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How Are Pine Species Responding to Soil Drought and Climate Change in the Iberian Peninsula?

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Abstract: This study investigates the relationship between soil moisture and the growth of *Pinus halepensis*, *P. nigra*, *P. sylvestris* and *P. uncinata*, which are some of the main pine species of the Iberian Peninsula, and the response of these species to soil drought. The role played by climatic and geographic factors in the resilience of these species to drought events is also evaluated. A total of 110 locations of the four species studied were selected, with data ranging from 1950 to 2007. The results show that the species that are less dependent on soil moisture best withstood droughts, while those more dependent on it showed better adaptability. Additionally, climatic and geographic factors had a stronger influence on the species' resilience to soil drought at higher altitudes. The results of this study can help us to better understand forest ecosystem dynamics and their reaction to droughts in Mediterranean areas, where this phenomenon will be much more severe in the future due to climate change.

Keywords: soil moisture; drought; pine; Mediterranean climate; environmental factors

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1. Introduction

Forests are one of the ecosystems that are the most vulnerable to extreme weather events because their natural adaptation to change is very slow [1]. Water scarcity due to the increase in the frequency and intensity of droughts has already caused a decrease in forest productivity [2,3] as well as widespread tree death worldwide [1,4,5]. Where existing forests have not yet reached maturity, there is a strong need to develop short-term adaptation strategies [6]. In general, the development of active adaptation strategies, such as planting more drought-resistant tree species, can achieve greater forest resistance and resilience [7,8]. These strategies are crucial in areas where water availability is limited since droughts have a greater impact on the physiology and growth of trees [9,10].

The Mediterranean region and especially the Iberian Peninsula have been identified as prominent hotspots of unprecedented climate change due to limited water availability [11]. As a result of rapidly progressing environmental changes associated with episodic droughts and heat waves, this region is expected to become hotter and drier, leading to more intense and prolonged droughts and thus a decrease in water available for plants [12–14]. This will have consequences in terms of tree growth and productivity, which can lead to an increase in tree mortality [15–17].

A drought is considered a major cause of abiotic stress that reduces forest growth, affects forest health and determines the geographic distribution of tree species [18]. The effects of droughts on tree growth are influenced by the physiological characteristics of individual species, as they tolerate droughts differently [19–21]. Therefore, the response of different tree species to changes caused by environmental factors, in terms of growth and optimization in the use of available water, is a very important issue, especially in Mediterranean areas [22].

When trees are under drought conditions, both the low water content in the soil and the high evaporation cause alterations in their physiology, with cambial activity being one of the processes that are affected from the outset [23]. This is because the formation of xylem cells is limited by the following two drought-related effects: the loss of turgor and the closure of stomata that reduce carbon assimilation [24,25]. This occurs for drought events that range from very severe to less severe, being the most limiting factor in tree growth worldwide [26]. The effect of a drought and its consequences on trees can be studied by measuring the width of the rings. This variable is commonly used as the main indicator of the response of trees to drought, both on large spatial and temporal scales [27]. Furthermore, in previous works, it was shown that this variable is more sensitive, and therefore a better indicator than other commonly used indicators [28].

The vast majority of research investigating the relationship between droughts and tree growth is performed through the study of climatic variables [29–33]. In this type of study, droughts have been identified using climatic variables such as precipitation, temperature or evapotranspiration. However, soil moisture is much more relevant in terms of droughts, since soils act as a water reservoir during dry periods, with tree roots having access to deep soil water [34].

In addition, most studies considering droughts refer to climatic or hydrological droughts instead of soil drought [18,35]. There are very few studies that use the soil moisture variable and investigate its relationship with tree growth [36–38]. This is because until recently, there were no long-term soil moisture databases available [36]. However, in recent years, this lack of data has been filled with both satellite and modeling soil moisture data [39–41]. For instance, recently, a few studies have investigated the role of soil moisture on *Pinus halepensis* growth, one of the dominant tree species in the Iberian Peninsula [36–38]. Therefore, effort is needed to characterize the response of other major pine species that can also be found in this region.

Forest ecosystems in the Iberian Peninsula cover an area of approximately 26 million hectares, a large part of which are coniferous stands, occupying an area of 5.7 million hectares [42]. Seven different pine species can be found in the Iberian Peninsula, five of which are autochthonous species (*Pinus halepensis* Mill, *P. nigra* J. F. Arnold, *P. uncinata* Ramond ex A. DC, *P. sylvestris* L. and *P. pinaster* Ait.) and two of which were introduced (*P. pinea* L. and *P. radiata* D. Don) [43,44].

The growth of these species has been primarily related to climatic variables [20], since the role of these variables as environmental factors is beyond question and the related data are commonly available. Most of the studies on tree resilience to droughts only take into account the effect of meteorological conditions in the same period in which the drought event occurs, ignoring the conditions that existed before and after said period. However, it was shown in different studies that these conditions can explain a large part of the resilience response [45,46]. Some studies have come to integrate the conditions after drought events, and the observed effects have not been consistent with the characteristics of the drought event of study [47,48]. The use of drought vulnerability indices in combination with tree-ring data is the method that is commonly used [35,49–51]. Among these indices, the most widely used approach in the literature was proposed by the authors of [52], who defined recovery, resistance and resilience indices based only on the ring width index (TRI) values before, during and after a drought event. Although several published works discussed some specific issues related to the Lloret indices [53], others [54] proved its suitability. These indices have been widely used in different forest species and under different types of climates worldwide, showing the specific vulnerability pattern of each case [8,28,47,55].

