Annals of Botany **128**: 205–215, 2021
doi: 10.1093/aob/mcab056, available online at www.academic.oup.com/aob

ANNALS OF BOTANY
Founded 1887

In situ radiation explains the frequency of dioecious palms on islands

Cibele Cássia-Silva[1,*], Cíntia G. Freitas[2], Lucas Jardim[3], Christine D. Bacon[4,5] and Rosane G. Collevatti[1]

[1]Laboratório de Genética & Biodiversidade, Instituto de Ciências Biológicas, Universidade Federal de Goiás, 74001-970, Goiânia, GO, Brazil, [2]Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná, 81531-990, Curitiba, PR, Brazil, [3]Laboratório de Ecologia Teórica e Síntese, Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, 74001-970, Goiânia, GO, Brazil, [4]Department of Biological and Environmental Sciences, University of Gothenburg, Box 461, 405 30, Gothenburg, Sweden and [5]Gothenburg Global Biodiversity Centre, 405 30, Gothenburg, Sweden
**For correspondence. E-mail cibelecassia01@gmail.com*

Received: 30 January 2021 Returned for revision: 22 April 2021 Editorial decision: 26 April 2021 Accepted: 28 April 2021
Electronically published: 5 May 2021

• **Background and Aims** Dioecy has evolved up to 5000 times in angiosperms, despite the potentially high intrinsic costs to unisexuality. Dioecy prevents inbreeding, which is especially relevant on isolated islands when gene pools are small. Dioecy is also associated with certain dispersal traits, such as fruit size and type. However, the influence of dioecy on other life history traits and island distribution remains poorly understood. Here, we test the effect of dioecy on palm (Arecaceae) speciation rates, fruit size and frequency on islands.
• **Methods** We used phylogenetic comparative methods to estimate the ancestral state of the sexual system and its impact on speciation rates and fruit size. Frequency of sexual systems, effect of insularity on the probability of being dioecious, and phylogenetic clustering of island dioecious vs. mainland species were inferred. Lastly, we determined the interplay of insularity and sexual system on speciation rates.
• **Key Results** Palms repeatedly evolved different sexual systems (dioecy, monoecy and polygamy) from a hermaphrodite origin. Differences in speciation rates and fruit size among the different sexual systems were not identified. An effect of islands on the probability of the palms being dioecious was also not found. However, we found a high frequency and phylogenetic clustering of dioecious palms on islands, which were not correlated with higher speciation rates.
• **Conclusions** The high frequency and phylogenetic clustering may be the result of *in situ* radiation and suggest an 'island effect' for dioecious palms, which was not explained by differential speciation rates. This island effect also cannot be attributed to long-distance dispersal due to the lack of fruit size difference among sexual systems, and particularly because palm dispersal to islands is highly constrained by the interaction between the sizes of fruit and frugivores. Taken together, we suggest that trait flexibility in sexual system evolution and the *in situ* radiation of dioecious lineages are the underlying causes of the outstanding distribution of palms on islands.

Key words: Arecaceae, dioecy, fruit size, hermaphroditism, island rule, macroevolution, monoecy, sexual system evolution.

INTRODUCTION

The diversity of angiosperms can be directly linked to their striking variation and evolutionary lability of sexual systems (Barrett, 2013; Onstein, 2020). The most common angiosperm sexual systems are bisexual flowers (e.g. hermaphroditism), bisexual individuals (i.e. monoecy: unisexual flowers within the same individual) and unisexual individuals (i.e. dioecy: the total separation of female and male functions in different individuals; Barrett, 2002). The large variation in the frequency distribution of the main sexual systems has long raised questions about the causes of the widespread nature of hermaphroditism compared with the rarity of dioecy (Käfer *et al.*, 2014; Renner, 2014). The majority of angiosperms (approx. 72 %) retain their ancestral condition of hermaphroditism (de Jong and Klinkhamer, 2005; Sauquet *et al.*, 2017), while the derived condition of dioecy is found in only 6 % of species (Renner, 2014). Despite this low frequency, recent findings show that dioecy is an important driver of angiosperm diversification (Käfer *et al.*, 2014; Käfer and Mousset, 2014; Onstein, 2020), in opposition to the classic view of dioecy as an evolutionary dead-end (Bull and Charnov, 1985), or at least as having elevated extinction rates (Vamosi and Vamosi, 2005). However, the potential effects of dioecy on speciation and extinction remain extremely controversial mainly due to its idiosyncratic nature (Sabath *et al.*, 2016; Goldberg *et al.*, 2017).

The evolution of dioecy is potentially costly for angiosperms, which is expressed in obligatory mate availability (Barrett, 2002). Dioecious species lack reproductive assurance, which could favour self-compatible hermaphroditic and monoecious counterparts (Barrett, 2002; Käfer *et al.*, 2014). Also, in a dioecious population, only half of the individuals are seed bearing, which leads to a competitive disadvantage in the presence of bisexual (hermaphroditic and monoecious) competitors (Heilbuth *et al.*, 2001). Despite these potential disadvantages, dioecy has evolved up to 5000 times across angiosperms

(Renner, 2014). The most widely accepted hypothesis for the evolution of dioecy is the avoidance of inbreeding, a frequent cost of hermaphroditism (Barrett, 2013). Indeed, inbreeding depression represents the main selective force driving the evolution of reproductive strategies on angiosperms (Charlesworth and Charlesworth, 1987), with dioecy as the most extreme and effective mechanism, especially in self-compatible clades (Barrett, 2002). The maintenance of dioecy in angiosperms may also reflect the evolution of strategies related to increased reproductive success (Heilbuth *et al.*, 2001; Bruijning *et al.*, 2017), which are in many cases associated with other life history or ecological traits (Renner and Ricklefs, 1995; Vamosi and Vamosi, 2004; Duan *et al.*, 2018).

Dioecious species, for example, are expected to invest more in increased dispersal-, survival- and/or reproduction-related traits (Renner and Ricklefs, 1995; Vamosi *et al.*, 2008; Bruijning *et al.*, 2017). Dioecious species have evolved larger and better-defended seeds (Vamosi *et al.*, 2008) and fruit, as a mechanism to increase the likelihood of seedling establishment and survival (i.e. 'k' strategists, Richards, 1997; Heilbuth *et al.*, 2001). Large fruits and seeds are often correlated with a higher quantity of endosperm (Westoby *et al.*, 2002), which is necessary to keep seeds viable for longer periods, even under intense competition or adverse environmental conditions (Westoby *et al.*, 2002; Vamosi *et al.*, 2008), such as ocean drift and establishment on remote islands.

Baker's law states that after long-distance dispersal, reproductive assurance via selfing may favour the colonization and persistence of hermaphrodite and self-compatible species in mate-limited and remote ecosystems (Baker, 1955), such as islands (e.g. Grossenbacher *et al.*, 2017; Razanajatovo *et al.*, 2019). Baker's law also states that dioecy should be rare on islands because dioecious individuals cannot successfully colonize without a mate (Baker, 1955). Contrary to Baker's law, a high incidence of dioecy has been reported for islands (Carlquist, 1966; Bawa, 1982; Baker and Cox, 1984), with growing evidence through time (Sakai *et al.*, 1995*a*; Richards, 1997; Webb *et al.*, 1999; Schlessman *et al.*, 2014). By hindering inbreeding depression and increasing the genetic variability of small colonizing populations through obligatory outcrossing, selection may favour the evolution of dioecy on islands compared with the mainland as a response to new selective pressures (Carlquist, 1966; Bawa, 1980, 1982). These lasting benefits could outweigh the need for at least two propagules for the colonization of isolated habitats by dioecious species (Carlquist, 1966; Bawa, 1980, 1982). The high proportion of dioecy on islands is also attributed to fleshy fruits, an important ecological correlate of dioecy (Renner and Ricklefs, 1995). The specialization and ability of fleshy fruits to be dispersed long distances by birds and other vertebrates might help dioecious species overcome the strong dispersal filter of island colonization (Sakai *et al.*, 1995*b*). In order to evaluate the evolution of different sexual systems in island habitats, it is thus essential to identify clade-specific constraints on long-distance dispersal.

