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ORIGINAL PAPER

What are palm groves of *Phoenix*? Conservation of *Phoenix* palm groves in the European Union

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Abstract There are three species of *Phoenix* (Arecaceae) in the territory of the European Union, *P. canariensis*, *P. dactylifera* and *P. theophrasti*, found in wild-native populations, feral, planted and intermediate states, accounting each for thousands of individuals. The EU Habitats Directive has addressed the conservation of *P. theophrasti* and *P. canariensis* under the habitat type 9370, 'Palm groves of *Phoenix*,' but neglected to include

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D. Johnson djohn37@aol.com the wild-growing populations of *P. dactylifera* palms in southern Spain. In this paper, we survey the habitats and status of both representative native and naturalized populations of *Phoenix*, in total 103, through fieldwork, image analysis and review of literature. We underline the significance of feral populations and palms originating from ancient abandoned plantations, existing in protected areas as a reservoir of genetic variation. We conclude that, in order to improve their conservation status by adequate protection and conservation management, the concept of *Phoenix* palm groves in the Habitats Directive should be redefined to include the western group of *P. dactylifera* and the various habitats of *P. canariensis* and *P. theophrasti* that do not appear in the current definition.

Keywords Canary Islands · Crete · EU habitats directive · Greece · Spain

Introduction

Accepted European species of *Phoenix* (Arecaceae) are *P. canariensis*, *P. dactylifera* and *P. theophrasti* (Barrow 1998; Euro+Med 2006). The Canary Island date palm (*P. canariensis*) is distinguished by thick solitary trunks, acanthophylls congested in short pseudopetiole, deep green leaflets closely and regularly inserted in one plane of orientation, and by smaller fruits (Rivera et al. 2013). The chloroplast mini-satellite CpfM typically has 269 base pairs (Ballardini et al. 2013). Natural hybridization events between *P. canariensis* and *P. dactylifera*, the latter introduced in the Canary Islands, are common (González-Pérez et al. 2004). Hybrids cannot be identified with the plastid marker alone, but require the analysis of morphological characters as well as nuclear molecular markers (Billotte et al. 2004; Carreño 2012).

The presence of thick trunks, commonly multiple-stemmed, smaller fruits and seeds, very thin mesocarp, robust long acanthophylls congested in short pseudopetioles, and glaucous leaflets laxly and irregularly inserted in cruciate planes of orientation morphologically distinguish the Cretan date palm *Phoenix theophrasti* (Greuter 1967; Barrow 1998), which occurs in scattered populations around the Cretan coast and in SW Anatolia. The chloroplast minisatellite CpfM presents 280 base pairs as a rule (Ballardini et al. 2013).

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Although in Crete hybridization has not yet been observed, planted *P. canariensis* trees in tourist resorts close to Cretan date palm trees pose a risk to the genetic integrity of the native populations.

Phoenix dactylifera is characterized morphologically by relatively longer thin trunks, a tendency to produce basal offshoots and "Rákib" or "Rakoub", plur. "Rawákeeb," offshoots produced near the base of the date palm or higher up on the trunk (Täckholm and Drar 1950), long pseudopetioles with relatively shorter acanthophylls, glaucous leaflets and especially larger fruits and seeds (Carreño 2017). This species constitutes a complex of planted and semi-natural palm populations extending from the Cape Verde Islands in the Atlantic Ocean to Pakistan in the East. Being of uncertain native origin it has been cultivated for thousands of years (Terral et al. 2012; Zohary et al. 2012; Rivera et al. 2014a, b; Al-Khayri et al. 2015). Recent studies distinguished two geographically well-defined types, showing exclusive alleles for the CpfM chloroplast minisatellite, 257 bp long for East Mediterranean and West Asian date palms and 246 bp long for West Mediterranean palms, which suggest the existence of at least two separate centres of origin (Pintaud et al. 2013). This was further confirmed with nuclear data (Zehdi-Azouzi et al. 2015) and whole genome re-sequencing (Hazzourt et al. 2015).

Southeastern Spain is the main area of date palm in continental Europe, with nearly 1 million trees as of the late 1990s, before the spread of the exotic deadly red palm weevil (*Rhynchophorus ferrugineus*) (Rivera et al. 2015). These date palm populations represent more than 98% of the allele typical of the western type, making it, thus, an Ibero-North African endemic (Carreño 2012). Among these palms, clusters occur of individuals morphologically characterized by smaller fruits (similar to those of *Phoenix canariensis* and of the South Asian *P. sylvestris*), with thin mesocarp, robust glaucous leaves, and short robust acanthophylls. Known as "palmera de rambla," described as *P. iberica*, but not recognized as a distinct species, they grow in natural habitats, sometimes mixed with other individuals with more "domesticated" features (Rivera et al. 1997, 2015). Cultivated date palm populations receive legal protection in the Palmeral de Elche (Lerma 1986) and other localities of Southeastern Spain. This is not the case for those in natural habitats (Rivera et al. 2015).

