.83 µmol PNF g^{-1} soil h^{-1}, and 0.1 and 2.1 µmol N-NH_4^+ g^{-1} soil h^{-1}), respectively. Daily and cumulative values of BSR were in the range 42.3 to 100.8 mg of C-CO_2 kg^{-1} d^{-1}, and 1355 to 3226 mg of C-CO_2 kg^{-1}, respectively (Figure 6).



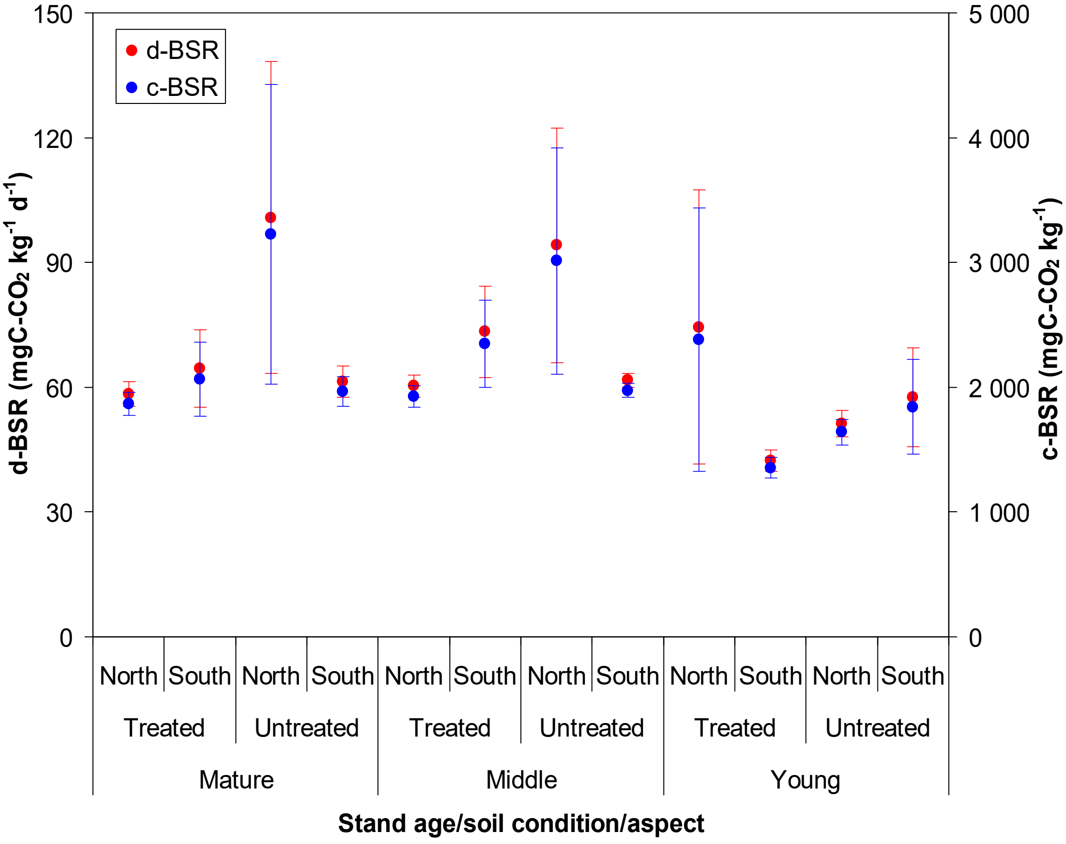


Figure 6 – Mean ± standard error (n = 3) of the main biochemical properties of soils (BGA = β-glucosidase activity; DHA = dehydrogenase activity; PA = alkaline phosphatase activity; UA =

urease activity; d-BSR = daily basal soil respiration; c-BSR = cumulative basal soil respiration) sampled in forests with different stand age (mature, middle, young), soil condition (with or without treatment) and aspect (south or north) in the study area (Vall d'Ebo, Comunidad Valenciana, Spain).

Marginal tests of DistLM showed that only pH was a significant factor of the model, while the sequential tests revealed that all variables must be added to the best distance linear model (R^2 = 0.36) to explain the variance of the variables (Table 1). According to the variations (out of the fitted model and out of the total variation) explained by the axes of dbRDA, the axis one (dbRDA1) explained 26.7% of the total variation of the fitted model and 9% of the total variation of the variables, whereas the axis two (dbRDA2) explained 16% of the fitted model and 5.4% of the total variation (Figure 7).

Table 1 – Marginal and sequential tests of the relationships between the soil properties sampled in forests with different stand age (mature, middle, young), soil condition (with or without treatment) and aspect (south or north) in the study area (Vall d’Ebo, Comunidad Valenciana, Spain).

MARGINAL TESTS

Variable	**SS(trace)**	**Pseudo-F**	**P**	**Prop.**
EC	3476	1.363	0.169	0.039
pH	4854	1.933	**0.021**	0.054
TOC	2077	0.801	0.701	0.023
FC	3297	1.290	0.197	0.037
WP	3321	1.300	0.164	0.037
AW	2569	0.996	0.457	0.028
SWC	1845	0.710	0.817	0.020
DHA	2576	1.000	0.450	0.029
BGA	3330	1.303	0.175	0.037
UA	3560	1.397	0.133	0.039
PA	1953	0.752	0.776	0.022
d-BSR	1734	0.666	0.882	0.019
c-BSR	1734	0.666	0.879	0.019

SEQUENTIAL TESTS

Variable	**R^2**	**SS(trace)**	**Pseudo-F**	**P**	**Prop.**	**Cumul.**	**Res. df**
+EC	0.039	3476	1.363	0.148	0.039	0.039	34
+pH	0.091	4709	1.894	0.020	0.052	0.091	33

+TOC	0.116	2269	0.910	0.582	0.025	0.116	32
+FC	0.147	2826	1.139	0.305	0.031	0.147	31
+WP	0.179	2879	1.166	0.264	0.032	0.179	30
+AW	0.210	2805	1.141	0.302	0.031	0.210	29
+SWC	0.231	1848	0.746	0.765	0.020	0.231	28
+DHA	0.249	1643	0.655	0.859	0.018	0.249	27
+BGA	0.278	2669	1.066	0.364	0.030	0.278	26
+UA	0.304	2309	0.920	0.512	0.026	0.304	25
+PA	0.338	3086	1.241	0.228	0.034	0.338	24
+d-BSR	0.359	1914	0.762	0.734	0.021	0.359	23
+c-BSR	0.359	0	0.000	1	0.000	0.359	23

Notes: EC = electrical conductivity; TOC = total organic carbon; AW = available water; FC = field capacity; WP = wilting point; SWC = soil water content; BGA = β-glucosidase activity; DHA = dehydrogenase activity; PA = alkaline phosphatase activity; UA = urease activity; d-BSR = daily basal soil respiration; c-BSR = cumulative basal soil respiration). Bold characters indicate statistical significance ($P < 0.05$).