Iconic elements of tropical islands, palms (Arecaceae) are a species-rich pantropical clade with approx. 2600 species (Baker and Dransfield, 2016). Given that most palm species have fleshy fruits (Zona and Henderson, 1989), palm dispersal to islands is likely to be constrained by the interaction between the sizes of fruit and frugivores (Onstein *et al.*, 2017; but see Bellot *et al.*, 2020). Also, a strong link between fruit size and reproductive success, particularly under stressful conditions, has been suggested in palms (Göldel *et al.*, 2015). The largest fruits of palms are found in three tribes, two of which are dioecious (Borasseae and Phytelepheae; Dransfield *et al.*, 2008). However, the interaction between sexual system and fruit size remains poorly understood for the Arecaceae family. Likewise, despite the role of islands in palm speciation (Savolainen *et al.*, 2006; Kissling *et al.*, 2012*a*, *b*; Weigelt *et al.*, 2015), gaps in our understanding persist; for example, are speciation rates on islands influenced by sexual systems? Does the relative frequency of different sexual systems of palms change between islands and the mainland (Pannell *et al.*, 2015; Grossenbacher *et al.*, 2017; Razanajatovo *et al.*, 2019)?

Palms are particularly diverse in their sexual system, with dioecious, hermaphrodite, monoecious and polygamous (i.e. a combination of bisexual and unisexual flowers in the same individual) species (Fig. 1), all most probably derived from a monoecious ancestor (Nadot *et al.*, 2016). Despite rare self-fertilization rates in nature (Richards, 1997; Henderson, 2002), palms lack self-incompatibility mechanisms such as the ability to recognize and reject their own pollen (Nadot *et al.*, 2016); thus dioecy is the most effective outcrossing mechanism within palms (Barrett, 2002). Taxonomically comprehensive sexual system (Dransfield *et al.*, 2008; Nadot *et al.*, 2016) and fruit size data (e.g. Kissling *et al.*, 2019; Cássia-Silva *et al.*, 2020), information on species occurrence (http://apps.kew.org/wcsp) and a species-level phylogeny (Faurby *et al.*, 2016) are available for palms. Such factors make palms a model clade to study the potential influence of the sexual systems on speciation rates and their potential ecological correlates.

Here, we leverage the variation of sexual system in palms to test for the potential effects of dioecy on speciation rates, reproductive success through increased fruit size and macroecological patterns of geographical distribution in mainland vs. island habitats. Specifically, we hypothesize that dioecy has a significant correlation with palm (1) speciation rates; (2) large fruit size (Richards, 1997); and (3) frequency on islands (Carlquist, 1966; Bawa, 1980; Pannell *et al.*, 2015). We also expect that the higher relative frequency of dioecious palms on islands compared with the mainland is explained by their higher speciation rates when compared with their (1) non-dioecious island and (2) dioecious mainland counterparts, and that (3) *in situ* radiation is evidenced by their high phylogenetic clustering when compared with non-dioecious counterparts on islands.

MATERIALS AND METHODS

Data

We used a time-calibrated phylogenetic tree for all 2539 palm species (Faurby *et al.*, 2016), based on the taxonomy from Govaerts *et al.* (2011). For analyses, we used either a subset of 100 random trees or the maximum clade credibility (MCC) tree, which was calculated from the posterior distribution (Cássia-Silva *et al.*, 2019). Data on sexual systems were obtained from the literature (Dransfield *et al.*, 2008;

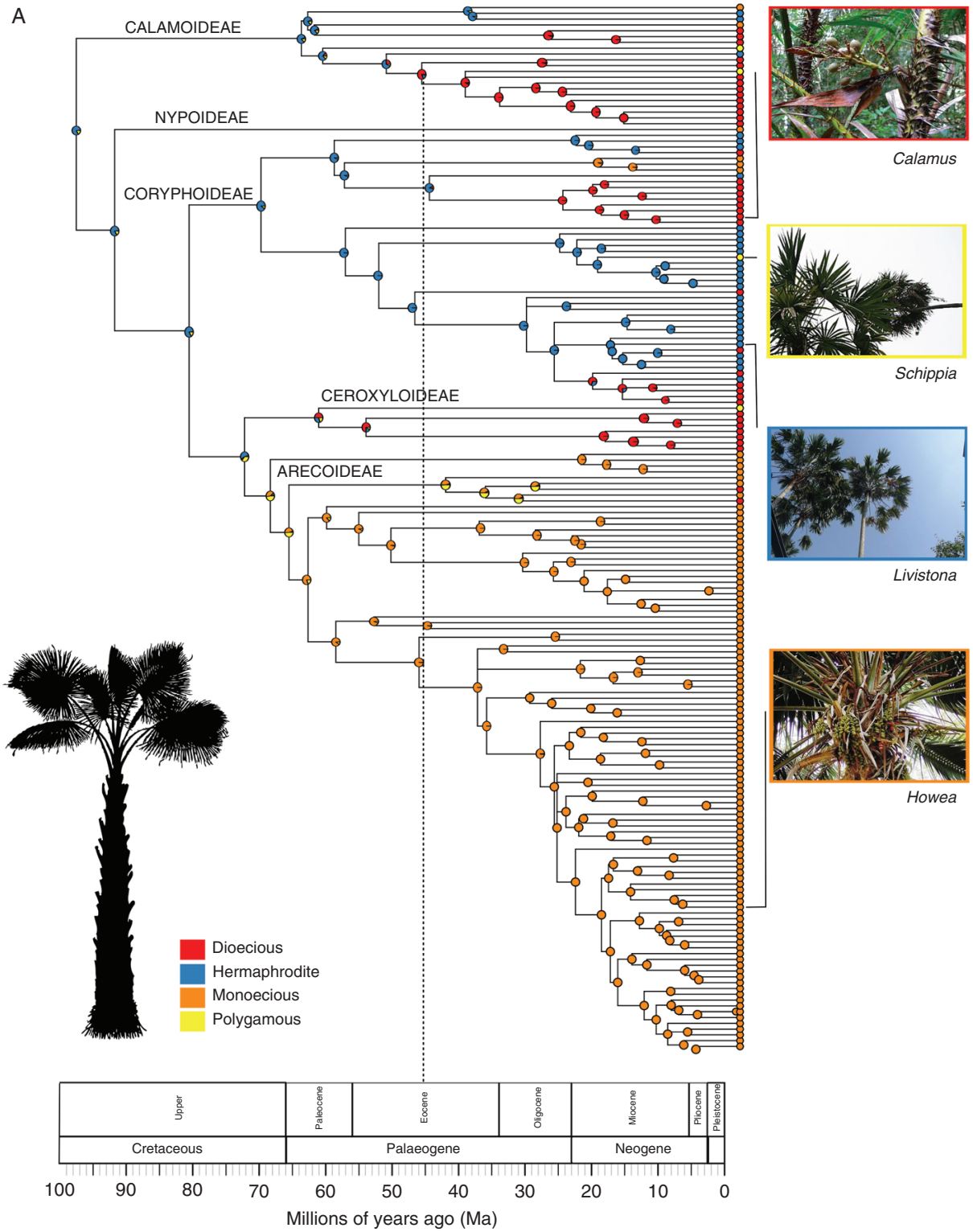

FIG. 1. Bayesian stochastic character mapping of palm sexual system evolution performed across 100 random genus-level trees. (A) Pie charts at nodes in the consensus tree represent ancestral states, which were calculated as the posterior probability of dioecy (red), hermaphroditism (blue), monoecy (orange) and polygamy (yellow), the sexual system states of palms. (B) The lineage diversity through time obtained from Bayesian stochastic character mapping with the palm maximum clade credibility tree with 1000 iterations and all different rates model. The palm silhouette was obtained from PhyloPic (http://phylopic.org), and representative genera photos were obtained from Wikispecies (http://species.wikimedia.org/) under the Creative Commons License.