The EU Habitats Directive (EEC, European Economic Community now European Communities) (Directive 92/43/EEC; European Union 1992) established as a priority habitat "Palm groves of *Phoenix*," coded 9370 and defined as "Woods, often riparian, formed by the two endemic palm trees, *Phoenix theophrasti* and *Phoenix canariensis*"(European Commission 2013). The Interpretation Manual specifies forest habitats of Annex I of the Directive, including 9370 palm groves, as "forests of native species [...] with a high degree of naturalness." Further criteria for forest habitats include "rare or residual, and/or hosting species of Community interest" (European Commission 2013). The current definition of European "Palm groves of *Phoenix*" explicitly covers only the palm groves of Crete and the Canarian palm groves, but excludes continental European date palm groves, not only modern plantations but also ancient human-made groves. This appears inconsistent as in other forest habitat types, such as "*Castanea sativa* woods" (9260) and "Mediterranean pine forests with endemic Mesogean pines" (9540) chestnut and stone pine plantations are included, provided that they are "old established" or "naturalized."

The current definition of *Phoenix* groves in the Interpretation Manual has thus several shortcomings causing difficulties in interpreting the habitat type and conveying and advocating the EU Directive in nature conservation practice:

- 1. Degradation stages of palm groves, which are common particularly on the Canary Islands but occur also in Crete, are not addressed, causing inconsistent recognition, interpretation, mapping, monitoring and management.
- 2. *Phoenix* groves derived from plantations, no matter how old and naturalized, are not referred to.
- Phoenix groves on the European mainland are currently ignored altogether, although phylogenetic and taxonomic evidence as well as vegetation studies suggest a high degree of evolutionary individuality and naturalness to date palm stands in southern Spain (Carreño 2017; Rivera et al. 2017).

In this paper, we outline the significance, habitat variation and distribution of *Phoenix* groves in Europe and the Canary Islands. We review briefly the habitats associated with *Phoenix*, both natural, semi-natural, and degraded, based on fieldwork and literature evaluation as well as aerial imagery analysis. By introducing the different regional subtypes of *Phoenix* habitats, we attempt to increase their international recognition and suggest a revision of the circumscription of the Annex I habitat type 9370.

Methods

Data collection

Bibliographical sources

Records of *Phoenix* species, their distribution, ecology, vegetation and conservation status were taken for Crete (Greece) from Barclay (1974), Gradstein and Smittenberg (1977), Turland et al. (1993), Greuter (1995), Fournaraki and Delipetrou (2003a, b), Boteva et al. (2004), Fielding and Turland (2005), Bergmeier and Abrahamczyk (2008), Dimopoulos and Bergmeier (2008), Thymakis (2009), Fassoulas (2013), NHMC (Natural History Museum of Crete) (2015), and Strid (2016), for the Bordighera-Sanremo area (Italy) from Carassale and Dore (2013), for the Canary Islands from Santos (1983), Rivas-Martínez et al. (1993a, b), Del Arco (2006), Del Arco et al. (2006, 2009, 2010), Naranjo et al. (2009), Salinas and Cueto (2009), Sosa et al. (2007), Saro et al. (2015), and Carqué et al. (2015), for SE Iberia (Spain) from Alcaraz et al. (1989), Peinado et al. (1992), Salinas and Cueto (2009), Costa et al. (2011), Carreño (2012), and Ruiz (2015).

The nomenclature of scientific names of species follows Euro+Med (2006), that of syntaxa Rivas-Martinez et al. (1993a, b) and Mucina et al. (2016). A reference to phytosociological community types and their syntaxonomical position are provided in the Supplement.

Field work and imagery analysis

We conducted fieldwork during the creation of the Spanish national germplasm bank (PhoenixSpain 2015) in continental Europe (2007–2016), Canary Islands (2011–2013) and Crete (2014 and 2017). We surveyed 103 localities with natural and semi-natural *Phoenix* populations, 69 of which are distributed in the Canary Islands, 14 in Crete, and 20 in continental Europe. Further studies on the vegetation and conservation status of Cretan habitats of *Phoenix theophrasti* were carried out during the Greek Natura 2000 mapping and

monitoring project in 2013–2015. We collected fruit and seed samples that were further processed, measured and included in the germplasm bank. A portion of each sample was

put to germinate. In the field, the sampled palms and their habitat were photographed and the accompanying species were annotated. We surveyed the localities and the areal extent of the palm groves using Google Earth[®] and Street View[®]. The protection status was extracted from NHMC (2015), IDE (2016), Generalidad Valenciana (1986, 2016), Ideandalucia (2016) and Cartomur (2016). Details of habitate and localities are summerized in Sumfementary Tables.

of habitats and localities are summarized in Supplementary Tables. Those of *Phoenix canariensis* appear in Supplementary Tables S1a and b, *Phoenix theophrasti* in Supplementary Tables S2a and b and *Phoenix dactylifera* in Supplementary Tables S3a, b.

Categories of data

For each of the 103 localities seven different descriptors were established (Table 1). Descriptor states are not mutually exclusive and often more than one is present in a single locality.

Status Levadoux (1956) distinguished different types of wild populations of grapevine (*lambrusques*), based on their origin and taxonomic status. Rivera et al. (2016) expanded this approach to different genera of fruit trees and date palms including available data on the distribution of genetic variation following Franks (1999) who proposed ecogeographic surveys to identify populations of plants for food and agriculture, and the genetic variation within and between these populations. Apart from "Planted" we distinguished the following states: Wild native, Abandoned, Escaped, and Naturalized.

Abandoned palms extend a previously established but now abandoned fruit palm plantation. Individual palms or plantations have been left by the owner devoid of cultivation. The presence of remains of agricultural structures, artificial terraces or plots, or the regular shape of the alignments, reveal the existence of a previous cultivation of these palm trees. Given sufficient time, the abandoned plantation may reach a wild-like aspect.

