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Phenotypic Diversity in Wild and Cultivated Date Palm (*Phoenix*, Arecaceae): Quantitative Analysis Using Information Theory

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Abstract: The quantitative study of genetic diversity requires tools to describe quantitatively and in parallel the whole phenotypic diversity in order to produce meaningful comparisons. The genus *Phoenix* offers examples of species with very different levels of diversity or heterogeneity. Within *Phoenix*, date palm (*Phoenix dactylifera* L.) is a major food crop of global relevance. The concept of information entropy was introduced by Claude Shannon; although initially intended to evaluate data communication systems, it has been used to measure biodiversity in terms of richness, evenness and dominance. In the present work, we will use it to describe heterogeneity within the different taxonomic units in the genus *Phoenix*. The description of the *Phoenix* morphological diversity in the present work is based on 596 accessions or populations belonging to 43 mutually exclusive taxonomic units (species, subspecies, varieties, landrace groups and hybrids). As *Phoenix* is a dioecious palm genus, female and male individuals are described separately. Each accession or sample is described using 116 characters totaling 449 states. The Shannon information entropy index allows the quantitative representation of the different levels of heterogeneity in the various taxonomic units of the genus *Phoenix*. Morphology, consistency and coloration of fruit and seed, followed by the inflorescences and female flowers, comprise the taxonomic characters that contribute the most to heterogeneity. Vegetative characters contribute less than the characters of the reproductive organs as a whole. *Phoenix dactylifera* and related Mediterranean and Macaronesian taxa present the maximum heterogeneity. Immediately afterwards we find *P. loureiroi* and, behind, the group of *P. pusilla*. At the lower limit of heterogeneity, we find species restricted in their distribution area: *P. rupicola*, *P. theophrasti*, *P. roebelenii* and *P. acaulis*. *Phoenix dactylifera* conforms to a complex of landraces and cultivars that coexist as phenotypically well-defined geographical groups with numerous intermediate forms and the long-distance translocation of otherwise local cultivars. This results in high heterogeneity. For the western and eastern groups of *Phoenix dactylifera*, it is extremely difficult to find a set of well-defined differential characters. However, some of the variables analyzed here allow us to propose a set of their respective syndromes. The high phenotypic heterogeneity in various *Phoenix* species is related to the genetic diversity, age and ancestry of different taxa, hybridization events and introgressions prior to domestication, and selective pressures after domestication and, again, interspecific crosses after domestication.

Keywords: biodiversity; diversity indices; taxonomy; Arecaceae; heterozygosis; phenotyping

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1. Introduction

The quantitative study of genetic diversity requires the development of tools to describe quantitatively and in parallel the whole phenotypic diversity in order to produce

meaningful comparisons. The quantitative assessment of phenotypic diversity within different species and other taxonomic ranks within the same genus, in a way that allows comparison—at least between them within the same study—is therefore an ongoing challenge that we address here. To avoid confusion, we will use the term "intraspecific taxonomic heterogeneity" or simply "taxonomic heterogeneity" throughout the text, leaving the use of "taxonomic diversity" or "species diversity" in the sense in which ecologists apply it [1].

The concept of information entropy was introduced by Claude Shannon in his 1948 paper "A Mathematical Theory of Communication" [2,3] and is also referred to as Shannon entropy. Although initially intended to evaluate data communication systems, information entropy has been used to measure biodiversity in terms of richness, evenness and dominance [4]. In the present work, we will use it to describe the heterogeneity within the different taxonomic units recognizable in the genus *Phoenix.*

Heterogeneity presents two well differentiated faces that are, to a great extent, opposed. On the one hand, we find that high heterogeneity is found in polymorphic organisms, which we can link to high levels of heterozygosity and a high potential to survive in constantly changing environments [5]. However, from a taxonomic point of view, these organisms are difficult to classify into distinct entities and exclusive distinguishing characters are scarce. In contrast, sets of organisms that as a whole (i.e., populations or groups of populations) are homogeneous in themselves are easy to characterize and exhibit unique distinguishing characters. These organisms have low levels of heterozygosity and, in many cases, run a real risk of extinction that is associated with their low capacity to adapt to a changing environment [6].

The genus *Phoenix* offers several examples of species with very different levels of diversity or heterogeneity. Within the genus *Phoenix*, date palm (*Phoenix dactylifera* L.) is a major food crop of global relevance. The date palm area harvested in 2019 was 1,396,727 ha, with the largest crops in Iraq (31%), Algeria, Iran, Saudi Arabia, Pakistan, Tunisia, Morocco, Egypt, Sudan, United Arab Emirates States and Libya. In 2019, a production of 9,248,033 tons was achieved, the main producers being Egypt (17%), Saudi Arabia, Iran, Algeria, Iraq, Pakistan, Sudan, Oman, United Arab Emirates and Tunisia [7].

Of the world production of dates, the amount exported in 2019 was approximately 20% (1,837,127 tons); the main exporters were Iraq (39%), United Arab Emirates, Saudi Arabia, Iran, Israel and Tunisia. With an export value of two billion USD, the main importers were India (22%), United Arab Emirates, Morocco, France, Turkey, Yemen, Indonesia, Bangladesh, Kazakhstan, the United States of America, Germany, and the United Kingdom of Great Britain and Northern Ireland [7].

Date palm is not only relevant in terms of food production, but also culturally; since as early as the Neolithic period, palms appear represented in wall paintings, sculptures, wood carvings, and coins for their symbolic value [8,9]. In addition, the palm grove has received, in the case of the "Palmeral of Elche" (Spain), the qualification of World Heritage by UNESCO [10] as an example of cultural transfer of a landscape from one continent to another.

Our objective is to address the quantitative evaluation of phenotypic heterogeneity, based on the use of descriptors and Shannon's information theory, and its comparison with parameters representing genetic diversity, such as heterozygosity, using as an example the case of *Phoenix* (Arecaceae).

We also intend to evaluate the intraindividual and intrapopulation variability within the analyzed accessions.

2. Materials and Methods

The description of the morphological diversity of the genus *Phoenix* in the present work (Figures 1–5) is based on 596 accessions or populations belonging to 43 mutually exclusive taxonomic units (species, subspecies, varieties and landrace groups and hybrids)

(Table 1). As *Phoenix* is a dioecious palm genus, female and male individuals are described separately.

Figure 1. Diversity of *Phoenix:* palm trees. (**a**), *Phoenix theophrasti* (Preveli, Crete, Greece); (**b**), *P. iberica* (Abanilla, Spain); (**c**), *P. loureiroi* Manipur (Huerto del Cura, Elche, Spain); (**d**), *P. rupicola* (Jardín Botánico de Valencia, Spain); (**e**) *P. farinifera* (Colección Tomás-Font, Valencia, Spain) (**f**), *P. dactylifera* "Candits" Western Group (W_DAC) (Elche, Spain); (**g**), *P. canariensis* var. *canariensis* (Geneva, Switzerland); (**h**), *P. reclinata* (Jardín Botánico La Concepción, Málaga, Spain); (**i**), *P. pusilla* (Menton, France); (**j**), *P. canariensis* var. *porphyrococca* (Lisboa, Portugal); (**k**), *P. roebelenii* (Orihuela, Spain); (**l**), *P. dactylifera* "Sarafana" Eastern Group (E_DAC) (Socotra, Yemen). Abbreviations for the major *P. dactylifera* geographical groups: E_DAC: North Africa and West Asia *P. dactylifera.* W_DAC: North Africa and Mediterranean *P. dactylifera.* Scale bar: 1 m. Images: (**a**). Jorge Sánchez-Balibrea. (**b**–**d**,**j**). Diego Rivera and Concepción Obón, (**l**). Joel Lode.

Figure 2. Diversity of *Phoenix:* leaves. (**a**), *Phoenix theophrasti* (Palmasur, Alicante, Spain); (**b**), *P. iberica* (Abanilla, Spain); (**c**), *P. loureiroi* Manipur (Huerto del Cura, Elche, Spain); (**d**), *P. rupicola* (Medipalm, Almería, Spain); (**e**) *P. arabica* (Djebel Bura, Yemen) (**f**), *P. loureiroi* var. *loureiroi* (Orihuela, Spain); (**g**), *P. canariensis* var. *canariensis* (Toulon, France); (**h**), *P. reclinata* (Medipalm, Almería, Spain); (**i**), *P. pusilla* (Menton, France); (**j**), *P. paludosa* (Orihuela, Spain); (**k**), *P. dactylifera* Eastern Group (E_DAC) (Palmyra, Syria); (**l**), *P. dactylifera* Western Group (W_DAC) (Jacarilla, Spain). Abbreviations for the major *P. dactylifera* geographical groups: E_DAC: North Africa and West Asia *P. dactylifera.* W_DAC: North Africa and Mediterranean *P. dactylifera.* Scale bar: 10 mm. Images: (**a**–**d**,**f**–**l**). Diego Rivera and Concepción Obón, (**e**). Joel Lode.

Figure 3. Diversity of *Phoenix:* flowers. (**a**), *P. dactylifera* "Candits" Male Western Group (W_DAC) (Elche, Spain); (**b**), *P. dactylifera* "Candits" Female (Elche, Spain); (**c**), *P. dactylifera* var. *costata* Male Western Group (W_DAC) (Santomera, Spain); (**d**), *P. loureiroi* var. *pedunculata* Female (Huerto del Cura, Elche, Spain); (**e**) *P. loureiroi* var. *loureiroi* Male (Orihuela, Spain); (**f**), *P. arabica* Male (Djebel Bura, Yemen); (**g**), *P. canariensis* var. *canariensis* (San Pedro, Spain) Male and Female; (**h**), *P. iberica* Female (Abanilla, Spain); (**i**), *P. iberica* Male (Abanilla, Spain); (**j**), *P. roebelenii* Male (Orihuela, Spain); (**k**), *P. roebelenii* Female (Orihuela, Spain); (**l**), *Phoenix theophrasti* Female (Palmasur, Alicante, Spain). Abbreviations for the major *P. dactylifera* geographical groups: W_DAC: North Africa and Mediterranean *P. dactylifera.* Scale bar: 5 mm. Images: (**a**–**l**). Diego Rivera and Concepción Obón.

