Overstory Effects on the Understory of Aleppo Pine Plantations—Implications for Ecosystem Restoration

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Abstract: At the end of the 19th century and along the first half of the 20th century, public policies in Mediterranean countries and elsewhere in Europe strongly promoted pine afforestation for land reclamation and wood production. In many cases, the transition to native forests, more resilient and more diverse, was also foreseen. This study aims to find the overstory characteristics that are best related to the understory of Aleppo pine (*Pinus halepensis*) plantations, to assist ecosystem restoration goals. We installed 33 circular plots in mature Aleppo pine plantations located in the southeastern Salento peninsula, Apulia, Italy. We measured overstory characteristics and the corresponding understory on these plots. We assessed the effects of overstory variables on understory development (plant density, plant height, and the Magini regeneration index) and diversity (species richness and the Shannon–Wiener index) using linear mixed models (LMM). Understory development and diversity were positively correlated with the Hart–Becking spacing index and negatively correlated with basal area and canopy cover, the three overstory variables that best explained variance. We used polynomial fitting and the subsequent derivation of these functions to determine the values of the Hart–Becking index and of the canopy cover that corresponded to the maximum development (33.7% and 84.6%, respectively) and diversity (32.6% and 86.5%, respectively) of the understory. Redundancy analysis (RDA) showed that late-successional species, including *Quercus coccifera*, were associated with higher levels of understory development and stand spacing. These results may assist in the restoration of native ecosystems in Aleppo pine plantations installed in similar ecological conditions.

Keywords: ecological restoration; overstory variables; forest management; *Pinus halepensis*; plant diversity; understory development

1. Introduction

There has been extensive use of pines and other conifers for land reclamation in sandy soils, mountain areas, and disturbed sites worldwide [1–3]. In the particular case of the Mediterranean Basin, large afforestation campaigns using pines, both for timber production and reclamation, were started in the 19th century and continued along the 20th century [4]. There are examples of such afforestation programs in several Mediterranean countries, including Portugal [5], France [6], Algeria [7] and Spain [8]. In many of these cases, pines were deliberately used as pioneer species to promote soil recovery and facilitate the regeneration of late-successional hardwoods [9], with the intention of driving ecological succession towards native hardwood forests. Some researchers argue that the strategy has had little success in the Mediterranean context because of the costly silvicultural post-plantation operations required, the recurrent fires, and the low dispersal ability of Mediterranean hardwoods [4]. We should also take into consideration that ecological succession is not a linear unidirectional process.

Multiple metastable states, irreversible changes and hysteresis are common in ecosystem dynamics [10], affecting the predictability of restoration results. Other authors argue that pine plantations are not adequate for ecological restoration, because of their impact on soil, flora and fauna, even in the long term [11,12]. However, there are several reported examples of a successful establishment of native broadleaf trees in conifer plantations in Mediterranean countries such as France [6], Israel [3], Italy [13,14] and Spain [15].

The decision to proceed in the ecological succession or, inversely, go back by regularly clearing the understory of a forest plantation depends on the specific goals involved and on the availability of financial resources [16]. This decision should consider the multiple benefits of mature broadleaf forests. Previous works have shown that broadleaf forests may be an effective way of preventing fire propagation by creating a more humid environment [17–19]. In the case of Mediterranean vegetation, the so-called forest understory may become a forest itself, if dominated by woody plants that have the potential to grow into trees. In the Mediterranean environment, species such as *Olea europaea* var. *sylvestris, Arbutus unedo* or *Quercus coccifera*, although often known as shrubs, have indeed the potential of reaching a tree habit, which assures fuel discontinuity between the canopy and the forest floor. A clear advantage of this strategy is its stability, compared to the recurrent disturbance associated with fuel management, because of the quick recovery of the suppressed plant community [20]. Plant invasions are an increasingly important aspect to consider since recurrently disturbed areas are more prone to be colonised by exotic species (e.g., [21]). Finally, there is an increasing body of literature showing that forest restoration is one of the most effective strategies to mitigate climate change [22–24].

However, there are many authors that advocate the opposite strategy, normally based on the principle that understory suppression is the best short-term solution to prevent wildfires in conifer stands, e.g., [25,26]. Several authors have tried to set silvicultural guidelines for fuel management purposes [25,27], based on the principle that closed canopies tend to suppress the understory vegetation, which results in lower fire hazard [28,29]. Following this basic relationship, it is possible to estimate the characteristics of the understory, using overstory variables such as density and dominant height [28]. Fonseca and Duarte [26] have used the Wilson factor (Fw) to determine the optimal spacing to prevent understory development in pine plantations in Portugal. A stand density criterion based on Fw = 0.21 was proposed as the minimum tree cover that ensures enough shading to prevent understory development and, therefore, to reduce fire hazard.

In the context of ecological restoration, it is possible to define the level of canopy closure or tree spacing that facilitates the establishment and development of plant communities in the understory of pine plantations. Although general trends are quite abundant in the available literature, fine-grained studies are still needed to provide forest managers with more detailed information about the effects of forest cover on understory characteristics [27]. In particular, it is important to determine which overstory variables commonly used in forestry (such as basal area and spacing indices) are better related to understory characteristics in order to set guidelines that favour understory development and diversity. This knowledge gap clearly exists in the case of *P. halepensis* forests, for which previous works have confirmed a negative relationship between forest cover and understory development and diversity, e.g., [30,31]. The present study aims to find the overstory characteristics that favour the development and diversity of the understory of *P. halepensis* plantations, with implications on ecosystem restoration. The specific objectives of this work are (a) to find the overstory variables that best explain the development and diversity of the understory in an area afforested with *P. halepensis*; (b) to determine the values of those variables allowing maximum development and diversity of the understory; (c) to assess the influence of overstory variables on the floristic composition of the understory.