Escaped palms grow in uncultivated ground, from seeds originated from planted palms. Escaped palms are often confounded with naturally wild individuals. Where wild relatives and cultivars grow in proximity and are morphologically similar it is often difficult to ascertain whether the direct progenitors have been planted.

Naturalized palms originate from cultivated or, more precisely, domesticated ancestors which, over several generations, have become established in the wild. Escaped populations constitute the first generation of a successful naturalization process.

Wild native or indigenous palms descend from ancestors which have never gone through the cultural stage. However, wild native (indigenous) palms may hybridize with palms of one of the above status forms. Resulting hybrid populations may become locally dominant in the natural vegetation. The fear of genetic dilution of the native *Phoenix canariensis* through wind-blown pollen of cultivated *P. dactylifera* led Spanish authorities to ban cultivation of the true date palm in the Canary Islands through its classification as an Invasive Species (Arias 2013). The inclusion in the list of Invasive Species entails the general prohibition of the possession, transport, traffic and trade of live or dead specimens, of their remains or propagules, including foreign trade (Arias 2013).

Grouping We distinguish *Scattered* (palm populations where individual palms are distant on average more than twice the diameter of the crowns); *Clusters* (small groups of up to 10 palm trees densely clustered, with crowns overlapping) and *Groves* (more or less dense linear or polygonal formations, usually with over 100 palm trees).

Type	Canary Islands	Crete	Continental Spain	Italy
Number of sites	69	14	19	1
Status				
Wild native	58.0	71.4	21.1	0
Planted	49.3	35.7	21.1	100
Abandoned	53.6	14.3	68.4	100
Escaped	50.7	14.3	68.4	100
Naturalized	58.0	57.1	68.4	0
Grouping				
Scattered	91.3	78.6	94.7	100
Cluster	20.3	57.1	73.7	100
Groves	14.5	21.4	26.3	0
Main habitat				
Ramblas	8.7	7.1	21.1	0
Gullies	42.0	42.9	31.6	100
Ravines	11.6	14.3	5.3	0
Fields	29.0	35.7	26.3	0
Slopes and hills	42.0	14.3	5.3	0
Cliffs	1.4	7.1	5.3	0
Sandy seashore more or less saline	0.0	14.3	10.5	0
Basins and reservoirs	4.3	0.0	10.5	0
Rivers	0.0	21.4	10.5	0
Protection				
Protected areas	42.0	50.0	68.4	0
Elevation				
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Type	Canary Islands	Crete	Continental Spain	Italy
Medium (151–400)	46.4	14.3	36.8	0
Moderately high (401–900)	52.2	0.0	5.3	0
High elevation (901–1200)	7.2	0.0	0.0	0
Vegetation				
CL. Phragmito-Magnocaricetea Klika in Klika & Novak 1941	4.3	28.6	15.8	0
CL. Molinio-Arrhenatheretea Tüxen 1937	17.4	14.3	26.3	100
CL. Quercetea ilicis BrBl. ex A. Bòlos & O. de Bolòs in A. Bolòs y Vayreda 1950	0.0	14.3	5.3	0
CL. Ononido Rosmarinetea BrBl.in A. Bolòs & Vayreda 1950. ROS04	0.0	0.0	21.1	0
CL. Ononido Rosmarinetea BrBl.in A. Bolòs & Vayreda 1950. ROS07	0.0	28.6	0.0	0
CL. Nerio-Tamaricetea BrBl. & O. de Bolòs 1958	40.6	57.1	57.9	100
CL. Oleo cerasiformis-Rhamnetea crenulatae Santos ex Rivas-Mart. 1987	55.1	0.0	0.0	0
CL. Pruno lusitanicae-Lauretea azoricae Oberd. ex Rivas-Mart. & al. 1977	1.5	0.0	0.0	0
CL. Salicetea purpureae Moor 1958	2.9	0.0	0.0	0
CL. Kleinio-Euphorbietea canariensis (Rivas Goday & Esteve 1965) Santos 1976	5.8	0.0	0.0	0
CL. Pegano-Salsoletea BrBl. and O. de Bolòs 1958	5.8	0.0	0.0	0
Anthropic	63.8	71.4	68.4	100
Main activity				
Natural	88.4	78.6	84.2	100
Agricultural	37.7	21.4	316	100

Multiple scoring in a single site is possible Data in percentage of sites

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Main habitat We distinguish nine categories mainly based on topography and land use: "Ramblas" (wide and open dry riverbeds periodically or occasionally flooded); Gullies (long narrow valleys with steep sides); Ravines (very deep narrow valleys with steep sides); Fields (areas of land on which crops are grown); Slopes (sides) of mountains and hills; Cliffs (high areas of land with a very steep side, next to the sea); Sandy seashore; Basins and reservoirs; Rivers (Table 1).

Protection For each palm population we determined whether or not it was conferred protection status.

Elevation The elevational range of the locality was classified as *low* (1–150 m above sea level), *medium* (151–400 m), *moderately high* (401–900 m), or *high* (901–1200 m).

