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Local-scale factors matter for tree cover modelling in Mediterranean drylands

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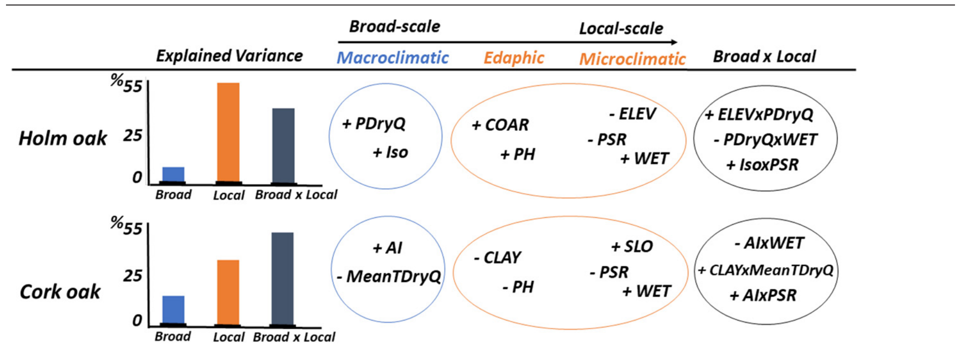
HIGHLIGHTS

- Current tree cover models focus on factors at a broad scale ignoring local-scale factors.
- We assessed the relative importance of broad- and local-scale factors on tree cover.
- Local-scale factors alone explained more variance than broad-scale factors.
- Future models must consider local-scale factors to improve forest management.

GRAPHICAL ABSTRACT



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ABSTRACT

Forests contribute directly to ecosystem structure and functioning, maintaining biodiversity, acting as a climate regulator and reducing desertification. To better manage forests, it is essential to have high-resolution forest models and appropriate spatial-explicit variables able to explain tree cover at different scales, including the management scale. Most tree cover models rely only on broad-scale variables (>500 m), such as macroclimate, while only few studies include also local-scale variables (<500 m). This study aimed to identify the importance of local-scale factors relative to broad-scale factors and identify the environmental variables at different scales that explain tree cover in oak woodlands in Mediterranean drylands. Sixty sites previously identified as being covered with Holm oak or Cork oak were stratified by precipitation. Normalized Difference Vegetation Index, used here as a surrogate of tree cover, was modelled using simultaneously broad-scale factors (macroclimate) and local-scale factors (microclimatic and edaphic conditions). The percentage of variance explained by local- and broad-scale factors and the effect size of each environmental variable on tree cover was determined for the study site. It was found that local-scale factors and their interaction with broad-scale factors explained more variance than broad-scale factors alone. The most important local-scale factors explaining tree cover were elevation, potential solar radiation, used as a surrogate of microclimatic conditions, and wetness evaluated terrain used as an indicator of water flow accumulation. The main broad-scale factors were related to temperature and precipitation. The effect of some local-scale variables in tree cover seems to increase in areas where water as a limiting factor is more important. This study demonstrates the critical importance of including local-scale factors in multi-scale modelling of tree cover to obtain better predictions. These models will support well-suited forest management decisions, such as reforestation and afforestation plans to reverse evergreen oaks decline in Mediterranean drylands.

1. Introduction

Changes in tree cover, whether due to increased tree canopy size or increased tree density, play a crucial role in decreasing drylands' susceptibility to desertification and land degradation (FAO and Plan Bleu, 2018).

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Forest cover contributes to water retention, improves soil fertility, reduces soil erosion, increases carbon sequestration, ameliorates climate conditions and maintains biodiversity and food provisioning (Aronson et al., 2009; Mitchell et al., 2014; Bugalho et al., 2016; FAO, 2019). In drylands, trees play a key role in the delivery of important ecosystem services which contribute to the United Nations' Sustainable Development Goals and the three Sister United Nations Conventions, increasing biodiversity, reducing climate change and halting desertification and land degradation. In the largely humanized Mediterranean landscapes, the distribution patterns of tree cover are multifactorial depending on factors such as precipitation, aridity, elevation, slope, the type of land use and management (Crowther et al., 2015).

To better manage the forest in Mediterranean drylands and comply with the multifunctionality potential of forests is essential to have high-resolution forest models to support decision making at the management scale. The challenge in building high spatial resolution models is to find appropriate spatial-explicit variables able to explain tree cover at different scales, including the management scale. Forest cover and tree productivity have been estimated using empirical global vegetation models. Most of these models are based on broad-scale factors, such as climate data with low spatial resolution, e.g. the aridity index and average monthly temperature and precipitation (Crowther et al., 2015; Madani et al., 2018; Nemani et al., 2003). Global vegetation models have the advantage of explaining vegetation productivity at the global scale, but they do not explain vegetation productivity at the scale needed for land management decisions. Variations in natural tree cover at the local scale are largely caused by differences in microclimatic conditions and/or edaphic factors (Maltez-Mouro et al., 2005; Príncipe et al., 2014; Wu and Archer, 2005; Ukkola et al., 2021). Although the importance of these local-scale factors is recognized, and data are often available (e.g., Costa et al., 2008; David et al., 2007), they are rarely included in tree cover spatial explicit models (e.g., Fricker et al., 2019; Bennett et al., 2020). These predictive models of forest cover potential at the local scale are needed for precision forest management across different site conditions, especially in areas with topographic complex terrains, where local abiotic conditions (e.g., potential solar radiation) are changing within a few meters (Alexander et al., 2016; Miller and Franklin, 2002; Príncipe et al., 2014; Zellweger et al., 2020). Previous works (Príncipe et al., 2014, 2019) showed that tree cover varied considerably at the local scale, within a few meters, from up to 90% tree cover in the northern slopes to less than 20% in south slopes, even after 60 years of natural regeneration. This considerable variation in tree cover was mostly explained by topographic variables with 10 m spatial resolution (Príncipe et al., 2014). However, it is still missing information about how these changes in tree cover at the local scale compare with the changes in tree cover due to variation in broad-scale drivers and whether there is an interaction between drivers acting on the local- and broad-scales.