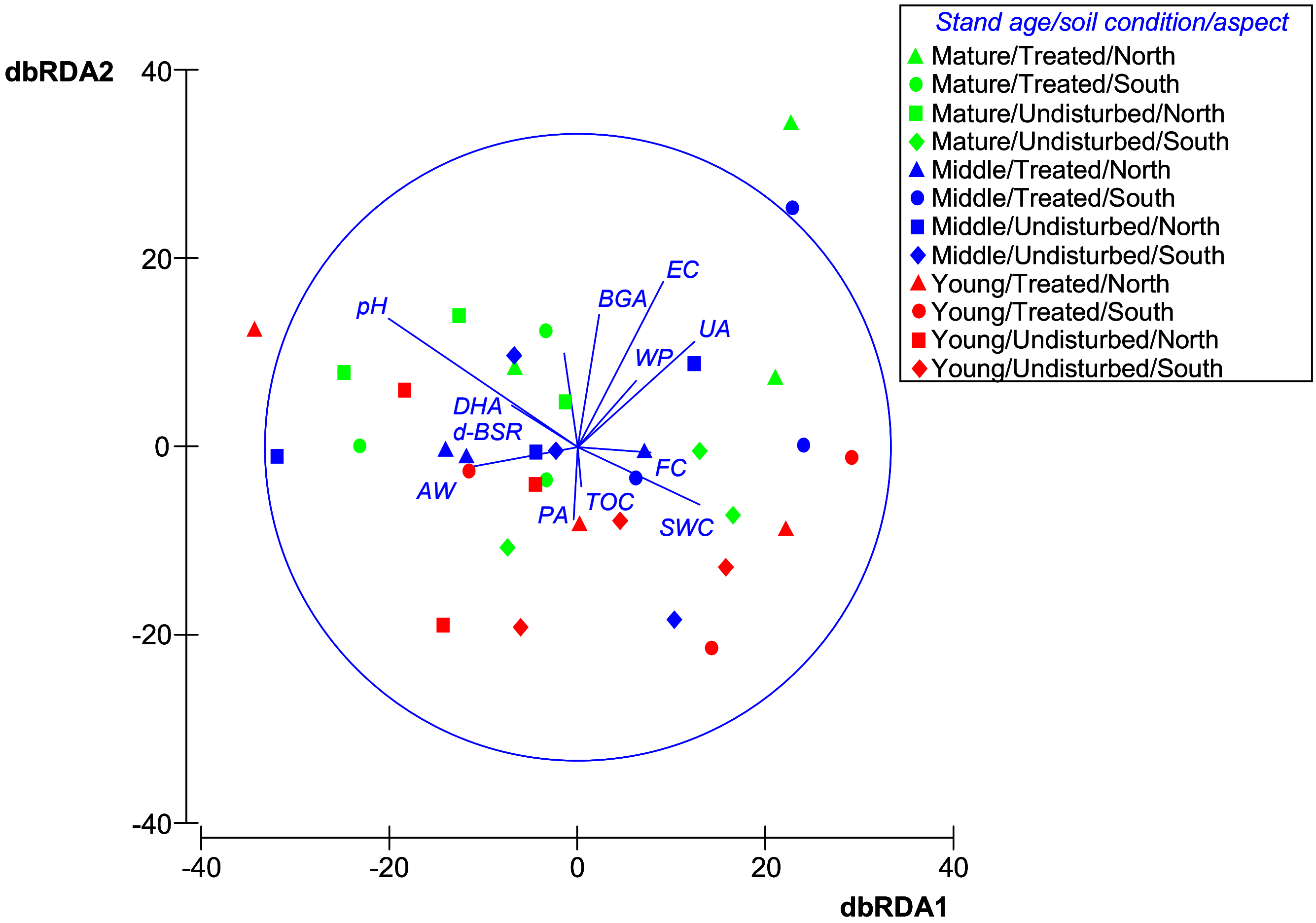
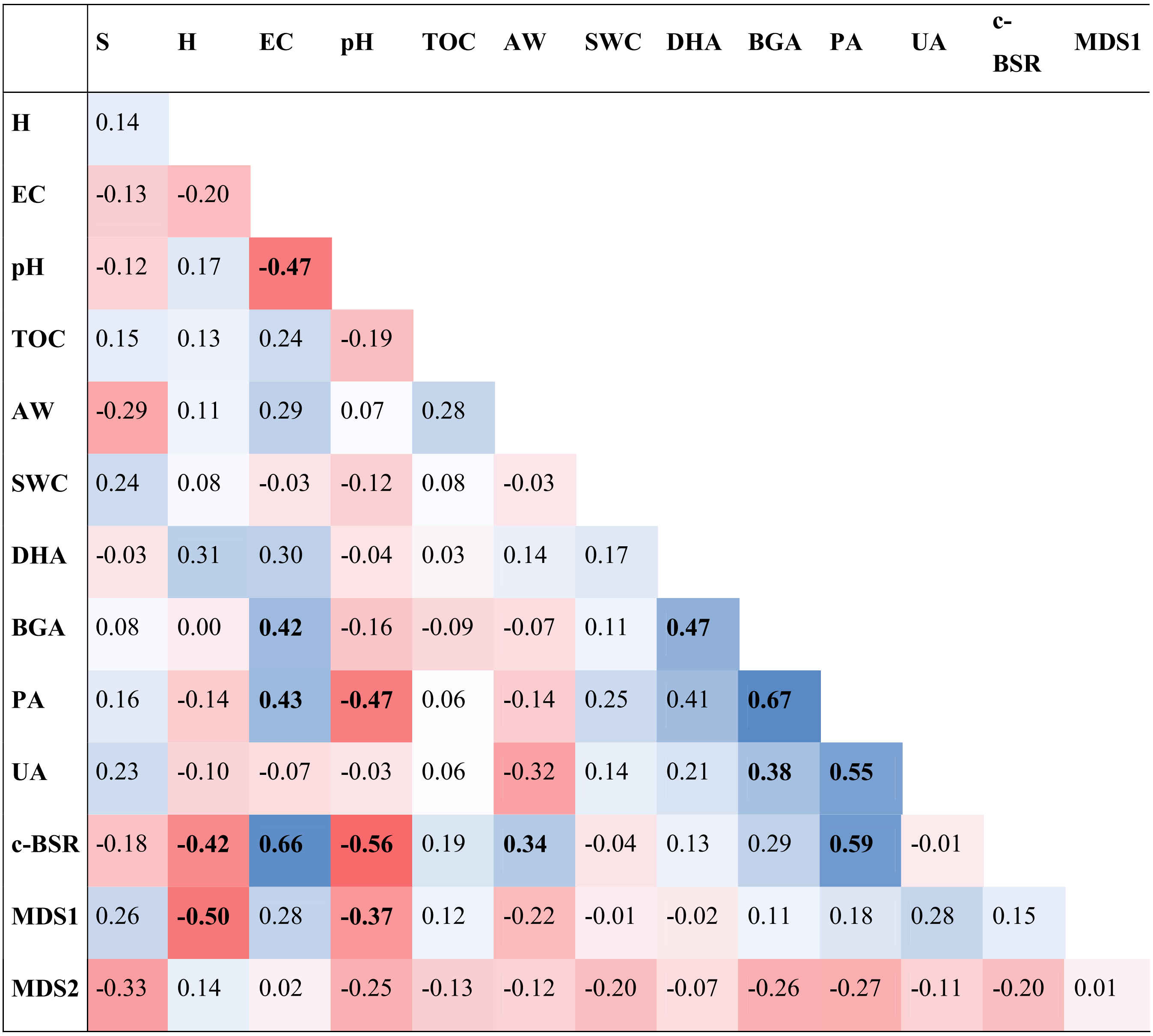


