



UvA-DARE (Digital Academic Repository)

PalmTraits 1.0, a species-level functional trait database of palms worldwide

Kissling, W.D.; Balslev, H.; Baker, W.J.; Dransfield, J.; Gödel, B.; Lim, J.Y.; Onstein, R.E.; Svenning, J.-C.

DOI

[10.1038/s41597-019-0189-0](https://doi.org/10.1038/s41597-019-0189-0)

Publication date

2019

Document Version

Final published version

Published in

Scientific Data

License

CC BY

[Link to publication](#)

Citation for published version (APA):

Kissling, W. D., Balslev, H., Baker, W. J., Dransfield, J., Gödel, B., Lim, J. Y., Onstein, R. E., & Svenning, J.-C. (2019). PalmTraits 1.0, a species-level functional trait database of palms worldwide. *Scientific Data*, 6, [178]. <https://doi.org/10.1038/s41597-019-0189-0>

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.

SCIENTIFIC DATA

OPEN

DATA DESCRIPTOR

PalmTraits 1.0, a species-level functional trait database of palms worldwide

W. Daniel Kissling¹, Henrik Balslev², William J. Baker³, John Dransfield³, Bastian Gödel², Jun Ying Lim¹, Renske E. Onstein⁴ & Jens-Christian Svenning^{2,5}

Received: 3 June 2019

Accepted: 9 August 2019

Published online: 24 September 2019

Plant traits are critical to plant form and function—including growth, survival and reproduction—and therefore shape fundamental aspects of population and ecosystem dynamics as well as ecosystem services. Here, we present a global species-level compilation of key functional traits for palms (Arecaceae), a plant family with keystone importance in tropical and subtropical ecosystems. We derived measurements of essential functional traits for all (>2500) palm species from key sources such as monographs, books, other scientific publications, as well as herbarium collections. This includes traits related to growth form, stems, armature, leaves and fruits. Although many species are still lacking trait information, the standardized and global coverage of the data set will be important for supporting future studies in tropical ecology, rainforest evolution, paleoecology, biogeography, macroecology, macroevolution, global change biology and conservation. Potential uses are comparative evolutionary studies, ecological research on community dynamics, plant-animal interactions and ecosystem functioning, studies on plant-based ecosystem services, as well as conservation science concerned with the loss and restoration of functional diversity in a changing world.

Background & Summary

Most ecosystems are composed of a large number of species with different characteristics. These characteristics (i.e. traits) reflect morphological, reproductive, physiological, phenological, or behavioural measurements of species that are usually collected to study intraspecific trait variation (i.e. among individuals or populations of the same species) or interspecific trait variation (i.e. among species)^{1–5}. Many traits have an important functional role for species and ecosystems and are therefore referred to as ‘functional traits’. For instance, functional traits such as plant morphological and physiological properties are often directly linked to ecosystem structure and ecosystem functioning^{6,7}. Such functional traits are further important for the response of organisms to their environment (‘response traits’) and the effects of organisms on ecosystems and other species (‘effect traits’)^{2,6,8}. Hence, functional traits are key to understanding ecosystem dynamics and the response of organisms to human-induced disturbances and changing environmental conditions such as climate change^{4,9,10}, habitat fragmentation¹¹ or harvesting pressure¹².

Over the last few years, comprehensive trait databases with continental or global scope have become available, covering diverse taxa in the marine^{13,14} and freshwater realm¹⁵ as well as terrestrial taxa such as plants¹⁶ and vertebrates^{17–20}. Despite these monumental efforts that have involved community contributions as well as advanced techniques in data mining and data integration, digitally available information on functional traits is still missing for the majority of taxa on Earth^{3,21}. Even for well-studied organisms such as vascular plants, information remains taxonomically and geographically limited. For instance, the TRY plant trait database¹⁶ has achieved an impressive compilation of almost 12 million trait records for currently 280,000 plant species (TRY database version 5 released in March 2019, www.try-db.org), but often only a few trait records are available per species. Moreover, as

¹Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, P.O. Box 94240, 1090 GE, Amsterdam, The Netherlands. ²Section for Ecoinformatics & Biodiversity, Department of Bioscience, Ny Munkegade 114, DK-8000, Aarhus C, Denmark. ³Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE, UK. ⁴German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103, Leipzig, Germany. ⁵Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Department of Bioscience, Ny Munkegade 114, DK-8000, Aarhus C, Denmark. Correspondence and requests for materials should be addressed to W.D.K. (email: wdkissling@gmail.com)

for other ecological information such as species occurrences²², digitally accessible information on traits remains particularly scarce in the tropics where most biodiversity occurs^{16,23–25}. This is a major bottleneck for ecological and evolutionary science because tropical ecosystems such as rainforests are one of Earth's greatest biological treasures, a major source of ecosystem services for a large proportion of the global human population, and a key component of the Earth system^{26,27}.

In the tropics, palms are an iconic plant family with keystone importance in many forest and savanna ecosystems^{28–30}. The pantropical palm family (Areaceae or Palmae) is species-rich and contains nearly 2600 species in 181 genera and 5 subfamilies³¹. The ecology and evolution of palms is strongly linked to interspecific variation in growth, reproduction and morphology of stems, leaves, inflorescences, fruits and seeds³². Palms are a major resource for herbivores, pollinators and fruit- as well as seed-eating animals in the tropics^{29,30,32–34}, provide provisioning services such as food, construction material and medicine to people (especially in rural communities)³⁵, and belong to one of the most economically important plant groups globally³⁶. Moreover, palms can provide important insights into the evolution of tropical rainforests^{28,37–39}, historical biogeography^{40–42}, past climate change^{43–45} and the vulnerability and response of ecosystems to ongoing and future global change^{46–48}. Despite this outstanding role of palms in tropical ecosystems and tropical biological science, studies using palm functional trait data across broad spatial scales remain scarce^{35,38,49,50}.

Here, we introduce the PalmTraits 1.0 database, an extensive database containing functional traits for palm species globally. PalmTraits 1.0 releases information on error-checked and referenced traits to capture interspecific variation in growth forms, armature and the morphology of stems, leaves and fruits of palms. Species-level trait information was assembled from >130 sources including monographs and taxonomic revisions as well as credible online sources and two herbaria with extensive palm collections. By making these data available to the scientific community, we aim to advance the sharing and digitalization of ecological trait data and understanding of the global ecology, biogeography and evolution of palms and the tropical rainforests they inhabit.

Methods

The data collection of the PalmTraits 1.0 database involved three major steps (Fig. 1a–c): (1) the identification of data sources, (2) the digitalization and encoding of trait values, and (3) the harmonization of fruit size data. Overall, the database was designed to capture species-level (interspecific) trait variation of palms rather than individual-level (intraspecific) variability. Such aggregated data (e.g. average values of continuous traits) facilitate biodiversity data integration across large spatial, temporal, and taxonomic scales, but are limited in their capacity to resolve fine-grained ecological patterns⁵¹. The PalmTraits 1.0 database captures trait variation of palms in terms of growth forms, stems, armature, leaves, and fruits (Online-only Table 1). This represents a large variation of trait diversity in palms (Fig. 1d–f). Some fundamental traits like wood density, specific leaf area or N-content⁵ are not represented because these traits are not commonly measured by palm taxonomists and hence are not available from palm books, monographs, species descriptions or herbarium specimens. Nevertheless, some of the available traits reflect major dimensions of plant form and function⁵, including the size of whole plants (e.g. growth form and stem height) and their organs (e.g. blade length). Other traits also capture characteristics that are relevant for studying plant–animal interactions such as herbivory (e.g. stem and leaf armature)⁴⁸ and frugivory and animal-mediated seed dispersal (e.g. fruit length and width, fruit shape, and fruit colour)^{37,50,52}. Below we describe the data collection (Fig. 1a–c) in more detail.

Data sources. The main data sources for extracting the palm trait data were books and monographs, scientific articles (e.g. taxonomic revisions and species descriptions), herbarium specimen and specialized websites (Fig. 1a). We first extracted trait data from books, monographs and taxonomic revisions because these contain trait descriptions in a standardized way and for major clades or specific regions. We started the trait data extraction by obtaining maximum values for stem height, stem diameter, leaf number and fruit diameter as well as binary information (yes/no) for acaulescence and stem clustering for about 850–1250 species from the appendix I of the palm ecology and evolution book of A. Henderson³². We then extracted additional information for continuous traits (minimum, maximum and average values) as well as binary or categorical traits from books that synthesized species-specific palm knowledge for particular countries or regions (e.g. Africa^{53–56}, Americas⁵⁷, Australia⁵⁸, Brazil⁵⁹, Colombia⁶⁰, Costa Rica⁶¹, Ecuador⁶², Hawaii⁶³, Indonesia⁶⁴, Madagascar^{65–67}, Malaysia^{68,69}, Mascarene Islands⁷⁰, New Caledonia⁷¹, Philippines⁷², Sabah⁷³, Southern Asia⁷⁴, Thailand⁷⁵, Vietnam⁷⁶). Additionally, we went through taxonomic revisions, monographs and other publications that provided trait data for specific taxonomic groups such as palm genera or tribes (e.g. *Acrocomia*⁷⁷, *Aiphanes*⁷⁸, *Archontophoenix*⁷⁹, *Areca*⁸⁰, *Asterogyne*⁸¹, *Astrocaryum*^{82,83}, *Attalea*⁸⁴, *Bactris*^{85,86}, *Balaka*⁸⁷, *Borassodendron*⁸⁸, *Butia*⁸⁹, *Calyptrocalyx*⁹⁰, *Calyptrogyne*⁹¹, *Calamus*^{92–94}, *Caryota*^{95,96}, *Chamaedorea*^{97–103}, *Cyrtostachys*¹⁰⁴, *Drymophloeus*¹⁰⁵, *Eremospatha*^{55,106}, *Geonoma*¹⁰⁷, *Heterospatha*¹⁰⁸, *Hydriastele*^{109,110}, *Hyospatha*¹¹¹, *Johannesteijsmannia*¹¹², *Laccosperma*^{55,106}, *Lanonia*¹¹³, *Licuala*^{114–116}, *Linospadix*^{90,117}, *Livistona*^{118,119}, *Metroxylon*¹²⁰, *Nenga*¹²¹, *Oncocalamus*^{55,106}, *Orania*¹²², *Parajubaea*¹²³, *Phoenix*¹²⁴, *Pinanga*¹²⁵, *Ptychosperma*¹²⁶, *Pritchardia*¹²⁷, *Rhapis*¹²⁸, *Sabal*¹²⁹, *Syagrus*^{130–134}, *Veitchia*¹³⁵, *Wallichia*¹³⁶). We further obtained raw data (i.e. individual-level trait measurements) from A. Henderson that were used in taxonomic revisions for a number of palm genera, including *Calyptrogyne*⁹¹, *Chuniophoenix*¹³⁷, *Desmoncus*¹³⁸, *Geonoma*¹⁰⁷, *Hyospatha*^{139,140}, *Leopoldinia*¹⁴¹, *Pholidostachys*¹⁴², *Rhapis*¹⁴³, *Synechanthus*¹⁴⁴ and *Welfia*¹⁴⁵. These raw data allowed us to add a few additional trait data (especially minimum, mean and maximum fruit sizes) for 139 species. We additionally used other scientific literature on palms^{146–174} as well as specialized palm websites^{175–179}, and the book *Genera Palmarum*¹⁸⁰ for traits that do not vary within single genera (e.g. some genera have only climbers). Finally, we visited two major herbaria (Aarhus University Herbarium, Denmark, and the Royal Botanic Gardens, Kew, UK) harbouring very large palm collections to fill gaps in the database by obtaining trait information from herbarium specimens (e.g. measuring fruit sizes or recording fruit colour from specimen descriptions). All sources are provided together with the trait dataset in DRYAD¹⁸¹.

