

## An all-evidence species-level supertree for the palms (Arecaceae)



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### ARTICLE INFO

#### Article history:

Received 13 June 2015

Revised 19 February 2016

Accepted 1 March 2016

Available online 5 April 2016

#### Keywords:

Arecaceae

Diversification

Palms

Palmae

Phylogenetic diversity

Species-level phylogeny

Supermatrix

### ABSTRACT

Several attempts have been made to generate complete species-level phylogenies for large clades, enabling comprehensive analyses of ecological or evolutionary hypotheses at the species level. No such phylogeny has, however, been generated for any major plant group yet, but here we generate such a phylogeny for the palm family (Arecaceae). We do this using a novel Bayesian approach, estimating the validity of intra-generic taxonomic groupings as topological constraints to assist in placing species without genetic or morphological data. From these we implement those that are supported by genetic or morphological data for a given genus or for related genera. The intergeneric relationships in our new phylogeny are surprisingly different from earlier phylogenies in the placement of genera within tribes, but largely identical to previous findings in the deeper branches in the phylogeny, pointing to the need for incorporating phylogenetic uncertainty in analyses based on this phylogeny. Initial analyses of the new phylogeny suggest non-constancy in diversification rates over time within genera, with an apparent increase in diversification rate over time, but no evidence for any geographic variation in the magnitude of this increase. We hope that our study will stimulate further evolutionary or ecological studies using palms as study organisms as well as discussions of the optimal way to place the many species without genetic or morphological data.

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### 1. Introduction

Evolutionary, ecological and biogeographical studies depend on phylogenetic trees as a source of information on macroevolutionary processes. The hypotheses addressed in those studies are commonly formulated at the species level and therefore testing them requires species-level phylogenetic data. However, phylogenetic trees are often highly incomplete at this level, as both the availability of suitable samples and the costs of molecular analysis present major bottlenecks. Thus, it is widely accepted that all analyses need to accommodate incomplete phylogenetic trees. The handling of missing species can either be built into the analysis itself (e.g., [FitzJohn, 2012](#)), or missing species can be added to the tree prior to analysis. The latter approach has the advantage that available information on the likely phylogenetic placement of the species – notably the taxonomic hierarchy – can be incorporated relatively easily if desired. Moreover, a tree that has been “completed” this way can subsequently be used for a wide range of downstream analyses. Such completed species-level phylogenies have recently

been constructed for several large animal groups, most notably mammals and birds ([Jetz et al., 2012](#); [Faurby and Svenning, 2015](#)), but not yet for any large plant group. Adding missing species to a phylogenetic tree is not a trivial task. One must carefully consider functional, geographic or phylogenetic biases in the missing species that potentially may influence the conclusions drawn from the tree, and make informed and well-documented choices as to what accessory information (e.g., taxonomy) is exploited to narrow down the phylogenetic placement of species. Here, we present a workflow for doing this, and use it to produce a species-level phylogeny for palms.

The palm family (Arecaceae) is an important model system for research on the processes structuring tropical biodiversity ([Couvreur and Baker, 2013](#)), and several recent studies have tested ecological, evolutionary, and biogeographical hypotheses across the whole palm family using phylogenetic data (e.g., [Kissling et al., 2012](#); [Baker and Couvreur, 2013](#); [Couvreur et al., 2015](#)). Since the 1990s, the palms have been the subject of intense phylogenetic research. Many of the phylogenetic studies so far have focused on higher-level relationships, aiming to establishing a rigorous systematic framework across the family (e.g., [Uhl et al., 1995](#); [Baker et al., 1999, 2009](#); [Asmussen et al., 2000, 2006](#); [Asmussen and Chase, 2001](#); [Hahn, 2002](#)). Detailed studies have been made of

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the species relationships in some subclades in almost all parts of the family (e.g., Trénel et al., 2007; Eiserhardt et al., 2011), but no study has so far attempted to integrate all available species-level data, and to add the missing species to obtain a tree that can be used for eco-evolutionary hypothesis testing. Previous macroevolutionary and macroecological studies have largely relied on a complete genus-level tree of the palm family (Baker et al., 2009), either using methods to account for the missing species in the analysis (e.g., Couvreur et al., 2011), adding species as polytomies to their genera (e.g., Kissling et al., 2012), or adding information from species-level studies for specific parts of the tree (Eiserhardt et al., 2013). Instead of finding a different way of dealing with missing species for each study, future studies should be able to rely on a single species-level phylogenetic framework for the whole palm family that explicitly deals with issues of bias and missing data.

In addition to providing a species-level phylogenetic framework as a resource for the palm family as the first large plant group, we also wish to reanalyze the intergeneric relationships of palms. Several relationships in the genus-level tree of palms remain problematic, as indicated by the fact that the topologies based on individual markers frequently were different from the combined topology in a genus-level study based on supertree and supermatrix methods (Baker et al., 2009). The study of Baker et al. (2009) aimed to synthesize molecular and morphological data from palms to establish the best hypothesis of relationships among palm genera using all data available at the time. Baker et al. (2009) used parsimony methods, but did not explore model-based methods, which generally outperform maximum parsimony methods especially for fairly deep nodes (Smith, 2011; Lee and Worthy, 2012). The use of distant outgroups is known to reduce phylogenetic performance (Rosenfeld et al., 2012), and the old age of the palm clade means that any potential outgroup is distant. To reduce such potential problems we do not use any external outgroups phylogenetic reconstruction, since they are not necessary for models applying molecular clocks, unless required for temporal calibration. We will use a Bayesian approach, which has the additional advantage of producing a probability distribution of phylogenetic trees, which can be used to represent phylogenetic uncertainty in subsequent evolutionary and other downstream analyses. We will mainly compare our results with the supermatrix tree of Baker et al. (2009), which is analytically closest to the new tree constructed here and will refer to this tree as the 2009 supermatrix tree throughout this paper.

The aims of this study are thus four-fold: (1) outline a workflow for the construction of a complete species-level phylogenetic tree based on all available molecular and morphological characters for a group of interest, with unsampled species being added using a novel approach to incorporate taxonomic groupings below genus level; (2) provide a species-level phylogenetic framework for future evolutionary, ecological, and biogeographic studies of the palm family; (3) re-address intergeneric relationships within the palms to test their robustness to different methodologies; and (4) illustrate the effect of the use of the species-level phylogenetic framework with an analysis of global patterns of palm phylogenetic diversity.

## 2. Materials and methods

Throughout the paper we generally used the taxonomy initially generated by Govaerts et al. (2011), but later updated (downloaded from <http://apps.kew.org/wcsp/> on 1 November 2013), excluding all hybrid species. We used a partial exception to this taxonomy for the genus *Calamus* where Andrew Henderson (New York Botanical Garden) kindly allowed us to use his unpublished morphological database; thus, we chose to construct two versions

of the phylogeny, one based on his newer taxonomic opinion and one based on Govaerts et al. (2011). Based on the taxonomy of Govaerts et al. (2011) there are 2539 species of palms in 184 genera. We used genetic data for all genera and for 901 species as well as morphological data for 547 with a total of 1255 species having data of at least one of the types. Based on the Govaerts et al. (2011) taxonomy there are 379 species of *Calamus* s.s. of which 301 have morphological or genetic data. Based on Henderson's taxonomy there are 326 species of *Calamus* s.s., all with morphological and or genetic data. The lower species number in Henderson's taxonomy is partly due to the fact that this account does not explicitly address the status of some potentially ambiguous species, described long ago and provisionally accepted in the Govaerts et al. (2011) taxonomy.

### 2.1. Intergeneric relationships

#### 2.1.1. The backbone phylogeny

We based our study on the same alignment and markers as the ones used in Baker et al. (2009) (9 plastid markers, 4 nuclear markers, a morphological dataset and a rflp dataset), but removed the outgroup taxa. We added sequences for the genera *Tahina* from Dransfield et al. (2008a) and *Lanonia* from Henderson and Bacon (2011). We used five calibration points, four of which were identical to calibration points used in the most recent molecular dating analysis of palms of Couvreur et al. (2011): (1) an exponential prior on the stem age of the subfamily Coryphoideae (hard lower bound 85.8 million years, 95% upper bound 88.8 million years), (2) an exponential prior on the stem age of the subtribe Hyphaeninae (Borasseae: Coryphoideae) (hard lower bound 27 million years, 95% upper bound 28.5 million years), (3) an exponential prior on the stem age of the subtribe Attaleinae (Cocoseae: Arecoideae) (hard lower bound 54.8 million years, 95% upper bound 60.79 million years) and (4) an exponential prior on the stem age of the subtribe Mauritiinae (Lepidocaryeae: Calamoideae) (hard lower bound 65 million years, 95% upper bound 69.49 million years). The fifth was the crown age of all palms (a normal prior, mean 100 million years, standard deviation 2.5 million years). The age of the fifth calibration point was based on the estimated phylogeny from Couvreur et al. (2011) and is thus a secondary calibration. This estimated secondary point was chosen rather than the primary dating point of the stem age chosen in Couvreur et al. (2011) because it meant that we could run the analyses without any external outgroup. Preliminary analyses showed that the problems of different chains getting stuck near different topologies (discussed later) were even greater for analyses conducted with an external outgroup.

