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Spatio-temporal patterns of defoliation in agro-forestry *Quercus ilex* L. systems

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Abstract Agroforestry systems such as holm oak (*Quercus ilex* subsp. *ballota*) dehesas face increased vulnerability due to the abandonment of sustainable practices, extreme droughts, and emerging pathogens. Despite the adaptability of *Q. ilex* to adverse conditions, signs of deterioration such as defoliation, reduced growth, and increased mortality have been observed in recent years. However, few national-wide studies have quantified the spatial and temporal components of defoliation in *Q. ilex* dehesas. This study aims to evaluate the spatio-temporal dynamics of defoliation in *Q. ilex* dehesa systems distributed across western Spain. Furthermore, we aim to study the potential effects of climate and site conditions on defoliation in *Q. ilex* stands. Defoliation was analysed over a 31-year period (1987–2018) in 254 monitoring plots, examining correlations with site variables (elevation, latitude, slope, orientation, soil texture, nitrogen, and carbon) and climate factors (temperature, precipitation). Average defoliation ranged from 17.9% to 21.5%, with northern *Q. ilex* dehesas in cooler, wetter regions exhibiting less defoliation than southern populations in harsher environments. Between 1987 and 1998, defoliation increased markedly across the region, especially in the northern dehesas of the study area (up to an 88% rise), compared to a 40–50% increase at more favourable sites. Defoliation was negatively correlated with soil nitrogen content, latitude, and elevation, and positively correlated with clay content and average annual temperature. Therefore, the forecasted harsher climatic conditions may contribute to increased defoliation of entire populations of *Q. ilex* growing in dehesas. This could threaten the persistence of these agroforestry systems and the ecosystem services provided by them, especially in the southern populations.

Keywords Climate · Site conditions · Socio-ecosystems · Decline · Crown condition

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Introduction

The vulnerability of forest ecosystems to climate change is contingent upon the climatic variation to which the ecosystem is exposed, its sensitivity, and its adaptive capacity in response to potential impacts (Füssel and Klein 2006). Forests are particularly sensitive to climate change, because the long life span of trees does not allow for rapid adaptation to environmental changes (Lindner et al. 2010). The effect of climate change factors will vary depending on, among other factors, the bioclimatic zones; and in

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this context, Spanish forest ecosystems, especially Mediterranean forests, have been and continue to be exposed to disturbances such as increased temperature and altered precipitation regimes (Peñuelas and Sardans 2021).

One of the most representative forests of the Mediterranean area is that of holm oak (*Quercus ilex* L. subsp. *ballota* [Desf.] Samp.) forest formations, which account for the largest amount of forested area on the Iberian Peninsula, covering 5,614,183 hectares, of which approximately 3.5 million hectares are dehesas (MITECO 2023). These formations extend across a wide range of climatic and edaphic conditions throughout the Iberian Peninsula. Dehesas are agro-silvo-pastoral systems resulting from the application of traditional Mediterranean forest management techniques (thinning and soil ploughing), whereby native species (*Q. ilex*, *Quercus suber* L., *Quercus pyrenaica* Willd., etc.) are either spaced out or incorporated into continuous grasslands (Gómez-Limón and de Lucío Fernández 1999). This creates a savannah-like landscape with widely spaced oak trees (around 40 trees per hectare) and open grasslands used for extensive livestock rearing (Pulido et al. 2001). Dehesas maintain an important balance between exploited resources and biodiversity conservation (Montero et al. 2000) and have been designated as habitats to be preserved under the EU Habitats Directive due to their high biological diversity. However, this diversity is increasingly threatened by climate change, extreme droughts and legacy uses (Camarero et al. 2004; Short and Hawe 2012; Pérez-Ramos et al. 2013; Moreno-Fernández et al. 2019).

To cope with these adverse factors, this key tree species of our Mediterranean forests has developed physiological defence mechanisms at leaf and xylem levels (Gimeno et al. 2009; Alderotti and Verdiani 2023). However, evidence from various studies indicates a progressive decline in *Q. ilex* (Moreno-Fernández et al. 2019; Sánchez-Cuesta et al. 2021), showing unexpectedly mediocre eco-physiological tolerance to severe droughts (Joffre et al. 2001; Martínez-Vilalta et al. 2002), poor competitiveness under intense drought conditions (Ogaya and Peñuelas 2003) and low water-use efficiency during drought (Reichstein et al. 2002). In this regard, Alderotti, et al. (2023) stated that use of water is, to some extent, dependent on the genotype. Observed symptoms of this decline include decreased diameter growth rates (Gea-Izquierdo et al. 2009), accelerated phenological phases (La Mantia et al. 2003), increased defoliation, and reduced acorn production (Olmo 2017; Garcia-Barreda et al. 2023), along with higher mortality rates due to processes known as dieback (Carnicier et al. 2011), and increased vulnerability to pathogens such as *Phytophthora cinnamomi* Rands (Corcobado et al. 2017; Sánchez-Cuesta et al. 2021).

Defoliation is an important indicator of tree health, integrating the effects of various factors such as site characteristics (soil, slope, etc.), intrinsic factors (age, phenology, etc.), biotic stress (insect pests, fungi), climatic conditions, and inadequate management practices (Carnicier et al. 2011; Sánchez-Salguero et al. 2017; Eckenscheidt et al. 2019b; Moreno-Fernández et al. 2019). The interaction of all these factors, which vary spatially and temporally, makes the study of large-scale defoliation challenging. Therefore, it is crucial to study defoliation in the same species under different site, climatic, and edaphic conditions to obtain more reliable results.

Another important aspect to consider is that defoliation studies should include long-term monitoring due to the marked intra- and interannual oscillations of this parameter in response to varying environmental conditions (Valladares et al. 2002). Obtaining long-term time series will allow trends to be identified and response dynamics to be analysed. In this regard, Spain has several monitoring networks, such as the International Cooperative Program on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests) (de Vries et al. 2003; Fischer et al. 2010). This program aims to assess the spatial and temporal variation of forest conditions with regard to natural and anthropogenic factors and to better understand the cause-effect relationships between these factors and forest ecosystem conditions (Seidling et al. 2018). Within the ICP-Forests program, defoliation is evaluated as one of the main indicators of forest health. Additionally, Spain has established parallel networks for monitoring and evaluating national parks and regional damage assessment networks.

