The cork oak in the Mountains of Palermo (Italy): ecological insights from the south-eastern edge of its distribution range

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The uneven presence of the cork oak (*Quercus suber* L.) within its distribution range is not only determined by its climatic requirements but also by specific edaphic needs. Although most of the natural populations thrive in acidic soils deriving from metamorphic or volcanic rock outcrops, some cork oak populations are found growing in soils deriving from calcareous bedrock, which are considered less suitable. We carried out a multidisciplinary investigation at the south eastern edge of the *Q. suber* distribution range (Mountains of Palermo, NW Sicily), including soil, floristic, and vegetation surveys, aimed at: (i) assessing the native or introduced origin of some peculiar cork oak populations; (ii) describing the associated plant communities and soils; (iii) identifying the ecological factors which could explain the local adaptation to soils deriving from calcareous bedrock; (iv) discussing the ecological role played by this species in the study area and within its distribution range. The collected information suggest that the detected cork oak stands are native to these areas. We hypothesized that the co-occurrence of high fire frequency, high soil calcium content and erosion, which caused the intermixing of different parent materials, might favor its competitive interactions with other Mediterranean tree species, thus accounting for the local presence of *Q. suber*. The study of cork oak populations thriving in peculiar substrates at the driest end of the range could be of great importance for the future conservation of this species, which is expected to face growing threats in the coming decades.

Keywords: Mediterranean Evergreen Forest, Soil Chemistry, Vegetation Science, Wildfire, Landscape, Tree Species, *Quercus suber*

Introduction

The cork oak (*Quercus suber* L.) is one of the most important tree species in the Mediterranean Basin, where its presence is of high ecological, landscape and socio-economic importance (Pollastrini et al. 2018, EUFORGEN 2019). Cork oak forests cover altogether more than 2 million ha (Matías et al. 2019), almost 1.5 million of which in Europe and 700,000 ha in North Africa (Houston Durrant et al. 2016). Its distribution area encompasses the western portion of the Mediterranean Basin and the southern portion of the European Atlantic coasts (Houston Durrant et al. 2016).

The cork oak shows a discontinuous geographical distribution, much more restricted and fragmented than might be expected based on its climatic requirements. However, compared to other evergreen oaks, *Q. suber* is characterized by a more restricted ecological niche, as particularly demanding in terms of soil humidity (Petroselli et al. 2013). The species grows in warm-humid Mediterranean areas with oceanic features, receiving at least 450 mm of mean annual rainfall, from sea level up to 2000 m a.s.l., although most cork oak stands are found below 800 m a.s.l. (Houston Durrant et al. 2016).

Soil physical-chemical characteristics are regarded as being among the ecological factors most correlated to the occurrence of the cork oak in its natural range (Petroselli et al. 2013). *Q. suber* generally prefers sandy soils derived from siliceous rocks with acid reaction, while usually avoids soils from base-rich, calcareous bedrocks such as dolomitic limestones, calcareous sandstones, and marls (Serrasolses et al. 2009). Indeed, the importance of various substrate-related variables, particularly lithology and soil type (Costa et al. 2008), for the distribution of cork oak has been repeatedly acknowledged. The preference for well drained soils with coarse textures is known (Laakili et al. 2016). Conversely, reduced organic matter availability or soil acidification have negative effects on cork oak regeneration in the longer term (Dias et al. 2016).

There is increasing evidence of a declining trend in cork oak populations, especially at the edge of the species' natural distribution range (Vessella et al. 2017, Matías et al. 2019). Many factors have been invoked to explain the ongoing process, which is bound to increase in the forthcoming decades based on current climate change scenarios (Matías et al. 2019), and due to other growing threats, such as overgrazing, soil pathogens and land-use changes (Dettori et al. 2018). In the Mediterranean

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region, climatic forecasting seem to indicate a rise in temperatures and a reduction in precipitation, which will probably decrease the potentially suitable areas for cork oak, especially in the southern edge and at lower altitudes; accordingly, northward and upward shifts could occur (Vessella et al. 2017). Indeed, the expected reduction in soil water availability could favor other co-occurring and more drought-tolerant woody species, such as holm oak (*Quercus ilex* L. – Petroselli et al. 2013). Aridity has been found to play a key role in *Q. suber* regeneration ability, markedly hindering seedling recruitment chance and originating over time an aged demographic structure (Matías et al. 2019).

In Italy, the most extensive cork oak forests occur in Sardinia (82.7% of total national area), followed by Sicily, Tuscany and Calabria, while more discontinuous and smaller nuclei are found in Campania, Lazio and Apulia (INFC 2007). In Sicily, *Quercus suber* is a native species which covers approx. 19,000 ha, from sea level up to 1000 m a.s.l. It accounts for approx. 7% of total regional forest cover (Camerano et al. 2011), in some cases characterizing old growth stands (Badalamenti et al. 2018). Only 41.3% of the Sicilian cork oak stands are currently managed for production and the progressive abandonment of cork cultivation is considered to be a threat to the conservation of these ecosystems on a regional scale. Furthermore, since these populations grow at the driest end of the spe-

cies' range, they are particularly prone to the effects of climate change, and could suffer from a marked reduction and local extinction in the next future (Vessella et al. 2017). For this reason, they are of particular interest for the future dynamics of cork oak in the whole Mediterranean Basin. In specific reference to the cork oak, according to Aronson et al. (2009): "Knowledge of species requirements and constraints can be used to promote conservation and restoration efforts or to expand its current distribution limits in view of the current climate and land use changes".