Environmental variables influence tree cover at different spatial scales. The appropriate scale of analysis depends on the variance of environmental variables over space (Box, 1995; Copeland et al., 2021). While climatic data available at lower spatial resolutions do not have enough spatial variation to explain vegetation patterns at local scales, topographic and edaphic factors are useful as surrogates of temperature and humidity at this scale. Recently, the high spatial resolution of digital elevation models (DEM) obtained from remote sensing data (e.g. satellite radar, Airborne LiDAR), led to the development of new spatially explicit surrogates of edaphic and microclimatic indicators (e.g., Lenoir et al., 2017; Zellweger et al., 2019). Soil physical and chemical properties can have high variability at local scales and are important drivers of tree species distribution and performance patterns, influencing water retention capacity and limiting tree root development (Brady and Weil, 1999; Fisher and Binkley, 2000). Despite its importance, edaphic data are challenging to obtain with a high spatial resolution for large areas. Spatially explicit models are estimating soil physical properties for 100 m^2 to 500 m^2 resolution (e.g., Ballabio et al., 2016) and are being used as a factor to better understand vegetation distribution (e.g., Sanchez-Ruiz et al., 2018). Similarly, climatic data at the local scale can be estimated using proxies of climatic conditions close to the ground using topographic indices derived from the DEM (Lenoir et al., 2017; Zellweger et al., 2019). For example, potential solar radiation derived from topography (Fu and Rich, 2002) at high spatial resolution (10 m) proved to be an important environmental factor to model tree cover (Príncipe et al., 2014), tree height (Fricker et al., 2019) and tree mortality (Dorman et al., 2015). These high-resolution topographic variables have the advantage of being spatially explicit and globally available at the local scale.

Modelling forest cover with both broad- and local-scale factors is particularly important in Mediterranean areas, where water is a strong limiting factor. Mediterranean evergreen oak woodlands exhibit different vegetation spatial structures, from open woodlands in silvopastoral systems to more closed woodlands and dense forests with lower disturbance intensity (Aronson et al., 2009; Pinto-Correia et al., 2011; Acácio et al., 2017). Moreover, these ecosystems are submitted to many pressures such as agriculture intensification, overgrazing, climate change, fire and desertification (FAO and Plan Bleu, 2018; Godinho et al., 2016). Indeed, in the last decades, increasing tree decline and decreasing natural regeneration of key tree species have been observed in Mediterranean evergreen oak woodlands (Aronson et al., 2009; Brasier, 1999). The functioning of these ecosystems is largely maintained by tree key species of evergreen oaks, namely Holm oak (*Quercus* [*ilex*] *rotundifolia* Lam.) and Cork oak (*Quercus suber* L.), which will be the focus of our work. Although Holm oak and Cork oak distribution models are available, they are not comparing broad- and local-scale factors importance (Hidalgo et al., 2008) and often make predictions to spatial resolutions equal or larger than 1 km (e.g., López-Tirado and Hidalgo, 2018; Vessella and Schirone, 2013; Paulo et al., 2015). Therefore, a critical step towards more precise tree cover predictions is the development of models with spatial explicit outputs with high spatial resolution and that integrate different spatial scales (Crowther et al., 2015; Franklin et al., 2013; Hannah et al., 2014; Copeland et al., 2021).

This study aims to determine the importance of broad- and local-scale factors and estimate the relative importance of relevant environmental variables on Holm oak and Cork oak cover distribution in Mediterranean drylands. The hypothesis of this study is that local-scale factors are critical for tree cover in Mediterranean woodlands. Sites over a precipitation gradient were selected and environmental variables were measured at different scales (broad- and local-scale factors) to model Normalized Difference Vegetation Index (NDVI) used as a surrogate of Holm oak and Cork oak cover.

2. Material and methods

2.1. Study area

The study area included the region in the southwest Iberian Peninsula dominated by Holm and Cork oak forests (Fig. 1 A and B). The National Forest Inventory (NFI) 2005/06 (AFN, 2010) and the Land Use and Land Cover Map of Continental Portugal (COS) 2007 v2.0 (DGT, 2010) were the basis for the sampling sites selection. The forest type in the NFI is defined systematically in a mesh grid of 500 m with field validation over a grid of 2 km. The forest classification considers tree species with a minimum height of 5 m and 10% tree cover within a minimum area of 0.5 ha. The tree species that dominates at least 75% of the sampling site is classified as dominant. COS uses a minimum of 1 ha as a cartographic unit classified according to dominant land use occupation in 75% of the area. In COS the land use occupation classified as "forest" includes a minimum of 30% tree cover with 5 m tree height, where the undercover was not explicitly used for farming. Both datasets have been combined because while NFI has more precise data with field validation in a regular grid of 500 m, COS has high detailed vectorial maps with high spatial resolution on the extent of the land use occupations. The following common criteria were used to select all the sites where: i) tree species had principal and secondary occupation of Holm oak and Cork oak (NFI) and land cover classified as Holm oak or Cork oak forests and no sign of crop cultivation in the understory (COS); ii) no record of fires since 1990 (National Cartography of Burned Areas: ICNF, 2021) and iii) mean slope between 9 and 25°, to select topographic complex areas