Figure 4. Diversity of *Phoenix*: fruits. (**a**), *Phoenix reclinata* (Orihuela, Spain); (**b**), *P.* "Palmer" (Orihuela, Spain); (**c**), *P. acaulis* (India); (**d**), *P. hanceana* (Riverside, USA); (**e**), *P. dactylifera* Eastern Group (E_DAC) (Palmyra, Syria); (**f**), *P. roebelenii* (Jardines de Albarda, Pedreguer, Spain); (**g**), *P. dactylifera* "Negros" Western Group (W_DAC) (Orihuela, Spain); (**h**), *P. canariensis* var. *porphyrococca* (Menton, France); (**i**), *P. dactylifera* Eastern Group (E_DAC) (Palmyra, Syria); (**j**), *P. dactylifera* "Barhee" Eastern Group (E_DAC) (Jordan Valley, Israel); (**k**), *P. dactylifera* Chowhara-style dehydrated dates Eastern Group (E_DAC) (Pakistan); (**l**), *P. dactylifera* Eastern Group (E_DAC) (Socotra, Yemen). Abbreviations for the major *P. dactylifera* geographical groups: E_DAC: North Africa and West Asia *P. dactylifera.* W_DAC: North Africa and Mediterranean *P. dactylifera.* Scale bar: 5 cm. Images: (**a**,**b**,**d**–**k**). Diego Rivera and Concepción Obón, (**c**). MNHN/Vascular plants (P)/P01796536 https://science.mnhn.fr/institution/mnhn/collection/p/item/p01796536?listIndex=11&listCount=16, (accessed on 15 March 2022), (**l**). Joel Lode.

Figure 5. Diversity of *Phoenix:* seeds. (**a**), *P. atlantica* (Ilha Sao Tiago, Cabo Verde); (**b**), *P. dactylifera* "Medjool" Western Group (W_DAC) (Morocco); (**c**), *P. dactylifera* "Haziz" Western Group (W_DAC) (US); (**d**), *P. paludosa* (near Bangkok, Thailand); (**e**,**f**), *P. sylvestris* (India); (**g**), *P. loureiroi* (Manipur, India); (**h**), *P. dactylifera* Eastern Group (E_DAC) (Socotra, Yemen); (**i**), *P. roebelenii* (Orihuela, Spain); (**j**), *P. theophrasti* (Crete, Greece); (**k**), *P. reclinata* var. *reclinata* (Rwanda); (**l**,**m**), *P. andamanensis* (North Andaman, India); (**n**), *P. dactylifera* "Dairy" Eastern Group (E_DAC) (UAE). Abbreviations for the major *P. dactylifera* geographical groups: E_DAC: North Africa and West Asia *P. dactylifera.* W_DAC: North Africa and Mediterranean *P. dactylifera.* Scale bar: 1 cm. Images: (**a**–**k**,**n**). Diego Rivera and Concepción Obón; l. Teresa Egea Molines in the herbarium FI; m. Royal Botanic Gardens Kew, http://apps.kew.org/herbcat/getImage.do?imageBarcode=K000736131, (accessed on 16 March 2022).

Table 1. Accepted taxa and their operative taxonomic units analyzed.

Recognised Species and Major Groups	OTUs that Include Typical and Related Taxa still under Study and Groups of Landraces
***Phoenix acaulis* Roxb.**	*P. acaulis* (10) [1]
***Phoenix canariensis* H.Wildpret**	*P. canariensis* var. *canariensis* (24) [1], *P. canariensis* "Macrocarpa" (20) [1], *P. canariensis* var. *porphyrococca* Vasc. & Franco (32) [1]
***Phoenix dactylifera* L. Eastern Group**	*P. dactylifera* "Mesopotamia" (32) [1], *P. dactylifera* "Nile" (12) [1], *P. dactylifera* "Persia" (4) [1], *P. dactylifera* "Socotra" (18) [1]
***Phoenix dactylifera* L. Western Group**	*P. atlantica* A.Chev. (15) [1], *P. dactylifera* "Chevalier" (8) [1], *P. dactylifera* var. *costata* Becc. (10) [1], *P. dactylifera* var. *cylindrocarpa* Mart. (66) [1], *P. dactylifera* "Mednoor" (10) [1], *P. excelsior* Cav. (61) [1], *P. iberica* D.Rivera, S.Ríos & Obón (10) [1], *P. iberica* "Abanilla" (6) [1]
***Phoenix loureiroi* Kunth**	*P. andamanensis* W.Mill., J.G.Sm. & N.Taylor (8) [1], *P. hanceana* Naudin (8) [1], *P. loureiroi* "Huerto del Cura" (4) [1], *P. loureiroi* var. *loureiroi* (10) [1], *P. loureiroi* var. *pedunculata* (Griff.) Govaerts (4) [1], *P loureiroi* "Tomás Font" (8) [1]
***Phoenix paludosa* Roxb.**	*P. paludosa* Roxb. (15) [1]
***Phoenix pusilla* Gaertn.**	*P. farinifera* Roxb. (10) [1], *P. zeylanica* Trimen (12) [1]
***Phoenix reclinata* Jacq.**	*P. abyssinica* Drude (10) [1], *P. arabica* Burret (10) [1], *P. caespitosa* Chiov. (11) [1], *P. reclinata* var. *reclinata* (11) [1], *P.* "Palmer" (10) [1], *P. spinosa* Schumach. & Thonn. (8) [1]
***Phoenix roebelenii* O'Brien**	*P. roebelenii* O'Brien (20) [1]
***Phoenix rupicola* T.Anderson**	*P. rupicola* var. *rupicola* (10) [1], *P. rupicola* "Medipalm" (5) [1]
***Phoenix sylvestris* (L.) Roxb.**	*P. sylvestris* var. *sylvestris* (15) [1], *P. sylvestris* "Edulis" (6) [1]
***Phoenix theophrasti* Greuter**	*P. theophrasti* var. *theophrasti* (14) [1], *P. theophrasti* "Datça" (10) [1], *P theophrasti* "Gölköy" (10) [1]
Hybrids	
Phoenix canariensis* × *P. reclinata	*P. canariensis* × *P. reclinata* (7) [1]
Phoenix dactylifera* × *P. canariensis	*P. dactylifera* × *P. canariensis* (12) [1]
Phoenix dactylifera* × *P. reclinata	*P. dactylifera* × *P. reclinata* (4) [1]
Phoenix dactylifera* × *P. sylvestris	*P. dactylifera* × *P. sylvestris* (6) [1]

[1] The number between parentheses is the number of samples (accessions or localities, including male and female) analyzed.

Although accessions in the National *Phoenix* Collection at Orihuela (Spain) and living individuals from botanic gardens and natural populations were the main source of data, numerous herbarium specimens were analyzed to refine the list of characters. The list of accessions and herbarium specimens is available as Supplementary Table S1. The basic data of the study are made available in a repository: the matrix of individual descriptions, the matrix of OTU/variable-frequencies and the dissimilarity matrix can be downloaded from Phoenix-Spain.org.

The system adopted for the description of the different taxonomic units (species, subspecies, varieties, hybrids and groups of *Phoenix* landraces) is based on the standardized descriptors for the date palm (IPGRI, INRAA, INRAM, INRAT, FEM, PNUD) [11] expanded to cover characteristics not present in the date palm but in other species. The descriptors are divided into several categories:

- Descriptors of the environment and the locality. Especially those of an ethnobotanical character.
- Characterization descriptors. Essentially, they focus on macromorphological characters easily discernible in the field, although they also include other characters of interest that require the study of samples in the laboratory. With reference to the colors, the Munsell Color Chart for Plant Tissues has been used.
- Evaluation descriptors. These include, among others, resistance to various types of stress.

Each accession or sample is described using 116 characters with 449 states that are summarized in Table 2. Only 63 among these have their equivalent in the "*Descripteurs du palmier dattier*" system [11]. The number of states per character vary from two to eight; the average is 3.85.

Table 2. Categories and types of characters and their states.

Group	Subgroups	Characters	States
Category	Evaluation	2	7
	Phenology	2	11
	Vegetative	42	163
	Male reproductive	11	31
	Female reproductive	13	46
	Fruit and seed	46	191
Type	Qualitative ordinal	12	43
	Quantitative discrete	7	37
	Quantitative continuous discretized	48	231
	Qualitative nominal	29	104
	Binary qualitative	6	6
	Binary qualitative duplicate	14	28

For dichotomous or binary characters, the notation 0/1 is adopted to indicate absence or presence. In the case of the fourteen characters (Table 2) for which both alternative states could occur in the same individual (for instance, the presence of wings or auricles on the seed surface), the columns have been duplicated using the same notation.

Continuous variables (for example lengths) have been divided in the database into intervals, thus transforming them into discrete ones. The intervals for which the sample is true are scored 1 (present) and the rest 0 (absent). A similar approach is adopted for quantitative discrete and qualitative ordinal or nominal characters.

For individuals or accessions that are not uniform for a descriptor (character), since they present more than one state, each of those registered states has been marked as present.

Intraindividual or intrapopulation variability is evaluated in our study by the proportion of variables scored as 1 in each sample in relation to the total number of variables, n = 418 in female and 212 in male individuals (Figure 6).

Therefore, the description of each accession is presented in the form of a message with a length of 449 binary characters with values of 0/1. Taking into account that *Phoenix* species are dioecious, male and female individuals can only give rise to messages of 212 and 418 characters, respectively. This difference is due to the high number of characters based on flowers and inflorescences and on fruits and seeds (Figure 6).

Here, taxonomic heterogeneity of the different OTUs is measured in terms of information or entropy. In information theory, the entropy of a random variable is the average level of "information", "surprise" or "uncertainty" inherent in the variable's possible outcomes. The basic idea of applying information theory to quantitative description matrices is that the "degree of uniformity" of a given taxon depends on the degree to which the content of the message (description) is striking. If an event is highly probable, it is no surprise (and generally uninteresting) when that event occurs as expected (Figure 2). The average uncertainty of a variable X is summarized by its entropy H(X). If we are told the value of X, then the amount of information we have been given is, on average, exactly equal to its entropy [12].

Shannon's choice of a logarithmic base corresponds to the choice of a unit to measure information: if base 2 is used, the resulting units can be called binary digits, or more briefly bits. Two of the fundamental concepts in information theory are: redundancy and noise.

Redundancy provides a quantitative measure of order. The redundancy measures the fractional difference between H(X) and its maximum possible value, $\log_2 (|A_X|)$ [13].

The redundancy of X is:

$$1 - H(X)/\log_2 |A_X| \quad (1)$$

Notation: the vertical bars '| . . . |' have two meanings. If AX is a set, |AX| denotes the number of elements in AX; if x is a number, then |x| is the absolute value of x.