Previous studies addressing health status or defoliation of *Q. ilex* have identified that this species, despite being able to endure a broad range of climatic conditions (De Dios Garcia et al. 2018), is also sensitive to climatic conditions (Sánchez-Salguero et al. 2017; Moreno-Fernández et al. 2019; Hernández-Lambraño et al. 2024). However,

most of the large-extent studies are based on static analyses (i.e., neglecting the temporal component), whereas the information on spatio-temporal defoliation patterns for *Q. ilex* dehesas is limited (Sánchez-Cuesta et al. 2021; López-Ballesteros et al. 2023). Among the few studies that have addressed this dynamic beyond the regional scale, the study conducted by López-Ballesteros et al. (2023) stands out for evaluating *Q. ilex* defoliation trends across 134 plots distributed throughout Spain, considering different land uses (forests vs. savannahs), topographic settings, and climatic conditions.

The objective of this study is to evaluate the spatio-temporal dynamics of defoliation in *Q. ilex* dehesa systems distributed across different regions characterized by contrasting bioclimatic and edaphic variables. Furthermore, we aim to study the potential effects of climate and site conditions on defoliation in *Q. ilex* dehesa stands. We hypothesized that hasher climatic conditions (i.e., warmer temperatures and less abundant precipitations) would be related to larger defoliation level. The results of this study will improve our understanding of dehesas dynamics and the potential effects of changing climatic conditions on the persistence of these agroforestry systems.

Material and methods

Study area and forest monitoring networks in Spain

To assess nationwide dehesa defoliation levels, data from various sources that applied a similar field protocol were analysed for the period 1987 to 2018, covering a total of 254 holm oak (*Quercus ilex* subsp. *ballota*) dehesa plots (Fig. 1). These included 54 plots from the national ICP-Forest network Level I, situated on a 16×16 km grid, 198 plots from the regional damage monitoring network on an 8×8 km grid, and 2 plots from the national parks monitoring and assessment network on a 4×4 km grid (See Supplementary Material Table SM1). The three data sources used in this study were harmonized prior to analysis to ensure comparability (Adame et al. 2022). This process included the standardization of nomenclature when the same variables had different names, the removal of non-matching data, and the use of conversion frameworks to align variables when classification categories or measurement units differed (Adame et al. 2022). The dataset structure was aligned with the ICP-Forests network format to facilitate integration and maintain consistency across datasets.

In the three forest monitoring networks used in this study, defoliation percentage was visually estimated for each tree. Defoliation was defined as the loss or absence of a certain amount of leaves resulting in

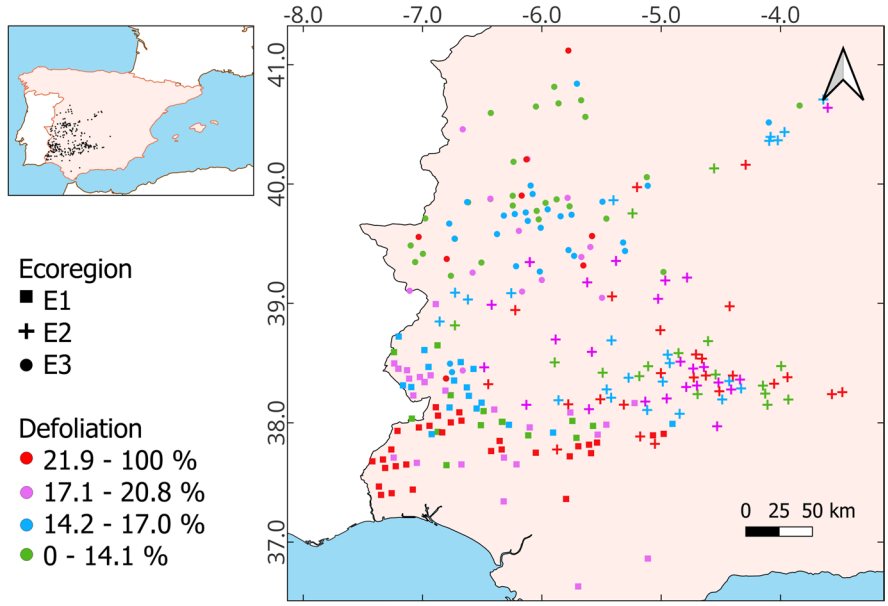

Fig. 1 Location of the plots used and their classification by ecoregion and defoliation (DEFOL). Defoliation bins were calculated using the quartiles. Ecoregions were defined using the K-medoids algorithm (see Sect. "Delimitation and characterization of the ecoregions")

incomplete canopy, compared to a perfectly healthy tree of the same species and zone following IPC Forest methodology (Eichhorn et al. 2020). This method divides the canopy frontally into four quadrants, qualitatively determining their defoliation degree and averaging the values. Defoliation is calculated in 5% increments relative to trees with full foliage. Five classes are defined: null, where there is < 10% defoliation; light, from 11 to 25% defoliation; moderate, from 26 to 60% defoliation; severe, over 60% defoliation (> 60%); and dead trees in the case of 100% defoliation. Defoliation is typically assessed for 24 trees per plot, unless site conditions restrict the assessment to fewer trees. We calculated the plot defoliation (*defol_year*) in each year as the arithmetic mean of the sampled *Q. ilex* trees in the plot, and the average defoliation over the entire period for each plot (DEFOL), i.e., the ratio of the sum of *defol_year* and the length of the monitoring period.

Environmental variables

We derived soil data from SoilGrid 2.0, which has a 250 m resolution (Poggio et al. 2021). Specifically, we focused on the pH of the water as well as the content of sand (SAND; in %), clay (CLAY; in %), nitrogen (N; in g/kg) and soil organic carbon (SOC; in g/kg) of the uppermost 60 cm of the soil. We also derived plot elevation (ELEV; in m) and slope (SLOPE; in degrees) from the EU-DEM, which is a digital elevation model covering Europe with a 25 m resolution.

