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REGULAR PAPER

Assessment of plant species diversity associated with the carob tree (*Ceratonia siliqua*, Fabaceae) at the Mediterranean scale

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Background and aims – The thermophilous woodlands of the Mediterranean region constitute reservoirs of genetic resources for several fruit trees. Among them, the carob tree (*Ceratonia siliqua*) is a key component of traditional Mediterranean agroecosystems but its ecology was never assessed at the scale of its whole distribution area. Fortunately, phytosociological literature shelters invaluable resources for several issues in conservation, among them the possibility to analyse plant biodiversity at regional or continental scale. Here, we present the results of a comprehensive survey of the phytosociological literature associated to carob tree.
Methods – We collected 1542 floristic relevés performed in 18 geographical areas distributed around the Mediterranean in which the presence of *C. siliqua* was recorded. Species composition of the plant communities was analysed by multivariate ordination and hierarchical classification, and species diversity was evaluated by rarefaction and prediction analyses of Hill numbers.
Key results – Multivariate analyses revealed that plant communities associated with the carob tree are well differentiated between the Western and Eastern basins. A wider range of floristic differentiation is revealed in the Western basin where the vegetation reaches its maximal heterogeneity. By comparison, in the Eastern basin the plant assemblages associated with the carob tree are more homogeneous and with a lower species richness but a higher Simpson diversity.
Conclusions – The large ecological range of the Mediterranean carob trees is potentially an important evolutionary legacy for the conservation of genetic resources and seed sourcing for new uses such as restoration ecology.

Key words – Biodiversity, biogeography, Mediterranean, species diversity, conservation, natural resources, carob tree, *Ceratonia siliqua*, crop wild relative.

INTRODUCTION

The Mediterranean thermophilous woodlands shelter several relictual taxa that were more widespread during the Miocene warmer climate (de Saporta 1888, Quézel & Médail 2003, Thompson 2005). Due to their higher incidence along the coasts and within the lowlands, thermophilous forests were very early impacted by human activities, mainly for forage and fruits harvest (Grove & Rackham 2001, Blondel 2006). The recurring exchanges between natural ecosystems and cultivated areas constituted a pivotal aspect in the long-term process of Mediterranean fruit tree domestication (Miller & Gross 2011, Weiss 2015, Aumeeruddy-Thomas et al. 2017) and they still play an important role for genetic resources in

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sight of global change (Besnard 2016). Natural and semi-natural forests, as well as traditional Mediterranean agroecosystems, harbor fruit tree populations throughout environmental gradients, and thereby they constitute reservoirs of evolutionary and genetic resources of crop wild relatives.

The carob tree (*Ceratonia siliqua* L.), is a Mediterranean thermophilous fruit tree widely exploited for food and forage since antiquity and currently for industrial, agricultural and soil restoration purposes (Battlle & Tous 1997). Despite its contribution to Mediterranean agroecosystems, the native status of the carob tree is still source of debate. On the basis of archaeological and etymological evidences several authors consider that after its domestication in the Middle-East around 6000–4000 BC the carob tree was disseminated by humans to the West (de Candolle 1883, Battlle & Tous 1997, Ramón-Laca & Mabberley 2004). As a consequence wild carob trees are a "semi-natural" or "semi-domestic" component, beside other fruit tree species, such as oaks, pistachios and almonds that were also extensively exploited since millennia (Blondel 2006). On the other hand, phytosociological studies usually included the carob in spontaneous vegetation as a native (i.e. as opposed to feral), considering it as a bioindicator of Mediterranean thermophilous maquis and forest communities (Zohary & Orshan 1959, de Bolòs 1970, Quézel & Médail 2003). However, a comprehensive survey of plant diversity associated to carob tree is still lacking despite the constantly emphasized importance of the tree in the Mediterranean human culture and the long-standing interest of botanists (e.g. de Candolle 1883, Hillcoat et al. 1980, Batlle & Tous 1997, Ramón-Laca & Mabberley 2004).

A comprehensive conservation of carob tree habitats requires to define the main patterns of plant species diversity through its range. After decades of investigation the phytosociological literature potentially contains this knowledge. In this study we use available phytosociological data to examine geographical patterns of plant species diversity associated with carob tree all over the Mediterranean region.