2. Materials and Methods

2.1. Study Area

The present study was conducted in a public forest dominated by *Pinus halepensis*, with some scattered Mediterranean cypress (*Cupressus sempervirens* L.). This forest was planted after World War II as part of a reclamation campaign covering around 150 ha of a sandy area in the southeastern part of the Salento peninsula near the Alimini lakes in the Apulia Region, Italy (Figure 1). At the time of the survey, the forest was around 50 years old, with the average tree height reaching 15 m and a diameter of 30 cm (Table 1). The area has a mild Mediterranean climate, with an average rainfall of 781 mm year^{-1} and an average temperature of 16.6 °C. This corresponds to a humid mesothermic climate, according to Köppen's classification. Soils are sandy-clay loams, classified as Vertisols, according to the USDA classification. A detailed description of the study area and its soil and climate can be found in Tartarino et al. [32].
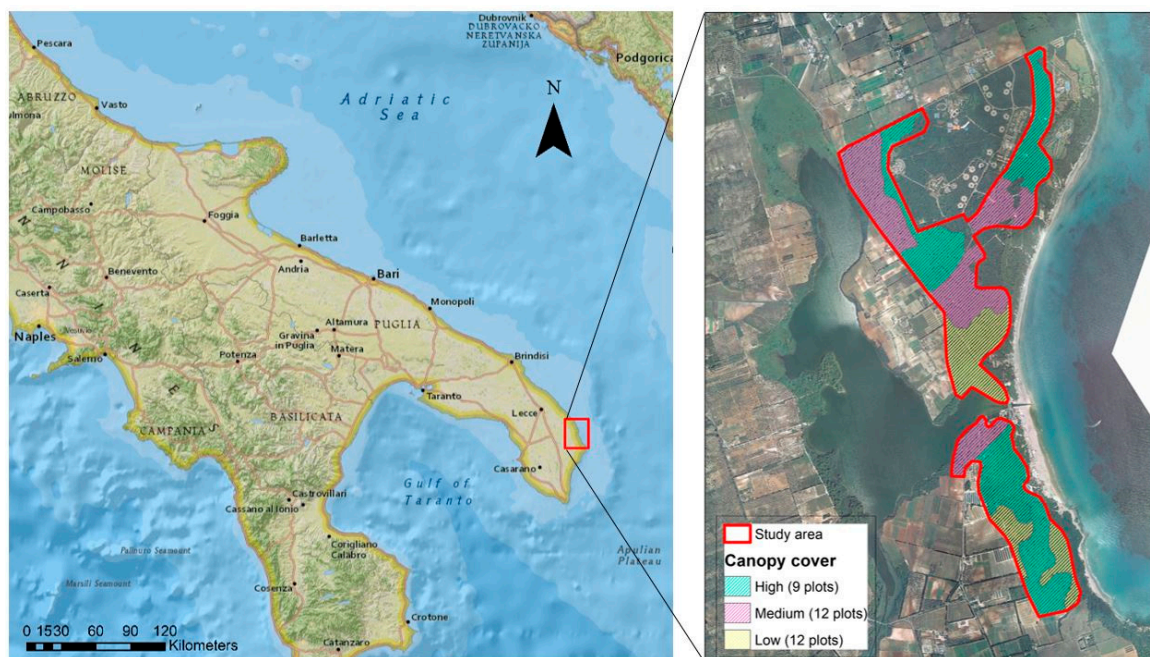
Figure 1. Location of the study area, and plot distribution across three sampling strata, defined according to the predominant canopy cover.

Along their development, these stands were thinned, but these operations were irregularly implemented, which led to different stocking levels of the stands. There are no precise registrations available of the forest interventions in the area that would allow us to locate these interventions in terms of time or space. From local reports, it is known that thinning operations were scattered and sometimes illegal, i.e., not led by the Forest Service. Given the role of these forests for soil reclamation, no intervention was carried out on the understory, so the vegetation has just grown naturally across the years. Differences in stocking levels have allowed the establishment and development of patches of understory vegetation with distinct patterns of composition and development. The understory that emerged beneath the tree canopies corresponds to a typical Mediterranean *maquis* composed mainly by the shrubs/trees: *Quercus coccifera* L., *Phillyrea latifolia* L., *Rhamnus alaternus* L., *Myrtus communis* L., *Olea europaea* L., var. *sylvestris* Brot., *Pistacia lentiscus* L., and *Ruscus aculeatus* L., and the climbers *Lonicera implexa* Aiton and *Smilax aspera* L. These species have been part of the natural ecosystems of this region along the Holocene [33], but *P. halepensis* is also native to the Salento peninsula [34]. However, the origin of current *P. halepensis* stands is mostly artificial, and the role of this species in the former natural forests of this region is uncertain [34]. *Pinus halepensis* depends partly on fire to

regenerate [35], but there are no records of forest fires. This somewhat explains the near absence of pine regeneration in the area.

Table 1. List of 13 overstory variables and five understory variables. Tree density and Average tree distance were not considered for model building but are presented here for additional information about stand and vegetation characteristics.

Variables	Abbreviation	Min.	Max.	Mean ± SD
Overstory				
Tree density (n ha^{-1}) *	Tree Density	297	594	432.8 ± 74.2
Average diameter at breast height (cm)	DBH	26.6	33.9	29.8 ± 1.8
Average tree height (m)	Tree Height	12.2	17.7	15.1 ± 1.3
Dominant height (m)	Hdom	14.1	18.9	16.8 ± 1.2
Average base height green canopy (m)	Canopy Green Height	5.7	10.1	8.2 ± 0.9
Average base height full canopy (m)	Canopy Base Height	2.3	6.5	3.9 ± 1.4
Average length of full canopy (m)	Canopy Length	5.4	8.6	7.0 ± 0.8
Basal area (m^2 ha^{-1})	Basal Area	23.0	37.8	30.0 ± 4.2
Canopy cover (%)	Canopy Cover	82.5	97.1	90.9 ± 36.0
Average taper ratio	Taper Ratio	42.0	61.5	50.7 ± 4.3
Average percent. green canopy	Perc. Green Canopy	19.3	55.7	44.3 ± 5.9
Average tree distance (m) *	Tree Distance	4.1	5.8	4.9 ± 0.4
Hart-Becking index (%)	Hart-Becking	22.5	36.5	29.2 ± 3.5
Understory				
Number of species	Richness	1	12	7.2 ± 2.9
Plant density (plants m^{-2})	Density	1.8	45.3	22.6 ± 11.0
Average plant height (m)	Height	0.1	1.3	0.5 ± 0.2
Magini index	Magini	0.4	28.2	11.8 ± 8.0
Shannon-Wiener index	Shannon	0.07	1.66	1.06 ± 0.39

* Not considered for model building.

2.2. Sampling

Fieldwork took place in 2006, aimed at characterizing the forest stands and the development of the associated understory. With that purpose, we installed 33 circular sampling plots, with a diameter of 30 m, distributed across the study area, trying to evenly cover the whole range of understory developmental stages. This was achieved by estimating in the field the height of the plant community to obtain a balanced distribution of plots for different height classes. This procedure resulted in the following plot distribution by average height class: <30 cm, six plots; 30–39 cm, six plots; 40–49 cm, six plots; 50–59 cm, eight plots; ≥60 cm, seven plots. We did not collect the geographical coordinates of each plot, but an approximate location of the sampling sites allowed us to produce the map shown in Figure 1. This map shows three classes of canopy cover (low, medium, high), obtained by photointerpretation of orthophotos from the Apulia Region dated from 2006, using ArcGIS 10.7.1, (ESRI). We then estimated the approximate number of plots that were established within each patch of canopy cover. Plots were regularly spaced, as much as possible, across the study area and were always away from the edges of the pine stands.