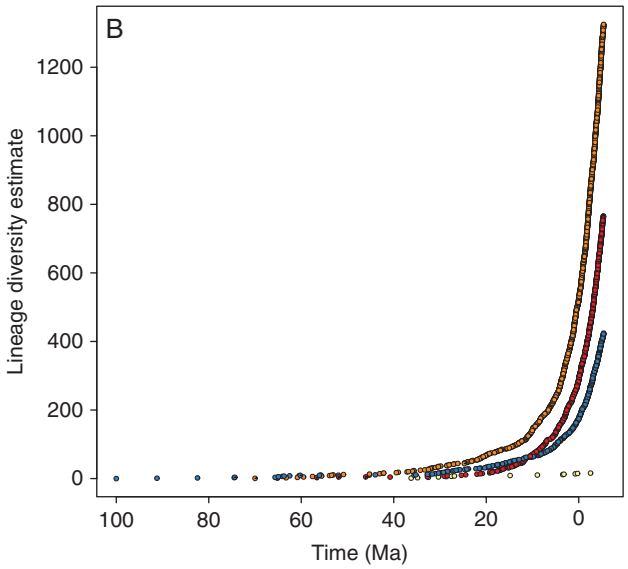

FIG. 1. Continued.

Henderson and Bacon, 2011; Nadot *et al.*, 2016). Following Nadot *et al.* (2016), we classified palms as dioecious, hermaphrodite, monoecious or polygamous based on the genus level (see details in Supplementary data Appendix S1). Treating the family at the genus level is justified because variation in the sexual system within genera is reported for only *Arenga*, *Chuniophoenix*, *Licuala*, *Livistona*, *Maxburretia*, *Rhapis*, *Trachycarpus* and *Wallichia* (eight genera out of 181; Baker and Dransfield, 2016). We coded these polymorphic genera based on their most frequent sexual system (see Supplementary data Table S1), following Nadot *et al.* (2016).

We obtained presence and absence data on islands for palms from the World Checklist of Selected Plant Families (http://apps.kew.org/wcsp accessed on 15 July 2019). In this global plant database, species presences and absences are recorded across the world within geographic units categorized as 'botanical countries' or 'level 3 geographic units' as defined by the International Working Group on Taxonomic Databases (TDWG), being the largest countries (i.e. Australia, Brazil, China and the USA) split into smaller states or provinces. All level 3 geographic units from the TDWG were classified into islands or mainland habitats (e.g. Kissling *et al.*, 2012*a*; Onstein *et al.*, 2017). Islands were defined as landmasses smaller than Australia and surrounded by ocean (Kreft *et al.*, 2008), which we then classified according to their geological origin as continental or oceanic islands based on data obtained from the United Nations Environment Program Island Directory (http://islands.unep.ch/isldir.htm accessed on 10 August 2019). Here, island species were only those with occurrence records on islands of oceanic origin, since higher speciation rates of dioecious species in insular habitats are expected only on islands that are isolated (Bawa, 1980). Oceanic islands, such as atolls and volcanic islands, have never been connected to the continental shelf (Kreft *et al.*, 2008), so geological origin was leveraged as a surrogate of isolation. Species occurring on continental islands and on the mainland were classified as 'mainland' (we refer only to mainland habitat hereafter).

We used fruit diameter to represent palm fruit size due to the strong correlation between different dimensions, such as diameter and length (Onstein *et al.*, 2018). We obtained fruit diameter data from a global dataset for palms (Cássia-Silva *et al.*, 2020). All analyses were performed using the R platform version 3.6.1 (R Core Team, 2019).

Ancestral character reconstruction of palm sexual systems

To identify the ancestral state of sexual systems for all palm lineages, we performed stochastic character mapping (Huelsenbeck *et al.*, 2003) using the MCC tree. We performed the analysis with the empirical Bayesian method with 100 iterations using the optimal transition model with the 'make.simmap' function (Bollback, 2006) implemented in 'phytools' (Revell, 2012). As the transition model can directly impact the ancestral state reconstruction (Pagel, 1994), we first selected between two models of discrete trait evolution for stochastic mapping analyses to avoid any potential bias in the estimates of the ancestral states along phylogeny. We compared the fit of the all-rates-different (ARD: a different rate for each possible transition between states) and the equal-rates (ER: a single rate for all possible transitions between states) models using the corrected Akaike information criteria (AIC_c) and weighted AIC (AIC_w; Burnham and Anderson, 2002) in 'geiger' (Harmon *et al.*, 2008). The ARD was the model that fitted best (Supplementary data Table S2), and was thus used as the transition model for stochastic mapping. Then, we estimated the dioecious, hermaphrodite, monoecious and polygamous lineage diversity across the MCC tree using the 'estDiversity' function in 'phytools'.

We assessed the phylogenetic uncertainty in ancestral sexual system state reconstruction using genus-level data. Because the addition of redundant tips (i.e. 2539 species rather than 181 genera) would add unnecessary parameters and time without increasing the performance of stochastic character mapping (Huelsenbeck *et al.*, 2003; Bollback, 2006), we pruned 100 randomly sampled genus-level trees taken from the posterior distribution, maintaining only a single species to represent each genus. Similarly to the MCC tree, we performed the stochastic character mapping for genus-level trees using 'make.simmap' with the ARD model and 1000 iterations.

State-dependent speciation rates

To test whether speciation rates (λ) of palms differ among sexual systems (Hypothesis 1), we used two complementary approaches: the structured rate permutation in phylogenies correlation (STRAPP; Rabosky and Huang, 2016) and the multistate state version of hidden state speciation and extinction – HiSSE – model (Beaulieu and O'Meara, 2016), namely MuHiSSE (Nakov *et al.*, 2019), which accommodates four trait states rather than only binary traits required for HiSSE. For both approaches, we focused our analyses on speciation rates because our Hypothesis 1 refers directly to speciation rather

than diversification rates. Additionally, we evaluated the impact of sexual systems on net diversification (speciation minus extinction) rates of palms using the MuHiSSE approach, although the inference of extinction rates from molecular phylogenies remains controversial and challenging, especially for large trees (Rabosky, 2010; Beaulieu and O'Meara, 2015).