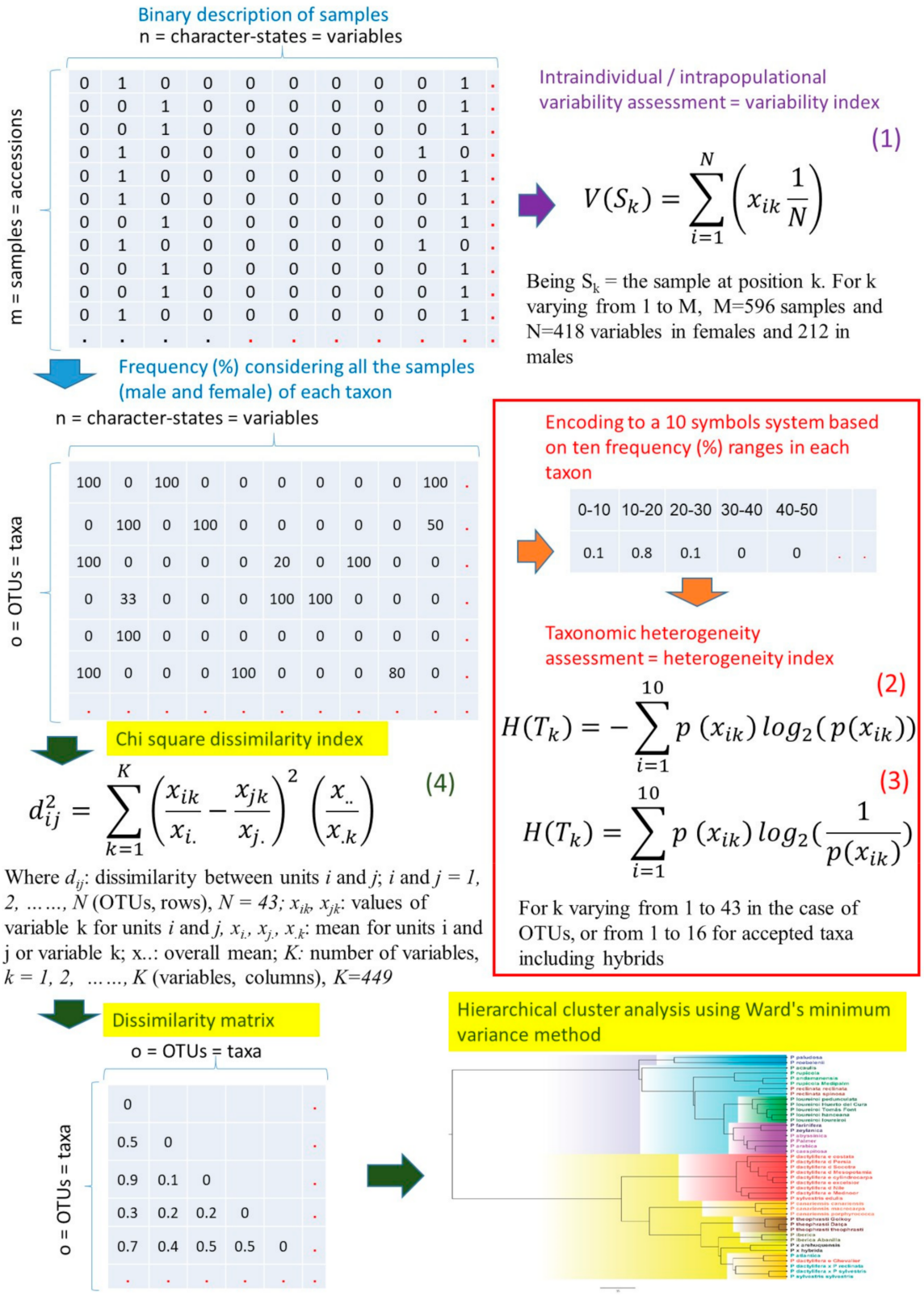

Figure 6. Diagram of the sequence of analysis.

With redundancy, we have a measure of predictability that varies from 1 for total order to 0 for total disorder. However for other authors [14], redundancy is a composite concept combining true redundancy and partial redundancy.

Noise changes the signal from a more probable to a less probable state, and from a more certain to a less certain state; the information content of the message is increased. The paradox that noise should increase the information content of a message is resolved by distinguishing between desirable and undesirable information [15,16]. In this article, we do not address the problem of encoding and decoding the message or the use of a channel for its transmission, so noise does not affect it.

Here, we are concerned with messages formed out of discrete symbols, as words are formed of letters, sentences of words, or a melody of notes [3]. This is such a general theory that it is not necessary to say what types of symbols are being considered. In the case at hand, we reduce our language to the use of ten symbols, i.e., the 10 possible ranges of 10 for the frequencies, ranging from 0 to 100, in each of the possible states of the descriptors (variables). The maximum information for the set of 10 symbols is 3.32 bits per symbol.

Each of the 43 OTUs is described using between 4 and 66 samples depending on its complexity and the available accessions, in terms of the relative frequency of each of the 449 variables into which the descriptors are divided. Therefore, we transform a written message using only two symbols (0 or 1 or presence/absence) with which the individual samples are described into another one in which ten corresponding symbols are used with the ten ranges adopted for the relative frequencies.

When working with a variable number of samples or accessions between the various OTUs, it is expected that the parameters related to entropy or information, such as heterogeneity and redundancy, may present values depending on the number of accessions or populations analyzed per OTU. It seems that the optimal size is around ten accessions. It can be seen (Figure 7) that when the available accessions are fewer than ten, there may have been an underestimation of heterogeneity and, consequently, an overvaluation of redundancy.

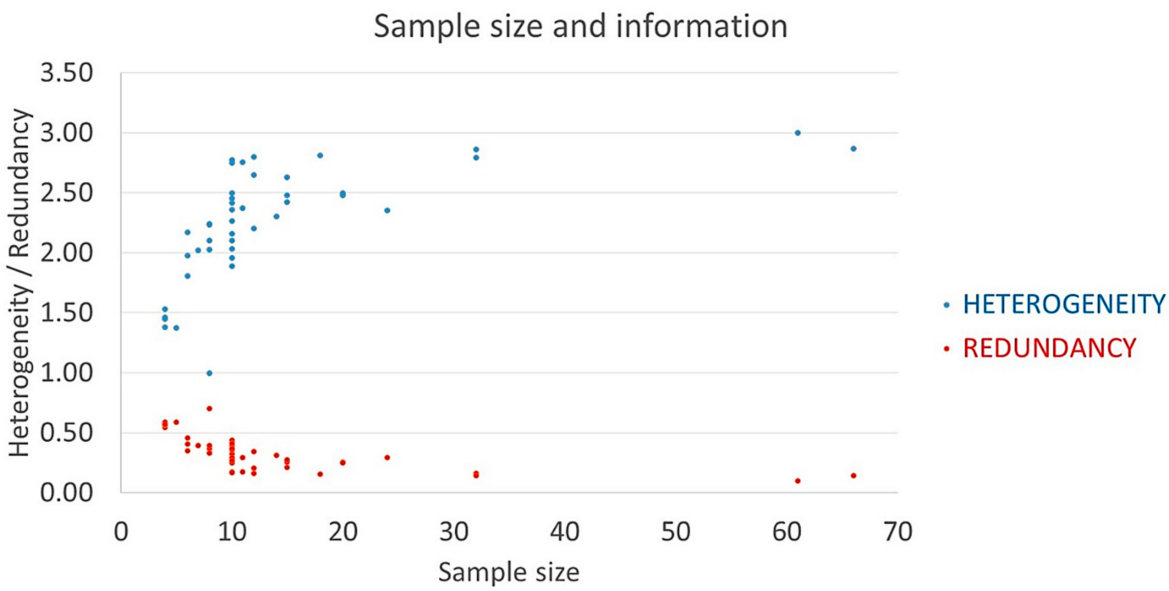

Figure 7. Sample size and information parameters.

For the purpose of comparing and classifying the different OTUs, the chi square dissimilarity index was calculated (which is optimal for such a type of data). This measure expresses a value x_{ik} as its contribution to the sum x_i on all variables and is a comparison of unit profiles (Figure 6) [17–19].

3. Results

3.1. Phenotypic Heterogeneity

3.1.1. Morphological Heterogeneity and Main Descriptor Categories

The main categories of descriptors that are established according to the parts of the plants analyzed contribute unevenly to the heterogeneity of the samples (Table 3). It is worth highlighting the importance of the morphology, consistency and coloration of the fruit and the seed, followed at a distance by the reproductive characters, to which those of the inflorescences and female flowers contribute specifically. The vegetative characters contribute less to the heterogeneity than the characters of the reproductive organs as a whole. Nevertheless, heterogeneity of vegetative organs is higher than that provided by the male or female organs when considered separately.

Table 3. Contribution to the total heterogeneity of *Phoenix* by the different groups of descriptors [1].

Group	Heterogeneity	Normalized Heterogeneity
Total	2.49	1
Fruit and seed	2.04	0.82
Reproductive	1.99	0.79
Vegetative	1.50	0.61
Female inflorescence and flower	1.04	0.42
Male inflorescence and flower	0.87	0.35

[1] Sets of characters.

The higher heterogeneity found in fruits and seeds can, in part, be due to the xenic and metaxenic effects of the different donors of pollen on date palm cultivars and even on wild female *Phoenix*.

Many of the descriptors or characters are independent of others in their inheritance, and, through their different combinations, form thousands of varieties. However, in the case of cultivated palms, many characters are used by farmers to identify known cultivars and probably as markers for the traditional selection of optimal palms.

Some of these phenotypic characters were found by Bedjaoui and Benbouza [20] in their study as the most discriminating, while also presenting an adaptive value. For example, the cultivar Hamraya is well known to farmers in the Ziban region of Algeria as being the most resistant to dryness. The results of the phenotypic characterization showed that the pseudopetiole is well developed in this cultivar and the width of the palm leaf is one of the lowest, probably associated with the reduction of evapotranspiration.

Based on the foregoing, it cannot be ruled out that some characters are grouped into sets that have been selected with a preference for their interest or usefulness by farmers, taking into account their preferences and the restrictions that the climate and in general the environment impose on the cultivation of the crop.