We ran PARTITIONFINDER (Lanfear et al., 2012) and implemented the preferred model as well as the calibration points into BEAST 1.7.5 (Drummond et al., 2012) thereafter we estimated the overall phylogeny assuming a birth-death model. We ran four chains for 100 million generations post burn-in sampling every 100,000th generation, with the length of burn-in estimated in by visual inspection of the chains in TRACER 1.5 (Drummond et al., 2012). All four chains converged to apparent optima, but the combined chain of the four had very low ESS (Estimated Sample Size) values for several parameters (mainly the estimated likelihoods for individual partitions) showing that each chain converged to individual local optima (and likely local topologies) fitting different markers. This problem could potentially be due to variation of mutational parameters across the tree, which makes it difficult to estimate the shortest internal branches on a tree containing distantly related organisms. The low ESS values for the tree-liability parameters for individual parameters indicated that parts of the topology were unreliable, but this should not be a problem for the parts where all chains converged to the same topology. We

therefore generated the Bayesian post burn-in consensus tree and identified all parts of the tree with posterior support above 0.75 (which requires at least partial support in all four chains) and considered these parts as the reliably inferred regions of the tree, whereas the remaining parts should be reanalyzed by separate analyses. In order to make the merging of tree parts simple we considered these smaller parts as the smallest clades with posterior support of 1 containing at least one node with posterior support below 0.75. We found six such clades in the tree; subfamilies Calamoideae and Coryphoideae, the tribe Ceroxyleae within subfamily Ceroxyloideae and three groups within subfamily Arecoideae: (1) Iriarteeae, (2) Cocoseae: Attaleinae except *Beccario-phoenix* and (3) a group containing six tribes; Euterpeae, Leopoldiniae, Pelagodoxeae, Manicarieae, Geonomateae and Areceae.

### 2.1.2. The shallower parts of the backbone phylogeny

For each of the six new analyses we re-ran PARTITIONFINDER (Lanfear et al., 2012) to find the optimal model and ran four chains in BEAST 1.7.5 (Drummond et al., 2012) for 50 million generations post burn-in sampling every 50,000 generation, with the length of burn-in estimated in TRACER 1.5 (Drummond et al., 2012). The mean rates of the clocks for each marker were initially set as wide (uniform between 0 and 1000), but were restricted for markers with low ESS and mean values substantially larger than the median values. The models were occasionally simplified from the optimal model as inferred by PARTITIONFINDER when the ESS values of individual mutation parameters or for the overall prior were low.

No further calibration was used for four of the six analyses (the analyses within Ceroxyloideae and Arecoideae), but the subfamily analyses of Calamoideae and Coryphoideae included fossil calibration points within them and therefore needed extra care in the new subclade analysis. The analysis of Calamoideae had a root age calibration of 70.74 million years as found in the backbone phylogeny (a normal prior with a sd of 2.36 million years) as well as an exponential prior on the stem age of Mauritiinae (hard lower bound 65 million years, 95% upper bound 95% upper bound 60.79 million years). The analysis of Coryphoideae had a root age calibration of 75.87 million years as found in the backbone phylogeny (a normal prior with a sd of 2.87 million years) as well as an exponential prior on the stem age of Hyphaeninae (hard lower bound 27 million years, 95% upper bound 28.5 million years). There were no convergence problems in five of the six analyses, which produced combined chains with all ESS values above 200, but there were problems within Coryphoideae where only three chains converged to an apparent global maximum and the fourth chain therefore was discarded. After the new analysis the shallower phylogenies were merged with the main backbone phylogeny with all branch lengths in the smaller phylogenies scaled so that the root age of the clade in the smaller phylogenies became identical to the clade's root age in the larger phylogeny.

## 2.2. Intrageneric relationships

### 2.2.1. Intrageneric analyses

Intrageneric relationships were analyzed in MrBAYES 3.2 (Ronquist et al., 2012). The shift in program from BEAST was chosen because MrBAYES has the potential to incorporate partial topological constraints, which we wanted for some of the intrageneric phylogenies (discussed later), while BEAST allows the use of multiple calibration points under birth–death species model, which were required for the intergeneric phylogeny. Input files for all analyses (both inter and intrageneric) are available in Appendix B.

We constructed individual MrBAYES analyses for each genus and its closest relatives in the intergeneric tree. This was generally defined as the smallest possible clades with posterior support of at least 0.9, but for a few genera with large potential outgroups

and uncertain placement (*Masoala*, *Cyrtostachys*, *Washingtonia* and the genera of the tribe Euterpeae), the phylogenies were reconstructed for the smallest clades containing the genus in the consensus tree irrespective of posterior support. The intergeneric relationships of these analyses were not used in our final tree and our results are thus essentially the same as if we had produced individual trees of each genus and all the closest outgroups. We constrained all genera to be monophyletic in these analyses. The sole exception of this was *Calamus*, which in its definition applied here probably is not monophyletic (Baker, 2015), and for these palms we instead constrained the monophyly of the subtribe Calaminae as well as the genera *Ceratolobus*, *Daemonorops* and *Pogonotium*.

For each group of genera, genetic data were found using PHYLOTA 1.5 (Sanderson et al., 2008) to identify markers with a sufficient number of homologous sequences from different species. The sequences were initially aligned using the default options in MUSCLE 3.8.31 (Edgar, 2004), but was frequently modified by hand using in BioEDIT 7.0.5.3 (Hall, 1999). Following this, we used PARTITIONFINDER to find the optimal substitution models and partitioning scheme just like in the higher scale phylogenies. Finally, we searched primary literature for published morphological studies and included these by adding the morphological characters as a separate partition in the MrBAYES analyses assuming gamma rate variation between sites (sources of the morphological data are given in Appendix A).

All trees were inferred using a birth–death model with an independent gamma rate clock model. We specified relative extinction rates in the birth–death models, but kept the remaining priors at their default values. The relative extinction rates for each genus were estimated by running the TURBOMEDUSA update to the MEDUSA algorithm (Alfaro et al., 2009; Brown, 2013) on 1000 trees of the overall intergeneric relationships and using the median value for each genus as a fixed prior for the relative extinction rates in the MrBAYES analyses. When the difference between the median relative extinction rates for different genera in the small clades were less than 0.05 we used the mean value as input. When they were over than 0.05 we ran separate MrBAYES analyses with the different extinction rates for the different genera.

The MrBAYES analyses were initially run with two runs for 10 million generations, but if the standard deviation of split frequencies of all partitions was higher than 0.01 the analyses were expanded by additional steps of 10 million generations until the standard deviation of split frequencies of all partitions were below 0.01, up to a maximum of 50 million generations. The results were analyzed in TRACER 1.5 (Drummond et al., 2012) with burn-in generally set to 25%, but occasionally manually changed based on visual inspection of the posterior distributions. If the ESS for the combination of the two runs was above 200 for all parameters the analysis was stopped. If the ESS for at least one parameter was lower than that, but with no obvious difference between the two runs the analysis was run longer to reach higher ESS up to a maximum of 100 million generations. If the low ESS was a consequence of convergence to different optima in the two runs, additional analyses were run for up to a total of ten runs of 50 million generations until at least two runs converge to the apparently global optimum (as defined by the total likelihood of the analysis). If after ten such runs only one of them had reached the apparent global optimum this run was continued for a total of 100 million generations and was used as the sole basis. Information on these convergence issues within each genus can be found in Appendix A. We substituted each terminal branch in the intergeneric phylogeny with the estimated phylogeny of the corresponding genus, except for Calaminae where we replaced the entire subtribe from the intergeneric analysis with the subtribe from the analysis including all species.