Figure 7 - Biplots of dbRDA (distance-based Redundance Analysis) applied to soil properties sampled in forests with different stand age (mature, middle, young), soil condition (with or without treatment) and aspect (south or north) in the study area (Vall d'Ebo, Comunidad Valenciana, Spain). Legend: EC = electrical conductivity; TOC = total organic carbon; AW = available water; FC = field capacity; WP = wilting point; SWC = soil water content; BGA = β-glucosidase activity; DHA = dehydrogenase activity; PA = alkaline phosphatase activity; UA = urease activity; d-BSR = daily basal soil respiration; c-BSR = cumulative basal soil respiration)

The Spearman's correlation analysis generally showed low correlations between soil properties and plant diversity with some exceptions. In more detail, among the soil properties, some enzymatic activities were correlated each to other with positive Spearman's coefficients (e.g., BGA with DHA, PA and UA, and PA and UA) as well as EC with pH (negative correlation), BGA and PA (positive correlations). Moreover, c-BSR was significantly correlated with several other soil properties, such as EC, pH, AW and PA. Among the parameters related to plant diversity, significant correlations were only detected between MDS1 and H (-0.50). Finally, no reciprocal associations between soil properties on one side, and plant diversity were revealed by the correlation analysis, except between

H and c-BSR (-0.42) and pH and MDS1 (-0.37), while MDS2 were never correlated to other variables (Figure 8).



	S	H	EC	pH	TOC	AW	SWC	DHA	BGA	PA	UA	c-BSR	MDS1
H	0.14												
EC	-0.13	-0.20											
pH	-0.12	0.17	**-0.47**										
TOC	0.15	0.13	0.24	-0.19									
AW	-0.29	0.11	0.29	0.07	0.28								
SWC	0.24	0.08	-0.03	-0.12	0.08	-0.03							
DHA	-0.03	0.31	0.30	-0.04	0.03	0.14	0.17						
BGA	0.08	0.00	**0.42**	-0.16	-0.09	-0.07	0.11	**0.47**					
PA	0.16	-0.14	**0.43**	**-0.47**	0.06	-0.14	0.25	0.41	**0.67**				
UA	0.23	-0.10	-0.07	-0.03	0.06	-0.32	0.14	0.21	**0.38**	**0.55**			
c-BSR	-0.18	**-0.42**	**0.66**	**-0.56**	0.19	**0.34**	-0.04	0.13	0.29	**0.59**	-0.01		
MDS1	0.26	**-0.50**	0.28	**-0.37**	0.12	-0.22	-0.01	-0.02	0.11	0.18	0.28	0.15	
MDS2	-0.33	0.14	0.02	-0.25	-0.13	-0.12	-0.20	-0.07	-0.26	-0.27	-0.11	-0.20	0.01

Figure 8 - Spearman correlation heatmap reporting the correlation coefficients between including the correlation coefficients between soil properties (EC, pH, TOC, AW, SWC, DHA, BGA, PA, UA, c-BSR and d-BSR) and plant diversity (S, H, MDS 1 and 2, the latter being the axes of the multidimensional scaling analyses of plant diversity). Significant coefficients ($p < 0.05$) are shown in bold. Legend: S = species richness; H = Shannon's index; EC = electrical conductivity; TOC = total organic carbon; AW = available water; SWC = soil water content; BGA = β-glucosidase activity; DHA = dehydrogenase activity; PA = alkaline phosphatase activity; UA = urease activity; d-BSR = daily basal soil respiration; c-BSR = cumulative basal soil respiration)

4. DISCUSSIONS

4.1 Variability of plant cover and diversity

In this study, the presence/absence of pre-fire treatments did not generally affect plant diversity and soil properties. However, stand age and aspect turned out to be important factors. When we look separately at stand age, the latter only influenced the life forms, with alterations in the distribution of geophytes and herbaceous chamaephytes, these were generally more abundant in mid-age stands. The combined effect of stand age and slope aspect significantly affected the regeneration mechanism. This can be observed in the significantly lower abundance of germinating species in mature stands compared to both young and mid-age stands. This can be caused by the loss seed viability with time. On the other hand, there is a lower abundance of resprouters in young stands compared to stands with middle age. In both cases, the hillslopes were exposed to south. In this case, plant succession processes may be delayed or hampered due to increased aridity conditions.

As for ground cover, the richness and evenness were not affected by stand age, presence of treatments, and hillslope aspect. This may be due to the high number of species surveyed in all different plots, which did not evidence a prevalence of some species over others. Among all species, a prevalence of *Brachypodium retusum, Cistus albidus,* and *Ulex parviflorus* was observed, although these species did not affect the overall distribution of all vegetal complexes among the different stands. The noticeable presence of *Pinus halepensis* in stands with younger age may be due to the fact that the percentage of pine cones that remain thanks to serotiny varies with age. On the other hand, it is worrying that the regeneration of *Pinus halepensis* showed such low values, probably due to the low precipitation that has characterized the climate in the 12 months after the fire (Ne'eman et al., 2004; Osem et al., 2013). In this regard, Capitanio and Carcaillet (2008) found low recruitment of Aleppo pine – in spite of the high adaptation capacity of this species to fire (Fournier et al., 2013) - in the first year after a wildfire, while 70% and 100% recruitments were observed one and three years after. Lucas-Borja et al. (2017) observed a lower early recruitment of *Pinus sylvestris* compared to *Pinus nigra* in the same environment of this study, while Thanos et al. (1996) reported a progressively declining regeneration of *Pinus halepensis* in the period from few months to three years after a wildfire in Greek mountains. Different factors such as microclimate, seed rain, or seed predation may influence post-fire recruitment (Calama et al., 2017). The finding of the present study indicates the need for monitoring of the future regeneration, which should be supported by proper techniques (e.g., biomass reduction, pruning of tree canopies, prescribed fire), but caring for a limited development of shrub cover, which may lead to more flammable and pyrophytic formations (De Luis et al., 2004; Alloza et al., 2006; Pausas and Moreira, 2012).

The scientific literature has widely demonstrated that Mediterranean species are able to regenerate after wildfire through different post-fire strategies, including resprouting, serotiny, soil seed banks or wind seed dispersion into a fire-affected site (e.g., Arnan et al., 2007; Enríquez-de-Salamanca, 2023; Rodrigues et al., 2024). Moreover, it is worth mentioning other circumstances, such as the land use prior to the wildfire event, to properly understand plant species composition in the study area. The presence of *Euphorbia segetalis* and *Avena sterilis* in middle-age stands may be due to three reasons: (i) the existence of old crop fields nestled in the mountains, with a seed bank very close to the forest area (which, however, requires further investigation, since there is no evident correlation between seedling emergence from seed banks from burial experiments (Saatkamp et al., 2009); (ii) crushing and incorporating of forest residues into the soil from silvicultural treatments; and (iii) the amount of ashes left by fire, which act as fertilizers (Zavala et al., 2009; Pereira et al., 2018).