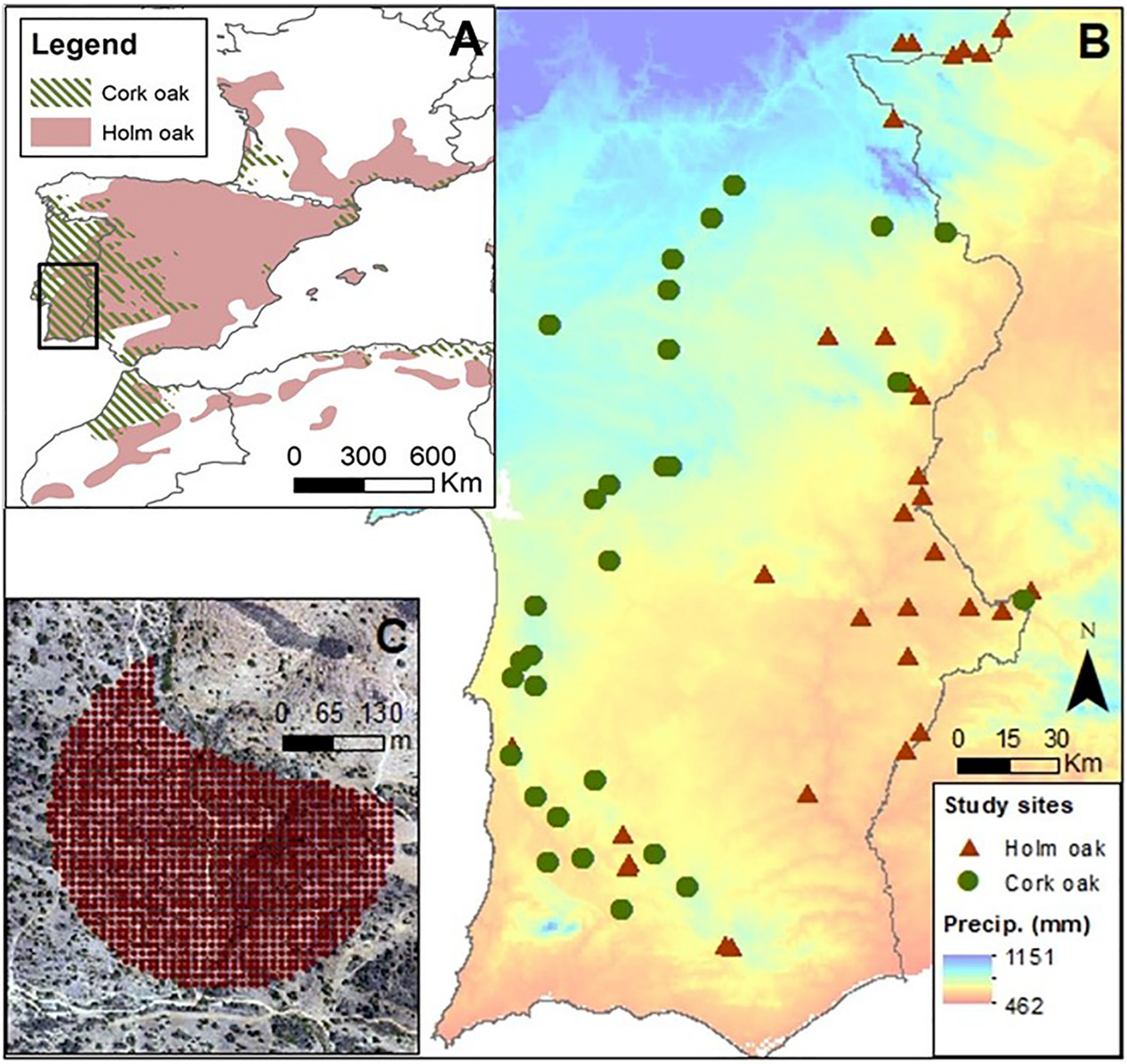

Fig. 1. A. General location of the study area (black square) and distribution range of Holm oak or Cork oak (Gil and Varela, 2008; Caudullo et al., 2017). B. Distribution of the 60 sampling sites along a precipitation gradient within semi-arid and dry-subhumid climates (WorldClim v2.0, 1970–2000, Fick and Hijmans, 2017). C. Detail of one sampling site within the sampling of 10 × 10 m grid of points. For detailed information about the 60 sites see Supplementary Material A Table A.1.

where farming is most likely to be excluded due to the difficult accessibility (Supplementary material A Fig. A.1). The sites were stratified by mean annual precipitation (1970–2000) collected from WorldClim dataset (Fick and Hijmans, 2017), to access different macroclimatic conditions in the semi-arid and dry-subhumid climates of the southwest of the Iberian Peninsula. Sixty sampling sites were selected, 31 sites dominated by Holm oak cover and 29 sites dominated by Cork oak cover, with 11.7 ha on average (Fig. 1 B). The selected sites were then visually inspected using orthophotos from 2004 to guarantee the presence of tree cover and low management intensity in the understory. Over the sampling sites, mean annual temperature ranged from 15 to 17 °C, mean annual precipitation from 525 to 704 mm, and elevation ranged between 50 and 482 m (for a detailed description of sampling sites see Supplementary Material Table A.1). To assess tree cover at high spatial resolution a grid of points (10 × 10 m, 1200 sampling points on average) was used for each sampling site (Fig. 1 C).