### 2.2.2. Intrageneric constraints

As previously stated, we included morphological data directly into the analyses whenever possible, but we also wanted some way to include the morphological knowledge contained in taxonomic information (e.g., subgenera, sections, species groups, previously suggested synonymy, etc.) as well. We therefore tested intrageneric groupings based on the species with genetic or cladistic morphological data and incorporated groupings when they were found to be significantly better than random. These constraints, when judged to be reliable, were used to guide the placement of species without genetic and direct morphological data and whenever possible were implemented to avoid having any effect on the species where genetic or morphological data was available. Such potential constraints were found for 35 genera, totaling 1083 species. Of the remaining 149 genera and 1456 species, 103 species belong to 79 genera with only 1–2 species and therefore a fixed internal topology, while the last 1353 species belong to 70 genera for which we could not find any taxonomic groupings in the literature. For genera without constraints and/or genera where the tested constraints were found to be untrustworthy, unsampled species were placed freely within the genera without constraints.

In order to estimate the precision of taxonomic groupings for intrageneric phylogeny, we compared the sum of pairwise branch lengths separating all species within a given group that were represented in the molecular or morphological phylogeny ( $\text{Dist}_{\text{Real}}$ ) (Fig. 1a) to the sum of pairwise branch lengths separating these species in random trees ( $\text{Dist}_{\text{Rand}}$ ) (Fig. 1b) and to the sum of pairwise distances between the species if the groups analyzed were constrained to be monophyletic ( $\text{Dist}_{\text{Monop}}$ ) (Fig. 1c). We only focus on the topology rather than the branch lengths and therefore we transformed the branch length of all trees based on the [Grafen \(1989\)](#) method. This method constructs ultrametric trees by assigning a number to all nodes equal to the number of descendant species minus one (and therefore zero to all tips) and letting all branch lengths be equal to the difference between these values for the two nodes they connect. Following this, the branch lengths are standardized, so the age of the most recent common ancestor of all species is 1.

We calculated *Constraint trustworthiness* as the number of trees satisfying the inequality  $\text{Dist}_{\text{Rand}} - \text{Dist}_{\text{Real}} \geq \text{Dist}_{\text{Real}} - \text{Dist}_{\text{Monop}}$  with  $\text{Dist}_{\text{Real}}$  calculated from each of 1000 trees from the posterior distribution,  $\text{Dist}_{\text{Rand}}$  calculated for 1000 random trees and  $\text{Dist}_{\text{Monop}}$  equal to the minimum value for 1000 random trees with the groups in question constrained to be monophyletic. This inequality is satisfied if the difference between the topology assuming monophyly of the suggested groupings and the actual tree is smaller than the difference between random trees and actual trees. It can therefore be seen as an estimate of the probability that the implementation of the taxonomic groupings as constraints leads to a topological improvement relative to assuming random placement of the missing species within the genus.

We note that calculated *Constraint trustworthiness* shows the general reliability of the constraints, but not if one or more of them are not fully monophyletic. We therefore occasionally chose to constrain slightly different groupings than the ones we tested. Clades supported by the consensus tree, or any clade with genetic or morphological data for zero or only one species were directly implemented. Clades violated in the consensus tree were either not implemented when there was no apparent phylogenetic pattern in the species belonging to it, implemented as they are (Fig. S1a) when we judged that the evidence against them was only minor, or alternatively implemented in a modified form. For the latter option (illustrated in Fig. S1) the clades were modified to remove violations between the constraints and the consensus tree by combining some of the clades (Fig. S1b), making one or more clades paraphyletic (Fig. S1d), or by removing individual species

with uncertain placement from the clade to make the rest monophyletic (Fig. S1c). We only implemented constraints where at least one of the species specified in the constraint lacked other data. The implementation of the constraints using an empirical example of the genus *Attalea* is illustrated in Fig. 1e and f.

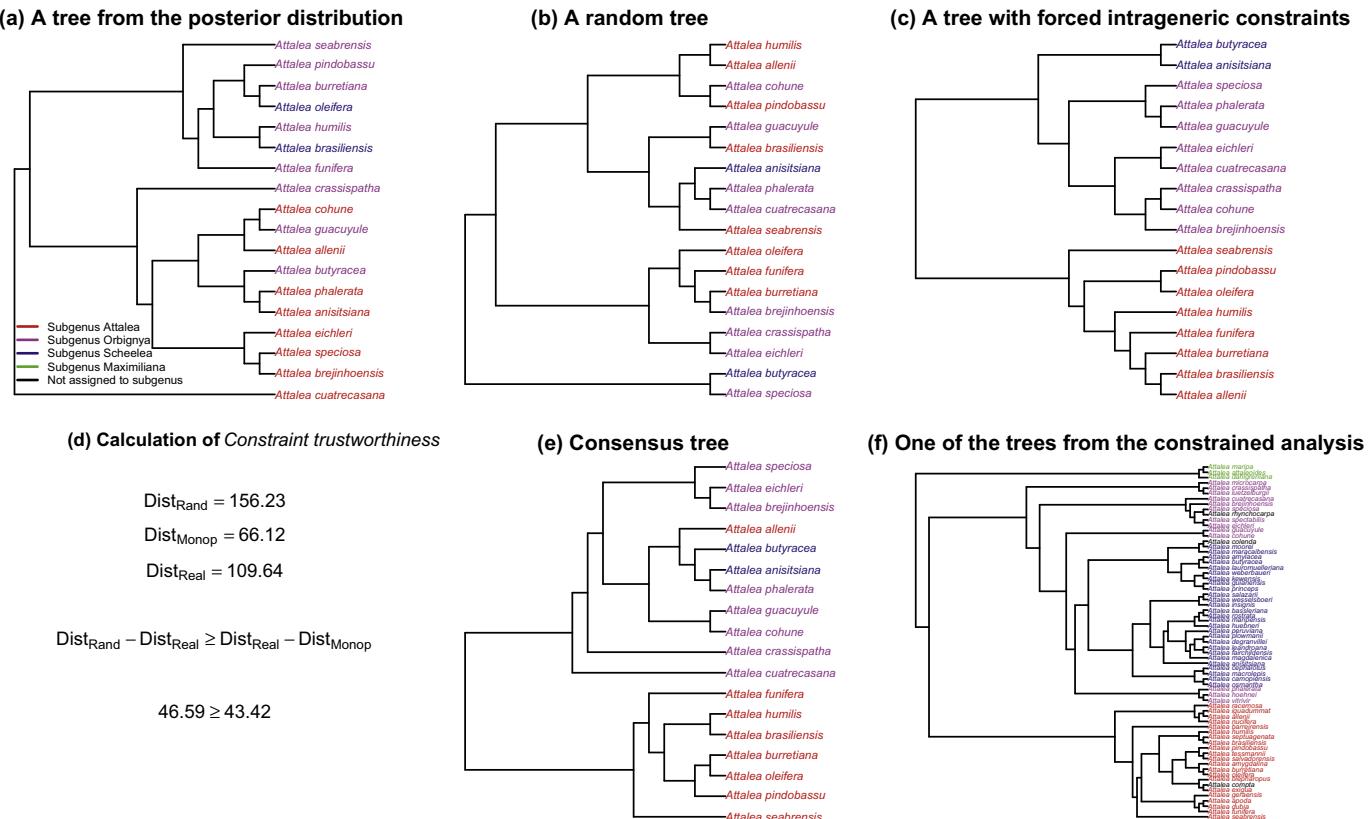
We generally used all species with genetic or morphological data in these analyses, except for the genus *Daemonorops* where there was poor overlap between the species sampled for different markers and therefore little knowledge of the internal relationships. For this genus we only tested the validity based on the species sampled in the morphological data matrix developed by Andrew Henderson, which, despite its primary focus for *Calamus*, contained species from both *Daemonorops* subgenera.

Separate analysis were run in MrBayes with and without these constraints and were then combined with *Constraint trustworthiness* as the frequency of all trees coming from the analysis with morphological constraints enforced (i.e., if *Constraint trustworthiness* was 0.8, 80% of the trees would use topological constraints and 20% would not). From a Bayesian perspective the output of this analysis produces a distribution of trees equivalent to the one produced with a reversible jump MCMC chain. In this context *Constraint trustworthiness* would be a hard prior for jumping from an analysis without constraints to one with constraints and  $(1 - \text{Constraint trustworthiness})$  the similar prior for jumping back to the unconstrained chain.

