SYSTEMATICS AND PHYLOGENY

Iconic, threatened, but largely unknown: Biogeography of the Macaronesian dragon trees (*Dracaena* spp.) as inferred from plastid DNA markers

Iván Durán,[1] Águedo Marrero,[2] Fouad Msanda,[3] Cherif Harrouni,[4] Michael Gruenstaeudl,[5] Jairo Patiño,[6,7] Juli Caujapé-Castells[1]* & Carlos García-Verdugo[8]*

1 *Departamento de Biodiversidad Molecular y Banco de ADN, Jardín Botánico Canario 'Viera y Clavijo' – Unidad Asociada CSIC, Cabildo de Gran Canaria, 35017 Las Palmas de Gran Canaria, Spain*
2 *Departamento de Sistemática Vegetal y Herbario, Jardín Botánico Canario 'Viera y Clavijo' – Unidad Asociada CSIC, Cabildo de Gran Canaria, 35017 Las Palmas de Gran Canaria, Spain*
3 *Faculty of Sciences, Ibn Zohr University, 80070 Agadir, Morocco*
4 *Hassan II Institute of Agronomy and Veterinary Sciences, 80070 Agadir, Morocco*
5 *Institut für Biologie, Systematische Botanik und Pflanzengeographie, Freie Universität Berlin, Altensteinstraße 6, 14195 Berlin, Germany*
6 *Plant Conservation and Biogeography Group, Departamento de Botánica, Universidad de La Laguna, 38200 La Laguna, Spain*
7 *Island Ecology and Evolution Research Group, Institute of Natural Products and Agrobiology (IPNA-CSIC), C/ Astrofísico Francisco Sánchez 3, La Laguna, 38206 Tenerife, Canary Islands, Spain*
8 *Universitat de les Illes Balears – Institut Mediterrani d'Estudis Avançats (CSIC-UIB), 07122 Mallorca, Spain*
* These two authors share the senior authorhip
Address for correspondence: *Carlos García-Verdugo*, *carlosgarciaverdugo@gmail.com*

DOI https://doi.org/10.1002/tax.12215

Abstract The genus *Dracaena* in Macaronesia comprises two threatened species of arborescent monocots that are often associated with one of the most intriguing biogeographic disjunctions: the Rand Flora pattern. Molecular information is, however, largely missing for the Macaronesian *Dracaena* taxa ("MDT", hereafter), and the biogeographic or population genetic patterns of this lineage have not yet been thoroughly assessed. To fill this gap, we generated plastid DNA sequence data of 14 *Dracaena* populations representing the entire natural distribution of MDT (including mainland Morocco and all recognized subspecies), 9 additional populations of subspontaneous origin, and a set of related species of the genus. We performed phylogenetic, biogeographic, and population genetic analyses at different spatial scales and conducted a comparative review on plant haplotype diversity in Macaronesian plants. The results of our phylogenetic analyses indicated the monophyly of the MDT and an origin separate from a clade of geographically distant species that so far were postulated as their closest living relatives (*D. cinnabari*, *D. ombet*, *D. schizantha*, *D. serrulata*). The results of our phylogeographic analyses indicated that diversification within *D. draco* occurred throughout the Pleistocene and that wild peripheral populations (Madeira, mainland Morocco) may have a recent origin from Canarian source populations. Recent dispersals, coupled with remarkably low levels of haplotype diversity, probably account for the weak phylogeographic signal observed across wild populations. However, our results suggested that human-assisted expansion of *Dracaena* inflates the extant phylogeographic signal by non-random translocation of a specific subset of haplotypes. Our study demonstrates that many of the previous biogeographic scenarios on MDT are not supported by molecular data. Instead, our results highlight (i) the impact that human activity may have on the phylogeographic pattern of island plants, and (ii) the need of a deeper taxonomic sampling in future investigations on MDT and close relatives.

Keywords biogeographic disjunction; *Dracaena draco*; haplotype diversity; human-mediated dispersal; island biogeography; Rand Flora

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

The Macaronesian islands in the Atlantic Ocean are home to one of the most iconic plant species in the region: the dragon tree (*Dracaena draco* (L.) L., Asparagaceae). Peculiar features such as its arborescent, pachycaulous growth form (Fig. 1) and the production of valuable resin (known as "dragon's blood") led it to become an emblematic symbol of Macaronesia (Lyons, 1974; Gupta & al., 2007; Marrero, 2010; Sánchez-Pinto & Zárate, 2010). Since the 20th century, the species is found across the globe, primarily due to human cultivation (e.g., Anonymous, 1905). The dragon tree is of interest not only due to its ethnobotanical and ornamental value, but also due to its intriguing evolutionary history. Thus,

Article history: Received: 21 Sep 2019 | returned for (first) revision: 12 Dec 2019 | (last) revision received: 21 Feb 2020 | accepted: 21 Feb 2020
Associate Editor: Levent Can

striking similarities between *D. draco* and several congeneric species inhabiting the opposite margin of the African continent and Arabia exist, and have led to the description of *Dracaena* as a premier example of the enigmatic Rand Flora distribution pattern (Quézel, 1978; Bramwell, 1985; Marrero & al., 1998; Sanmartín & al., 2010).

Research on *Dracaena* has recently focused on the fields of comparative physiology and anatomy (Jura-Morawiec & Tulik, 2016; Nadezhdina & Nadezhdin, 2017; Klimko & al., 2018). In addition, relatively recent taxonomic work revealed that the genus not only inhabits the Macaronesian islands, but also neighbouring mainland areas (Benabid & Cuzin, 1997; Médail & Quézel, 1999). Today, the Macaronesian lineage of *Dracaena* (collectively called "MDT" hereafter) is known to comprise *D. tamaranae* Marrero Rodr. & al., a species endemic to the island of Gran Canaria (Marrero & al., 1998), and three subspecies of *D. draco*. These subspecies naturally occur in the Macaronesian enclave of mainland SW Morocco (*D. draco* subsp. *ajgal* Benabid & Cuzin; Benabid & Cuzin, 1997), the Cape Verde Islands (*D. draco* subsp. *caboverdeana* Marrero Rodr. & R.S. Almeida; Marrero & Almeida Perez, 2012), and the Canary Islands and Madeira (*D. draco* subsp. *draco*; Almeida Pérez & Beech, 2017). Despite this enigmatic geographic distribution, the evolutionary history of the MDT and their biogeographic diversification have remained largely unexplored. In particular, the idea that the MDT display a close evolutionary affinity with their East African and Arabian congeners has never been thoroughly examined using molecular data.

The hypothesis of common ancestry of the Macaronesian and the East African and Arabian species of *Dracaena* was first presented in early biogeographic and morphological investigations (Meusel, 1965 [cited in Marrero & al., 1998]; Axelrod, 1975; Quézel, 1978; Sunding, 1979; Bramwell, 1985). According to these studies, the dragon tree group would include arborescent *Dracaena* taxa inhabiting xerophilous habitats in East Africa (*D. ombet* Heuglin ex Kotschy & Peyr, *D. schizantha* Baker), Arabia (*D. serrulata* Baker) and the islands of Socotra (*D. cinnabari* Balf.f.) and Macaronesia (*D. draco*). Despite some discrepancies concerning the precise species composition of the group (e.g., Bramwell, 1985, included *D. ellenbeckiana* Engl., a species inhabiting mountain areas of East Africa, while Quézel, 1978, excluded *D. ombet*), the hypothesis of a common ancestry of the MDT and the East African and Arabian species of *Dracaena* has been reiterated by several recent investigations (Marrero & al., 1998; Sanmartín & al., 2010; Nadezhdina & Nadezhdin, 2017; Del Arco Aguilar & Rodríguez Delgado, 2018). However, the description of a new Macaronesian species of *Dracaena* also led to a re-evaluation of the original hypothesis (Marrero & al., 1998). Based on morphological and ecological traits, Marrero & al. (1998) suggested that *D. tamaranae* may be closely related to the group of species found in the Horn of Africa and Arabia (*D. ombet*, *D. schizantha*, *D. serrulata*), whereas the second Macaronesian species (*D. draco*) would show closer affinities with the Socotran species *D. cinnabari*. Recent taxonomic assessments have broadened the circumscription of the Macaronesian lineage of *Dracaena* to include several Southeast Asian species (Wilkin & al., 2012), whereas paleobotanical records relate the MDT to an extinct species from the East Mediterranean region rather than to East African taxa (Denk & al., 2014). Molecular phylogenetic reconstructions could therefore shed some light on the conflicting biogeographic patterns described by previous studies.

As island species with restricted geographic distributions, the relevance of the MDT for biogeographic research is

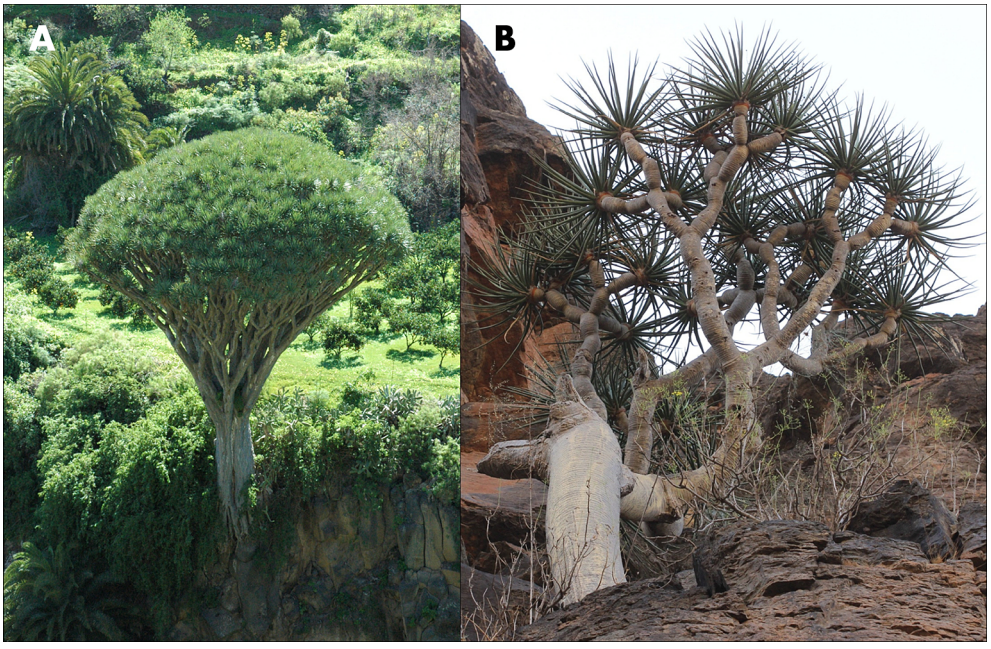

Fig. 1. Growth habit of *Dracaena draco* (**A**) and *D. tamaranae* (**B**), the two *Dracaena* species naturally occurring in Macaronesia. — Photographs: A. Marrero.

paralleled by the challenges that this plant group poses to biodiversity conservation. *Dracaena* individuals of wild origin are extremely rare in Macaronesia, occupy areas with very limited accessibility, and show a declining trend in effective population size (Almeida Pérez, 2003; Marrero, 2010). As a consequence, recent conservation assessments consider both Macaronesian species of *Dracaena* as threatened (Almeida Pérez & Beech, 2017; Marrero Rodríguez & al., 2017). The small population sizes of the MDT also raise the question of effective conservation strategies, particularly if levels of genetic diversity are low in the island habitats (e.g., García-Verdugo & al., 2015). The low abundance of the MDT in the wild sharply contrasts with the occurrence of *D. draco* in human-inhabited areas of the islands where, due to its emblematic status, the species has been frequently propagated for traditional or ornamental purposes (Marrero & Almeida Perez, 2012; Almeida Pérez & Beech, 2017). Being a commonly cultivated plant, animal-mediated dispersal has also promoted the establishment of several subspontaneous populations throughout the general distribution area (Almeida Pérez & Beech, 2017). Therefore, human-assisted expansion of *Dracaena* in the Macaronesian region also proves useful for testing emergent patterns in biogeography. There is rising concern that island biogeography is profoundly impacted by human-mediated translocations (Helmus & al., 2014; Graham & al., 2017; Hofman & Rick, 2017), yet the effect of anthropogenic impacts on the phylogeographic pattern of island endemic plants is poorly understood (Hofman & Rick, 2017).

The current lack of molecular information on the MDT also precludes the assessment of the levels of genetic structure as well as a detailed evaluation of the biogeographic diversification of this lineage (e.g., Quézel, 1978; Médail & Quézel, 1999). This lack of information can be partially explained by the relatively recent taxonomic delimitation of the MDT from the rest of the genus, and because previous molecular phylogenetic analyses on *Dracaena* employed only a few accessions (e.g., Bogler & Simpson, 1996). The only molecular phylogenetic investigation with a taxon sampling sufficient to partly evaluate the hypothesis of a Rand Flora distribution pattern was performed by Lu & Morden (2014). However, *D. tamaranae* and most of the subspecies of *D. draco* were not included in their analysis, thus leaving the biogeographic hypotheses untested.