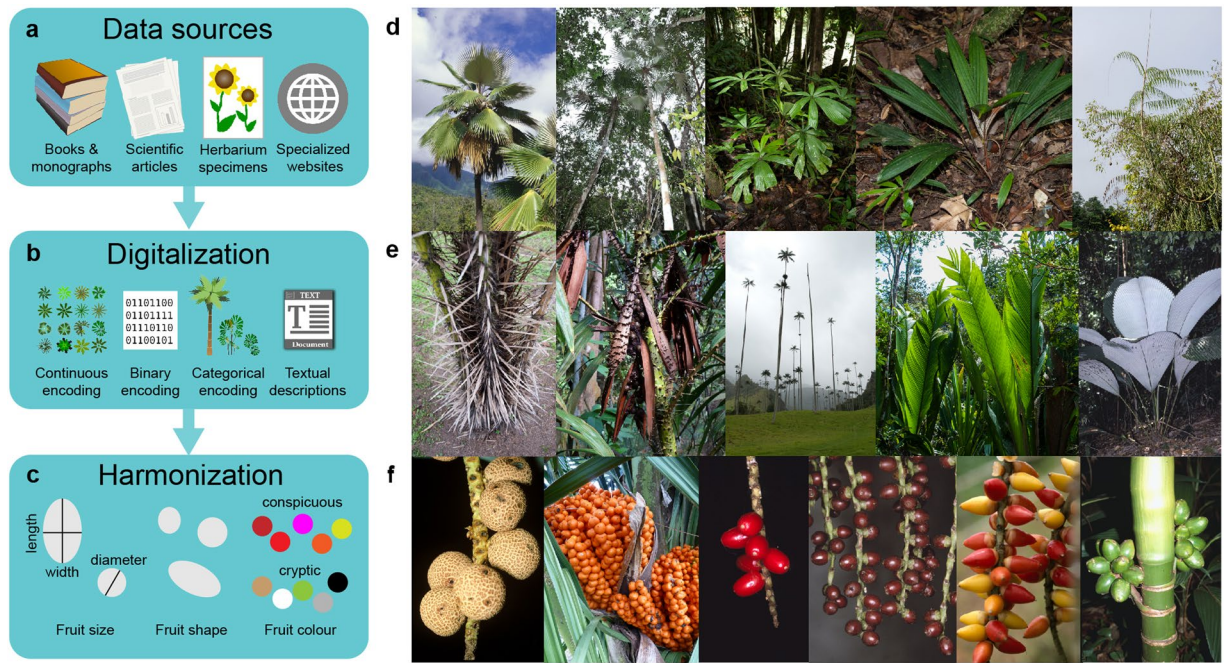


Fig. 1 Trait compilation and trait variation in palms. The workflow (a–c) illustrates key steps in the compilation of palm trait data whereas the images (d–f) represent examples of trait variation in palms. (a) Main data sources for extracting trait data for PalmTraits 1.0. (b) Digitalization of the original trait information through different ways of encoding. (c) Standardization and harmonization of fruit trait information (size, shape and colour). (d) Palm growth forms (from left to right): *Pritchardia viscosa*, an erect canopy palm from Hawaii. Two erect palms (*Thrinax radiata* and *Coccothrinax argentata*) growing under a canopy gap in Mexico. *Licuala telifera*, an understory palm from New Guinea. *Dypsis acaulis*, an acaulescent understory palm from Madagascar. *Plectocomiopsis geminiflora*, a climbing rattan palm from Borneo. (e) Stem and leaf variation (from left to right): *Astrocaryum standleyanum* from Colombia, armed with long black spines. *Daemonorops didymophylla* from Southeast Asia, a climbing rattan palm armed with spines on the petiole of the leaf. *Ceroxylon quinduense* from Colombia, with about 60 m stem height the tallest non-climbing palm in the world. *Marojejya darianii* from Madagascar, a medium-sized tree palm with large leaves of up to 5 m blade length. *Johannesteijsmannia magnifica* from Malaysia, an acaulescent palm with up to 2 metres long leaf blades covered with fine white hairs. (f) Fruit variation (from left to right): *Lemurophoenix halleuxii* from Madagascar, a canopy palm with large (5 cm) chestnut-brown fruits that have corky warts. *Ravenea dransfieldii* from Madagascar, a mid-story palm with small (1.5–2 cm) orange fruits. *Calyptrocalyx* sp., representing a genus of predominantly understory palms that have mostly small (1–2 cm) bright red fruits. *Hydriastele microspadix* from New Guinea, a mid-story palm with small dark red fruits. *Drymophloeus litigiosus* from New Guinea, an understory palm with small (1 cm) yellow to red fruits. *Areca ipot* from the Philippines, with large (5 cm long) fruits that ripen from green through yellow to red. Image credits: J. Dransfield, H. Balslev, and W.J. Baker.

Digitalization. The digitalization of trait data from the original data sources into a database required to encode the information as continuous, binary, categorical or as text descriptions (Fig. 1b). For most traits, trait information was encoded either as continuous or binary (Online-only Table 1). For continuous traits, we usually recorded maximum values (e.g. for stem and leaf size) or minimum, maximum and average values (e.g. for fruit size) as reported in monographs and taxonomic revisions (Online-only Table 1). Binary traits were encoded as 0/1 (e.g. presence/absence of climbing, acaulescent or erect growth form, stem clustering, armature) and additionally as 2 if populations of the same species showed intraspecific trait variation (Online-only Table 1). Three traits were encoded as categorical information. This included understory/canopy information (a derived trait based on whether maximum stem height is ≤ 5 m or > 5 m, and/or whether species have an acaulescent growth form or not)⁵⁰, small/large fruit sizes (a derived trait based on whether fruit length is < 4 cm or ≥ 4 cm in length, i.e. classifying small vs. megafaunal fruits)^{50,182}, and fruit shape (Online-only Table 1). Two other traits (fruit colour and fruit shape) were encoded with text descriptions (Online-only Table 1). For those, we extracted verbatim text descriptions from the literature and herbarium sheets (e.g. glossy black, bright orange, or reddish brown as examples of fruit colour information) and later standardized and harmonized the information (see below).

Harmonization. Since our research has a particular focus on palm-frugivore interactions^{37,50,52,183}, we further standardized and harmonized trait information on fruit size, fruit shape, and fruit colour (Fig. 1c).

For fruit size, the PalmTraits 1.0 database provides information on average, minimum and maximum values for both fruit length and fruit width (Online-only Table 1). However, in some monographs, species descriptions and taxonomic revisions the original information on fruit size was reported as fruit diameter rather than fruit length and fruit width. This typically included palm species that tend to have roundish fruits. We initially recorded these fruit diameter measurements in a separate column, but then merged it into the fruit length and/or fruit width columns. There was a

measurement difference between fruit diameter compared to fruit width and length estimates for 168 palm species. For 74 of those 168 species, this difference was ≤ 0.1 cm and we therefore ignored (deleted) fruit diameter information. For the remaining 94 species, we revisited the original sources and additionally checked available online sources. In 82 cases, fruit diameter/width/length did not differ much (0.1–0.5 cm), and we updated the fruit width information based on the fruit diameter measurements. In the 12 remaining cases, fruit diameter values were much smaller or larger than fruit length (difference > 0.5 cm), and we decided to omit these fruit diameter values to avoid biases and outliers.

For fruit shape, we harmonized the original trait descriptions from the literature into seven categories (ellipsoid, elongate, fusiform, globose, ovoid, pyramidal, and rounded) (Online-only Table 1). We chose those categories as they were most widely used. Note that these fruit shape descriptions are not necessarily distinctively different because no quantitative formulas are used when taxonomists describe the fruits.

For fruit colour, we kept the extracted verbatim text descriptions from the literature ('FruitColorDescription' in Online-only Table 1), but we additionally aggregated and harmonized the verbatim text descriptions in two ways. First, we derived the main fruit colour(s) from the verbatim text descriptions ('MainFruitColors' in Online-only Table 1) and separated them by semicolons (e.g. 'black; blue', or 'brown; orange; yellow'). This allowed to keep the main fruit colour descriptions, but simplified and reduced the verbatim text. Immature fruit colours were excluded in this step, and fruit colours described with a suffix -ish or -ey were usually reduced to the main fruit colours. Second, we classified fruit colours into 'cryptic' and 'conspicuous' colours ('Conspicuousness' in Online-only Table 1). This was done because fruit-eating animals can differ in their colour vision, for instance birds vs. bats or dichromatic vs. trichromatic primates³³. We classified fruit colours as cryptic if their reflectance spectra are difficult to detect against a background of leaves, and as conspicuous if reflectance spectra appear to be in strong contrast to the background of leaves¹⁸⁴. Consequently, orange, red, yellow, pink, crimson and scarlet fruits were classified as conspicuous, and brown, black, green, blue, cream, grey, ivory, straw-coloured, white and purple fruits as cryptic (following ref.¹⁸⁵). When a fruit colour description contained a combination of cryptic and conspicuous colours (e.g. 'green/yellow', 'yellow-brown', 'brown orange'), or when colours were described with a suffix -ish or -ey (indicating to have only a touch of that colour), we inferred that the cryptic colour is the dominant hue and the fruit colour was classified as cryptic. The classification of cryptic vs. conspicuous is here provided as an example to show how the verbatim text descriptions of fruit colours could be used for ecological or evolutionary analyses, e.g. when analysing the colour vision of primates in relation to the distribution of palms with conspicuous fruit colours. Other colour classifications can be developed from the colour verbatim text descriptions as originally extracted from the data sources (column 'FruitColorDescription', Online-only Table 1).