MATERIAL AND METHODS

Collection of floristic relevés

A set of 1683 phytosociological relevés performed according to the method of Braun-Blanquet (1964) and including *C. siliqua* were gathered from databases (56.5%) and from a large literature survey (43.5%). The sources of this information are detailed in electronic appendix 1B. The nomenclatural homogenization was performed according to the following steps: first the homogenization was done progressively, country by country, and according to the Euro+Med PlantBase (2015) and the African Plant Database version 3.4.0 (2015). For a final correction of synonyms and plant name authorships the files were merged and submitted to The Plant list (2013) using the function TPL() of the Taxonstand R package (Cayuela et al. 2012). The list of all names of taxa with their authorships is available in electronic appendix 3. After removing those relevés with a lack of precision to assign geographical coordinates, the final data set included 1542 relevés and 1823 taxa (species and subspecies). Information about the plot size of each relevé was available for 961 of them, and the 75% ranged from 100 to 400 m^2 whereas the 25% remaining were distributed from 4 to 90 m^2 with a dominance of relevés of 50 m^2 (11%). The correlation between plot size and species richness was low and non-significant (Kendall τ = -0.04, p = 0.09) and therefore was not considered as a bias in the analyses. Moreover relevés done on plot size below 100 m^2 were not concentrated in one region and where found in areas where a lot of relevés were collected. The table of species occurrences with their abundance and geographical coordinates of relevés is available in electronic appendix 3.

Multivariate analyses of floristic structure

Multivariate analyses of floristic structure were carried out with a reduced data set of 1542 relevés for 1141 species, in which singletons (i.e. species observed in only one relevé) were removed. To investigate the geographical patterns of plant diversity, the relevés were gathered into areas containing at least 25 relevés; 18 areas were defined, 11 in the Western and 7 in the Eastern Mediterranean. These areas were selected to best reflect the Mediterranean geography (table 1, see map of the 18 areas in electronic appendix 1A). The geographical split between Western and Eastern Mediterranean was based on biogeographical literature (Finnie et al. 2007). A principal coordinate analysis (PCoA; dudi.pco() function, ade4 R package, Dray & Dufour 2007) was performed based on the Bray-Curtis dissimilarity index (vegdist() function, vegan R package, Oksanen et al. 2016). Species abundance was obtained from Braun-Blanquet's abundance-dominance codes using the scores of 0.5, 1, 2, 3, 4 and 5. The first 100 axes of the PCoA were kept, as they included 75% of total variance, and were submitted to a between-class analysis (BCA, bca() function, ade4 R package) using geographical area as the explanatory variable to test for geographical trends (randomization test, 999 iterations).

Plant species composition and diversity associated to the carob tree

Analyses of plant species diversity were done on the data set with all species, i.e. including singletons (1542 relevés for 1823 taxa). A constancy table reporting the frequency of species in each of the 18 areas was built to summarize the composition of main floristic groups at the scale of the study and only the species present in at least 25% of the relevés of one area were kept. To summarize the pattern of species composition at a coarser level, the 18 areas were gathered in five groups according to their floristic similarity within the constancy table, by a hierarchical cluster analysis (HCA; Bray Curtis distance and Ward algorithm; functions vegdist(), vegan R package, and hclust()). The dendrogram was truncated to retain five main clusters or floristic groups, which we consider a good compromise to describe the main geographical pattern at the Mediterranean level. To characterize the composition of these floristic groups the functions indval() and const() (labdsv R package, Roberts 2016) were used to list the indicator and most frequent plant taxa. These lists were used to assign a phytosociological alliance to each floristic group (species indicator values available in electronic appendix 4). The floristic group were assigned to phytosociologi-

Table 1 – **Species diversity associated with carob tree in the Mediterranean.**
Diversity estimates produced by rarefaction analyses (iNEXT R package) to compare plant species diversity associated to carob tree among five geographical areas. LCL= lower confidence limit, UCL= upper confidence limit.