To run STRAPP, we used speciation rates previously inferred for the palm MCC tree (see Cássia-Silva *et al.*, 2019) employing Bayesian analysis of macroevolutionary mixtures (BAMM; Rabosky, 2014) and correlated them with the sexual systems using the Kruskal–Wallis test implemented in the 'BAMMtools' package (Rabosky *et al.*, 2014). We compared the resulting statistics with a null distribution obtained by permutation of the evolutionary rates at the tips of the phylogeny. The proportion of permutations of the posterior samples where the correlation of the null distribution was more different than the observed correlations was used as a measurement of statistical significance utilizing the Kruskal–Wallis test (Rabosky and Huang, 2016). We also built eight different MuHiSSE models for the palm MCC tree, all departing from a full model with no parameter constraints following Nakov *et al.* (2019). The full model identifies whether and which sexual system state is associated with variation in the diversification rates (Supplementary data Fig. S1). Then, we built seven character-independent diversification (CID) models with increasing numbers of unobserved states (1–7) and equal diversification parameters for the four observed sexual system states (Supplementary data Fig. S1). The CID models assume that diversification rate differences are associated with unobserved states and this number of unobserved states (i.e. 1–7), which were previously estimated in the MCC tree (Supplementary data Table S3). For all MuHiSSE models, we used the transition matrix of the sexual system states estimated in the stochastic character mapping (see above), but we constrained the transitions by not allowing simultaneous transitions between observed (i.e. 0A and 1A) and hidden states (0B and 1B), following Nakov *et al.* (2019). For instance, the state 'dioecious A' could change to 'dioecious B', but not to 'hermaphrodite B', where the hidden states (A, B) could change only within a single sexual system state. We ran MuHiSSE models and selected the best-fitted model using the AIC_c and AIC_w in 'hisse' (Beaulieu and O'Meara, 2016). We estimated the speciation and net diversification rates for the best-fitting model using GetModelAverates also available in 'hisse'.

Sexual system and fruit size

We evaluated whether dioecious palms have larger fruit sizes when compared with other sexual systems (Hypothesis 2) with a phylogenetic analysis of variance (i.e. phyANOVA). We used the phylANOVA function based on the MCC tree with 10 000 simulations in 'phytools'. To access phylogenetic uncertainty, we also performed the phyANOVA across 100 randomly selected trees taken from the posterior distribution and reported the *F*-statistic and *P*-values across these phylogenies. Due to the allometric relationship between palm height and fruit diameter (Cássia-Silva *et al.*, 2020), we performed an additional phylogenetic generalized least squares (PGLS) regression analysis (Martins and Hansen, 1997) to assess the differences in fruit size as a function of the sexual system, taking into account height as an interaction factor. We performed the PGLS with the MCC tree in 'caper' (Orme, 2013) using the $\log_{10}$ of palm stem height and fruit diameter in all analyses to improve data normality. Data on maximum stem height were taken from the PalmTraits 1.0 dataset (Kissling *et al.*, 2019).

Sexual system and islands

To determine whether islands have a higher relative frequency of dioecious palms compared with the mainland (Hypothesis 3), we first defined island specialists as those species that occur exclusively on oceanic islands (n = 368). Mainland specialists were defined as palms that occur on both mainland and continental islands, as explained above (n = 1932; Supplementary data Appendix S1). We refer to either the island or mainland specialist assemblages as 'habitat specialists' hereafter. Species that occur on both an oceanic island and the mainland were defined as 'widespread' (n = 239). To compare the effects of islands on the probability of the palms being dioecious, we fitted a phylogenetically corrected generalized linear mixed model (PGLMM; Ives and Helmus, 2011) using the MCC tree and 'pglmm' function in the 'phyr' package (Li *et al.*, 2020). We built the PGLMM using dioecy as a binary response variable (dioecious or non-dioecious) and habitat as the independent variable (island specialist, mainland specialist or widespread). The phylogenetic autocorrelation was fitted as a random effect in the intercept of the model. We also took phylogenetic uncertainty into account by running PGLMM over the distribution of 100 phylogenies.

To test for a combined effect of sexual systems and island occurrence on speciation rates (Predictions 1 and 2), we used the several examined and concealed states-dependent speciation and extinction model (SecSSE; Herrera-Alsina *et al.*, 2019). SecSSE allows for the identification of simultaneous action of multiple states (i.e. more than four allowed for MuHiSSE) on diversification rates of clades while accounting for the role of hidden states (Herrera-Alsina *et al.*, 2019). Here, by combining the four sexual systems and two habitat types, we classified all palms into eight observed trait states (i.e. dioecious insular and mainland; hermaphrodite insular and mainland; monoecious insular and mainland; and polygamous insular and mainland). As each species must be assigned to only one habitat type, we thus assigned the widespread species into island categories due to their potential to colonize islands (e.g. Onstein *et al.*, 2017; Razanajatovo *et al.*, 2019). We built ten different SecSSE diversification models using the MCC tree, encompassing these eight states, and varied the number of hidden states (see Supplementary data Fig. S2 for details), as with the MuHiSSE approach described above. Among these ten models, we included a 'dioecious model' and an 'island dioecious model' to explicitly test for higher speciation rates in dioecious compared with non-dioecious palms on islands (Prediction 1), as well as higher speciation rates of insular dioecious species compared with their mainland counterparts (Prediction 2). We maintained speciation rates constant for all states in the 'dioecious model', except for dioecious species with two unobserved states. In the 'insular dioecious model', we maintained the speciation rates

constant for all states except for the insular dioecious with two hidden states, which we expect to have higher rates. The transition matrices for all SecSSE models were the same as for MuHiSSE, but here we restricted the transitions among sexual systems and habitat types at the same time. For example, an island dioecious species could evolve another sexual system state if it remained on an island. We ran all SecSSE diversification models and identified the best-fitting model using 'SecSSE' (Herrera-Alsina *et al.*, 2019). The model selection was also done using AIC_c and AIC_w.

We used phylogenetic species variability (PSV), which is statistically independent of species richness (Helmus *et al.*, 2007), to test for higher phylogenetic clustering of dioecious island compared with non-dioecious island palms (Prediction 3). PSV averages the phylogenetic relatedness among members of an assemblage by quantifying how phylogenetic relatedness decreases the variance of a hypothetical neutral trait shared by all species (Helmus *et al.*, 2007; Tucker *et al.*, 2017). PSV values range from 0 to 1, where PSV = 1 indicates that all species in an assemblage are unrelated (i.e. a star phylogeny) and, as the values approach zero, species are increasingly related (i.e. phylogenetic clustering; Helmus *et al.*, 2007). To calculate the PSV, we used the presence–absence matrix taking into account the island dioecious and island non-dioecious palm assemblages, and the MCC.

RESULTS

Ancestral sexual system and speciation/diversification rates

Hermaphroditism is the most likely ancestral state of palms (Fig. 1A, B), based on both the MCC species-level tree (probability = 1 for the ancestral node) and 100 genus-level trees (probability = 0.811 for the ancestral node; Supplementary data Appendix S1). The most common transition between sexual systems in palm evolutionary history was hermaphrodite to dioecious (approx. 30 %), followed by polygamous to monoecious (approx. 19 %). Meanwhile, shifts from monoecious to hermaphroditism and polygamous were not detected at all in the stochastic mapping analysis (Supplementary data Table S4). Based on the MCC species-level tree, we also found a high accumulation of monoecious and dioecious over hermaphrodite and polygamous palm lineages through time (Fig. 1B).

According to the MuHiSSE approach, the polygamous sexual system had lower speciation and diversification rates, while the other systems presented higher variation, although the rate heterogeneity in the former is better explained by unmeasured (hidden) states and is independent of the sexual systems (i.e. a CID as the best-fitting model; Supplementary data Table S5; Supplementary data Figs S3 and S4). This result was corroborated by the STRAPP correlative approach, in which none of the sexual systems was significantly associated (P = 0.837; $r_{dioecious}$ = 0.450; $r_{hermaphrodite}$ = 0.406; $r_{monoecious}$ = 0.247; $r_{polygamous}$ = 0.071) with speciation rates in palms (Supplementary data Fig. S3A, B).