In this study, we aimed to gain ecological insights from the cork oak stands occurring in NW Sicily in soils deriving from calcareous bedrock, which are generally considered to be less suitable for the species. In particular, we characterized soil and plant communities associated to cork oak stands, occurring at the southeastern edge of its natural distribution range. The main objectives of the study were to: (i) identify and quantify the area covered by cork oak populations in the Mountains of Palermo (NW Sicily); (ii) investigate the effective origin of these populations (whether natural or artificial) based on historical and floristic information; (iii) identify the ecological factors responsible for the presence of the species in soils that developed on calcareous substrates; (iv) propose a synthetic interpretation of the ecological role played by the cork oak within local potential vegetation.

Materials and methods

Identification and characterization of the study areas

In order to detect any cork oak population, either as forest stand, small nucleus or isolated individual, the main botanical literature concerning the Mountains of Palermo (the mounts surrounding Palermo city) was consulted (Marcenò & Trapani 1978). The historical information gathered was used to identify potential areas covered by *Q. suber*. After being validated through dedicated field surveys, the detected areas were characterized by adopting the hierarchical classification developed by Blasi et al. (2000); this method entailed overlapping the pedological map (scale 1:250.000 – Fierotti 1988) with the geological map (scale 1:250.000 – Lentini & Carbone 2014), the bioclimatic map (scale 1:250.000 – Bazan et al. 2015), and the map of Sicilian potential vegetation (scale 1:250.000 – Anonymous 1996; see Tab. S1 in Supplementary material). Three macro-areas, geographically distinct from one other and fairly homogeneous in terms of substrate (geology and soil types), were identified (Tab. 1): (i) macro-area A: "Pianetto" (municipalities of Altofonte and Santa Cristina Gela); (ii) macro-area B: "Cozzo Secco" (municipality of Borgetto); (iii) macro-area C: "Colline della media valle del fiume Oreto e del Monrealese" (municipalities of Altofonte and Monreale).

The occurrence of the cork oak had al-

Tab. 1 - Main characteristics of the study areas. Sources: (1): Fierotti (1988); (2): Lentini & Carbone (2014); (3): Bazan et al. (2015).

Characteristics	Macro-area		
	A	B	C
Locality	Pianetto (Cozzo Giammeri and Costa Zolia)	Cozzo Secco	Colline della media Valle del fiume Oreto e del Monrealese
Stand description	Small, isolated and discontinuous, grazed, pure stand or mixed with holm and downy oak	Scattered and discontinuous stands, grazed, mixed with evergreen thermophilous sclerophyllous species or with downy oak	Isolated plants and small nuclei, discontinuous, pure stands or mixed with evergreen thermophilous species
Municipality	Altofonte, Santa Cristina Gela	Borgetto	Monreale, Altofonte, Marineo, Montelepre, Giardinello
Regional Technical Map 1:10.000 (Section no.)	595130 and 608010	594140	594120 and 594160
Maximum range of UTM Coordinates	E 2373518-2374629 N 4206720-4208280	E 2356966-2357797 N 4209665-4210804	E 2370475-2371368 N 4213457-4217808
Area (ha)	251	50	240
Mean altitude (m a.s.l.)	720	560	480
Altitudinal range (m a.s.l.)	597-835	432-659	240-680
Slope (%)	20	20	30
Main aspect	NO-SE	SW	None
Soil type[1]	Leptosols, Regosols, Phaeozem (Association 7)	Leptosols (Association 6)	Leptosols, Regosols, Phaeozem, Cambisols (Associations 21 and 29)
Lithotype[2]	Calcilutites and marls, calcarenites grading up to doloarenites and dolorudites (Geology 42)	Silicoclastic deposits, yellowish graded quartzarenites and brown clays (Geology 8 and 30)	Radiolarites and Spongolites with redeposited calcarenites and calcirudites, and red marls (Geology 41)
Bioclimate[3]	thermo-Mediterranean upper sub-humid	thermo-Mediterranean lower sub-humid	thermo-Mediterranean upper sub-humid

ready been reported in macro-area A (at Dingoli site) by Marcenò & Trapani (1978), while cork oak forests have been present in macro-area B at least since XIII century, when the territory was owned by the Abbey of "Santa Maria di Altofonte" (Bresc 1983). Conversely, no previous historical data was available on the occurrence of *Q. suber* in macro-area C.

Subsequently, we searched for local data on wildfires, as they are an important factor explaining the natural distribution of the cork oak in the Mediterranean, as well as in our study areas. Information collected by the Special Office of the Firefighting Forest Fire Service (USSAB 2005), for the period preceding our field surveys, and by the Command of the Forest Service of Sicily for more recent data (2007-2019 – https://sifweb.regione.sicilia.it/arcgis/rest/services/Censimento_Incendi/MapServer), was considered. The oldest data are sorted by municipality and they provide information on the occurrence of wildfires in Sicily in the years 1986-2002 (USSAB 2005). In detail, in the framework of the Regional plan for the protection of vegetation from fires, a regional map of fire risk was developed, not only considering the factors which enhance the likelihood of wildfire (*e.g.*, vegetation types or climate traits), but also taking into account the frequency of wildfires occurring in a given area, as well as the average affected area and the average affected wooded area, thus including a quantitative assessment. In particular, this map was elaborated through the overlapping of different base maps, including a statistical risk map, a vegetation risk map, a climate risk map, and a morphological risk map.

For a climatic and bioclimatic characterization of the study areas, the thermopluviometric stations of Partinico (189 m a.s.l.) and Monreale (310 m a.s.l. – Duro et al. 1993, SIAS, http://www.sias.regione.sicilia.it/) were considered the most suitable (Tab. 2). Taking into account their location, the Partinico station was used to characterize macro-area B, while the Monreale station was used for macroareas A and C. Annual precipitation ranged from 706 mm (Partinico) to 991 mm (Monreale), while mean temperature ranged from 16.2 °C (Monreale) to 17.8 °C (Partinico). Raw climatic data were used to identify the duration of the drought-stress period, which generally spans from the third ten-day period of April to the third ten-day period of September in both stations. According to Rivas-Martínez (1996), as well as local classification schemes (Bazan et al. 2015), the bioclimate for macro-area B is thermo-Mediterranean lower sub-humid, while for macro-areas A and C, the bioclimate is thermo-Mediterranean upper sub-humid.