The present study has two main objectives. The first is to study the response of four major pine species in the Iberian Peninsula—*P. halepensis* (PIHA), *P. nigra* (PINI), *P. sylvestris* (PISY) and *P. uncinata* (PIUN)—to droughts defined by the soil water content and using resilience indices. Secondly, the role played by environmental and geographic factors in these pine species' endurance to droughts is assessed. As environmental factors, the study uses soil moisture, temperature, radiation, evaporation, precipitation and dew point temperature for the period between 1950 and 2007 for the 110 locations where the tree growth series were selected.

2. Dataset and Methodology

2.1. Study Area and Dendrochronological Dataset

The study area includes most of the species' distribution range across the Iberian Peninsula, which climatically represents a transitional area between temperate and Mediterranean climates (Figure 1). Thus, the northern part of the study area is more strongly affected by the Atlantic influence, having, in general, a higher mean annual precipitation (>1500 mm) and a lower mean annual temperature (<12 °C) [56]. Coastal and southern areas have a more typical Mediterranean climate, with warm and dry summers and mild and relatively wet winters, but include semiarid areas where the mean annual precipitation locally can be lower than 300 mm [56].

The dendrochronological dataset contains 110 sites, including 28 for PIHA, 48 for PISY, 15 for PIUN and 19 for PINI. This specific dataset was selected from previous research [56,57] based on the homogeneity of the forestland cover and soil conditions (marls and limestone) at the sampled sites. Chronologies developed over open forest areas or inhomogeneous landscapes were discarded.

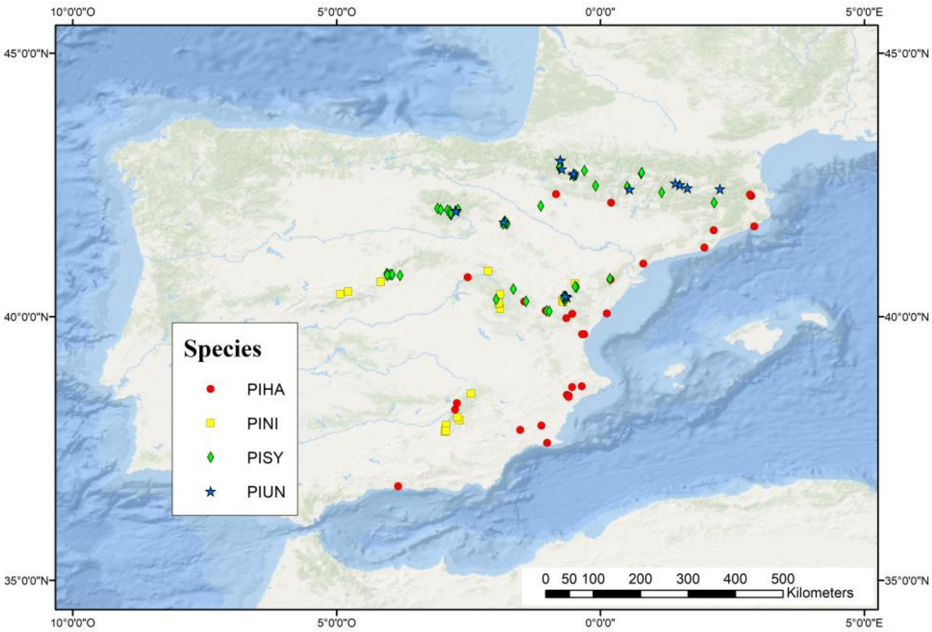

Figure 1. Location of the tree samples used in the study for the four pine species including *Pinus halepensis* (PIHA), *Pinus nigra* (PINI), *Pinus sylvestris* (PISY) and *Pinus uncinata* (PIUN). A more detailed description of the dendroclimatic dataset and climatic conditions across the study area can be found in [58,59].

Each of the study sites included in this study is represented by 10 to 35 dominant or codominant sample trees with healthy trunks and no signs of human intervention. These samples were processed according to standard procedures to identify and date the exact position of the annual rings (see specific details in [56,57]). Crossdating was verified using COFECHA [60]. Then, the tree ring width measurements were performed to the nearest 0.01 mm using the TSAP-Win program and a LINTAB™ 5 measuring device (Rinntech, Heidelberg, Germany).

Then, for each site, a TRI chronology was constructed. To remove the low-frequency variability from the tree ring width series and emphasize the high-frequency variability, we applied double detrending. Thus, a negative exponential function followed by a cubic smoothing spline with a 50% cutoff frequency and a 30-year response period was applied to each individual series. We then constructed the residual chronologies, which were produced after removing the first-order autoregression for each previously obtained detrended tree ring series. Finally, a biweight robust estimation of the mean was applied to construct the residual chronologies. These analyses were performed using the dplR library [61].