Climatic data was obtained from the CHELSA 2.1 repository (Karger et al. 2017) with a 30 arcsec resolution (~ 1 km). We considered both averaged values of the climatic variables for the period 1981–2010 (climatological averages), and temporal series of monthly values for temperature and precipitation. As regards the averaged climatic variables, we considered the following: (i) mean annual daily mean air temperatures averaged over 1 year (TEMP; in °C), (ii) standard deviation of the monthly mean temperatures (TEMP.SEA; in °C/100), (iii) accumulated precipitation amount over 1 year (PREP; in mm), (iv) the precipitation of the driest month (PREP.DRIEST; in mm), and (v) the coefficient of variation of the precipitation, i.e., is the standard deviation of the monthly precipitation estimates expressed as a percentage of the mean of those estimates (PREP.SEA; in %). Furthermore, we leveraged CHELSA 2.1. monthly temporal series of precipitation and daily mean air temperatures at a height of meters to calculate the two following variables at the annual resolution: cumulative amount of precipitation (*pr*, in mm) and mean annual temperature (*tas*, in ºC), respectively. Given that the series of *pr* and *tas* are complete for the period 1979–2018, but defoliation data are only available from 1987 onwards (see Supplementary Material, Table SM1), we restricted the analysis to the period 1987–2018.

For this study, we used lower-case letters in italics for variables with temporal resolution (*defol_year, tas, pr*) while capital letters were used for variables without temporal resolution, i.e., DEFOL, soil variables (CLAY, SLOPE, NITROGEN, PH, LAT) and averaged climatic variables (TEMP, TEMP.SEA, PREP, PREP.DRIEST, PREP.SEA). See Table 1 for mean values of the selected variables.

Delimitation and characterization of the ecoregions

We used the K-medoids (namely Partitioning Around Medoids) unsupervised learning approach to classify the plots into clusters or ecoregions according to environmental variables (Kaufman and Rousseeuw 1987). This algorithm divides a dataset into clusters by reducing the distance between data points assigned to a cluster and a central point representing that cluster. We proposed the following array of environmental variables, which include averaged values of climatic variables: PH, SAND, N, SLOPE, ELE, CLAY, SOC, TEMP, LAT (plot latitude), LONG (plot longitude), TEMP.SEA, PREP, PREP.DRIEST and PREP.SEA. However, we found high levels of correlation ($|r| > 0.7$) between some of these variables and so we filtered the original array of variables, maintaining the following: CLAY, SLOPE, N, PREP, PH, TEMP.SEA, TEMP, LAT (See Supplementary Material Figure SM1). We evaluated the degree of association between DEFOL and these eight variables using Pearson's correlation coefficient and the *p-value*.

We then classified all plots into ecoregions considering the selected eight variables (CLAY, SLOPE, N, PREP, PH, TEMP.SEA, TEMP, LAT). The number of ecoregions was selected using the gap statistics after 5000 bootstrapped interactions. We ran a Principal Analysis Component (PCA) to understand more in detail as well as represent in a reduced

Table 1 Mean and standard deviation of the variables used to run k-medoids algorithm (static variables) and the additive model (dynamic variables) for the complete data set (i.e. without distinguishing among ecoregions) and for each of the ecoregions separately

	Complete dataset	Ecoregion 1	Ecoregion 2	Ecoregion 3
Static variables				
Plot defoliation (DEFOL, %)	20.4 ± 7.2	21.5 ± 7.2	20.9 ± 7.3	17.9 ± 6.6
Content of clay (CLAY, %)	23.5 ± 4.5	23.1 ± 3.4	27.0 ± 3.2	18.6 ± 2.9
Slope (SLOPE, °)	1.7 ± 1.4	1.8 ± 1.4	1.7 ± 1.3	1.7 ± 1.6
Content of nitrogen (N, g/kg)	1.4 ± 0.2	1.3 ± 0.1	1.2 ± 0.1	1.6 ± 0.2
Accumulated precipitation (PREP, mm)	568 ± 172	553 ± 166	532 ± 152	647 ± 187
PH	6.4 ± 0.5	6.2 ± 0.3	6.7 ± 0.4	6.3 ± 0.5
Temperature seasonality (TEMP.SEA, °C/100)	637 ± .43	597 ± 32	672 ± 28	643 ± 30
Mean air temperatures (TEMP, °C)	16.4 ± 1.5	17.2 ± 0.9	16.4 ± 1.1	15.1 ± 1.8
Latitude (LAT, °)	38.7 ± 0.9	37.9 ± 0.4	38.6 ± 0.7	39.9 ± 0.6
Dynamic variables				
Precipitation amount (*pr*, mm)	651 ± 214	711 ± 217	567 ± 172	687 ± 165
Mean air temperatures (*tas*, °C)	16.3 ± 1.5	17.0 ± 0.5	16.4 ± 0.6	14.7 ± 0.7

For details on the classification of ecoregions, please refer to Sects. "Delimitation and characterization of the ecoregions" (Methodology) and "Static analyses of defoliation" (Results)

two-dimensional space (biplot) the relationships between the environmental variables and the ecoregions. The two axis of the biplot were the two components accounting for the highest variation through the data. We also drew ellipses around the observations of each ecoregion.

Finally, as the studied variable met the required statistical assumptions, a one-way analysis of variance (ANOVA) was performed, followed by Tukey's HSD post-hoc test to investigate potential differences in DEFOL among the ecoregions defined above. The ANOVA analyses were conducted using IBM SPSS Statistics, version 29.0.0.0 (IBM Corp. 2017).

Dynamics of defoliation

The temporal trends of climatic variables, the defoliation dynamics (*defol_year*) of *Q. ilex* at plot level over the study period (1987–2018), and their relationships with climatic variables were also analysed.

First, we regressed *tas* and *pr* with the variable *Year* for each ecoregion to investigate whether these variables have increased or decreased over the study period. Furthermore, we calculated the annual mean values of these two variables for the study area to identify drops or peaks.