When there were potential taxonomic constraints on several levels within a genus (e.g., subgenera, sections, species groups) we calculated *Constraint trustworthiness* at each level and furthermore we calculated *Constraint trustworthiness* for the lower levels both with and without assuming the monophyly of the higher levels in the calculations of  $\text{Dist}_{\text{Rand}}$  and  $\text{Dist}_{\text{Monop}}$ . The different levels were then combined based on multiplicity of the probabilities. Imagine that *Constraint trustworthiness* for subgenus monophyly is  $P(A)$ , the *Constraint trustworthiness* for section monophyly given subgenus monophyly is  $P(B)$  and the *Constraint trustworthiness* for section monophyly without assuming subgenus monophyly is  $P(C)$ . We would then sample  $P(A) \times P(B)$  from trees assuming both subgenus and section monophyly,  $P(A) \times (1 - P(B))$  assuming subgenus but not section monophyly  $(1 - P(A)) \times P(C)$  only assuming section monophyly, and  $(1 - P(A)) \times (1 - P(C))$  without any assumptions. In our phylogeny this complexity ended up not being needed because there were no cases with two different *Constraint trustworthiness* values that were both different from zero.

*Constraint trustworthiness* was not always calculable for all groupings at particular level (e.g. subgenera) because some of them may only have genetic data for one or even zero species. However, since we were calculating one *Constraint trustworthiness* for all constraints at a particular level we transfer the calculable values to the non-calculable ones for the same level, i.e. if we could test that one subgenus was trustworthy we used this to infer that subgenera in general were trustworthy for this particular genus. *Constraint trustworthiness* was generally not calculable at the shallowest levels since it requires genetic or cladistic morphological data for at least two species mentioned in the constraint (e.g., species group). For these lower levels, we assumed the *Constraint trustworthiness* to be identical to the mean of the *Constraint trustworthiness* for the calculable constraints within the genus. No analyses with constraint were run for any genera with a *Constraint trustworthiness* below 0.05.

When there were insufficient data to estimate *Constraint trustworthiness* for a particular genus we estimated it based on the closest related genera with a calculable *Constraint trustworthiness*. We first calculated the mean *Constraint trustworthiness* for genera with several levels of constraints (i.e., the mean of  $P(A)$  and  $P(C)$  in the example described above). Following this we



**Fig. 1.** The process of testing *Constraint trustworthiness* as exemplified by the genus *Attalea*: (a) shows one of 1000 trees from the posterior distribution of the phylogeny of the genus *Attalea*, (b) shows a random phylogeny of the same genus, and (c) shows a tree where the intrageneric clades we analyze (here the subgenera) are constrained to be monophyletic. In each case we only show the species with genetic or morphological data and therefore used to calculate *Constraint Trustworthiness*. In all figures, species are color-coded based on subgenus assignment; the subgenus *Attalea* with 14 species (8 with genetic data) is red, the subgenus *Orbignya* with 13 species (8 with genetic data) is purple, the subgenus *Scheelea* with 27 species (2 with genetic data) is blue and the subgenus *Maximiliana* with, 3 species (0 with genetic data) is green. The last three species, which are not assigned to subgenus, are shown in black. In (d) we calculate *Constraint trustworthiness* for this particular tree using the values from the trees shown in (a–c). The inequality is satisfied for 748 out of 1000 trees for *Attalea* and the *Constraint trustworthiness* for *Attalea* is therefore 0.748. (e) Bayesian consensus tree of the species with genetic or morphological data and included in an intrageneric constraint. (f) Illustrates a tree with the constraints applied for the genus *Attalea*. Based on (e) we constrained the monophyly of the subgenera *Attalea* (*Attalea allenii*, which is arguing against monophyly of subgenus *Attalea*, only has data for a single marker and all the species supporting it have data for at least seven), *Scheelea* and the combined monophyly of *Orbignya* and *Scheelea*, but not of *Orbignya*. We further constrained *Maximiliana* since there is no evidence against the monophyly of this group. Finally, three species have not been assigned to subgenera (marked in black) and are therefore allowed to be placed freely in the phylogeny.

estimated a *Constraint trustworthiness* for the remaining genera through maximum parsimony ancestral trait estimation. We acknowledge that the transfer *Constraint trustworthiness* to related genera may be considered problematic and we therefore constructed an additional set of phylogenies where we only used *Constraint trustworthiness* from genera where such was directly calculable. This set is available in Appendix C, but will not be discussed in further details in this paper. This set can be seen as intermediate between the results with and the results without constraints, which we later compare, and for all analyses of the sets, the results of this third set can therefore safely be assumed to be intermediate between the other two.

### 2.3. Estimation of effects of using a species level tree instead of a genus level one

In order to illustrate the effects of using the new tree we compared geographic variation in phylogenetic diversity (Faith, 1992) for species occurring in Taxonomic Databases Working Group (TDWG) Level 1 and 3 regions (Brummitt, 2001) as well as globally. The Level 3 regions generally correspond to countries, but some large countries (e.g., Australia or USA) are broken into states, while the Level 1 regions generally correspond to continents (although Asia is split into a temperate and a tropical part). We calculated

phylogenetic diversity based on three different sets of trees. One called *No Data*, where the intrageneric phylogenies are only based on the birth-death priors; one called *No Constraints*, including all genetic or morphological data, but no intrageneric topological constraints; and one called *Constraints*, where we include all data as well as the taxonomic constraints, which we found to be supported as explained in Section 2.2. Due to the limited number of Level 1 regions we used them to generate unique figures for each region illustrating both the mean and the spread of phylogenetic diversities between each of the 1000 trees and compared them with the global pattern. The higher number of Level 3 regions on the other hand is beneficial for statistical analyses and we used them to analyze the residuals of phylogenetic diversity as a function of species diversity in each region. We only analyzed the phylogenetic diversities for Level 3 regions with at least two species.

## 3. Results

### 3.1. Genus-level topology

The relationships among subfamilies were identical to those in the 2009 supermatrix tree as well as in most other recent studies (Calamoideae, (*Nypa*, (Coryphoideae (Ceroxyloideae, Arecoideae))))

with a strong posterior support (0.951), although there was also a limited support for *Nypa* as sister to all other palms (0.032), or for *Nypa* and Calamoideae as combined sisters to the remaining palms (0.017). Among the 28 lineages older than 50 million years in our phylogeny (Fig. S2) the only differences between our topology and the one of the 2009 supermatrix tree was the relationship of the two isolated genera *Sabal* (tribe Sabaleae) and *Phoenix* (tribe Phoenixae) to the other tribes within Coryphoideae, the internal relationship among the tribes and subtribes of Calamoideae, and the placement of Pelagodoxeae within the core Arecoid clade (Fig. 2). At shallower nodes, the intergeneric phylogeny produced a topology that was surprisingly different from the previous one, even though they were constructed with virtually identical data (Fig. 2).

Most of the many differences have limited taxonomic implications, since they almost exclusively relate to the placement of subtribes within tribes and genera within subtribes. Furthermore, many of the lineages with different placement in the current and the earlier tree had low support for their placement in at least one of the two studies. The only difference between the two phylogenies of potential taxonomic influence was the subtribe Dypsidinae (Arecoideae: Areceae), which was polyphyletic in the 2009 supermatrix tree, but monophyletic albeit only with a moderate support (0.756) in this study. Most of the tribes and subtribes discussed in Dransfield et al. (2008b) had posterior support of at least 0.99, with the only exceptions beyond Dypsidinae being tribes Euterpeae (Arecoideae) (support 0.765) and Lepidocaryeae (Calamoideae) (support 0.402) (since Lepidocaryeae has a support below 0.5 it is not shown as monophyletic in Fig. 2). A full list of support values for the intergeneric relationships and for some of the alternative relationships is found in Table S1.

### 3.2. Geographic variation in phylogenetic diversity

Global phylogenetic diversity for *No Constraints* was substantially lower than global phylogenetic diversity for *No Data*. This pattern was generally paralleled at the continental level, although to a varying degree, with the largest differences in temperate Asia, Australia and North America, differences similar to the global level in South America and Tropical Asia and apparently no differences between *No Data* and *No Constraints* for Africa and Oceania (Fig. 3). The standard deviations of the phylogenetic diversities between trees globally was lower for *No Constraints* than for *No Data*, and on a continental level the continents showing largest differences in the median phylogenetic diversity also showed largest differences in standard deviations. There was no apparent directional difference between the phylogenetic diversities on each continent between *Constraints* and *No Constraints* and also only limited effects on the variation of values between the 1000 trees although there was a small decrease in the standard deviations of the phylogenetic diversities in *Constraints*.