In the present investigation, we aim to evaluate the genetic variability, the phylogeographic structure, and the biogeographic diversification of the MDT using DNA sequence data of the plastid genome. Specifically, we aim to answer the following questions: (i) Is each of the two Macaronesian *Dracaena* species (i.e., *D. draco* and *D. tamaranae*) phylogenetically closer to different *Dracaena* taxa, as suggested by previous biogeographic hypotheses? (ii) When did *Dracaena* populations diverge within Macaronesia and which are the geographic areas of origin of the extant taxa? (iii) How is genetic (haplotype) diversity spatially distributed in the remaining wild populations, and how does human-aided expansion affect the natural pattern? By answering these questions, we will be able to postulate more refined hypotheses on the biogeographic history of this iconic plant group.

■ MATERIALS AND METHODS

Study taxa and sampling approach. — The Macaronesian members of *Dracaena* are currently represented by only a small number of wild populations. The most threatened of these taxa, *D. tamaranae*, exclusively occurs on a few escarpments at the SW sector of the island of Gran Canaria (Canary Islands). It is estimated to comprise as few as 12 mature individuals in the wild, which has led the IUCN to consider this species as critically endangered (CR) (Marrero Rodríguez & al., 2017). *Dracaena draco* subsp. *draco* only occurs naturally in two locations on the island of Gran Canaria and three massifs of the island of Tenerife (Canary Islands) (Almeida Pérez, 2003; Almeida Pérez & Beech, 2017). This taxon is regarded as endangered (EN) by recent conservation assessments, with an estimated total population of 674 mature individuals showing a decreasing trend (Almeida Pérez & Beech, 2017). For *D. draco* subsp. *caboverdeana*, wild populations can be currently found on three of the ten main Cape Verde islands, namely Santo Antão, Sao Nicolãu and Fogo (Marrero & Almeida Perez, 2012), whereas *D. draco* subsp. *ajgal* only occurs within an area of a few square kilometers in the Anti-Atlas mountains (SW Morocco) (Benabid & Cuzin, 1997). However, all of the current distribution areas of the subspecies of *D. draco* have been affected by human translocation, either through the transport of individuals within archipelagos from natural populations to other islands or by moving them to other Macaronesian archipelagos and continental areas ("subspontaneous populations", hereafter; Marrero & Almeida Perez, 2012; Almeida Pérez & Beech, 2017).

Population-level sampling. — For the present investigation, we sampled all known natural populations of the MDT. In each population, leaves were collected from one to five individuals, depending on population size and the accessibility of mature plants. Thus, in each of the *D. draco* populations on the islands of Madeira and Gran Canaria, we collected a sample from the only remaining individual considered to be of natural origin (Almeida Pérez & Beech, 2017). Leaves of *D. tamaranae* were collected from individuals propagated from seeds that were collected in the field and grown at the Jardín Botánico Canario "Viera y Clavijo" (Gran Canaria). In total, 30 individuals representing 14 populations of wild origin were included in our study (see Table 1). In order to appropriately represent the distribution areas of *Dracaena* that originated from human introduction, we additionally sampled individuals from a set of subspontaneous populations. These populations were selected based on the most updated IUCN assessment of the species (Almeida Pérez & Beech, 2017), in which populations are identified as non-natural if individuals occupy anthropogenic habitats or historical records indicate human-mediated introductions. These areas included atypical locations such as the Azores archipelago (island of

Table 1. Information on the Macaronesian *Dracaena* populations sampled in this study, including status of the population.

Taxon	Status	Island / Region	Locality	Collector(s)	Voucher	N	Haplotype/s	*psbJ-petA*	*rpl32-trnL*	*psbD-trnT*
D. tamaranae	W	Gran Canaria (Canary Islands)	Barranco Los Vicentillos	*A. Marrero & R. Almeida s.n.*	LPA34717	3	H1 (3)	LT909428–LT909430	LT909471–LT909473	LT909514–LT909516
D. draco subsp. *draco*	W	Gran Canaria (Canary Islands)	Barranco Alonso	*A. Marrero & R. Almeida s.n.*	LPA18503	1	H2 (1)	LT909406	LT909449	LT909492
D. draco subsp. *draco*	W	Gran Canaria (Canary Islands)	Tirma	*A. Marrero & R. Almeida s.n.*	LPA37237	1	H2 (1)	–	–	–
D. draco subsp. *draco*	I	Gran Canaria (Canary Islands)	Maspalomas	*A. Marrero s.n.*	–	1	H4 (1)	–	–	–
D. draco subsp. *draco*	W	Tenerife (Canary Islands)	Buenavista	*A. Marrero s.n.*	LPA18504	5	H4 (5)	LT909434–LT909437	LT909477–LT909480	LT909520–LT909523
D. draco subsp. *draco*	W	Tenerife (Canary Islands)	Adeje	*A. Marrero s.n.*	LPA18505	1	H3 (1)	LT909438	LT909481	LT909524
D. draco subsp. *draco*	W	Tenerife (Canary Islands)	Chamorga	*A. Marrero s.n.*	LPA37286	3	H5 (3)	LT909431–LT909433	LT909474–LT909476	LT909517–LT909519
D. draco subsp. *draco*	I	La Palma (Canary Islands)	Las Tricias	*A. Marrero s.n.*	LPA34706	2	H4 (2)	–	–	–
D. draco subsp. *draco*	W	Madeira (Madeira)	Ribeira Brava	*A. Marrero & F. Oliva s.n.*	LPA19384	1	H4 (1)	LT909417	LT909460	LT909503
D. draco subsp. (indet.)	I	Madeira (Madeira)	As Neves	*A. Marrero & F. Oliva s.n.*	LPA37252	4	H4 (2) + H6 (2)	LT909413–LT909416	LT909456–LT909459	LT909499–LT909502
D. draco subsp. *ajgal*	W	Anti-Atlas (mainland)	Jbel Imzi	*F. Msanda, C. Harrouni, C. García-Verdugo, J. Caujapé s.n.*	LPA22512	2	H2 (2)	LT909411–LT909412	LT909454–LT909455	LT909497–LT909498
D. draco subsp. (indet.)	I	Anti-Atlas (mainland)	Agadir Ouguejgal	*F. Msanda, C. Harrouni, C. García-Verdugo, J. Caujapé s.n.*	–	3	H2 (1) + H4 (2)	LT909408–LT909409	LT909451–LT909453	LT909494–LT909496
D. draco subsp. *caboverdeana*	W	Santo Antão (Cape Verde)	Matinho	*A. Marrero, F. Oliva, R. Almeida & B. Vilches s.n.*	LPA28880	3	H8 (3)	LT909418–LT909420	LT909461–LT909463	LT909504–LT909506
D. draco subsp. *caboverdeana*	W	Santo Antão (Cape Verde)	Paul	*A. Marrero, F. Oliva, R. Almeida & B. Vilches s.n.*	LPA28863	2	H6 (2)	LT909421–LT909422	LT909464–LT909465	LT909507–LT909508

(Continues)

Table 1. Continued.

Taxon	Status	Island / Region	Locality	Collector(s)	Voucher	N	Haplotype/s	*psbJ-petA*	*rpl32-trnL*	*psbD-trnT*
D. draco subsp. *caboverdeana*	W	Fogo (Cape Verde)	Monte Espia	*A. Marrero*, *F. Oliva*, *R. Almeida* & *B. Vilches s.n.*	LPA28883	2	H7 (2)	LT909402–LT909403	LT909445–LT909446	LT909488–LT909489
D. draco subsp. *caboverdeana*	W	Fogo (Cape Verde)	Relva	*A. Marrero*, *F. Oliva*, *R. Almeida* & *B. Vilches s.n.*	LPA28885	1	H6 (1)	LT909404	LT909447	LT909490
D. draco subsp. *caboverdeana*	W	São Nicolau (Cape Verde)	Cruzetinha	*A. Marrero*, *F. Oliva*, *R. Almeida* & *B. Vilches s.n.*	LPA28913	4	H6 (4)	LT909423–LT909426	LT909466–LT909469	LT909509–LT909512
D. draco subsp. *caboverdeana*	W	São Nicolau (Cape Verde)	Fajã	*A. Marrero*, *F. Oliva*, *R. Almeida* & *B. Vilches s.n.*	LPA28907	1	H6 (1)	LT909427	LT909470	LT909513
D. draco subsp. *caboverdeana*	I	Santiago (Cape Verde)	Santiago	*A. Marrero*, *F. Oliva*, *R. Almeida* & *B. Vilches s.n.*	LPA28915	1	H6 (1)	–	–	–
D. draco subsp. *draco*	I	Iberian Peninsula (mainland)	Cádiz	*A. Marrero* & *J. Caujapé s.n.*	LPA37275	4	H4 (4)	LT909397–LT909400	LT909440–LT909443	LT909483–LT909486
D. draco subsp. *draco*	I	Iberian Peninsula (mainland)	Gibraltar	*A. Marrero* & *J. Caujapé s.n.*	LPA37279	1	H2 (1)	LT909405	LT909448	LT909491
D. draco subsp. *caboverdeana*	I	Iberian Peninsula (mainland)	Lisbon	N.A.	–	1	H6 (1)	LT909407	LT909450	LT909493
D. draco subsp. *caboverdeana*	I	Pico (Azores)	Pico	N.A.	LPA26144	1	H6 (1)	LT909396	LT909439	LT909482

All sequences have been newly generated in this study.
(W = wild, I = subspontaneous / introduced), geographic location, number of individuals sampled (N), collector(s) and herbarium vouchers, haplotypes (number of individuals of each haplotype are indicated in parentheses), and GenBank accessions of the three plastid regions (*psbJ-petA*, *rpl32-trnL*, *psbD-trnT*) sequenced.

Pico) and the Iberian Peninsula (Gibraltar, Cádiz, Lisbon), as well as new populations within the areas previously represented by samples of wild origin (Madeira, Canary Islands, Cape Verde, mainland Morocco). A total of 18 individuals were sampled to represent 9 subspontaneous populations (Table 1).

Sampling of Macaronesian taxa and putative sister species. — To perform phylogenetic reconstructions of the target MDT in an ample taxonomic context, we aimed to combine our new DNA sequence data with the dataset of *Dracaena* and other closely related species (N = 101) as compiled by Lu & Morden (2014). To that end, we focused our taxon sampling on the core dragon tree group, with one specimen representative of each of the MDT previously collected in the field and one specimen of those *Dracaena* taxa hypothesized to be their closest relatives (*D. cinnabari*, *D. ombet*, *D. schizantha*, *D. serrulata*; Marrero & al., 1998). The African and Asian taxa of *Dracaena* that were either suggested to be members of the core dragon tree group (*D. cochinchinensis* (Lour.) S.C.Chen, *D. ellenbeckiana*; Bramwell, 1985; Wilkin & al., 2012) or recovered as sister to *D. draco* (*D. aubryana* Brongn. ex E.Morren; Lu & Morden, 2014) by previous investigations were also included in our taxon sampling. With the exception of the subspecies of *D. draco*, leaf material for molecular phylogenetic analysis was obtained from plants grown in botanic gardens (Appendix 1).

DNA extraction. — Most species of *Dracaena* display thick, leathery leaves that retain water for long time periods, which affects plant tissue conservation even if placed in silica gel. To desiccate leaf samples for subsequent DNA extraction, we cut two or three leaves of each individual into pieces of 2 cm^2 and dried them on a laboratory bench for approximately one week before storing them in a bag of silica gel until DNA extraction. Between 30 and 50 mg of dried leaf material was ground in a MM200 mixer mill (Retsch, Haan, Germany), and genomic DNA was extracted from the leaf powder using the protocol described in Dellaporta & al. (1983). In a second step, DNA extractions were purified using the UltraClean PCR Clean-up kit (MoBio Laboratories Carlsbad, California, U.S.A.). The final DNA concentration and quality of the isolations were confirmed with a Nanodrop 2000 spectrophotometer (Thermo Fisher Scientific, Wilmington, Delaware, U.S.A.). Aliquots with a concentration of 50 ng/µl were stored for further processing.