Vegetation The vegetation associated with *Phoenix* stands was identified at the level of phytosociological classes (Cl. Phragmito-Magnocaricetea, Cl. Molinio-Arrhenatheretea, Cl. Quercetea ilicis, Cl. Ononido-Rosmarinetea, Cl. Nerio-Tamaricetea, Cl. Oleo-Rhamnetea, Cl. Pruno-Lauretea, Cl. Salicetea, Cl., Kleinio-Euphorbietea, and Cl. Pegano-Salso-letea). We also recognized an eleventh category (Anthropic) for vegetation of deeply transformed areas due to buildings or agricultural activities. The scheme for this Sintaxonomy of the *Phoenix* communities in continental Europe and islands under Habitats Directive is presented in Supplementary Table S4, actualized following Mucina et al. (2016).

Environment The environment of palm stands was classified as *Natural* (including seminatural areas with forest or range management) or *Agricultural* (cultivated palm groves, plantations and fields.

Data analysis

With the aim of establishing a classification of the great number of types of situations in which we can find the three *Phoenix* species in the territory of the European Union, we calculated a dissimilarity matrix from the 103 *Phoenix* localities and 35 variables of status, grouping, habitat, elevation, protection, vegetation and environment using Darwin 6V.6.0.12 (2015-04-15) (Perrier et al. 2003; Perrier and Jacquemoud-Collet 2016). The Sokal–Sneath dissimilarity index was calculated as $d_{ij} = 2(b + c)/a + 2(b + c)$, where d_{ij} is the dissimilarity between sample units i and j; a, number of variables where i is present and j is present; b, number of variables where i is present and j is absent.

Further, we used the agglomerative hierarchical minimum variance clustering technique (Ward's method), available in Darwin 6, to arrange the clusters so that relationships between different groups became apparent. Ward's method focuses on determining how much variation is present within each cluster. In this way, the clusters will tend to be as distinct as possible, since the criterion for clustering is to have the least amount of variation (Kovach 2007). The resulting tree was drawn using Dendroscope 3 (Huson and Scornavacca 2012).

Results and discussion

Habitat variation

Five main clusters were found that group the 103 surveyed localities along their variables of status, grouping, habitat, elevation, protection, vegetation and environment (Fig. 1).

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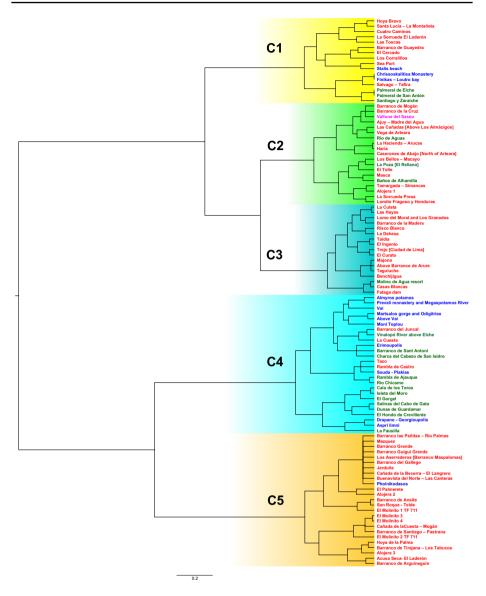


Fig. 1 Ward's minimum variance tree of the analyzed Phoenix localities in the European Union

Three clusters refer to localities which are highly cultivation-dependent and where wild native palms are rare or absent (C1–C3 in Figs. 1, 2). These comprise 41 sites in the Canary Islands, 3 in Crete, 1 in Italy and 7 in continental Spain. Two further clusters (C4 and C5 in Figs. 1, 2) comprise localities where wild native palms more or less prevail and which may occur together with abandoned, escaped or naturalized populations. These comprise 28 sites in the Canary Islands, 11 in Crete and 12 in Continental Spain.

"Grove" in English defines a group of trees that are close together, to small woods without underbrush or undergrowth, or to plantations of fruit trees (Collins 2017; Webster



C1. Cultivated or abandoned. Dense palm groves and clumps. Fields and sandy seashore. Anthropogenic. P. canariensis Las Toscas (La Gomera, Spain) F. Alcaraz. P. theophrasti Stalis Beach (Crete, Greece) D. Rivera. P. dactylifera San Antón (Orihuela, Spain) C. Obón.



C2. Cultivated, abandoned, escaped or naturalized. Scattered and clumps. Gullies, slopes and terraced fields. Molinio-Arrhenatheretea and Anthropogenic. P. canariensis La Sorrueda (Gran Canaria, Spain) F. Alcaraz. P. dactylifera Baños de Alhamilla (Almeria, Spain) D. Rivera and Vallone del Sasso (Bordighera, Italy) D. Rivera



C3. Cultivated, abandoned, escaped or naturalized. Scattered. Slopes and hills. Oleo-Rhamnetea and Anthropogenic. P. canariensis Barranco de Arure (La Gomera, Spain) F. Alcaraz, Arure (La Gomera, Spain) F. Alcaraz and Taguluche (La Gomera, Spain) F. Alcaraz.