It is worth mentioning that the low ground cover of the plant species surveyed that emerged the first year after the fire (approximately 27%) is not expected to play an important role in mitigating the possible water erosion from the burned soil (Shakesby, 2011; Moody et al., 2013). Therefore, post-fire management actions targeted at reducing the effects of erosivity of post-fire rainstorms are suggested, in order to avoid the off-site effects of vegetation removal (Lucas-Borja, 2021; Zema, 2021).

4.2 Variability of soil properties

In this study, neither the stand age nor the soil condition (treated or not) or aspect influenced almost all the soil physical-chemical and biochemical properties. Only pH significantly varied between stands, and this different significance may derive from the selective uptake of acids by trees and shrubs of different age (Elliott et al., 2013; Zavala et al., 2014). In this case, the well-known buffering capacity of soil against the pH variations was overcome by this process (Carra et al., 2021), which generates the aforementioned changes in this parameter. Since the wildfire is severe and homogenous in the studies sites, and the organic matter content of soil is not significantly different among the soil conditions, the variability in EC was not noticeable. The small differences in EC among the different sites should be due to the inconsistency of the quality and amount of ash - an important key driver for content of minerals and ions in burned soils - released by a so severe wildfire (Zavala et al., 2014; Prats et al., 2018).. In contrast, no similar effects on TOC and in those physical properties that are strictly associated with changes in organic matter (soil water repellency, aggregate stability, porosity (Doerr et al., 2000; Mataix-Solera et al., 2002; Agbeshie et al., 2022) were as evident as for pH, although both the pre-fire treatments and the soil aspect may have influenced the OM content (Certini et al., 2011; Barančíková et al., 2018). The general lack of influence of hillslope aspect should be due to presence of a stony ground on the experimental soils, which balanced the changes in soil properties and the subsequent response of vegetal complexes other than expected. What might be surprising at first sight is the similar values of SWC among sites of different aspect. However this may be justified by the severity of wildfire, which should have fully dried and compacted the soil, due to the high temperatures while burning (de Jonge et al., 1999; Pereira et al., 2018; Carrión-Paladines et al., 2022) as well as to shrinkage of soil macropores with reduction in porosity (Mirzaei et al., 2023).

Among the enzymatic activities and other biological properties of soil, only BGA showed a significant variability between the same stands, presumably due to the different digestion rate of cellulose due to microorganisms recovering after the wildfire, which could be different among the different stand ages and aspects (Carletti et al., 2009; Lucas-Borja et al., 2016; Walkiewicz et al., 2021). The other enzymatic activities and BSR were not affected by different variations of stand age, pre-fire treatment and aspect. An explanation could be the low levels of enzymatic activities due to the extreme damage to microbial communities determined by the high burning temperatures (Mataix-Solera et al., 2009; Rodríguez et al., 2017). The low changes in plant cover and diversity as well as in soil properties may be the main reason of the low accuracy of the dbRDA model to reproduce their variability among sites with different pre-fire characteristics. Finally, it is worthy to mention that the selection of plots burned at high severity may have homogenised wildfire impacts not allowing differences among studied factors (stand age, pre-fire forest management and slope).

4.3 Associations between plant diversity and soil properties

The negative correlation between H and c-BSR demonstrated by the correlation analysis (Figure 8) indicates a dominance of few species over the background vegetation with increasing soil basal respiration. This result is quite surprising, since a higher biochemical activity should support growth of most species. Presumably, some adverse factors other than soil basal respiration may significantly disturb the weakest species, such as BGA or pH. In overall, the relationships between plant and soil were weak, as demonstrated by the low or lack of influence of soil variables on MDS1 and MDS2 (Figure 8).

These results contrast with other studies about associations between plants and soils after burning and post-fire treatments in Mediterranean forests. For instance, Lucas-Borja et al. (2021) found significant relations between ecosystem multifunctionality and plant community species in the same environment, suggesting that fire-related changes in plant diversity can alter many forest functions. Furthermore, Gómez-Sánchez et al. (2023), again in Mediterranean severely-burned and treated forests and in the mid-term after fire, showed more resprouting species in treated sites (due to higher contents of organic matter and nitrogen compared to untreated soils) and more abundant tree and herbaceous species resulting from decreases in pH and increases in organic matter. However, the fire severity of those studies was lower and the treatment intensity (log erosion barriers and contour felled log debris) was more impacting on the ecosystem, which may justify these contrasts compared to our investigation.

The low number of associations between parameters that are related to plant diversity on one side, and soil properties on the other side shown by our study reveals that the three factors (stand age, pre-fire treatments, and hillslope aspect) played a limited role on relationships between plants and soils, and this further confirms the high influence of severe wildfires on post-fire recovery of the forest ecosystem. This is an important result, which shows the low resilience of vegetation and soil to an extreme disturbance such as wildfire, despite treatments and other natural drivers, such as stand maturity and north aspect under semi-arid Mediterranean conditions. Other authors have showed that important role of fire severity and post-fire management on both plant diversity and soil properties. For instance, Gómez-Sánchez et al. (2023) reported that increases in OM, N, and pH are associated with clear differences in the regeneration mechanisms as well as layer composition in sites treated with post-fire management techniques. Fires with different severity are associated to variable landscape-level biodiversity by increasing species turnover across landscapes with a diverse mosaic of habitats (Burkle et al., 2015). Fireseverity has a significant influence on soil status, and the microbiological properties show a particular sensitivity to fire characteristics (Fernández-García et al., 2019). Post-fire management play important impacts also on soil properties, and manual operations have less detrimental impacts compared to machinery (Francos et al., 2018).

4.4 Practical implications and limitations of the study

This study suggests some practical implications that may support a quicker regeneration of vegetation as well as recovery of the pre-fire soil characteristics. First of all, the high percentage of resprouting species (approximately 80%) and the large number of different pioneer species in the first year of regeneration ensure a good response in post-fire regeneration of the Mediterranean forests (e.g., Santana et al., 2012; Méndez et al., 2015; Castro, 2021). Fire is also important for supporting highly diversified fire-dependent plant communities, and its suppression may reduce diversity in Mediterranean forests (Fournier et al., 2020). Second, the pre-fire forest management practices do not negatively interfere with the ecosystem regeneration (as also demonstrated by Capitanio and Carcaillet, 2008), as the soil physico-chemical properties, enzymatic activities, and post-fire vegetation cover and diversity are not altered. Third, and finally, the implementation of silvicultural techniques should be taken into account when aiming to reduce the damage due to future wildfires and to accelerate vegetation and soil properties recovery after wildfire events (e.g., selection of tree species with serotiny mechanisms, which may ensure seed bank for post-fire regrowth of vegetation).

Given the impacts of hillslope aspect on plant regeneration, when reforestation with tree species is necessary to accelerate the recovery of forest ecosystem functions, it is essential to take into account the effect of microclimate, selecting species originating from warmer or drier places (Resco de Dios et al., 2007) and adopting the so-called "assisted migration" process (McLachlan et al., 2007). This process has emerged as a promising forestry strategy to mitigate the impacts of climate change (Xu and Prescott, 2024). As a matter of fact, translocating more conservative species in cooler climates may decrease the buffering capacity of forest canopies and facilitation for understory species as well as increase the wildfire risks with consequent acceleration of climate warming through negative atmospheric feedback (Michalet et al., 2023). This contrasts with the traditional approach that suggested planting based on the suitability of species to thrive under past climatic conditions.