2.2. NDVI as tree cover surrogate

Normalized Difference Vegetation Index (NDVI) was chosen to assess tree cover and overall tree condition of Holm oak and Cork oak in the study sites because it is widely used; it is available over time and space with high spatial resolution and is an efficient tool to assess areas that are difficult to sample in the field (e.g., private properties, hilly sites). Moreover, NDVI obtained from remote sensing has a significant relation with Holm oak and Cork oak cover under different tree density levels, as already shown by other studies (e.g., Carreiras et al., 2006; Godinho et al., 2017; Soares et al., 2018). Specifically, NDVI showed a good performance on predicting Holm oak cover in sites with high topographic complexity and with low management intensity (Soares et al., 2018) which are similar conditions to the sampling sites. Moreover, the sampling sites were individually verified using orthophotos from 2004 to guarantee the presence of tree cover and low management intensity in the understory. For NDVI determination, seven Sentinel-2A Level-1C (L1C) remote sensing images from late July to mid-August 2017 were used, which represented the driest season in the Mediterranean basin when only the evergreen vegetation is present. Tiles 29SND, 29SNC, 29SNB, 29TPE, 29SPD, 29SPC and 29SPB were downloaded from the ESA Sentinel Scientific Data Hub. Sentinel-2A L1C products have a 10 × 10 m pixel resolution with 13 multispectral bands (Copernicus Sentinel data, 2017, processed by ESA) and were extracted with less than 10% cloud cover. Sentinel-2 Toolbox (Sentinel

Application Platform, SNAP v5.0.0) was used for atmospheric correction and NDVI deriving. The NDVI was calculated using the following equation: NDVI = (NIR − Red) / (NIR + Red), where NIR is the near-infrared and Red is from the visible light spectrum.

2.3. Environmental variables

The division of environmental variables in broad-scale factors and local-scale factors was based on the sampling units of the sampling design which used the mesh grid of 500 m from the National Forest Inventory. Also, this division took into consideration the scale of variation of the environmental variables over space. The environmental variables classified as local-scale factors were the ones with variation within the 500 m and broad-scale factors the ones that varied over 500 m. While climatic variables have great variability at broad scales, microclimatic and edaphic factors have greater variability at the local scale. Therefore, seventeen variables were measured at different scales that potentially affect tree cover in topographic complex areas in Mediterranean woodlands. Topographic and edaphic variables with a resolution equal or lower than 500 m were considered local-scale factors, as is common in other studies in Mediterranean forests (e.g., Bacaro et al., 2008; Mammola et al., 2019), because of their high importance for tree cover at local scales (Fricker et al., 2019; Príncipe et al., 2014; Abadie et al., 2018).

Environmental variables were grouped according to their resolution: macroclimatic variables (broad-scale factors), microclimatic variables and edaphic variables (local-scale factors) (Table 1). Macroclimatic data, here defined as the climate at a broad scale, included the aridity index (Trabucco and Zomer, 2019), temperature and precipitation data available in WorldClim v2 (Fick and Hijmans, 2017), averaged for a period of 30 years from 1970 to 2000. Topographic vector data, derived from hypsometric curves of 10 m, (1:25,000 Portuguese Military Map M888 series from 2000 to 2010) were used to generate a raster digital elevation model for the study area with 10 m pixel resolution. This was used to calculate four microclimatic variables (Table 1): i) annual sum of potential solar radiation in 2017 (PSR) (Fu and Rich, 2002), i.e. the potential amount of solar radiation that reaches a surface on the ground with a clear sky (WH/m^2) calculated with Solar Analyst ArcMap tool (ESRI, 2018; Fu and Rich, 2002), ii) elevation (ELEV), iii) slope (SLO) and iv) wetness evaluated terrain (WET) (Neves, N., description in Supplementary Material B), which relates the upslope water contributing areas inside a drainage basin with the vertical distance to the water body and the natural logarithm of absolute terrain elevation. Soil texture (clay and coarse) and pH were selected as edaphic factors with potential impact on tree cover of Holm oak and Cork oak. Soil texture was available at finer scales (500 m^2 pixel resolution) at the European level. This database consists of physical characteristics of topsoil (top 20 cm), divided into soil texture classes: percentage of clay (CLAY) and coarse sediment grain size (COAR). These soil texture maps were obtained by the combination of LUCAS topsoil survey (Tóth et al., 2013), which includes 19,857 topsoil samples in 25 Members of the European Union collected in 2009, with climatic and land cover covariates (Ballabio et al., 2016). The soil pH was obtained from Pena et al., 2015 which integrates the Soil Map for Portugal (1:50,000, SROA/CNROA series published in 1973) and the LUCAS topsoil survey (476 points for Portugal in 2009, Tóth et al., 2013). The edaphic variables were extracted from the European Soil Data Centre (ESDAC, http://esdac.jrc.ec.europa.eu/; Panagos et al., 2012) and EPIC WebGIS (http://epic-webgis-portugal.isa.ulisboa.pt/) (Table 1). All the geospatial data collection and management was performed using ArcMap v.10.6 (ESRI, 2018).

2.4. Statistical analysis

The influence of macroclimatic, microclimatic and edaphic variables on NDVI of Holm oak and Cork oak derived from Sentinel-2A images was modelled using Linear Mixed Models (LMMs) (Zuur et al., 2009). Site (ID, Table A.1) was included as a random factor in all models. A grid of sampling points (10 × 10 m, total N = 75,878) nested within sites (N = 60) was used in statistical analysis to account for the hierarchical structure of the data. The selection of the fixed effects in the model was done using Maximum Likelihood estimation but in the final model selection, Restricted Maximum Likelihood was used instead (Zuur et al., 2009). The continuous explanatory variables were standardized before analysis using the Z score (Zuur et al., 2009). Variance Inflation Factors (VIF) were used to test for model multicollinearity (Zuur et al., 2009). The variables more strongly correlated were selected in pairs, where the variable with higher biological meaning was primarily considered to be included in the model. The selected variables included in the models had a Spearman correlation coefficient < 0.70 and VIF < 2 (correlations among predictors and VIF values are in Supplement Material Fig. A.2 and Table A.4, respectively). The significance of two-way interactions within broad-scale and local-scale variables were tested using the selected variables. The last step for the final selection

Table 1
Environmental variables used to model Holm oak and Cork oak cover. The variables range corresponds to the variation of the sampling points within the sampling sites (10 × 10 m, N = 75,878).