C4. Wild native, rarely abandoned, escaped or naturalized. Clumps. Mostly coastal ramblas, rivers and ravines. Nerio-Tamaricetea and Anthropogenic. P. theophrasti Aspri Limni (Crete, Greece) D. Rivera and Megalospotamos River (Crete, Greece) C.Obón. P. dactylifera El



C5. Wild native. Scattered. Gullies, slopes of mountains and hills. 150-900 m. Oleo-Rhamnetea, Nerio-Tamaricetea, rarely Pruno-Lauretea. *P. camriensis* Barranco de Arguineguin (Gran Canaria, Spain) E. Carreño. Santa Lucia de Tirajana (Gran Canaria, Spain) F. Alcaraz and Santa Lucia de Tirajana (Gran Canaria, Spain) E. Carreño

Fig. 2 Examples of the five main clusters of *Phoenix* localities in the European Union. Further images can be accessed at: http://www.phoenix-spain.org/galeria-habitats/

2017). Whatever meaning adopted for "Palm groves of *Phoenix*" it assumes dense *Phoenix* formations falling within Clusters 1 and 4 (Figs. 1, 2), independent of their mainly anthropic or more or less natural origin. This clearly excludes more open or discontinuous *Phoenix* formations like those in clusters 2, 3 and 5 (Figs. 1, 2), and natural or anthropogenic, which are also relevant for *Phoenix* conservation.

From a geographical perspective, cluster 1 includes *P. canariensis* populations in the Canary Islands, together with some of the *P. dactylifera* in continental Spain and *P. theophrasti* in Crete. Cluster 2 includes the single Italian *P. dactylifera* locality that shows similar features and is associated with other localities of *P. canariensis* in the Canary Islands and *P. dactylifera* in continental Spain. Cluster 3 is almost composed of *P. canariensis* localities from the Canary Islands and a single locality of *P. dactylifera* from Rio Aguas in continental Spain, that present similar features. Cluster 4 shows the coincidence in the analysed variables among mainly natural populations of *P. theophrasti* (Crete), *P. canariensis* (Canary Islands) and *P. dactylifera* (continental Spain). Finally cluster 5 is almost exclusively integrated by *P. canariensis* populations of, mainly, Gran Canaria (Canary Islands, Spain).

There is a clear gradient in the proportion of localities with *wild native palms*, from the single Italian site (0%) and continental Spain (21%) to Crete (71%). Abandoned palms are relatively frequent in the "ramblas" (dry riverbeds) and ravines of SE Spain, the Italian Riviera and the Canary Islands, as remnants of abandoned orchards and groves. Escaped palms are relatively easy to detect where outside their natural range, e.g. P. dactylifera in the Canary Islands and P. canariensis in continental Europe. However, where the native species may have been planted as ornamental trees, or have been cultivated, it is difficult to distinguish escaped individuals, e.g. P. theophrasti in semi-natural surroundings of monasteries in Crete, P. canariensis on slopes of the Canary Islands or P. dactylifera in "ramblas" of SE Spain. Phoenix canariensis tends to grow naturalized in forest and scrubland around Barcelona (Basnou et al. 2015) although there is insufficient long-term evidence to distinguish the recorded individuals from escaped ones.

We found a wide repertory of situations for populations of the three *Phoenix* species. These are summarized in the following paragraphs.

Phoenix canariensis

The Canary Island date palm is native to all major islands of the archipelago. It grows as isolated trees or as more or less dense palm groves, with the exception of El Hierro where fully developed palm groves are absent, and Lanzarote where those occurring do not seem autochthonous (Del Arco et al. 2006, 2010; Naranjo et al. 2009). The best-preserved populations and habitats for *Phoenix canariensis* are in La Gomera and Gran Canaria (Naranjo et al. 2009) (Supplementary Table S1b). This species presents the maximum diversity of situations, so it is represented in the five clusters (Fig. 1). It is almost exclusive in the fifth group composed of native indigenous sparse *Phoenix* populations (Fig. 2), and in the third that includes cultivated, abandoned, escaped or naturalized palms (Fig. 2).

Canary date palm grows in the wild in infra- and thermo-Mediterranean humid colluviums, dry ravines with temporary water flow (wadi), or near watercourses, palaeochannels and springs. Besides, in semi-natural habitats it has been found in more or less abandoned traditional farming areas, accompanied by diverse shrubby and sub-shrubby vegetation typical of successional stages with which the Canary Islands palm community (*Periploco-Phoenicetum canariensis*) is related, for instance *Echium* spp. and *Euphorbia* spp. ("taginastes," "tabaibas"), Kleinia neriifolia ("verodes"), Periploca laevigata, Artemisia *thuscula*, accompanied by introduced plants characteristic of rural areas (Supplementary Table S1a). In most thermophilic areas appear alongside wild olive (*Olea europaea* subsp. *guanchica*), *Cytisus proliferus* ("*escobonales*") and *Retama monosperma* subsp. *rhodor-hizoides* and *Teline* spp. ("*retamares*") (Naranjo et al. 2009) (Supplementary Table S1a). Vegetation records and inventories are mainly available from Tenerife and La Palma. On the islands of Gran Canaria and Tenerife a significant presence of *Phoenix canariensis*

and *Juniperus* sp. was detected in pollen records, declining progressively from 2000 BC (De Nascimento et al. 2009, 2015). Rivas-Martínez et al. (1993b) attributed the *Periploco-Phoenicetum canariensis* to the Macaronesian endemic vegetation class *Oleo cerasiformis-Rhamnetea crenulatae* (Supplementary Table S1a).

In the western islands of Gomera, La Palma and Tenerife the *Periploco-Phoenicetum* canariensis grows on ravine edges and humid colluvium, mainly in the climate zone of *Oleo cerasiformis- Rhamnetea crenulatae*, ranging into the climate zone of *Kleinio neriifo-liae-Euphorbietea canariensis*.