Factor	Geographical areas	N	Diversity metric	Estimator	LCL	UCL
Flo. Grp. 1	z01 South Portugal, z02 South Spain, z10 Northern Morocco	317	Species richness	398	388	407
			Shannon diversity	149	145	154
			Simpson diversity	78	76	81
Flo. Grp. 2	z03 Western Spain, z04 Baleares, z05 France, z06 Croatia, z07 Sicily, z08 Tunisia, z09 Algeria	609	Species richness	506	498	514
			Shannon diversity	203	199	208
			Simpson diversity	103	101	106
Flo. Grp. 3	z15 Turkey, z16 Cyprus, z17 Levant, z18 Libya	151	Species richness	325	316	334
			Shannon diversity	172	167	177
			Simpson diversity	108	103	112
Flo. Grp. 4	z11 Southern Morocco	164	Species richness	304	295	313
			Shannon diversity	151	146	156
			Simpson diversity	90	87	94
Flo. Grp. 5	z12 Western Greece, z13 South Greece, z14 Crete	352	Species richness	501	492	510
			Shannon diversity	241	236	247
			Simpson diversity	138	134	142
Eastern	z12 Western Greece, z13 South Greece, z14 Crete, z15 Turkey, z16 Cyprus, z17 Levant, z18 Libya	503	Species richness	745	738	761
			Shannon diversity	305	299	310
			Simpson diversity	154	153	159
Western	z01 South Portugal, z02 South Spain, z10 Northern Morocco, z03 Western Spain, z04 Baleares, z05 France, z06 Croatia, z07 Sicily, z08 Tunisia, z09 Algeria	1039	Species richness	1002	998	1012
			Shannon diversity	299	294	304
			Simpson diversity	129	128	131

cal alliances following Quézel & Médail (2003) and Tsiourlis et al. (2007).

Patterns of plant species diversity were summarized for each area and compared according to the five main floristic group obtained by the HCA and finally according to Western and Eastern Mediterranean. At the level of the 18 areas, Pearson correlation tests revealed a strong and significant bias caused by the number of relevés in each area for gamma species richness ($r = 0.93$, $p < 0.001$), but not for alpha species richness ($r = 0.35$, $p = 0.15$). To take into consideration the bias due to different sampling efforts, the comparison of species diversity among the five floristic groups or between the Western and Eastern Mediterranean was done with the sample-size based interpolation and extrapolation (R/E) of Hill numbers developed by Chao & Jost (2012). The rarefaction and prediction analysis of Hill numbers was applied to the three orders of taxonomic diversity (species richness, Shannon diversity and Simpson diversity) with the iNEXT() function (iNEXT R package, Hsieh et al. 2016); confidence intervals were based on 999 iterations and R/E curves were done with ggiNEXT() function. Rarefaction (interpolation) and extrapolation (prediction) of Hill numbers are a unified method to account for differences in sample size when comparing species diversity across several assemblages.

RESULTS

Geographical pattern of plant species diversity associated with carob tree

The plant diversity analyses revealed common association between carob and plant species of Mediterranean forest environments such as *Pistacia lentiscus*, *Olea europaea*, *Smilax aspera*, *Quercus coccifera*, *Rhamnus* spp. and *Phillyrea* spp. (table 2, electronic appendix 4). The BCA analysis indicated that a large part of the floristic variance was due to the within-area level: the between-area inertia percentage was 19% ($p = 0.001$, 999 permutations). However, the BCA ordination revealed a strong floristic differentiation between the Western and the Eastern basins, followed by the opposition between Southern Morocco and the French Riviera (fig. 1A & B). By contrast plant species diversity of the areas of East-

Table 2 – **Summary of the most frequent plant taxa associated with carob tree according to five floristic groups.**
Plant taxa were ordered according to their relative frequency, in decreasing order in each floristic group and the first twenty are shown here.