2.2. ERA5-Land

For this research, several climatic variables from the ERA5-Land reanalysis database of the European Center for Medium-Range Weather Forecasts (ECMWF) were used [62]. The database provides hourly values of several land variables on a regular 10 × 10 km resolution grid. The time series of the pixels containing the 110 pine sites for temperature, radiation, evaporation, precipitation and soil moisture at different depths were obtained. For the variables of radiation, precipitation and evaporation, the accumulated daily values were calculated. For the variables of temperature and soil moisture, the data at 12 h and 00 h were used to obtain an average daily value. In turn, for soil moisture, the values of the first three layers of the soil profile (0–100 cm depth) were used, thus obtaining a daily average root zone soil moisture value. The dew point temperature of the ERA5-Land database was adopted as an auxiliary variable to calculate, together with the temperature, the vapor pressure deficit following the method described in [63].

2.3. Analysis

To meet the two objectives of this study, different analyses were carried out for each objective. This study follows the approach adopted in [38] to study the role of soil moisture in the growth variability of the four considered pine species. First, from the 110 daily soil moisture time series corresponding to each pine sample, monthly average values were obtained. Subsequently, a monthly correlation analysis (Pearson method) was performed between these time series and the TRI values of each species, thus obtaining an R value and a percentage of samples with significant results for every month, from October of the previous year to December of the corresponding year.

To study the pines' response to droughts through resilience indices, the four indices presented in [52] were used. The first is the resistance index, which is the level of growth of a species during the drought event compared to the growth before it. Values less than 1 indicate that the pine grows less during the event. The recovery index is the ability of the pine species to restore growth after the event in comparison to the growth values during the event. Values greater than 1 indicate that the pine grows more after the event. The resilience index represents the ability of the pine to return the post-event growth values to those before the event. Values close to 1 indicate that the pines grow practically the same before and after the event. Finally, the relative resilience index is the weighting of the resilience based on the damage caused by the drought event. Prior to the calculation of these four indices, the drought events for the study period were defined based on the soil moisture anomaly time series of all 110 locations, verifying that there were no major differences among them on a similar temporal pattern (Figure 2). The close correspondence between the series shows the concurrence of events affecting all species along the entire spatial domain.

Subsequently, the 25th percentile threshold was applied to the annual soil moisture anomalies to establish dry years, and the 75th percentile was applied to establish humid years. Afterward, the drought events were chosen by considering the methodology of [52], by which the drought events, defined as periods of dry years regardless of the duration, have two years with normal or humid values before and after the event. Thus, within the study period, four drought events were defined, including 1953–55, 1958, 1994–95 and 1999–2001 (Figure 3).

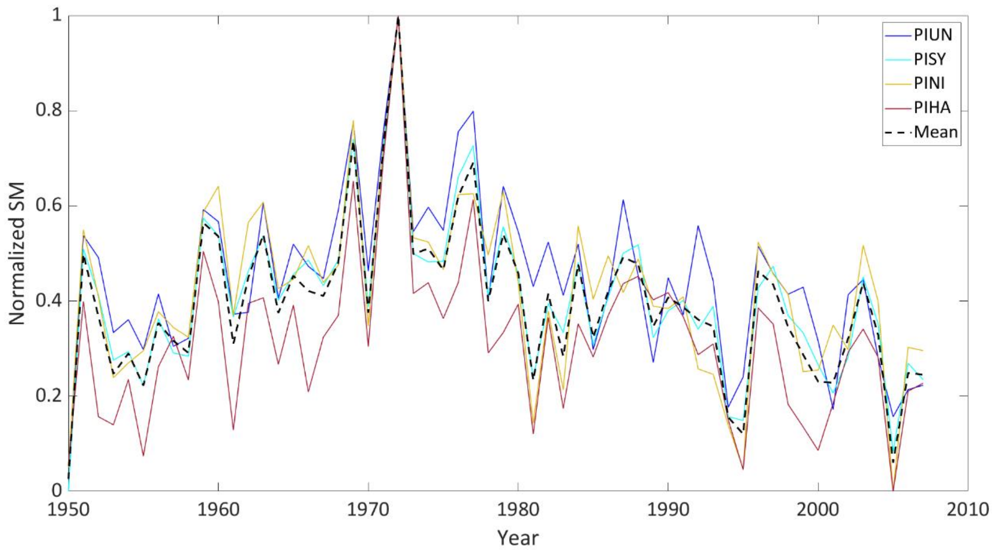

Figure 2. Temporal evolution of the normalized soil moisture mean series of the 110 locations and of the locations of each of the four pine species.