The cork oak distribution map

A distribution map of the cork oak, either found as forest stand, small nucleus and/or isolated individual, was made in a GIS environment. Field data were registered by means of a Trimble® GPS (Trimble Inc., Sunnyvale, CA, USA). Data referring to the UTM plane coordinate system, timed to share information, latitude and longitude, were exported as shapefiles to be treated with QGIS® ver. 3.10 (QGIS Development Team) and were overlapped with sections no. 594140, 595130, 594120, 594160 and 608010 of the Regional Technical Map (scale 1:10.000). The shape relative to punctual distribution files of cork oak was then overlapped with the soil, geological and bioclimatic maps.

Soil surveys

The choice of the most suitable areas for the pedological surveys was based on two steps: after superimposing the cork oak distribution map with the geological map, direct field observations of the soil features and plant species assemblages (acidophilous *vs.* basiphilous) were carried out. The benchmark pedons (=soil profiles) representative of the main soil types (Tab. 1) were described in the field after direct soil excavation and according to the genetic horizons defined by Schoeneberger et al. (2002). Overall, 5 pedons, sampled in bulk and undisturbed soil horizons, were described: four pedons belonging to macro-area A, and one pedon belonging to macro-area B. No pedon was considered in macro-area C because it was not possible to access the privately owned areas. Pedon 1 (Code Ag1) and pedon 2 (Code Ag2) were located at Cozzo Giammeri (38° 00′ 23.80″ N, 13° 20′ 34.41″ E), pedon 3 (Code Az3) and pedon 4 (Code Az4) were located at Costa Zolia (37° 59′ 50.75″ N, 13° 20′ 49.64″ E), and pedon 5 (Code B) was located at Cozzo Secco (38° 01′ 31.15″ N, 13° 09′ 07.21″ E). For each pedon, three soil samples were collected at several soil depths. Bulk soil samples were air dried, crushed and 2-mm sieved. Particle size distribution was determined by sieving and sedimentation (ISO 11277:2009): total carbonates volumetrically, pH potentiometrically (ISO 10390:2005) and soluble ions by ion chromatography of saturated-paste water extracts (Dionex DX-120®, Sunnyvale, CA, USA). Soil classification followed the IUSS Working Group (2015).

Floristic and vegetation surveys

Floristic and phytosociological surveys were carried out during spring 2004. Analysis of cover-value ranges available from vegetation surveys on evergreen forests in Sicily (see Brullo et al. 2009 and literature therein) suggested the use of 20% as a valuable threshold for the cover of *Q. suber*. Full vegetation surveys, within 100 m²-wide plots, were carried out only within the sub-populations where cork oak cover exceeded 20%. Four plots were established in macro-area A, and seven plots were established in each of the macro-areas B and C, which included the most interesting cork oak stands. For each plant species, the cover/dominance scale proposed by Braun-Blanquet (1932) was considered, with modifications subsequently proposed by Pignatti & Mengarda (1962). The Shannon diversity index (H' – Shannon 1948) and Evenness index (Pielou J) were calculated after converting Braun-Blanquet values according to Tüxen & Ellenberg (1937). Classification of the vascular plants followed Pignatti et al. (2017) and hierarchical classification of the plant communities followed Guarino et al. (2017). Each plant species surveyed was included in one of the following phytosociological alliances: (i) *Erico-Quercion ilicis*, including pure evergreen or mixed ever- and summer-green oak forest species linked to neutrocline-acid soils (EQi); (ii) *Quercion ilicis*, including pure evergreen or mixed ever- and summer-green oak forest species (Qi); *Oleo-Ceratonion siliquae*, including maquis species (OCs); (iii) *Pruno-Rubion ulmifolii*, including mantle species (PRu); (iv) *Cisto-Ericion multiflorae*, including garrigue species (CEm); (v) *Hyparrhenion hirtae*, including xerophilous grassland species (Hh); (vi) Other species belonging to other syntaxa.

Where only a few scattered individuals of cork oak occurred in open and discontinuous plant communities (cork oak cover <20%), we considered only the presence/absence of diagnostic vascular plants typical of forest and pre-forest communities (maquis, mantle, garrigue and grassland), as well as of species characteristic of rocky and scree habitats. In these areas, we aimed to highlight whether a high number

Tab. 2 - Precipitation and temperature data in the considered thermo-pluviometric stations.

Variable	Parameter	Meteo Stations	
		Partinico	**Monreale**
Precipitation (mm)	Mean annual	706	991
	Monthly maximum	97	129
	Monthly minimum	4.3	4.7
Temperature (°C)	Mean annual	17.8	16.2
	Average of the maximum	22.6	21.3
	Average of the minimum	12.7	11.4
	Maximum average of the hottest month	31.8	31.1
	Minimum average of the coldest month	6.6	5.3

of species characteristic of *Erico-Quercion ilicis* could support the past occurrence of cork oak forests. The authors of all scientific epithets concerning plants mentioned in the text are provided in Tab. S2 (Supplementary material).