Then, we fitted an additive model where *defol_year* was the response variable while *Ecoregion, Year, tas* and *pr* were the predictors (Eq. 1).

$$(defol\_\text{year})_{itk} = \mu + Ecoregion_k + f^k\left(Year_t\right) + \beta_1 tas_{ik} + \beta_2 pr_{ik} + \sigma_i + \varepsilon_{itk} \quad (1)$$

where μ is the intercept of the model, *defol*_year is the defoliation (%) of the *i*-th plot located in the *Ecoregion k*, $f^k(Year)$ is an ecoregional smooth term (Wood 2003) where the smoothing variable is the *Year* (subfix *t*). This model formulation allows each ecoregion to have different defoliation patterns over the study period (Pedersen et al. 2019). *tas* and *pr* are climatic variables defined above and β_1 and β_2 are the unknown but estimable parameters. Finally, σ_i is a random intercept plot effect and ε_{itk} is the model error, assumed to follow a normal distribution. Given that the number of sampled trees varied among plots and years, we weighted the model by the number of sampled trees (Eickenscheidt et al. 2019a). We used Akaike's Information Criterion (AIC) and a forward stepwise procedure for variable selection fixing five points of delta AIC as the cut-off value. We plotted the partial effect plots for the final pool of variables included in the additive model.

All the statistical analyses were performed in R 4.3.3. (R Core Team 2024). In particular, we used the

following packages: "cluster" (Maechler et al. 2023) and "factoextra" (Kassambara and Mundt 2020a, b) for K-medoids and PCA analysis as well as "mgcv" (Wood 2017) and "visreg" (Breheny and Burchett 2017) for the additive model and its visualization.

Results

Static analyses of defoliation

We found that DEFOL was positively and significantly associated with CLAY ($r = 0.22$, $p\text{-value} < 0.001$) and TEMP ($r = 0.28$, $p\text{-value} < 0.001$). The correlations between DEFOL and N ($r = -0.20$, $p\text{-value} < 0.001$) and LAT ($r = -0.34$, $p\text{-value} < 0.001$) were negative and significant while DEFOL was not statistically correlated with SLOPE ($r = 0.11$, $p\text{-value} = 0.086$), PREP ($r = -0.15$, $p\text{-value} = 0.613$), PH ($r = 0.05$, $p\text{-value} = 0.386$) and TEMP.SEA ($r = -0.12$, $p\text{-value} = 0.059$). This means that stands subjected to warm temperatures and located on soils with high clay content values, i.e., soils with low permeability and high soil water holding capacity, as well as low nitrogen content are related to higher mean values for *Q. ilex* defoliation. The negative association between plot LAT and DEFOL indicates that northern stands of the studied area display less intense defoliation processes than southern stands.

The optimum numbers of ecoregions or clusters determined by the gap statistics was three (Fig. 2A). Plots classified within the ecoregion 1 (E1) were mainly located in the South-West of the study area, plots included in the ecoregion 2 (E2) were more prevalent in the East of the study area, while plots of ecoregion 3 (E3) were dominant in the North of the study area (Fig. 1). According to the PCA (Fig. 2B), E1 is the warmest ecoregion whereas E3 is the coolest and also has the soils with the highest N values. Ecoregion E2 is characterized by the highest values for TEMP.SEA, PH and CLAY. SLOPE was the variable with the lowest contribution when differentiating between the ecoregions.

The mean value for plot defoliation throughout the study period (DEFOL) was 21.5% (standard deviation = 7.2%) for E1, 20.9 ± 7.3% for E2 and 17.9 ± 6.6% for E3 (Table 1). In this regard, we found a significant effect of the ecoregion factor on DEFOL ($p\text{-value} < 0.0001$). Furthermore,

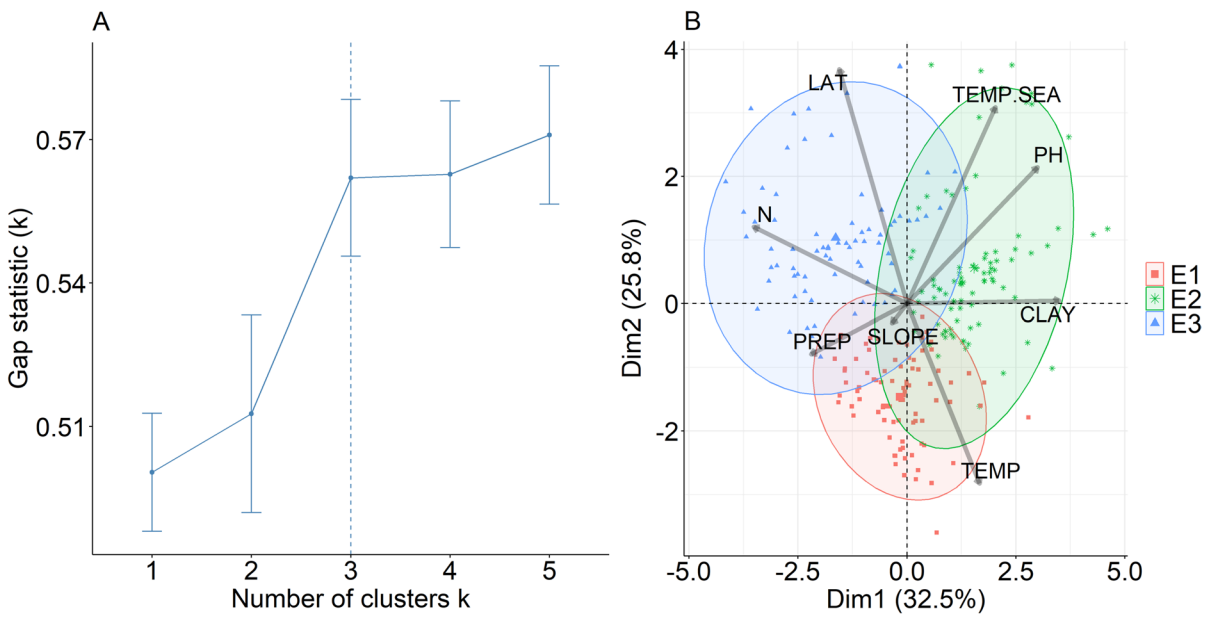

Fig. 2 A. Determination of the optimum number of clusters for the K-medoids algorithm using the gap statistics. B. PCA biplot of the variables included in the K-medoids algorithm. Colours refer to the ecoregions: red = ecoregion 1 (E1), green = ecoregion 2 (E2) and blue = ecoregion 3 (E3)

Tukey's test revealed that DEFOL for E3 was significantly lower than DEFOL for E2 ($p\text{-}value = 0.007$) and E1 ($p\text{-}value < 0.0001$) while the difference between E2 and E1 was not statistically significant ($p\text{-}value = 0.5053$).