Phylogenetic analysis: DNA marker selection, sequencing and combination with published data. — We aimed to generate new DNA sequences and combine them with previously generated sequence data in order to compile datasets suitable for the phylogenetic reconstruction of the MDT. Specific emphasis was hereby placed on the integration of high-quality DNA sequences of previous studies while simultaneously exercising caution regarding sequence misidentification. A cautious approach was particularly warranted due to concerns regarding the misidentification of the sequences generated by Lu & Morden (2014). Their investigation generated a great number of DNA sequences of *Dracaena* species, yet some of them were found to be dissimilar to those generated in this and other studies, despite representing the same taxa. Given the observed discrepancies, we confirmed the validity of our own sequences by repeating the DNA sequencing for selected taxa while starting from new DNA extractions. We obtained DNA sequences that were consistent with our previous sequence data, yet were dissimilar to those of Lu & Morden (2014). A potential confusion in taxon identity among the sequences of Lu & Morden (2014) is also indicated by conflicts of their results with the current taxonomic classification of *Dracaena*, as species considered to be close relatives (e.g., *D. ombet* and *D. schizantha* [syn. *D. ombet* subsp. *schizantha* (Baker) Bos; see Klimko & al., 2018]) were recovered in distantly related clades in their analyses. Other investigations (Jankalski, 2015; Takawira-Nyenya & al., 2018) have also reported concerns regarding potential species misidentification and sequence errors by Lu & Morden (2014). Based on these observations, we forewent the combination of our sequences with those generated by Lu & Morden (2014).

As an alternative approach, we amplified and sequenced four plastid DNA markers that appeared unaffected by species misidentification and low sequence quality in previous investigations. Specifically, we focused on the intergenic spacers *trnQ-rps16* and *rpl32-trnL*, as well as the genes *rbcL* and *matK* of the plastid genome. For each sequence sample, forward and reverse chromatograms were assembled to a consensus sequence using Bioedit v.7.2.5 (Hall, 1999). Final DNA sequences were inspected by eye and then submitted to the European Nucleotide Archive (http://www.ebi.ac.uk/ena/) upon conversion to checklist files using the software tool EMBL2-checklists (Gruenstaeudl & Hartmaring, 2019) (see Table 1).

Corresponding sequences of *Dracaena* of the same DNA markers from other studies were obtained from the European Nucleotide Archive (https://www.ebi.ac.uk/ena) and combined with our newly generated sequences in two different datasets. The combined matrix of the two plastid genes (*rbcL*, *matK*) was used to build the "Phylogen-1" dataset (N = 38 accessions, 22 taxa; Appendix 1), and the combined matrix of all four plastid DNA markers (*rbcL*, *matK*, *trnQ-rps16*, *rpl32-trnL*) constituted the "Phylogen-2" dataset (N = 12 accessions, 12 taxa; Appendix 1). In both datasets, DNA sequences of *Liriope muscari* (Decne.) L.H.Bailey (Asparagaceae) were included, which acted as an outgroup taxon in accordance with previous results on phylogenetic relationships among the Asparagaceae (e.g., Bogler & Simpson, 1996).

All sequences of the same plastid marker were trimmed to the same length and then aligned using MAFFT v.7.304b (Katoh & Standley, 2013) under default settings. Upon alignment, the individual plastid markers were concatenated into the datasets Phylogen-1 and Phylogen-2, respectively. During concatenation, information on marker length was maintained and written into the resulting NEXUS files, thus generating partitioned DNA matrices (suppl. Appendices S1 & S2).

Phylogenetic analysis: statistical methods. — Phylogenetic reconstructions were performed on both datasets via maximum likelihood (ML) and Bayesian phylogenetic inference (BI), using one data partition per DNA marker. Analyses via ML were conducted with RAxML v.8.2.9 (Stamatakis, 2014), using the nucleotide substitution model GTRGAMMAI for both partitions and the thorough ML optimization option. Branch support for ML analyses was calculated via 1000 bootstrap (BS) replicates. Analyses via BI were conducted with MrBayes v.3.2.5 (Ronquist & Huelsenbeck, 2003) under model GTR + I + Γ for both partitions, using four parallel Markov chain Monte Carlo (MCMC) runs and collecting a total of 50 million MCMC generations. Independent sampling of generations and convergence of Markov chains were confirmed via Tracer v.1.7 (Rambaut & al., 2018). The initial 50% of all MCMC trees were discarded as burn-in, and post burn-in trees were summarized as a maximum clade credibility tree, with branch support given as posterior probability (PP) values.

Phylogeographic analysis: DNA marker selection and sequencing. — To analyze the patterns of molecular diversity within Macaronesia, we initially screened 10 plastid regions following Shaw & al. (2007) by sequencing a subset of samples that included at least one specimen of each Macaronesian taxon. Most tested markers revealed genetic differentiation between *D. tamaranae* and *D. draco* s.l., but polymorphism was far less frequent among the subspecies of *D. draco*. In order to perform a phylogeographic analysis, we selected three plastid regions (*psbJ-petA*, *rpl32-trnL*, *psbD-trnT*) that displayed genetic variation within *D. draco* (suppl. Table S1). One specimen of *Dracaena* that represented an appropriate outgroup for the clade composed of the Macaronesian taxa (*D. ellenbeckiana*) was also sequenced. Forward and reverse contigs for each plastid region and sample were assembled into a consensus sequence using Bioedit v.7.2.5 (Hall, 1999). The concatenated sequences of the three plastid regions were employed to build the "Phylogeog-1" dataset (N = 31 accessions).

Phylogeographic analysis: estimates of genetic variability and human impact. — To infer the genetic relationships between the haplotypes contained in the Phylogeog-1 dataset, we constructed a maximum parsimony network based on the median joining algorithm implemented in the software Network v.4.5.1.0 (Bandelt & al., 1999). Genetic diversity estimates at both the population and island scales were calculated via Nei's unbiased haplotype diversity (*h*) (Nei, 1978) and the total number of haplotypes (*H*). Due to our interest in providing a comparative framework for assessing the levels of genetic diversity observed in the threatened MDT, we additionally performed a bibliographic search via the Web of Science (https://apps.webofknowledge.com, Clarivate Analytics). Different combinations of the terms "haplotyp* diversity", "gen* diversity", "plastid", "chloroplast", "phylogeogr*", "plant", "Macaronesia*", "island", "Cape Verde", and "Canar*" were employed in the search. Only those publications in which (i) the population sampling covered the entire distribution of the study species, and (ii) the number of plastid DNA markers assayed was equal or higher than three were retained for extracting data of interest such as haplotype frequency, number of plastid markers, and sample sizes.

The impact of human-mediated translocations on the patterns of genetic structure and phylogeographic signal in *Dracaena* was tested by comparing the results obtained for the Phylogeog-1 dataset with those obtained for an expanded data matrix which included the sequences generated for subspontaneous populations ("Phylogeog-2" dataset, N = 49 accessions). Our expectation was that human-mediated translocation of haplotypes should have blurred any biogeographic signal associated with geographic island isolation across the natural distribution of MDT (Helmus & al., 2014): i.e., low phylogeographic structure when subspontaneous populations are considered.

To test this expectation, we first conducted an AMOVA with the software Arlequin v.3.5.2 (Excoffier & Lischer, 2010) to examine how haplotype diversity was hierarchically structured within regions, among islands (within regions) and within islands. Three (Canary Islands + Madeira, Cape Verde islands, and mainland Morocco) or four (all the previous + the Iberian Peninsula) regions were considered for the analysis of "wild" or "wild + subspontaneous" populations, respectively. The AMOVA was performed in two independent runs using each of the datasets. Similarly, two independent runs of the software PERMUT v.1.2.1 (Pons & Petit, 1996) with input files extracted from both datasets were used to compare the effect of subspontaneous populations on the phylogeographic signal of *Dracaena* in Macaronesia. This software calculates two parameters: GST, as a measure of genetic differentiation based on haplotype frequencies, and NST, which additionally accounts for phylogenetic distance between haplotypes. A phylogeographic signal was detected if NST > GST, following 1000 permutation tests (Pons & Petit, 1996).

Temporal framework and ancestral area reconstructions at different geographic scales. — Since we were interested in examining the inferred patterns of genetic divergence in *Dracaena* within an explicit temporal framework, we ran dating analyses using BEAST v.1.8.4 (Drummond & al., 2012). The analyses were conducted at broad and regional geographic scales using the Phylogen-2 and Phylogeog-1 datasets, respectively. In both cases, we merged identical sequences into unique haplotypes using the online fasta sequence toolbox FaBox v.1.4 (Villesen, 2007) before all subsequent analyses because inclusion of identical sequences results in many zero length branches at the tip of the tree and can cause the model to oversplit the dataset (Reid & Carstens, 2012). Then, each dataset was analyzed with PartitionFinder v1.1.1 (Lanfear & al., 2012) to select the best partitioning scheme, using the greedy algorithm with linked branch lengths under the Bayesian information criterion. One partition was defined for each dataset, with the four plastid regions of the Phylogen-2 dataset distributed into two

partitions (*rbcL*: K80, *matK* + *rpl32-trnL* + *trnQ-rps16*: HKY + Γ), and three plastid regions of the Phylogeog-1 dataset combined (HKY).

We then ran BEAST analyses for four independent chains of 50 million generations each, sampling every 10^4 generations. While each plastid partition was assigned to a strict and uncorrelated lognormal relaxed clock model for the Phylogen-2 dataset, a strict clock model was applied to the Phylogeog-1 dataset. Under the different clock models, a mean rate of 5.0×10^{-4} substitutions/site/Myr with a standard deviation of 1.0×10^{-4}, sampled from a normal distribution (Palmer, 1991), was considered. Bayesian reconstructions were conducted under four different tree priors, including speciation models defined by Yule and birth–death Process priors, as well as coalescent models implemented by constant size and Bayesian skyline priors. Convergence and mixing of the four chains were assessed by checking that all parameters had reached stationarity and sufficient (>200) effective sample sizes using Tracer v.1.7 (Rambaut & al., 2018), and 10% trees were discarded as burn-in. Finally, we compared the posterior distributions of each combination of clock and tree priors using the marginal likelihood estimate (MLE) of each model, estimated from stepping-stone sampling and path sampling. We estimated MLE with 150 path steps, each with a chain length of one million iterations, and the other parameters were set by default. We directly calculated the log-Bayes factors (BF) from MLEs and used BF to compare the support of all the models tested. We considered BF values above 2 to indicate that one model was significantly favored over another. Based on BF, the uncorrelated lognormal relaxed clock (Phylogen-2; suppl. Table S2) and the strict clock (Phylogeog-1; suppl. Table S3) models were selected, in both cases under a coalescent constant size tree model. The two resulting maximum clade credibility (MCC) trees were employed in the subsequent analyses.

To estimate the geographic origin of the MDT, we used the package BioGeoBEARS v1.1 (BioGeography with Bayesian Evolutionary Analysis in R Scripts; Matzke, 2014) implemented in R v.3.5.1 (R Core Team, 2017). Since different approaches to estimate ancestral areas are based on different assumptions and can produce variable results (Matzke, 2013, 2014), we tested the likelihood of the three biogeographic models available in BioGeoBEARS: DEC (dispersal-extinction-cladogenesis), DIVALIKE (dispersal-cicariance) and BAYAREALIKE (Bayesian BayArea). BioGeoBEARS allows the use of the model that includes dispersal and extinction as free parameters and a model (DEC + J) that includes an additional parameter J taking founder event speciation into account (Matzke, 2014, and references therein). However, Ree & Sanmartín (2018) recently reported that "the DEC+J is a poor model of founder event speciation, and statistical comparisons of its likelihood with DEC are inappropriate". They suggested that, for simple inference of ancestral ranges on a fixed phylogeny, "a DEC-based model may be defensible if statistical model selection is not used to justify the choice", and we therefore refrained from using the DEC + J in our study. Depending on the dataset, we considered the following geographical regions: West Africa, East Africa, Asia and Macaronesia for Phylogen-2 and, following Marrero & al. (1998), Cape Verde, Canary Islands, Madeira, Morocco and East Africa for Phylogeog-1. Lineage distributions were coded as present or absent in each of the four or five areas, respectively. We set the maximum number of areas to three, as none of the taxa is distributed over more than two of the defined areas. Finally, we estimated ancestral areas on internal nodes of each *Dracaena* MCC tree from the divergence time analysis, and the likelihood values of each of the three BioGeoBEARS models were subsequently compared using the Akaike information criterion corrected for small sample size (AICc; Matzke, 2013, 2014). The analyses showed that DIVALIKE was the best model for both datasets (suppl. Tables S4, S5).

■ RESULTS

Molecular analysis of the core dragon tree taxa. — Our analyses using the Phylogen-1 dataset did not recover strongly supported clades by either ML or BI methods that may help elucidate the phylogenetic relationships of the Macaronesian taxa (suppl. Fig. S1). The largest, best-supported clade (BS = 0.94) from this analysis encompassed mostly African *Dracaena* species in a derived position within the phylogenetic tree. The tree topology generally suggested the monophyly of MDT (*D. tamaranae* sister to *D. draco* s.l; BS = 0.76) and a substantial phylogenetic distance between MDT and the congeneric taxa hypothesized to be their closest relatives (*D. cinnabari*, *D. ombet*, *D. schizantha*, *D. serrulata*; suppl. Fig. S1).