Fruit size and island occurrence

The variation in palm fruit size was not explained by sexual systems using the MCC tree (phyANOVA $F_{3,1683}$ = 10.92; P = 0.7; n = 1687; Supplementary data Fig. S5) or 100 random trees (Supplementary data Table S6). As we found a significant relationship in palm fruit size as a function of height and sexual systems ($F_{176,1339}$ = 3.687; P < 0.001; n = 1516), we also performed a phyANOVA considering the relative fruit size [i.e. palm fruit diameter (m)/stem height (m)] as response variable. However, again, the sexual systems did not significantly differ in relative fruit size using the MCC tree ($F_{3,1512}$ = 2.006; P = 1; n = 1516) or 100 random trees (Supplementary data Table S6).

Monoecy exhibits the highest frequency on island and mainland habitats (Fig. 2). However, we found a higher frequency of dioecy on islands than the mainland, whereas monoecious and hermaphrodite species show the opposite patterns (Fig. 2). The relative frequency of dioecy on islands (41.2 %) was highly similar to that of monoecy (approx. 44 %), whereas on the mainland, the frequency of dioecy was lower than that of monoecy (approx. 29.0 and approx. 53 %, respectively). Considering only habitat specialist palms, we found a higher relative frequency of dioecy (approx. 36 %) on islands than on the mainland (approx. 27 %; Fig. 2). However, we found no significant relationship between the occurrence on islands and the probability of species being dioecious using the MCC tree (Table 1; Supplementary data Fig. S6) or 100 random trees (Supplementary data Table S7).

We found that the dioecious island palms were phylogenetically more closely related (PSV = 0.364; species richness = 250) than their non-dioecious island counterparts (PSV = 0.581; species richness = 356), but this phylogenetic clustering was not associated with high speciation rates. Using the SecSSE approach, we found that the interactive effect between sexual system (all states) and habitat type (mainland and island) is better explained by unmeasured (hidden) states (i.e. the CID model; Supplementary data Table S8).

DISCUSSION

Here, we used a comprehensive dataset on phylogeny, fruit size and island occurrence to determine the role of sexual system on the macroevolution and macroecology of palms. Specifically, we tested for an effect of dioecy on speciation rates and fruit size, as well as on the presence and speciation rates on islands. We determined that palms were most likely to have originated from a hermaphroditic ancestor and, contrary to our hypotheses, palms showed no significant differences among sexual systems in either speciation rate (Hypothesis 1) or fruit size patterns (Hypothesis 2). Although not driven by higher speciation rates, we found palms on islands to be more frequently dioecious and phylogenetically clustered compared with the mainland assemblage and with non-dioecious island palms, respectively (Hypothesis 3). However, a relationship between islands and the probability of being dioecious was not supported for palms.

Sexual system evolution and patterns of speciation rates

Hermaphroditism is here supported as the most likely ancestral sexual system of palms, which is consistent with the evolutionary pathway of sexual systems in angiosperms (Sauquet *et al.*, 2017), but contrasts with previous understanding of the ancestral state of palms as monoecious (Nadot *et al.*, 2016).

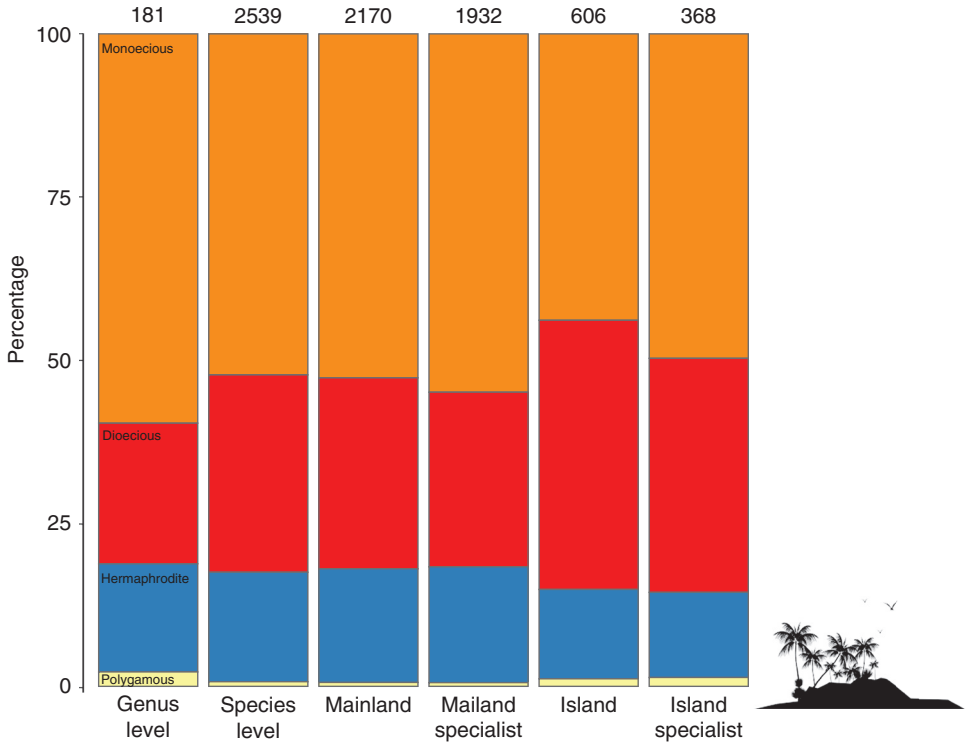

FIG. 2 Frequency of palm sexual systems (dioecy, red; hermaphroditism, blue; monoecy, orange; and polygamy, yellow) on the mainland and island habitats globally. The 'mainland' and 'island' palm assemblages include both species that occur exclusively in those habitats and widespread (occur on islands and the mainland) species. Mainland and island specialists refer to species that occur exclusively in one of those habitats.

TABLE 1. *Phylogenetic generalized linear model fitted for maximum clade credibility (MCC)* palm phylogeny with the probability of palms being dioecious as the dependent variable and habitat type (island, mainland and widespread) as the independent variable*

Fixed effects	**Estimate**	**s.e.**	***Z*-score**	***P***
Island	–2.90	1.81	–1.60	0.11
Mainland	0.62	0.87	0.72	0.47
Widespread	0.49	1.03	0.48	0.63
Random effects	**Variance**	**s.d.**		
Species	1.05 e-08	1.02 e-04		
Phylogeny	0.9	0.94		

Species and Phylogeny random effects are, respectively, species-specific variation and phylogenetic signal of dioecy probability. The table shows the intercept and slope (estimate) of each habitat type with their s.e. and *P*-values. The variance and s.d. of the random effects are also shown.

*The model estimates did not vary across 100 trees randomly sampled from the posterior distribution (Supplementary data Table S7).

Results from Nadot *et al.* (2016) were based on a previous phylogenetic tree for Arecaceae (Baker *et al.*, 2009) to reconstruct the evolution of sexual systems in the family based on parsimony and maximum likelihood optimizations. Results from stochastic character mapping identified sexual flexibility in the evolution of palms, where different states evolved repeatedly over time, which is in agreement with previous findings (Nadot *et al.*, 2016). Contrary to the classic view of dioecy as an irreversible evolutionary trait (i.e. an evolutionary dead-end; Bull and Charnov, 1985; Heilbuth, 2000; Käfer *et al.*, 2013), our results support the suggestion that dioecy is a labile trait across angiosperms (Renner, 2014; Zhang *et al.*, 2019). Dioecious lineages of palms exhibited unconstrained evolution towards other sexual systems (7.63 % towards polygamy; 5.91 % hermaphrodite; and 0.76 % towards monoecy; Supplementary data Table S4), whereas monoecy had constrained flexibility towards hermaphroditism and polygamy (Supplementary data Table S4).