Group 1	**Group 2**	**Group 3**	**Group 4**	**Group 5**
South Portugal, South Spain, Northern Morocco	Western Spain, Baleares, France, Croatia, Sicily, Tunisia, Algeria	Turkey, Cyprus, Levant, Libya	Southern Morocco	Western Greece, Southern Greece, Crete
Pistacia lentiscus	*Pistacia lentiscus*	*Smilax aspera*	*Lavandula dentata*	*Pistacia lentiscus*
Olea europaea subsp. *europaea*	*Olea europaea* subsp. *europaea*	*Pistacia lentiscus*	*Pistacia lentiscus*	*Olea europaea* subsp. *europaea*
Rhamnus lycioides subsp. *oleoides*	*Asparagus acutifolius*	*Quercus coccifera*	*Cistus creticus*	*Calicotome villosa*
Chamaerops humilis	*Rubia peregrina*	*Calicotome villosa*	*Tetraclinis articulata*	*Prasium majus*
Phlomis purpurea	*Smilax aspera*	*Phillyrea latifolia*	*Genista tricuspidata*	*Drimia maritima*
Smilax aspera	*Brachypodium retusum*	*Olea europaea* subsp. *europaea*	*Thymus saturejoides*	*Asparagus aphyllus* subsp. *orientalis*
Rubia peregrina	*Rhamnus alaternus*	*Cistus creticus*	*Olea europaea* subsp. *europaea*	*Brachypodium retusum*
Aristolochia baetica	*Pinus halepensis*	*Sarcopoterium spinosum*	*Globularia alypum*	*Thymbra capitata*
Quercus coccifera	*Rosmarinus officinalis*	*Rubia tenuifolia*	*Genista ferox*	*Quercus coccifera*
Daphne gnidium	*Arisarum vulgare*	*Asparagus acutifolius*	*Brachypodium distachyon*	*Phagnalon rupestre* subsp. *graecum*
Cistus albidus	*Lonicera implexa*	*Prasium majus*	*Chamaerops humilis*	*Smilax aspera*
Phillyrea latifolia	*Clematis flammula*	*Pinus brutia*	*Argania spinosa*	*Dactylis glomerata* subsp. *hispanica*
Arbutus unedo	*Chamaerops humilis*	*Dactylis glomerata* subsp. *hispanica*	*Phagnalon saxatile*	*Piptatherum miliaceum*
Asparagus albus	*Euphorbia dendroides*	*Juniperus phoenicea* subsp. *turbinata*	*Fumana laevipes*	*Piptatherum caerulescens*
Arisarum simorrhinum	*Quercus coccifera*	*Rhamnus punctata*	*Arisarum vulgare*	*Leontodon tuberosus*
Quercus ilex subsp. *ballota*	*Myrtus communis*	*Myrtus communis*	*Phillyrea angustifolia*	*Cistus creticus*
Rhamnus alaternus	*Calicotome spinosa*	*Pistacia palaestina*	*Quercus ilex* subsp. *ballota*	*Arisarum vulgare*
Drimia maritima	*Phillyrea latifolia*	*Cyclamen persicum*	*Eryngium tricuspidatum*	*Sarcopoterium spinosum*
Lonicera implexa	*Pistacia terebinthus*	*Hypericum thymifolium*	*Drimia maritima*	*Crucianella latifolia*
Cistus monspeliensis	*Ampelodesmos mauritanicus*	*Piptatherum miliaceum*	*Rhus tripartita*	*Phillyrea latifolia*

ern is weakly structured; only the area z17 gathering relevés from Lebanon and Syria appeared to be different and only from the fourth axis of the BCA (not shown).

Main plant species assemblages associated to carob tree

Floristic composition among the 18 areas was partitioned by a HCA in five floristic groups (table 1) which are described in tables 2 & 3 (the dendrogram is shown in electronic appendix 2C). The differences between these floristic groups are mainly due to taxa restricted to one or few areas or to the Western vs. Eastern part.

The first group is gathering relevés from areas adjacent to the Gilbraltar strait (North Morocco, Southern Portugal and Southern Spain). According to frequent and indicator taxa (tables 2 & 3) this group belongs to the phytosociological alliance *Asparago albi-Rhamnion oleoidis* Rivas-Goday 1964 emend. Rivas-Martínez 1975 characterizing a thermo-Mediterranean vegetation of Iberian Peninsula and North Morocco under semi-arid and sub-humid climate. The second group is composed of relevés of seven areas from Mediterranean Europa and North Africa (Western Spain, Baleares, France, Croatia, Sicily, Tunisia, Algeria). It corresponds to the alliance *Oleo sylvestris-Ceratonion siliquae* Br.-Bl. 1936 emend. Rivas-Martínez 1975, a thermo-Mediterranean forest vegetation mostly observed at the east of the meridian Valence-Oran under humid and sub-humid climates. The third group is constituted by relevés from Turkey, Lebanon, Syria, Cyprus and Libya, designed by the alliance *Ceratonio siliquae-Rhamnion oleoidis* Barbero & Quézel 1979; this is a thermo-Mediterranean vegetation from Greece to the Middle East mainly on limestone and near the coastline. The fourth