Phoenix canariensis rarely reaches into the potential area of laurel forest (*Visneo-Arbutetum canariensis*). In La Palma more or less natural stands occur on the E slopes; in Gomera around the island; in Tenerife along the N slope, but on the Macizo de Anaga mountain range also in the S. In general, the palms co-occur with various scrub communities, depending on elevation and degree of disturbance, including *Euphorba lamarckii* communities (La Palma, Tenerife), *Euphorbietum berthelotii* (La Gomera) and *Rhamno-Hypericetum canariensis*, and *Artemisio thusculae-Rumicetum lunariae* in more disturbed sites. *Cistus monspeliensis* associations may also occur adjacently. In the vicinity of water courses the *Periploco-Phoenicetum canariensis* grows next to the Canary willow (*Salix canariensis*) community that occupies the ravine beds together with brambles. The adjacent willow and Canary Islands palm communities of the "Ramblas" seem to be represented in pollen records of the distant past (until 7000 BC), indicating the possible natural environment of the palm on the western Canaries before the profound changes through anthropogenic forest fires (Nogue et al. 2013). Nowadays *Arundo donax* thickets fill ravine beds in many places and are in contact with the palm community.

On Gran Canaria palms also mainly grow within the *Oleo cerasiformis- Rhamnetea crenulatae* climate zone surrounding the island, but it extends further into the *Kleinio neri-ifoliae-Euphorbietea canariensis* zone, especially on N and NE slopes. In the SW, *Phoenix* enters the belt of thermo-sclerophyllous pine forest in the trachyte and phonolite areas of the island. Again, palms may grow together with various shrub communities such as in less disturbed areas *Euphorbia regis-jubae* community, *Rhamno crenulatae-Hypericetum canariensis*, and *Cytisus proliferus* community, and in more disturbed places *Artemisio thusculae-Rumicetum lunariae*. In Gran Canaria the *Periploco-Phoenicetum canariensis* co-occurs in ravines with willow-bramble scrub in much the same way as in the other western islands, and thickets of invasive *Arundo donax* are also widespread. Apart from that, the *Periploco-Phoenicetum canariensis* grows in the arid infra-Mediterranean belt of the NE trade windward slopes at desert like edges of ravines and on alluvial soils of wadis within the infra-Mediterranean semiarid belt of the S slope, the *Kleinio neriifoliae-Euphorbietea canariensis* climate zone.

In Fuerteventura, the *Periploco-Phoenicetum canariensis* grows chiefly in arid and semiarid infra-Mediterranean, and semiarid thermo-Mediterranean belts, in humid colluvial soils, wadis and near springs. The scrub *Kleinio neriifolia-Asparagetum pastoriani* in undisturbed places and the *Chenoleo tomentosae-Suaedetum mollis* in very disturbed sites are common companions of Canary Island palms, characteristically, such as at the Charca de Catalina García, where the *Suaedo-Tamaricetum canariensis* occupies the more saline

dry ravine beds, and the *Periploco-Phoenicetum canariensis* the less saline edges (Carqué et al. 2015).

Since *Phoenix canariensis* has been highly esteemed as a source of food and other resources (Rivera et al. 2014b), and as the best soils for the palm, deep and well watersupplied, have been transformed for agriculture, we observed that degraded anthropogenic palm stands prevail in the Canary Islands. To conclude, there are two key situations for palm trees in degraded habitats, one in "*ramblizos*" areas and dry ravines, on steeper stony slopes and usually accompanied by the neophytes *Agave americana* and, sometimes, *Opun-tia ficus-indica*, the other in gullies and ravine beds, on deep soil where *Arundo donax* interferes with the palms (Naranjo et al. 2009). Further degraded Canary palm stands grow in abandoned almond plantations or with feral almond trees (*Prunus dulcis*) (Naranjo et al. 2009).

Phoenix theophrasti

The Cretan palm, although known since antiquity, was not recognized as a separate species until 1967. Until then it was believed to be a feral form of the cultivated date palm (Greuter 1967). Its small dates are sweet and of pleasant taste. Mature palms are extremely variable in appearance. While it is commonly a tree of 3–12 m, low shrubby plants that are by no means young are known as well. As a tree, it is frequently multi-stemmed, forming clumps consisting of 2–5 or more trunks with basal offshoots. The trees may be scattered or form more or less extensive groups (Greuter 1995; Fielding and Turland 2005; Thymakis 2009) (Fig. 2).

The well-known population at Vai in eastern Crete stands out as the most extensive Cretan palm forest. It covers about 12 ha and comprises many hundreds of mature trees. Another fairly large population is at Preveli, a gallery forest of about 3 ha near the mouth of the Megalo Potamos (Kourtaliotis) at the south coast of central Crete (Fig. 2). The other locations with wild *Phoenix* in Crete, about twelve or so (Supplementary Table S2b), are smaller, each consisting of 10–100 mature trees. Maps showing the distribution of *P. theophrasti* in Crete and the Aegean have been provided by Turland et al. (1993), Greuter (1995), Rackham and Moody (1996), Thymakis (2009), and Strid (2016). Various ancient and present-day localities called Finikas on the island recall the palm. Apart from Crete, *P. theophrasti* occurs on a few other South Aegean islands, such as on Milos (Raus 2012), always in small numbers and sometimes of uncertain status. It is further known from a couple of sites on the Datça Peninsula in Southwest Turkey (Boydak 1985; Yaltirik and Boydak 1991). Small Aegean populations on coastal sites and near monasteries may originate from trees planted for ornament.