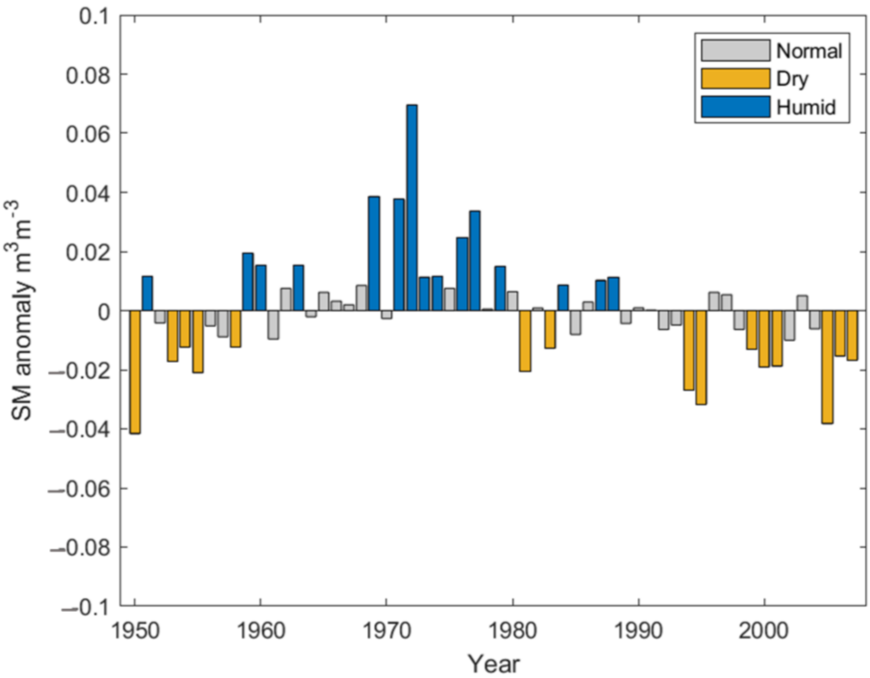

Figure 3. Mean annual soil moisture anomalies for the entire spatial domain. Normal years (grey), 25–75th percentile; dry years (brown), below 25th percentile; and humid years (blue), above 75th percentile.

Once the drought events were defined and identified, the four resilience indices were calculated for each sample using the following formulas:

$$\text{Resistance } (R_t) = \text{TRI\_Ev}/\text{TRI\_PreEv}, \quad (1)$$

$$\text{Recovery } (R_c) = \text{TRI\_PostEv}/\text{TRI\_Ev}, \quad (2)$$

$$\text{Resilience } (R_s) = \text{TRI\_PostEv}/\text{TRI\_PreEv}, \quad (3)$$

$$\text{Relative Resilience } (RR_s) = R_s - R_t, \quad (4)$$

where TRI_PreEv, TRI_Ev and TRI_PostEv are the TRI values before the drought event, during the drought event and after the drought event, respectively. The TRI_PreEv and TRI_PostEv were calculated as the averages of the TRI values of the two years before and after the event, respectively, and the TRI_Ev was calculated as the average of the TRI values during the event. In addition, differences among the species for each of the four resilience indices were tested using the Kruskall–Wallis test ($p < 0.05$).

To study the role played by environmental and geographic factors in the drought resilience of the four considered pine species, a multivariate regression analysis was conducted. The variables considered were soil moisture, temperature, radiation, evaporation, precipitation, vapor pressure deficit, latitude, longitude, altitude and distance to the coast. They were normalized to facilitate the subsequent analyses. The set of variables preferable for multivariate modeling was filtered based on collinearity using the variance inflation factor (VIF). The VIF is an indicator of the collinearity of each variable that is dependent on the correlation coefficient R_i between the i variable and the remaining variables of the model as follows:

$$\mathrm{VIF} = 1/(1 - R_i^2), \quad (5)$$

Variables with VIF values >10 are usually considered highly collinear and removed from the set of variables [64], while variables with 5 > VIF > 3 have an admissible degree of collinearity [65,66]. One combination of three, four and five variables was selected for the assessment of the models. The selection of the multivariate models was based on the corrected Akaike information criterion (AICc) [67,68]. The model with the lowest AICc was the one considered optimal, while in the case of equal AICc between the evaluated models, the best R^2-adjusted (R^2-adj) value determined the best model.

The results of the models were evaluated regarding the relative contribution of each variable. The relative contribution of each variable was computed using the weights of the AIC scores (referred to as AICw) of all possible combinations of models for the set of variables in use, following the method described in [69]. The probabilities of occurrence of each variable can be used (AICcmodavg and relaimpo R packages) to obtain the relative importance of each variable [70], which is a metric that indicates the proportion of the variance explained by the variable within the model. The relative importance can even be expressed in relative terms so that the results can be depicted in terms of the total percentage of the variance caused by each variable.

3. Results and Discussion

3.1. Relationship between Soil Moisture and Tree Growth

The results obtained in the correlation analysis between the soil moisture and TRI (Figure 4) on a monthly scale show how the PIHA species obtained the highest correlation values throughout the months, as well as the highest percentage of samples with significant results. The maximum values, both in terms of correlation and percentage of significant samples, were obtained in May and June (median of 0.41 and 82%, respectively), as observed in previous studies [36–38]. PINI stood out for its high correlation values in the months of the previous year, while in the corresponding year, it obtained negative R values, reaching the highest percentage of significant samples in March. PISY obtained low correlation values throughout the period, with the median oscillating between −0.15 and 0.2, reaching the maximum percentage of significant samples in June-July with positive R values, while another maximum of significant samples was reached in April, but with negative values. PIUN was the species that obtained the lowest values in terms of correlation and percentage of significant samples (between −0.1 and 0.15 for the median of R and between 0 and 20% for the percentage of significant samples), except in July, when the maximum R value was obtained (median of 0.2) and the percentage of significant samples reached 40%. Therefore, the PINI, PISY and PIUN species obtained much lower percentage values of significant correlations than PIHA.