3.1.2. Intraindividual/Intrapopulational Variability

Intraindividual or intrapopulational variability ranges within the 596 accessions, or populations, between 0.27 and 0.46 following an asymmetric right-skewed unimodal probability distribution for female samples and a less clearly right-skewed and almost bimodal for male samples (Figure 8) with mean = 0.313 (99% CI 0.311 to 0.315) (female), 0.36 (99% CI 0.356 to 0.363) (males) and median = 0.311 (female), and 0.356 (males).

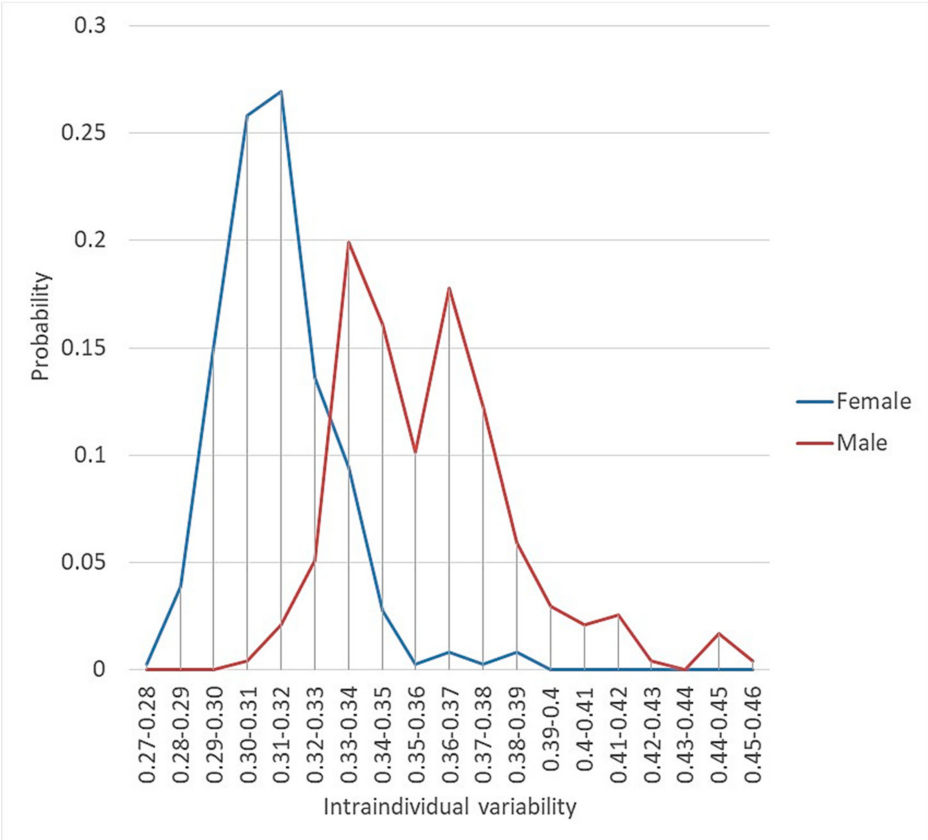

Figure 8. Probability distribution of the *Phoenix* intraindividual/intrapopulational variability.

While the values of intraindividual/intrapopulational variability (including both female and male samples) within each of the populations or accessions analyzed present similar levels, of 0.33 ± 0.03, which represents a deviation of 9% from the mean value, the heterogeneity within the 43 OTUs, where each one is composed of four or more accessions, presents a greater variability of 2.25 ± 0.47 (Table 4), which represents a deviation from the mean above 20%. This suggests that the diversity or heterogeneity of each OTU depends to a great extent on the differences between accessions or localities there included and to a lesser extent on the intrapopulational variability.

Table 4. Operative taxonomic units (OTUs), their intraindividual/intrapopulational morphological variability and morphological/taxonomic heterogeneity.

Taxa	Geog.	AVarIntr (Average) [1]	Heter. [2]	Redund. [3]	Pond. Heter.	Accessions	SF/SM
P. abyssinica Drude	AFR	0.32	2.03	0.39	1.72	10	1.00
P. acaulis Roxb.	S_AS	0.31	2.26	0.32	2.02	10	1.00
P. andamanensis W.Mill., J.G.Sm. & N.Taylor	S_AS	0.31	2.23	0.33	2.17	8	3.00
P. arabica Burret	AFR	0.33	2.16	0.35	2.00	10	1.00
P. atlantica A.Chev.	MED	0.31	2.48	0.25	1.96	15	4.00
P. caespitosa Chiov.	AFR	0.34	2.37	0.29	2.09	11	1.20
P. canariensis var. *canariensis*	MED	0.33	2.35	0.29	1.77	24	3.80
P. canariensis "Macrocarpa"	MED	0.32	2.48	0.25	1.89	20	3.00
***P. canariensis* var. *porphyrococca* Vasc. & Franco**	**MED**	**0.33**	**2.79**	**0.16**	**2.32**	**32**	1.91
***P. dactylifera* "Mesopotamia"**	**E_DAC**	**0.33**	**2.86**	**0.14**	**2.89**	**32**	1.00
***P. dactylifera* "Nile"**	**E_DAC**	**0.32**	**2.65**	**0.20**	**2.68**	**12**	1.00
P. dactylifera "Persia"	E_DAC	0.33	1.53	0.54	2.01	4	1.00

Table 4. *Cont.*

Taxa	Geog.	AVarIntr (Average) [1]	Heter. [2]	Redund. [3]	Pond. Heter.	Accessions	SF/SM
***P. dactylifera* "Socotra"**	**E_DAC**	**0.33**	**2.81**	**0.15**	**2.99**	**18**	1.00
P. dactylifera "Chevalier"	W_DAC	0.33	2.10	0.37	**2.56**	8	1.00
P. dactylifera var. *costata* Becc.	W_DAC	0.32	2.41	0.27	**2.46**	10	1.00
***P. dactylifera*var. *cylindrocarpa* Mart.**	**W_DAC**	**0.32**	**2.86**	**0.14**	**2.45**	**66**	1.00
***P. excelsior* Cav.**	**W_DAC**	**0.33**	**3.00**	**0.10**	**2.58**	**61**	3.36
***P. dactylifera* "Mednoor"**	**W_DAC**	**0.33**	**2.75**	**0.17**	**3.18**	**10**	1.00
P. farinifera Roxb.	S_AS	0.35	2.36	0.29	2.37	10	1.00
P. iberica D.Rivera, S.Ríos & Obón	MED	0.35	2.49	0.25	2.49	10	1.00
P. iberica "Abanilla"	MED	0.32	1.97	0.41	2.09	6	2.00
P. hanceana Naudin	E_AS	0.39	2.24	0.33	**2.65**	8	1.00
P. loureiroi "Huerto del Cura"	S_AS	0.35	1.46	0.56	1.97	4	1.00
P. loureiroi*var. *loureiroi	**SE_AS**	**0.34**	**2.77**	**0.16**	**2.96**	**10**	1.00
P.loureiroi var. *pedunculata* (Griff.) Govaerts	S_AS	0.34	1.44	0.57	1.88	4	1.00
P. loureiroi "Tomás Font"	S_AS	0.39	1.00	0.70	0.96	8	1.00
P. "Palmer"	AFR	0.37	1.88	0.43	1.83	10	1.00
P. paludosa Roxb.	S_AS, SE_AS	0.31	2.42	0.27	1.86	15	2.00
P. reclinata*var. *reclinata	**AFR**	**0.32**	**2.75**	**0.17**	**2.55**	**11**	1.75
P. spinosa Schumach. & Thonn.	AFR	0.31	2.02	0.39	1.89	8	3.00
P. roebelenii O'Brien	SE_AS	0.32	2.49	0.25	1.79	20	2.33
P. rupícola var. *rupícola*	S_AS	0.32	1.95	0.41	1.62	10	1.00
P. rupicola "Medipalm"	S_AS	0.34	1.37	0.59	1.48	5	1.50
P. sylvestris "Edulis"	S_AS	0.32	1.81	0.46	1.86	6	1.00
P. sylvestris var. *sylvestris*	S_AS	0.33	2.63	0.21	2.20	15	2.00
P. theophrasti "Datça"	MED	0.34	2.45	0.26	2.43	10	1.00
P theophrasti "Gölköy"	MED	0.34	2.29	0.31	2.00	10	1.00
P. theophrasti var. *theophrasti*	MED	0.36	2.30	0.31	2.05	14	1.00
***P. zeylanica* Trimen**	**S_AS**	**0.33**	**2.80**	**0.16**	**2.68**	**12**	1.40
Hybrids							
P. canariensis × *P. reclinata*	-	0.35	2.01	0.39	2.26	7	2.50
P. dactylifera × *P. canariensis*	-	0.35	2.20	0.34	1.99	12	5.00
P. dactylifera × *P. reclinata*	-	0.31	1.38	0.59	1.66	4	1.00
P. dactylifera* × *P. sylvestris	**-**	**0.34**	**2.17**	**0.35**	**3.04**	**6**	2.00

Notice: Highly heterogeneous OTUs appear in **bold type** and those with lower values are underlined. Abbreviations: [1] AvarIntr = Variability intraindividual/intrapopulational; [2] Heter. = Heterogeneity; [3] Redund. = Redundancy; Pond. Heter. = Heterogeneity pondered considering the number of accessions. SF/SM = proportion female vs. male samples. Abbreviations for the geographical groups: E_DAC: North Africa and West Asia *P. dactylifera*. W_DAC: North Africa and Mediterranean *P. dactylifera*. S_AS: Southern Asia. E_AS: Eastern Asia., SE_AS: South-East Asia. AFR: Taxa from Africa and Western Arabian Peninsula. MED: Mediterranean and Macaronesia.

3.2. Operative Taxonomic Units' Heterogeneity and Taxonomy

Morphological heterogeneity at the OTU level, in crude values of the Shannon index, follows an almost multimodal distribution (Figure 9) ranging from 1 to 3.

The maximum of morphological heterogeneity (3) in this study is reached within the set of *Phoenix dactylifera* (Tables 4 and 5; Figure 9) and related or subordinate Mediterranean and Macaronesian taxa, notably by *P. excelsior* and *P. dactylifera* "Mednoor" groups in the western and by *P. dactylifera* "Socotra", and *P. dactylifera* "Mesopotamia" in the eastern group of *P. dactylifera*.

Immediately afterwards, we find within the Asiatic taxa a large group of *P. loureiroi* and notably the type of the species *P. loureiroi* var. *loureiroi* and, behind, the smallest group of *P. pusilla*.