Statistical analysis

To test the effects of the environmental variables, namely altitude, main aspect (north or south) and lithology (calcareous or flysch) on richness, diversity (Shannon H') and evenness (Pielou J), we used a general linear model (GLM). Before running the model, we first checked that the three dependent variables followed a normal distribution (Shapiro-Wilk test: p = 0.55, 0.23 and 0.85, respectively). Spatial autocorrelation across the sampling plots using Moran's I index, calculated from three different weight matrices (*i.e.*, distance to the nearest neighbor) was also checked (Dormann et al. 2007). We set the distance range at 2300 m, which was the minimum distance to allow all plots to have at least one neighbor. We then set the range at 4300 m to connect all plots inside the same macro-area, and finally we used a "queen" matrix, searching for the first closest neighbor without a maximum distance threshold, thus connecting at least one neighbor from all macro areas. To test for differences in richness, diversity, and evenness between the three macro-areas, we used one-way ANOVA, after verifying the homogeneity of variances in the residuals

of the model (Levene's test: p = 0.69, 0.50 and 0.12, respectively). All statistical analysis was performed in R v. 3.6.1 (R Core Team 2019) and spatial autocorrelation was assessed with GEODA 1.8.16 (Anselin et al. 2006).

Results

Distribution and characterization of the study areas

The distribution map of the areas where cork oak occurs in the Mountains of Palermo is shown in Fig. 1. Macroarea A is mainly characterized by calcilutites, marls, and calcarenites grading up to doloarenites and dolorudites, and Leptosols, Regosols, and Phaeozem (Fierotti 1988, Lentini & Carbone 2014). Macroarea B is mainly characterized by Silicoclastic deposits, Numidian Flysch, and mainly Leptosols (Fierotti 1988, Lentini & Carbone 2014). Macroarea C is mainly characterized by Radiolarites and Spongolites with redeposited calcarenites and calcirudites, red marls, and Leptosols, Regosols, Phaeozem, and Cambisols (Fierotti 1988, Lentini & Carbone 2014).

Macro-area A has a surface of about 251 ha and is localized in the south-east sector of the map. Macro-area B is around 50 ha wide and is localized in the south-west sector of the map. Macro-area C is approx. 240 ha wide, encompassing much more fragmented and isolated stands, localized in the northern sectors of the map. Overall, the areas under investigation, covered by

more or less dense cork oak forests, cover approximately 540 ha. Concerning fire occurrence, all investigated areas fall within areas classified as high or very high fire risk, according to the regional classification scheme (USSAB 2005). This means that these areas not only have a high likelihood of suffering from wildfire but they have been effectively burned with high frequency at least at the end of the last century (USSAB 2005). Such a trend has been confirmed by recent data (2007-2019), showing a high mean annual frequency of wildfire passage, ranging from one wildfire every two years elsewhere in macro-area B to one wildfire per year elsewhere in macro-area C. Hence, although the total area is considerably large, the intense human pressure may represent a serious threat for the conservation of these forest ecosystems.

Soil surveys

Most of the investigated soil profiles showed marked limitations in root growth, mostly belonging to Leptosols. The five pedons showed a taproot plus shallow horizontal roots. The main portion of root biomass is located in the root crown just below the trunk base at a soil depth < 0.3 m. As we sampled by horizontal profiles, the horizontal extension of the whole root system, including roots thinner than 1 cm, is unknown. In macro-area A, pedon 1 and pedon 2 (Ag1 and Ag2) belonged to Leptosols / Regosols (sporadically Phaeozems) soil associations, while pedon 3 and pedon 4 (Az3 and Az4) belonged to Leptosols. These soils evolved from lithological substrates made of siliceous shales, radiolarites and marls, with interbedded lenticular resedimented breccias. Graded and laminated calcareous sandstone with elements from Middle-Upper Triassic Cretaceous platforms occurred in pedon 3 and pedon 4. Cozzo Giammeri profiles (Ag1 and Ag2) evolved on slopes with a gradient of 15 and 25%, respectively, while Costa Zolia profiles (Az3 and Az4) evolved on slopes with a gradient of 10%. The pedon differed in terms of stoniness and rockiness. The main land use was overgrown pastureland. In macro-area B, pedon 5 belonged to Leptosols, which evolved on lithological substrates made of graded doloarenites and dolorudites, and re-sedimented dolomite breccias with megabreccias from Triassic carbonate platforms. This profile was open on one side in a slope with a gradient of 35%, stoniness of 25%, rockiness of 20% and moderately rapid drainage. A morphological description of all pedons is given in Tab. S3 (Supplementary material). Average soil pH ranged between 6 and 7 in all study sites. Variability of soil pH increased almost linearly with a soil depth of up to 80 cm (ranging from 5.0 to 7.8); conversely, it decreased progressively at higher soil depths (Fig. 2). Overall, the large variability in soil pH (from 4.6 to 7.8) showed good plasticity of cork oak to this edaphic factor. Na/Ca
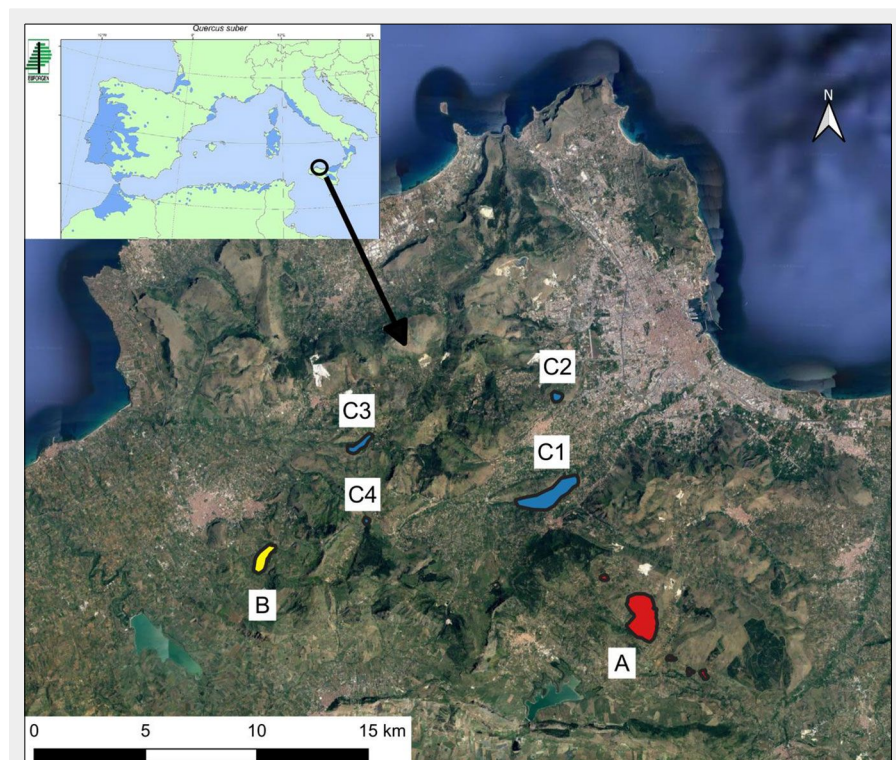