Cretan palm habitats are extraordinarily diverse and many are transformed by human activities (Supplementary Tables S2a and b). Not all sites can be attributed to the habitat type 9370, "Palm groves of *Phoenix*," for instance the population near Georgioupolis where the palms occur scattered on seaward cliffs and slopes (Boteva et al. 2004). Most Cretan palm stands are referable to the community class of Mediterranean riparian scrub, *Nerio-Tamaricetea*, such as near Vai and Preveli. Cretan palm trees have further been observed in riparian gallery woods (*Platanion orientalis*) (Fig. 3) and, as single trees or clusters never far from the coast, in thermomediterranean sclerophyllous macchia (*Ceratonio-Pistacion lentisci*).

Phoenix theophrasti typically grows on alluvial, fluvial or coastal, sandy deposits of estuaries and landward sections of beaches, on the bottom of ravines with a permanent or temporary water supply, close to the sea and chiefly up to 20 m above sea level, rarely

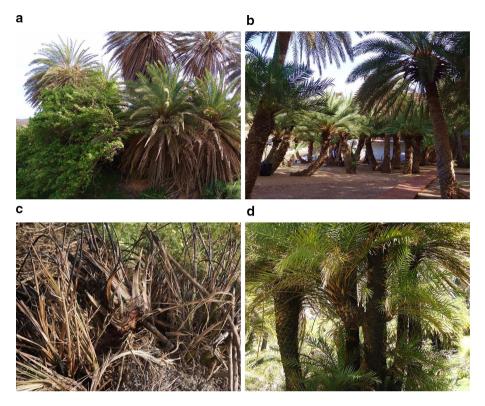


Fig. 3 *Phoenix theophrasti* **a** in a riparian gallery wood (*Platanion orientalis*) above Vai (Crete, Greece) Photo: C. Obón. **b** Outside the fence in the Vai beach (Crete, Greece). Photo: C. Obón. **c** Along the road above Vai beach (Crete, Greece). Photo: D. Rivera. **d** Recovery of the burnt palm forest along the Megalo Potamo River at Preveli beach (Crete, Greece). Photo: J. Sánchez-Balibrea

higher than 100 m (Fig. 2). The sandy soils are mostly deep and of neutral to alkaline reaction; the underlying rock of the ravine sites may be calcareous, quartzitic or serpentine. Species commonly associated with the Cretan palm are *Arundo donax*, *Juncus heldreichianus*, *Nerium oleander*, *Pistacia lentiscus*, *Rubus sanctus*, *Scirpoides holoschoenus* and *Smilax aspera* (Dimopoulos and Bergmeier 2008; Zaimes et al. 2010) (Supplementary Tables S2a, b).

The plant community of the palm stands of Vai, Preveli and other representative sites await formal description but is assignable to the class *Nerio-Tamaricetea*, and its eastern Mediterranean alliance *Rubo sancti-Nerion oleandri*. Marginal habitats of *Phoenix* in Crete, with only few trees or clusters, include coastal phrygana, a low Aegean shrub formation mostly used as rangeland (such as *Aspri Limni* near *Moni Chrisoskalitisa* in the far west of the island) (Fig. 2), *Platanus* riparian forest (e.g., Richti gorge in the northeast; Bergmeier, obs.) and, as mentioned above, edges of a calcareous coastal cliff (near Georgioupolis, in the north; Boteva et al. 2004). Unusual occurrences in phrygana, ravines and on cliffs (Supplementary Tables S2a, b) may be due to water resources underground or in crevices. They do not represent the habitat type 9370 (Palm groves of *Phoenix*) but rather the habitat types 5420 (*Sarcopoterium phrygana*), 92C0 (*Platanus* woods) and 8210 (Calcareous cliffs), respectively. The assignation of *Phoenix theophrasti* communities of the

habitat type 9370 to the class *Quercetea ilicis* (as in Papastergiadou et al. 1997) and Rod-well et al. (2002) is erroneous.

Anthropic pressure is extreme at the beach of Vai where in some parts *Phoenix theophrasti* is the only plant species left as a shadow ornamental palm (Fig. 3b). To overcome the anthropic impact there a fence is set to protect the Vai main palm grove and recent plantations.

Accessible *Phoenix* stands are very often degraded by trampling and garbage, especially at sandy beaches such as at the sites of Preveli and Vai, where palms close to the beach have been integrated into touristic facilities and beach life as ornamental trees. The major part of the famous "palm beach" of Vai, formerly heavily disturbed by touristic activities throughout, has been fenced off and is no longer accessible. At both sites, Vai and Preveli, vigorous rejuvenation can be observed, and extensive replanting of the Cretan palm as recently established at Vai may serve to increase rapidly the size of the grove but is not necessary a conservation measure.

Wildfires, unless very frequent, do not appear harmful to the stands, as most trees of *Phoenix theophrasti* regenerate vegetatively by basal offshoots. However combined burning and uprooting of offshoots is still used to remove palm trees (Fig. 3c). Burn marks can be observed on the trunks of many living palms. The enormous fire of August 2011, which demolished the palm forest of Preveli, was without lasting damage (Fig. 3d).