Defoliation dynamics

No significant linear trend of *pr* was found over the study period for any ecoregion ($p\text{-}value > 0.05$). However, in the case of temperature (*tas*), we found statically significant ($p\text{-}value < 0.05$) and positive linear trends (estimation coefficient of Year for E1, E2 and E3 = 0.015, 0.014 and 0.036, respectively) for the three ecoregions, which indicates that on average, the temperature has increased over the period 1987 to 2018.

The annual average temperature (*tas*) for the study period (1987–2018) was also lower in E3 compared to E1 and E2, with the lowest average values corresponding to the period from 1992 to 2005. The temperature variation pattern was very similar across all three ecoregions, with high values in 1995, 2009, 2011, 2015 and 2017 (Fig. 3A). The annual precipitation (*pr*) also exhibited a similar variation pattern across the three ecoregions, with the lowest precipitation observed in E2. There was a notably prolonged period of low precipitation in all three ecoregions between 1990 and 1995, which coincided with the significant defoliation increase during this period (Fig. 3B and 5B). Additionally, a sharp drop in precipitation was observed in 2005, 2015 and 2017.

In all three ecoregions, the light defoliation class was the most common, accounting for 77%, 75%, and 82% of cases in E1, E2, and E3, respectively (Fig. 4). E1 and E2 presented a higher percentage of plots with moderate defoliation (20% and 11%, respectively) compared to E3.

As regards the additive model, the inclusion of all the predictors resulted in a reduction of more than five points in AIC, with the exception of *pr* (see Table 2 for the complete model formulation). The other climatic variable evaluated here, *tas*, displayed a significant and positive relationship (estimation coefficient = 0.63) with *Q. ilex* defoliation (Fig. 5A and Table 2). Figure 5B revealed that the *Q. ilex* defoliation trends differed significantly among ecoregions (p-values of smooth terms lower than 0.0001; Table 2). In the defoliation dynamics observed across the three ecoregions (Fig. 5B), it can be observed that there was a progressive increase from 1987 to 1997, although with varying intensities (a 50%, 41%, and 88% increase for E1, E2, and E3, respectively). This was followed by a stabilization period from 1998 to 2011, and then another albeit less pronounced increase between 2012 and 2018, also showing different levels of intensity (an increase of 11%, 25%, and 27% for E1, E2, and E3, respectively). Throughout the entire time series, the average defoliation was lower in E3, with the most significant difference occurring between 1995 and 2005 (Fig. 5B).

Discussion

This study provides a large-scale, long-term assessment of defoliation patterns in *Q. ilex* dehesas, offering updated insights into the spatial and temporal dynamics of forest decline in Mediterranean agroforestry systems. One of the main strengths of our approach lies in the robustness of the dataset, which spans more than three decades and integrates harmonized information from 254 monitoring plots. This comprehensive coverage enhances the reliability of the observed trends and provides a solid foundation for identifying patterns and drivers of forest deterioration across the study area.

Moreover, our results highlight the decisive role of climate and site conditions, particularly soil characteristics and temperature regimes, in shaping defoliation levels. The strong spatial signal detected, with northern populations in our study exhibiting lower defoliation compared to those located in harsher southern environments, underscores the importance of incorporating edaphoclimatic factors into assessments of forest health and vulnerability. Overlooking these site-specific variables may lead to misleading generalizations and reduce the effectiveness of conservation or adaptive management strategies. In the following sections, we discuss in detail the influence of climate and soil conditions on defoliation patterns.

Influence of climate on defoliation

Q. ilex has demonstrated an ability to activate various adaptation mechanisms in response to adverse climatic conditions (Barbeta and Peñuelas 2016). Crown defoliation can be a short-term response to