Fig. 1 - The cork oak distribution map in the Mountains of Palermo. The different letters indicate the three macro-areas (A, B and C). Up on the left, the natural distribution range of *Quercus suber* is reported (EUFORGEN 2019).

molar ratios were constantly higher than 1, Mg/Ca ratio exceeded 0.6, while Na/K ratio exceeded 20 (Fig. 3).

*Floristic and vegetation surveys*

Despite evenness being autocorrelated in the two close range matrices, source variable richness as well as diversity were not autocorrelated in all matrices (Moran's I *p* > 0.05 in all cases – Tab. S4), suggesting high local scale variability. GLM indicated that richness, diversity and evenness are not predicted by altitude, aspect and lithology (p > 0.05 in all cases – Tab. 3), and they did not differ between the macro areas (richness: F = 0.24, p = 0.78; diversity: F = 0.74, p = 0.49; evenness: F = 1.01, p = 0.38). However, significant differences (F = 7.92, p < 0.01) were found in the richness of species belonging to the alliance dominated by *Q. suber* (EQi), which was significantly higher in macro-area B than in C, although not differing from A (after Tukey HSD test). High degradation and fragmentation of forest habitats in the surveyed areas can be inferred from the number of plant taxa not framed within any alliance (see "Other Species" in Fig. 4 and Tab. S2 in Supplementary material), as well as from those belonging to the alliance Hh. In all macro-areas, plant taxa belonging to "other species" represented the dominant component of plant communities, ranging from 38.6% in macro-area B, 39.8% in C and up to 42.5% in A (Fig. 4).

Macro-area A is characterised by a complex and heterogeneous landscape, due to extreme variability in local topography (aspect and slope), continuous shifts from carbonate (compact calcarenites and calcilutites) to acid (quartz sandstones) outcropping rocks, as well as to major disturbance factors (mostly cattle grazing and fires). Here, cork oak stands, pure or mixed with a number of evergreen or deciduous trees, are intermingled with more open thermophilous maquis on S-facing ridges and summits. *Quercus suber* does not seem to play a dominant role in the absence of human disturbance. These forest communities show excellent potential for recovery and future development, although the possibility of establishing the potential vegetation (*Quercetalia pubescenti-petraeae*) with downy oak as the dominant tree species (Anonymous 1996) is currently low. In fact, the current floristic composition of local communities is rich in plants linked to rocky habitats and overgrazed pasturelands, showing clear signs of soil degradation and thinning processes. Some cooler and shady microhabitats are suitable for *Cephalanthera longifolia*, *Quercus congesta* and *Iris foetidissima*, which are rare species on the Mountains of Palermo (Pasta & Troìa 1994).

In macro-area B, the cork oak stand is uneven-aged, almost pure, mostly sparse and discontinuous, and rather plant species poor. High wildfire frequency is witnessed by the extremely high number of species
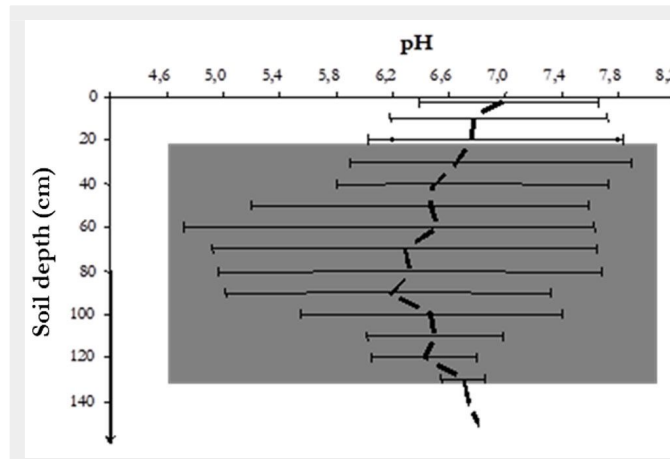
Fig. 2 - Soil pH variation with soil depth (average of pedons 1-5). The dashed line represents the median of pH values while whiskers indicate the range. The shaded area represents the range of soil pH in *Quercus suber* stands found in literature.
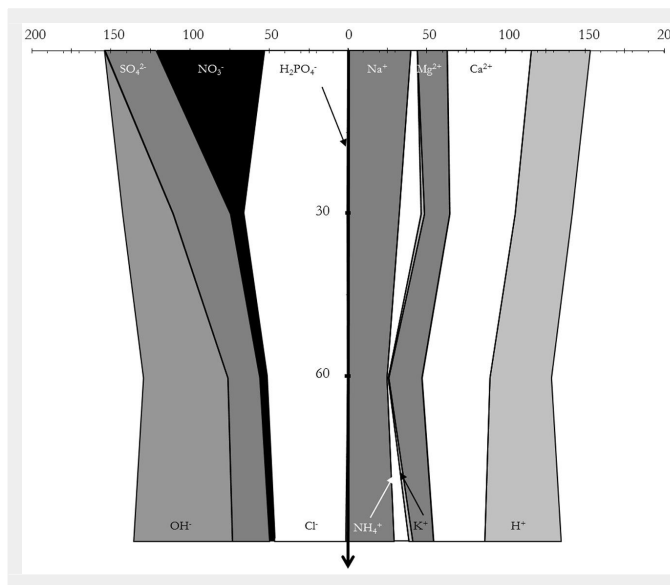
Fig. 3 - Ionic species within the saturated extracts from soils. Average concentrations in nM (x-axis) and depth (y-axis) in cm.