Despite a hermaphroditic origin, palms evolved towards greater (dioecy) or lesser (monoecy) sexual differentiation (Goldberg *et al.*, 2017). Dioecy and monoecy led to high lineage diversity through time (Fig. 1B). Indeed, transitions away from hermaphroditism towards intermediate sexual differentiation, such as monoecy, is a common evolutionary pathway in angiosperms (Goldberg *et al.*, 2017). Monoecy shares some of the advantages of dioecy, such as reduced inbreeding and the elimination of trade-offs between male and female function at the flower level (Barrett, 2002). Unlike dioecy, monoecy provides reproductive assurance through the combined male and female functions within a single individual (Barrett, 2002). Such mixed advantages may explain the highest lineage diversity of monoecy compared with other sexual systems. However, in contrast to recent findings for angiosperms (Onstein, 2020), the high diversity through time of monoecious and dioecious palm lineages was not triggered by high speciation rates.

Despite the strong phylogenetic structure in palm sexual systems (Fig. 1A), none of them (dioecy, hermaphroditism, monoecy and polygamy) was associated with differential speciation rates. This result rejects our hypothesis that dioecy leads to high speciation rates (Hypothesis 1). Although we did not directly assess extinction rates, the placement of dioecy on the palm phylogeny suggests that it also is not associated with higher extinction rates (Vamosi *et al.*, 2018), as suggested (Bull and Charnov, 1985; Heilbuth, 2000; Vamosi and Vamosi, 2005). Traits that increase extinction rates often show limited life span, and the presence of these traits in extant species is likely to be due to a recent origin and thus often appears only at the tips of trees (Bromham *et al.*, 2016; Vamosi *et al.*, 2018), which is not the case of dioecy in palms (Fig. 1A). That is the case because younger lineages probably have not yet had time to experience extinction (Bromham *et al.*, 2016; Vamosi *et al.*, 2018). Indeed, we found no consistent difference in diversification rates (speciation–extinction) among sexual systems in palms. Similarly to Sabath *et al.* (2016), our analysis suggests that the effect of dioecy (and other sexual systems) on speciation as well as on diversification rates is relatively weak, being overwhelmed by other unmeasured traits affecting diversification. The temporal separation of the sexual phases (i.e. dichogamy), for instance, is widespread in palms (Henderson, 2002; Nadot *et al.*, 2016). Dichogamy can superimpose on the sexual system function and favour outcrossing even in monoecious palms that occur sympatrically in small islands (Savolainen *et al.*, 2006). Hence, our work adds evidence to the idiosyncratic and complex nature of sexual system evolution (Goldberg *et al.*, 2017).

Fruit size and an 'island effect' in dioecious palms

The largest fruits of Borasseae and Phytelepheae clades (Dransfield *et al.*, 2008; Bellot *et al.*, 2020) are not explained by dioecy, as we expected (Hypothesis 2). We found that fruit size variation in palms is independent of their sexual system (Supplementary data Fig. S5). One possible explanation is that variation in maximum fruit size of palms is strongly constrained by extrinsic selection pressures related to frugivores (Galetti *et al.*, 2013; Lim *et al.*, 2020) or climatic factors (Göldel *et al.*, 2015; Lim *et al.*, 2020). With rare exceptions such as *Cocos nucifera* and *Nypa fruticans* that are dispersed by water, palms rely on animals for seed dispersal (Zona and Henderson, 1989; Lim *et al.*, 2020). Consequently, a strong relationship of frugivore body size–fruit size is fundamental to dispersal effectiveness. As a result, the frugivore–fruit relationship shapes the variation in maximum fruit size of palms across time and space (Onstein *et al.*, 2018; Lim *et al.*, 2020). The strong selective pressure keeping this body–fruit size relationship could thus overcome the role of intrinsic traits such as the sexual system in fruit size variation of palms. On the one hand, the lack of variation in fruit size among palm sexual systems indicates that the obligate outcrossing in dioecious species may not lead to reproductive investment focused on large fruit (Richards, 1997). On the other hand, this lack of variation indicates that differences in the proportion of dioecious species between thee mainland and islands cannot be attributed to the role of dispersal-related traits (Sakai *et al.*, 1995b; Vamosi and Vamosi, 2004).

Although the relationship between island occurrence and the probability of dioecy was not supported, there is an increased proportion of the dioecious state on islands. Therefore, we suggest that an 'island effect' on dioecy distribution cannot be fully ruled out for palms. The frequency of dioecy in palms is high (approx. 30 %), representing more than five times the frequency in angiosperms (approx. 6 %; Renner, 2014). Moreover, we found an increased frequency of dioecious palms on islands, whereas monoecious and hermaphrodite species show the opposite pattern (Fig. 2). The higher relative frequency of dioecious species on islands (Hypothesis 3) and higher phylogenetic clustering of island dioecious palms, when compared with non-dioecious counterparts (Prediction 3), are in line with the longstanding view of the higher evolutionary success (i.e. abundance, species richness and range size) of dioecy on islands than on the mainland (Carlquist, 1966; Bawa, 1980; Pannell *et al.*, 2015). However, the higher frequency and the phylogenetic clustering of dioecious palms on islands were not triggered by higher speciation rates (Predictions 1 and 2). This lack of differential speciation rates causing the increased frequency of dioecious palms on islands can be explained by the complex interplay of other unmeasured traits, as suggested here by interactive (sexual system and island distribution) state-dependent diversification models. Growth form, dispersal and pollination modes, for instance, are phylogenetically constrained and frequently coincident with dioecy (Käfer *et al.*, 2014; Duan *et al.*, 2018), besides being important traits triggering plant diversification on islands (Givnish *et al.*, 2009).

A disproportionately high frequency of dioecy and monoecy over hermaphroditism on islands, especially when we consider all potential island colonizers such as widespread species (i.e. non-specialist island assemblage; Fig. 2), contradicts Baker's law that hermaphrodites should be the most successful at colonizing islands (Baker, 1955). The higher frequency of dioecy in island assemblages when compared with island specialists (Fig. 2) suggests that some colonizers were dioecious, while the higher phylogenetic clustering suggests a potential *in situ* radiation of dioecious lineages within islands (Kissling *et al.*, 2012*b*). Dioecy evolved early in clades that are currently species rich and widespread on islands such as Calameae (Calamoideae; Henderson, 2009) at approx. 45 million years ago (Fig. 1A), which suggests a potential mainland origin of this sexual system. However, previous studies suggest an early dispersal of Calameae from ancestral mainland ecosystem to islands (Couvreur *et al.*, 2011; Baker and Couvreur, 2013). Fossil pollen records and phylogenetic reconstruction suggest that radiation of Calameae lineages throughout islands from south-east Asia took place during the Eocene (Baker and Couvreur, 2013). Overall, our results suggest that the adaptive value of dioecy in insular conditions might be great enough to overcome the need for the colonization and establishment of two propagules, and posterior radiation on islands (Carlquist, 1966; Bawa, 1980).