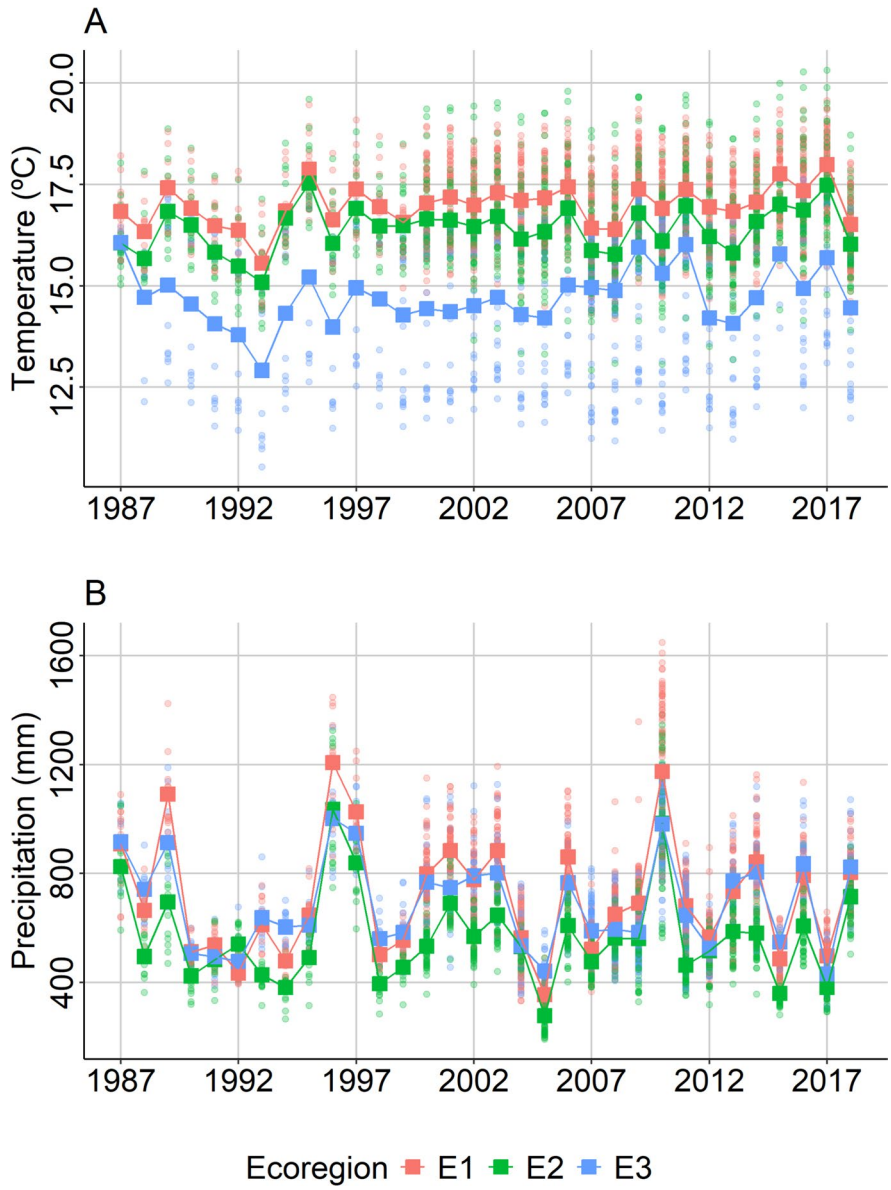

Fig. 3 Observed values (points) and mean values (squares) of the temperature (A; *tas*) and precipitation (B; *pr*) by ecoregion over the study period (1987–2018). Colours refer to ecoregions. E1 = ecoregion 1; E2 = ecoregion 2; and E3 = ecoregion 3

drought, allowing the plant to adjust its transpiration area as water availability decreases, thus preventing excessive water loss through the canopy (Montserrat-Martí et al. 2009; Bucci et al. 2012; Liu et al. 2015). However, in periods of extreme drought, significant leaf loss can reduce photosynthetic capacity, thereby decreasing carbon assimilation and leading to a reduction in carbohydrate reserves of up to 60%, which increases the long-term mortality risk (McDowell et al. 2008; Galiano et al. 2012). Defoliation as a response to periods of low precipitation combined with increased temperatures has been confirmed by various studies, showing correlations between crown defoliation in *Q. ilex* and increased water stress over the last 20 years (Peñuelas et al. 2000; Barbeta et al. 2013, 2015; Camarero et al. 2015). Similarly, our results show that dehesas in ecoregion 3 (E3), located in more favourable environments (lower temperatures, higher water availability, and situated further north of the study area), show significantly lower crown defoliation percentages compared to dehesas in ecoregions 1 (E1) and 2 (E2), which are located further south in more xeric and thus less favourable conditions for growth (Table 1). This is consistent

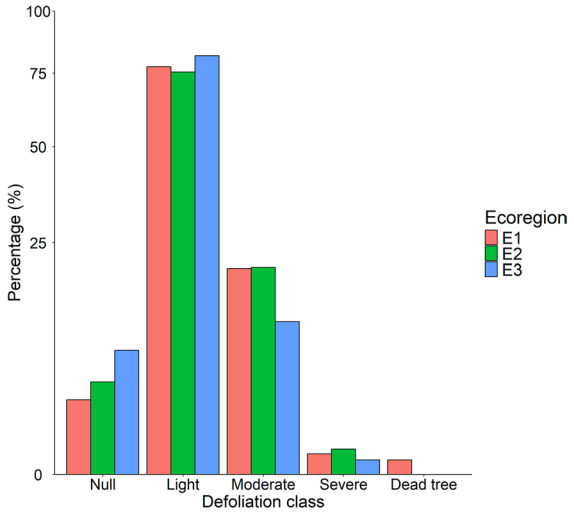

Fig. 4 Percentage of dehesas that belong to the different defoliation classes according to the three differentiated ecoregions (E1 = ecoregion 1, E2 = ecoregion 2 and E3 = ecoregion 3): Null class (defoliation < 10%), light class (11–25%), moderate class (26–60%), severe class (> 60%) and dead tree (100%)

with the findings of Moreno-Fernández et al. (2019) on dehesa decline in the western Iberian Peninsula, using health condition data from the Third National Forest Inventory. However, it is worth to note that the light defoliation class is the most common class for all the ecoregions. Our study also found a significant correlation between defoliation and annual average temperature, though no significant relationship was found with precipitation. This suggests that in the dehesas of the south-western Iberian Peninsula, temperature increments may have a greater influence on defoliation. This conclusion aligns with the findings by de la Cruz et al. (2014), and Sánchez-Cuesta et al. (2021), who also identified annual average temperature as the best predictor of defoliation percentages in dehesas, similarly concluding that defoliation varies based on the geographic location of the plots.

Variation in drought-related defoliation over time depends on both the intensity, duration and frequency of drought events. In some cases, defoliation increases during prolonged drought periods (Lloret et al. 2004; Carnicier et al. 2011; de la Cruz et al. 2014; Barbeta et al. 2015), while in other cases, it occurs during shorter periods of severe drought (Barbeta et al. 2013). In this study, the most significant defoliation increase across all three ecoregions occurred during a prolonged period of low precipitation from 1990 to 1996, coinciding with a sharp rise in temperature in 1995, when the average temperature increased by 2 °C between 1993 and 1995 (Figs. 3 and Fig. 5B). This likely led to an increase in evapotranspiration, which could have caused negative water balances. During this period (1990–1995), defoliation increased more sharply in E3 than in E1 and E2, indicating that a period of decreasing precipitation had a greater effect on dehesas located in more favourable conditions. This supports the premise that trees adapted to