We measured all trees within each plot. Tree measurements included diameter at breast height (using tree callipers), tree height, and base canopy height (using a Blume–Leiss hypsometer). A distinction was made between the base of the green canopy and the base of the full canopy (including dead branches), so two values were registered for base canopy height. The canopy cover of each tree was estimated by measuring four canopy diameters, according to four regularly distributed directions (N–S, E–W, NE–SW, NW–SE). The surface occupied by each canopy (S_i) was calculated as the surface of a circle with a diameter corresponding to the average of four measurements.

We characterised the understory by establishing two perpendicular (N–S and E–W directions) 1.5-m-wide transects within each plot. Each transect was subdivided into 1.5 × 1.5 m subplots, numbered

sequentially from 1 to 20. The understory vegetation was characterized in three randomly chosen subplots, with 2.25 m^2 each. In each subplot, plant individuals were identified at the species/genus level and their height (cm) was measured, therefore allowing us to assess the average plant density (plants m^{-2}).

2.3. Data Analysis

Tree measurements allowed us to compute the 13 overstory variables listed in Table 1 for each sampled plot. The Hart–Becking spacing index is widely used to regulate the intensity of thinning, particularly in coniferous stands planted for timber, similar to the Wilson spacing factor. The Hart–Becking index is computed as Tree Distance/Hdom*100. The Taper Ratio is equal to Tree Height/diameter at breast height (DBH). The Hdom is the mean height of the seven trees with the largest DBH in each plot. Basal Area is the sum of the trunk sectional areas, measured at breast height, per hectare. The Canopy Cover (%) was computed as $\sum S_i/10{,}000$ m$^2 \times 100$, where $\sum S_i$ is the sum of individual canopy covers in one hectare. The Tree Distance was computed in each plot as the square root of the average surface occupied by each tree, based on the number of trees of the plot.

To assess the development of the understory plant community, we calculated three distinct variables for each sampled subplot: Plant Height, Plant Density, and a composite index that includes both these variables, the Magini index [36]. The Magini regeneration index is equal to Plant Height × Plant Density. We adopted two widely used vegetation indices to assess the diversity of the understory plant communities: the Shannon index and the number of species (Richness) found in the subplots. Therefore, we use five variables to describe the understory.

Given that several overstory variables were highly correlated, we did a screening of these variables to detect collinearity and simplify the dataset. Therefore, we produced a correlation matrix using the Pearson correlation coefficient to eliminate all correlations with absolute values > 0.5. From each pair of highly correlated variables, we preferably retained the one that was easier to measure in the field. The Hart–Becking index, the Basal Area, and the Canopy Cover were highly correlated, but according to the observation of exploratory scatterplots, they were all highly related to the five understory variables. Therefore, we considered three sets of explanatory variables, each one including one of the three selected overstory variables, plus those that had not been discarded: DBH, Canopy Base Height, and Canopy Length. We used variance inflation factors (VIF) [37] to perform an additional check on collinearity within each of the three groups of the four variables and verified that they all presented VIF < 1.3, therefore, with very little correlation.

Each of the three groups of the four overstory variables was used in nested linear mixed models (LMM) to determine their effect on the five understory variables (three structural indices and two diversity indices). Therefore, 15 models were produced: 5 dependent understory variables × 3 groups of four explanatory overstory variables. The initial models (full models) were composed of four fixed terms (four overstory variables) and two nested random terms (the subplot, nested within the plot), using a normal distribution with an identity link. Then, we used a backward variable selection to obtain more parsimonious models [37,38]. Variable removal was processed by testing the coefficients of the fixed terms through likelihood-ratio tests and by verifying that the final model corresponded to the lowest value of the second-order Akaike information criterion (AICc), normally preferred (over AIC) for small samples [38]. The assessment of model performance follows Nakagawa and Schielzeth [39]. We computed the marginal pseudo-R^2, representing the variance explained by the fixed effects (R^2 fix.) and the conditional pseudo-R^2, representing the variance explained by the whole model (R^2 tot.). The R package *lme4* was used to produce the models [40].

The examination of the LMM resulted in the conclusion that the Hart–Becking index, the Basal Area and the Canopy Cover were the most performant overstory variables and could be used as alternative standalone indicators to guide the restoration of the understory in the studied *P. halepensis* forest. Therefore, after analysing the graphics of each of the three variables plotted against the Magini and the Shannon indices (six plots), we decided to fit first-, second-, and third-order polynomial

functions to the data. We opted to use just the two composite indices (Magini and Shannon), given that these are more informative, from a management point of view, about the overall development and diversity of the plant community and because the respective models were more performant (higher R^2). In this analysis, we opted to average the values of the three subplots within each plot (n = 33). For those fitted lines presenting a "shoulder" (second- and third-order polynomials), we determined the maximum of the function by finding the first derivative and setting the resulting equation equal to zero. This procedure was aimed at finding the optimal values of the overstory variable that would maximise, according to the model, the development and the diversity of the understory. Model selection (among the three polynomial functions) was performed using AICc and the Bayesian information criterion (BIC), always in search of the most parsimonious model in order to avoid overfitting [38].

The third analytical approach was aimed at assessing the relationships between species composition and the ensemble of overstory and understory variables. This analysis is relevant in terms of ecological restoration, to know if taller species, with a tree habit and the potential to form a forest canopy, are positively or negatively influenced by those variables. We used redundancy analysis (RDA), a method of constrained ordination in which the canonical axes are linear combinations of the explanatory variables, i.e., the constraints [41]. In our case, the matrix of explanatory variables was formed by the selected overstory variables and the two understory indices (eight columns) averaged for each plot (33 rows). The matrix of dependent variables was composed by species abundance (24 columns, one for each species) averaged for each plot (33 rows), and standardized using the Hellinger transformation [42]. The selection of explanatory variables was performed with permutation tests (using the pseudo-F statistic; minimum of 1000 permutations), allowing us to assess the significance of the overall RDA and of each of the first two axes [43]. Several variable combinations provided significant results, so we chose the model with the highest explained variance given by the adjusted R^2. As in multiple regression, the adjusted R^2 corrects the bias originated by the accumulation of explanatory variables [42]. Finally, we produced a tri-plot based on the final model. We used the package *vegan* to perform this analysis [44]. All analyses in this study were performed using R software [45].