Conclusions

With great trait flexibility, palms evolved towards monoecy and dioecy from an ancestral hermaphrodite sexual system. The evolution of monoecy and dioecy leads to accumulation of high palm lineage diversity over time, which was not triggered by differential speciation rates even when associated with island occurrence. However, an island effect on the evolution of dioecy in palms can be evidenced by (1) the higher frequency of dioecious palms on islands than on the mainland and (2) the higher phylogenetic clustering of dioecious island palms, supporting the role of *in situ* radiation (Kissling *et al.*, 2012*b*). Our results indicate that the differential frequency of dioecy on islands cannot be attributed to long-distance dispersal correlates (Sakai *et al.*, 1995*b*; Vamosi and Vamosi, 2004) such as fruit size for palms (Onstein *et al.*, 2017, 2018), due to the lack of variation in fruit size among sexual systems. High trait flexibility requires sufficient pre-existing genetic variation or at least plasticity in this trait, which would allow for faster adaptation to new selective pressures (Onstein, 2020). Therefore, we suggest that the trait flexibility in the sexual system evidenced here by repeated evolution of different sexual systems, and the *in situ* radiation of dioecious lineages, are the underlying factors explaining the evolutionary success (i.e. abundance, species richness and range size) of palms across the tropical region, especially on islands.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following. Appendix S1: sexual system and fruit size datasets used in the analyses and ancestral sexual system nodes. Table S1: palm genera with variation in the sexual system. Table S2: comparative fit of two alternative transition models for sexual system ancestral state reconstruction. Table S3: comparative fit of alternative models ranging from one to 15 hidden states using the missing state speciation and extinction model and the palm maximum clade credibility tree. Table S4: changes between sexual systems in palm phylogeny obtained from stochastic character mapping. Table S5: comparative fit of MuHiSSE models fitted to the palm MCC tree. Table S6: the distribution of *F*-statistic values estimated with phylogenetic ANOVA for palm fruit size and relative fruit size as a function of sexual systems. Table S7: phylogenetic generalized linear model for 100 trees randomly sampled from the posterior distribution, with the probability of palms being dioecious as the dependent variable and habitat type as the independent variable. Table S8: comparative fit of SecSSE fitted to the palm MCC tree. Figure S1: conceptual models of the effect of sexual system or hidden states on palm diversification rates. Figure S2: conceptual models of the effect of sexual system, habitat type and hidden states on palm diversification rates. Figure S3: speciation rates of palms regarding their sexual systems. Figure S4: net diversification rates of palms regarding their sexual systems. Figure S5: traitgram visualizing palm fruit size trajectory through time. Figure S6: phylogenetic distribution of palm dioecious versus non-dioecious sexual systems and habitat type.

FUNDING

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brasil (CAPES) – Finance Code 001. This work was also supported by the Conselho Nacional de Desenvolvimento Cientifico e Tecnológico (CNPq; CNPq/PVE #407310/2013-4) and the Biodiversity and Ecosystem Services in a Changing Climate Initiative at the University of Gothenburg, Sweden to C.D.B. R.G.C. was supported by Rede Cerrado CNPq/PPBio (project no. 457406/2012-7) and PROCAD/CAPES (project no. 88881.068425/2014-01). C.D.B. was supported by the Swedish Research Council (2017-04980). C.C.S. and C.G.F. received fellowships from CAPES. L.J. received a fellowship from the National Institutes for Science and Technology in Ecology, Evolution and Biodiversity Conservation (INCT-EECBio), supported by MCTIC/CNPq (proc. 465610/2014-5) and FAPEG (proc. 201810267000023). R.G.C. has continuously been supported by productivity grants from the CNPq, which we gratefully acknowledge.

ACKNOWLEDGEMENTS

We thank Anne Brysting and two anonymous referees for their detailed reviews and constructive comments that helped to improve the manuscript. We also thank Mário Almeida-Neto and Luísa Carvalheiro for constructive comments on an earlier version of the manuscript. C.S.S. designed the study. C.C.S., C.G.F. and L.J. performed the analyses. C.C.S. wrote the first version of the manuscript with substantial input from C.D.B. and R.G.C. All authors contributed to revisions and approved the final version of the manuscript. The authors declare no conflict of interest.

LITERATURE CITED

Baker HG. 1955. Self-compatibility and establishment after 'long-distance' dispersal. *Evolution* **9**: 347–349.

Baker WJ, Couvreur TLP. 2013. 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.

Baker HG, Cox PA. 1984. Further thoughts on dioecism and islands. *Annals of the Missouri Botanical Garden* **71**: 244–253.

Baker WJ, Dransfield J. 2016. Beyond genera palmarum: progress and prospects in palm systematics. *Botanical Journal of the Linnean Society* **182**: 207–233.

Baker WJ, Savolainen V, Asmussen-Lange CB, *et al.* 2009. Complete generic-level phylogenetic analyses of palms (Arecaceae) with comparisons of supertree and supermatrix approaches. *Systematic Biology* **58**: 240–256.

Barrett SCH. 2002. The evolution of plant sexual diversity. *Nature Reviews Genetics* **3**: 274–284.

Barrett SCH. 2013. The evolution of plant reproductive systems: how often are transitions irreversible? *Proceedings of the Royal Society B: Biological Sciences* **280**: 20130913.

Bawa KS. 1980. Evolution of dioecy in flowering plants. *Annual Review of Ecology and Systematics* **11**: 15–39.

Bawa KS. 1982. Outcrossing and the incidence of dioecism in island floras. *The American Naturalist* **119**: 866–871.