The pattern weakly supported by the former dataset was reinforced by the results of the phylogenetic analyses performed on the Phylogen-2 dataset (Fig. 2). In this case, *D. tamaranae* was recovered as sister to all *D. draco* taxa with strong support (BS = 100, PP = 1.0), whereas *D. serrulata*, *D. schizantha* and *D. ombet* constituted a phylogenetically distant subclade (BS = 98, PP = 1.0). The relationship of *D. cinnabari* as sister to this latter subclade was weakly supported (BS = 76, PP = 0.89). Our analyses, however, did not clearly identify the closest relative of the *D. tamaranae–D. draco* subclade: the sister position of the Asian *D. cochinchinensis* received poor statistical support (BS = 0.56, PP = 0.60). Furthermore, all these latter taxa plus the African *D. aubryana–D. ellenbeckiana* constituted a clade (BS = 87, PP = 1.0) clearly differentiated from the putative East African–Arabian relatives of the MDT (Fig. 2).

BioGeoBEARS results showed that deep nodes in our phylogenetic reconstructions were subjected to high biogeographic uncertainty (Fig. 2). However, a Macaronesian origin for the *D. tamaranae–D. draco* subclade (including the mainland taxon *D. draco* subsp. *ajgal*) and an East African–Arabian origin for the *D. serrulata–D. ombet* s.l. subclade were strongly supported. Dating analyses suggested that

diversification in the East African–Arabian subclade probably started before (i.e., around the late Miocene) diversification in the MDT subclade (Fig. 2).

Regional-scale analyses of Macaronesian *Dracaena* taxa. — Sequencing of 2600 bp of plastid DNA revealed eight haplotypes among MDT samples (suppl. Table S1, Fig. 3A). Haplotype distribution was generally restricted to specific taxonomic groups: the three sampled individuals of *D. tamaranae* displayed one private haplotype; *D. draco* subsp. *caboverdeana*, three private haplotypes; and *D. draco* subsp. *draco*, four haplotypes, but one of these (haplotype H2) was shared with *D. draco* subsp. *ajgal* (Table 1, Fig. 3B). In contrast, geographic structure of haplotypes was less evident within *D. draco*, as half of these showed widespread distributions. Thus, haplotype H6 was found on three islands of the Cape Verde archipelago (Fig. 3D), haplotype H4 on Tenerife and Madeira (Fig. 3C), and haplotype H2 on Gran Canaria and mainland Morocco (Fig. 3B,C).

Considering the number of taxa sampled and their geographic distribution, our results suggested that levels of genetic diversity were low for MDT (Fig. 3B). This observation was reinforced by our literature review. We found that Macaronesian species with large distribution areas (i.e., those occurring on more than tree islands such as *Olea*, *Kleinia*, *Cistus* or *Periploca*) displayed the highest levels of plastid DNA diversity (Table 2). In contrast, our focal taxa (*D. draco* subsp. *draco*, *D. draco* subsp. *caboverdeana*) were ranked among the Macaronesian island taxa with the lowest intra-population and total haplotype diversity analyzed thus far (Table 2).

In line with the results obtained with the Phylogen-2 dataset, BioGeoBEARS revealed a high probability of a Canarian origin for the *D.tamaranae–D. draco* clade based on the analysis of sequence data generated at the regional scale (Fig. 4). However, the results showed a low probability of a single ancestral range for the *D. draco* subclade: node C received combined support for the Cape Verde and Canary Islands (Fig. 4). Dating analyses suggested that the split between *D. tamaranae* and *D. draco* may have started in the Plio-Pleistocene (node B: 2.3 [0.7– 5.8] Myr; Table 3), whereas

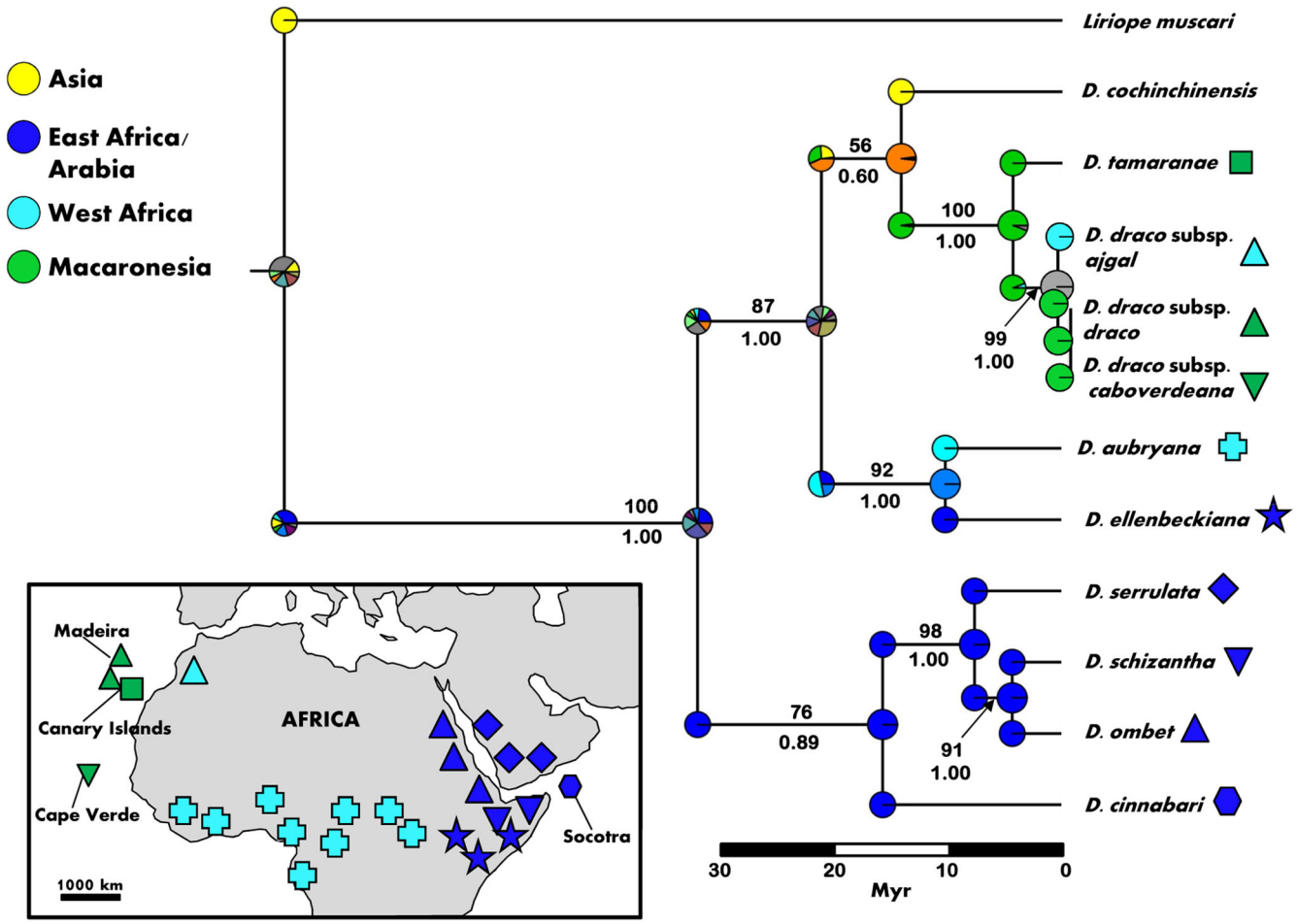

Fig. 2. Phylogenetic reconstructions based on maximum likelihood and Bayesian inference, and estimation of ancestral distributions based on BioGeoBEARS using the Phylogen-2 *Dracaena* dataset. Numbers next to branches indicate statistical (above = bootstrap, below = posterior probability) support. Pie charts on each node depict the relative probabilities of ancestral ranges, which are represented by colors. The map in the inset shows the distribution of the African and Arabian taxa of *Dracaena* included in the analyses. Main parameters: $d = 0.0042$; $e = 1.00E\text{-}12$; LnL = −18.74.

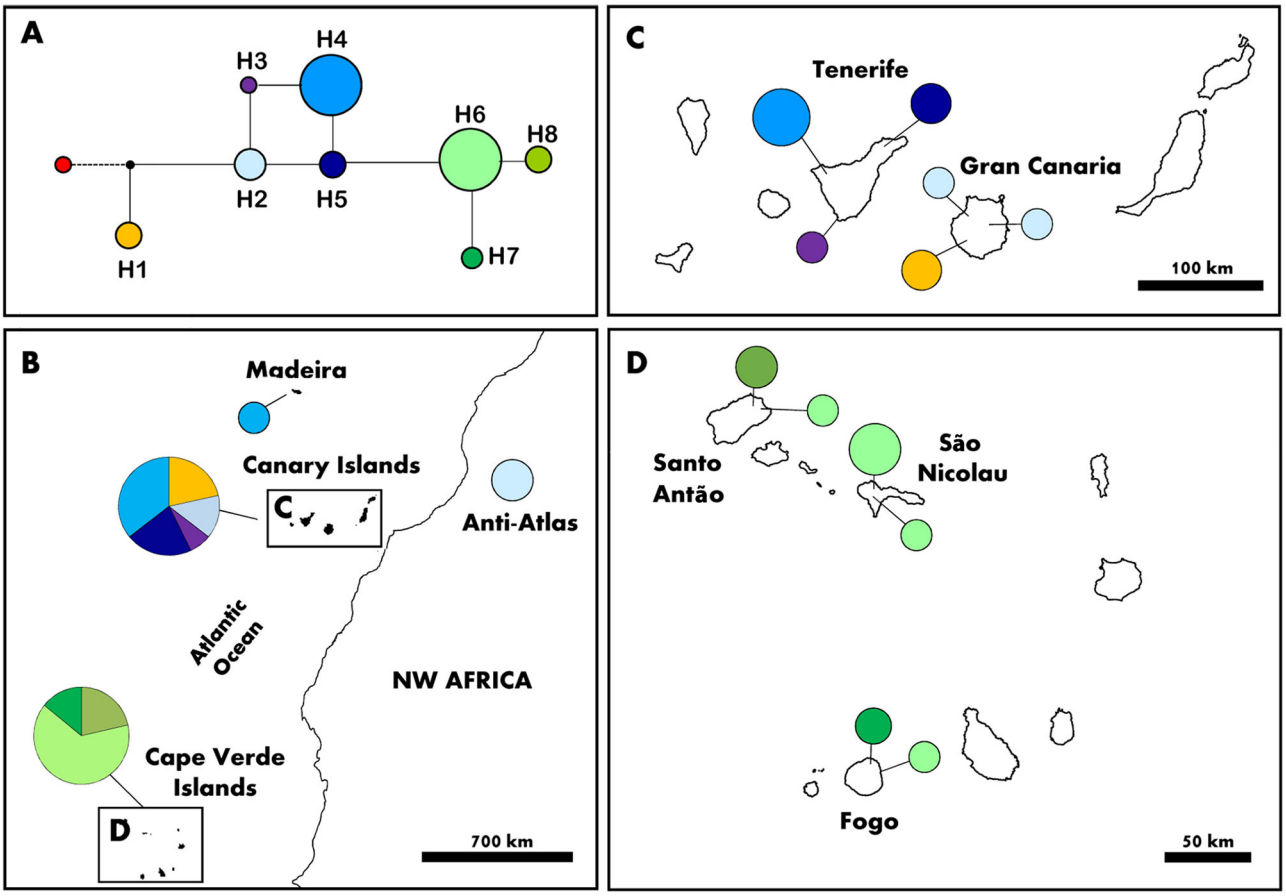

Fig. 3. Parsimony haplotype network (**A**) based on three plastid (*psbJ-petA*, *rpl32-trnL*, *psbD-trnT*) regions and distribution of haplotypes across wild populations of *Dracaena* taxa in Macaronesia (**B**), Canary Islands (**C**) and Cape Verde islands (**D**). The size of each pie chart corresponds with the sample size of each population or geographic area.

Table 2. Levels of plastid genetic diversity (h = unbiased haplotype diversity; H = number of haplotypes) of Macaronesian plant taxa at different spatial scales (POP = population, ISL = island, TOT = total) following a literature review.