3. Results

The pine stands were relatively homogeneous (Table 1) in terms of tree development, with an average Tree Height of 15.1 ± 1.31 m (mean ± SD) and an average DBH of 29.8 ± 1.8 cm. On the contrary, the stands showed considerable variability in density and stocking, with an average Tree Density of 432.8 ± 74.2 trees ha^{-1}, an average Basal Area of 30.0 ± 4.2 m^2 ha^{-1}, and an average Canopy Cover of 90.9 ± 36.0%. As to the understory, there was also a large variability across samples. The average species Richness was 7.2 ± 2.9, the average Plant Density was 22.6 ± 11.0 plants m^{-2}, and the average Plant Height was 0.5 ± 0.2 cm.

The understory was composed of a total of 24 species (Table 2), from which 12 were present in more than 50% of the sampled plots. *Rubia peregrina* was the most frequent herbaceous species, being present in all plots. *Phillyrea latifolia*, *Pistacia lentiscus* and *Olea europaea* var. *sylvestris* were the most frequent woody species, being present in 85% of the plots. Eight species were present in less than 10% of the plots. The inventoried plants included one exotic species of Australian origin, *Pittosporum tobira*, present in only one plot. Plant Height was quite different across species, ranging from 0.22 m for *Arbutus unedo*, to 1.75 m for *Quercus ilex*, but this latter value corresponded to only two samples. Plant Density by species ranged from 0.15 plants m^{-2} (*Crataegus monogyna*, *Coronilla emerus*, *Pittosporum tobira*) to 7.68 plants m^{-2} (*Rubia peregrina*). The three species that presented higher values of the Magini index were *Rubia peregrina*, *Quercus coccifera* and *Rhamnus alaternus*.

Table 2. List of the 24 inventoried understory species, ranked by decreasing order of their frequency. The table presents the species names and respective symbols, the absolute number of plots where they occurred, relative frequencies, Plant Height, Plant Density (only considering the plots where the species occurred), and the Magini index calculated by species.

Species	Symbol	Abs. freq.	Rel. freq.	Height (m)	Density (n m^{-2})	Magini (m m^{-2})
Rubia peregrina L. *	Rp	33	1.00	0.36	7.68	2.76
Smilax aspera L. *	Sa	30	0.91	0.91	1.39	1.26
Phillyrea latifolia L.	Pla	28	0.85	0.55	1.94	1.07
Pistacia lentiscus L.	Ple	28	0.85	0.63	0.53	0.33
Olea europaea L. *var. sylvestris*	Oe	28	0.85	0.46	0.61	0.28
Rhamnus alaternus L.	Ral	27	0.82	0.75	2.60	1.95
Asparagus acutifolius L. *	Aa	27	0.82	0.58	0.83	0.48
Quercus coccifera L.	Qc	25	0.76	0.47	5.69	2.67
Myrtus communis L.	Mc	21	0.64	0.62	1.35	0.84
Rosa sempervirens L.	Rs	20	0.61	0.49	1.73	0.85
Ruscus aculeatus L.	Rac	19	0.58	0.35	1.54	0.54
Lonicera implexa Aiton *	Li	17	0.52	0.68	0.72	0.49
Rubus spp.	Rsp	15	0.45	0.77	0.65	0.50
Arbutus unedo L.	Au	11	0.33	0.22	0.30	0.07
Osyris alba L.	Oa	9	0.27	0.57	0.59	0.34
Clematis flammula L. *	Cf	6	0.18	0.82	0.22	0.18
Crataegus monogyna Jacq.	Cm	3	0.09	0.28	0.15	0.04
Viburnum tinus L.	Vt	3	0.09	0.53	0.79	0.42
Coronilla emerus L.	Ce	2	0.06	0.55	0.15	0.08
Quercus ilex L.	Qi	2	0.06	1.75	0.22	0.39
Prunus spinosa L.	Ps	2	0.06	0.54	0.44	0.24
Prasium majus L.	Pm	2	0.06	0.61	0.74	0.45
Laurus nobilis L.	Ln	1	0.03	0.32	0.74	0.24
Pittosporum tobira L. (Thunb.) Ait.	Pt	1	0.03	0.52	0.15	0.08

* Herbaceous species.

The LMM only include one explanatory variable each (Table 3), with the exception of models *Dc* and *Mc*, which include two variables. In general, the model predictabilities for Richness and Shannon were lower ($0.17 < R^2 < 0.34$) than those for Density, Height, and Magini ($0.25 < R^2 < 0.66$). The Richness and Shannon models had similar performance with very similar values of R^2. In these models, there was an important part of variance that was explained by the random terms, i.e., the location of the samples across the sampled area, as shown by the values presented by the total R^2. The Magini models explained more variance ($0.37 < R^2 < 0.66$) than the Height models ($0.36 < R^2 < 0.59$) and these latter models had better performance than the Density models ($0.25 < R^2 < 0.42$).

Variables related to understory development (Density, Height, Magini) were positively influenced by the Hart–Becking spacing index and the Canopy Base Height and negatively influenced by the Canopy Cover and Basal Area. The same effect was also observed for the species composition variables (Canopy Cover and Shannon), which were also positively influenced by a larger spacing of trees and a higher base of the canopies. The higher model coefficients (in absolute value) were observed for the Hart–Becking index and the Basal Area, both having a strong effect on Density and Magini.

The comparison of polynomial functions using information criteria resulted in the selection of second-order polynomials for the Hart–Becking index, linear models for Basal Area and third-order polynomials for Canopy Cover. In the case of the Hart–Becking index, there was just a slight improvement using a third-order polynomial compared to the second-order (less than 1%, both for AICc and AIC), so the second-order was adopted. In the other two variables, there was a considerable change in the AICc and the BIC indices (always above 1%, with one single exception), so there was a clear choice in these cases. These univariate models explained between 0.50 and 0.80 of the variance of the Magini index and between 0.19 and 0.54 of the Shannon index.

Table 3. Linear mixed models (LMMs) developed to show the relationships between overstory variables (explanatory) and understory variables (independent). Table columns represent the models, the dependent variables, the coefficients of the fixed terms, the respective standard errors, the *t*-value for each tested coefficient, the AICc of the model, the R^2 of the fixed terms and the total R^2. Test significance: *** $p < 0.001$; [ns] non-significant.