Taxonomy. To standardize the taxonomic names of palms, we followed the World Checklist of palms¹⁸⁶, using a version download from July 2015. This included a total of 2557 accepted palm species names. Since the palm taxonomy is regularly updated by taxonomic experts from the Royal Botanic Gardens in Kew, we recommend to use their taxonomic resources to search for synonyms and currently accepted names. Two useful online resources are the World Checklist of Selected Plant Families (WCSP, <https://wcsp.science.kew.org>, searching for 'Arecaceae') and PalmWeb (<http://www.palmweb.org/>).

Data Records

The PalmTraits 1.0 database can be downloaded from the DRYAD data repository¹⁸¹ under the terms of a Creative Commons Zero (CC0) waiver. The CC0 waiver facilitates the discovery, re-use, and interoperability of the data by removing any legal barriers. We also provide the PalmTraits 1.0 database in the TRY Plant Trait Database (<https://www.try-db.org/>; TRY DatasetID 540) which uses a Creative Commons Attribution License (CC BY 4.0). Regardless of the database version used, we ask users to cite this data paper when these data are used in publications or other activities (e.g. teaching and education), and to also cite the actual version of the database used in accord with emerging standards for data citation.

Data coverage. The PalmTraits 1.0 database covers 24 traits and additional taxonomic information (Online-only Table 1). The species coverage of trait information is complete for growth form (100% coverage), and particularly high for armature ($> 95\%$), stem habit ($> 84\%$), maximum stem height and diameter ($> 73\%$), and for average fruit size and width ($> 77\%$). Other traits are less covered (30–70%, Online-only Table 1), reflecting a lower availability of these traits in the published literature. Nevertheless, the high species coverage of several traits translates into a high geographic completeness of traits within country-level palm assemblages worldwide (Fig. 2, left column). For instance, global coverage of trait information is (near) complete for growth form and stem armature (Fig. 2, left top two maps). Other traits (e.g. maximum stem height, maximum blade length and average fruit length) have lower sampling completeness in species-rich tropical areas such as parts of South America, the Caribbean, Central Africa and Southeast Asia (Fig. 2, left bottom three maps).

Mapping species-level trait information to a phylogeny allows visualizing the phylogenetic coverage of traits. Using a recently published all-evidence species-level supertree of palms¹⁸⁷, we demonstrate that little phylogenetic bias exists in the coverage of key traits across the palm family (Fig. 3).

Applications. The PalmTraits 1.0 allows the analysis of trait variation within palm species assemblages worldwide (Fig. 2, right column). This includes mapping the predominance (i.e. proportion) of particular growth forms (e.g. climbers), the species richness of palms with particular traits (e.g. stem armature), or the average size of stems, leaves or fruits across species that are present within botanical countries (Fig. 2, right column). Another avenue of application is to combine the species-level trait information with phylogenies (e.g. the recently published all-evidence species-level supertree of palms¹⁸⁷) to perform macroevolutionary analyses such as trait-dependent models of speciation, extinction and transition rates^{50,52}.

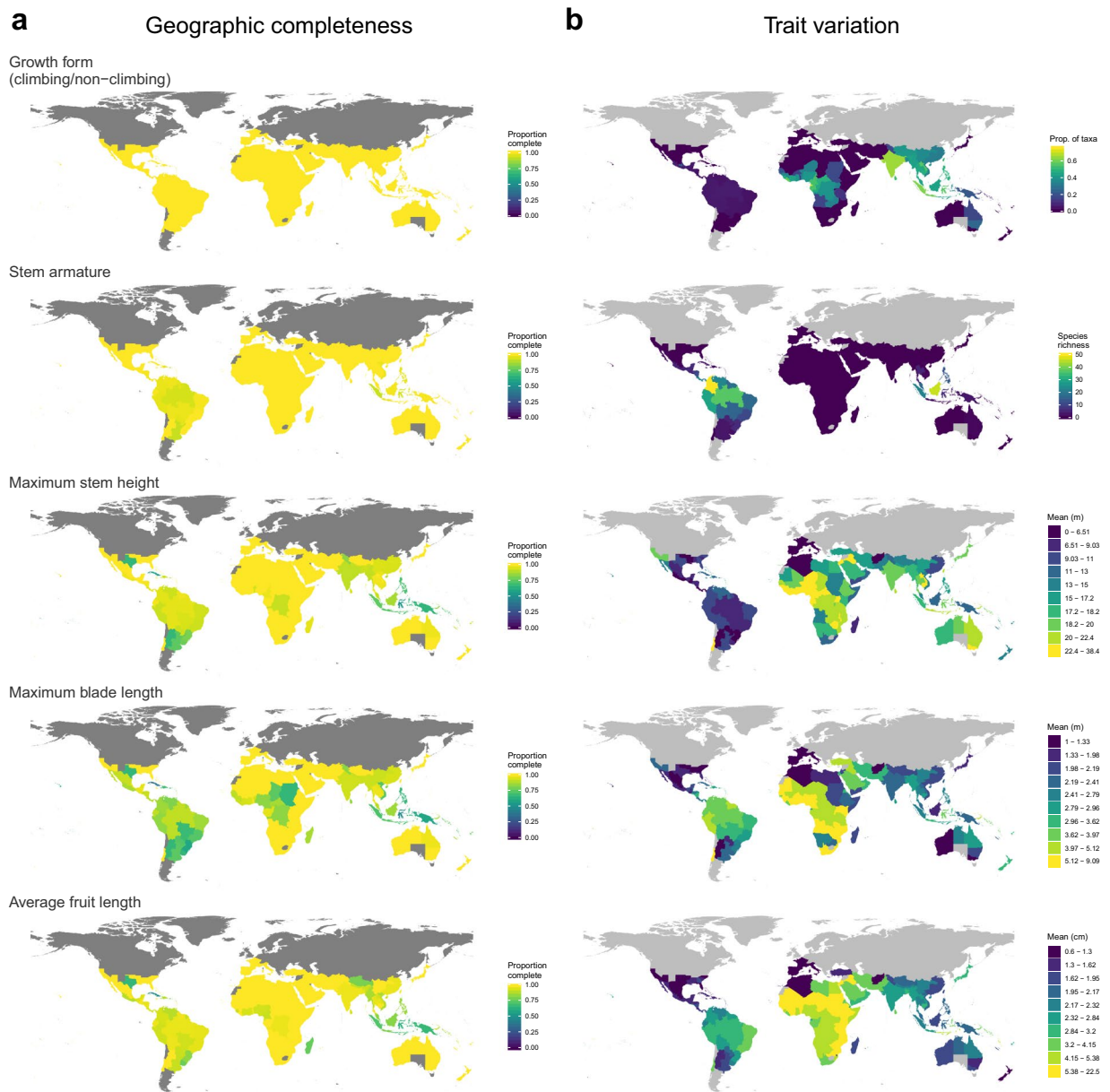


Fig. 2 Geographic variation of trait information for palm assemblages worldwide. In (a), geographic completeness of various palm trait data is shown at the spatial resolution of ‘botanical countries’ (TDWG level 3 units) which are standardized areas defined by the International Working Group on Taxonomic Databases (TDWG) for recording plant distributions¹⁹³. Global palm distribution data from the World Checklist of Palms are available as presence-absence data in TDWG level 3 units¹⁸⁶ and can be used to analyse the global distribution and biogeography of palm assemblages^{37,38,43,206}. Geographic completeness is represented here as the proportion of species having trait information, with yellow showing botanical countries with high completeness and dark blue showing botanical countries with low completeness. In (b), interspecific variation of traits is shown for palm assemblages in botanical countries. Trait variation is exemplified as the proportion of species having a specific growth form (e.g. proportion of climbers), as the species richness of palm species with a particular binary trait (e.g. stem armature), or by representing the mean value of a continuous trait (e.g. maximum stem height, maximum blade length, or average fruit length) across all palm species in a given botanical country. Yellow indicates botanical countries with high trait values and dark blue low trait values.

Technical Validation

All data were digitized by entering trait information from the original source (e.g. books, taxonomic revisions or specimen sheets) into an Excel spreadsheet, where each row represented a palm species and each column a single trait. Subsequent error detection and data quality control were done at three levels. First, trait information on growth forms (climbing, acaulescent, and erect) was carefully checked by a taxonomist (J.D.) with comprehensive experience with palms in the field and herbarium. Trait information of some specific palm genera was further