A possible limitation of the study is the short monitoring time, which, if it captures the sudden changes in vegetation characteristics, does not allow for a clear understanding of ecosystem dynamics some years after the wildfire, and the time of complete recovery to its pre-fire conditions. Indeed, a short-term monitoring of vegetation recruitment after severe wildfires is less meaningful compared to long-term chronosequences (Fournier et al., 2020) or succession modelling (Retana et al., 2002). Therefore, a long-term monitoring of the trajectory of the burned ecosystem is necessary, since many species that appeared in the first year after the disturbance may disappear in a short time (Fournier et al., 2020). On the contrary, coverage of species that now seem insignificant may take a very important role in the future ecosystem.

5. CONCLUSIONS

In contrast to the working hypothesis, this study has shown that forest stand age, presence of pre-fire treatments and hillslope aspect played a small influence on vegetation cover regeneration, plant diversity, and physico-chemical and biochemical properties of soil in pine forests of Castilla La Mancha (Central Eastern Spain) affected by a severe fire. In general, the damage to soil and vegetation was so high that both vegetation and pre-fire soil properties slowly recovered. These recovery rates were very similar in young to old stands regardless of the presence of pre-fire treatments and soil aspect. Regarding the plant cover, only a few life forms of vegetation were influenced by the pre-fire stand age (geophytes and herbaceous chamaephytes). If combined with soil aspect, stand age significantly affected the regeneration mechanism, resulting in lower germinating species in mature stands and lower resprouters in young stands, both cases on hillslopes exposed to south. The plant diversity at the experimental sites was very high, and the post-fire regeneration did not change the species richness and evenness. Due to the very high temperatures after the uniform burn severity, no significant changes in the physico-chemical and biochemical properties of soil were detected among the burned sites under different conditions, except for some small differences in pH and betaglucosidase among stands of different age. The low variance in plant cover and diversity as well as in soil properties resulted in a low accuracy of the dbRDA model to reproduce its variability among sites with different pre-fire characteristics.
Overall, this study contributes to better understand how plant and soil dynamics change in burned Mediterranean environments, which is a matter of primary interest for forest managers, especially in the Mediterranean ecosystems. This knowledge will reduce ecosystem degradation and preserve its health in changing fire and climate contexts.

NOMENCLATURE

SR = species richness
H = Shannon index
Ther. = Therophytes
Hemicr. = Hemicryptophytes
Geo. = Geophytes
Phan. = Phanerophytes
W. Cham. = Woody Chamaephytes

H. Cham. = Herbaceous Chamaephytes
EC = electrical conductivity
TOC = total organic carbon
AW = available water
FC = field capacity
WP = wilting point
SWC = soil water content
BGA = β-glucosidase activity
DHA = dehydrogenase activity
PA = alkaline phosphatase activity
UA = urease activity
d-BSR = daily basal soil respiration
c-BSR = cumulative basal soil respiration
distLM = distance-based linear modelling
dbRDA = distance-based redundancy analysis

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COMPETING INTERESTS

The authors have no relevant financial or non-financial interests to disclose.

DATA AVAILABILITY

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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SUPPLEMENTARY INFORMATION

Table 1.SI - Results of PERMANOVA analysis according to the regeneration strategy of plant species surveyed in the burned forest (Vall d'Ebo, Comunidad Valenciana, Spain). Significant values ($p < 0.05$) are marked in bold.

Factor	**df**	**SS**	**MS**	**Pseudo-F**	**P(perm)**
Resprouters					
Age	2	7267	3633	1.282	0.146
Aspect	1	2913	2913	1.028	0.431
Age (soil condition)	3	4943	1648	0.581	0.989
Age x Aspect	2	7374	3687	1.301	0.121
Age (soil condition) x Aspect	3	9708	3236	1.142	0.237
Residues	24	68026	2834		
Total	35	100230			
Seeders					
Age	2	4950	2475	1.158	0.297
Aspect	1	2843	2843	1.33	0.22
Age (soil condition)	3	8988	2996	1.402	0.115
Age x Aspect	2	7536	3768	1.763	**0.05**
Age (soil condition) x Aspect	3	6299	2070	0.982	0.471
Residues	24	51305	2138		
Total	35	81920			

Notes: df = degrees of freedom; SS = sum of squares; MS = mean sum of squares; Pseudo-F = F value by permutation; P(perm) = permutation test. Bold characters indicate statistical significance ($P < 0.05$).

Table 2.SI - Similarity within/among groups (“Aspect” as factor with levels “North” and “South”) according to the regeneration strategy of plant species surveyed in the burned forest (Vall d’Ebo, Comunidad Valenciana, Spain). The significant values (p < 0.059 are marked in red). Significant values are marked in bold.

<table>
<tr><td colspan="9">Resprouters</td></tr>
<tr><td rowspan="2">Group</td><td colspan="4">North plots</td><td colspan="4">South plots</td></tr>
<tr><td colspan="2">t</td><td colspan="2">P(perm)</td><td colspan="2">t</td><td colspan="2">P(perm)</td></tr>
<tr><td>Mature vs. Middle</td><td colspan="2">1.133</td><td colspan="2">0.252</td><td colspan="2">1.332</td><td colspan="2">0.069</td></tr>
<tr><td>Mature vs. Young</td><td colspan="2">0.991</td><td colspan="2">0.434</td><td colspan="2">1.024</td><td colspan="2">0.461</td></tr>
<tr><td>Middle vs. Young</td><td colspan="2">0.800</td><td colspan="2">0.748</td><td colspan="2">1.517</td><td colspan="2">0.040</td></tr>
<tr><td rowspan="5"></td><td colspan="8"><i>Average similarity between/within groups</i></td></tr>
<tr><td></td><td>Mature</td><td>Middle</td><td>Young</td><td></td><td>Mature</td><td>Middle</td><td>Young</td></tr>
<tr><td>Mature</td><td>23.688</td><td></td><td></td><td>Mature</td><td>22.817</td><td></td><td></td></tr>
<tr><td>Middle</td><td>26.239</td><td>32.551</td><td></td><td>Middle</td><td>29.139</td><td>46.593</td><td></td></tr>
<tr><td>Young</td><td>23.460</td><td>29.546</td><td>23.858</td><td>Young</td><td>18.839</td><td>22.544</td><td>15.013</td></tr>
<tr><td colspan="9">Seeders</td></tr>
<tr><td rowspan="2">Group</td><td colspan="4">North plots</td><td colspan="4">South plots</td></tr>
<tr><td colspan="2">t</td><td colspan="2">P(perm)</td><td colspan="2">t</td><td colspan="2">P(perm)</td></tr>
<tr><td>Mature vs. Middle</td><td colspan="2">0.913</td><td colspan="2">0.514</td><td colspan="2">1.586</td><td colspan="2">0.049</td></tr>
<tr><td>Mature vs. Young</td><td colspan="2">1.144</td><td colspan="2">0.222</td><td colspan="2">1.351</td><td colspan="2">0.037</td></tr>
<tr><td>Middle vs. Young</td><td colspan="2">1.073</td><td colspan="2">0.356</td><td colspan="2">1.063</td><td colspan="2">0.337</td></tr>
<tr><td></td><td colspan="8"><i>Average similarity between/within groups</i></td></tr>
</table>

		Mature	Middle	Young		Mature	Middle	Young
	Mature	23.026			Mature	42.906		
	Middle	37.351	51.416		Middle	23.328	16.83	
	Young	33.725	50.749	49.978	Young	36.203	26.525	36.894

Notes: t = test result; P(perm) = permutation test. Bold characters indicate statistical significance (P < 0.05).