Unless there is a substantial bias in the phylogenetic relationship between species having genetic or morphological data and the species lacking such data, so that species consistently younger than average are sampled more often, the *No Constraints* results must be closer to the truth than the *No Data* results. At the same time, the *No Constraints* results will likely be more similar to the *No Data* results than the true results would be. Thus, the difference between the two can be seen as a minimum estimate of the magnitude of bias generated by using the *No Data* (i.e., only using intergeneric data).

The fairly large differences between the *No Data* and the *No Constraints* analyses at the continental level was not reflected in the pattern of phylogenetic diversities at the TDWG3 level. Here we found a surprisingly small difference in the geographic pattern of the residuals between species and phylogenetic diversity for the *No Data* and the *No Constraints* (Fig. 4). The (Pearson) correlation between the residuals for the 1000 trees ranged from 0.837 to

0.989 (median 0.963), and the correlation between the median value for the 1000 trees for *No Data* and the 1000 trees for *No Constraints* was 0.976. This difference was likewise small when looking at the absolute difference in the ordering of the residuals by Spearman correlations. Here, the correlations for the 1000 trees ranged from 0.865 to 0.990 (median 0.973), and the correlation between the median value for the 1000 trees for *No Data* and the 1000 trees for *No Constraints* was 0.982. The difference between *Constraints* and *No Constraints* was even smaller. The Pearson correlation between the residuals for the 1000 trees ranged from 0.972 to 0.999 (median 0.996), while the Spearman correlations between the residuals for the 1000 trees ranged from 0.973 to 0.999 (median 0.996).

## 4. Discussion

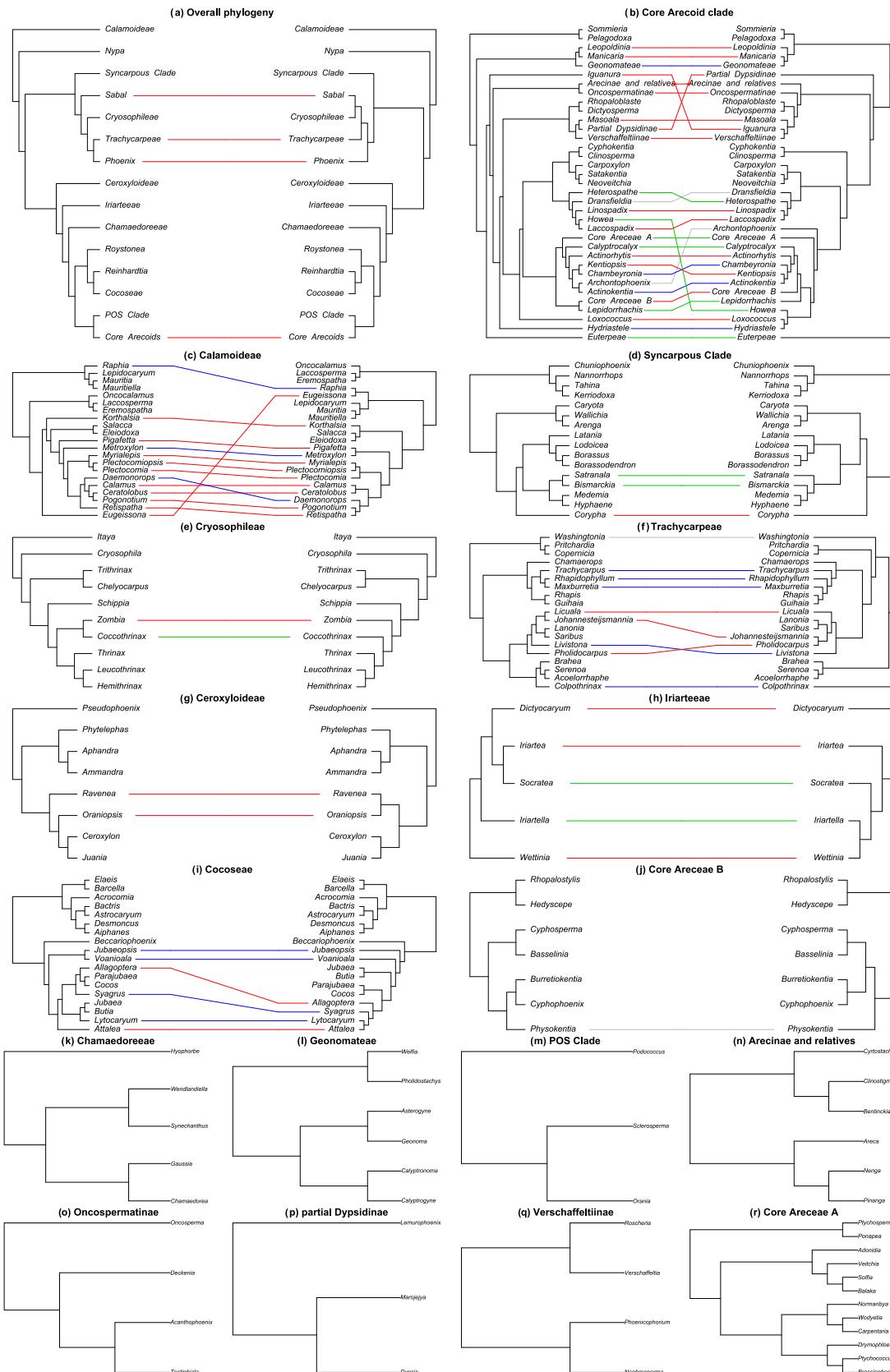
### 4.1. The pros and cons of the new workflow

Despite several attempts at an optimal workflow to create complete species-level trees (e.g., Thomas et al., 2013; Faurby and Svensson, 2015), no consensus has yet emerged as to the optimal approach, since different methods have different pros and cons. This is illustrated by a comparison of the two sets of trees we produce here. The *No Constraints* analysis has fewer assumptions than the *Constraints* analysis, but the distribution of trees generated by the *Constraints* analysis will be more precise than the distribution of trees generated by the *No Constraints* analysis if the assumptions are justifiable. The optimum would be to generate a set of trees that are as precise as possible with as few assumptions as possible. We suggest that each researcher carefully consider advantages and disadvantages of each method and selects the one they judge to be optimal for their study organisms.

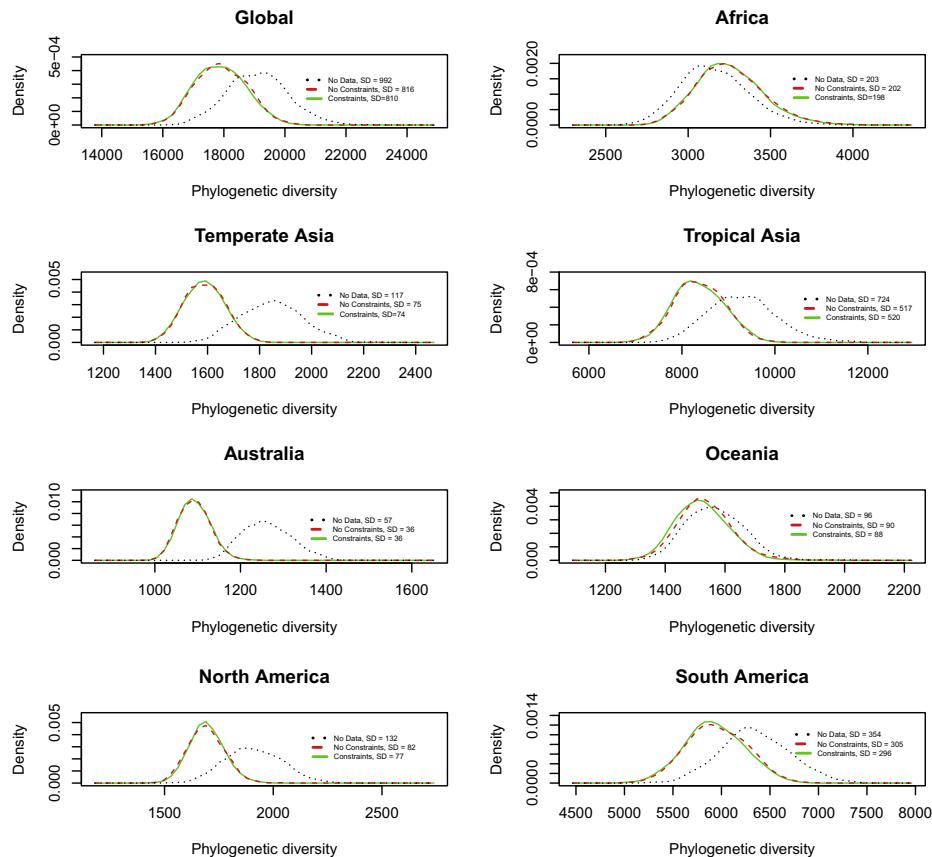
The frequency of species with available genetic or morphological data varies substantially between groups, and groups with a low proportion of species with data are scattered across the tree (Figs. 5 and S2; Appendix A). Further, there are some larger clades with consistently poor sampling, most notably Iriarteeae, while there are other clades like Geonomateae where almost all genera are well sampled. The effect of the choice of method used to incorporate missing species will therefore depend substantially on what group is being analyzed.