		Variable (units) [abbreviation]	Variables range (mean, standard deviation)		Source (resolution)
			Holm oak	Cork oak	
Broad-scale factors	Macroclimatic	Global Aridity Index [AI]	4189–6804 (4979, 697)	4446–6489 (5559, 543)	Trabucco and Zomer, 2018 (1 km, 1970–2000 period)
		Annual Mean Temperature (°C) [AMT]	15.44–17.27 (16.32, 0.39)	15.52–16.77 (16.20, 0.32)	WorldClim v2.0 (Fick and Hijmans, 2017) (1 km, 1970–2000 period)
		Mean Diurnal Range (°C) [MeanDR]	8.93–12.22 (11.28, 0.74)	9.03–12.15 (10.20, 0.71)	
		Isothermality (°C) [Iso]	39.63–46.80 (43.24, 1.77)	40.14–45.36 (43.61, 0.93)	
		Temperature Seasonality (°C) [Tseason]	432.3–619.5 (544.2, 42.11)	420.6–578.8 (486.2, 39.9)	
		Mean Temperature Driest Quarter (°C) [MeanTDryQ]	21.35–24.60 (23.19, 0.79)	21.43–23.48 (22.26, 0.45)	
		Mean Temperature Coldest Quarter (°C) [MeanTColdQ]	9.25–11.13 (10.11, 0.52)	9.17–11.55 (10.64, 0.63)	
		Precipitation Seasonality (mm) [Pseason]	55.39–69.16 (60.80, 4.21)	54.43–69.43 (63.33, 4.09)	
		Precipitation of Wettest Quarter (mm) [PWetQ]	227–299 (253.8, 21.38)	241–305 (280.8, 16.53)	
		Precipitation Driest Quarter (mm) [PDryQ]	20–36 (28.1, 4.84)	18–38 (27.39, 5.53)	
Local-scale factors	Edaphic	Clay soil (%) [CLAY]	6.50–26.92 (15.98, 3.94)	5.67–27.30 (14.88, 4.48)	European Soil Data Centre (Panagos et al., 2012; Ballabio et al., 2016) (500 m)
		Coarse soil (%) [COAR]	16.73–40.61 (28.62, 4.78)	11.25–42.19 (22.43, 5.06)	
		Soil pH [pH]	4.25–7.75 (5.35, 0.69)	4.0–7.75 (5.16, 0.93)	Pena et al., 2015 (1:25,000, 25 m)
	Microclimatic	Elevation (m.s.l.) [ELEV]	98.44–508.83 (227.69, 77.94)	26.44–445.82 (198.61, 101.7)	DTM derived from hypsometric curves of 10 m, Portuguese Military Map M888 series (10 m)
		Potential Solar Radiation (WH/m2) [PSR]	745,588–1,397,805 (1,180,346, 99,447)	805,469–130,961 (1,187,375, 94,222)	
		Slope (°) [SLO]	0–39.4 (13.507, 6.74)	0–32.75 (12.1, 5.99)	
		Wetness Evaluated Terrain [WET]	0.29–11.20 (1.8, 1.4)	0.51–10.87 (1.86, 1.31)	

of the variables to be included in the model was based on their importance, extracted using the sum of weights (Burnham and Anderson, 2002). Then, the predictors with their importance lower than 1 were excluded from the final models for Holm oak and Cork oak. The variance explained (R^2) by the final models was calculated using marginal R^2 (R^2m), i.e. variance explained by fixed effects only, and conditional R^2 (R^2c), i.e. variance explained by both fixed and random effects (Nakagawa and Schielzeth, 2013). The best fifteen models that resulted from the combination of the selected variables in the final model are available in Supplement Material Tables A.2 and A.3.

The final models were checked for the distribution of residuals and controlled for the absence of spatial autocorrelation using the Moran I Test. The goodness-of-fit of the models was evaluated using the root mean squared prediction error (RMSE) calculated by repeated 10-fold cross-validation (RMSE < 0.8 indicates good fit of the model). The model estimates, standard errors, p-values, variance inflation factors and variable importance values, are available in Supplement Material Table A.4.

The relative importance of predictor variables was estimated using the overall explanation of broad- and local-scale factors and the individual explanation of each selected variable in the final model. The percentage of variance explained by broad and local-scale factors, and their interaction was determined using a variance partitioning analysis based on the final model. Afterwards, the effect size of each variable on the prediction of Holm oak and Cork oak cover was estimated. The parameters and the associated averaged coefficients were estimated using a model averaging approach, calculated by the function "model.avg" from the MuMIn R package (Barton, 2020). All analyses were done in R version 4.0.2 (R Core Team, 2020) using packages Hmisc (Harrell Jr, 2020), nlme (Pinheiro et al., 2020), MuMIn (Barton, 2020) and cvTools (Alfons, 2012).

3. Results

Tree cover in the study sites was measured using NDVI as a surrogate. NDVI values in the study sites ranged from 0.03 to 0.96 (mean 0.41, standard deviation 0.16) for Holm oak and from 0.05 to 0.99 (mean 0.51, standard deviation 0.17) for Cork oak. Overall, local-scale factors together showed higher relative importance, in explaining Holm oak and Cork oak cover, than broad-scale factors. The local-scale factors alone explain most of the variance for Holm oak cover (52% of the marginal $R^2 = 0.22$) (Table 2). The interaction between broad- and local-scale factors explained 39% and broad-scale factors alone 9% of the proportion of the relative variance. On the other hand, the interaction between broad- and local-scale factors was the main factor explaining the Cork oak cover (49%), followed by local-scale factors (35%) and broad-scale factors (16%) (Table 2).