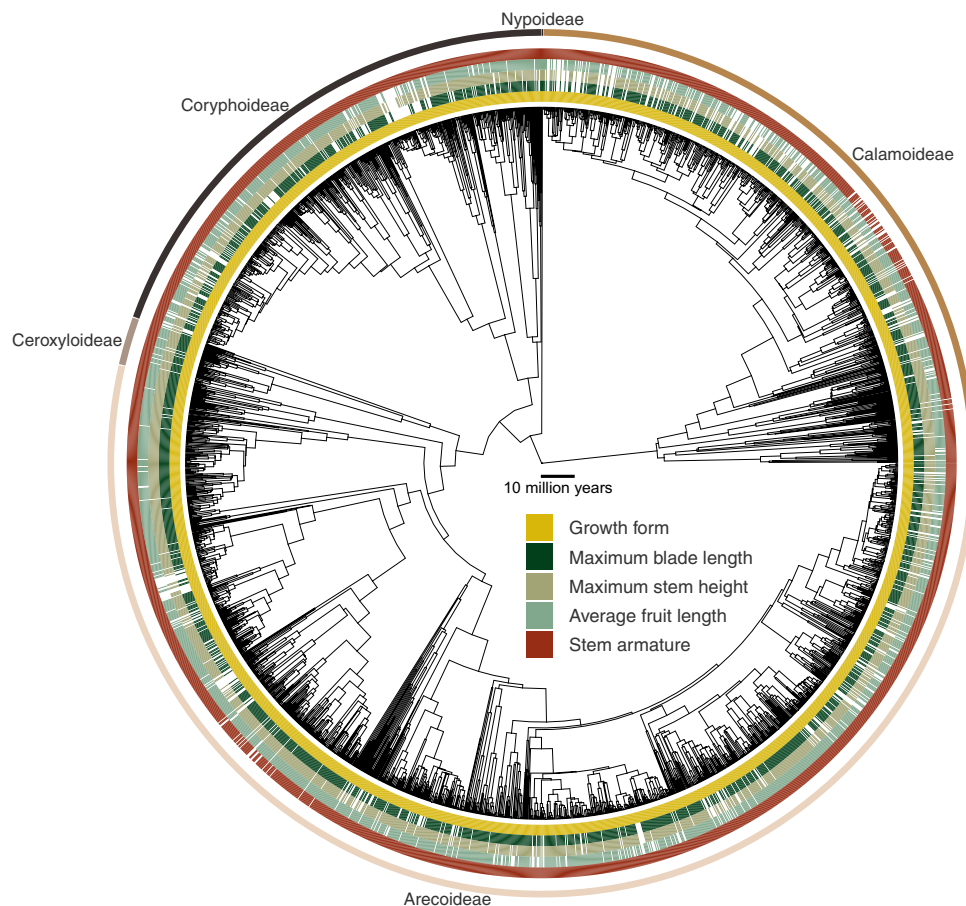


Fig. 3 Phylogenetic distribution of exemplar palm traits. The five inner coloured circles represent species-level presence of trait information for key traits (growth form, maximum blade length, maximum stem height, average fruit length and stem armature). The outer coloured circle represents the five subfamilies of palms (Arecoideae, Ceroxyloideae, Coryphoideae, Nypoideae and Calamoideae). The time-calibrated phylogenetic tree illustrated here is a maximum clade credibility (MCC) tree^{50,52} derived from a recently published all-evidence species-level supertree of palms¹⁸⁷.

checked by additional experts (see acknowledgements). Second, we sorted and filtered the Excel spreadsheet to search for erroneous entries (i.e. obvious errors in data entry) such as text or comma entries in columns with continuous data, or negative trait values and wrong values from unit conversion. These were corrected as much as possible. Third, we identified extreme values and detected outliers by looking at the most extreme (smallest and largest) values of each continuous trait across the whole family as well as within each tribe. These extreme values were checked for plausibility and reliability against external sources and our taxonomic and ecological knowledge of palms, and retained or corrected accordingly. For instance, several climbing palms (especially in the genus *Calamus*) have stem heights ≥ 100 m, with *Calamus manan* being the tallest climbing palm in the world (with 170 m stem height or more)¹⁸⁸. Among erect palms, *Ceroxylon quindiuense* is with >60 m the tallest¹⁸⁹. Fruit size is largest for *Lodoicea maldivica* (50 cm), the palm with the largest seed within the whole plant kingdom¹⁹⁰. In contrast, the smallest fruit sizes are found in palm species in the genus *Coccothrinax*¹⁹¹. Palms also hold the record of the largest leaf of the plant kingdom, with *Raphia regalis* having a maximum blade length of 25 m¹⁹².

Usage Notes

We provide the data via the Dryad digital repository¹⁸¹ and via the TRY plant trait database (www.try-db.org; TRY DatasetID 540). The Dryad release¹⁸¹ contains three files related to the PalmTraits 1.0 database:

1. A tab-delimited text file containing taxonomic information (species, genus, tribe, subfamily) together with all trait data
2. A tab-delimited text file containing all references that have been used for each species.
3. A tab-delimited text file containing the full details of all references that were used.
To facilitate integration with other datasets, we further provide the following files (also via the Dryad data repository¹⁸¹):
4. An R script containing code that allows to combine the PalmTraits 1.0 database with species distribution and phylogenetic information

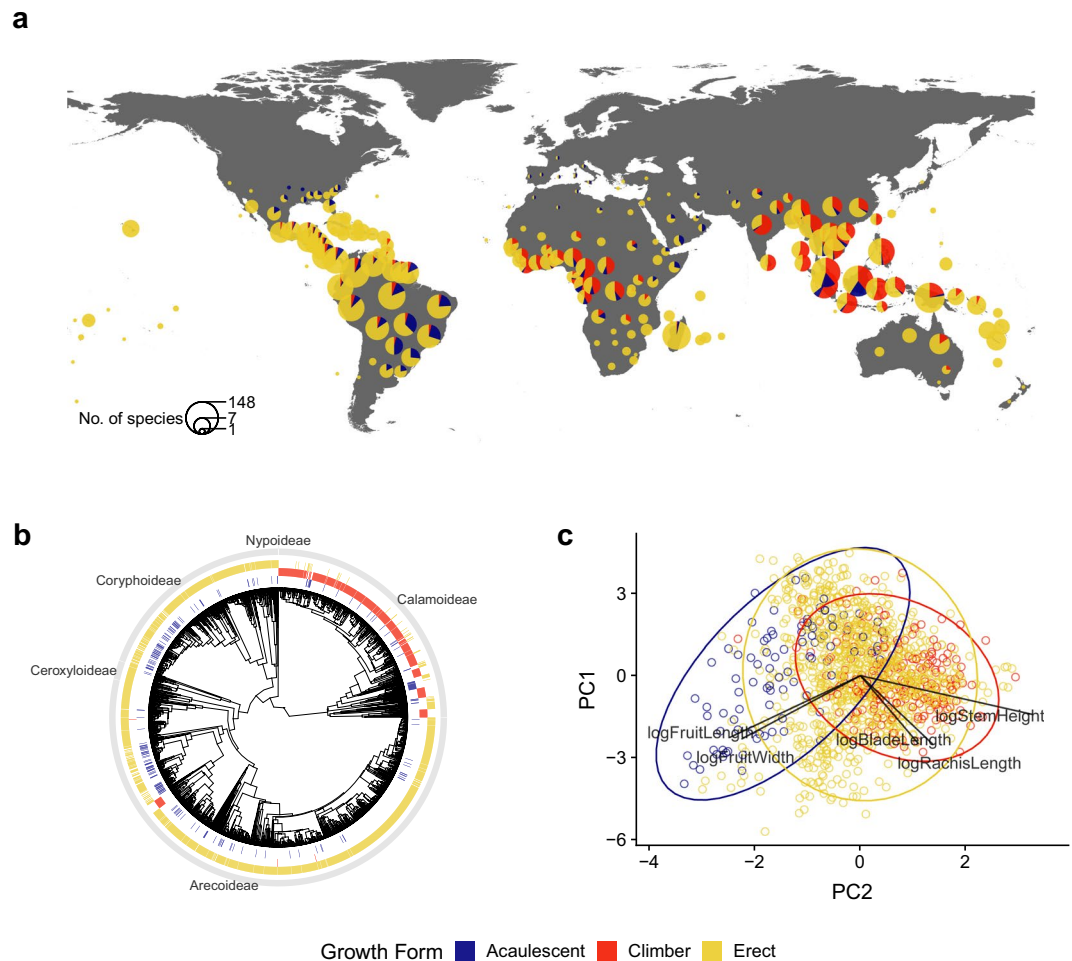


Fig. 4 Examples of combining palm trait data, species distribution and phylogenetic information. The global map in (a) shows the relative proportion of major palm growth forms within ‘botanical countries’ worldwide (i.e. geographic units as defined by the International Working Group on Taxonomic Databases, TDWG¹⁹³) by combining growth form information (climbing, acaulescent, and erect) with global species distribution data from the world checklist of palms¹⁸⁶. In (b), palm growth form information is linked to a species-level palm phylogeny¹⁸⁷ using a Maximum Clade Credibility (MCC) phylogenetic tree^{50,52} to illustrate the phylogenetic distribution of climbing, acaulescence and erect growth forms in palms. Climbing dominates in the subfamily Calamoideae whereas erect palms are common in subfamilies Coryphoideae, Ceroxyloideae and Arecoideae. Acaulescent palms are scattered across the palm phylogenetic tree. In (c), the location of different palm growth forms (climbing, acaulescent, and erect) in a multivariate trait space is illustrated by the first two axes of a Principal Component Analysis (PCA) based on continuous trait information on stem height (logStemHeight), leaf size (logBladeLength and logRachisLength) and fruit size of palms (logFruitLength and logFruitWidth). The figure can be reproduced with data and an R script that integrates the PalmTraits 1.0 database with spatial and phylogenetic data¹⁸¹.

5. A shape file with all botanical countries (TDWG level 3 units) worldwide
6. Presence-absence data of palms at the resolution of botanical countries
7. Phylogenetic information of palms represented as maximum clade credibility (MCC) tree

Tips for integrating the data records with other datasets. The R script that we provide contains guidance of how to integrate the PalmTraits 1.0 database with spatial and phylogenetic data and how to explore multi-variate trait variation¹⁸¹. We illustrate this by using the growth form information (climbing, acaulescent, and erect) from PalmTraits 1.0 (Fig. 4). We first load global species distribution data from the world checklist of palms¹⁸⁶ and then combine them with the new palm growth form data and a polygon file that represents geographic units (‘botanical countries’, i.e. TDWG level 3 units) as defined by the International Working Group on Taxonomic Databases (TDWG), a geographic standard for recording plant distributions¹⁹³. This allows plotting the proportion of growth forms in palm assemblages worldwide (Fig. 4a). We then map growth form information onto a species-level palm phylogeny¹⁸⁷ using a Maximum Clade Credibility (MCC) phylogenetic tree as recently used in macroevolutionary analyses of palms^{50,52}. This allows to explore growth form information in

a phylogenetic context (Fig. 4b). Finally, the R script illustrates how continuous trait information (e.g. on stem height, leaf size and fruit size) can be combined with growth form information to explore the multi-dimensional nature of species traits (Fig. 4c).

Imputation of missing trait data. As trait values are often not available for all species (Online-only Table 1), we recommend to explore data imputation methods to fill information for missing data. Data imputation might be especially important for analyses where complete trait-based representation of all palm species is crucial. For instance, metrics of functional diversity¹⁹⁴ can be systematically biased when trait data coverage is incomplete^{195,196} and gap-filling may allow to reduce errors when interpreting functional diversity patterns¹⁹⁷. Data imputation may be performed in a variety of ways, for example through the leveraging of phylogenetic comparative models¹⁹⁸, taxonomic hierarchies¹⁹⁹, or machine learning algorithms²⁰⁰. The relative performance and accuracy of the methods will depend on completeness and interspecific and intraspecific variation of traits. For instance, if correlations among traits are not strong, predictions based on observed covariation in existing trait data should be used with caution. We suggest that data imputation methods should be rigorously tested and accompanied with comprehensive sensitivity analyses to assess their performance²⁰¹.