tied to open patches of perennial grassland dominated by *Ampelodesmos mauritanicus* or of acidophilous garrigue dominated by *Cistus* spp. and *Lavandula stoechas*, while the current intensity of cattle grazing is underlined by high numbers of mantle and grassland species. Only near rocky outcrops, especially along ridges and on hilltops, a higher frequency of Mediterranean maquis species was recorded. In small valleys, where soils are deeper and the effect of wind is slightly mitigated, some scattered individuals of downy oak (*Quercus pubescens* Willd. s.l.) co-occur with cork oak, while the shrubby understory is dominated by *Cytisus villosus*. This plant community may be framed within the *Erico-Quer-*

cion ilicis, due to the high number of species referred to this alliance, in addition to acidophilous species such as *Lavandula stoechas*, *Limodorum abortivum*, *Pteridium aquilinum*, and *Tuberaria guttata*. We may hypothesize that local forest communities belonged in the past to the *Erico arboreae-Quercetum virgilianae*, rather widespread in the Tyrrhenian sector of Sicily (Brullo et al. 2009).

Macro-area C is subdivided into four subareas geographically disjoint from each other (Fig. 1). The most interesting cork oak stands occur in the southeast sub-area, where the semi-natural landscape appears rather uniform: a series of ridges whose S-facing slopes usually host thermophilous

Tab. 3 - Summary of the results of the GLM testing the effects of the three environmental variables on richness and diversity.

Variable	Richness (R² = 0.22)			Diversity (R² = 0.13)			Evenness (R² = 0.05)		
	Estimate	t	p	Estimate	t	p	Estimate	t	p
Intercept	35.506	3.1	<0.001	2.019	5.72	<0.001	0.558	8.26	<0.001
Altitude	0.028	1.36	0.2	0.001	0.83	0.42	0	0.49	0.63
Aspect	-0.027	0.02	0.98	0.003	0.03	0.98	0.002	0.11	0.91
Lithology	6.64	1.86	0.08	0.155	1.41	0.18	0.018	0.83	0.42
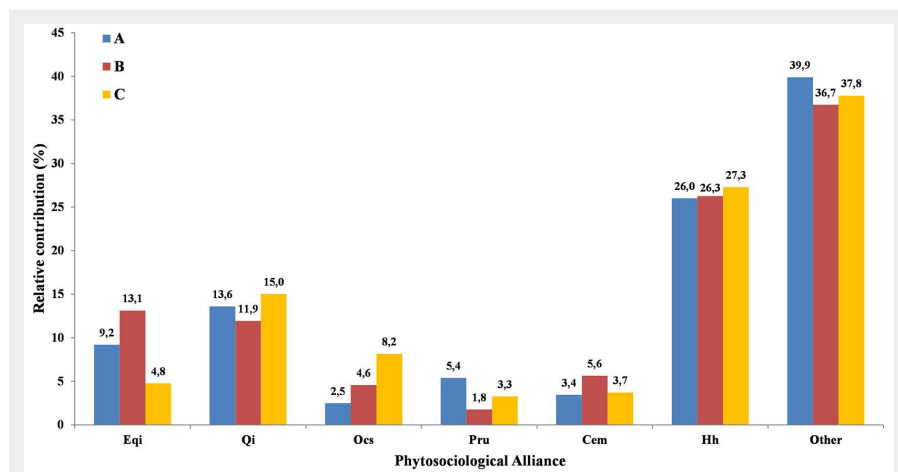
Fig. 4 - The relative contribution (in %) of each surveyed phytosociological alliance within each macro-area (A, B and C). (EQi): *Erico-Quercion ilicis*; (Qi): *Quercion ilicis*; (OCs): *Oleo-Ceratonion siliquae*; (PRu): *Pruno-Rubion ulmifolii*; (CEm): *Cisto-Ericion multiflorae*; (Hh): *Hyparrhenion hirtae*; (Other): species belonging to other syntaxa.

taxa and assemblages, while N-facing slopes host some remnant nuclei of Mediterranean oak forests. It is therefore quite difficult to assign local plant assemblages to a plant association. On more acidic substrates, like quartz sandstones and argillites, local forest communities probably belonged to the *Erico-Quercion ilicis* alliance, or alternatively to the *Erico arboreae-Quercetum virgilianae* plant association. Elsewhere, the high frequency of woody species typical of *Oleo-Ceratonion*, which represents the potential vegetation of this area (Anonymous 1996), supports the hypothesis that cork oak locally belonged to the *Oleo sylvestris-Quercetum virgilianae*. Most of the cork oak stands in this macro-area are very scattered and open, forming a patchwork with xeric perennial grasslands dominated by *Ampelodesmos mauritanicus* or with mantle communities physiognomized by *Crataegus monogyna*, *Cytisus infestus*, *Osyris alba*, *Daphne gnidium*, *Spartium junceum*, *Pistacia terebinthus* and *P. lentiscus*. Intense and widespread soil erosion processes, and frequent wildfires caused extreme soil and habitat degradation. The high degree of soil thinning may also be inferred by the high frequency of species adapted to cliffs, ledges and screes, as observed in the small stand of "Contrada Loghi Vecchi" (Monte Caputo – see Tab. S5 in Supplementary material).