The lower limit of calculated H values is equal to 1 and is found in the cultivar *P. loureiroi* "Tomas Font".

In the vicinity of the lower limit of heterogeneity (Table 4), we find almost invariable species such as: *P. rupicola, P. paludosa, P. roebelenii* and *P. acaulis*, which present redundancy levels of ca. 25%.

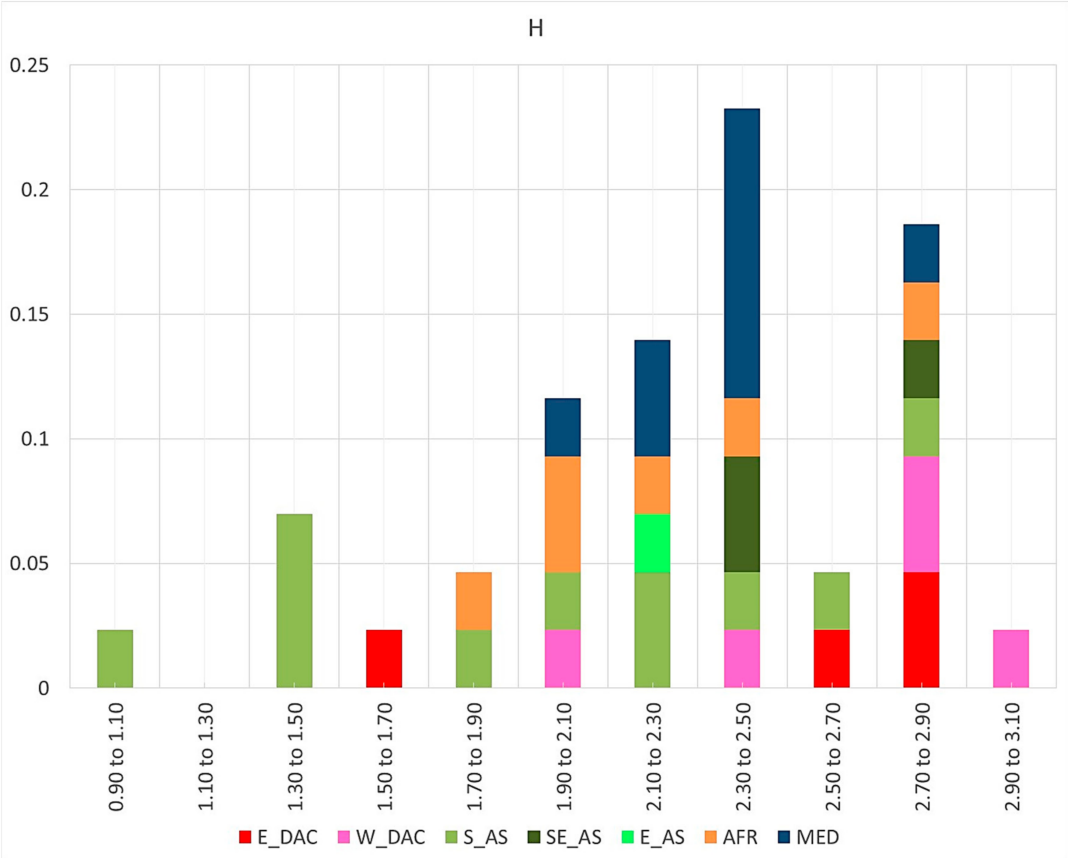

Figure 9. Probability distribution of *Phoenix* heterogeneity considering large geographical groups. **Notice:** Abbreviations for the geographical groups: E_DAC: North Africa and West Asia *P. dactylifera*. W_DAC: North Africa and Mediterranean *P. dactylifera*. S_AS: Southern Asia. E_AS: Eastern Asia., SE_AS: South-East Asia. AFR: Taxa from Africa and Western Arabian Peninsula. MED: Mediterranean and Macaronesia.

Table 5. Species and hybrids intraindividual/intrapopulational variability, heterogeneity and redundancy.

Recognised Species and Major Groups	Geog.	AVarIntr (Range) [1]	Heterogeneity [2]	Redundancy	Pondered Heterogeneity [3]	SM [4]	SF [4]
Phoenix acaulis Roxb.	S_AS	0.31	2.26	0.32	2.02	5	5
Phoenix canariensis H.Wildpret	MED	0.32–0.33	2.35–2.79, mean 2.54	0.16–0.29, mean 0.23	1.77–2.32, mean 1.99	21	55
Phoenix dactylifera L. Eastern Group	E_DAC	0.32–0.32	1.53–2.86, mean 2.46	0.14–0.54, mean 0.26	2.01–2.99, mean 2.64	33	33
Phoenix dactylifera L. Western Group	W_DAC	0.31–0.35	2.10–3.0, mean 2.62	0.10–0.37, mean 0.21	2.45–3.18, mean 2.65	61	94
Phoenix loureiroi Kunth	S_AS, E_AS, SE_AS	0.31–0.39	(1) [5] 1.46–2.77, mean 2.17	0.16–0.56 (0.70) [5], mean 0.35	(0.96) [5] 1.97–2.96, mean 2.53	15	15
Phoenix paludosa Roxb.	S_AS, SE_AS	0.31	2.42	0.27	1.86	5	10
Phoenix pusilla Gaertn.	S_AS	0.33–0.35	2.36–2.80, mean 2.58	0.16–0.29, mean 0.23	2.37–2.68, mean 2.53	10	12
Phoenix reclinata Jacq.	AFR	0.31–0.37	(1.88) [5] 2.02–2.75, mean 2.26	0.17–0.39 (0.43) [5], mean 0.32	(1.83) [5] 1.72–2.55, mean 2.05	26	34
Phoenix roebelenii O'Brien	SE_AS	0.32	2.49	0.25	1.79	6	14
Phoenix rupicola T.Anderson	S_AS	0.32–0.34	(1.37) [5] 1.95	0.41 (0.59) [5]	(1.62) [5] 1.82	7	8
Phoenix sylvestris (L.) Roxb.	S_AS	0.32–0.33	1.81–2.63, mean 2.22	0.21–0.46, mean 0.34	1.86–2.2, mean 2.03	8	13
Phoenix theophrasti Greuter	MED	0.34–0.36	2.1–2.45, mean 2.28	0.26–0.37, mean 0.33	2–2.43, mean 2.16	17	17
Hybrids							
Phoenix canariensis × *P. reclinata*	-	0.35	2.01	0.39	2.26	2	5
Phoenix dactylifera × *P. canariensis*	-	0.35	2.20	0.34	1.99	2	10
Phoenix dactylifera × *P. reclinata*	-	0.31	1.36	0.59	1.66	2	2
Phoenix dactylifera × *P. sylvestris*	-	0.34	2.17	0.35	3.04	2	4

[1] AVarIntr = Average intraindividual/intrapopulational variability. [2] Total information in bits per symbol. [3] Pondered information = 10*relative length*H/($\log_2$ sample size). [4] SM = males sampled, SF = females sampled [5] Heterogeneity and redundancy values of modern cultivars are presented between parentheses. Abbreviations for the geographical groups: E_DAC: North Africa and West Asia *P. dactylifera*. W_DAC: North Africa and Mediterranean *P. dactylifera*. S_AS: Southern Asia. E_AS: Eastern Asia., SE_AS: South-East Asia. AFR: Taxa from Africa and Western Arabian Peninsula. MED: Mediterranean and Macaronesia.

There are some taxa in which we have found extraordinarily polymorphic accessions and/or populations, such as in *P. hanceana* or even in cultivars such as *Phoenix* "Palmer".

Within *P. theophrasti* Turkish populations, the maximum of heterozygosity was recorded at Gölköy (0.7) while the populations of the Datça peninsula, and other southernmost places, presented values between 0.3 and 0.55 in the study of Vardareli et al. [21]. However, the phenotypic heterogeneity value is relatively lower for Gölköy. We should not discard the possibility of a hybrid origin (*P. theophrasti* × *P. dactylifera*) of the Gölköy population given the intermediate characteristics of their leaves, acanthophylls, inflorescences (male and female) and fruits.

4. Discussion

4.1. Heterogeneity of Commonly Accepted Phoenix Species

The maximum of phenotypic heterogeneity in this study is reached within the set of *Phoenix dactylifera* (Table 4) and related or subordinate taxa, either in the western or eastern groups of *P. dactylifera*. However, we should note that the range, and average, heterogeneity values are notably higher in the western group (Table 5). Immediately afterwards we find the large group of *P. loureiroi*, especially the type of the species, and, behind, the smallest of *P. pusilla*.

Phoenix dactylifera, *P. loureiroi* and *P. reclinata* scored higher genetic diversity in the study of Pintaud et al. [22]. This is coincident with our results, except for *P. reclinata*. However, we must notice that within *P. reclinata* there is a gradient from west to east in phenotypic heterogeneity with peaks in the eastern part where the samples analyzed by Pintaud et al. [22] were originally collected (Botswana, Kenya, Somalia, Tanzania, Zimbabwe).

The high phenotypic heterogeneity of the hybrid *P. dactylifera* × *P. sylvestris* (Table 5) is very notable, especially considering the relatively low values of *P. sylvestris* heterogeneity. This merits further study considering that, notwithstanding the limited sampling of *P. sylvestris*, Pintaud et al. [22] findings suggest a high genetic diversity within this species, which still needs to be explored. Low phenotypic heterogeneity values (Table 5) are associated with species originally restricted in their distribution area such as *P. roebelenii*, *P. rupicola*, *P. acaulis* and *P. canariensis*, but also *P. paludosa*. In the analysis in [22], *P. acaulis*, *P. canariensis*, *P. rupicola*, *P. pusilla*, *P. roebelenii*, and *P. theophrasti* had low genetic diversity and some fixed private alleles, a pattern consistent with an evolution of small populations in isolation. The only major discrepancy between phenotypic heterogeneity values and genetic diversity is found in *P. pusilla* and it is likely due to differences in sampling strategies.

Ballardini et al. [23] sequenced a longer cpDNA region (700 bp) comprising the CpfM minisatellite located between the psbZ and trnfM(CAU) genes; the minisatellite showed 2–7 repetitions of a 12 bp motif, with 1–3 out of seven haplotypes per species confirming most parts of the results of Pintaud et al. [22].