Taxon	Area	#pops. (ind.)	#reg. (bp)	h_{POP}	H_{POP}	h_{ISL}	H_{ISL}	H_{TOT}	Ref.
Olea cerasiformis	CI	9 (101)	5 (1.5K)	0.55 (0.05)	3.3 (0.3)	0.71 (0.04)	5.3 (1.1)	11	1
Kleinia neriifolia	CI	18 (80)	3 (2.5K)	0.54 (0.07)	2.4 (0.2)	0.52 (0.11)	3.3 (0.6)	16	2
Cistus monspeliensis	CI	25 (90)	3 (1.9K)	0.40 (0.08)	1.7 (0.2)	0.67 (0.05)	4.0 (0.7)	16	3
Periploca laevigata	CI	16 (80)	3 (2.8K)	0.23 (0.09)	1.6 (0.3)	0.17 (0.09)	2.8 (1.1)	14	4
Canarina canariensis	CI	16 (144)	3 (2.2K)	0.22 (0.07)	1.8 (0.2)	0.30 (0.11)	2.8 (1.1)	10	5
Euphorbia lamarckii	CI	6 (32)	3 (2.0K)	0.21 (0.15)	1.7 (0.5)	0.32 (0.18)	2.3 (0.9)	8	6
Periploca laevigata	CV	3 (15)	3 (2.8K)	0.20 (0.20)	1.3 (0.3)	0.47 (0.23)	1.5 (0.5)	3	4
Euphorbia regis-jubae	CI	4 (23)	4 (2.0K)	0.15 (0.14)	1.3 (0.3)	0.11 (0.10)	1.3 (0.3)	2	6
Umbilicus schmidtii	CV	7 (20)	3 (1.4K)	0.09 (0.08)	1.1 (0.1)	0.45 (0.15)	1.5 (0.3)	5	7
Dracaena draco subsp. *caboverdeana*	CV	6 (13)	3 (2.6K)	0.00 (0.00)	1.0 (0.0)	0.42 (0.21)	1.7 (0.3)	3	8
Dracaena draco subsp. *draco*	CI	5 (11)	3 (2.6K)	0.00 (0.00)	1.0 (0.0)	0.32 (0.31)	2.0 (1.0)	4	8
Echium stenosiphon	CV	9 (15)	5 (2.7K)	0.00 (0.00)	1.0 (0.0)	0.00 (0.00)	1.0 (0.0)	3	9

Number of populations and individuals, number of plastid regions analyzed, and geographic area (CI = Canary Islands, CV = Cape Verde Islands) are detailed for each case. Diversity indexes are expressed as mean values with standard errors in parentheses. Taxa are ranked according to decreasing levels of haplotype diversity. References: (1) García-Verdugo & al., 2010; (2) García-Verdugo & al., 2019a; (3) Coello & al., 2020; (4) García-Verdugo & al., 2017; (5) Mairal & al., 2015; (6) Sun & al., 2016; (7) Romeiras & al., 2015; (8) This study; (9) Romeiras & al., 2011

diversification within *D. draco* was placed within the Pleistocene (node C: 1.4 [0.4–3.6] Myr; Table 3).

Effect of human-mediated translocation of *Dracaena draco* within Macaronesia. — As expected, sequencing of individuals from subspontaneous populations did not render any new haplotype (Table 1). The AMOVA conducted with the Phylogeog-1 dataset (i.e., wild populations alone) revealed subtle, albeit significant, genetic structure among geographic areas (11% of total genetic variance), but this hierarchical level was no longer significant when subspontaneous populations (Phylogeog-2 dataset) were included in the analysis (Table 4). Subspontaneous populations thus favored genetic homogenization of *D. draco* across spatial scales by increasing the component of within-island haplotype diversity (from 44.3% of explained variance for Phylogeog-1 to 55.6% for the Phylogeog-2 dataset; AMOVA results, Table 4). As a result, inclusion of these populations caused an overall weak genetic structure (GST), but contrary to our expectation, the recurrent translocation of the same haplotypes resulted in a similar NST between both datasets (PERMUT results, Table 4). This pattern ultimately prompted a significant phylogeographic signal (NST > GST) that was not detected when wild populations were considered alone (Table 4).

Our results indicated that only two of the eight haplotypes detected in MDT have been extensively spread by human intervention: haplotype H6, originally private to the Cape Verde Islands, has been introduced to the island of Santiago

Table 3. Mean and 95% high posterior density (HPD) of divergence time estimates for each of the clades with high (PP > 0.9) statistical support, as inferred from BEAST analysis of Macaronesian *Dracaena* haplotypes.

Clade	Mean (Myr)	95% HPD (Myr)
A	11.8	4.9–16.3
B	2.3	0.7–5.8
C	1.4	0.4–3.6
D	0.5	0.1–1.5
E	0.1	0.0–0.7

Definition of clades follows Fig. 4.

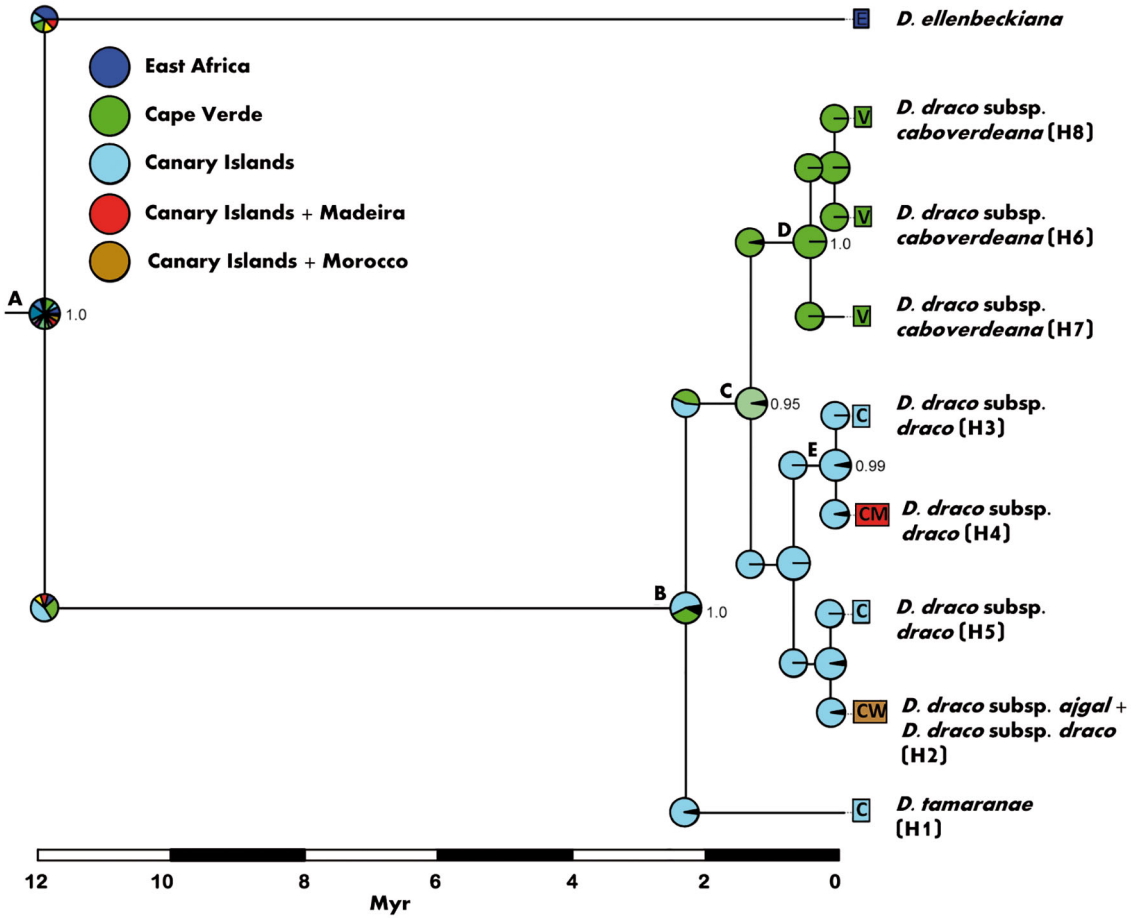

Fig. 4. BioGeoBEARS estimation of ancestral distributions of the Macaronesian *Dracaena* taxa based on the MCC tree resulting from BEAST analysis of the Phylogeogr-1 dataset. Numbers at nodes indicate posterior probabilities. Pie charts on each node depict the relative probabilities of ancestral ranges, which are represented by colors. C: Canary Islands; M: Madeira; V: Cape Verde; W: Morocco; E: East Africa. Main parameters: three areas maximum; $d = 0.091$; $e = 0.062$; LnL = −16.57.

Table 4. Results of the AMOVA and PERMUT analysis considering haplotype composition of wild populations alone (Phylogeog-1 dataset) and wild + subspontaneous populations together (Phylogeog-2).

	AMOVA					PERMUT		
Dataset	Source of variation	Df	Var Comp	%VAR	Fixation index	NST	GST	NST > GST
Phylogeog-1	Among regions	2	0.27	11.5	0.12**	0.637	0.608	No^{ns}
	Among islands (regions)	4	1.02	44.2	0.56***			
	Within islands	23	1.02	44.3	0.50***			
Phylogeog-2	Among regions	3	0.11	6.6	0.07^{ns}	0.491	0.340	Yes*
	Among islands (regions)	6	0.64	37.8	0.44***			
	Within islands	34	0.95	55.6	0.41***			

The hierarchical level "Region" includes the Canary Islands, Cape Verde, mainland Morocco (Phylogeog-1) and the Iberian Peninsula (Phylogeog-2). Df = degrees of freedom, VarComp = variance component, %VAR = percentage of explained genetic variance, NST = genetic differentiation considering genetic distances among haplotypes; GST = genetic differentiation based on allele frequencies (i.e., assuming that all haplotypes are equally divergent)
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns = non significant

(Cape Verde), Madeira, Azores (island of Pico), and mainland Iberian Peninsula (Lisbon); haplotype H4, most frequently found in NW Tenerife, has been introduced to other Canary Islands where it does not naturally occur (La Palma, Gran Canaria), in addition to two locations sampled in the mainland (SW Morocco, Cádiz) (suppl. Fig. S2).

■ DISCUSSION

Biogeographic connections of the Macaronesian *Dracaena* taxa. — Our phylogenetic and biogeographic results consistently rejected the long-held idea that the East African–Arabian *Dracaena* species (*D. cinnabari*, *D. ombet*, *D. schizantha*, *D. serrulata*) represent the closest relatives of the MDT (Quézel, 1978; Marrero & al., 1998; Sanmartín & al., 2010; Del Arco Aguilar & Rodríguez Delgado, 2018). None of our molecular reconstructions confidently recovered the sister-group relationship of Macaronesian and East African lineages that has sustained the Rand Flora pattern in other study cases (e.g., Thiv & al., 2010; Pokorny & al., 2015; Villaverde & al., 2018). Rather, the results of the first molecular analysis jointly considering the two Macaronesian species, *D. tamaranae* and *D. draco*, strongly supported (i) their sister relationship and (ii) a Macaronesian origin for the lineage that they both constitute. Our findings are at odds with previous interpretations of independent biogeographic connections of *D. tamaranae* and *D. draco* (Marrero & al., 1998), but are in line with the notable similarities recently reported in leaf anatomy between both species when compared to the rest of taxa included in the dragon tree group (Klimko & al., 2018).

Our study therefore represents a new case of lack of molecular support to early proposals regarding Rand Flora disjunctions (see Andrus & al., 2004). Divergence time estimates for the MDT, in addition, suggested a younger origin of their recent common ancestor (Plio-Pleistocene; Table 3) than the most comprehensive age estimates of the Sahara desert (Zhang & al., 2014). Although continental aridification may thus have played a minor role in the differentiation of the MDT lineage (cf. Sanmartín & al., 2010), its geographic link remains elusive. Hence, the closest living relative(s) of this species pair could not be identified with confidence by our molecular reconstructions. However, in keeping with recent morphological (Wilkin & al., 2012; Klimko & al., 2018) and phylogenetic (Takawira-Nyenya & al., 2018) studies, our results pointed to a *Dracaena* clade composed of taxa with disparate geographic distributions (including Asian species and, to a lesser extent, the African *D. ellenbeckiana*) that could qualify as potential sister species. Increased taxon and molecular sampling in future phylogenetic analyses, coupled with in-depth paleobotanic investigations (Denk & al., 2014), are needed to shed more light on the biogeographic connections of the Macaronesian dragon tree lineage. Concerning extended taxon sampling in forthcoming studies, the SE Asian group deserves particular consideration since our sampling considered only one out of the five species described (Wilkin & al., 2012).