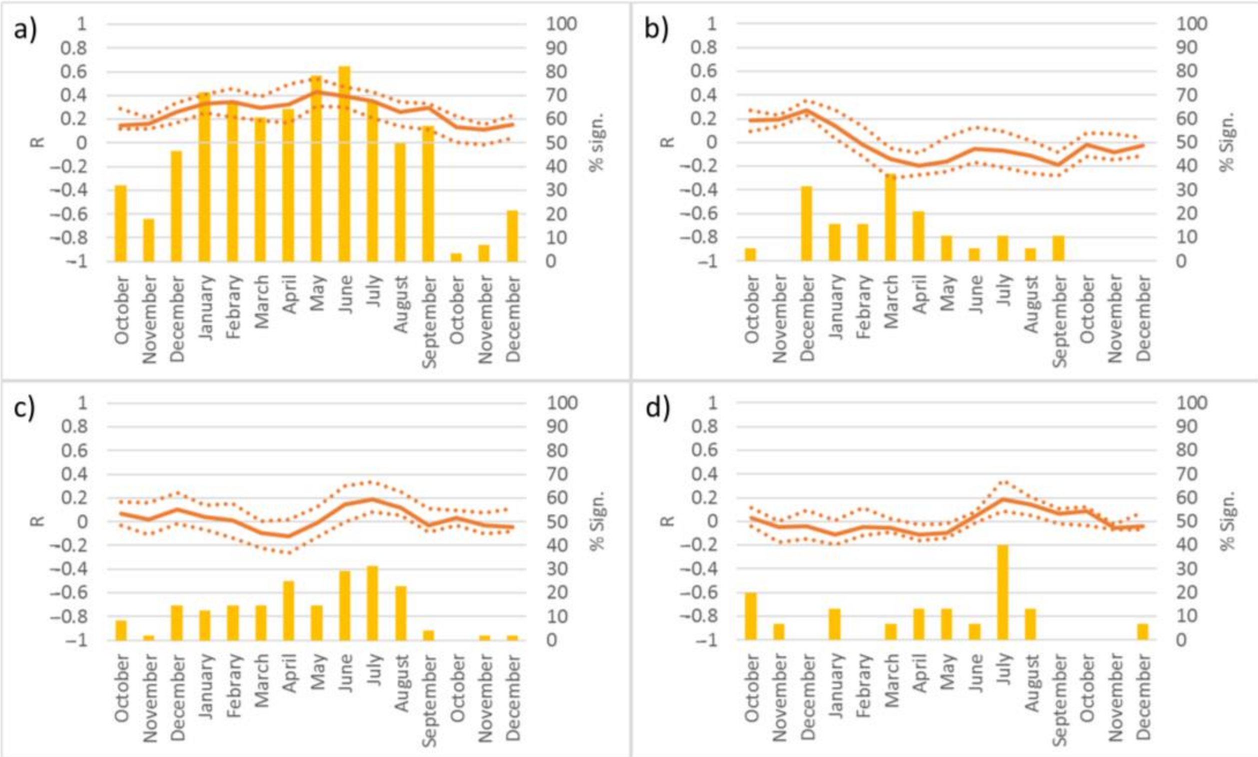

Figure 4. Monthly temporal evolution of the 75th percentile (top dashed line), median (solid line), and 25th percentile (bottom dashed line) of the coefficient of correlation (R) values between soil moisture and TRI and the percentage of significant ($p < 0.05$) cases (yellow bars) for (**a**) PIHA, (**b**) PINI, (**c**) PISY and (**d**) PIUN.

The difference among the species seems clear, with PIHA being the species that is the most sensitive to soil moisture compared to the other species, while PIUN is the least sensitive species. PINI depends, to a large extent, on soil moisture in the last months of the year prior to its growth, while in the corresponding year, it seems that excessive soil moisture may negatively affect its growth. PISY growth depends positively on soil moisture in the summer months, while in spring, it is negatively related to soil moisture.

Some studies show that the growth of these pine species is correlated with precipitation and temperature in areas with a Mediterranean climate [71]. Other studies show that soil temperature has a greater importance for the growth of pines than precipitation [72]. A study that examined how drought conditions affect the PISY species found that, although conditions are more favorable for growth in the summer, this pine grows more in the spring [73], but the study did not use soil moisture as an environmental variable. In the PIHA species, the results obtained with soil moisture in [38] show a similar behavior, with correlation values and percentages of samples with statistical significance similar to those obtained in this study, highlighting the importance of this variable compared to other climatic variables since it is the most suitable variable to characterize the growth of these pine trees. The soil water content is decisive for the growth of PIHA, and this variable is much more determinant as the environmental conditions are more arid [38].

Although variables related to soil moisture have been used to study tree growth, the absence of studies where this variable has been used to study the growth of PINI, PISY and PIUN makes comparisons difficult. However, the obtained results seem to be consistent with the species studied. PIHA is a species that is located mainly at low altitudes, where soil moisture is more critical, even more so in Mediterranean environments where water-limited conditions predominate. Therefore, it is consistent that its growth is highly dependent on soil moisture. In contrast, PIUN grows in high mountain areas (above 2000 m.a.s.l.), where other factors, such as temperature [55,74], are much more important than soil moisture. In contrast, PINI and PISY grow at altitudes between 1200 and 2000 m.a.s.l. but not as high as PIUN, and therefore, soil moisture gains slightly more prominence, although there are other factors that are even more important, such as snow water equivalent [75].