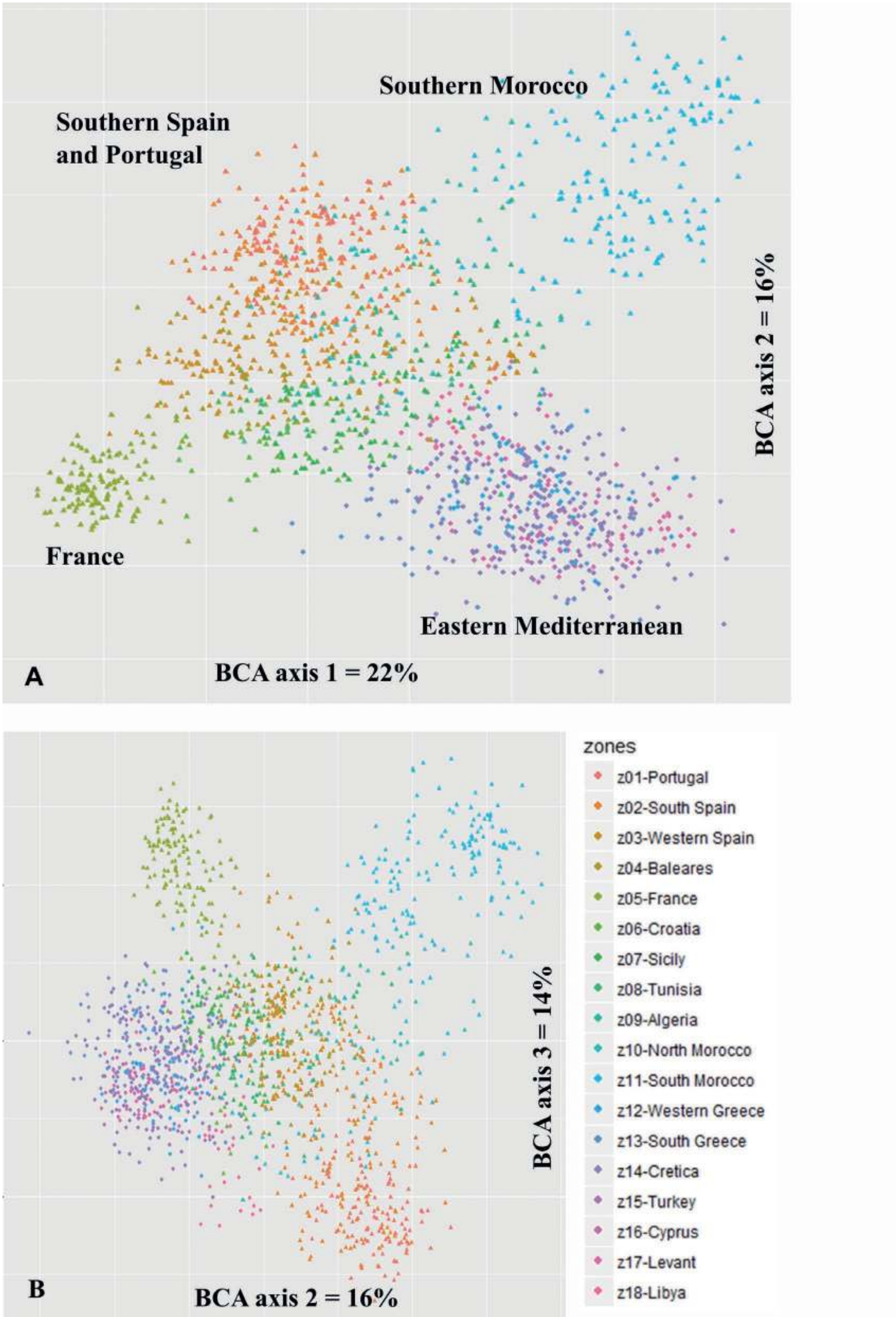

Figure 1 – Ordination of the 1542 relevés describing plant assemblages associated with the carob tree based on the Bray-Curtis dissimilarity index and a between-class analysis (BCA) with the geographical areas as the class factor, (A) plot with BCA axes 1 and 2, (B) plot with BCA axes 2 and 3. The relevés are coloured according to their geographical area. The BCA was performed on the 100 first components of a principal coordinate analysis (PCoA). BCA is accounting for 19% of the total inertia coming from the PCoA and the three first BCA axes are accounting for 52% of BCA inertia. A permutation test confirmed the significance of the structure bore by BCA ($p = 0.001$, 999 permutations).

Table 3 – **Summary of the indicator plant taxa associated with carob tree according to five floristic groups.**
Plant taxa were listed in decreasing order of their indicator value in each floristic group and the first twenty are shown here. The whole list is available in electronic appendix 4. The last row indicates the phytosociological alliance of the floristic group (see the text for the details).