Vardareli et al. [21], working with 12 SSR markers, reported low observed heterozygosity in *P. theophrasti*, *P. roebelenii*, *P. sylvestris* and *P. acaulis*, and high observed heterozygosity in *P. dactylifera*, *P. loureiroi* and *P. reclinata*, which is consistent with our heterogeneity values. However two among their results are contrasting: the high heterozygosity in *P. canariensis*, which differs from the low average heterozygosity determined by Saro [24] in her study of the whole of the Canary Islands, but working only with 8 SSR markers. The second discrepancy is the high heterozygosity in *P. rupicola*, which contrasts with our results on phenotypic heterogeneity and the genetic analyses of previous authors.

4.2. Heterogeneity of Genus Phoenix Geography and Origins

The seeds of *Phoenix* are the part of the plant that can best be identified and with the highest level of detail when studying fossil remains, which allows their comparison with modern samples in a multivariate analysis of the seed morphology of the entire genus *Phoenix* [25,26]. It is interesting to observe that the two large groups of recognizable species in the genus *Phoenix* (Figure 10) present seeds with well-differentiated shapes and

dimensions. These seed types are also found in the fossil record. In both major groups, the oldest materials are dated between the end of the Cretaceous and the beginning of the Paleocene.

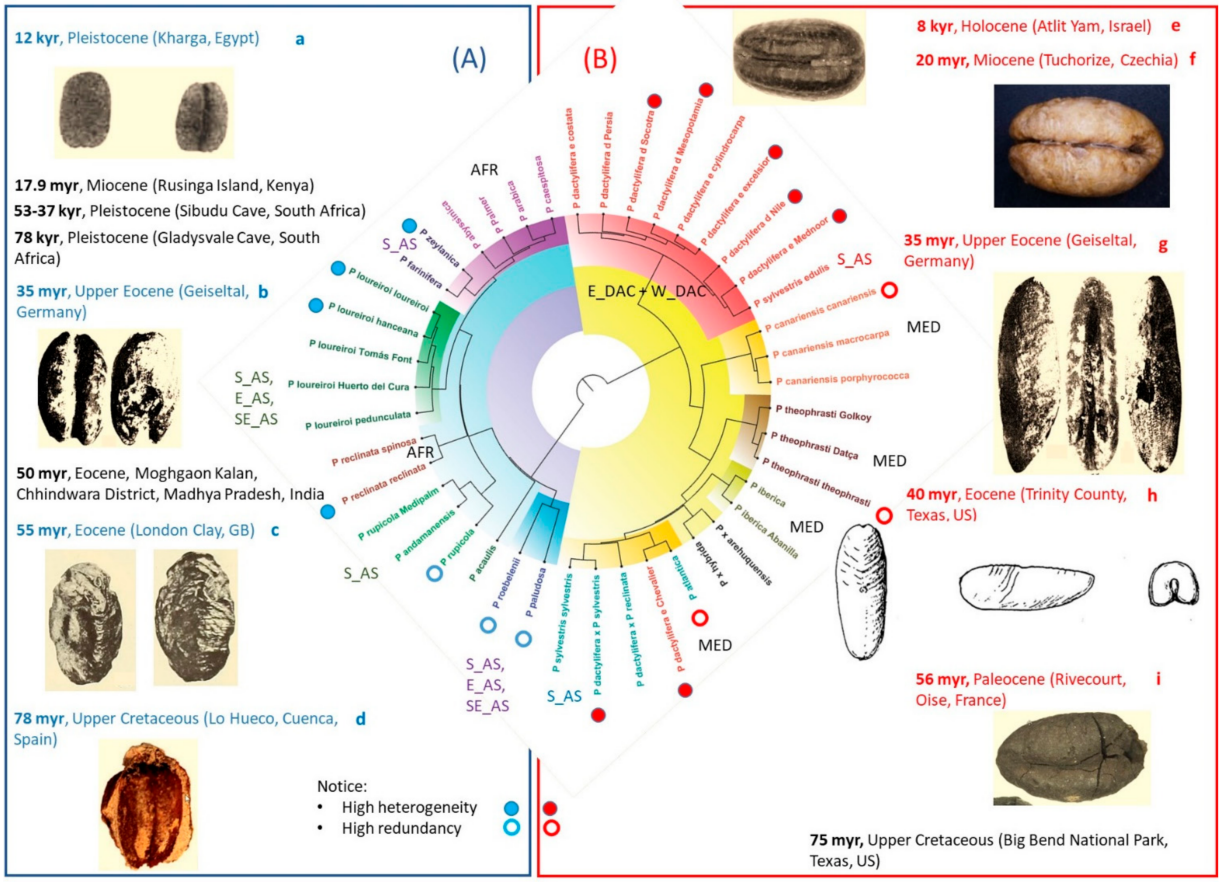

Figure 10. *Phoenix* OTUs and fossil *Phoenix* seeds. (**A**) Eastern group of *Phoenix* species; (**B**) Western group of *Phoenix* with, notably, *P. dactylifera.* a–d. Fossil seeds of *Phoenix* morphologically similar to those of species in the eastern group (A) of species. e–i. Fossil seeds of *Phoenix* morphologically similar to those of species in the western (B) species group. Abbreviations for the geographical groups: E_DAC: North Africa and West Asia *P. dactylifera*. W_DAC: North Africa and Mediterranean *P. dactylifera*. S_AS: Southern Asia. E_AS: Eastern Asia., SE_AS: South-East Asia. AFR: Taxa from Africa and Western Arabian Peninsula. MED: Mediterranean and Macaronesia. Images: fossil seeds: a. Gardner [27]; b. Mai, [28]; c. Chandler [29]; d. Ortega [30]; e. Anat Hartmann–Shenkman; f., Jiri Kvacek; g. Mai, [28]; h. Berry [31]; i. Smith [32].

The cluster characterized by relatively large ovoid to cylindrical seeds (Figure 10b) includes the subgroups MED, S_AS, E_DAC and W_DAC of Table 5 with, among others, species such as *P. dactylifera, P. canariensis, P. theophrasti* or *P. sylvestris* and is centered in North Africa, western Asia and the Mediterranean, reaching the Indus Valley in the east (Figure 11). In it the maximums of morphological heterogeneity within *Phoenix* genus have been registered. The group presently extends between 20 and 40 degrees north latitude. This group is represented by fossils at least 56 myr old from the Paleocene (Rivecourt, Oise, France) or the 35 myr old, Upper Eocene (Geiseltal, Germany) (Figures 10b and 11b). The oldest among these fossils were found in localities between 45 and 55 degrees north latitude on the European continent and approximately 30 degrees north latitude on the American continent.

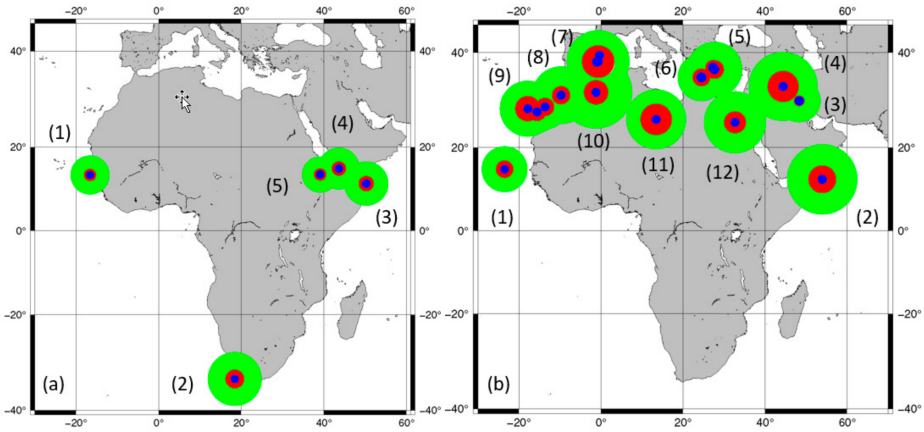

Figure 11. *Phoenix* heterogeneity in taxa from Africa, West Asia and the Mediterranean. The red and green circles are proportional to the heterogeneity of the group, before and after normalization, and the blue circles are proportional to the mean intraindividual variability of the accessions in each group. (**a**) AFR: 1, *P. spinosa*; 2, *P. reclinata* var. *reclinata*; 3, *P. caespitosa*; 4, *P. arabica*; 5, *P. abyssinica*; (**b**) MED: 1, *P. atlantica*; E_DAC: 2, *P. dactylifera "Socotra"*; 3, *P. dactylifera "Persia"*; 4, *P. dactylifera "Mesopotamia"*; MED: 5, *P. theophrasti "Datça"*; 5, *P. theophrasti "Gölköy"*; 6, *P. theophrasti* var. *theophrasti*; W_DAC: 7, *P. dactylifera* var. *costata*; *P. excelsior*; & MED: *P. iberica*; W_DAC: 8, *P. dactylifera "Chevalier"*; MED: 9, *P. canariensis* var. *canariensis*; *P. canariensis* var. *macrocarpa*; & *P. canariensis* var. *porphyrococca*; W_DAC: 10, *P. dactylifera "Mednoor"*; 11, *P. dactylifera* var. *cylindrocarpa*; E_DAC: 12, *P. dactylifera "Nile"*. Abbreviations for the major geographical groups: AFR: Taxa from Africa and Western Arabian Peninsula. E_DAC: North Africa and West Asia *P. dactylifera*. W_DAC: North Africa and Mediterranean *P. dactylifera*. MED: Mediterranean and Macaronesia.

The cluster with small seeds, usually ellipsoidal or oblong-elliptical (Figure 10a) includes groups E_AS, SE_AS and AFR, with species such as *P. loureiroi*, *P. paludosa* or *P. reclinata*. It ranges throughout tropical Africa (Figure 11a), the Indian subcontinent, and eastern Asia (Figure 12). The maximums of heterogeneity within this group were recorded in the *P. loureiroi* complex.

The small-seeded cluster presently extends between the Equator and 28 degrees north latitude and is represented by fossils at least 78 myr old, Upper Cretaceous (Lo Hueco, Cuenca, Spain) or the 55 myr old, Eocene (London Clay, GB). At the 35 myr old, Upper Eocene (Geiseltal, Germany) seems to have coexisted with *Phoenix*, producing seeds of the larger type (Figure 10a,b). The oldest fossils identified as belonging to this cluster were found between 40 and 55 degrees north latitude on the European continent and approximately 23 degrees north latitude on India. The center of morphological diversity for this group extends from India to Hong Kong (Figure 12).