Biogeographic history of *Dracaena* within Macaronesia. — Our analyses suggested a complex biogeogeographic scenario to satisfactorily explain the observed genetic pattern of *Dracaena* across Macaronesian populations. Thus, based on the higher levels of genetic diversity detected in the insular populations than in the mainland, we found support for the idea that the Atlantic islands might have served as a refuge for this plant lineage (Marrero & al., 1998). Additionally, our results highlighted the role of the Canary Islands as a relatively recent source of biodiversity to other Macaronesian areas, including the neighboring mainland (Carine & al., 2004; Caujapé-Castells & al., 2017). The Canarian refuge hypothesis for *Dracaena* is further suggested by two additional lines of evidence. Our biogeographic analyses (Fig. 2) and the central position of Canarian haplotypes in the parsimony network (Fig. 3A) identified these island populations

as ancestral, whereas the concentration of haplotype diversity (five haplotypes) within this area may be indicative of longer residence times than in the rest of the extant distribution range (Mairal & al., 2015; Coello & al., 2020).

Considering the crown age of the Macaronesian lineage and its associated uncertainty (node C; Fig. 4, Table 3) (García-Verdugo & al., 2019b), dating analyses suggested a period of island residence for *Dracaena* since the Plio-Pleistocene. Such an estimate agrees well with the discovery of fossil dragon tree imprints dating back to the late Pliocene (Marrero, 2013). Under the temporal framework depicted by fossil and molecular data, it is quite probable that, following successful dispersal, the islands provided *Dracaena* with habitat suitability throughout episodes of widespread extinction, such as those derived from Quaternary climatic oscillations (reviewed in García-Verdugo & al., 2019c; see also Schüßler & al., 2019).

In turn, extant populations outside the putative source area represented by the Canarian islands (Cape Verde, Madeira, mainland Morocco) may have been the result of different episodes of dispersal during the Quaternary. Hence, dating analyses suggested that diversification of *D. draco* subsp. *caboverdeana* started in the middle Pleistocene (Fig. 4, Table 3), i.e., much later than the inferred primary colonization of Macaronesia. This result, in addition to limited morphological (Marrero & Almeida Perez, 2012) and genetic (Fig. 3A, suppl. Table S1) divergence from *D. draco* subsp. *draco*, is indicative of ongoing allopatric differentiation between both taxa. Although the exact geographic origin of Cape Verde populations remains unclear (i.e., a combined ancestral area for the most recent common ancestor of *D. draco* s.l., Canary Islands + Cape Verde in Fig. 4), our biogeographic analyses found strong support for a Canarian origin for the shared common ancestor (i.e., stem branch) of the *D. draco* and *D. tamaranae* populations. Alternatively, our results are compatible with a scenario of independent episodes of archipelago colonization from the mainland (i.e., the Canaries in the Plio-Pleistocene, Cape Verde in the Pleistocene), but extinction on the mainland should be invoked. Sunding (1979), for instance, cited *Dracaena* as an example of colonization of the Cape Verde archipelago by African source populations already extinct in the mainland; he regarded as unlikely the alternative of dispersal from an area located 1400 km away to the north (i.e., direct dispersal from the Canarian archipelago). The impact of extinction on mainland and easternmost island populations of *Dracaena* during the Pleistocene probably limits the accuracy of our biogeographic reconstructions at regional scales (García-Verdugo & al., 2019c), but what the information available to date clearly rules out is the possibility that the extant mainland population could have acted as a direct source of Cape Verde colonizers (Figs. 3B, 4).

The two other populations geographically peripheral to the Canary Islands were inferred as the youngest. The relatively recent split between the only *Dracaena* haplotype that naturally occurs on Madeira (plus Tenerife; haplotype H4) and haplotype H3 (private to Tenerife), provides another example of the colonization route that links the central Canaries with this latter archipelago (e.g., Jones & al., 2014; Valtueña & al., 2017). In addition, our results are in sharp contrast with the view of SW Morocco as a refuge area for *D. draco* subsp. *ajgal* (Médail & Quézel, 1999). Lack of private haplotypes and the BioGeoBears results suggesting a Canarian origin for *D. draco* s.l. both coincide with Marrero & al.'s (1998) contention that subspecies *ajgal* may be a taxon at early stages of speciation, i.e., in light of our results, a subpopulation experiencing recent allopatric differentiation from the island source area.

Extant genetic patterns of *Dracaena* in Macaronesia: implications for conservation. — Our literature review evidenced that levels of haplotype diversity in extant Macaronesian populations of *Dracaena* are remarkably low. While our results may be an underestimation due to small within-population sample sizes or other sampling biases (Waples & Yokota, 2007), the first assessment of genetic diversity in this lineage strongly relates extinction threat due to population decline (Almeida Pérez & Beech, 2017; Marrero Rodríguez & al., 2017) to limited genetic variability. Furthermore, our preliminary results revealed a marked population-specific haplotype composition, particularly among wild Canarian populations (Fig. 3C), but more variable markers are needed to better characterize the levels of population genetic diversity and identify provenances for genetic reinforcement (Breed & al., 2013).

Implementing a rigorous assessment of genetic provenance in conservation plans is particularly important in the case of Macaronesian dragon trees. Our analyses showed that the translocation of non-native haplotypes has enhanced genetic diversity within islands, thus causing an artificial phylogeographic signal across distribution areas. Such an expansion of *Dracaena* haplotypes is far from being random. The widespread occurrence of a subset of haplotypes among subspontaneous populations reflects the impact of human activity on the genetic structure of the Macaronesian *Dracaena* taxa. For instance, the most frequent haplotype of subspecies *caboverdeana* (haplotype H6) was the only genetic variant found in introduced areas that belong to Portugal (Lisbon, Madeira, Azores), apart from its natural area of origin in the Cape Verde Islands (a former colony of the Portuguese overseas empire for nearly 500 years). In addition to previous studies in the region (De la Rúa & al., 2001; Saro & al., 2015), our results illustrate that anthropogenic translocation of commercially valuable species may obscure our inferences on island biogeographic patterns.

Conclusions. — Our molecular reconstructions suggested a close genetic relationship between the two extant Macaronesian *Dracaena* species, but they ruled out previous biogeographic hypotheses that postulated a close relationship between this lineage and some geographically distant species. Extinction, however, coupled with limited taxonomic sampling of putative sister species, probably hinders accurate inference on biogeographic patterns in our study group depending on the spatial scale. Thus, broad-scale reconstructions could benefit from a more complete sampling of SE

Asian species, although accurate inferences could be additionally constrained by the loss of putative closely related species (Denk & al., 2014). In turn, haplotype reconstructions at regional scales are probably impacted by extinction of key populations (García-Verdugo & al., 2019c). Despite these limitations, our analyses suggested a Canary Island origin for the MDT lineage, followed by Pleistocene expansion of *D. draco* across Macaronesia that triggered allopatric differentiation (e.g., *D. draco* subsp. *caboverdeana*). However, human-mediated expansion of haplotypes arises as a confounding factor that may be interfering with natural processes of dispersal and differentiation.

■ AUTHOR CONTRIBUTIONS

CG-V and JC-C conceived the project. ID, JC-C, AM and CG-V participated in the study design. AM, JC-C, ID, FM, CH, and CG-V collected the samples. ID and CG-V conducted the laboratory work. MG, JP and CG-V analyzed the data. CG-V wrote the paper with contributions from all co-authors. — MG, https://orcid.org/0000-0002-1666-1773; JP, https://orcid.org/0000-0001-5532-166X; JC-C, https://orcid.org/0000-0003-0600-1496; CG-V, https://orcid.org/0000-0003-0332-5583

■ ACKNOWLEDGEMENTS

We greatly appreciate the assistance of F. Oliva, R. Almeida, B. Vilches, R. Jaén and P. Monroy during field sampling and laboratory analyses. P. Brownless (RBGE, Scotland), F. Van Caekenberghe, M. Reynders (Botanic Garden Meise, Belgium), D. Orr, and J. Hoh (Waimea Valley Arboretum and Botanical Garden, U.S.A.) kindly provided *Dracaena* samples for analysis. JP acknowledges the contribution of the Teide High-Performance Computing facility (TeideHPC) provided by the Instituto Tecnológico y de Energías Renovables. This research was funded by the European Regional Development Fund (Intereg projects CAVEGEN and ENCLAVES). JP was funded by the Marie Sklodowska-Curie COFUND, Researchers' Night and Individual Fellowships Global (MSCA grant agreement No 747238, "UNISLAND"'), and the Ramón y Cajal program (RYC-2016-20506). CG-V was financially supported by a "Vicenç Mut" postdoctoral fellowship (Conselleria d'Innovació, Recerca i Turisme, Govern de les Illes Balears and the European Social Fund).

■ LITERATURE CITED

Almeida Pérez, R.S. 2003. Sobre la presencia de *Dracaena draco* (L.) L. en Gran Canaria (Islas Canarias): Aportación corológica, estado actual y significación biogeográfica. *Bot. Macaronés.* 24: 17–38.

Almeida Pérez, R.S. & Beech, E. 2017. *Dracaena draco*. The IUCN Red List of Threatened Species 2017: e.T30394A103368016. https://doi.org/10.2305/IUCN.UK.1998.RLTS.T30394A9535771.en (accessed on 2 May 2019).

Andrus, N., Trusty, J., Santos-Guerra, A., Jansen, R.K. & Francisco-Ortega, J. 2004. Using molecular phylogenies to test phytogeographical links between East/South Africa-Southern Arabia and the Macaronesian islands – A review, and the case of *Vierea* and *Pulicaria* section *Vieraeopsis* (Asteraceae). *Taxon* 53: 333–346. https://doi.org/10.2307/4135612

Anonymous 1905. *Dracaena draco*. In: Gilman, D.C., Peck, H.T. & Colby, F.M. (eds.), *The New International Encyclopedia*, 1st ed., vol. 6. New York: Dodd, Mead. https://archive.org/details/newinternational06gilm

Axelrod, D.I. 1975. Evolution and biogeography of Madrean–Tethyan sclerophyll vegetation. *Ann. Missouri Bot. Gard.* 62: 280–334. https://doi.org/10.2307/2395199

Bandelt, H.J., Forster, P. & Röhl, A. 1999. Median-joining networks for inferring intraspecific phylogenies. *Molec. Biol. Evol.* 16: 37–48. https://doi.org/10.1093/oxfordjournals.molbev.a026036

Benabid, A. & Cuzin, F. 1997. Dragon tree (*Dracaena draco* subsp. *ajgal* Benabid et Cuzin) populations in Morocco: Taxonomical, biogeographical and phytosociological values. *Compt. Rend. Acad. Sci. Paris*, *Sér. 3*, *Sci. Vie* 320: 267–277. https://doi.org/10.1016/S0764-4469(97)86935-1

Bogler, D.J. & Simpson, B.B. 1996. Phylogeny of Agavaceae based on ITS rDNA sequence variation. *Amer. J. Bot.* 83: 1225–1235. https://doi.org/10.1002/j.1537-2197.1996.tb13903.x

Bramwell, D. 1985. Contribución a la biogeografía de las Islas Canarias. *Bot. Macaronés.* 14: 3–34.

Breed, M., Stead, M., Ottewell, K., Gardner, M. & Lowe, A. 2013. Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. *Conservation Genet.* 14: 1–10. https://doi.org/10.1007/s10592-012-0425-z

Carine, M.A., Russell, S.J., Santos-Guerra, A. & Francisco-Ortega, J. 2004. Relationships of the Macaronesian and Mediterranean floras: Molecular evidence for multiple colonizations into Macaronesia and back-colonization of the continent in *Convolvulus* (Convolvulaceae). *Amer. J. Bot.* 91: 1070–1085. https://doi.org/10.3732/ajb.91.7.1070

Caujapé-Castells, J., García-Verdugo, C., Marrero-Rodríguez, A., Fernández-Palacios, J.M., Crawford, D.J. & Mort, M.E. 2017. Island ontogenies, syngameons, and the origins and evolution of genetic diversity in the Canarian endemic flora. *Perspect. Pl. Ecol. Evol. Syst.* 27: 9–22. https://doi.org/10.1016/j.ppees.2017.03.003

Charles-Dominique, T., Davies, T.J., Hempson, G.P., Bezeng, B.S., Daru, B.H., Kabongo, R.M., Maurin, O., Muthama Muasya, A., Van der Bank, M. & Bond, W.J. 2016. Spiny plants, mammal browsers, and the origin of African savannas. *Proc. Natl. Acad. Sci. U.S.A.* 113: E5572–E6557. https://doi.org/10.1073/pnas.1607493113

Chen, S., Kim, D.K., Chase, M.W. & Kim, J.H. 2013. Networks in a large-scale phylogenetic analysis: Reconstructing evolutionary history of Asparagales (Lilianae) based on four plastid genes. *PLoS One* 8: e59472. https://doi.org/10.1371/journal.pone.0059472

Coello, A.J., Fernández-Mazuecos, M., García-Verdugo, C. & Vargas, P. 2020. Phylogeographic sampling guided by species distribution modeling reveals the Quaternary history of the Mediterranean-Canarian *Cistus monspeliensis* (Cistaceae). *J. Syst. Evol.*, early view. https://doi.org/10.1111/jse.12570