Semantic integration with other plant trait data. Plant trait data are measured in a multitude of ways²⁰², and this heterogeneity together with a lack of standards for acquiring, organizing and describing trait data makes their integration often difficult^{3,203,204}. Trait data of palms are usually described in a standardized and systematic way within taxonomic descriptions and revisions. This makes the extraction of palm trait data relatively straightforward. However, many of the palm trait terms and measurements are not directly captured in semantic descriptions of plant traits such as the global handbook for standardised measurement of plant functional traits²⁰⁵ or the thesaurus of plant characteristics (TOP)²⁰³. During the collection of palm trait data, we did not harmonize the terminology of palm trait definitions with other plant trait terminologies because they were internally consistent (i.e. within the palm family). However, after finalizing the data collection we mapped the palm trait definitions to the TOP (see Online-only Table 1). Several palm traits are currently not represented in the TOP. For instance, fruit colour is currently not represented within the dispersule trait category of the TOP. Similarly, maximum number of leaves as well as armature on leaves and stems are currently not captured by the TOP. This highlights the need for further development of the TOP and other semantic resources to facilitate the integration of trait data from multiple sources³. Such efforts will also allow better interoperability and effectiveness of automated data exchange among different sources. We therefore urge the research community to further develop and harmonize existing plant traits terminologies and semantic relations.

Code Availability

The original data collection was done by entering trait information into an Excel spreadsheet (Microsoft Office 2013). No code is available for this step. The final PalmTraits 1.0 dataset was saved as tab-delimited text file¹⁸¹. Scripts to load the PalmTraits 1.0 dataset into R, to plot multi-variate trait variation and to combine it with phylogenetic and species distribution data are available in the accompanying dataset¹⁸¹. The scripts were developed in R version 3.5.0, and using the associated libraries as indicated in the scripts. There are no restrictions to use the provided code.

References

1. Violle, C. *et al.* Let the concept of trait be functional! *Oikos* **116**, 882–892, <https://doi.org/10.1111/j.0030-1299.2007.15559.x> (2007).
2. Diaz, S. *et al.* Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution* **3**, 2958–2975, <https://doi.org/10.1002/ece3.601> (2013).
3. Kissling, W. D. *et al.* Towards global data products of Essential Biodiversity Variables on species traits. *Nature Ecology & Evolution* **2**, 1531–1540, <https://doi.org/10.1038/s41559-018-0667-3> (2018).
4. Bjorkman, A. D. *et al.* Plant functional trait change across a warming tundra biome. *Nature* **562**, 57–62, <https://doi.org/10.1038/s41586-018-0563-7> (2018).
5. Diaz, S. *et al.* The global spectrum of plant form and function. *Nature* **529**, 167–171, <https://doi.org/10.1038/nature16489> (2016).
6. Lavorel, S. & Garnier, E. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16**, 545–556 (2002).
7. Schneider, F. D. *et al.* Mapping functional diversity from remotely sensed morphological and physiological forest traits. *Nature Communications* **8**, 1441, <https://doi.org/10.1038/s41467-017-01530-3> (2017).
8. Lavorel, S. *et al.* A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *Journal of Vegetation Science* **24**, 942–948, <https://doi.org/10.1111/jvs.12083> (2013).
9. Eskildsen, A. *et al.* Ecological specialization matters: long-term trends in butterfly species richness and assemblage composition depend on multiple functional traits. *Diversity and Distributions* **21**, 792–802, <https://doi.org/10.1111/ddi.12340> (2015).
10. Pacifici, M. *et al.* Species' traits influenced their response to recent climate change. *Nature Climate Change* **7**, 205–208, <https://doi.org/10.1038/nclimate3223> (2017).
11. Hagen, M. *et al.* Biodiversity, species interactions and ecological networks in a fragmented world. *Advances in Ecological Research* **46**, 89–210 (2012).
12. Genner, M. J. *et al.* Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. *Global Change Biology* **16**, 517–527, <https://doi.org/10.1111/j.1365-2486.2009.02027.x> (2010).
13. Costello, M. J. *et al.* Biological and ecological traits of marine species. *PeerJ* **3**, e1201 (2015).
14. Madin, J. S. *et al.* The Coral Trait Database, a curated database of trait information for coral species from the global oceans. *Scientific Data* **3**, 160017, <https://doi.org/10.1038/sdata.2016.17> (2016).
15. Schmidt-Kloiber, A. & Hering, D. www.freshwaterecology.info – An online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecological Indicators* **53**, 271–282, <https://doi.org/10.1016/j.ecolind.2015.02.007> (2015).
16. Kattge, J. *et al.* TRY – a global database of plant traits. *Global Change Biology* **17**, 2905–2935, <https://doi.org/10.1111/j.1365-2486.2011.02451.x> (2011).

17. Wilman, H. *et al.* EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* **95**, 2027–2027, <https://doi.org/10.1890/13-1917.1> (2014).
18. Kissling, W. D. *et al.* Establishing macroecological trait datasets: Digitalization, extrapolation, and validation of diet preferences in terrestrial mammals worldwide. *Ecology and Evolution* **4**, 2913–2930, <https://doi.org/10.1002/ece3.1136> (2014).
19. Oliveira, B. F., São-Pedro, V. A., Santos-Barrera, G., Penone, C. & Costa, G. C. AmphiBIO, a global database for amphibian ecological traits **4**, 170123, <https://doi.org/10.1038/sdata.2017.123> (2017).
20. Guralnick, R. P. *et al.* The importance of digitized biocollections as a source of trait data and a new VertNet resource. *Database* **2016**, baw158, <https://doi.org/10.1093/database/baw158> (2016).
21. Hortal, J. *et al.* Seven shortfalls that beset large-scale knowledge of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* **46**, 523–549, <https://doi.org/10.1146/annurev-ecolsys-112414-054400> (2015).
22. Meyer, C., Kreft, H., Guralnick, R. & Jetz, W. Global priorities for an effective information basis of biodiversity distributions. *Nature Communications* **6**, 8221, <https://doi.org/10.1038/ncomms9221> (2015).
23. Bruehlheide, H. *et al.* Global trait–environment relationships of plant communities. *Nature Ecology & Evolution* **2**, 1906–1917, <https://doi.org/10.1038/s41559-018-0699-8> (2018).
24. Salguero-Gómez, R. *et al.* COMADRE: a global data base of animal demography. *Journal of Animal Ecology* **85**, 371–384, <https://doi.org/10.1111/1365-2656.12482> (2016).
25. Salguero-Gómez, R. *et al.* The COMPADRE Plant Matrix Database: an open online repository for plant demography. *Journal of Ecology* **103**, 202–218, <https://doi.org/10.1111/1365-2745.12334> (2015).
26. Malhi, Y. *et al.* Climate change, deforestation, and the fate of the Amazon. *Science* **319**, 169–172, <https://doi.org/10.1126/science.1146961> (2008).
27. Richardson, J. E. & Pennington, R. T. *Origin of tropical diversity: from clades to communities*. (Frontiers Media, 2016).
28. Couvreur, T. L. P. & Baker, W. J. Tropical rain forest evolution: palms as a model group. *BMC Biology* **11**, 48 (2013).
29. Eiserhardt, W. L., Svenning, J.-C., Kissling, W. D. & Balslev, H. Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. *Annals of Botany* **108**, 1391–1416, <https://doi.org/10.1093/aob/mcr146> (2011).
30. Zona, S. & Henderson, A. A review of animal mediated seed dispersal of palms. *Selbyana* **11**, 6–21 (1989).
31. Baker, W. J. & Dransfield, J. Beyond Genera Palmarum: progress and prospects in palm systematics. *Botanical Journal of the Linnean Society* **182**, 207–233, <https://doi.org/10.1111/boj.12401> (2016).
32. Henderson, A. *Evolution and ecology of palms*. (The New York Botanical Garden Press, 2002).
33. Fleming, T. H. & Kress, W. J. *The ornaments of life: coevolution and conservation in the tropics*. (Chicago University Press, 2013).
34. Barfod, A. S., Hagen, M. & Borchsenius, F. Twenty-five years of progress in understanding pollination mechanisms in palms (Arecaceae). *Annals of Botany* **108**, 1503–1516, <https://doi.org/10.1093/aob/mcr192> (2011).
35. Cámara-Leret, R. *et al.* Fundamental species traits explain provisioning services of tropical American palms. *Nature. Plants* **3**, 16220, <https://doi.org/10.1038/nplants.2016.220> (2017).
36. Johnson, D. V. *Tropical palms*. (Food and Agriculture Organization of the United Nations, 2010).
37. Kissling, W. D. Has frugivory influenced the macroecology and diversification of a tropical keystone plant family? *Research Ideas and Outcomes* **3**, e14944, <https://doi.org/10.3897/rio.3.e14944> (2017).
38. Couvreur, T. L. P. *et al.* Global diversification of a tropical plant growth form: environmental correlates and historical contingencies in climbing palms. *Frontiers in Genetics* **5**, 452, <https://doi.org/10.3389/fgene.2014.00452> (2015).
39. Morley, R. J. *Origin and evolution of tropical rain forests*. (John Wiley & Sons, 2000).
40. Baker, W. J. & Couvreur, T. L. P. Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. I. Historical biogeography. *Journal of Biogeography* **40**, 274–285, <https://doi.org/10.1111/j.1365-2699.2012.02795.x> (2013).
41. Baker, W. J. & Couvreur, T. L. P. Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. II. *Diversification history and origin of regional assemblages*. *Journal of Biogeography* **40**, 286–298, <https://doi.org/10.1111/j.1365-2699.2012.02794.x> (2013).
42. Moore, H. E. The major groups of palms and their distribution. *Gentes Herbarum* **11**, 27–140 (1973).
43. Kissling, W. D. *et al.* Quaternary and pre-Quaternary historical legacies in the global distribution of a major tropical plant lineage. *Global Ecology and Biogeography* **21**, 909–921, <https://doi.org/10.1111/j.1466-8238.2011.00728.x> (2012).
44. Greenwood, D. R. & Wing, S. L. Eocene continental climates and latitudinal temperature gradients. *Geology* **23**, 1044–1048 (1995).
45. Blach-Overgaard, A., Kissling, W. D., Dransfield, J., Balslev, H. & Svenning, J.-C. Multimillion-year climatic effects on palm species diversity in Africa. *Ecology* **94**, 2426–2435, <https://doi.org/10.1890/12-1577.1> (2013).
46. Blach-Overgaard, A., Balslev, H., Dransfield, J., Normand, S. & Svenning, J.-C. Global-change vulnerability of a key plant resource, the African palms. *Scientific Reports* **5**, 12611, <https://doi.org/10.1038/srep12611> (2015).
47. Galetti, M. *et al.* Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* **340**, 1086–1090, <https://doi.org/10.1126/science.1233774> (2013).
48. Göldel, B., Araujo, A. C., Kissling, W. D. & Svenning, J.-C. Impacts of large herbivores on spinescence and abundance of palms in the Pantanal, Brazil. *Botanical Journal of the Linnean Society* **182**, 465–479, <https://doi.org/10.1111/boj.12420> (2016).
49. Göldel, B., Kissling, W. D. & Svenning, J.-C. Geographical variation and environmental correlates of functional trait distributions in palms (Arecaceae) across the New World. *Botanical Journal of the Linnean Society* **179**, 602–617, <https://doi.org/10.1111/boj.12349> (2015).
50. Onstein, R. E. *et al.* Frugivory-related traits promote speciation of tropical palms. *Nature Ecology & Evolution* **1**, 1903–1911, <https://doi.org/10.1038/s41559-017-0348-7> (2017).
51. König, C. *et al.* Biodiversity data integration—The significance of data resolution and domain. *PLOS Biology* **17**, e3000183, <https://doi.org/10.1371/journal.pbio.3000183> (2019).
52. Onstein, R. E. *et al.* To adapt or go extinct? The fate of megafaunal palm fruits under past global change. *Proceedings of the Royal Society B: Biological Sciences* **285**, 20180882, <https://doi.org/10.1098/rspb.2018.0882> (2018).
53. Dransfield, J. In *Flora of tropical East Africa* (ed. Polhill, R. M.) (A. A. Balkema, 1986).
54. Russell, T. A. In *Flora of west tropical Africa* Vol. 2 (ed. Hepper, F. N.) (Whitefriars Press, 1968).
55. Sunderland, T. C. H. *Field guide to the rattans of Africa*. (Royal Botanic Gardens, 2007).
56. Tuley, P. *The palms of Africa*. (The Trendrine Press, 1995).
57. Henderson, A., Galeano, G. & Bernal, R. *Field guide to the palms of the Americas*. (Princeton University Press, 1995).
58. Dowe, J. L. *Australian palms: biogeography, ecology and systematics*. (CSIRO Publishing, 2010).
59. Lorenzi, H. *Brazilian Flora Arecaceae (Palms)*. (Instituto Plantarum, 2010).
60. Galeano, G. & Bernal, R. *Palmas de Colombia: guía de campo*. (Panamericana Formas e Impresos S.A., 2010).
61. Grayum, M. H. Nomenclatural and taxonomic notes on Costa Rican palms (Arecaceae), with five new species. *Phytologia* **84**, 307–327 (1998).
62. Borchsenius, F., Pedersen, H. B. & Balslev, H. *Manual to the palms of Ecuador*. *AAU Reports* **37**. (Aarhus University Press, 1998).
63. Read, R. & Hodel, D. R. In *Manual of the flowering plants of Hawai'i*. *Bishop Museum Special Publication* **83** (eds Wagner, W. L., Herbst, D. R. & Sohmer, S. H.) (B.P. Bishop Museum, 1990).
64. Mogege, J. P. In *Palms for human needs in Asia* (ed. Johnson, D.) (A.A. Balkema, 1991).
65. Dransfield, J. & Beentje, H. *The palms of Madagascar*. (Royal Botanic Gardens Kew and The International Palm Society, 1995).