When Billotte et al. [33] characterized 16 nuclear simple sequence repeat (SSR) loci in *Phoenix dactylifera*, the across-taxa amplification and genotyping tests showed the utility of most SSR markers in eleven other *Phoenix* species with one exception of their transferability in one of the same group b (*P. canariensis*) and some exceptions in group a: two markers were not transferable to *Phoenix paludosa*, and *P. roebelenii* and *P. pusilla* presented this problem with only one single SSR marker.

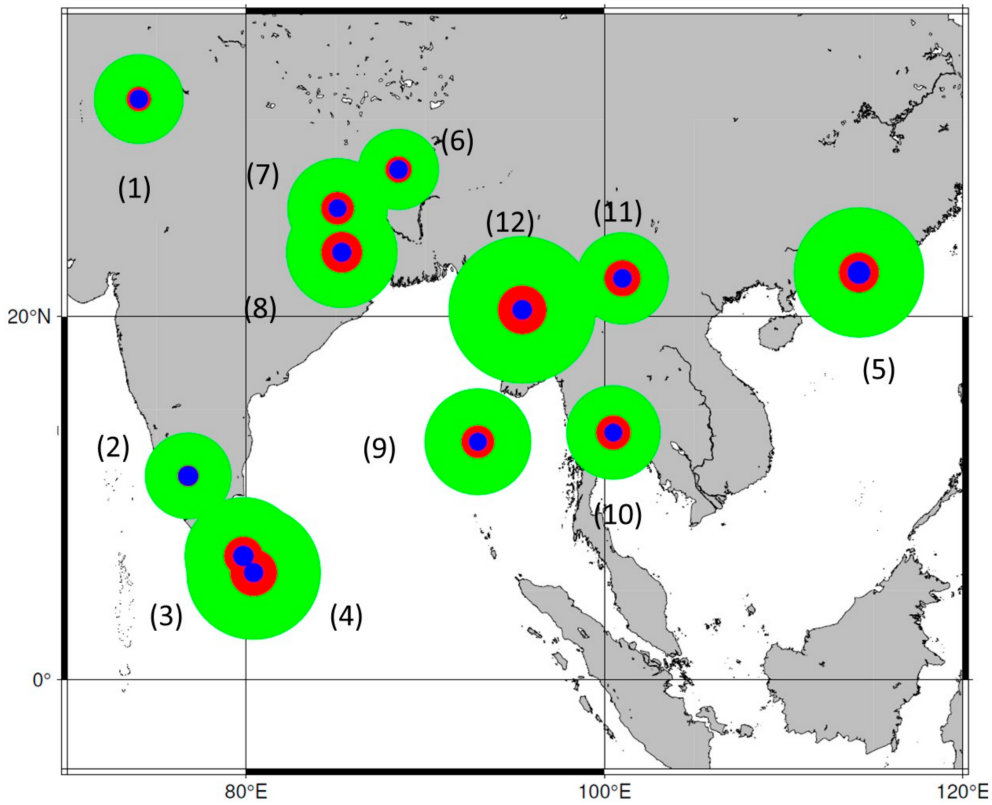

Figure 12. *Phoenix* heterogeneity in taxa from Middle and East Asia. The red and green circles are proportional to the heterogeneity of the group, before and after normalization, and the blue circles are proportional to the mean intraindividual variability of the accessions in each group. S_AS: 1, *P. sylvestris "Edulis"*; 2, *P. loureiroi* var. *pedunculata*; 3, *P. farinifera*; 4, *P. zeylanica*; E_AS: 5, *P. hanceana*; S_AS: 6, *P. rupicola*; 7, *P. acaulis*; 8, *P. sylvestris sylvestris*; 9, *P. andamanensis*; SE_AS: 10, *P. paludosa*; 11, *P. roebelenii*; 12, *P. loureiroi loureiroi*;. Abbreviations for the major geographical groups: E_AS: Eastern Asia; S_AS: Southern Asia. SE_AS: South-East Asia.

4.3. Patterns of Date Palm (Phoenix dactylifera) Phenotypic Diversity

4.3.1. Phenotypic Heterogeneity and Heterozygosis in *Phoenix dactylifera*

Phoenix dactylifera conforms a complex of landraces and cultivars that coexist with phenotypically well-defined geographical groups with numerous intermediate forms and long-distance translocation of otherwise local cultivars, i.e., the case of Moroccan Medjoul that became a widespread cultivar within a century. This entails high heterogeneity. The careful analysis of shared alleles led Pintaud et al. [22] to suggest that isolated hybridization events with other species, such as *P. sylvestris*, *P. caespitosa* and *P. reclinata*, are likely to have occurred during the expansion of date palm cultivation outside the Fertile Crescent, towards the Middle East and the southern limit of Sahara. Such a process could have resulted in particular local varieties having introgressed some allospecific genes.

Elshibli and Korpelainen [34], working with 16 SSR markers, recorded in the Upper Nile Valley of Sudan values of observed heterozygosity above 0.9, closely followed by those from Morocco, 0.88. This agrees with the high phenotypic heterogeneity of the *P. dactylifera* "Nile" (Egypt and Sudan) and *P. dactylifera* "Mednoor" (Morocco and Algeria) groups (Table 4).

The high heterogeneity detected in *Phoenix dactylifera* "Mesopotamia" from the lower Euphrates (Table 4) is parallel with the results of Chaluvadi et al. [35], where Iraqi accessions were found to have the richest allelic diversity, as well as the most private alleles.

Observed heterozygosity values between 0.6 and 0.7 were recorded by Naqvi [36], working with 18 SSR markers, in Pakistan, regions of Muzafargarh, Faisalabad and Kech, and by Moussoni et al. [37], for 18 SSR markers, in Algeria (Ghardaia, Timimoun, Ouargla

and Oued Souf). This coincides with the high values of phenotypic heterogeneity registered in the hybrid of *P. dactylifera* × *P. sylvestris* in Pakistan, and the high values of *P. dactylifera* var. *cylindrocarpa* (Table 4).

The genetic structure of the date palm (*Phoenix dactylifera*) in the Old World presents a strong differentiation between eastern and western populations. Zehdi-Azouzi and collaborators [38], analyzing nuclear SSRs, confirmed the existence of two pools named Eastern and Western within what is known as *Phoenix dactylifera*. Eastern accessions are substantially different from the Western ones, suggesting that they each have their own autochthonous origin. Mathew et al. [39] conducted genotyping-by-sequencing and generated genome-wide genotyping data for 13,000–65,000 SNPs (single nucleotide polymorphisms) in a diverse set of date palm fruit and leaf samples mainly from *P. dactylifera*, but also from *P. sylvestris* and *P. hanceana*. Their analysis provides the first genome-wide evidence for the date palm cultivars segregation into two main regions of shared genetic background from North Africa and the Arabian Gulf. Their results fit a model with two centers of earliest cultivation, including date palms autochthonous to North Africa. Hazzouri et al. [40] generated a catalog of circa seven million SNPs in date palms. Their population structure analysis also indicated a major genetic divide between North Africa and the Middle East/South Asian date palms, with evidence of admixture in cultivars from Egypt and Sudan.

Therefore, this strong differentiation suggests the existence of at least two domestication events. Northern Africa would have been either a primary or a secondary dome. Therefore, it would be expected that this differentiation at the genetic level entails the existence of perceptible phenotypic differences at the morphological level and two major pools of heterogeneity, which is partly consistent with the results of our analysis (Table 5).

Mohamoud et al. [41] identified four *Phoenix dactylifera* haplotypes instead of two by population-wide organellar genome sequencing. The North African haplotype (NA1) is highly deviated from the Arabian Gulf (AG) haplotypes and likely represents a distinct, early center of date palm cultivation. Altogether, the genetic distinction among the three major haplotypes (AG1, AG2, and NA1) suggests their geographic separation at the time of initial cultivation. The similarity of the major North African haplotype (NA1) to *P. sylvestris* is important to note and agrees with the findings of Flowers and colleagues in their analyses of the date palm chloroplast and mitochondrial genomes, and those of Chaluvadi et al. [35] based on nuclear markers, where Indian and Pakistani date palms were found to be most closely related to the North African germplasm. These studies coincide with the results of our present morphological analysis in which *P. sylvestris* is closer to *P. atlantica* and related North African *P. dactylifera* cultivars of "Chevalieri" group than to any other taxa (Figure 10b). The NA2 haplotype is more similar to the AG1 than any other haplotype and it suggests that the NA2 haplotype derived from the AG1 as they are both closer to the other Arabian Gulf haplotype (AG2) than the major North African 1 haplotype [41]. In parallel, Flowers et al. [42] resequenced the genomes of date palm varieties and five other *Phoenix* species. Their results indicate that the North African population, at least in part, has mixed ancestry with components from Middle Eastern *P. dactylifera* and *P. theophrasti*. Analysis of ancestry ratios indicates that up to 18% of the genome of North African varieties of *P. dactylifera* is shared with *P. theophrasti* and that a large percentage of loci in this population are segregated for single nucleotide polymorphisms (SNPs) that are fixed in *P. theophrasti* and absent in the Middle Eastern date palm (*P. dactylifera*). Nevertheless, this can be seen from other perspectives in terms of *P. theophrasti* and North African *P. dactylifera* varieties sharing a common ancestor, which could be traced to the Tertiary of Europe. Or, alternatively, that the ancestral populations of Western *P. dactylifera* cohabited and introgressed with those of *P. theophrasti*, in the glacial refuges of the Mediterranean that they shared, after having segregated from the Eastern ones, which would have experienced independent evolution during the glaciations.

The analysis of Niger date palms allowed Zango et al. [43] to establish a secondary genetic structure within the Western gene pool of *P. dactylifera*; therefore, it is advisable to verify its relationships with the above mentioned subgroups. Overall, the Western group

presents regional patterns of morphological and genetic variability that are relatively well structured but highly heterogeneous.

4.3.2. Differential Characters for *Phoenix dactylifera* Western and Eastern Populations

Given the high levels of morphological heterogeneity that occur in the western and eastern groups of *Phoenix dactylifera*, it is extremely difficult to find a set of well-defined differential characters. The genome-wide scans for selection in the study of Hazzouri et al. suggest [40] at least 56 genomic regions associated with selective sweeps that may underlie geographic adaptation. These patterns of post-domestication diversification may have blurred the distinction between groups. However, some of the variables analyzed allow us to propose a set that could constitute the respective syndromes (Table 6). In any case, it is quite possible that the inclusion of new varieties and landraces in the study will further blur even these slight differences.

Table 6. Morphological differences between *Phoenix dactylifera* Western and Eastern groups.