The models for Holm oak and Cork oak cover included 7 environmental variables with different scales and 3 variables interactions. Holm oak was explained by precipitation of driest quarter, isothermality, coarse soil, soil pH, elevation, potential solar radiation and wetness evaluated terrain. Moreover, three interactions within the former variables were also significant: i) elevation and precipitation of driest quarter, ii) wetness evaluated terrain and precipitation of driest quarter and iii) isothermality and potential solar radiation. The environmental variables explained 22% of the variance of Holm oak cover (R^2m = 0.22), but with random effects, the model explained 85% (R^2c = 0.85), with RMSE of 0.10 (Supplement Material Fig. A.3). The precipitation of driest quarter, elevation, potential solar radiation and the interaction of precipitation of driest quarter and elevation were the variables with the highest effect on modelling tree cover of Holm oak ($PDryQ_{avr.coef.} = 0.044$, $ELEV_{avr.coef.} = -0.074$, $PSR_{avr.coef.} = -0.044$ and $ELEVxPDryQ_{avr.coef.} = 0.043$) (see the abbreviation in Table 1, Fig. 2). All the variables included in the model that explained Holm oak were positively related, except for potential solar radiation, and elevation that had a negative effect. The precipitation of the driest quarter showed a significant positive interaction with elevation ($PDryQxELEV_{avr.coef.} = 0.042$) and a weaker negative interaction with wetness evaluated terrain ($PDryQxWET_{avr.coef.} = -0.013$). This means the higher the precipitation of the driest quarter, the stronger the negative effect of elevation on Holm oak cover. A weak positive interaction was found between isothermality and potential solar radiation, meaning that the negative effect of solar radiation exposition on tree cover is stronger in more isothermal areas (i.e., areas where daily temperature oscillations are higher relative to the annual temperature oscillations).

Cork oak cover was explained by aridity index, mean temperature of driest quarter, clay content in the soil, soil pH, slope, potential solar radiation and wetness evaluated terrain. Three interactions within the former variables, were significant and also included in the model, the interaction between i) clay content in the soil and mean temperature of driest quarter, ii) aridity index and wetness evaluated terrain and iii) aridity index and potential solar radiation. The environmental variables explained 48% of the variance of Cork oak cover (R^2m = 0.48), but the overall explanation of the selected model with the random effects was 86% (R^2c = 0.86), with RMSE of 0.13 (Supplement Material Fig. A.3). Cork oak cover decreased significantly with mean temperature of driest quarter (avr.coef. = −0.196) and potential solar radiation (avr.coef. = −0.036). The significant negative relations were with soil clay content and pH (avr.coef. =

Table 2
Summary of the best models selected examining the effects of the predictor variables on the NDVI of Holm oak and Cork oak, using Restricted Maximum Likelihood method. The proportion of the explained variance by macroclimate, edaphic and microclimate was calculated using a variance partitioning analysis based on each model, *** p-value < 0.001 (*t*-test).

Predictors			Holm oak		Cork oak	
			R^2m = 0.22 R^2c = 0.85		R^2m = 0.48 R^2c = 0.86	
			Coeff.	Prop. explain. var. (%)	Coeff.	Prop. explain. var. (%)
Broad-scale factors	Macroclimatic	Intercept	0.41***	9	0.53***	16
		Precipitation of Driest Quarter	0.04***			
		Isothermality	0.02***			
		Aridity Index			0.11***	
		Mean Temperature Driest Quarter			−0.20***	
Local-scale factors	Edaphic	Coarse soil	0.02***	52		35
		Clay soil			−0.02***	
		Soil pH	0.02***		−0.02***	
	Microclimatic	Elevation	−0.07***			
		Slope			0.02***	
		Potential Solar Radiation	−0.04***		−0.04***	
		Wetness Evaluated Terrain	0.01***		0.04***	
Broad-scale × local-scale factors		Elevation × Precipitation of Driest Quarter	0.04***	39		49
		Precipitation Driest Quarter × Wetness Evaluated Terrain	−0.01***			
		Isothermality × Potential Solar Radiation	0.01***			
		Clay soil × Mean Temperature Driest Quarter			0.04***	
		Aridity Index × Wetness Evaluated Terrain			−0.02***	
		Aridity Index × Potential Solar Radiation			0.05***	