Table 2 Summary of the results for the defoliation additive model

Parametric coefficients				
	Estimate	Std. error	t value	Pr (>|t|)
Intercept	10.32	2.38	4.33	< 0.0001
Ecoregion 2	− 0.31	0.59	− 0.53	0.597
Ecoregion 3	− 2.57	0.68	− 3.77	< 0.0001
tas	0.63	0.14	4.53	< 0.0001
Approximate significance of smooth terms				
	edf	Ref.df	F	p-value
$f^1(Time_t)$	8.00	8.69	44.64	< 0.0001
$f^2(Time_t)$	8.00	8.68	46.52	< 0.0001
$f^3(Time_t)$	7.45	8.38	40.42	< 0.0001
$f(Plot)$	207.12	251.00	7.75	< 0.0001
Variance explained: 54.7%				

tas mean daily air temperature; *edf* estimated degrees of freedom; *Ref.df* reference degrees of freedom

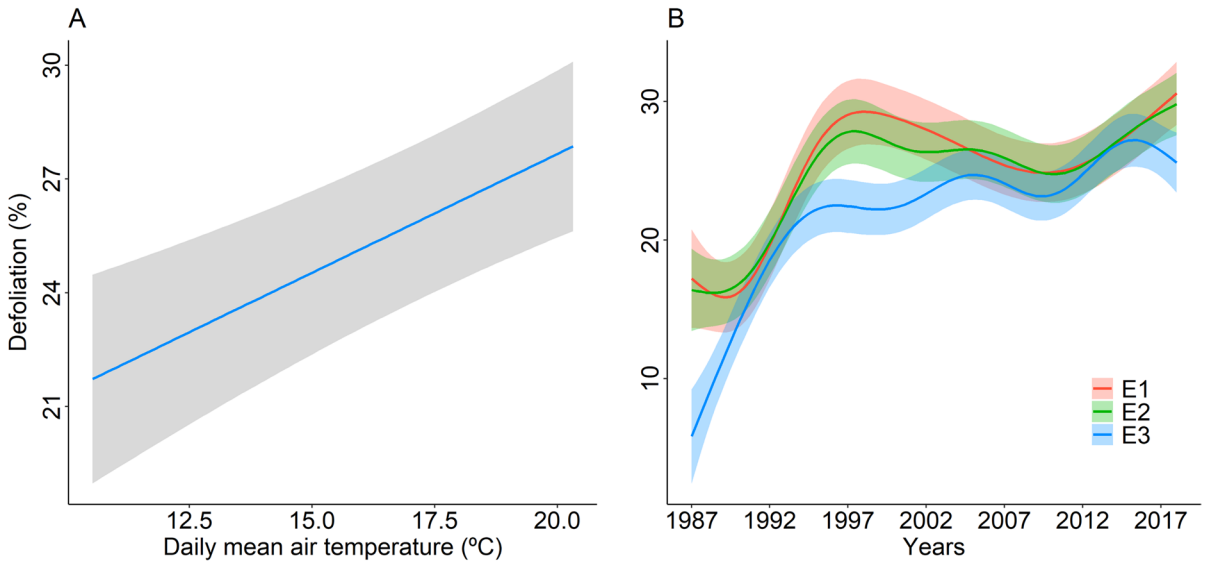

Fig. 5 Model-derived partial effects plots for daily mean air temperature (**A**) and year (**B**); colours refer to ecoregions (E1 = ecoregion 1, E2 = ecoregion 2 and E3 = ecoregion 3) defined by the K-medoids algorithm. Shaded areas refer to the 95% confidence bands. Y axis refers to the yearly defoliation (*defol_year*)

harsher conditions show greater resistance to extreme droughts (Breda et al. 2006; Barbeta and Peñuelas 2016). In 2005, there was also a significant decrease in precipitation; however, reduced water availability did not lead to increased crown defoliation, indicating that *Q. ilex* has lower tolerance to prolonged periods of low precipitation. This result is consistent with the findings of Barbeta et al. (2013, 2015), who reported 51% stem mortality in *Q. ilex* stands during prolonged droughts, compared to 5% stem mortality during shorter droughts. Sánchez-Cuesta el al. (2021) similarly concluded that defoliation is a cumulative process that primarily responds to prolonged drought periods in dehesas in the southern peninsula.

Additionally, adaptive responses are transient and can be reversed when limiting factors disappear (Oliva et al. 2014; Wolkovich et al. 2014; Domingo et al. 2020). However, in this study, no recovery was observed following the prolonged period of low precipitation (1990–1995). In E3, defoliation did not decrease and remained stable until 2011, while in E1 and E2 only a slight reduction in defoliation was observed during that time. This result was also observed by Carnicier et al. (2011), where recovery in *Q. ilex* was only partial. This finding suggests that drought produces a chronic, long-lasting and legacy effect on the crown that could limit the tree's investment in foliage production (Breda et al. 2006; Gazol et al. 2018), in addition to reducing tree resilience due to cumulative effects and decreased recovery time between drought episodes (Lloret et al. 2004; Gazol el al. 2018, 2022).

The most abundant defoliation class in the three *Q. ilex* dehesa ecoregions (78% of total dehesas) corresponded to the light defoliation class (11–25%) (Fig. 4). The average defoliation values in the three ecoregions (Table 1) were similar to those obtained by other authors for dehesas in south-western Iberian Peninsula (Sanchez-Cuesta et al. 2021; Lopez-Ballesteros et al. 2023) and in *Q. ilex* forests widely distributed across the Iberian Peninsula (Carnicier et al. 2011; Vitale et al. 2014; Sanchez-Salguero et al. 2017; Lopez-Ballesteros et al. 2023). The mean defoliation reported by Carnicier et al. (2011) for other broadleaf species located at higher northern latitudes (*Quercus- pyrenaica, Quercus robur* L., *Fagus sylvatica* L., and *Castanea sativa* Mill.) was also similar to that obtained in this study for *Q. ilex*. Despite the adverse climatic conditions present, particularly in ecoregions 1 and 2, with prolonged periods of low precipitation combined with rising temperatures, light defoliation still predominated in the dehesas. This could be attributed to the activation of several adaptation mechanisms in this species under stress

conditions, such as (1) sclerophylly, which facilitates water conservation at the cellular level (Bartlett et al. 2012); (2) stomatal closure to reduce xylem tension, with its water regulation strategy described as isohydric (Ogaya et al. 2014) or partially isohydric (Martinez-Vilalta et al. 2014), while some studies classify it as anisohydric (Baquedano and Castillo 2006; Aguadé et al. 2015) depending on the co-occurring reference species and the study context; (3) osmotic adjustment to maintain cell turgor through increased soluble sugars during drought periods (Zhang et al. 2020); (4) the development of a deep root system (Canadell et al. 1999) or (5) increasing the phenotypic plasticity of fine roots (Encinas-Valero et al. 2022), all of which may reduce leaf loss in response to stress. Additionally, tree density, which indicates greater competition for resources, positively influences defoliation (Moreno and Cubera 2008; Carnicier et al. 2011; Galiano et al. 2012; Jump et al. 2017; Rebollo et al. 2024). However, in dehesa systems with low tree density, the joint effect of drought and stand density on defoliation may be less pronounced.