Group 1	**Group 2**	**Group 3**	**Group 4**	**Group 5**
South Portugal, South Spain, Northern Morocco	Western Spain, Baleares, France, Croatia, Sicily, Tunisia, Algeria	Turkey, Cyprus, Levant, Libya	Southern Morocco	Western Greece, Southern Greece, Crete
Phlomis purpurea	*Asparagus acutifolius*	*Rubia tenuifolia*	*Lavandula dentata*	*Thymbra capitata*
Aristolochia baetica	*Rubia peregrina*	*Rhamnus punctata*	*Genista tricuspidata*	*Drimia maritima*
Rhamnus lycioides subsp. *oleoides*	*Pinus halepensis*	*Sarcopoterium spinosum*	*Tetraclinis articulata*	*Lamyropsis cynaroides*
Daphne gnidium	*Rhamnus alaternus*	*Calicotome villosa*	*Thymus saturejoides*	*Crucianella latifolia*
Arisarum simorrhinum	*Brachypodium retusum*	*Pistacia palaestina*	*Genista ferox*	*Leontodon tuberosus*
Chamaerops humilis	*Euphorbia dendroides*	*Hypericum thymifolium*	*Argania spinosa*	*Phlomis fruticosa*
Cistus albidus	*Calicotome spinosa*	*Cyclamen persicum*	*Globularia alypum*	*Genista acanthoclada*
Arbutus unedo	*Thymus vulgaris*	*Pinus brutia*	*Carlina involucrata*	*Hypericum empetrifolium*
Crataegus monogyna	*Rosmarinus officinalis*	*Stachys distans*	*Eryngium tricuspidatum*	*Scaligeria napiformis*
Quercus ilex subsp. *ballota*	*Ononis minutissima*	*Origanum syriacum*	*Phagnalon saxatile*	*Urospermum picrioides*
Cistus monspeliensis	*Ampelodesmos mauritanicus*	*Phillyrea latifolia*	*Thymus maroccanus*	*Dracunculus vulgaris*
Asparagus albus	*Lonicera implexa*	*Lotus longisiliquosus*	*Rhus tripartita*	*Petromarula pinnata*
Vinca difformis	*Quercus ilex* subsp. *ilex*	*Calicotome rigida*	*Genista tamarrutii*	*Valantia hispida*
Jasminum fruticans	*Clematis flammula*	*Eryngium falcatum*	*Fumana laevipes*	*Hypochaeris achyrophorus*
Stipa tenacissima	*Euphorbia spinosa*	*Arbutus andrachne*	*Lavandula maroccana*	*Phlomis lanata*
Osyris lanceolata	*Erica multiflora*	*Rhamnus lycioides* subsp. *graeca*	*Acacia gummifera*	*Teucrium microphyllum*
Viburnum tinus	*Allium acutiflorum*	*Arbutus pavarii*	*Coronilla ramosissima*	*Galium murale*
Jasminum fruticans	*Galium obliquum*	*Micromeria myrtifolia*	*Lavandula pedunculata*	*Avena barbata*
Stipa tenacissima	*Ruta angustifolia*	*Micromeria nervosa*	*Asphodelus tenuifolius*	*Lagoecia cuminoides*
Melica minuta subsp. *latifolia*	*Helictochloa bromoides*	*Phlomis floccosa*	*Teucrium demnatense*	*Bromus fasciculatus*
Asparago albi-Rhamnion oleoidis	***Oleo sylvestris-Ceratonion siliquae***	***Ceratonio siliquae-Rhamnion oleoidis***	***Senecio anteuphorbii-Arganion spinosae***	***Sarcopoterion spinosi***

group gathered relevés from Southern Morocco only, it corresponds to the alliance *Senecio anteuphorbii-Arganion spinosae* Barbero et al. 1982, endemic of South-Western Morocco and characterizing a quasi-steppic vegetation under semi-arid climate. Finally, the fifth group corresponds to the three areas from Greece and belongs to the *Sarcopoterion spinosi* Zohary 1973, a phrygana vegetation of the Eastern Mediterranean.

Comparisons of species diversity

Overall, a mean of 23 plant species by sample (i.e. by relevé) is reported; minimum alpha diversity values ranged from 15 to 17 species by sample for the Balearic Islands, Tunisia and Croatia, whereas maximum values of 29, 31 and 40 species by sample are obtained for Crete, Lybia and France respectively (electronic appendix 2A). Comparison of species pools between the five floristic groups described above is done on rarefaction/prediction of Hill numbers to account for differences in sample size (table 1). The highest species richness estimates are obtained for floristic group 2 (Western Spain, Baleares, France, Croatia, Sicily, Tunisia, Algeria) and floristic group 5 (Greece); they have similar value for species richness but Greece have higher estimates for Shannon and Simpson diversities. The highest Simpson diversity estimates are predicted for floristic groups 3 and 5 belonging to the Eastern Mediterranean and for group 2 belonging to the Western.