3.2. Tree Species' Response to Droughts

Resilience indices were calculated for drought episodes defined by soil moisture anomalies (Figure 5). In terms of resistance, PIHA showed values less than 1, which indicates that it is the species that is the most affected by drought events. PINI and PISY obtained values close to 1, which indicates that they are not greatly affected by droughts in terms of resistance. PIUN was the least affected by this type of event, since most of its resistance values were above 1. In terms of recovery, PIHA obtained values above 1 in all cases, which means that it recovers well after a drought event. The recovery values obtained by PINI and PISY were slightly above 1, which indicates that they once again show growth values similar to those prior to the drought event. However, the samples corresponding to the PIUN species, while not affected as much by droughts in terms of resistance, show lower recovery values. The results for both the absolute and relative resilience indices show that PIHA once again obtained the highest values, that is, it grows more than before the drought event regardless of the damage caused by the drought. Low values of resilience were obtained by PIUN, perhaps because it is the species that is the least affected by droughts in terms of recovery and resistance, as was seen before.

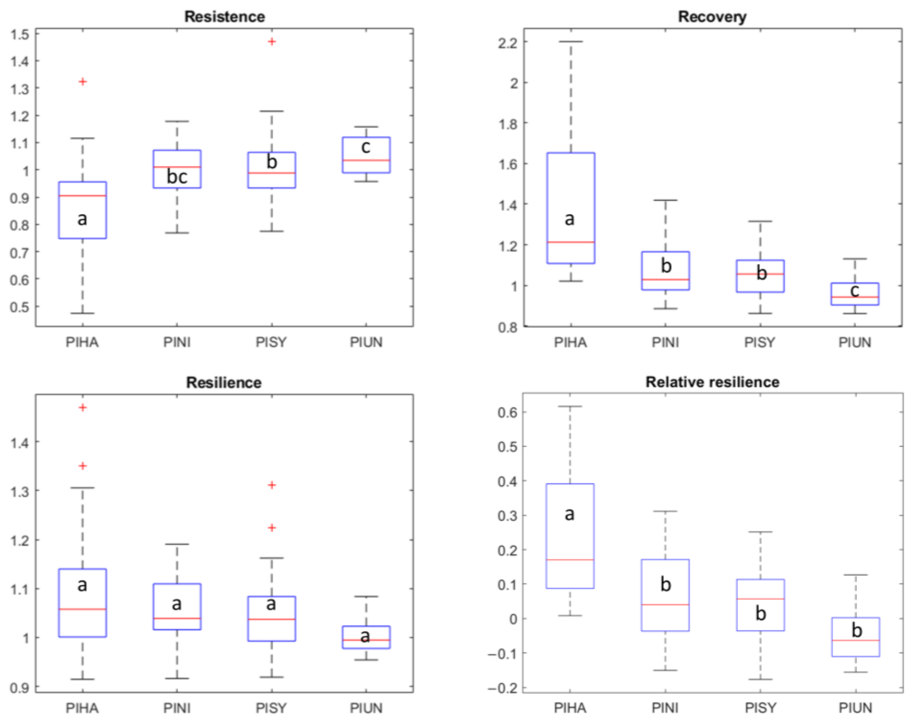

Figure 5. Resistance, recovery, resilience and relative resilience indices observed for the four studied pine species. The central lines of boxplots indicate the median value, vertical hinges indicate first and third quartiles, error bars indicate the 95% confidence interval of the median and + symbol indicate outlier values, which are values beyond the 95% confidence interval threshold. Different letters in the boxes indicate significant differences between species (Kruskall–Wallis test, $p < 0.05$).

Regarding the pattern observed in the results, PIHA showed a greater range of values for the four indices, followed by PINI and PISY, with PIUN showing the least variability. This is probably related to the spatial variability of the samples used in the study. As shown in Figure 1, PIHA is more spatially distributed over the Iberian Peninsula. In turn, PINI and PISY occupy less surface within the studied area, while the PIUN samples are only located in the northern half of the peninsula. Although it was found that the pattern of soil moisture was very similar in all areas, other factors may have a different spatial pattern and may influence these species to be more or less sensitive to droughts.

The results shown by the four pine species studied through the resilience indices are in line with those of previous studies in which the method of [52] was used. However, those studies used other drought indices or approaches and other variables, such as precipitation, mean temperature or NDVI, to study the relationship between droughts and resilience [16,28,76]. In turn, the present results are in line with those obtained in the correlation analysis shown in the preceding section. It seems coherent that PIHA, being the species that is the most dependent on soil moisture, is the one that is the most influenced by droughts. Drought events also affect the growth of both PINI and PISY, although not as much as PIHA, while PIUN, as the species that is the least dependent on soil moisture, shows a lower impact of soil drought on its growth.

These results are in agreement with the studies that demonstrated that the plastic character of pines is related to the adaptation of their cambial activity and growth rate to climate variability [59,77,78]. When subjected to soil moisture scarcity, PIHA reduces its growth, and later, when the soil water content is recovered, it properly grows again. That is, its biophysical activity stops when the climatic conditions are not favorable in terms of water availability, which demonstrates its adaptability [58]. However, this is not the case with the rest of the species studied, and according to climate change projections, those species could be more stressed by drought events in the future than PIHA [56,59].

Differential growth responses to droughts between taxonomic groups may be relevant in drought-prone and diverse regions, such as the Mediterranean basin [79].