Moderate grazing does not seem to represent a serious obstacle to natural rejuvenation either, although trampling and browsing mainly affect juvenile plants and offshoots. The possible effects of grazing goats in *Phoenix* sites requires a monitoring scheme. The invasive weed *Oxalis pes-caprae*, a spring geophyte of South African origin, occurs abundantly at almost all *Phoenix* stands. Any soil disturbance, as for instance through the tree replanting, but also from crop, tree or vine cultivation upstream, increases the competitive abilities of *O. pes-caprae*.

A high proportion of palm trees at Vai were found to be infested with the fungus *Graphi*ola phoenicis (Tsiaoussi et al. 2002), which is, however, rarely fatal to trees. More important is the red palm weevil, *Rhynchophorus ferrugineus*, the most serious pest of palm trees worldwide, found on Crete for the first time in 2005, infesting ornamental Canary Island palms (*Phoenix canariensis*). *Phoenix theophrasti* also was found to be susceptible to the weevil (Kontodimas et al. 2006). To preserve *P. theophrasti*, it is essential, as a first step, to halt any further planting of ornamental palm trees in the wider surroundings of the Cretan palm stands, and to refrain from importing palms into Crete, from whatever source.

Phoenix dactylifera

Semi-natural populations (either escaped, naturalized or wild indigenous native) of date palm in the Iberian Peninsula grow in stream and ravine beds and drier side branches (Supplementary Tables S3a, b).

These plant communities may be integrated into the alliance *Tamaricion africanae* (class *Nerio-Tamaricetea*). In the lower basin of the Segura River, from Cieza (Murcia) to the mouth at Guardamar (Alicante), the riparian forest (*Lonicero biflorae–Populetum albae*), despite being dominated by a deciduous broad-leaved tree (*Populus alba*), has a floristic composition peculiar to the class *Nerio-Tamaricetea*. One may conclude that the Segura River is the single permanent Iberian river with a section in which the vegetation is south-Mediterranean and indeed more North African than European (Alcaraz et al. 1997).

The date palm appears in the original table records of the *Lonicero-Populetum albae* and the *Rubo-Loniceretum biflorae*, co-occurring mainly in the region of Valle de Ricote

(Murcia). There, date palms also appear in the shrublands or "baladrales" of the Rubo-Nerietum oleandri (Ríos 1994) (Supplementary Table S3a). In the interpretation manual for habitats in the region of Murcia (Alcaraz et al. 2008), Nerio-Tamaricetea riparian galleries and thickets (92D0) are defined accordingly, including hydrophilous woods with poplars, tamarisks, oleanders and palm trees. Perhaps the most accurate descriptions of these clumps of tamarisks and poplars with date palm trees is in the studies by Alcaraz et al. (2008) and Velasco et al. (2008), even proposing a new subtype within the priority habitat 9370, for date palm groves. Further inventories would be required to assess the thermophilic "tarayales," Saccharo ravennae–Tamaricetum canariensis, appearing in the Iberian southeast, where both the date palm and the subspontaneous pomegranate are relatively common and characteristic.

Scattered individual date palms, clumps and clusters occur among abandoned orchards in valleys and ravines of SE Spain, often with *Agave americana*, *Opuntia ficus-indica* or *Nicotiana glauca*, similar to what can be observed between Bordighera and Sanremo in Liguria, Italy. There, the historic date palm grove (Fig. 2) forms a remnant of the 19th century *Giardino Moreno*, covering parts of the "*Beodo*" channel along the Sasso di Bordighera stream.

Conclusions

Many wild populations of *Phoenix* palms in Europe do not form "groves" according to the definition of habitat type 9370, Palm groves of *Phoenix*, but form clusters or groups of individuals of limited extension that may or may not form part of other habitat types of Annex I of the Habitats Directive. Furthermore, a high proportion of palm occurrences are anthropogenic and, as shown above, may be considered naturalized and occur partly in semi-natural environments. Independent of their origin these palm groves are relevant reservoirs of *Phoenix* genetic diversity.

This is inconsistent with the approach taken by the Directive concerning date palms as compared to chestnut trees (*Castanea sativa*), which are included regardless of their genuine wild or autochthonous origin or stone pine forests (*Pinus pinea*), which require reaching only a sufficient degree of naturalness, up to and including old plantations.

We propose to adapt the definition of the habitat type 9370 accordingly, to encompass native palm populations of Crete and the Canary Islands outside of the then known "palm groves," and not covered by other Annex I habitat types. Subtypes of 9370 should be specified. Of particular relevance is moreover the inclusion of *Phoenix dactylifera* (represented in continental Spain by the western genetic type including the group known as *P. iberica*), to highlight the genetic and ecological significance of the Iberian populations and to facilitate measures to protect populations in natural habitats. Naturalized palms originating from ancient plantations and semi-natural formations both in the context of the Iberian Peninsula, the Canary Islands and Crete are part of the European natural-cultural heritage. They should be covered by the Habitats Directive in consistency with the approach adopted concerning chestnut (*Castanea sativa*) and stone pine (*Pinus pinea*) woods, discussed above.

We do not see appropriate a redefinition of "Palm grove of *Phoenix*" but instead a more inclusive approach for defining *Phoenix* habitats worthy of conservation.

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