Table 3.SI - Results of PERMANOVA analysis according to the life form of plant species surveyed in the burned forest (Vall d'Ebo, Comunidad Valenciana, Spain).

Factor	**df**	**SS**	**MS**	**Pseudo-F**	**P(perm)**
Therophytes					
Age	2	4.011	2.005	1.128	0.314
Aspect	1	1.906	1.906	1.072	0.377
Age (soil condition)	3	4.411	1.471	0.827	0.745
Age x Aspect	2	4.483	2.241	1.261	0.195
Age (soil condition) x Aspect	3	4.010	1.337	0.752	0.83
Residues	24	42.667	1.778		
Total	35	61.487			
Hemicryptophytes					
Age	2	5.300	2.650	1.101	0.342
Aspect	1	2.135	2.135	0.887	0.536
Age (soil condition)	3	5.156	1.719	0.714	0.865
Age x Aspect	2	3.356	1.678	0.697	0.863
Age (soil condition) x Aspect	3	8.801	2.934	1.219	0.202
Residues	24	57.771	2.407		
Total	35	82.519			
Geophytes					
Age	2	1.122	0.561	2.373	**0.04**
Aspect	1	0.125	0.125	0.530	0.63
Age (soil condition)	3	0.908	0.303	1.280	0.273
Age x Aspect	2	0.943	0.471	1.994	0.081
Age (soil condition) x Aspect	3	0.908	0.303	1.280	0.286
Residues	24	5.674	0.236		
Total	35	9.6798			
Phanerophytes					
Age	2	3.626	1.813	1.157	0.267
Aspect	1	2.728	2.728	1.741	0.054
Age (soil condition)	3	6.748	2.250	1.435	0.062

Age x Aspect	2	5.129	2.565	1.636	**0.046**
Age (soil condition) x Aspect	3	6.208	2.069	1.321	0.09
Residues	24	37.612	1.567		
Total	35	62.051			
Woody Chamaephytes					
Age	2	1.2304	0.61521	0.51506	0.901
Aspect	1	0.7865	0.7865	0.65847	0.679
Age (soil condition)	3	2.803	0.93432	0.78222	0.689
Age x Aspect	2	0.96771	0.48386	0.40509	0.975
Age (soil condition) x Aspect	3	3.2256	1.0752	0.90017	0.547
Residues	24	28.667	1.1944		
Total	35	37.68			
Herbaceous Chamaephytes					
Age	2	26.573	13.287	4.045	**0.031**
Aspect	1	3.172	3.172	0.966	0.322
Age (soil condition)	3	1.690	0.563	0.172	0.987
Age x Aspect	2	18.326	9.163	2.79	**0.073**
Age (soil condition) x Aspect	3	4.841	1.614	0.491	0.766
Residues	24	78.831	3.285		
Total	35	133.43			

Notes: df = degrees of freedom; SS = sum of squares; MS = mean sum of squares; Pseudo-F = F value by permutation; P(perm) = permutation test. Bold characters indicate statistical significance ($P < 0.05$).

Table 4.SI - Similarity within/among groups ("Aspect" as factor with levels "North" and "South") according to the life form of plant species surveyed in the burned forest (Vall d'Ebo, Comunidad Valenciana, Spain). Significant values (p < 0.059 are marked in red). Significant values are marked in bold.

Therophytes

Group	North plots		South plots	
	t	P(perm)	t	P(perm)
Mature vs. Middle	1.024	0.512	1.237	0.138
Mature vs. Young	1.048	0.484	1.231	0.188
Middle vs. Young	1.245	0.164	0.909	0.597

Average Similarity between/within groups

	Mature	Middle	Young		Mature	Middle	Young
Mature	2.248			Mature	1.295		
Middle	1.721	1.168		Middle	1.583	1.782	
Young	1.794	1.248	1.260	Young	1.893	2.008	2.326

Hemicryptophytes

	North plots		South plots	
	t	P(perm)	t	P(perm)
Mature vs. Middle	0.889	0.653	0.890	0.669
Mature vs. Young	1.116	0.381	0.797	0.840
Middle vs. Young	1.064	0.361	0.840	0.756

Average similarity between/within groups

		Mature	Middle	Young		Mature	Middle	Young
	Mature	2.897			Mature	1.942		
	Middle	2.415	1.950		Middle	1.893	1.914	
	Young	2.390	1.834	1.660	Young	0.847	1.856	1.844
Geophytes								
	North plots				South plots			
	t		P(perm)		t		P(perm)	
Mature vs. Middle	1.414		0.211		1.527		0.128	
Mature vs. Young	1.291		0.299		1.001		0.648	
Middle vs. Young	1.291		0.314		1.607		0.108	
	Average similarity between/within groups							
		Mature	Middle	Young		Mature	Middle	Young
	Mature	0.369			Mature	0.435		
	Middle	0.416	0.369		Middle	0.828	1.122	
	Young	0.324	0.324	0.230	Young	0.231	0.679	0.001
Phanerophytes								
	North plots				South plots			
	t		P(perm)		t		P(perm)	
Mature vs. Middle	1.301		0.078		1.013		0.415	
Mature vs. Young	1.324		**0.049**		1.312		0.1	
Middle vs. Young	0.807		0.806		1.189		0.215	
	Average similarity between/within groups							

	Mature	Middle	Young		Mature	Middle	Young
Mature	2.421			Mature	1.882		
Middle	2.082	1.472		Middle	1.834	1.780	
Young	2.196	1.502	1.674	Young	1.667	1.590	1.252

Woody Chamaephytes

	North plots		South plots	
	t	P(perm)	t	P(perm)
Mature vs. Middle	0.516	0.885	0.816	0.785
Mature vs. Young	0.516	0.910	0.881	0.664
Middle vs. Young	0.534	0.913	0.612	0.836

Average similarity between/within groups

	Mature	Middle	Young		Mature	Middle	Young
Mature	1.192			Mature	1.497		
Middle	1.093	1.222		Middle	1.233	0.949	
Young	1.135	1.153	1.292	Young	1.481	1.106	1.470

Herbaceous Chamaephytes

	North plots		South plots	
	t	P(perm)	t	P(perm)
Mature vs. Middle	0.484	0.808	3.980	**0.006**
Mature vs. Young	0.451	0.795	0.505	0.730
Middle vs. Young	0.558	0.662	3.156	**0.020**

Average Similarity between/within groups

		Mature	Middle	Young		Mature	Middle	Young
	Mature	2.532			Mature	1.822		
	Middle	2.021	1.630		Middle	3.237	1.413	
	Young	2.188	1.837	2.206	Young	2.180	3.701	2.728

Notes: t = test result; P(perm) = permutation test. Bold characters indicate statistical significance ($P < 0.05$).

Table 5.SI - Results of PERMANOVA analysis of diversity indexes of plants surveyed in the burned forest (Vall d'Ebo, Comunidad Valenciana, Spain). The significant values ($p < 0.05$) are marked in red.