Discussion

Our study provides ecological insights from *Quercus suber* stands occurring on the Mountains of Palermo, at the southeast edge of its distribution range. The pedological characteristics obtained by direct soil excavation and pedon observation (Corona et al. 2005) allowed to infer some interesting indications on the ecological range of *Q. suber* in terms of soil variables. Recent research has emphasized the need for very detailed field data when studying cork oak stands (Vessella et al. 2017). The

same is true for our study sites, as the calcareous nature of the substrates is different from the typical siliceous rocks with acid reaction, where most of the cork oak stands occur.

Our study sites fall within areas considered to be of particular interest for the future dynamics of cork oak, as they could face growing risk of local extinction, or a significant reduction in the population size (Vessella et al. 2017) due to many interacting detrimental factors (climate change, fire frequency, etc.) driven by man (Matías et al. 2019). Our field observations and wildfire data clearly proved that the surveyed cork oak stands are highly exposed to these risks.

The occurrence of species typical of the *Erico-Quercion ilicis* (EQi) may represent an effective proxy for assessing the native status of local *Q. suber* populations. A high frequency of base-avoiding plant species typical of the EQi was recorded in the understory of the surveyed cork oak stands. Since many of these species show high fidelity to cork oak stands throughout the whole island (Brullo et al. 2009), all the macro-areas have very good potentiality for *Q. suber*. As historical data (Bresc 1983, Gussone 1842, Lojacono-Pojero 1888, Parlatore 1848) testify the local occurrence of *Q. suber* at least since the Middle Ages, and considering that the first afforestations in Sicily started around 1920s, cork oaks should be considered locally native in these areas and the hypothesis of a past introduction in pre-existing woodlands should be discarded.

Cork oak stands growing on alkaline or neutral-alkaline soils have been already observed in western and southeastern Sicily (Minissale et al. 2006), as well as in southern Latium (central Italy), where they have been interpreted as steady "disclimax" communities favoured by century-long fire disturbance to the detriment of local "climax" forests dominated by holm and/or

downy oak (Blasi et al. 1997). In our study areas, three main factors, probably acting in synergy, could account for the scattered but persistent occurrence of *Q. suber*: (i) local fire disturbance; (ii) the peculiar characteristics of local soils; and (iii) the effect of erosion processes on the local geological framework.

High fire frequency, as observed in all macro-areas, could have hindered evolution towards more mature forest ecosystems, favouring the more fire-resistant cork oak, once a minor component of pristine mixed oak forests (Barberis et al. 2003). Indeed, *Q. suber* is a fire-resistant tree species with a thick bark acting as an insulating material and protecting the inner woody structures. After fire passage, the cork oak is also able to resprout both from stem and basal buds (Pausas 1997), showing a notably high survival rate (Sirca et al. 2015). The marked effect of human disturbance on local plant communities can also be derived by the fact that none of the abiotic factors assessed (altitude, aspect and lithology) proved to be a predictor of the observed richness, diversity and evenness of the cork oak stands.

Regarding pedological traits, we found large plasticity in *Q. suber* to substrate conditions, including the pH of the rhizosphere and the geological substrate. Average soil pH ranged between 6 and 7 in all study sites, which is consistent with values reported in the literature (Cucchi 1963). Our results also match the preference of *Q. suber* for soils with acid or sub-acid reaction, together with a tendency to avoid limestone soils (Duque-Lazo et al. 2018). However, the total calcium content in soils and its active portion should be distinguished. The cork oak, like the sweet chestnut (*Castanea sativa* Mill.) and the common bracken (*Pteridium aquilinum* (L.) Kuhn), may tolerate a rather high content of soluble limestone (Ozenda 1982). Interestingly, recent research has found natural cork oak populations growing in soils with an active lime content below 26% and soil pH close to 8 (Duque-Lazo et al. 2018). *Q. suber* rarely develops in podzols and regosols (Simões et al. 2016), whereas more frequently is found in cambisols (Aponte et al. 2013) with a moderately thick humic horizon and subacidic soil pH. In the pedon profiles, the presence of nitrates proves that rhizosphere activity is mostly concentrated in the first 30 centimeters of soil depth. Subsequently, the scarcity of phosphorus, the excess of calcium and sodium, counterbalanced by similar concentrations of chlorides and sulphates, characterize all the pedon profiles. The average depth of the described pedons falls within the range reported in the literature (Dettori et al. 2001). Soluble ions, particularly sodium, do not disturb the cork oak, though excess calcium most likely does (Maghnia et al. 2017). In fact, at each depth, molar ratios Na/Ca were always higher than 1, while Mg/Ca ratio was at maximum 0.6, and Na/K ratio

was permanently higher than 20. It is plausible that the high Ca content, deriving from parent material, may represent a major obstacle for the colonization of forest species typical of more mature stages, thus favouring the cork oak. Furthermore, cork oak may produce changes in soil nutrient content, particularly N and Ca, affecting the composition of soil microbial community (Aponte et al. 2013). This would explain the good establishment and natural regeneration even on dolomitic limestones found on Mt. Gibilmesi, Mt. Petroso and Costa Sant'Anna near Mt. Cuccio, where *Q. suber* was planted during the second half of the twentieth century (Cutino et al. 2018). In agreement with its general ecological behaviour, on the Mountains of Palermo *Q. suber* seems to play a dominant role only in macro-area B, characterized by acidic soils and rocky outcrops. This finding suggests some peculiar adaptation to local conditions in the other macro-areas; for instance, the ability of cork oak seedlings to withstand iron deficiency has been proved (Gogorcena et al. 2001).