Comparison of diversity showed a much higher species richness in the Western than in the Eastern basin (fig. 2B), with species richness reaching values of 1002 and 745, respectively (table 1). Although Shannon diversity index was similar across basins, Simpson diversity index was slightly but significantly higher in the Eastern than in the Western Mediterranean (table 1), indicating higher cover-abundance scores of species in the relevés of the Eastern basin. Besides, this result also indicates that the higher species richness in the Western basin is related to the recording of more numerous rare species (table 1).

DISCUSSION

The thermophilous woodlands of the Mediterranean region constitute reservoirs of genetic resources for several fruit trees. To our knowledge the ecological range of wild relatives of domesticated fruit trees has been overlooked and very rarely examined at the scale of the Mediterranean region. This study illustrates the potential of phytosociological literature to characterize the plant species biodiversity in a broad geographic range and confirms that phytosociological literature shelters invaluable resources for ecological and environmental surveys. An initiative of a systematic collection of phytosociological data as done in Mediterranean databases SIVIM (Font et al. 2012), SILENE (2015) and VEGHELLAS (Dimopoulos et al. 2012) is indispensable for the ecological scientific community.

By means of data from these three databases (SIVIM, SILENE, VEGHELLAS) and of an extensive literature investigation the plant species diversity associated with carob tree was described throughout its current distribution in the Mediterranean based on 1542 floristic relevés. All the plant assemblages associated to carob tree described here have in common the overall high frequency of *Olea europea* and *Pistacia lentiscus* and the dominance of trees, shrubs or lianas such as *Smilax aspera*. Alongside these forest and maquis elements our analyses revealed that the vegetation associated with carob trees is diversified at the scale of the Mediterranean; the *Oleo sylvestris-Ceratonion siliquae* phytosociological alliance being only one of the five alliances described in this study (table 3 and see Results). The range of floristic differentiation is higher in the Western Mediterranean where three poles of diversity are shown in the BCA plot (fig. 1): Southern Morocco (an endemic phytosociological alliance), France and Southern Spain and Portugal. By contrast the areas of the Eastern basin are less differentiated and more overlapping (fig. 1) indicating a more homogeneous floristic diversity. Rarefaction/extrapolation sampling analyses of Hill numbers (table 1, fig. 2) converged to show that the plant assemblages associated with the carob tree contained higher species-richness in the Western than in the Eastern basin with more infrequent species in the Western (see differences in Simpson diversity, table 1).

In summary, carob tree habitats are characterized in the Western basin by a higher species richness due to higher number of rare species and a stronger floristic differentiation due to the strong latitudinal gradient of the Western range. In the Eastern basin, the floristic differentiation is less pronounced but Simpson diversity is higher indicating a greater diversity of abundant species. However, when geographical patterns were summarized according to five floristic groups a more nuanced pattern was revealed with a level of species richness in Greece similar or higher to those observed in the West and highest Simpson diversity in the East (table 1). The lowest estimates of plant species richness (extrapolation curve fig. 2A) are found for the southern and eastern limits of carob tree range. This pattern might be regarded as the consequence of either biogeography *per se* or different anthropogenic activities (Quézel & Médail 2003). For example in Greece, the carob tree is extensively exploited in multi-use agrosystems