Models	Variables	Coeff.	SE	*t*-Value	AICc	R^2 fix.	R^2 tot.
Density							
Dh	Hart–Becking	1.5979	0.4210	3.7950 ***	696.5	0.25	0.73
Db	Basal Area	−1.4194	0.3415	−4.1561 ***	694.9	0.28	0.73
Dc	*Can. Cover*	−0.0188	0.0034	−5.4708 ***	694.4	0.42	0.73
	Can. Base Heig.	1.8134	0.9065	2.0003 [ns]			
Height							
Hh	Hart–Becking	0.0407	0.0082	4.9633 ***	−62.0	0.36	0.75
Hb	Basal Area	−0.0316	0.0072	−4.3687 ***	−58.4	0.31	0.75
Hc	*Can. Cover*	−0.0005	0.0001	−8.7896 ***	−73.4	0.59	0.75
Magini							
Mh	Hart–Becking	1.4262	0.2840	5.0225 ***	610.4	0.37	0.80
Mb	Basal Area	−1.2835	0.2217	−5.7884 ***	606.5	0.44	0.80
Mc	*Can. Cover*	−0.0179	0.0017	−10.2877 ***	592.0	0.66	0.80
	Can. Base Heig.	0.9810	0.4592	2.1362 ***			
Richness							
Rh	Hart–Becking	0.3826	0.1191	3.2121 ***	439.2	0.20	0.75
Rb	Basal Area	−0.3004	0.1016	−2.9570 ***	440.8	0.18	0.75
Rc	*Can. Cover*	−0.0048	0.0010	−4.6366 ***	441.1	0.33	0.75
Shannon							
Sh	Hart–Becking	0.0544	0.0156	3.4818 ***	47.9	0.22	0.75
Sb	Basal Area	−0.0395	0.0137	−2.8932 ***	51.1	0.17	0.75
Sc	*Can. Cover*	−0.0006	0.0001	−4.7772 ***	50.3	0.34	0.75

Since the best models for Basal Area were linear models, we only computed the derivatives for the Hart–Becking index and Canopy Cover. The value obtained for the Hart–Becking index that maximised the Magini index was 33.7%, and the maximum value for the Shannon index was obtained with a Hart–Becking value of 32.6%. Likewise, the value obtained for Canopy Cover that maximised the Magini index was 84.6%, and the value that maximised the Shannon index was 86.5% (Figure 2 and Table 4).

Table 4. Description of the univariate polynomial functions shown in Figure 2, relating three chosen overstory variables (Hart–Becking, Basal Area and Canopy Cover) with the Magini and Shannon indices. The first column identifies the model and shows the order of the polynomial in brackets. The table shows the *F* statistic, the standard error of residuals, and the values of the second-order Akaike information criterion, the Bayesian information criterion, the R^2, and the adjusted R^2. Test significance: *** $p < 0.001$.

Function	Variables	*F*	SE	AICc	BIC	R^2	adj. R^2
Magini							
P_Mh (2)	Hart–Becking	17.2687 ***	5.296	209.95	214.51	0.53	0.50
P_Mb (1)	Basal Area	33.7739 ***	5.287	208.31	211.97	0.52	0.51
P_Mc (3)	*Can. Cover*	43.9490 ***	3.355	181.49	186.75	0.82	0.80
Shannon							
P_Sh (2)	Hart–Becking	9.4909 ***	0.292	18.84	23.40	0.39	0.35
P_Sb (1)	Basal Area	8.4057 ***	0.326	24.50	28.17	0.21	0.19
P_Sc (3)	*Can. Cover*	13.5110 ***	0.245	8.96	14.22	0.58	0.54
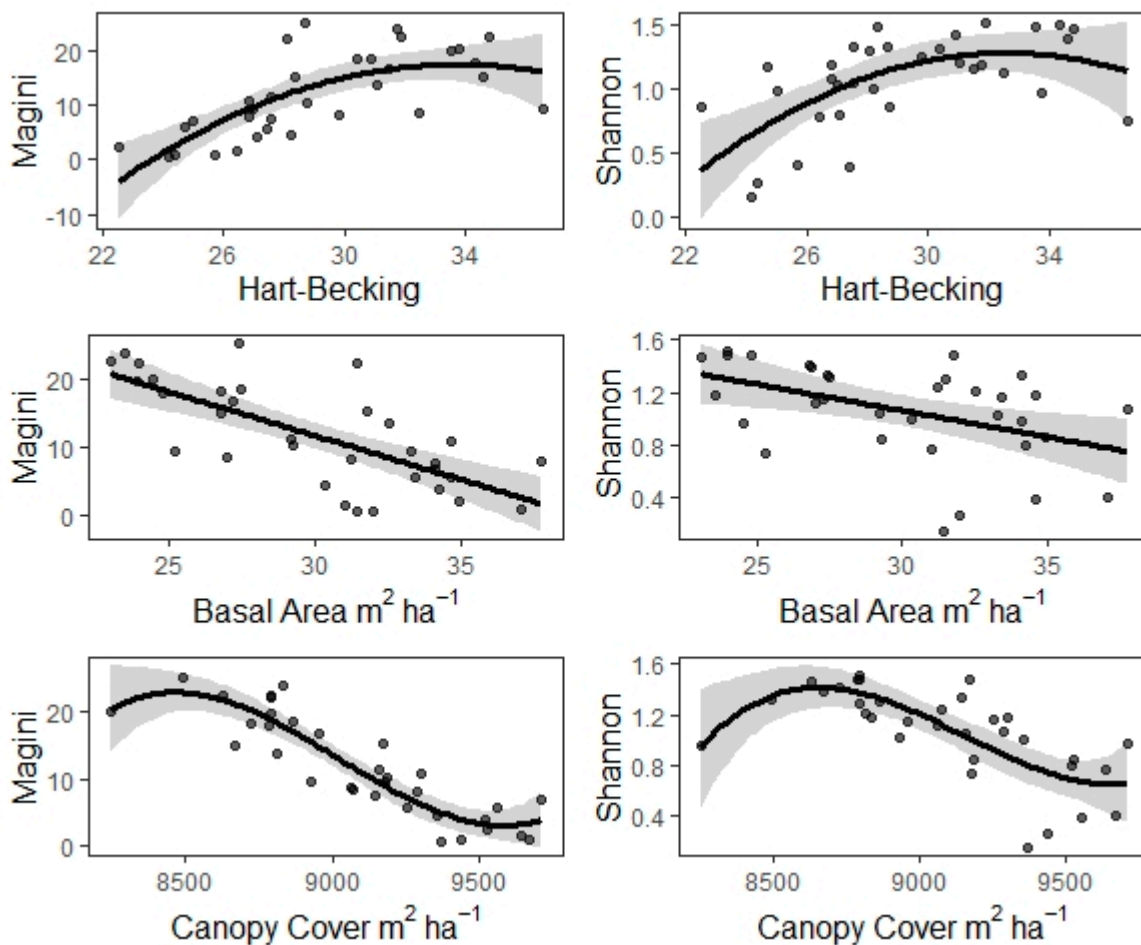
Figure 2. Polynomial fits and respective 95% confidence intervals for the Magini and Shannon indices as functions of the Hart–Becking spacing index, Basal Area and Canopy Cover. Dots represent the 33 sampling plots.