As far as soil erosion is concerned, the calcareous substrates colonized by *Q. suber* are in tight contact with (and once were underneath) the flysch outcrops, mainly quartz sandstones and argillites (Catalano et al. 1978). Due to the heavy impact of human activities since prehistoric and protohistoric times, the upper lithological layers (flysch) may have been eroded, remaining obliterated or reduced to small pockets in cracks of the underlying carbonate layers. In any case, if the general conditions for establishment of the species exist, the plasticity of the cork oak (Maghnia et al. 2017) may induce deep transformations on soil characteristics over time.

The issue of how to interpret the dynamic role played by cork oak in the vegetation of the thermo- and meso-Mediterranean is still under debate (Brullo et al. 2009). In the progressive succession of the Mediterranean vegetation, many authors (Di Benedetto et al. 1985) are in agreement when considering the cork oak stands as an edaphic and stable climax, linked to loose soils with an acid reaction, and assigning them to the *Quercion ilicis* alliance. Conversely, other authors framed them within the *Erico-Quercion ilicis*, which includes all the evergreen western Mediterranean forests dominated by evergreen oaks (Brullo et al. 2009, Guarino & Pasta 2017). Within its natural distribution range, including Sicily, the cork oak seems chiefly to characterize sub-optimal *facies* compared to local climax forests, whereas only rarely playing a primary role (Selvi & Viciani 1999). However, due to the total lack of examples of undisturbed forest vegetation within the whole range of the Mountains of Palermo (Pasta 1993), forecasting the possible dynamic evolution of cork oak stands is rather complex, making impossible to assess which were the most mature "final" forests adapted to local edapho-climatic con-

straints. Mixed oak woods must have been the rule before man favoured holm oak, cork oak and manna-ashes (*Fraxinus ornus*) to the detriment of deciduous oaks (*e.g., Quercus pubescens* and *Quercus cerris*) by coppicing native woodlands. Conversely, it is well known that regressive processes affect these ecosystems when the disturbance is more intense and/or more frequent than the cork oak's regeneration and recovery ability. Due to the combined effects of overgrazing and wildfires, cork oak stands are initially replaced by species-poor and structurally simplified mantle and shrubland communities, dominated by fast resprouters such as *Cytisus infestus, Spartium junceum* and *Euphorbia characias*, but also by species that are largely dispersed by wild animals, such as *Pistacia lentiscus, Pistacia terebinthus, Osyris alba, Prunus spinosa, Pyrus spinosa, Rubus ulmifolius* and *Crataegus monogyna* (La Mantia et al. 2019). If the disturbance regime is further intensified, perennial grasslands dominated by *Ampelodesmos mauritanicus* are the most likely fate of *Q. suber* stands, as has largely occurred in other areas of the western Mediterranean basin (Vilà et al. 2001). Contrarily, open and scattered cork oak stands could evolve towards more complex woodlands if grazing pressure and fire frequency decrease (Bueno et al. 2020). However, a similar scenario, consistent with the hypothesis of many authors who attribute the meaning of steady disclimax to cork oak stands, maintained by moderate disturbance regimes, especially wildfires (Barberis & Mariotti 1979), should be supported by further qualitative and quantitative investigations.

As far as our study sites are concerned, they have been particularly prone to intense and frequent human pressure (mostly wildfires and overgrazing) for millennia. Natural woodlands, including cork oak stands, have been exploited or cleared since proto-historical times. The land patches between these forests have been historically devoted to other agro-pastoral land uses (leaving no tree species), because agroforestry systems like *dehesa* do not belong to local Sicilian farming tradition. Accordingly, the surveyed cork oak stands can be interpreted as the last remnant nuclei of once more widespread forest patches. Such worrying conditions of the territory under investigation are further exacerbated by the lack of effective protection regime as none of the surveyed forest stands falls within protected sites, and by the still high impact of wildfires. Hence, we deem that these cork oak stands would deserve full protection as their survival in a medium to long-term perspective is far from guaranteed.

Conclusions

Compared to other evergreen oaks, cork oak has a more restricted ecological niche, particularly concerning soil humidity. Moreover, a decline of *Q. suber* is foreseen, es-

pecially at the edge of its natural range, due to overgrazing, high fire frequency, soil pathogens and land-use changes. We studied several cork oak populations on soils deriving from calcareous bedrock, which are generally less suited to the species. Based on our results, we hypothesized that the local presence of *Q. suber* could depend on high fire frequency, the peculiar biogeochemistry of local soils (*e.g.*, high Ca content), and erosion, which caused the re-emergence of calcareous substrates. The evolution of these stands is hardly predictable as strictly linked to disturbance frequency and intensity (mostly wildfires). Monitoring activities and protection measures are highly necessary to contrast the likely future shrinkage of these populations, which are threatened by extremely high fire frequency and overgrazing, as well as the likely negative effects of climate change on regeneration ability and survival rate.

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Supplementary Material

Tab. S1 - Land units of the surveyed areas according to the methodology developed by Blasi et al. (2000).

Tab. S2 - Results of the full phytosociological surveys.

Tab. S3 - Morphological characteristics of the pedons collected in the field.

Tab. S4 - Results of spatial autocorrelation analysis.

Tab. S5 - Results of the simplified phytosociological surveys.

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