De la Rúa, P., Galián, J., Serrano, J. & Moritz, R.F.A. 2001. Genetic structure and distinctness of *Apis mellifera* L. populations from the Canary Islands. *Molec. Ecol.* 10: 1733–1742. https://doi.org/10.1046/j.1365-294X.2001.01303.x

Del Arco Aguilar, M.J. & Rodríguez Delgado, O. 2018. *Vegetation of the Canary Islands*. Springer: Cham. https://doi.org/10.1007/978-3-319-77255-4

Dellaporta, S., Wood, J. & Hicks, J. 1983. A plant DNA minipreparation: Version II. *Pl. Molec. Biol. Reporter* 1: 19–21. https://doi.org/10.1007/BF02712670

Denk, T., Güner, H.T. & Grimm, G.W. 2014. From mesic to arid: Leaf epidermal features suggest preadaptation in Miocene dragon trees (*Dracaena*). *Rev. Palaeobot. Palynol.* 200: 211–228. https://doi.org/10.1016/j.revpalbo.2013.09.009

Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molec.*

Biol. Evol. 29: 1969–1973. https://doi.org/10.1093/molbev/mss075

Elansary, H.O. 2013. Towards a DNA barcode library for Egyptian flora, with a preliminary focus on ornamental trees and shrubs of two major gardens. *DNA Barcodes* 1: 46–55. https://doi.org/10.2478/dna-2013-0004

Elansary, H.O., Ashfaq, M., Ali, H.M. & Yessoufou, K. 2017. The first initiative of DNA barcoding of ornamental plants from Egypt and potential applications in horticulture industry. *PLoS ONE* 12: e0172170. https://doi.org/10.1371/journal.pone.0172170

Excoffier, L. & Lischer, H.E.L. 2010. Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Molec. Ecol. Resources* 10: 564–567. https://doi.org/10.1111/j.1755-0998.2010.02847.x

García-Verdugo, C., Forrest, A.D., Fay, M.F. & Vargas, P. 2010. The relevance of gene flow in metapopulation dynamics of an oceanic island endemic, *Olea europaea* subsp. *guanchica*. *Evolution* 64: 3525–3536. https://doi.org/10.1111/j.1558-5646.2010.01091.x

García-Verdugo, C., Sajeva, M., La Mantia, T., Harrouni, C., Msanda, F. & Caujapé-Castells, J. 2015. Do island plant populations really have lower genetic variation than mainland populations? Effects of selection and distribution range on genetic diversity estimates. *Molec. Ecol.* 24: 726–741. https://doi.org/10.1111/mec.13060

García-Verdugo, C., Mairal, M., Monroy, P., Sajeva, M. & Caujapé-Castells, J. 2017. The loss of dispersal on islands hypothesis revisited: Implementing phylogeography to investigate evolution of dispersal traits in *Periploca* (Apocynaceae). *J. Biogeogr.* 44: 2595– 2606. https://doi.org/10.1111/jbi.13050

García-Verdugo, C., Caujapé-Castells, J., Mairal, M. & Monroy, P. 2019a. How repeatable is microevolution on islands? Patterns of dispersal and colonization-related plant traits in a phylogeographical context. *Ann. Bot. (Oxford)* 123: 557–568. https://doi.org/10.1093/aob/mcy191

García-Verdugo, C., Caujapé-Castells, J. & Sanmartín, I. 2019b. Colonization time on island settings: Lessons from the Hawaiian and Canary Island floras, *Bot. J. Linn. Soc.* 191: 155–163. https://doi.org/10.1093/botlinnean/boz044

García-Verdugo, C., Caujapé-Castells, J., Illera, J.C., Mairal, M., Patiño, J., Reyes-Betancort, J. & Scholz, S. 2019c. Pleistocene extinctions as drivers of biogeographical patterns on the easternmost Canary Islands. *J. Biogeogr.* 46: 845–859. https://doi.org/10.1111/jbi.13563

Graham, N.R., Gruner, D.S., Lim, J.Y. & Gillespie, R.G. 2017. Island ecology and evolution: Challenges in the Anthropocene. *Environm. Conservation* 44: 323–335. https://doi.org/10.1017/S0376892917000315

Gruenstaeudl, M. & Hartmaring, Y. 2019. EMBL2checklists: A Python package to facilitate the user-friendly submission of plant and fungal DNA barcoding sequences to ENA. *PLoS ONE* 14: e0210347. https://doi.org/10.1371/journal.pone.0210347

Gupta, D., Bleakley, B. & Gupta, R.K. 2007. Dragon's blood: Botany, chemistry and therapeutic uses. *J. Ethnopharmacol.* 115: 361–380. https://doi.org/10.1016/j.jep.2007.10.018

Hall, T.A. 1999. BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucl. Acids Symp. Ser.* 41: 95–98.

Helmus, M.R., Mahler, D.L. & Losos, J.B. 2014. Island biogeography of the Anthropocene. *Nature* 513: 543–546. https://doi.org/10.1038/nature13739

Hofman, C.A. & Rick, T.C. 2017. Ancient biological invasions and island ecosystems: Tracking translocations of wild plants and animals. *J. Archaeol. Res.* 26: 65–115. https://doi.org/10.1007/s10814-017-9105-3

Jankalski, S. 2015. *Chrysodracon* in Hawaii. *Sansevieria* 33: 26–28.

Jones, K.E., Reyes-Betancort, J.A., Hiscock, S.J. & Carine, M.A. 2014. Allopatric diversification, multiple habitat shifts, and hybridization in the evolution of *Pericallis* (Asteraceae), a Macaronesian endemic genus. *Amer. J. Bot.* 101: 637–665. https://doi.org/10.3732/ajb.1300390

Jura-Morawiec, J. & Tulik, M. 2016. Dragon's blood secretion and its ecological significance. *Chemoecology* 26: 101–105. https://doi.org/10.1007/s00049-016-0212-2

Katoh, K. & Standley, D.M. 2013. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molec. Biol. Evol.* 30: 772–780. https://doi.org/10.1093/molbev/mst010

Kim, J.H., Kim, D.K., Forest, F., Fay, M.F. & Chase, M.W. 2010. Molecular phylogenetics of Ruscaceae sensu lato and related families (Asparagales) based on plastid and nuclear DNA sequences. *Ann. Bot. (Oxford)* 106: 775–790. https://doi.org/10.1093/aob/mcq167

Klimko, M., Nowinska, R., Wilkin, P. & Wiland-Szymanska, J. 2018: Comparative leaf micromorphology and anatomy of the dragon tree group of *Dracaena* (Asparagaceae) and their taxonomic implications. *Pl. Syst. Evol.* 304: 1041–1055. https://doi.org/10.1007/s00606-018-1530-3

Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. 2012. PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molec. Biol. Evol.* 29: 1695–1701. https://doi.org/10.1093/molbev/mss020

Lu, P.-L. & Morden, C.W. 2014. Phylogenetic relationships among dracaenoid genera (Asparagaceae: Nolinoideae) inferred from chloroplast DNA loci. *Syst. Bot.* 39: 90–104. https://doi.org/10.1600/036364414X678035

Lyons, G. 1974. In search of dragons; or The plant that roared. *Cact. Succ. J. (Los Angeles)* 44: 267–282.

Mairal, M., Sanmartín, I., Aldasoro, J.J., Culshaw, V., Manolopoulou, I. & Alarcón, M. 2015. Palaeo-islands as refugia and sources of genetic diversity within volcanic archipelagos: The case of the widespread endemic *Canaria canariensis* (Campanulaceae). *Molec. Ecol.* 24: 3944–3963. https://doi.org/10.1111/mec.13282

Marrero, A. 2010. Dragos. *Rincones del Atlántico* 6/7: 130–140.

Marrero, A. 2013. Aportaciones a la flora pliocena de la isla de Gran Canaria: avances a los estudios florísticos y paleoambientales. *Vieraea* 41: 371–384.

Marrero, A. & Almeida Perez, R.S. 2012. A new subspecies, *Dracaena draco* (L.) L. subsp. *caboverdeana* Marrero Rodr. and R. Almeida (Dracaenaceae) from Cape Verde Islands. *Int. J. Geobot. Res.* 2: 35–40. https://doi.org/10.5616/ijgr120004

Marrero, A., Almeida, R.S. & González-Martín, M. 1998. A new species of the wild dragon tree, *Dracaena* (Dracaenaceae) from Gran Canaria and its taxonomic and biogeographic implications. *Bot. J. Linn. Soc.* 128: 291–314. https://doi.org/10.1111/j.1095-8339.1998.tb02123.x

Marrero Rodríguez, A, Almeida Pérez, R.S., Beech, E. & Rivers, M.C. 2017. *Dracaena tamaranae*. The IUCN Red List of Threatened Species 2017: e.T79726923A79726929. https://doi.org/10.2305/IUCN.UK.2017-3.RLTS.T79726923A79726929.en (accessed on 2 May 2019).

Matzke, N.J. 2013. Probabilistic historical biogeography: New models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. *Frontiers Biogeogr.* 5: 242–248. https://doi.org/10.21425/F5FBG19694

Matzke, N.J. 2014. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Syst. Biol.* 63: 951–970. https://doi.org/10.1093/sysbio/syu056

Médail, F. & Quézel, P. 1999. The phytogeographical significance of SW Morocco compared to the Canary Islands. *Pl. Ecol.* 140: 221– 244. https://doi.org/10.1023/A:1009775327616

Meusel, H. 1965. Die Reliktvegetation der Kanarischen Inseln in ihren Beziehungen zur süd- und mitteleuropäischen Flora. Pp. 17–136 in: Gersch, M. (ed.), *Gesammelte Vorträge über moderne Probleme der Abstammunslehre*, vol. 1. Jena Friedrich-Schiller-Universität.

Miller, S.E., Hrcek, J., Novotny, V., Weiblen, G.D. & Hebert, P.D.N. 2013. DNA barcodes of caterpillars (Lepidoptera) from Papua New Guinea. *Proc. Entomol. Soc. Wash.* 115: 107–109. https://doi.org/10.4289/0013-8797.115.1.107

Nadezhdina, N. & Nadezhdin, V. 2017. Are *Dracaena* nebulophytes able to drink atmospheric water? *Environm. Exp. Bot.* 139: 57–66. https://doi.org/10.1016/j.envexpbot.2017.04.005

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* 89: 583–590.

Palmer, J.D. 1991. Plastid chromosome, structure and evolution. Pp. 5–53 in: Bogorad, L. & Vasil, I.K. (eds.), *The molecular biology of plastids*. San Diego: Academic Press. https://doi.org/10.1016/B978-0-12-715007-9.50009-8

Parmentier, I., Duminil, J., Kuzmina, M., Philippe, M., Thomas, D.W., Kenfack, D., Chuyong, G.B., Cruaud, C. & Hardy, O.J. 2013. How effective are DNA barcodes in the identification of African rainforest trees? *PLoS ONE* 8: e54921. https://doi.org/10.1371/journal.pone.0054921

Pokorny, L., Riina, R., Mairal, M., Meseguer, A.S., Culshaw, V., Cendoya, J., Serrano, M., Carbajal, R., Ortiz, S., Heuertz, M. & Sanmartín, I. 2015. Living on the edge: Timing of Rand Flora disjunctions congruent with ongoing aridification in Africa. *Frontiers Genet.* 6: 154. https://doi.org/10.3389/fgene.2015.00154

Pons, O. & Petit, R.J. 1996. Measuring and testing genetic differentiation with ordered versus unordered alleles. *Genetics* 144: 1237–1245.

Quézel, P. 1978. Analysis of the flora of Mediterranean and Saharan Africa. *Ann. Missouri Bot. Gard.* 65: 479–534. https://doi.org/10.2307/2398860

R Core Team 2017. *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org

Rambaut, A., Drummond, A.J., Xie, D., Baele, G. & Suchard, M.A. 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Syst. Biol.* 67: 901–904. https://doi.org/10.1093/sysbio/syy032

Ree, R.H. & Sanmartín, I. 2018. Conceptual and statistical problems with the DEC+J model of founder-event speciation and its comparison with DEC via model selection. *J. Biogeogr.* 45: 741–749. https://doi.org/10.1111/jbi.13173

Reid, N.M. & Carstens, B.C. 2012. Phylogenetic estimation error can decrease the accuracy of species delimitation: A Bayesian implementation of the General Mixed Yule Coalescent model. *B. M. C. Evol. Biol.* 12: 196. https://doi.org/10.1186/1471-2148-12-196

Romeiras, M.M., Paulo, O.S., Duarte, M.C., Pina-Martins, F., Cotrim, M.H., Carine, M.A. & Pais, M.S. 2011. Origin and diversification of the genus *Echium* (Boraginaceae) in the Cape Verde archipelago. *Taxon* 60: 1375–1385. https://doi.org/10.1002/tax.605013

Romeiras, M.M., Monteiro, F., Duarte, M.C., Schaefer, H. & Carine, M. 2015. Patterns of genetic diversity in three plant lineages endemic to the Cape Verde Islands. *AoB Plants* 7: plv051. https://doi.org/10.1093/aobpla/plv051

Ronquist, F. & Huelsenbeck, J.P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Rudall, P.J., Furness, C.A., Chase, M.W. & Fay, M.F. 1997. Microsporogenesis and pollen sulcus type in Asparagales (Lilianae). *Canad. J. Bot.* 75: 408–430. https://doi.org/10.1139/b97-044

Sánchez-Pinto, L. & Zárate, R. 2010. Sangre de drago. *Rincones del Atlántico* 6/7: 130–140.