Based on the permutation tests, we chose the Canopy Cover, the Hart–Becking index, the Magini index, and the Shannon index for the final model. The model was significant at $p < 0.001$ and so were both axes ($p < 0.001$ for RDA1 and $p = 0.036$ for RDA2). The unadjusted R^2 was 0.32, with the first two axes representing 18% and 8%, respectively, of the total explained variance. The adjusted R^2 was reduced to 0.23. The RDA tri-plot confirmed the results obtained by the LMM analysis, showing that the Hart–Becking index had a high positive correlation with the Magini index and a high negative correlation with the Canopy Cover (Figure 3). The inclusion of highly correlated variables is often avoided in ordination methods such as PCA and RDA [46]. However, just including the two least correlated variables (Magini and Shannon) yielded results very similar to those obtained with our chosen model. The Shannon index was very aligned with the second axis, RDA2. Some species were associated with higher diversity levels, including *Asparagus acutifolius* and *Ruscus aculeatus*, but these species were quite indifferent to structural changes in the under- and the overstory. On the other hand, two late-successional species, *Quercus coccifera* and *Rhamnus alaternus*, were positively associated with the Magini and Hart–Becking indices. In general, most species presented scores positively associated with understory development, species diversity and tree spacing. The most important exception was the widespread climber *Rubia peregrina*, apparently associated with lower species diversity.
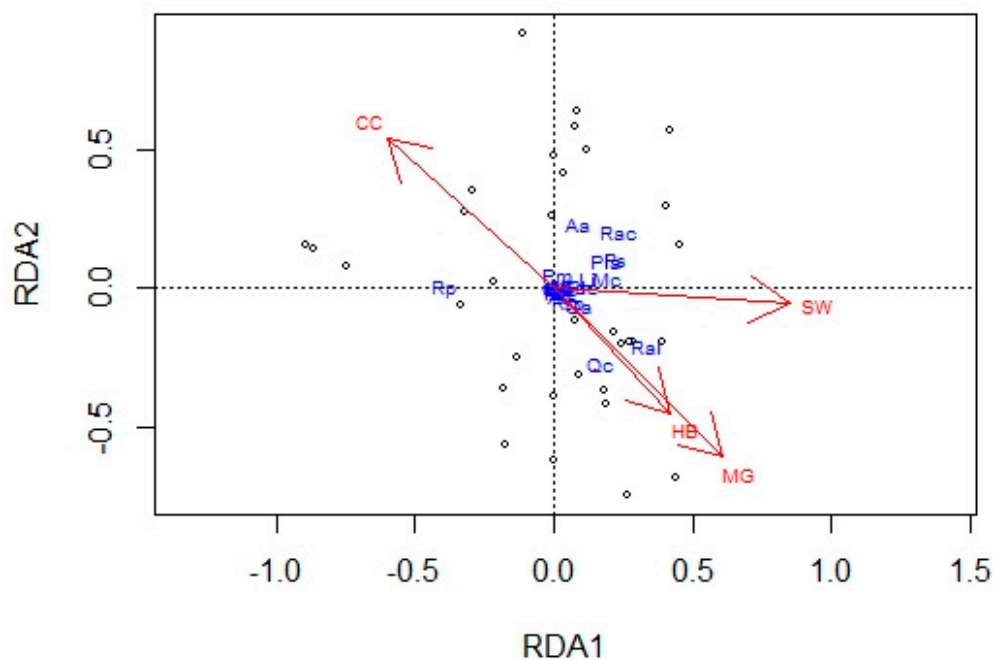
Figure 3. RDA tri-plot exploring the relationships between the frequency of each species, the overstory variables (CC—Canopy Cover, HB—Hart–Becking) and the understory indices (SW—Shannon, MG—Magini). White circles represent the plots. For species symbols (in blue), see Table 2.

4. Discussion

4.1. Overstory Effects on Understory Development

Our results showed a strong negative effect of overstory cover on the development of the understory plant community in terms of plant height and density; the effect was even stronger on the composite index proposed by Magini [36]. This composite index closely reflects the amount of light that crosses the canopy, directly affected by the tree cover and the height of the canopy base. Besides the role of light interception, other possible concomitant effects should be considered, such as chemical (e.g., allelopathy) and physical (e.g., soil water) effects on the soil, which may affect the development of understory plants [12,47]. On the other hand, the existence of negative interactions between the tree canopy and understory species can be mediated by other life forms, such as the case reported by Maestre et al. [48] between *P. halepensis* and *Pistacia lentiscus*. This strong dependency of understory plants on the canopy cover of trees has been demonstrated for many other understory and overstory types, including, for example, pastures under *Pinus radiata* in New Zealand [49], *Picea abies* regeneration under *Betula pubescens* in Norway [50] or herbaceous cover under *Pinus palustris* plantations in the USA [51]. Nonetheless, this influence is not similar for all forest and climate types, and it was found to be weak in mesophilous forests studied by Halpern and Lutz [52] in the USA. Changes in this effect can even be found on a smaller scale, as, for example, along altitudinal gradients [27].

In Mediterranean plant communities, typically exposed to high levels of light, canopy cover may play an important role in the development of the understory. In the case of *P. halepensis* stands, this was fully shown by different authors under different conditions. Tables 5 and 6 present a summary of previous studies that have shown the effect of overstory stocking and density on the understory of *P. halepensis* stands in the Mediterranean region. A negative influence of the basal area on plant cover and plant biomass was found by Jiménez et al. [31] in a thinning experiment in Spain. Using thinning experiments, Nunes et al. [2] and Navarro et al. [53] have also found a negative effect of tree density on understory density and biomass, respectively. Coll et al. [27] did not find a negative relationship between the basal area of *P. halepensis* on understory cover and argue

that in dryer areas, both competition and facilitation might be occurring simultaneously. However, as shown in Tables 5 and 6, this does not seem to be confirmed by other works for similar conditions. The interpretation by Coll et al. [27] may, however, hold true in our case since growth conditions at the soil level in our study area are apparently more favourable (higher annual rainfall). Therefore, canopy cover may indeed be a more limiting factor in our case, compared to drier areas.