In our analysis, only a fairly small proportion of species are influenced by intrageneric constraints. Out of 2539 species in 184 genera, 713 species in 19 genera have a *Constraint trustworthiness* above 0.5 and are therefore substantially influenced by the constraints, 109 species in 6 genera have a *Constraint trustworthiness* more than 0 but less than 0.5 and are therefore influenced to a smaller extent, while 1372 species in 62 genera have a *Constraint trustworthiness* of 0 (Appendix A). The remaining 345 species in 107 genera also have a *Constraint trustworthiness* of 0, but this is because they cannot be influenced by the intrageneric constraints since there are only one or two species in them or all species have genetic or morphological data. Some of the genera with large *Constraint trustworthiness*, however, include older genera such as *Orania* and *Roystonea*. The intrageneric constraints may therefore, despite their limited number, substantially influence analyses of the overall tree particularly related to phylogenetic diversity or diversification.

We only found limited effects of intrageneric constraints in our PD analyses (Figs. 3 and 4), but this only shows that some analyses are essentially unaffected by them, not that all analyses are. As an example of a type of analysis likely to be more influenced by intrageneric constraints, the ages of the most recent common ancestors of the three groups *Attalea*, Caribbean *Copernicia* and Malagasy *Orania* have substantially different estimates for *No Constraints*



**Fig. 2.** A newly inferred genus-level phylogenetic tree of the palm family, compared to the tree of Baker et al. (2009, supermatrix analysis). Panel (a) shows the relationships among major clades, the internal relationships of which are shown in more detail in panels (b–r). In (a–j), the new tree is shown on the left side and the Baker et al. (2009) tree on the right. Where the two are identical (panels k–r), only one tree is shown. Taxa that differ in position between the two trees are highlighted in red where the difference is well supported in both trees (posterior support above 0.9 in our new tree and resolved in the semistrict consensus tree from the 2009 supermatrix tree), green where the placement is well supported only in the new tree, blue when the placement is only well supported in the tree of Baker et al. (2009), and grey where the placement is not well-supported in either tree.



**Fig. 3.** Global and continental phylogenetic diversity of the trees from the posterior distributions of trees. The results of three sets of trees are shown, *No Data*, where the intrageneric phylogenies are only based on the birth–death priors; *No Constraints*, including all genetic or morphological data, but not intrageneric topological constraints; and *Constraints*, where all genetic or morphological data as well as intrageneric topological constraints are included (see Section 2.2.2 for additional details). No plot is shown for Europe because the only two species on the continent belong to different genera making the results identical for all three sets of trees.

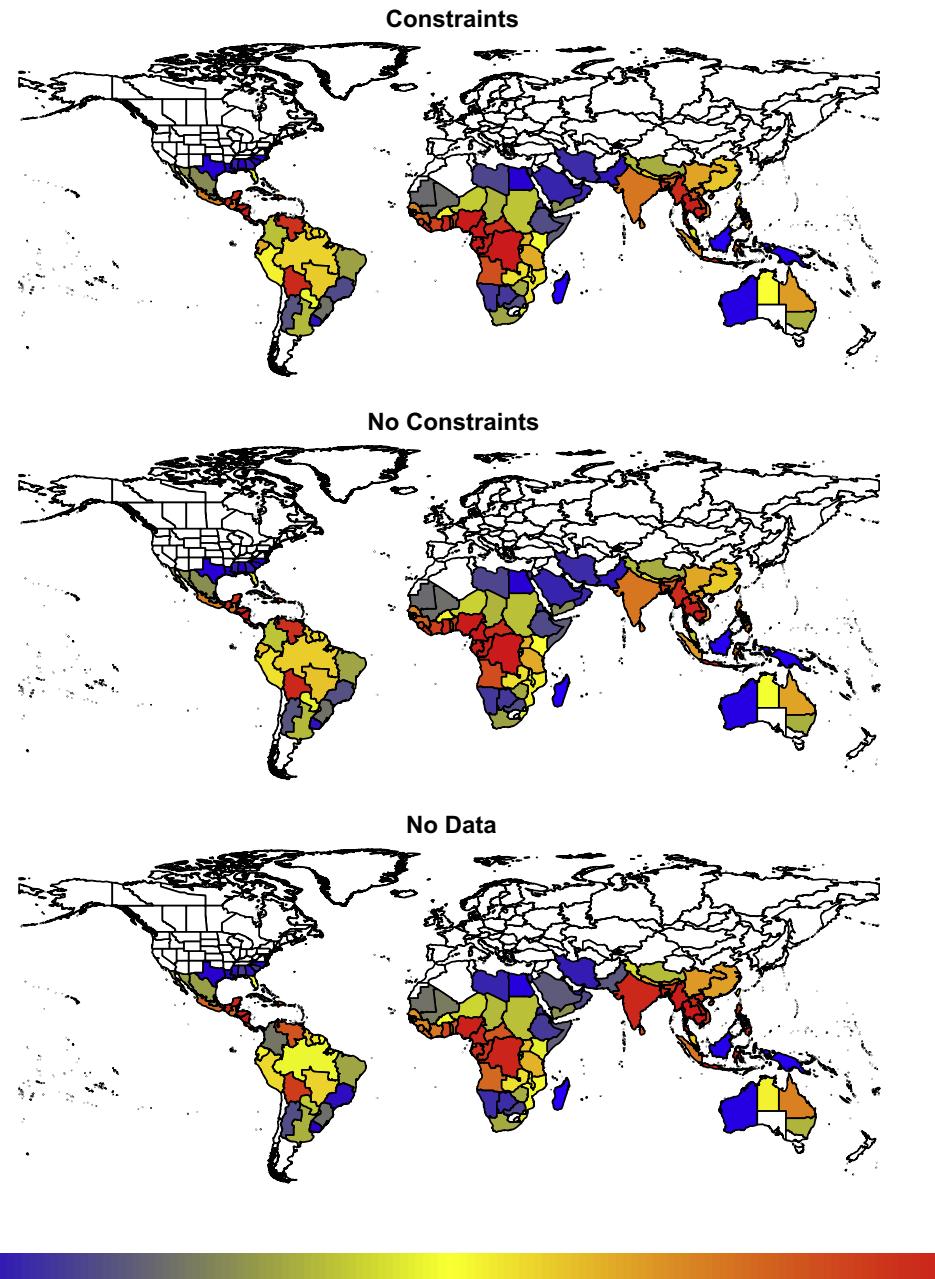
and *Constraint*, but much smaller differences between *No Constraints* and *No Data* (Fig. 6). These three examples are selected among genera with relatively limited sampling of species, but taxonomic constraints in place for the majority of the unsampled species. Since the constraints are deliberately only enforced when they influence the placement of at least one unsampled species, the differences between *No Constraints* and *Constraint* will diminish as species sampling is improved in future phylogenies.

These three examples also illustrate some of the potential problems of implementing intrageneric constraints. For *Orania*, the tested and employed constraints are identical, but the available data is very limited. We have only genetic data for three out of 28 species to support the suggested monophyly of the Malagasy and the South-East Asian species (Keim and Dransfield, 2012). While the posterior support in this case for the monophyly of the two sampled Malagasy species relative to the single Southeast Asian species is 1.000, the species sampling is problematically low. The sampling for *Copernicia* with 13 out of 22 species and *Attalea* with 18 out of 67 species is better, but both represent cases where we employ slightly different constraints than we test for (Figs. 1 and S1, Appendix A). In this case we note that while the constraints we test for (in both cases based on subgenus assignment) and therefore the *Constraint trustworthiness* (see materials and methods) can be considered objective, the modifications of the constraints we employ may not be, since other researchers could have interpreted these modifications of the constraints (employed to minimize conflicts with the genetic data) differently.