Influence of soil on defoliation

In addition to climate, soil is a factor that also influences defoliation, with a positive relationship observed between defoliation and clay content. However, this result contradicts findings from other studies (Drohan et al. 2002; Martins et al. 2006; Sánchez-Cuesta et al. 2023) which found that soils with high clay content had lower levels of defoliation compared to soils with lower clay content. This discrepancy may be due to the properties of clay soils, which despite their high water holding capacity and high nutrient availability will dry out, crack, and compact easily under drought conditions, thus hindering root penetration and in turn reducing water absorption, which will negatively affect tree growth. This finding is supported by other studies which have shown that soil compaction is one of physical properties of soil that most influences the decline of *Q. ilex*, limiting root penetration and access to water in deeper soil layers (Lloret et al. 2004; de Sampaio e Paiva Camilo-Alves et al. 2013; Barbeta et al. 2015). Additionally, clay soils are also characterized by slow drainage, which can lead to waterlogging, potentially causing root hypoxia and contributing to tree decline (Jin 2023). Furthermore, various studies have confirmed that pathogens like *Phytophthora cinnamomi* Rands are more common in clayey, compact soils, which have greater base saturation and higher nutrient content, potentially leading to increased defoliation (Jönsson et al. 2005; Moreno et al. 2009; de Sampaio e Paiva Camilo-Alves et al. 2013; Corcobado 2013).

Nitrogen and organic carbon content also influence defoliation, although data for the latter were not presented due to their autocorrelation with nitrogen content in the soil. Dehesas developed on more fertile soils exhibited lower levels of defoliation, which may be because nitrogen is a nutrient known to be related to increased foliar biomass production (van den Driessche 1991; Fathi 2022). This result also suggests that under stressful conditions, defoliation tends to be higher in less fertile soils, a finding supported by other authors (Demchik and Sharpe 2000). Additionally, greater nutrient availability may improve plant defences, thereby increasing resistance to biotic attacks, which could indirectly reduce defoliation (Anderegg et al. 2015). Other authors have also reported a negative correlation between defoliation and nitrogen and carbon content in the soil for *Q. ilex* (García-Angulo et al. 2020; Sánchez-Cuesta et al. 2023).

Although the role of biotic agents such as insects and fungi in defoliation was not specifically studied in this research, the importance of these agents is well known, particularly certain pathogens like *P. cinnamomi*, which are major causes of defoliation and mortality in *Q. ilex* (Ruiz-Gómez et al. 2019; Sánchez-Cuesta et al. 2021, 2023). However, there is insufficient information on the combined effect of adverse climatic conditions and infection by these pathogens, with conflicting results having been obtained. For example, some studies have reported that plants subjected to drought have a higher probability of pathogen attack (Oliva et al. 2014; Corcobado et al. 2013). Some authors point to the impact of insects and fungi on defoliation being lower under extreme drought conditions in the case of *Q. ilex* (Carnicier et al. 2011), while others have detected no significant influence (González et al. 2020). Soil properties also influence pathogen activity. For instance, organic matter content appears to be related to increased fungal impact, which could indirectly contribute to defoliation (Sánchez-Cuesta et al. 2021).

The influence of climate on defoliation and its interaction with other factors not addressed in this

study, such as tree age or management practices, should also be mentioned. In arid environments, older trees may be more susceptible to drought or pathogen attack, leading to increased tree decline (Eickenscheidt et al. 2019b; Rebollo et al. 2024). Additionally, it has been observed that in dehesa systems with intensive silvicultural management, there is reduced regeneration, which negatively affects tree health and crown condition (López-Sánchez et al. 2018; Moreno-Fernández et al. 2019). However, Gazol et al. (2021) found that the abandonment of traditional management practices can lead to increased vegetation cover and improved soil microbial health, but at the expense of *Q. ilex* vitality and associated ecosystem services, particularly under drier and hotter scenarios. Given all of the above, it would be of interest to further explore the influence of the relationships between climate, soil, management, and biotic agents on defoliation.

Our results are supported by data from three different but harmonized monitoring networks. The consistency in average defoliation values across networks, despite differences in data collection timelines (Supplementary Material Table SM1), along with the homogeneous distribution of ecoregions in both space and time, supports the robustness of the dataset and ensures that observed patterns are not biased by sampling design or network-specific effects.

Conclusions

In dehesa systems, both geographic location and site conditions are factors that must be considered in crown defoliation studies, with mean annual temperature being the most important climatic predictor. Defoliation also appears to be associated with soil fertility and soil texture.

Long periods of low precipitation combined with increased temperatures have had a greater influence on increased defoliation compared to shorter periods. Therefore, given the potential for increased frequency of extreme events with reduced water availability and rising temperatures in the future, it would be advisable to continue developing models based on defoliation and climate data obtained from long time series. These models could help predict the interactions between climate change and the adaptive responses of *Q. ilex*, and support the implementation of appropriate dehesa management measures to mitigate the impact of adverse conditions.

Besides climate, soil, and site conditions, it would be beneficial to study other factors, such as biotic agents and agro-silvicultural management, as well as the combined effects of these factors on defoliation. Applying these factors to predictive models of defoliation dynamics patterns could be of considerable importance, as increased defoliation is a key early indicator of forest decline.

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Declarations

Competing interests The authors declare no competing interests.

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