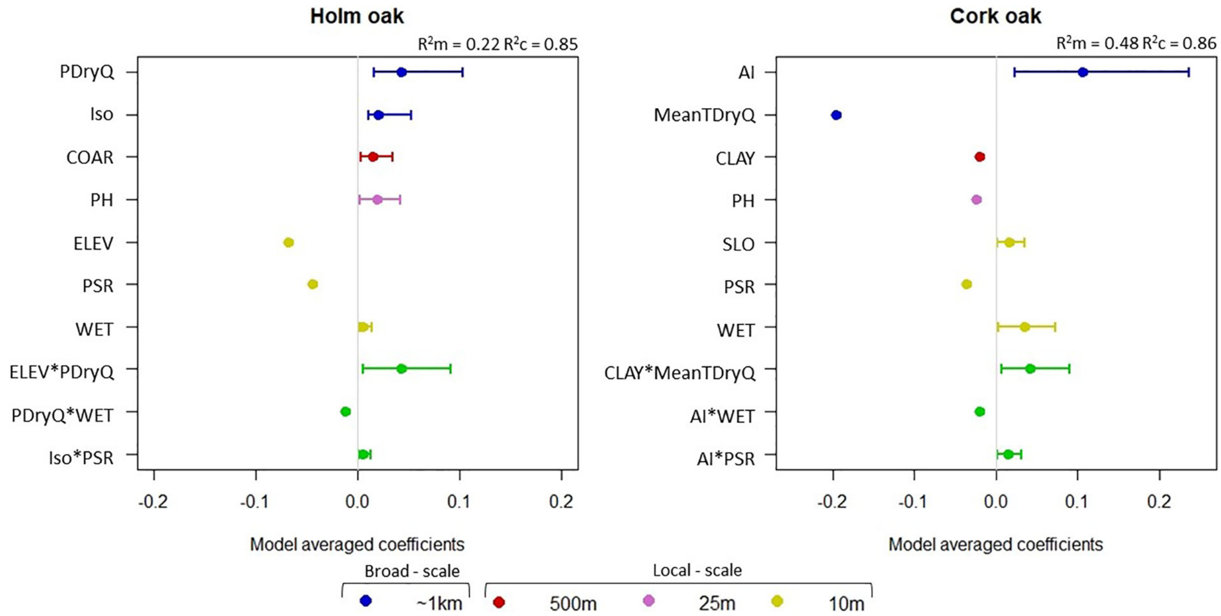

Fig. 2. Standardized model-averaged coefficients of predictor variables of Holm oak and Cork oak cover. Coefficients were averaged across models, means and 95% confidence intervals are shown. Different colours represent the different scales of the environmental variables (blue, 1 km resolution; red, 500 m; pink, 25 m and yellow, 10 m). AI Aridity Index, Iso Isothermality, MeanTDryQ Mean Temperature Driest Quarter, PDryQ Precipitation Driest Quarter, CLAY Clay soil, COAR Coarse soil, PH Soil pH, ELEV Elevation, PSR Potential Solar Radiation, SLO Slope, WET Wetness Evaluated Terrain.

−0.024). On the other hand, the Cork oak cover increased significantly with wetness evaluated terrain (avr.coef. = 0.036) and with slope, but with a weaker influence (avr.coef. = 0.017). Clay content in the soil has significant positive interaction with the mean temperature of the driest quarter on the Cork oak cover (avr.coef. = 0.042). Therefore, the higher is the soil clay content, the stronger the effect of the mean temperature of the driest quarter on the Cork oak cover. The aridity index showed a weaker interactions with wetness evaluated terrain (avr.coef. = −0.020) and potential solar radiation (avr.coef. = 0.015).

4. Discussion

In this work, it was found that Holm oak and Cork oak cover in the Mediterranean drylands were mostly explained by local-scale factors and the interactions between local- and broad-scale factors. Surprisingly, local-scale factors alone had higher relative importance than broad-scale factors. This confirms the hypothesis that the local-scale factors are crucial to better predict tree cover with high spatial resolution and that models at this scale are important since this is the scale where decision-making is often required. Additionally, the importance of local-scale factors, namely those related to favourable microclimatic conditions, was found to be higher in areas where water is a more limiting factor for plant productivity. The most important local-scale factors were related to microclimatic and edaphic variables associated with topography, soil texture and pH. As expected, the most important macroclimatic variables were related to precipitation of the dry season and temperature. Therefore, water availability for the trees was the critical factor underlying the effect of the most important variables at both spatial scales. For example, Fricker et al. (2019) showed that macroclimate was the most important factor at local and broad scales (25–1000 m), but topography and edaphic factors increased its importance at finer scales (25–50 m). However, after a search in the literature, no previous studies were found that measured the importance of broad-scale factors relatively to local-scale factors on Mediterranean woodlands dominated by Holm oak and Cork oak.

Microclimatic and edaphic variables were important drivers of tree cover at the local level for both tree species. Regarding microclimatic variables, both potential solar radiation and wetness evaluated terrain were relevant variables explaining Holm oak and Cork oak cover variation. The cover of the two oaks increased when potential solar radiation decreased, which is here used as a surrogate of microclimatic conditions. This suggests that where potential solar radiation is high (sun-exposed areas) evaporation and soil temperature increase and soil moisture decreases. These microclimatic conditions can lead to an overall decrease in water availability which is the most limiting factor for productivity in dryland areas, where water and high evaporation due to high temperatures constrain the establishment and growth of plant species (Breshears et al., 1997). This suggests that the two oaks in areas with low potential solar radiation may be taking advantage of microclimatic refugia where water availability is higher compared with the areas with high potential solar radiation, increasing tree regeneration in these sites (McLaughlin et al., 2017; Príncipe et al., 2014). Other authors found similar results on the effect of solar radiation on increasing tree mortality of adult trees (Costa et al., 2010) and seedlings (Ritsche et al., 2021). Also, Príncipe et al. (2014, 2019) found that Potential Solar Radiation was the most important factor influencing Holm oak natural regeneration at the local scale. Holm oak and Cork oak cover increased with higher wetness evaluated terrain in the sampling points (Table 1). This is a topography related variable that plays a strong role in the spatial distribution of soil moisture and groundwater flow and similarly to other topographic wetness indices was used to predict potential water content in the soil from flow accumulation (Nobre et al., 2011). These results show the importance of high spatial resolution data, here as local-scale variables, on the distribution of tree productivity in drylands. Holm oak cover decreased with increasing altitude, other authors also found a negative relationship between elevation and Holm oak cover over time (Lloret et al., 2004; Aubard et al., 2019). Higher elevation can be associated with shallow soils, due to erosion processes and water flow that come from ridges to valleys. Therefore, lower elevations can have the accumulation of nutrients, sediments, and water availability associated with higher tree cover. Cork oaks showed to have more cover in areas with higher slopes. Although unexpected, even in these sites where management is reduced, sites with higher slopes are more inaccessible discouraging land use management as cork stripping. The reduction of management, as Cork oak pruning and seasonal clearing of understory vegetation, can contribute to more natural regeneration and consequently increase the canopy cover in the long term. Overall, microclimatic variables at high spatial resolution seem to determine the tree cover of these two important oaks in Mediterranean drylands.