Table 5. List of studies investigating the influence of overstory variables on the understory of *P. halepensis* stands. The information shown in the table was directly retrieved from the respective papers; NFI—National Forest Inventory. The results of these studies are displayed in Table 6.

Studies	Stand Age	Soil	Climate	Precip. mm	Country: Region(s)	Study Type
Coll et al. [27]	Nonspecified	Non-specified	Nonspecified	500–750	Spain: Catalonia	Data from NFI
Jiménez et al. [31]	10–15 years	Petric calcisol	Semiarid	302	Spain: Granada	Thinning experiment
De las Heras et al. [54]	5 years	Sandy, sandy loam	Arid, semiarid	226, 845	Spain: Albacete, Murcia	Thinning experiment
Pasta et al. [30]	15–46 years	From limestone, marls	Infra-Mediterranean upper semiarid	300	Italy: Lampedusa	Field survey
Nunes et al. [2]	Nonspecified	From limestone	Dry subhumid	650	Portugal: Setúbal	Thinning experiment
Navarro et al. [53]	11 years	Petric calcisol	Semiarid	302	Spain: Granada	Thinning experiment

Table 6. Summary of results from the studies listed in Table 5. The table shows the effect of stand stocking (including basal area and canopy cover) and stand density on five understory variables: plant cover, plant density, plant biomass, plant richness and the Shannon-Wiener index; ns—nonsignificant results/nonconclusive relationships.

Overstory Variables	Understory Variables				
	Cover	Density	Biomass	Richness	Shannon
Stocking	ns [27] negative [31]		negative [31]	negative [30,31,54]	negative [31]
Density	ns [54]	negative [2]	negative [53]	negative [54] ns [2]	ns [2,54]

4.2. Overstory Effects on Understory Diversity and Composition

Our results regarding the negative effect of canopy cover on species diversity are consistent with other works dealing with different stand types [55–57]. Other variables may mask the overstory effect, such as the case of *Pinus sylvestris* in Eastern Pyrenees reported by Pausas [58], where environmental variables were far more important than overstory variables in explaining species diversity. Fire can also have a confounding influence as it contributes to canopy openings while having a direct effect in plant community dynamics, often fostering biodiversity levels, as in the case of *Pinus palustris* forests [59,60].

In the specific case of *P. halepensis* forests, previous works have consistently shown a negative relationship between tree stocking and tree density with understory diversity (Tables 5 and 6). Using thinning experiments in Spain, Jiménez et al. [31] and De las Heras et al. [54] demonstrated the positive effect of canopy reduction on species richness, also in line with Pasta et al. [30]. However, another thinning experiment on *P. halepensis* stands, in this case, established in a former quarry in Portugal [2], did not show the existence of significant short-term effects on plant diversity. Local characteristics and sampling constraints may have been at the origin of these nonconclusive results.

The strong negative relationship between canopy cover and plant diversity seems to be valid for early-developmental stages, as in our study, but not necessarily to more advanced stages, where a few understory species may take over, thus reducing diversity [61]. Long-term studies obviously provide better insights into the complex mechanisms that rule the development and species composition of the understory that grows under a forest cover [52]. Worth mentioning in this respect is the review by

Royo and Carson [62] on the formation of a recalcitrant homogeneous, understory layer that precludes advances in the forest succession. Remarkably, Mediterranean ecosystems were not included in this review, which may show that different processes are associated with the successional trajectories of the understory of Mediterranean forests, compared to those analysed in the review.

In our study, *Quercus coccifera* and *Rhamnus alaternus* were the only species clearly showing a positive association with the Hart–Becking spacing index. Although the analysis of functional or taxonomical groups is not in the scope of the present study, it is relevant to distinguish those species that have the potential of acquiring a tree habit, such as the case of *Quercus coccifera*, from the remaining species. The importance of broadleaf species with the potential to develop a tree habit is very high because these species determine the capacity to reach more mature stages in ecological succession, with higher stability and lower fire hazard [17]. It is worth noting that the contribution of these species to the overall Magini index was more related with the number of individuals than with their development (Table 2), which indicates the predominance of an early successional stage in most of the surveyed area. In line with this result, Lookingbill and Zavala [15] reported a positive association of two oak species seedlings (*Quercus ilex* and *Quercus pubescens*) with the presence of adult *P. halepensis* individuals. However, the positive role of *P. halepensis* afforestation in fostering ecological succession has been contested by other authors. Jiménez et al. [31] found that the development of the understory plant community in thinned stands was not accompanied by the recruitment of species that are typical of native forests. In addition, Maestre and Cortina [11], based on a literature review on the ecological effects of *P. halepensis* plantations, and Maestre et al. [48], based on experimental evidence, have refuted the ecological benefits of *P. halepensis* afforestation. Likewise, Bellot et al. [12] suggest that *P. halepensis* afforestation has a negative effect on late-successional shrubs, and therefore has a detrimental effect on ecological succession. These authors argue that improved microclimatic conditions associated with *P. halepensis* cannot counterbalance the reduction in soil water, therefore resulting in a negative effect on native shrubs. However, if soil water is not likely to be a serious constraint, as in our study area, this reasoning may not apply, which may explain the successful establishment of late-successional species such as *Quercus coccifera* and *Rhamnus alaternus*, if favoured by canopy opening. Nonetheless, although *P. halepensis* stands seem to allow the development of late-successional species, it is impossible to know whether this development would be more successful with or without the afforestation. To our knowledge, there are no paired studies comparing the long-term development of ecological succession with and without the presence of *P. halepensis*.

The study also showed species that were either indifferently or negatively related to increases in diversity and ecosystem complexity. This was the case of the climber *Rubia peregrina*, which seems to be associated with less diverse communities, although it was found in all survey samples. Among the species with higher scores, *Lonicera implexa* and *Ruscus aculeatus* were those that did not show any relationship with the axis formed by Canopy Cover—Magini index. These are widespread species in Mediterranean ecosystems, therefore showing no relationship with the development and diversity of the plant communities.

The differentiated response of understory species to increased canopy opening in *P. halepensis* stands was also shown by Nunes et al. [2]. These authors found a differentiated response of functional groups, with a positive effect of thinning on the density of plants with N-fixing capacity. Bonari et al. [63] found that a lower canopy cover of *P. halepensis* was associated with herbaceous and shrub species of natural dune succession, such as *Lonicera implexa* and *Ruscus aculeatus*, whereas higher canopy cover was associated with generalist species such as *Asparagus acutifolius*.