66. Rakotoarinivo, M. & Dransfield, J. New species of *Dypsis* and *Ravenea* (Arecaceae) from Madagascar. *Kew Bulletin* **65**, 279–303, <https://doi.org/10.1007/s12225-010-9210-7> (2010).
67. Rakotoarinivo, M., Trudgen, M. S. & Baker, W. J. The palms of the Makira Protected Area, Madagascar. *Palms* **53**, 125–146 (2009).
68. Dransfield, J. *A manual of the rattans of the Malay Peninsula*. *Malayan Forest Records* **29**. (Forest Department, Ministry of Primary Industries, 1979).
69. Kiew, R. In *Proceedings 1st International Sago Symposium* (ed. Tan, K.) (Demajuan Kanji Sdn. Bhd., 1977).
70. Moore, H. E. & Guého, L. J. In *Flore des Mascareignes* (eds Bosser, J., Cadet, T., Guého, J. & Marais, W.) (The Sugar Industry Research Institute, l'Office de la Recherche Scientifique Outre-Mer & Royal Botanic Gardens, Kew, 1984).
71. Hodel, D. R. & Pintaud, J.-C. *The palms of New Caledonia*. (Kampon Tansacha, Nong Nooch Tropical Garden, 1998).
72. de Guzman, E. D. & Fernando, E. S. *Guide to Philippine flora and fauna*. (1986).
73. Dransfield, J. *The rattans of Sabah*. (Forest Department, 1984).
74. Henderson, A. *Palms of Southern Asia*. (Princeton University Press, 2009).
75. Hodel, D. R. *The palms of Thailand*. (Allen Press, 1998).
76. Henderson, A. & Dung, N. Q. Notes on rattans (Arecaceae) from Vietnam. *Phytotaxa* **8**, 25–33 (2010).
77. Vianna, S. A., Berton, L. H. C., Pott, A., Guerreiro, S. M. C. & Colombo, C. A. Biometric characterization of fruits and morphoanatomy of the mesocarp of *Acrocomia* species (Arecaceae). *International Journal of Biology* **9**, 78–92, <https://doi.org/10.5539/ijb.v9n3p78> (2017).
78. Borchsenius, F. & Bernal, R. Aiphanes (Palmae). *Flora Neotropica* **70**, 1–94 (1996).
79. Dowe, J. L. & Hodel, D. R. A revision of *Archontophoenix* H.Wendl. & Drude (Arecaceae). *Austrobaileya* **4**, 227–244 (1994).
80. Heatubun, C. D. Seven New Species of *Areca* (Arecaceae). *Phytotaxa* **28**, 6–26 (2011).
81. Stauffer, F. W., Asmussen, C. B., Henderson, A. & Endress, P. K. A revision of *Asterogyne* (Arecaceae: Arecoideae: Geonomeae). *Brittonia* **55**, 326–356, [https://doi.org/10.1663/0007-196x\(2003\)055\[0326:arocaa\]2.0.co;2](https://doi.org/10.1663/0007-196x(2003)055[0326:arocaa]2.0.co;2) (2003).
82. Kahn, F. The genus *Astrocaryum* (Arecaceae). *Revista Peruana de Biología* **15**, 31–48 (2008).
83. Kahn, E. & Ferreira, E. J. L. A new species of *Astrocaryum* (Palmae) from Acre, Brazil. *Candollea* **50**, 321–328 (1995).
84. Pintaud, J.-C., Del Castillo, A. M. R., Ferreira, E. J. L. & R, M. M. Towards a revision of *Attalea* in Western Amazonia. *Palms* **60**, 57–78 (2016).
85. Henderson, A. *Bactris* (Palmae). *Flora Neotropica Monographs* **79**, 1–181 (2000).
86. Cascante, A. Additions to the Genus *Bactris* (Arecaceae) of Mesoamerica. *Palms* **44**, 146–153 (2000).
87. Hodel, D. R. A synopsis of the genus *Balaka*. *Palms* **54**, 161–188 (2010).
88. Dransfield, J. The genus *Borassodendron* in Malesia. *Reinwardtia* **8**, 351–363 (1972).
89. Noblick, L. R. *Butia*: What we think we know about the genus. *Journal of Oil Palm Research* **208**, 5–23 (2014).
90. Dowe, J. L. & Ferrero, M. D. Revision of *Calyptrocalyx* and the New Guinea species of *Linospadix* (Linospadicinae: Arecaceae: Blumea - Biodiversity, Evolution and Biogeography of Plants **46**, 207–251 (2001).
91. Henderson, A. A multivariate study of *Calyptrogyne* (Palmae). *Systematic Botany* **30**, 60–83, <https://doi.org/10.1600/0363644053661913> (2005).
92. Dransfield, J. & Baker, W. J. An account of the Papuan species of *Calamus* (Arecaceae) with paired fruit. *Kew Bulletin* **58**, 371–387, <https://doi.org/10.2307/4120621> (2003).
93. Henderson, A., Ban, N. K. & Dung, N. Q. New species of *Calamus* (Palmae) from Vietnam. *Palms* **52**, 187–197 (2008).
94. Jacob, J., Mohanan, N. & Kariyappa, K. C. A new species of *Calamus* L. (Arecaceae) from Silent Valley, the Western Ghats, India. *Rheedea* **18**, 29–31 (2008).
95. Hahn, W. *Biosystematics and evolution of the genus Caryota* (Palmae: Arecoideae) PhD thesis, University of Wisconsin, (1993).
96. Jeanson, M. L., Yusuf, Z. & Labat, J.-N. A new species of *Caryota* (Arecaceae, Coryphoideae) from Central and North Sulawesi. *Systematic Botany* **36**, 600–604 (2011).
97. Hodel, D. R. *Chamaedorea palms: the species and their cultivation*. (The International Palm Society, Allen Press, 1992).
98. Hodel, D. R. Two new species of *Chamaedorea* (Arecaceae). *Novon* **7**, 35–37, <https://doi.org/10.2307/3392071> (1997).
99. Hodel, D. R. Additions to *Chamaedorea* palms: new species from Mexico and Guatemala and miscellaneous notes. *Principes* **36**, 188–202 (1992).
100. Hodel, D. R. Three new species of *Chamaedorea* from Panama. *Principes* **39**, 14–20 (1995).
101. Hodel, D. R. Two new species of *Chamaedorea* from Costa Rica. *Principes* **40**, 212–216 (1996).
102. Hodel, D. R., Herrera, G. & Cascante, A. A remarkable new species and additional novelties of *Chamaedorea* from Costa Rica and Panama. *Palm. Journal* **137**, 32–44 (1997).
103. Hodel, D. R., Mont, J. J. C. & Zuniga, R. Two new species of *Chamaedorea* from Honduras. *Principes* **39**, 183–189 (1995).
104. Heatubun, C. D. *et al.* A monograph of *Cyrtostachys* (Arecaceae). *Kew Bulletin* **64**, 67–94, <https://doi.org/10.1007/s12225-009-9096-4> (2009).
105. Zona, S. Revision of *Drymophloeus* (Arecaceae: Arecoideae). *Blumea - Biodiversity, Evolution and Biogeography of Plants* **44**, 1–24 (1999).
106. Sunderland, T. C. H. A taxonomic revision of the rattans of Africa (Arecaceae: Calamoideae). *Phytotaxa* **51**, 1–76 (2012).
107. Henderson, A. A revision of *Geonoma* (Arecaceae). *Phytotaxa* **17**, 1–271 (2011).
108. Trudgen, M. S. & Baker, W. J. A revision of the *Heterospathe elegans* (Arecaceae) complex in New Guinea. *Kew Bulletin* **63**, 639–647 (2008).
109. Heatubun, C. D., Petoe, P. & Baker, W. J. A monograph of the *Nengella* group of *Hydriastele* (Arecaceae). *Kew Bulletin* **73**, 18, <https://doi.org/10.1007/s12225-018-9743-8> (2018).
110. Petoe, P., Cámara-Leret, R. & Baker, W. J. A monograph of the *Hydriastele wendlandiana* group (Arecaceae: Hydriastele). *Kew Bulletin* **73**, 17, <https://doi.org/10.1007/s12225-018-9736-7> (2018).
111. Skov, F. & Balslev, H. A revision of *Hyospathe* (Arecaceae). *Nordic Journal of Botany* **9**, 189–202, <https://doi.org/10.1111/j.1756-1051.1989.tb02114.x> (1989).
112. Dransfield, J. The genus *Johannesteijsmannia* H.E. Moore Jr. *Garden Bulletin Singapore* **26**, 63–83 (1972).
113. Henderson, A. J. & Bacon, C. D. *Lanonia* (Arecaceae: Palmae), a new genus from Asia, with a revision of the species. *Systematic Botany* **36**, 883–895, <https://doi.org/10.1600/036364411x604903> (2011).
114. Saw, L. G., Dransfield, J. & Keith-Lucas, D. M. Morphological diversity of the genus *Licuala* (Palmae). *Telopea* **10**, 187–206 (2003).
115. Saw, L. G. A revision of *Licuala* (Palmae) in the Malay Peninsula. *Sandakania* **10**, 1–95 (1997).
116. Saw, L. G. A revision of *Licuala* (Arecaceae, Coryphoideae) in Borneo. *Kew Bulletin* **67**, 577–654, <https://doi.org/10.1007/s12225-012-9414-0> (2012).
117. Dowe, J. L. & Irvine, A. K. A revision of *Linospadix* in Australia, with the description of a new species. *Principes* **41**, 192–197 (1997).
118. Rodd, A. N. Revision of *Livistona* (Arecaceae) in Australia. *Telopea* **8**, 49–153 (1998).
119. Dowe, J. L. A taxonomic account of *Livistona* R.Br. (Arecaceae). *Garden's Bulletin Singapore* **60**, 185–344 (2009).
120. Rauwerdink, J. B. An essay on *Metroxylon*, the sago palm. *Principes* **30**, 165–180 (1986).
121. Fernando, E. S. A revision of the genus *Nenga*. *Principes* **27**, 55–70 (1983).
122. Keim, A. P. & Dransfield, J. A monograph of the genus *Orania* (Arecaceae: Oranieae). *Kew Bulletin* **67**, 127–190, <https://doi.org/10.1007/s12225-012-9356-6> (2012).
123. Mónica, M. R. & Henderson, A. The genus *Parajubaea* (Palmae). *Brittonia* **42**, 92–99, <https://doi.org/10.2307/2807619> (1990).