We believe that the constrained trees are more likely to represent the true phylogenetic history, but the insufficiently tested assumptions and partial subjectivity employed in the

implementation of them may concern some end-users. We would therefore suggest that end-users of our phylogeny compare the results of any analysis for the *Constraints* and *No Constraints* sets of trees and consider conclusions, which are independent of the dataset that is used to be more certain than conclusions, which only hold for one of them.

We suggest that potential users carefully consider whether our approach or alternative approaches (e.g. Thomas et al., 2013; Faurby and Svensen, 2015) are most appropriate for their study group. The main difference between the approaches is the use of topological constraints. The approach of Thomas et al. (2013) can essentially be seen as a specialized case of our new approach where all *constraint trustworthiness* values are set to either 0 or 1 based on prior information on the particular taxon. The approach may therefore be faster than ours since our approach requires two analyses of all genera whereas the approach of Thomas et al. (2013) may only require one. The approach of Faurby and Svensen (2015) allows enforcing constraints for species without data without influencing the position of species with data (this is achieved through a complex set of post-analysis modifications of the phylogenies), but comes at a cost of losing branch length information. If there is strong knowledge about the placement of all species without molecular or morphological data there may be no need for our new approach, and the solution of Thomas et al. (2013) may be simpler and faster. If topological precision is considered more important than branch lengths and if the information used to place the missing species is judged to be likely, rather than certain the approach of Faurby and Svensen (2015) may be preferred. Otherwise the approach described in this paper is likely the best of the three.



**Fig. 4.** Geographic variation in the residuals between species diversity and phylogenetic diversity. Colors represent the order of the value so the country with the smallest residual value (i.e., the country with the lowest phylogenetic diversity relative to its species diversity), which is Madagascar for both *No Data* and *No Constraints*, is deep blue while the country with the highest phylogenetic diversity relative to its species diversity (Thailand for *No Data*, Cameroon for *No Constraints*) is colored deep red.

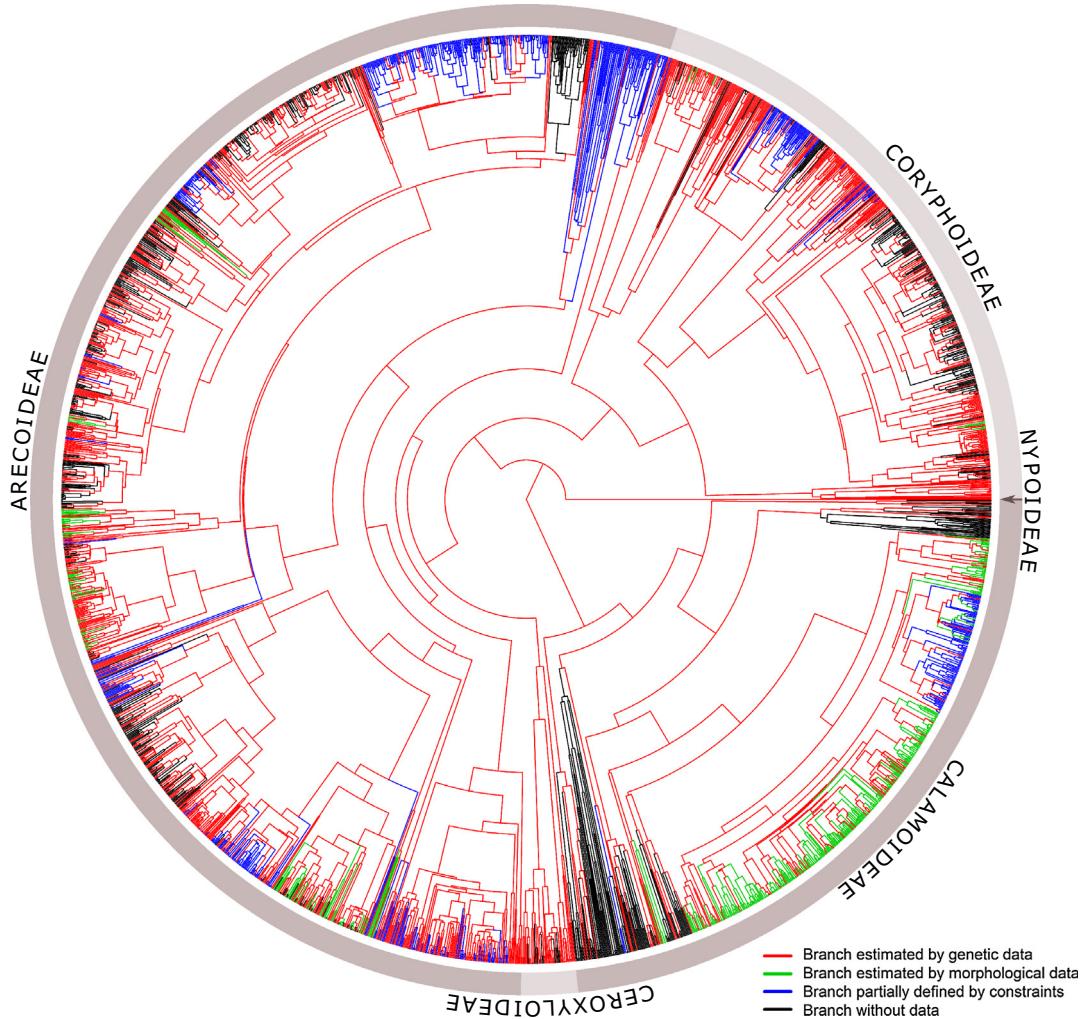
#### 4.2. The intergeneric relationships

Despite the strong similarities in the topology among older lineages, our new analysis recovered surprisingly large differences regarding the internal organization of the younger lineages i.e., the relationship among genera within tribes or subtribes relative to the 2009 supermatrix tree (Fig. 2). The substantial differences despite similar input data highlight the substantial remaining uncertainty and the need for additional data to fully settle the intergeneric phylogeny of palms.

As we noted earlier the Bayesian approaches we employ here may on average be slightly better than parsimony methods as employed in Baker et al. (2009). Regarding potential improvement of the tree, we can note that the placement of *Masoala* as sister to the remaining Dypsidinae appears more plausible since it is in

agreement with standard taxonomic opinions. In contrast, the placement of the genus *Sabal* as sister to *Cryosophileae*, *Phoeniceae* and *Trachycarpeae* instead of just *Cryosophileae* seems surprising given the biogeography of *Sabal* and the previous analyses containing the genus discussed in Dransfield et al. (2008b).

The existence of multiple local optima for many of the analyses highlight problems in the reconstruction of the phylogeny of palms and we cannot know for certain if our treatment of the problem is adequate. This depends on whether the problems are (mainly) caused by incomplete lineage sorting or by the non-constancy of mutational parameters. If the problem is (mainly) incomplete lineage sorting, species-tree algorithms like BEAST (Heled and Drummond, 2010) could be the solution. Alternatively, the problem could be a non-constancy of mutational parameters, since constancy is assumed by most phylogenetic analyses (including ours).



**Fig. 5.** A representative tree from the posterior distribution of trees. The figure shows one of the 1000 trees from the posterior distribution of trees from the dataset including topological constraints. The names of the subfamilies is shown at the root of each subfamily. We stress that the plotted trees is no more representative of the underlying set than any other of the 1000 trees.

One of the most readily visible examples of variation in such parameters is variation in GC content, which has been shown to be able to bias phylogenetic reconstruction and create false sister groups of distantly related taxa with similar GC content (Gruber et al., 2007). Similar problems can arise for any of the many other parameters.