Factor	**df**	**SS**	**MS**	**Pseudo-F**	**P(perm)**
Species richness					
Age	2	360.730	180.370	1.986	0.15
Aspect	1	196.290	196.290	2.161	0.117
Age (soil condition)	3	171.920	57.307	0.631	0.6
Age x Aspect	2	238.500	119.250	1.313	0.276
Age (soil condition) x Aspect	3	555.860	185.290	2.04	0.145
Residues	24	2179.900	90.828		
Total	35	3703.200			
Shannon index					
Age	2	316.670	158.340	1.626	0.197
Aspect	1	288.190	288.190	2.959	0.073
Age (soil condition)	3	172.320	57.440	0.590	0.69
Age x Aspect	2	127.100	63.552	0.653	0.574
Age (soil condition) x Aspect	3	526.740	175.580	1.803	0.143
Residues	24	2337.600	97.400		
Total	35	3768.600			

Notes: df = degrees of freedom; SS = sum of squares; MS = mean sum of squares; Pseudo-F = F value by permutation; P(perm) = permutation test. Bold characters indicate statistical significance ($P < 0.05$).

Table 6.SI - Similarity within/among groups (“Aspect” as factor with levels “north” and “south”) of diversity indexes of plants surveyed in the burned forest (Vall d’Ebo, Comunidad Valenciana, Spain). Significant values (p < 0.059 are marked in red). Significant values are marked in red.

Group	**North plots**		**South plots**	
	t	P(perm)	t	P(perm)
Mature vs. Middle	1.093	0.285	1.510	0.028
Mature vs. Young	1.113	0.206	1.089	0.251
Middle vs. Young	0.863	0.734	1.524	**0.013**

	Average similarity between/within groups							
		Mature	Middle	Young		Mature	Middle	Young
	Mature	23.309			Mature	29.350		
	Middle	29.407	38.920		Middle	27.603	39.019	
	Young	26.381	37.080	33.449	Young	25.489	24.375	23.793

Notes: t = test result; P(perm) = permutation test. Bold characters indicate statistical significance (P < 0.05).

Table 7.SI - Species contribution to similarity within groups of all plant species surveyed in the burned forest (Vall d'Ebo, Comunidad Valenciana, Spain). The significant values ($p < 0.059$ are marked in red). Significant values are marked in red.

Species	**Average abundance**	**Average similarity**	**Contribution (%)**	**Cumulated value (%)**
Group Adult/Treated/North				
Average similarity: 21.20				
Brachypodium retusum	3.12	10.35	48.79	48.79
Mercurialis tomentosa	1.22	2.05	9.67	58.46
Rhamnus alaternus	0.67	1.84	8.67	67.14
Scorzonera graminifolia	0.67	1.84	8.67	75.81
Sonchus oleraceus	0.67	1.84	8.67	84.49
Ulex parviflorus	0.67	1.84	8.67	93.16
Group Adult/Treated/South				
Average similarity: 27.55				
Brachypodium retusum	2.45	10.73	38.96	38.96
Cistus albidus	1.38	9.03	32.78	71.74
Rosmarinus officinalis	0.67	2.67	9.69	81.43
Ulex parviflorus	0.67	2.67	9.69	91.12
Group Adult/Untreated/North				
Average similarity: 26.78				
Cistus albidus	1.47	5.16	19.27	19.27
Brachypodium retusum	2.47	5.11	19.08	38.35
Ulex parviflorus	1.24	4.55	16.98	55.33
Erica multiflora	0.91	1.7	6.35	61.68
Asparagus acutifolius	0.67	1.48	5.54	67.22
Brachypodium phoenicoides	2.52	1.48	5.54	72.76
Clematis flamula	0.67	1.48	5.54	78.3
Daphne gnidium	0.67	1.48	5.54	83.84
Pistacia lentiscus	0.67	1.48	5.54	89.38
Rubus ulmifolius	0.8	1.48	5.54	94.92
Group Adult/Untreated/South				

Average similarity: 28.84				
Brachypodium retusum	2.26	11.42	39.62	39.62
Cistus albidus	1.24	6.6	22.87	62.49
Ulex parviflorus	1	6.6	22.87	85.37
Lotus scorpiurus	0.67	2.26	7.85	93.21
Group Middle/Treated/North				
Average similarity: 23.70				
Brachypodium retusum	2.59	13.37	56.42	56.42
Ulex parviflorus	1.14	6.3	26.6	83.02
Cistus albidus	0.8	2.32	9.79	92.81
Group Middle/Treated/South				
Average similarity: 50.00				
Brachypodium retusum	5.91	29.42	58.84	58.84
Avena sterilis	1	5.75	11.5	70.34
Crepis foetida	0.67	2.01	4.02	74.36
Leuzea conifera	0.67	2.01	4.02	78.38
Mercurialis tomentosa	1.08	1.97	3.94	82.32
Allium roseum	1.33	1.77	3.54	85.86
Asphodelus cerasiferus	0.67	1.77	3.54	89.39
Eryngium campestre	0.67	1.77	3.54	92.93
Group Middle/Untreated/North				
Average similarity: 46.10				
Brachypodium retusum	3.31	18.39	39.88	39.88
Cistus albidus	1.61	11.56	25.09	64.97
Ulex parviflorus	1.14	8.18	17.74	82.71
Scorzonera graminifolia	0.8	3.06	6.65	89.35
Euphorbia isatidifolia	0.67	2.45	5.32	94.68
Group Middle/Untreated/South				
Average similarity: 32.83				
Brachypodium retusum	5.02	26.84	81.76	81.76
Cistus albidus	1	2	6.08	87.84
Rhamnus alaternus	0.67	2	6.08	93.92
Group Young/Treated/North				

Average similarity: 28.83				
Brachypodium retusum	3.01	12.88	44.68	44.68
Ulex parviflorus	1.24	6.21	21.55	66.23
Cistus albidus	1.05	2.49	8.63	74.86
Pinus halepensis	0.67	1.97	6.83	81.69
Eryngium campestre	0.67	1.76	6.1	87.79
Silene mellifera	0.67	1.76	6.1	93.9
Group Young/Treated/South				
Average similarity: 19.58				
Ulex parviflorus	1	10.49	53.6	53.6
Daphne gnidium	0.67	5	25.54	79.14
Brachypodium retusum	1.76	4.08	20.86	100
Group Young/Untreated/North				
Average similarity: 33.53				
Cistus albidus	1.52	11.67	34.8	34.8
Ulex parviflorus	1.14	8.25	24.61	59.41
Brachypodium retusum	1.95	5.39	16.08	75.49
Pinus halepensis	0.67	3.11	9.28	84.78
Conyza bonariensis	0.67	2.55	7.61	92.39
Group Young/Untreated/South				
Average similarity: 27.35				
Ulex parviflorus	1.28	7.86	28.75	28.75
Cistus albidus	1	6.56	23.99	52.74
Brachypodium retusum	2.41	3.36	12.29	65.02
Thapsia villosa	0.67	3.14	11.49	76.51
Euphorbia segetalis	0.8	1.92	7	83.52
Convolvulus althaeoides	0.67	1.5	5.49	89.01
Euphorbia isatidifolia	0.67	1.5	5.49	94.51

Table 8.SI - Results of PERMANOVA applied to the main physico-chemical properties of soils sampled in forests with different stand age (mature, middle, young), soil condition (with or without treatment) and aspect (south or north) in the study area (Vall d'Ebo, Comunidad Valenciana, Spain).