124. Barrow, S. C. A monograph of *Phoenix* L. (Palmae: Coryphoideae). *Kew Bulletin* **53**, 513–575, <https://doi.org/10.2307/4110478> (1998).
125. Dransfield, J. Systematic notes on *Pinanga* (Palmae) in Borneo. *Kew Bulletin* **34**, 769–788, <https://doi.org/10.2307/4119070> (1980).
126. Essig, F. B. A revision of the genus *Ptychosperma* Labill. (Arecaceae). *Allertonia* **1**, 415–478 (1978).
127. Hodel, D. R. A review of the genus *Pritchardia*. *Palms* **51**, S1–S53 (2007).
128. Hastings, L. A revision of *Rhapis*, the lady palms. *Palms* **47**, 62–78 (2003).
129. Zona, S. A monograph of *Sabal* (Arecaceae: Coryphoideae). *Aliso* **12**, 583–666 (1990).
130. Glassman, S. F. Revisions of the palm genus *Syagrus* Mart. and other selected genera in the *Cocos* alliance. *Illinois Biological Monographs* **59**, 1–414 (1987).
131. Noblick, L. R. A revision of the genus *Syagrus* (Arecaceae). *Phytotaxa* **294**, 1–262 (2018).
132. Hodel, D. R. Hybrids in the genus *Syagrus*. *Palms* **55**, 141–154 (2011).
133. Noblick, L. R. *Syagrus* × *mirandana*, a naturally occurring hybrid of *S. coronata* and *S. microphylla*. *Palms* **56**, 57–60 (2012).
134. Noblick, L. R. & Lorenzi, H. New *Syagrus* species from Brazil. *Palms* **54**, 18–42 (2010).
135. Moore, H. E. Synopses of various genera of Arecaceae: *Veitchia*. *Gentes Herbarum* **8**, 483–536 (1957).
136. Henderson, A. A revision of *Wallichia* (Palmae). *Taiwania* **52**, 1–11, [https://doi.org/10.6165/tai.2007.52\(1\).1](https://doi.org/10.6165/tai.2007.52(1).1) (2007).
137. Henderson, A. A revision of *Chuniophoenix* (Arecaceae). *Phytotaxa* **218**, 163–170 (2015).
138. Henderson, A. A revision of *Desmoncus* (Arecaceae). *Phytotaxa* **35**, 1–88 (2011).
139. Henderson, A. J. A multivariate analysis of *Hyospathe* (Palmae). *American Journal of Botany* **91**, 953–965 (2004).
140. Henderson, A. *Hyospathe*. *Palms* **48**, 161–166 (2004).
141. Henderson, A. A revision of *Leopoldinia* (Arecaceae). *Phytotaxa* **32**, 1–17 (2011).
142. Henderson, A. A revision of *Pholidostachys* (Arecaceae). *Phytotaxa* **43**, 1–48, <https://doi.org/10.11646/phytotaxa.43.1.1> (2012).
143. Henderson, A. A revision of *Rhapis* (Arecaceae). *Phytotaxa* **258**, 137–152 (2016).
144. Henderson, A. & Ferreira, E. A morphometric study of *Synechanthus* (Palmae). *Systematic Botany* **27**, 693–702 (2002).
145. Henderson, A. & Villalba, I. A revision of *Welfia* (Arecaceae). *Phytotaxa* **119**, 33–44 (2013).
146. Aliaga-Rossel, E., Moraes, R. & Mamíferos, M. consumidores de frutas y semillas de la chonta (*Astrocaryum gratum*, Arecaceae) en bosques submontanos y aluviales de Bolivia. *Ecología en Bolivia* **49**, 98–103 (2014).
147. Bacon, C. D. & Baker, W. J. *Saribus* resurrected. *Palms* **55**, 109–116 (2011).
148. Balick, M. J., Anderson, A. B. & de Medeiros-Costa, J. T. Hybridization in the babassu palm complex. II. *Attalea compta* × *Orbignya oleifera* (Palmae). *Brittonia* **39**, 26–36, <https://doi.org/10.2307/2806969> (1987).
149. Barfod, A. S. A monographic study of the subfamily Phytelephantoideae (Arecaceae). *Opera Botanica* **105**, 1–73 (1991).
150. Barfod, A. S. & Heatubun, C. D. Two new species of *Licuala* Thunb. (Arecaceae: Coryphoideae) from North Moluccas and Western New Guinea. *Kew Bulletin* **64**, 553–557, <https://doi.org/10.1007/s12225-009-9129-z> (2009).
151. Bernal, R. Demography of the vegetable ivory palm *Phytelephas seemannii* in Colombia, and the impact of seed harvesting. *Journal of Applied Ecology* **35**, 64–74, <https://doi.org/10.1046/j.1365-2664.1998.00280.x> (1998).
152. Bernal, R., Galeano, G. & Hodel, D. R. A new species of *Chamaedorea* from Columbia. *Palms* **48**, 27–29 (2004).
153. Bernal, R. & Borchsenius, F. Taxonomic novelties in *Aiphanes* (Palmae) from Colombia and Venezuela. *Caldasia* **32**, 117–127 (2010).
154. Dowe, J. L. & Ferrero, M. D. A new species of rheophytic palm from New Guinea. *Palms* **44**, 194–197 (2000).
155. Dransfield, J. In *Tropical trees as living systems* (eds P. B. Tomlinson & M. H. Zimmermann) 232–246 (Cambridge University Press, 1978).
156. Dupuyoo, J.-M. Two palms with surprising qualities. *Palms* **50**, 179–183 (2006).
157. Essig, F. B. & Hernandez, N. A systematic histological study of palm fruits. V. Subtribe Archontophoenicinae (Arecaceae). *Brittonia* **54**, 65–71 (2002).
158. Essig, F. B. & Litten, L. A systematic histological analysis of palm fruits VII. The Cyrtostachyinae (Arecaceae). *Brittonia* **56**, 375–379 (2004).
159. Essig, F. B. A systematic histological study of palm fruits. VI. Subtribe Linospadicinae (Arecaceae). *Brittonia* **54**, 196–201 (2002).
160. Essig, F. B. A systematic histological study of palm fruits. VIII. Subtribe Dypsidinae (Arecaceae). *Brittonia* **60**, 82–92 (2008).
161. Essig, F. B., Bussard, L. & Hernandez, N. A systematic histological study of palm fruits. IV. Subtribe Oncospermatinae (Arecaceae). *Brittonia* **53**, 466–471 (2001).
162. Essig, F. B., Manka, T. J. & Bussard, L. A systematic histological study of palm fruits. III. Subtribe Iguanurinae (Arecaceae). *Brittonia* **51**, 307–325 (1999).
163. Evans, T. & Sengdala, K. The Indochinese rattan *Calamus acanthophyllus*: a fire-loving palm. *Palms* **45**, 25–28 (2001).
164. Fong, F. *Studies on the population structure, growth dynamics and resource importance of nipa palm (Nypa fruticans Wurmb.)* Ph.D. thesis, University of Malaya (1986).
165. Gibbons, M. & Spanner, T. W. Medemia argun lives! *Principes* **40**, 65–74 (1996).
166. Henderson, A., Ban, N. K. & Thanh, B. V. New species of *Areca*, *Pinanga*, and *Licuala* (Arecaceae) from Vietnam. *Phytotaxa* **8**, 34–40 (2010).
167. Henderson, A. Arecaceae part I. Introduction and the Iriarteinae. *Flora Neotropica* **53**, 1–101 (1990).
168. Jones, D. L. *Palms throughout the world*. (Smithsonian Institution Press, 1995).
169. Keat, L. C. Notes on recent palm species and records from Peninsular Thailand. *Principes* **42**, 110–119 (1998).
170. Kumagai, L. & Hanazaki, N. Ethnobotanical and ethnoecological study of *Butia catarinensis* Noblick & Lorenzi: contributions to the conservation of an endangered area in southern Brazil. *Acta Botanica Brasiliica* **27**, 13–20 (2013).
171. McClatchey, W. C. Phylogenetic analysis of morphological characters of *Metroxylon* section *Coelococcus* (Palmae) and resulting implications for studies of other Calamoideae genera. *Memoirs of the New York Botanical Garden* **83**, 285–306 (1999).
172. Moraes, R. M. & Pintaud, J.-C. *Attalea blepharopus* Mart. (Arecaceae) from Bolivia revisited since Martius. *Candollea* **71**, 27–32 (2016).
173. Skov, F. *Geonoma polyandra* (Arecaceae), a new species from Ecuador. *Nordic Journal of Botany* **14**, 39–41, <https://doi.org/10.1111/j.1756-1051.1994.tb00567.x> (1994).
174. Soares, K. P., Longhi, S. J., Witeck Neto, L. & Assis, L. C. D. Palmeiras (Arecaceae) no Rio Grande do Sul, Brasil. *Rodriguésia* **65**, 113–139 (2014).
175. Palmweb. *Palmweb - palms of the world online*, <http://www.palmweb.org/> (2019).
176. Palmpedia. *Palmpedia - palm grower's guide*, <http://www.palmpedia.net/> (2019).
177. Fern, K. *The useful tropical plants database*, <http://tropical.theferns.info/> (2014).
178. Couvreur, T. L. P. *Palms of Africa*, <http://palms.myspecies.info/> (2019).
179. Virtual Herbarium. *The Fairchild tropical botanic garden virtual herbarium (FTG)*, <http://www.virtualherbarium.org/> (2011).
180. Dransfield, J. et al. *Genera palmarum - the evolution and classification of palms*. (Royal Botanical Gardens, 2008).
181. Kissling, W. D. et al. Data from: PalmTraits 1.0, a species-level functional trait database of palms worldwide. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.ts45225> (2019).
182. Guimarães, P. R. Jr., Galetti, M. & Jordano, P. Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate. *PLoS ONE* **3**, e1745 (2008).