4.3. Management Applications of This Study

The four overstory variables that best explained the development of the plant community have a direct relationship with the amount of light that reaches the ground. Among the four overstory variables, Canopy Cover, being a direct measurement of light interception, was consistently better than the other three. The Hart–Becking index had a performance similar to Basal Area. The polynomial

models developed to derive the value of the Hart–Becking index, corresponding to maximum understory development (as given by the Magini index) and to the maximum diversity (as given by the Shannon–Wiener index), somehow complement the results obtained by Fonseca and Duarte [26] for *Pinus pinaster* in northern Portugal. The authors were seeking a stand stocking threshold, using the Wilson spacing factor—Fw, [64] in order to minimise understory development and to prevent the occurrence of wildfires. The value suggested by these authors was Fw = 0.21. The Wilson spacing factor is given by Fw = $100N^{-0.5}$ Hdom^{-1}, where N is tree density and Hdom is dominant height. The relationship between the two indices is H–B = 100 × Fw, where H–B is the Hart–Becking index. Therefore, Fw = 0.21 is close to the minimum value of the Hart–Becking index (22.5) found in our study, as shown in Table 1. According to our models, this value corresponds to conditions where the understory is nearly absent. Although we are comparing species that have different ecological characteristics, the two pine species seem to share similar effects on the understory, as suggested by Bonari et al. [63], who even recommends similar management strategies.

In Italy, Pasta et al. [30] found that species richness decreased drastically when *P. halepensis* cover exceeded 80%. In our case, this drop occurred for higher canopy cover (86.5%), as shown by the polynomial model relating Canopy Cover and the Shannon–Wiener index. Although in our study we used the sum of individual canopies, which may represent an overestimation of the actual cover due to some canopy overlap, this overlap should not be high, considering the even-aged structure of the stand. The polynomial models also showed a slight decrease in the Shannon and Magini indices for very open stands. In fact, a very sparse overstory can reduce species richness by favouring invasive species [65]. In the case of the present study, the climber blackberry (*Rubus* sp.) plays this role by covering the remaining vegetation, preventing new species from regenerating and developing, as shown by local observations in the studied area.

The values obtained for Canopy Cover and Hart–Becking are useful to guide thinning operations in *P. halepensis* stands when ecosystem restoration is foreseen. Although Canopy Cover performed better than the Hart-Becking index, there are some practical advantages in using the latter since only the average tree distance and the dominant height are needed to calculate it. In fact, dominant height does not change when thinning is applied, so it is enough to measure tree distance to regulate thinning intensity. Contrarily, when using the basal area, we need to measure all diameters before and after the thinning, which is more time-consuming than simply using a spacing index.

Although these plots were not remeasured after 2016 for a longer-term perspective of the ecological succession, we did visit them in 2019 and observed the transition of the plant community from understory to overstory. Species such as *Quercus coccifera*, *Olea europaea* var. *sylvestris*, and *Arbutus unedo* grew to 4–5 m in height, therefore presenting a tree habit. We could foresee the future development of this plant community by surveying a nearby forest reserve that has been untouched for 40 years, where the three tree species dominated the ecosystem (Figure 4), forming a natural broadleaf forest with 6 to 8 m height.

Although proceeding in ecological succession in a disturbance-free environment may be a desirable goal from a conservationist perspective, we should be aware of the risks involved because of fuel accumulation across time. Therefore, there are important tradeoffs to consider between the short-term risk of fire due to fuel accumulation [25] and the benefits of restoring a system that will be less fire-prone in the long-term [17,18]. Hence and again, the best decision depends on the specific goals involved and on the availability of financial resources [16] to implement the adequate measures.

Figure 4. Images (**A–E**) were taken in 2006, in the afforested area, showing an increasing development of the understory, associated with decreasing levels of canopy cover. Image (**F**) was taken in 2019, showing the transition from understory to overstory. Image (**G**) was taken in 2019 in a nearby reserve not afforested with *P. halepensis*, where ecological succession along 40 years has resulted in the development of a broadleaf forest dominated by *Quercus coccifera*, *Quercus ilex* and *Arbutus unedo*.

5. Conclusions

A deep understanding of the processes that shape ecosystems is critical to anticipating the effects of any measures taken to restore native vegetation [66]. In the present paper, we have contributed to this understanding by providing concrete information on the relationships between the manageable forest cover of an afforested area and the development of a native ecosystem growing beneath the tree canopies. Among the related literature, authors are divided between the need for understory suppression, either for better stand performance or, more frequently, to prevent wildfires, and those who defend the need to foster ecological succession towards more stable and diverse forest systems. Authors are also divided between the benefits and negative effects of *P. halepensis* afforestation for the purpose of restoring native ecosystems. In any case, as stated by Gómez-Aparicio et al. [67], plantations are dynamic systems where successional trajectories and diversity levels are determined by abiotic constraints, complex balances of competitive and facilitative interactions, the spatial configuration of native seed sources, and species life-history traits. Therefore, different combinations of these factors may result in different outcomes in terms of the successional trajectories of the vegetation growing beneath the canopy.

We have found a strong negative correlation between the canopy cover of a *P. halepensis* forest and the development and diversity of the respective understory. This finding is supported by other works on *P. halepensis* and is relevant about the potential role of classical forest management, including

thinning operations, to change the characteristics of the vegetation growing beneath the canopy. According to our findings, this goal may be attained through the control of stand stocking/spacing by using overstory variables that are widely used in forestry: basal area, canopy cover or spacing indicators such as the Hart–Becking index or the Wilson factor. Moreover, we could estimate the values of the Hart–Becking index and canopy cover corresponding to maximum development (33.7% and 84.6%, respectively) and diversity (32.6% and 86.5%, respectively) of the understory plant community.

Our study also demonstrates that some species are more associated than others with canopy openings and with changes in understory diversity and development. The present work not only shows that lower overstory cover may favour understory development and diversity, but also that this change is accompanied by the establishment of late-successional species, such as *Quercus coccifera* and *Rhamnus alaternus*.

Our results, obtained in a specific location in Southern Italy, are compatible with other studies describing the effects of pine overstory on the vegetation growing beneath the canopy, therefore supporting the generalization of our findings to other areas. Comparable results were obtained by other authors for distinct environmental conditions and even for different pine species. Therefore, we believe these findings may be useful for the management of other pine forests, particularly for the management of *P. halepensis* plantations, with the aim of ecosystem restoration.

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