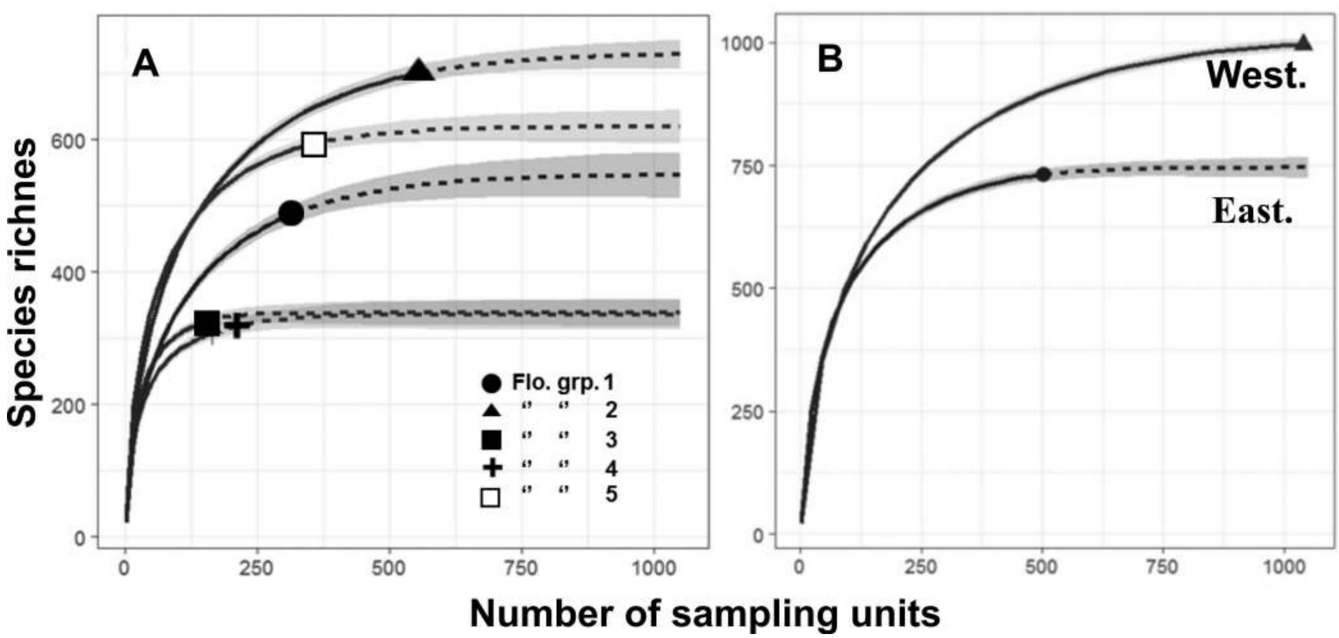

Figure 2 – Comparison of plant species richness associated to carob trees according to: A, the five floristic groups of table 1; and B, Western and Eastern Mediterranean. Sampling-unit-based rarefaction (solid lines) and extrapolation (dashed lines) curves are shown with 95% confidence intervals (grey-shaded regions).

(Blondel 2006) and it is also very abundant in rocky outcrops, cliffs and canyons where it is spread by the profusion of goats in landscapes. Thus, in Greece carob trees spread in an open vegetation, the *Sarcopoterion spinosi* alliance, associated to a large diversity of plant species (table 1). By contrast, toward the Eastern range limit, such as in Lebanon, the vegetation with carob tree that was investigated in the literature correspond in general to abandoned fields and orchards that are colonized by thermophilous shrubs (Talhouk et al. 2005).

Conclusions

The debate about the status of the carob tree – native, or introduced for cultivation – in the Western Mediterranean (Ramón-Laca & Mabberley 2004) will remain open until adequate investigations such as phylogeographical and paleoecological studies are conducted. In the context of forthcoming research on the history of the carob tree in the Mediterranean, the extensive data survey reported here bore evidence of the presence of carob tree along a large ecological gradient in the Western Mediterranean, where it is very well integrated to spontaneous vegetation within hotspots of plant biodiversity well known to be also biogeographical refugia (Benabid & Cuzin 1997, Médail & Quézel 1999, Molina-Venegas et al. 2017). Within the context of the aggravation of global changes, the ecological resilience capabilities have become a major issue in Mediterranean basin (see Thiébault & Moatti 2016). This issue is crucial, notably for Mediterranean orchards based on fruit trees, for which high productivity practices lead to a drastic decrease and homogenization of millenary biodiversity. The large ecological range of the Mediterranean carob trees is potentially an important evolutionary legacy for the conservation of genetic resources and seed sourcing for new uses such as restoration ecology (e.g. Domínguez et al. 2010), and also to develop a more water-efficient fruit farming in the drier areas of the Mediterranean basin.

SUPPLEMENTARY DATA

Supplementary data are available at *Plant Ecology and Evolution*, Supplementary Data Site (https://www.ingentaconnect.com/content/botbel/plecevo/supp-data) and consist of: (1) sources and geographical distribution of floristic data (pdf); (2) supplementary results on species diversity structure (pdf); (3) floristic data (Excel file); and (4) species indicator values of the floristic groups (Excel file).

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