183. Muñoz, G., Trøjelsgaard, K. & Kissling, W. D. A synthesis of animal-mediated seed dispersal of palms reveals distinct biogeographical differences in species interactions. *Journal of Biogeography* **46**, 466–484, <https://doi.org/10.1111/jbi.13493> (2019).
184. Regan, B. C. *et al.* Fruits, foliage and the evolution of primate colour vision. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **356**, 229–283, <https://doi.org/10.1098/rstb.2000.0773> (2001).
185. Dominy, N. J., Svenning, J. C. & Li, W. H. Historical contingency in the evolution of primate color vision. *Journal of Human Evolution* **44**, 25–45, [https://doi.org/10.1016/s0047-2484\(02\)00167-7](https://doi.org/10.1016/s0047-2484(02)00167-7) (2003).
186. Govaerts, R. & Dransfield, J. *World checklist of palms*. (Royal Botanic Gardens Kew, 2005).
187. Faurby, S., Eiserhardt, W. L., Baker, W. J. & Svenning, J.-C. An all-evidence species-level supertree for the palms (Arecaceae). *Molecular Phylogenetics and Evolution* **100**, 57–69, <https://doi.org/10.1016/j.ympev.2016.03.002> (2016).
188. Burkill, I. H. *A dictionary of the economic products of the Malay Peninsula*. (Ministry of Agriculture and Cooperatives, 1966).
189. Bernal, R., Martinez, B. & Sanin, M. J. The World's tallest palms. *Palms* **62**, 5–16 (2018).
190. Bailey, L. H. Palms of the Seychelles Islands. *Gentes Herbarum* **6**, 3–48 (1942).
191. Craft, P. *The palms of Cuba*. (Palm Nut Pages, 2018).
192. Hallé, F. The longest leaf in palms? *Principes* **21**, 18 (1977).
193. Brummitt, R. K. *World Geographical Scheme for Recording Plant Distributions*. 2nd edn, (Hunt Institute for Botanical Documentation Carnegie Mellon University, 2001).
194. Laliberté, E. & Legendre, P. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**, 299–305, <https://doi.org/10.1890/08-2244.1> (2010).
195. Pakeman, R. J. Functional trait metrics are sensitive to the completeness of the species' trait data? *Methods in Ecology and Evolution* **5**, 9–15, <https://doi.org/10.1111/2041-210x.12136> (2014).
196. van der Plas, F., van Klink, R., Manning, P., Olf, H. & Fischer, M. Sensitivity of functional diversity metrics to sampling intensity. *Methods in Ecology and Evolution* **8**, 1072–1080, <https://doi.org/10.1111/2041-210x.12728> (2017).
197. Kim, S. W., Blomberg, S. P. & Pandolfi, J. M. Transcending data gaps: a framework to reduce inferential errors in ecological analyses. *Ecology Letters* **21**, 1200–1210, <https://doi.org/10.1111/ele.13089> (2018).
198. Swenson, N. G. Phylogenetic imputation of plant functional trait databases. *Ecography* **37**, 105–110, <https://doi.org/10.1111/j.1600-0587.2013.00528.x> (2014).
199. Schrodt, F. *et al.* BHPMF – a hierarchical Bayesian approach to gap-filling and trait prediction for macroecology and functional biogeography. *Global Ecology and Biogeography* **24**, 1510–1521, <https://doi.org/10.1111/geb.12335> (2015).
200. Stekhoven, D. J. & Bühlmann, P. MissForest—non-parametric missing value imputation for mixed-type data. *Bioinformatics* **28**, 112–118, <https://doi.org/10.1093/bioinformatics/btr597> (2011).
201. Penone, C. *et al.* Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods in Ecology and Evolution* **5**, 961–970, <https://doi.org/10.1111/2041-210x.12232> (2014).
202. Cornelissen, J. H. C. *et al.* A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**, 335–380, <https://doi.org/10.1071/BT02124> (2003).
203. Garnier, E. *et al.* Towards a thesaurus of plant characteristics: an ecological contribution. *Journal of Ecology* **105**, 298–309, <https://doi.org/10.1111/1365-2745.12698> (2017).
204. Parr, C. S. *et al.* TraitBank: Practical semantics for organism attribute data. *Semantic Web* **7**, 577–588, <https://doi.org/10.3233/SW-150190> (2016).
205. Pérez-Harguindeguy, N. *et al.* New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* **61**, 167–234, <https://doi.org/10.1071/BT12225> (2013).
206. Kissling, W. D. *et al.* Cenozoic imprints on the phylogenetic structure of palm species assemblages worldwide. *Proceedings of the National Academy of Sciences of the United States of America* **109**, 7379–7384, <https://doi.org/10.1073/pnas.1120467109> (2012).

Acknowledgements

We thank Birgitte Bergmann (Aarhus University) for help with data entry, and Andrew Henderson (New York Botanical Garden) for providing individual trait measurements for species from several palm genera (*Calyptrogyne*, *Chuniophoenix*, *Desmoncus*, *Geonoma*, *Hyospathe*, *Leopoldinia*, *Pholidostachys*, *Rhapis*, *Synechanthus*, *Welfia*). We acknowledge additional cross-checking of trait information for specific palm genera by Lauren Gardiner (*Heterospathe*), Finn Borchsenius (*Aiphanes*, *Bactris*, *Desmoncus*, *Geonoma*), Anders Barfod (*Licuala*), Rodrigo Bernal (*Syagrus* hybrids) and Donald Hodel (some *Chamaedorea* species). W.D.K. was supported by the University of Amsterdam (starting grant), the Danish Council for Independent Research–Natural Sciences (grant 11-106163) and the Netherlands Organisation for Scientific Research (Grant 824.15.007), H.B. by the European Union 7th Framework Programme (FP7-PALMS-Contract no. 212631) and by the Danish National Science Research Council (272-06-0476), W.J.B. by a grant from the Garfield Weston Foundation to the Global Tree Seed Bank Project at the Royal Botanic Gardens, Kew, and J.C.S. by the European Research Council (ERC-2012-StG-310886-HISTFUNC). J.C.S. also considers this work a contribution to his VILLUM Investigator project ‘Biodiversity Dynamics in a Changing World’ funded by VILLUM FONDEN. R.E.O. acknowledges the support of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation)—FZT 118. R.E.O. further acknowledges SYNTHESYS grant GB-TAF-6695.

Author Contributions

W.D.K., H.B. and J.C.S. conceived the idea; W.D.K. designed the study; W.D.K., B.G., R.E.O., J.D., W.J.B. collected data and/or facilitated data collection; W.D.K., R.E.O. and J.Y.L. assembled the dataset and prepared figures and code; W.D.K. wrote the manuscript; all authors discussed the results and commented on the manuscript.

Additional Information

Competing Interests: The authors declare no competing interests.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

The Creative Commons Public Domain Dedication waiver <http://creativecommons.org/publicdomain/zero/1.0/> applies to the metadata files associated with this article.

© The Author(s) 2019