Sanmartín, I., Anderson, C.L., Alarcon, M., Ronquist, F. & Aldasoro, J.J. 2010. Bayesian island biogeography in a continental setting: The Rand Flora case. *Biol. Lett.* 6: 703–707. https://doi.org/10.1098/rsbl.2010.0095

Saro, I., González-Pérez, M.A., García-Verdugo, C. & Sosa, P.A. 2015. Patterns of genetic diversity in *Phoenix canariensis*, a widespread oceanic palm (species) endemic from the Canarian archipelago. *Tree Genet. Genomes* 11: 815. https://doi.org/10.1007/s11295-014-0815-0

Schaefer, H., Hardy, O.J., Silva, L., Barraclough, T.G. & Savolainen, V. 2011. Testing Darwin's naturalization hypothesis in the Azores. *Ecol. Letters* 14: 389–396. https://doi.org/10.1111/j.1461-0248.2011.01600.x

Schüßler, C., Bräuchler, C., Reyes-Betancort, J.A., Koch, M.A. & Thiv, M. 2019. Island biogeography of the Macaronesian *Gesnouinia* and Mediterranean *Soleirolia* (Parietarieae, Urticaceae) with implications for the evolution of insular woodiness. *Taxon* 68: 537–556. https://doi.org/10.1002/tax.12061.

Shaw, J., Lickey, E.B., Schilling, E.E. & Small, R.L. 2007. Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: The tortoise and the hare. III. *Amer. J. Bot.* 94: 275–288. https://doi.org/10.3732/ajb.94.3.275

Stamatakis, A. 2014. RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Sun, Y., Li, Y.S., Vargas-Mendoza, C.F., Wang, F.G. & Xing, F.W. 2016. Colonization and diversification of the *Euphorbia* species (Sect. *Aphyllis* subsect. *Macaronesicae*) on the Canary Islands. *Sci. Rep.* 6: 34454. https://doi.org/10.1038/srep34454

Sunding, P. 1979. Origins of the Macaronesia flora. Pp. 13–40 in: Bramwell, D. (ed.), *Plants and islands*. London: Academic Press.

Takawira-Nyenya, R., Mucina, L., Cardinal-McTeague, W.M. & Thiele, K.R. 2018. *Sansevieria* (Asparagaceae, Nolinoideae) is a herbaceous clade within *Dracaena*: Inference from non-coding plastid and nuclear DNA sequence data. *Phytotaxa* 376: 254–276. https://doi.org/10.11646/phytotaxa.376.6.2

Tamura, M.N., Yamashita, J., Fuse, S. & Haraguchi, M. 2004. Molecular phylogeny of monocotyledons inferred from combined analysis of plastid *matK* and *rbcL* gene sequences. *J. Pl. Res.* 117: 109–120. https://doi.org/10.1007/s10265-003-0133-3

Thiv, M., Thulin, M., Hjertson, M., Kropf, M. & Linder, H.P. 2010. Evidence for a vicariant origin of Macaronesian-Eritreo/Arabian disjunctions in *Campylanthus* Roth (Plantaginaceae). *Molec. Phylogen. Evol.* 54: 607–616. https://doi.org/10.1016/j.ympev.2009.10.009

Toyama, H., Kajisa, T., Tagane, S., Mase, K., Chhang, P., Samreth, V., Ma, V., Sokh, H., Ichihashi, R., Onoda, Y., Mizoue, N. & Yahara, T. 2015. Effects of logging and recruitment on community phylogenetic structure in 32 permanent forest plots of Kampong Thom, Cambodia. *Philos. Trans., Ser. B* 370: 20140008. https://doi.org/10.1098/rstb.2014.0008

Valtueña, F.J., Rodríguez-Riaño, T., López, J., Mayo, C. & Ortega-Olivencia, A. 2017. Peripatric speciation in an endemic Macaronesian plant after recent divergence from a widespread relative. *PLoS ONE* 12: e0178459. https://doi.org/10.1371/journal.pone.0178459

Villaverde, T., Pokorny, L., Olsson, S., Rincón-Barrado, M., Johnson, M.G., Gardner, E.M., Wickett, N.J., Molero, J., Riina, R. & Sanmartín, I. 2018. Bridging the micro- and macroevolutionary levels in phylogenomics: Hyb-Seq solves relationships from populations to species and above. *New Phytol.* 220: 636–650. https://doi.org/10.1111/nph.15312

Villesen, P. 2007. FaBox: An online toolbox for fasta sequences. *Molec. Ecol. Notes* 7: 965–968. https://doi.org/10.1111/j.1471-8286.2007.01821.x

Waples, R.S. & Yokota, M. 2007. Temporal estimates of effective population size in species with overlapping generations. *Genetics* 175: 219–233. https://doi.org/10.1534/genetics.106.065300

Wilkin, P., Piyakaset, S., Kaweesak, K., Van Welzen, P. & Wiland-Szymańska, J. 2012. A new threatened endemic species from central and northeastern Thailand, *Dracaena jayniana* (Asparagaceae: tribe Nolinoideae). *Kew Bull.* 67: 697–705. https://doi.org/10.1007/s12225-012-9412-2

Yamashita, J. & Tamura, M.N. 2000. Molecular phylogeny of the Convallariaceae (Asparagales). Pp. 387–400 in: Wilson, K.L.

& Morrison, D.A. (eds.), *Monocots: Systematics and evolution*. CSIRO: Melbourne.

Yessoufou, K., Davies, T.J., Maurin, O., Kuzmina, M., Schaefer, H., Van der Bank, M. & Savolainen, V. 2013. Large herbivores favour species diversity but have mixed impacts on phylogenetic community structure in an African savanna ecosystem. *J. Ecol.* 101: 614–625. https://doi.org/10.1111/1365-2745.12059

Zhang, Z., Ramstein, G., Schuster, M., Li, C., Contoux, C. & Yan, Q. 2014. Aridification of the Sahara desert caused by Tethys Sea shrinkage during the Late Miocene. *Nature* 513: 401–404. https://doi.org/10.1038/nature13705

Appendix 1. Sequence information for the *Dracaena* samples used for the construction of Phylogen-1 (38 accessions; *matK* + *rbcL* markers) and Phylogen-2 (12 accessions; *matK* + *rbcL* + *rpl32-trnL* + *trnQ-rps16* markers) datasets.

Taxon, accession numbers (*matK*, *rbcL*, *rpl32-trnL*, *trnQ-rps16*), publication or source.

Dracaena aletriformis (Haw.) Bos **1,** JX517850, AFV48994, –, –, Maurin & al., unpub.; ***Dracaena aletriformis*** (Haw.) Bos **2,** JX903540, –, –, –, Chen & al., 2013; ***Dracaena aletriformis*** (Haw.) Bos **3,** –, ADZ61821, –, –, Yessoufou & al., 2013; ***Dracaena angustifolia*** (Medik.) Roxb. **1,** AB029802, –, –, –, Yamashita & Tamura, 2000; ***Dracaena angustifolia*** (Medik.) Roxb. **2,** AB924769, BAO72419, –, –, Toyama & al., 2015; ***Dracaena angustifolia*** (Medik.) Roxb. **3,** –, AER29281, –, –, Miller & al., 2013; ***Dracaena angustifolia*** (Medik.) Roxb. **4,** –, AER29361, –, –, Miller & al., 2013; ***Dracaena angustifolia*** (Medik.) Roxb. **5,** –, AER29622, –, –, Miller & al., 2013; ***Dracaena angustifolia*** (Medik.) Roxb. **6,** –, AER29701, –, –, Miller & al., 2013; ***Dracaena aubryana*** Brongn. ex E.Morren **1,** AB088791, AB088823, –, –, Tamura & al., 2004; ***Dracaena aubryana*** Brongn. ex E.Morren **2,** HM640583, HM640470, –, –, Kim & al., 2010; ***Dracaena aubryana*** Brongn. ex E.Morren **3,** LT934268*, LT934244*, LT934256*, LT934280*, This study: Waimea Valley Arboretum and Botanical Garden (*ex horto*); ***Dracaena aubryana*** Brongn. ex E.Morren **4,** –, Z77270, –, –, Rudall & al., 1997; ***Dracaena cinnabari*** Balf.f., LT934269*, LT934245*, LT934257*, LT934281*, This study: Jardín Botánico Viera y Clavijo (*ex horto*) – LPA18513; ***Dracaena cochinchinensis*** (Lour.) S.C.Chen, LT934270*, LT934246*, LT934258*, LT934282*, This study: Waimea Valley Arboretum and Botanical Garden (*ex horto*); ***Dracaena deremensis*** Engl. **1** (syn. ***D. fragrans***), JX903539, –, –, –, Chen & al., 2013; ***Dracaena deremensis*** Engl. **2** (syn. ***D. fragrans***), KX783666, ART88308, –, –, Elansary & al., 2017; ***Dracaena draco*** subsp. ***ajgal*** Benabid & Cuzin, LT934271*, LT934247*, LT934259*, LT934283*, This study: LPA22512; ***Dracaena draco*** subsp. ***caboverdeana*** Marrero Rodr. & Almeida, LT934272*, LT934248*, LT934260*, LT934284*, This study: LPA28912; ***Dracaena draco*** (L.) L. subsp. ***draco*** **1,** AB029803, AB029848, –, –, Yamashita & Tamura, 2000; ***Dracaena draco*** (L.) L. subsp. ***draco*** **2,** HM850497, HM849958, –, –, Schaefer & al., 2011; ***Dracaena draco*** (L.) L. subsp. ***draco*** **3,** JX495705, JX571820, –, –, Elansary, 2013; ***Dracaena draco*** (L.) L. subsp. ***draco*** **4,** LT934273*, LT934249*, LT934261*, LT934285*, This study: LPA37286; ***Dracaena ellenbeckiana*** Engl., LT934274*, LT934250*, LT934262*, LT934286*, This study: Jardín Botánico Viera y Clavijo (*ex horto*) – LPA19404; ***Dracaena fragrans*** (L.) Ker Gawl. **1,** –, AFG32688, –, –, Kalyankar & al., unpub.; ***Dracaena fragrans*** (L.) Ker Gawl. **2,** KX783667, ART88309, –, –, Elansary & al., 2017; ***Dracaena laxissima*** Engl., KC627876, AGJ76159, –, –, Parmentier & al., 2013; ***Dracaena mannii*** Baker, JX517338, AFV48995, –, –, Maurin & al., unpub.; ***Dracaena marginata*** Lam. (syn. ***Dracaena reflexa*** var. ***angustifolia***), KX783668, ART88310, –, –, Elansary & al., 2017; ***Dracaena ombet*** Heuglin ex Kotschy & Peyr., LT934275*, LT934251*, LT934263*, LT934287*, This study: Jardín Botánico Viera y Clavijo (*ex horto*) – LPA18515; ***Dracaena reflexa*** Lam., KX783669, ART88311, –, –, Elansary & al., 2017; ***Dracaena schizantha*** Baker **1,** LT934276*, LT934252*, LT934264*, LT934288*, This study: Meise Botanic Garden (*ex horto*); ***Dracaena schizantha*** Baker **2,** HM640582, HM640469, –, –, Kim & al., 2010; ***Dracaena serrulata*** Baker, LT934277*, LT934253*, LT934265*, LT934289*, This study: Jardín Botánico Viera y Clavijo (*ex horto*) – 146/03; ***Dracaena steudneri*** Engl., KX146227, AOP18845, –, –, Charles-Dominique & al., 2016; ***Dracaena tamaranae*** Marrero Rodr., Almeida & González, LT934278*, LT934254*, LT934266*, LT934290*, This study: Jardín Botánico Viera y Clavijo (*ex horto*) – LPA34717; ***Dracaena transvaalensis*** Baker, JX517732, AFV48996, –, –, Maurin & al., unpub.; ***Liriope muscari*** (Decne.) L.H.Bailey, LT934279*, LT934255*, LT934267*, LT934291*, This study: Meise Botanic Garden (*ex horto*).