Distinctive Characters	Western Syndrome	W Cultivars Examples	Eastern Syndrome	E Cultivars Examples
Leaf				
Basal neck length in the upper spines	0–15 mm	Abel, Alig, Candits, Criollo, Deglet Nour, Ghars, Haziz	15–30 (60) mm	Apdandon, Barhee, Dairy, Khalas, Koroch, Lulu
Leaf base width	15–30 (35) cm	Candits, Medjool, Rhars, Thoory	8–20 (25) cm	Apdandon, Korosh, Sarafana, Sayir, Sudra
Spines (acanthophylls) *	10–30	Abel, Abu Faqqus, Alig, Blonde Beauty, Criollo, Deglet Nour, Ghars, Maurs, Thoory	2–17	Khadrawy, Kustawy, Sudra, Sarafana
Fruits				
Fruiting Peduncle Colour	Orange, greenish orange or reddish orange	Beser Helou, Candits, Criollo, Medjool, Thoory	Greenish yellow, yellow or orange	Barhee, Braim, Dairy, Lulu, Sarafana, Sudra
Fruit Apex	Obtuse	Aziza, Candits, Maurs, Rhars, Tenats, Thoory	Obtuse, acute, truncate, mucronate, ovate-oblique, retuse emarginate	Barhee, Braim, Dairy, Kustawy, Maktoom, Piarom
Epicarp	Epicarp usually not adherent	Abel, Alig, Candits, Medjool, Thoory	Epicarp usually adherent	Barhee, Braim, Dairy, Piarom, Sayir
Seeds				
Seed width	6–12 mm	Abel, Candits, Criollo, Ghars, Medjool, Tenats	5–10 mm	Apdandon, Kessab, Maktoom, Muzawati, Sarafana, Sudra, Zahidi
Seed shape	Seed ovate to triangular, elliptical, elliptical-oblong, but also cylindrical-narrow	Blonde Beauty, Brunette Beauty, Candits, Criollo, Deglet Nour, Haziz, Medjool Thoory	Seed usually cylindrical-narrow	Apdandon, Dairy, Halawy, Khadrawy, Khalas, Muzawaty, Sarafana, Sayir, Sudra, Zahidi
Seed ventral furrow	Seed ventral furrow shallow or U-shaped, rarely deep V-shaped	Abel, Alig, Blonde Beauty, Brunette Beauty, Deglet Nour, Haziz, Medjool, San Ignacio	Seed ventral furrow usually deep V-shaped, less often U-shaped	Apdandon, Dairy, Halawy, Khadrawy, Khalas, Maktoom, Muzawaty, Sarafana, Sayir, Sudra, Zahidi
Seed surface	Rough or irregular, rarely smooth	Aziza, Beser Helou, Candits, Criollo, Medjool, Rhars, Tenats, Thoory	About 40% are smooth, the rest rough or irregular	Apdandon, Koroch, Lulu, Muzawati, Piarom

Notice: (*) counted only on one side of the rachis.

Vavilov's law of homologous series in variation [44] offers a satisfactory model for this parallel in polymorphism between the Western and Eastern *Phoenix dactylifera* groups, which can be seen as closely related "Linneons", provided that we can find their "Radicals", which can be understood as specific morphological and physiological complexes for each series. Homologous series are characterized by similar series of variation with such regularity that, knowing a succession of varieties in a "Linneon", the existence of similar forms and even genotypic differences similar to other "Linneon" can be predicted. The similarity is more complete when the "Linneons" are more related. For example, following Vavilov's hypothesis, the existence of varieties with winged or auriculate seeds, such as Medjool (Figure 5b), in the Western group, would lead us to anticipate finding varieties with this peculiar type of seed in the Eastern group as well.

Although on a theoretical basis it would be possible to morphologically define a Western and an Eastern date palm, both typical and well differentiated, the reality is that when a good number of varieties and landraces characterized according to their chlorotype as Western or Eastern are considered, the limits become imprecise. This is largely due to the existence of hybridizations and introgressions along an extensive strip stretching from the Nile Valley to the oases of Morocco, which has been especially well characterized in Algeria by Moussouni and collaborators [37].

If we consider the utility of adopting specific or infraspecific taxa to systematize variability within *Phoenix dactylifera*, in light of the available evidence that shows extremely high heterogeneity within Eastern and Western groups, it seems unwise to divide into species or even subspecies the *Phoenix dactylifera* complex. On the other hand, the existence of groups of landraces sharing morphological and physiological traits whose origins are geographically well defined seems evident and, in some cases, it is manifested both in the morphological characteristics of the members of the group and in the existence of privative alleles. This is the case of the "candits" in Elche (Spain) [45] (Figures 1f, 3a,b and 4g)

This suggests that if we continue to search for differential morphological characters taking into account the four groups recognized by Mohamoud et al. [35] and not the two generally accepted, we could achieve better differentiation.

The traditional propagation of date palms based on seedlings leads to the existence of a high morphological diversity [46]. Regions such as Mesopotamia and neighboring areas, the Arabian Peninsula, the Western Mediterranean and the Saharan oases are home to an extraordinary repertoire of date palm diversity [47]. Consequently, within *Phoenix dactylifera*, the OTUs with the greatest heterogeneity are those associated with regions where there is a long tradition of date palm cultivation, with a very high varietal diversity linked to the use of seed propagation. This makes it difficult to distinguish these geographical groups morphologically.

4.4. Role of Hybrids and Hybrid Swarms in Phenotypic Diversity

4.4.1. Large-Scale Hybrid Swarms

Hybrids, in the case of terrestrial vascular plants, are usually found in the areas of contact between two different but genetically compatible species, where they cohabit in proximity. If the hybrids are more or less fertile, crosses can occur between them and with their offspring, as well as with the parental species, giving rise to introgressions and the appearance of hybrid zones where these hybrid swarms coexist. The morphological complexity of these hybrid swarms is very high since all the transits between the parental species can be found, although in other cases one of the hybrids is more successful than the parental species and ends up occupying the entire space and, as a consequence, the morphological diversity is significantly reduced [48].

Introgression in *Phoenix* is so common that it is sometimes questionable what the true species is supposed to look like, as it was reported concerning *P. roebelenii* [49,50]. However, in the case of *P. roebelenii* it is not clear which part of this hybrid swarm occurred in its natural habitat along the Mekong River, with populations of *P. loureiroi*, and which part occurred with other species, in cultivation, outside Indochina.

Moussouni and collaborators [37] employed 18 microsatellite markers and a chloroplast minisatellite to characterize 414 individual palm trees corresponding to 114 local varieties from 10 different Algerian oases. They found a significant negative inbreeding coefficient, suggesting active farmer selection for heterozygous individuals. Three distinct genetic clusters were identified: an ubiquitous set of varieties found across the different oases, and two clusters, one of which was specific to the northern area, and the other to the drier southern area of the Algerian Sahara. The ubiquitous cluster presented very striking chloroplast diversity, with haplotypes found in Saudi Arabia, the most eastern part of the date palm range. Exchanges of Middle Eastern and Algerian date palms are known to have occurred and could have led to the introduction of this particular chlorotype. However, Algerian nuclear diversity was not of eastern origin. Their study strongly suggests that the peculiar chloroplastic diversity of date palm is maintained by farmers and could originate from date palms introduced from the Middle East a long time ago, which have subsequently strongly introgressed. Within this area, from Morocco to Tunisia, we have detected an extraordinary morphological heterogeneity, inside *P. dactylifera* var. *cylindrocarpa* and the group of landraces "mednoor", which includes well-known cultivar groups such as "deglet noor" or "medjoul", even when considering those landraces present exclusively as the Western chlorotype.

In Algeria, the maximum numbers of cultivars, as an index of diversity, were recorded in the Gourara, a region of western Algeria formed by a set of oases, the mountainous areas and plateaus of the northeast (Aurés and Nemamcha) and the valleys of the mountainous massifs of the southeast (Tassili); these numbers are much lower in other large Saharan oases where most of the palm trees of the country are grown [51,52]. This suggests an origin of the diversity prior to the relatively recent homogenization of the large oases that affected the peripheral regions to a lesser extent.

At a global level, Mohamoud et al. [41] suggest that there were likely three distinct centers of *P. dactylifera* cultivation from which cultivars in those regions all derived from a single maternal contributor followed by a fourth that developed from the AG1 haplotype. These centers of cultivation were then responsible for hundreds of future cultivars that are now available with admixture of the nuclear genome occurring at the boundaries of these centers.

4.4.2. *Phoenix* Interspecific Hybrids

The specimens of each of the known F1 direct hybrids, first filial generation, among the different *Phoenix* species, which are available and complete enough to be useful for morphological analysis, are scarce; this has limited the adequate appreciation of heterogeneity in the different hybrids. Their identification as hybrids on exclusively morphological grounds is difficult when the parent species are relatively similar. Additionally, hybrids of several generations must be even harder to distinguish by morphology alone [49]. Moreover, the variability (heterogeneity) is high within species, especially in *P. dactylifera*; thus, differentiating hybrids from ecotypes or landraces based on morphology alone is challenging.

Within the analyzed material for which the hybrid nature was determined using morphological and molecular analyses, it is worth highlighting the very remarkable heterogeneity of the *Phoenix dactylifera* × *P. sylvestris* hybrids.

5. Conclusions

Using a homogeneous descriptor system and an appropriate symbol scale, the Shannon information entropy index allows the quantitative representation the different levels of heterogeneity in the various taxonomic units of the genus *Phoenix*.

The high phenotypic heterogeneity in various *Phoenix* species is related to the genetic diversity, age and ancestry of different taxa, hybridization events and introgressions prior to domestication, and selective pressures after domestication and, again, interspecific crosses after domestication.

The most heterogeneous taxon as a whole and several of its units is *Phoenix dactylifera*, which is associated with its wide geographical distribution; while the most uniform or less heterogeneous taxa are *P. rupicola*, *P. theophrasti* and *P. roebelenii*, which have very small natural ranges. Furthermore, within *Phoenix dactylifera*, the OTUs with the greatest heterogeneity are those associated with regions where there is a long tradition of date palm cultivation, with a very high varietal diversity linked to the use of seed propagation.

The lower limits of heterogeneity are found in ornamental cultivars within *P. loureiroi* and *P. rupicola*, which is coherent with the definition of cultivars.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/horticulturae8040287/s1, Table S1: List of analyzed accessions, herbarium specimens, and included cultivars.

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