Edaphic characteristics were also important local-scale predictors of tree cover, although with lower relative importance than that of microclimatic factors. Soil texture and pH were important in explaining Holm oak and Cork oak cover. Soil texture has a direct influence on soil water availability for plants. For example, coarse soils in dry environments can be an indicator of non-compacted soils where water can infiltrate saving reservoirs of water (Hatten and Liles, 2019). On the other hand, soils with high clay content have small pores which difficult water infiltration and water drainage (Hatten and Liles, 2019), creating unfavorable conditions for Cork oak performance (Costa et al., 2008; Hidalgo et al., 2008). Soil pH can change at short distances influencing tree cover spatial patterns. For instance, Cork oak has a high tolerance to acidic soils, being common in areas where soil pH ranges from 4.4 to 7 and is estimated to have optimal conditions at a pH of 5.67 (Laiseca, 1949, Aronson et al., 2009).

Macroclimatic variables were important for both Holm oak and Cork oak cover, despite their lower explanation. Tree cover of both species was negatively influenced by high temperatures (i.e., higher isothermality for Holm oak and lower MeanTDryQ for Cork oak) and positively by rainfall (i.e., higher PDryQ for Holm oak and higher aridity index for Cork oak). This is supported by previous studies reporting an overall decrease in tree cover with aridity at the landscape scale (Scholes et al., 2002; Schulze et al., 1996; Vessella and Schirone, 2013; Duque-Lazo et al., 2018). Drought can negatively affect Holm oak reproductive success decreasing viable seeds (Bykova et al., 2018) and tree growth (Ogaya et al., 2003). Additionally, the Cork oak cover was negatively influenced by summer temperatures. High temperatures increase evapotranspiration which, together with summer droughts, have a negative synergistic effect on Cork oak growth (Caritat et al., 2000; David et al., 2007) and induce oak mortality mainly in water-limited areas, decreasing tree cover (Gea-Izquierdo et al., 2009; Lloret et al., 2004).

The effect of local-scale variables on tree cover was also influenced in some cases by macroclimatic variables, as evidenced by the significant interactions between local- and broad-scale factors found in the models. Macroclimatic variables can amplify, reduce, or modulate the effect of local-scale factors (i.e., soil texture and local topography) in explaining tree cover. For example, severe droughts can reduce tree cover only in sites where potential solar radiation is higher (Peñuelas et al., 2000), or affect trees in higher elevations (Asner et al., 2015). In this study, Holm oak cover on high elevations was more dependent on the precipitation availability during the dry season. On the other hand, the Cork oak cover was more affected by high temperatures in soils with high clay content. Cork oaks growing in clay soils had in general lower performance and they can be more susceptible to water stress caused by increasing temperatures in the summer (Caritat et al., 2000; David et al., 2007). Moreover, Holm oak and Cork oak cover showed to have a higher dependence on wetness evaluated terrain in drier climates. Overall, the effect of favourable microclimatic conditions in tree cover seems to increase in areas with a drier climate, showing the importance of having high spatial resolution data to explain tree cover across more arid areas.

The high relevance of local-scale factors to explain tree cover shows that topographic and edaphic variables at 10 m to 500 m spatial resolutions are undoubtedly important. Yet, the environmental variables considered in models built for both species explain a relatively modest amount of variation in oak tree cover (i.e., by the fixed effects), suggesting it is also influenced by other variables not addressed in this study. Factors such as management practices and historical land use, such as crop cultivation, grazing pressure, understory clearance and tree cutting are common drivers in Mediterranean woodlands affecting tree cover at the landscape level (e.g., Jones et al., 2011; Moreno-Fernández et al., 2019). Despite the influence of such variables, difficult to quantify, the selected environmental variables in this study explained 22% and 48% of the variance for Holm oak and Cork oak cover, respectively. The percentage of explanation of the selected variables demonstrate the importance of microclimatic and edaphic variables, as well as macroclimate, to explain tree cover. According to this study's findings local-scale factors are important drivers of forest cover in dryland forests on sites with high complex topography. However, the particular conditions of the sampling sites such as the dominant tree species in Mediterranean drylands and the annual precipitation range from 500 to 700 mm, limits the generalization about the importance of specific environmental variables beyond these conditions. In other dryland forests, local-scale factors will have high importance but they should be evaluated case by case for its specific environmental conditions.

5. Conclusion

Local-scale factors and their interaction with broad-scale factors are more important for modelling Holm oak and Cork oak cover in Mediterranean woodlands than broad-scale factors alone. Microclimatic and edaphic variables namely potential solar radiation, wetness evaluated terrain and soil texture and pH were important drivers of tree cover at the local level for both tree species. Topography derived variables, such as potential solar radiation, used here as an indicator of microclimatic conditions, are possible to calculate at higher resolutions and they can be included in models to map NDVI potential at the landscape level. Overall, the most important broad- and local-scale factors were related to water availability for the trees, reflecting the importance of water for tree productivity in drylands. Understanding the contribution of local-scale factors for tree distribution and canopy cover has important applications in the conservation and restoration of forest cover in semi-arid regions, where they play a critical role in the delivery of many ecosystem services which are being highly affected by climate change. Then, this work expects to increase the awareness about the high importance of taking into consideration local-scale factors in Mediterranean woodland ecosystems. Similar approaches can be applied to other forest types using the selected environmental variables to improve high spatial resolution planning of reforestation and forest management.

CRediT authorship contribution statement

Adriana Príncipe: Conceptualization, Methodology, Formal analysis, Investigation, Writing. **Alice Nunes:** Conceptualization, Methodology, Formal Analysis, Writing – Review & Editing. **Pedro Pinho:** Conceptualization, Methodology, Writing – Review & Editing. **Cristiana Aleixo:** Investigation, Methodology, Writing – Review & Editing. **Nuno Neves:** Methodology, Resources, Writing – Review & Editing. **Cristina Branquinho:** Conceptualization, Methodology, Investigation, Writing – Review & Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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