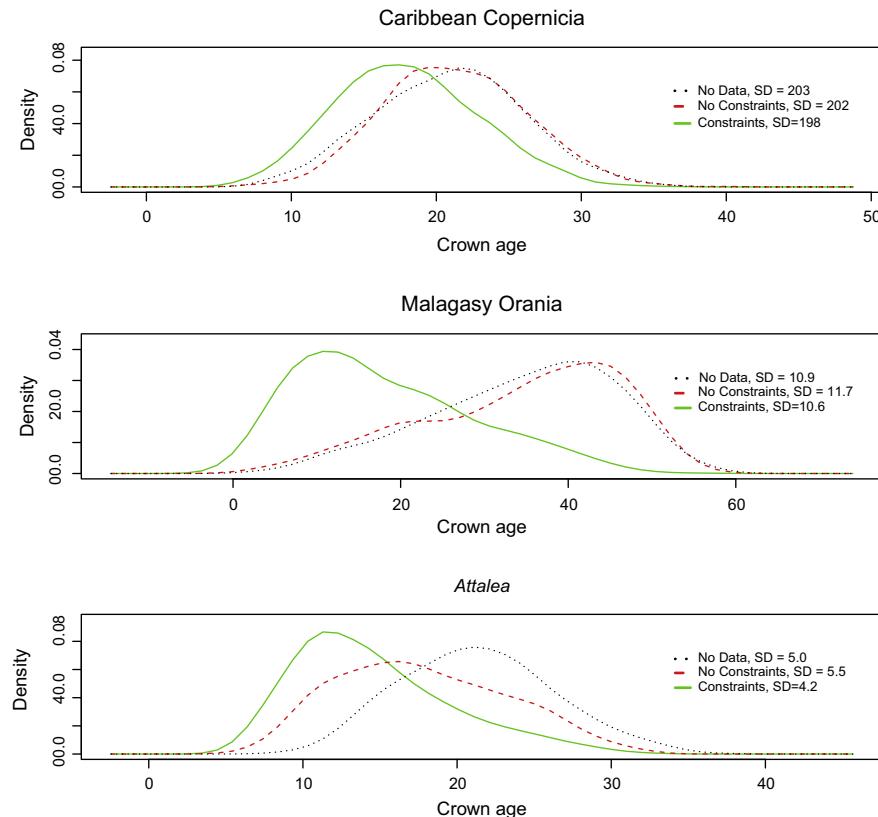
In our analysis we assumed this latter cause to be the underlying problem. We tried reducing it by reanalyzing the parts of the intrageneric tree with convergence problems only using closer related groups of genera. This makes the assumption of constancy of parameters more likely, but on the other hand means that fewer mutations are available to estimate each parameter, giving a lower precision on the estimate of all mutational parameters. We cannot know for certain if this assumption was valid, but the fact that the convergence issues in these analyses were substantially smaller than in the overall tree suggests that it was at least part of the problem for the overall phylogeny.

#### 4.3. Potential bias of using genus-level trees in species-level analyses

Our analysis of phylogenetic diversity using different versions of the tree indicated that analyses that are exclusively based on genus-level relationships (*No Data* analysis) may overestimate phylogenetic diversity, at least at large spatial scales. The variation in this effect among continents further indicates a geographic

pattern in the magnitude of the bias. Such a geographic pattern may not be real, however, and could reflect geographic variation in our ability to estimate the bias instead, since incomplete species sampling will cause the resulting phylogenetic diversity to be closer to the estimate of *No Data* (because the placement of the species without data are entirely governed by the same birth-death priors that govern the placement of all species in the *No Data* set). Temperate Asia, Australia and North America exhibit the largest differences between the *No Data* and *No Constraints* results, but also have genetic or morphological data for most species (78.4%, 90% and 81%), Tropical Asia and South America have intermediate differences and intermediate data levels (46.8% and 56%), while Africa has the smallest differences, but also only genetic or morphological data for 26.9% of all species. The only potential exception to this was Oceania, which only has a small difference between the pattern for *No Data* and *No Constraints* despite genetic or morphological data for 71% of the species. However, Oceania is dominated by relatively young genera, with relatively low precision in their relative placement (Baker and Couvreur, 2013), which reduced the influence of intrageneric distances for overall phylogenetic diversity.

We cannot know the underlying pattern generating the apparent bias in phylogenetic diversity, but can suggest at least four potential reasons. (1) A true recent increase in diversification rate, (2) miscalculations of extinction rates, (3) taxonomic overinflation,



**Fig. 6.** Variation in the age of the most recent common ancestor of selected clades from the posterior distributions of trees. The results of three sets of trees are shown, *No Data*, where the intrageneric phylogenies are only based on the birth–death priors; *No Constraints*, including all genetic or morphological data, but not intrageneric topological constraints; and *Constraints*, where all genetic or morphological data as well as intrageneric topological constraints are included (see Section 2.2.2 for additional details).

(4) biased sampling of species for genetic or morphological analyses. The first of these is the biologically most interesting one. It goes against a frequent scenario with decreasing diversification rate over time potentially intercropped with new innovations causing initially high, but again decreasing diversification rates (e.g., Rabosky et al., 2014a, 2014b). A recent synchronous increase in numerous lineages has, however, been observed in another plant lineage, the cycads (Nagalingum et al., 2011), showing that such a pattern is occurring in some plant lineages.

The second potential explanation of the pattern could be problems estimating extinction rates, which has been discussed numerous places (e.g., Rabosky, 2010). In this case the question is whether the extinction priors, which we estimated with the MEDUSA algorithm (Alfaro et al., 2009), were systematically underestimated (a higher extinction rate results in lower phylogenetic diversity). This may not be the whole answer, but our approach may be problematic in two separate circumstances that both may create a small part of the bias. The first is that for some genera, which the MEDUSA algorithm inferred to have separate unique diversification rates not shared with any other genera (in our case the two American genera *Coccothrinax* and *Chamaedorea*), it is impossible to estimate both an extinction and a speciation rate and the algorithm therefore assumes Yule-like evolution. The second is that the best model is inferred by AIC meaning that a genuine small, but non-zero, extinction rate will never be inferred since a Yule model has one parameter less than a birth–death model and will therefore be inferred instead.

The third potential cause is taxonomic inflation, which for instance has been suggested to be the cause of an apparent recent diversification increase across all eukaryotes (Hedges et al., 2015). There used to be a substantial variation in taxonomic opinions in palms, for instance exemplified with the approximately

contemporary taxonomic treatments of the American genus *Attalea* by Henderson et al. (1995) and Glassman (1999) who understood the genus as containing 29 and 65 species, respectively. With such large variation it would be possible that oversplitting could have dominated large parts of the family. This variation is reduced at present with a more standardized treatment by Govaerts et al. (2011), but we cannot rule out that taxonomic inflation may bias the estimation of phylogenetic diversity in a likely small manner.

The fourth potential cause is nonrandom species sampling in genetic studies. Most phylogenetic studies try as hard as possible to sample all the oldest lineages within a clade (Mooers, 1995). If most genetic data comes from studies with a primary phylogenetic focus near the genus level, the majority of the missing species could therefore be expected to be closely related to the sampled ones, whereas we assume them to be randomly placed within their genera, in which case the bias could be even higher than our results indicate. If, on the other hand, most of the genetic data comes from studies investigating species limits in difficult groups or focus on the species within a limited region (and they are closer related to one another than random species in the genus), the nonrandom sampling could generate part of the observed apparent bias instead.

#### 4.4. The implication of the new trees in future studies

The clear bias in the estimation of phylogenetic diversity at large spatial scales (Fig. 3) seems at odds with the comparison of residuals between countries (Fig. 4), which partially may be because the bias is comparable between many regions. If all input data are biased to the same extent in the same direction the result may not be. This would therefore indicate that the biases are unlikely to have substantially affected the conclusions of earlier geographic studies on palm diversification.

We anticipate that the new trees obtained here will increase confidence in the conclusions that are drawn in future studies. As discussed elsewhere (e.g., Faurby and Svenning, 2015) the likelihood for any given tree (including the maximum likelihood estimate) is extremely small. Given the massive uncertainty even at the genus level (Fig. S2), it will therefore be highly beneficial for new studies to be able to directly integrate a set of trees from the posterior distribution instead of restricting the analyses to a single tree. Another improvement with this new set of trees is an expected increase in the power of the analyses. As illustrated in Fig. 3 any parameter such as the phylogenetic diversity can be estimated more precisely when more data is included, which is illustrated in the decreased in the standard deviations for the *No Constraints* and *Constraints* analyses relative to the *No Data* ones. Analyses using the new trees would therefore be suspected to have a substantially lower false negative rate than analyses not incorporating information below the genus level.

We are convinced that the new sets of trees we have included will stimulate the interesting macroevolutionary and macroecological research performed on palms and have included both the *No Constraints*, the *Conservative constraints* and the *Constraints* set of trees (Appendix C) and hope they will be useful to analyze novel hypotheses in palms. The data is also available on the homepage <http://bios.au.dk/en/about-bioscience/organisation/ecoinformatics-and-biodiversity/data/> where they will be updated as new genetic or morphological data becomes available.

## Acknowledgements

We are grateful to the Danish Council for Independent Research | Natural Sciences (grant 12-125079 to JCS and 4090-00227 to SF) and the European Union's FP7-PEOPLE programme (grant 327259 to WLE) for financial support. In addition we are deeply grateful to Andrew Henderson for allowing us to use his unpublished morphological database for the subtribe Calaminae. We thank an anonymous reviewer and the editor for their constructive comments on the manuscript.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ympev.2016.03.002>.

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