Evergreen gymnosperms dominating the semi-arid and drought-prone areas displayed lower resistance but faster recovery than evergreen gymnosperms and deciduous angiosperms dominating the temperate and wet regions [28]. This seems to be the case for *Pinus halepensis*, which inhabits dry regions, and which displays a lower resistance to droughts but a great capacity to recover. This trade-off between forest resistance to droughts and recovery after droughts has been previously reported [16,76].

It is plausible that such a difference in the species resilience may be due to the existence of species-specific adaptations and physiological mechanisms to cope with droughts. However, the involved mechanisms remain unclear and poorly understood [25].

In this sense, the isohydric/anisohydric framework was proposed to clarify tree species in relation to their different responses to stomatal closure at different vapor pressure deficits, or leaf water potentials during droughts [25,80]. The anisohydric behavior is related with species that regulate water potential within a narrow range, reducing the cavitation risk at the cost of a reduced carbon uptake [81]. On the contrary, species with a higher isohydricity tend to decrease their water potential during droughts, allowing for trees to maintain C assimilation rates at the risk of the occurrence of hydraulic failures [82].

Within this framework, our study suggests that, along the spectrum of isohydric to anisohydric, the PIHA species will demonstrate more isohydric behavior, while PIUN will be the more anisohydric one, with PISY and PIUN located in an intermediate position.

3.3. Environmental Modulation of Pine Resilience

Some environmental factors closely related to soil moisture can also participate in the differences in drought response among the four pine species. Among them, both climatic and geographic variables are of relevance. The concurrent role of these variables was evaluated via multivariate analyses of the resistance, recovery, resilience and relative resilience indices of each tree species.

The filtering of the suitable environmental variables for the drought response of the four pine species indicated that the optimal set of variables included three climatic variables (temperature, radiation, vapor pressure deficit), soil moisture and one geographic variable among latitude, longitude and distance to the coast. The geographic variable differs depending on the resilience index and species, as shown in Table 1.

Table 1. Average R^2 values obtained from the multivariate modeling of the four resilience indices (resistance, R_t; recovery, R_c; resilience, R_s; relative resilience, RR_s) for each pine species with details of the main geographic variable included in the optimal model.

R^2	R_t	R_c	R_s	RR_s
PIHA Geo.	0.26 Latitude	0.79 Latitude	0.35 Longitude	0.09 Longitude
PINI Geo.	0.14 Coast	0.57 Latitude	0.37 Altitude	0.26 Latitude
PISY Geo.	0.19 Longitude	0.28 Longitude	0.11 Coast	0.44 Longitude
PIUN Geo.	0.11 Altitude	0.58 Altitude	0.39 Coast	0.28 Altitude

The mean R^2 obtained by the optimal model for each species (Table 1) shows the highest mean values for PIHA (R^2 = 0.37), followed by PINI and PIUN (R^2 = 0.34), with PISY showing the lowest value (R^2 = 0.26). A comparison of the R^2 values among the studied indices shows the highest values for recovery, followed by resilience, relative resilience and resistance. These results indicate that other types of factors also play a role in droughts in forests, such as the type of soil in which the trees are found or the extent of the rocky cover and soil stoniness [83].

The results of the relative contribution of the main environmental factors influencing the variance of the resilience indices shown in Figure 6 indicate differences among the pine species. PIHA is primarily driven by soil moisture both in terms of resistance and recovery (over 40% of variance explained by soil moisture). The vapor pressure deficit is the second most relevant variable for PIHA in terms of resistance, recovery and relative resilience. Radiation plays a key role in the resilience of PIHA. Geographic variables dominated by latitude and longitude play a moderate role.

The relative contribution of the energy-related variables is dominant in the case of PINI and notable in the case of PIUN. The vapor pressure deficit stands out among the rest of the variables in the case of the resistance, recovery and relative resilience indices of PINI, indicating a remarkable sensitivity of this tree species to the evaporation processes related to that variable. The geographic variable primarily contributes to the variability of the resilience of PINI. PINI is also notably influenced by radiation compared to the other three species and is the second most responsive species to temperature, after PIUN.

The relative contribution of temperature to the variance in the recovery, resilience and relative resilience indices of PIUN is high compared to the rest of the participating variables, except for the notable case of the geographic variable. The relative contributions of radiation, vapor pressure deficit and soil moisture remain low. Radiation and vapor pressure deficit fall within the range of low contribution, which is also shown by PISY.

PISY shows a reduced effect of climatic variables on the variance of the indices. Among the climatic variables, temperature and vapor pressure deficit prevail over radiation, while this last variable shows a more consistent contribution to all indices, similar to the case of soil moisture. Temperature and radiation show the largest contribution to resilience over relative resilience, recovery and resistance for this species. These results are under the uncertainty of the R^2 values shown in Table 1.

While the contribution of soil moisture is considerable for PIHA, it presents a minor influence on the variation in the four indices for the other pine species. This is consistent with the quick response to droughts that is characteristic of PIHA, which is singular on its ability to quickly halt or resume growth depending on stress, up to the point of presenting recurrent ring discontinuities [32]. However, the difference is inconsistent with the isohydric approach that PIHA has in common with PINI, PISY and PIUN and the relatively high sensitivity to xylem embolism compared to those species [84]. Among the many uncertain exogenous (e.g., fires) or endogenous (e.g., lifecycle) aspects that may be involved in this paradox observed for PIHA, physiological and phylogenetic factors have been the focus of investigation [85]. These factors reveal what confers the barely diverse PIHA with such an advanced drought response, as it is the most phylogenetically recent Mediterranean species [86].