Factor	**df**	**SS**	**MS**	**Pseudo-F**	**P(perm)**
All variables					
Age	2	19.515	9.758	1.367	0.198
Aspect	1	3.314	3.314	0.464	0.785
Age (soil condition)	3	7.480	2.493	0.349	0.980
Age x Aspect	2	9.753	4.876	0.683	0.714
Age (soil condition) x Aspect	3	33.662	11.221	1.572	0.114
Residues	24	171.280	7.137		
Total	35	245.000			
TOC					
Age	2	12.007	6.004	0.568	0.602
Aspect	1	1.003	1.003	0.095	0.767
Age (soil condition)	3	26.355	8.785	0.831	0.469
Age x Aspect	2	49.114	24.557	2.323	0.120
Age (soil condition) x Aspect	3	26.913	8.971	0.849	0.510
Residues	24	253.680	10.570		
Total	35	369.070			
pH					
Age	2	0.198	0.099	4.316	**0.034**
Aspect	1	0.005	0.005	0.204	0.671
Age (soil condition)	3	0.002	0.001	0.036	0.996
Age x Aspect	2	0.007	0.003	0.149	0.870
Age (soil condition) x Aspect	3	0.113	0.038	1.647	0.215
Residues	24	0.549	0.023		
Total	35	0.874			
Available Water					
Age	2	284.880	142.440	0.968	0.380
Aspect	1	15.029	15.029	0.102	0.761
Age (soil condition)	3	87.475	29.158	0.198	0.893

Age x Aspect	2	276.480	138.240	0.939	0.418
Age (soil condition) x Aspect	3	666.250	222.080	1.509	0.236
Residues	24	3532.700	147.200		
Total	35	4862.800			
Wilting Point					
Age	2	197.530	98.765	0.861	0.440
Aspect	1	73.302	73.302	0.639	0.458
Age (soil condition)	3	37.910	12.637	0.110	0.947
Age x Aspect	2	1.660	0.830	0.007	0.996
Age (soil condition) x Aspect	3	124.200	41.402	0.361	0.786
Residues	24	2752.900	114.710		
Total	35	3187.500			
Field Capacity					
Age	2	52.122	26.061	0.152	0.860
Aspect	1	17.153	17.153	0.100	0.754
Age (soil condition)	3	85.412	28.471	0.166	0.922
Age x Aspect	2	303.650	151.820	0.888	0.415
Age (soil condition) x Aspect	3	362.040	120.680	0.706	0.553
Residues	24	4105.300	171.050		
Total	35	4925.700			
Soil Water Content					
Age	2	0.732	0.366	0.139	0.870
Aspect	1	4.681	4.681	1.778	0.200
Age (soil condition)	3	3.560	1.187	0.451	0.712
Age x Aspect	2	0.914	0.457	0.174	0.837
Age (soil condition) x Aspect	3	0.345	0.115	0.044	0.987
Residues	24	63.176	2.632		
Total	35	73.408			
Electrical Conductivity					
Age	2	1222.900	611.450	5.055	0.138
Aspect	1	4.681	4.681	1.778	0.200
Age (soil condition)	3	362.900	120.970	0.115	0.979
Age x Aspect	2	0.914	0.457	0.174	0.837

Age (soil condition) x Aspect	6	6320.700	1053.500	2.206	0.063
Residues	24	11462.000	477.590		
Total	35	19369.000			

Notes: df = degrees of freedom; SS = sum of squares; MS = mean sum of squares; Pseudo-F = F value by permutation; P(perm) = permutation test. Bold characters indicate statistical significance ($P < 0.05$).

Table 9.SI - Results of PERMANOVA applied to the main biochemical properties of soils sampled in forests with different stand age (mature, middle, young), soil condition (with or without treatment) and aspect (South or North) in the study area (Vall d'Ebo, Comunidad Valenciana, Spain). Significant values are marked in bold.

Factor	**df**	**SS**	**MS**	**Pseudo-F**	**P(perm)**
All parameters					
Age	2	31.146	15.573	1.359	0.191
Aspect	1	8.321	8.321	0.726	0.556
Age (soil condition)	3	14.945	4.982	0.435	0.950
Age x Aspect	2	10.478	5.239	0.457	0.915
Age (soil condition) x Aspect	3	45.020	15.007	1.309	0.231
Residues	24	275.090	11.462		
Total	35	385.000			
Dehydrogenase Activity					
Age	2	2.757	1.379	0.720	0.522
Aspect	1	0.679	0.679	0.354	0.589
Age (soil condition)	3	4.650	1.550	0.809	0.555
Age x Aspect	2	0.673	0.336	0.176	0.883
Age (soil condition) x Aspect	3	1.363	0.454	0.237	0.903
Residues	24	45.970	1.915		
Total	35	56.092			
Beta Glucosidase Activity					
Age	2	23.281	11.641	3.434	**0.030**
Aspect	1	1.336	1.336	0.394	0.549
Age (soil condition)	3	1.709	0.570	0.168	0.944
Age x Aspect	2	0.250	0.125	0.037	0.962
Age (soil condition) x Aspect	3	11.463	3.821	1.127	0.390
Residues	24	81.353	3.390		
Total	35	119.390			
Phosphatase Activity					
Age	2	6.537	3.269	0.513	0.629
Aspect	1	13.684	13.684	2.150	0.139

Age (soil condition)	3	7.354	2.451	0.385	0.794
Age x Aspect	2	3.209	1.604	0.252	0.791
Age (soil condition) x Aspect	3	16.810	5.603	0.880	0.492
Residues	24	152.790	6.366		
Total	35	200.380			
Urease Activity					
Age	2	0.724	0.362	0.301	0.826
Aspect	1	0.086	0.086	0.071	0.804
Age (soil condition)	3	3.404	1.135	0.942	0.444
Age x Aspect	2	3.120	1.560	1.296	0.329
Age (soil condition) x Aspect	3	1.640	0.547	0.454	0.796
Residues	24	28.892	1.204		
Total	35	37.865			
Daily Basal Soil Respiration					
Age	2	1906.400	953.220	1.032	0.408
Aspect	1	1533.600	1533.600	1.661	0.196
Age (soil condition)	3	1584.900	528.290	0.572	0.647
Age x Aspect	2	73.864	36.932	0.040	0.972
Age (soil condition) x Aspect	3	4218.600	1406.200	1.523	0.228
Residues	24	22165.000	923.540		
Total	35	31482.000			
Cumulative Basal Soil Respiration					
Age	2	1952200	976100	1.032	0.403
Aspect	1	1570400	1570400	1.661	0.226
Age (soil condition)	3	1622900	540970	0.572	0.666
Age x Aspect	2	75637	37819	0.040	0.978
Age (soil condition) x Aspect	3	4319800	1439900	1.523	0.237
Residues	24	22697000	945700		
Total	35	32238000			

Notes: df = degrees of freedom; SS = sum of squares; MS = mean sum of squares; Pseudo-F = F value by permutation; P(perm) = permutation test. Bold characters indicate statistical significance ($P < 0.05$).