Figure 6. Relative contribution of the different climatic and geographic variables to the total variance of the R_t, R_c, R_s and RR_s indices of each pine species. (Temperature, T; radiation, RAD; vapor pressure deficit, VPD; soil moisture, SM; geographic variable, GEO).

Nevertheless, the distinct exposure of each species to a dominant factor (e.g., soil moisture for PIHA, vapor pressure deficit for PINI, geographic variable for PISY and temperature for PIUN) reflects their different biogeographic niches and expresses their distinct traits of response to drought-induced stress. Interestingly, an individual factor seems to dominate the response of each species to droughts.

In the case of soil moisture, the plasticity of PIHA growth in relation to soil moisture implies an advantage of this pine species over the medium-altitude species (PINI, PISY) and high-altitude species (PIUN) under the scenario of decreasing trends in soil moisture in the Iberian Peninsula [87]. This result indicates that PIHA may better endure this type of sustained climate anomaly and outcompete or expand its biogeographic distribution into the low-altitude locations of PINI and PISY in soils and exposures experiencing increasing soil water restrictions [88,89].

In contrast, the temperature increase in Spain [90], while not showing a uniform trend in all time periods and areas [91,92], poses both an opportunity and a limitation to the temperature-sensitive PIUN [93,94]. However, even the relatively limited contribution of soil moisture can pose a threat, since PIUN growth is affected by snow cover, whose temporal change may alter the influence of soil moisture on this species [75], including its phenology [95]. The results imply a reduction in the biogeographic distribution of PIUN due to the limited altitudinal belt available in the Pyrenees, especially in the Iberian range, for the upward tree line shift of this species [96].

The notable responsiveness of PINI to the increasingly relevant vapor pressure deficit [97] warns against neglecting the importance of this factor on tree growth [98] in combination with soil moisture [99]. There is an increased concern about the major role of evapotranspiration processes on drought stress in areas with a Mediterranean climate [100]. Therefore, rising vapor pressure deficit levels may jeopardize the status of PINI forests, particularly among the widespread reforestation plantations of the species in Spain that are located beyond its ecological niche [101].

Finally, it was observed that the geographic variable has a remarkable influence on the variance of the four tree growth indices analyzed for PISY. This result may lead to a misperception of the endurance of the species to climate change compared to the other Iberian pines, which is at least not true compared to PINI [102]. However, until there is further evidence of such an insensitive response, the results merely imply that the variance is spurred by the geographic diversity of the species in the Iberian Peninsula [103], regardless of the samples evaluated in this study. Diversity is also high in PIUN, which is the second most affected species by geographic factors in our results. The gradient of continentality from SW to NE is correlated with longitude and coastal distance in the Iberian Peninsula [104] and may be under the geographic signal of PISY. This was corroborated in this work, since the longitude and distance to the coast are the most relevant geographic variables (Table 1).

Overall, the results illustrate the distinct response of pine species to drought events, which has implications for the long-term sustainability of medium-altitude (PINI and PISY) and high-altitude (PIUN) pine forests in Spain [105], and the favorable drought response traits found for PIHA. Recent studies [106,107] made in several European regions other than the Mediterranean one also show the limitations of the acclimatation of pine species to the changing climate.

Negative effects of an altered forest status due to droughts can propagate to the rest of the land system, from reductions or increases in water yields with consequences on water availability [108,109] to feedbacks of the land–atmosphere system [110] of these Mediterranean regions, which are increasingly prone to extreme events [111,112].

4. Conclusions

The results obtained in this research show that soil moisture is a very important variable in the growth of pines, but for the pine species that are located at higher altitudes, the influence of other environmental factors increases. In addition, for the species in which soil moisture is the most important variable for growth (*P. halepensis*), soil moisture was found to be critical in the spring months, as observed in previous studies.

In line with these results, it was found that when the growth of a pine species is more dependent on soil moisture, it is more influenced by soil drought. This means that when soil moisture is scarce, these species stop growing as they normally grow. Once the drought event passes, these species grow the most compared to the others.

It was observed that the variables that most influence the growth of pine species in the Iberian Peninsula during soil drought events, in addition to soil moisture, are temperature, radiation, vapor pressure deficit and some of the geographic variables linked to each species. Nevertheless, this study shows that soil moisture is the most influential variable on soil drought resilience in the pine species growing at lower altitudes. Similarly, in species growing at higher altitudes, energy-related variables and geographic features play a greater role in the resilience of pines after soil drought events.

The results obtained in this study can help us to understand the dynamics of existing pine species in the Iberian Peninsula in periods of soil drought and their consequences in areas with a Mediterranean climate. This study can be very valuable for the adaptive management of Mediterranean pine forests, since, as has been seen, *Pinus halepensis* seems to be a species that is particularly adapted to soil drought and, therefore, is a model species for an extension of its distribution range in Mediterranean areas. However, more research should be carried out since, according to many studies, climate change will intensely affect these areas. This scenario will make the droughts more intense and longer lasting, making these forests one of the most threatened ecosystems.

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