Beaulieu JM, O'Meara BC. 2015. Extinction can be estimated from moderately sized molecular phylogenies. *Evolution* **69**: 1036–1043.
Beaulieu JM, O'Meara BC. 2016. Detecting hidden diversification shifts in models of trait-dependent speciation and extinction. *Systematic Biology* **65**: 583–601.
Bellot S, Bayton RP, Couvreur TLP, *et al.* 2020. On the origin of giant seeds: the macroevolution of the double coconut (*Lodoicea maldivica*) and its relatives (Borasseae, Arecaceae). *New Phytologist* **228**: 1134–1148.
Bollback JP. 2006. SIMMAP: stochastic character mapping of discrete traits on phylogenies. *BMC Bioinformatics* **7**: 88.
Bromham L, Hua X, Cardillo M. 2016. Detecting macroevolutionary self-destruction from phylogenies. *Systematic Biology* **65**: 109–127.
Bruijning M, Visser MD, Muller-Landau HC, *et al.* 2017. Surviving in a cosexual world: a cost–benefit analysis of dioecy in tropical trees. *The American Naturalist* **189**: 297–314.
Bull JJ, Charnov EL. 1985. On irreversible evolution. *Evolution* **39**: 1149–1155.
Burnham KP, Anderson DR. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer New York.
Carlquist S. 1966. The biota of long-distance dispersal. IV. Genetic systems in the floras of Oceanic Islands. *Evolution* **20**: 433–455.
Cássia-Silva C, Freitas CG, Alves DMCC, Bacon CD, Collevatti RG. 2019. Niche conservatism drives a global discrepancy in palm species richness between seasonally dry and moist habitats. *Global Ecology and Biogeography* **28**: 814–825.
Cássia-Silva C, Freitas CG, Lemes LP, *et al.* 2020. Higher evolutionary rates in life-history traits in insular than in mainland palms. *Scientific Reports* **10**: 21125.
Charlesworth D, Charlesworth B. 1987. Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics* **18**: 237–268.
Couvreur TL, Forest F, Baker WJ. 2011. Origin and global diversification patterns of tropical rain forests: inferences from a complete genus-level phylogeny of palms. *BMC Biology* **9**: 44.
Dransfield, J, Uhl N, Asmussen C, Baker W, Harley M, Lewis C. 2008. *Genera Palmarum. The evolution and classification of palms*. Royal Botanic Gardens Kew: Kew Publishing.
Duan T, Deng X, Chen S, *et al.* 2018. Evolution of sexual systems and growth habit in *Mussaenda* (Rubiaceae): insights into the evolutionary pathways of dioecy. *Molecular Phylogenetics and Evolution* **123**: 113–122.
Faurby S, Eiserhardt WL, Baker WJ, Svenning JC. 2016. An all-evidence species-level supertree for the palms (Arecaceae). *Molecular Phylogenetics and Evolution* **100**: 57–69.
Galetti M, Guevara R, Côrtes MC, *et al.* 2013. Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* **340**: 1086–1090.
Givnish TJ, Millam KC, Mast AR, *et al.* 2009. Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proceedingsof the Royal Society B: Biological Sciences* **276**: 407–416.
Goldberg EE, Otto SP, Vamosi JC, *et al.* 2017. Macroevolutionary synthesis of flowering plant sexual systems. *Evolution* **71**: 898–912.
Göldel B, Kissling WD, Svenning JC. 2015. 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.
Govaerts R, Dransfield J, Zona SF, Hodel DR, Henderson A. 2011. World checklist of Arecaceae facilitated by the Royal Botanic Gardens. apps.kew.org/wcsp (15 July 2018, date last accessed).
Grossenbacher DL, Brandvain Y, Auld JR, *et al.* 2017. Self-compatibility is over-represented on islands. *New Phytologist* **215**: 469–478.
Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W. 2008. GEIGER: investigating evolutionary radiations. *Bioinformatics* **24**: 129–131.
Heilbuth JC. 2000. Lower species richness in dioecious clades. *The American Naturalist* **156**: 221–241.
Heilbuth JC, Ilves KL, Otto SP. 2001. The consequences of dioecy for seed dispersal: modeling the seed-shadow handicap. *Evolution* **55**: 880–888.
Helmus MR, Bland TJ, Williams CK, Ives AR. 2007. Phylogenetic measures of biodiversity. *The American Naturalist* **169**: E68–E83.
Henderson A. 2002. *Evolution and ecology of palms.* New York: New York Botanical Garden Press.
Henderson A. 2009. *Palms of Southern Asia*. Princeton, NJ: Princeton University Press.
Henderson AJ, Bacon CD. 2011. *Lanonia* (Arecaceae: Palmae), a new genus from Asia, with a revision of the species. *Systematic Botany* **36**: 883–895.
Herrera-Alsina L, van Els P, Etienne RS. 2019. Detecting the dependence of diversification on multiple traits from phylogenetic trees and trait data. *Systematic Biology* **68**: 317–328.
Huelsenbeck JP, Nielsen R, Bollback JP. 2003. Stochastic mapping of morphological characters. *Systematic Biology* **52**: 131–158.
Ives AR, Helmus MR. 2011. Generalized linear mixed models for phylogenetic analyses of community structure. *Ecological Monographs* **81**: 511–525.
de Jong T, Klinkhamer P. 2005. *Evolutionary ecology of plant reproductive strategies*. Cambridge: Cambridge University Press.
Käfer J, Mousset S. 2014. Standard sister clade comparison fails when testing derived character states. *Systematic Biology* **63**: 601–609.
Käfer J, Talianová M, Bigot T, *et al.* 2013. Patterns of molecular evolution in dioecious and non-dioecious Silene. *Journal of Evolutionary Biology* **26**: 335–346.
Käfer J, de Boer HJ, Mousset S, Kool A, Dufay M, Marais GA. 2014. Dioecy is associated with higher diversification rates in flowering plants. *Journal of Evolutionary Biology* **27**: 1478–1490.
Kissling W, Baker W, Balslev H, *et al.* 2012*a*. Quaternary and pre Quaternary historical legacies in the global distribution of a major tropical plant lineage. *Global Ecology and Biogeography* **21**: 909–921.
Kissling WD, Eiserhardt WL, Baker WJ, *et al.* 2012*b*. Cenozoic imprints on the phylogenetic structure of palm species assemblages worldwide. *Proceedings of the National Academy of Sciences, USA* **109**: 7379–7384.
Kissling WD, Balslev H, Baker WJ, *et al.* 2019. PalmTraits 1.0, a species-level functional trait database of palms worldwide. *Scientific Data* **6**: 178.
Kreft H, Jetz W, Mutke J, Kier G, Barthlott W. 2008. Global diversity of island floras from a macroecological perspective. *Ecology Letters* **11**: 116–127.
Li D, Dinnage R, Nell LA, Helmus MR, Ives AR. 2020. phyr: an R package for phylogenetic species-distribution modelling in ecological communities. *Methods in Ecology and Evolution* **11**: 1455–1463.
Lim JY, Svenning JC, Göldel B, Faurby S, Kissling WD. 2020. Frugivore–fruit size relationships between palms and mammals reveal past and future defaunation impacts. *Nature Communications* **11**: 4904.
Martins EP, Hansen TF. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *The American Naturalist* **149**: 646–667.
Nadot S, Alapetite E, Baker WJ, Tregear JW, Barfod AS. 2016. The palm family (Arecaceae): a microcosm of sexual system evolution. *Botanical Journal of the Linnean Society* **182**: 376–388.
Nakov T, Beaulieu JM, Alverson AJ. 2019. Diatoms diversify and turn over faster in freshwater than marine environments. *Evolution* **73**: 2497–2511.
Onstein RE. 2020. Darwin's second 'abominable mystery': trait flexibility as the innovation leading to angiosperm diversity. *New Phytologist* **228**: 1741–1747.
Onstein RE, Baker WJ, Couvreur TLP, Faurby S, Svenning JC, Kissling WD. 2017. Frugivory-related traits promote speciation of tropical palms. *Nature Ecology & Evolution* **1**: 1903–1911.
Onstein RE, Baker WJ, Couvreur TLP, *et al.* 2018. 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.
Orme D. 2013. The caper package: comparative analysis of phylogenetics and evolution in R. R package version 0.5, 2: 1–36.
Pagel M. 1994. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society B: Biological Sciences* **255**: 37–45.
Pannell JR, Auld JR, Brandvain Y, *et al.* 2015. Tansley review: the scope of Baker's law. *New Phytologist* **208**: 656–667.
Rabosky DL. 2010. Extinction rates should not be estimated from molecular phylogenies. *Evolution* **64**: 1816–1824.
Rabosky DL. 2014. Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS One* **9**: e89543.
Rabosky DL, Huang H. 2016. A robust semi-parametric test for detecting trait-dependent diversification. *Systematic Biology* **65**: 181–193.
Rabosky DL, Grundler M, Anderson C, *et al.* 2014. BAMMtools: an R package for the analysis of evolutionary dynamics on phylogenetic trees. *Methods in Ecology and Evolution* **5**: 701–707.
Razanajatovo M, van Kleunen M, Kreft H, *et al.* 2019. Autofertility and self-compatibility moderately benefit island colonization of plants. *Global Ecology and Biogeography* **28**: 341–352.

R Core Team. **2019.** *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Renner SS. 2014. The relative and absolute frequencies of angiosperm sexual systems: dioecy, monoecy, gynodioecy, and an updated online database. *American Journal of Botany* **101**: 1588–1596.

Renner SS, Ricklefs RE. 1995. Dioecy and its correlates in the flowering plants. *American Journal of Botany* **82**: 596–606.

Revell LJ. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**: 217–223.

Richards AJ. 1997. *Plant breeding systems*. Garland Science Press.

Sabath N, Goldberg EE, Glick L, *et al.* 2016. Dioecy does not consistently accelerate or slow lineage diversification across multiple genera of angiosperms. *New Phytologist* **209**: 1290–1300.

Sakai AK, Wagner Warren L, Ferguson DM, Herbst DR. 1995*a*. Origins of dioecy in the Hawaiian flora. *Ecology* **76**: 2517–2529.

Sakai AK, Wagner Warren L, Ferguson DM, Herbst DR. 1995*b*. Biogeographical and ecological correlates of dioecy in the Hawaiian flora. *Ecology* **76**: 2530–2543.

Sauquet H, von Balthazar M, Magallón S, *et al.* 2017. The ancestral flower of angiosperms and its early diversification. *Nature Communications* **8**: 16047.

Savolainen V, Anstett MC, Lexer C, *et al.* 2006. Sympatric speciation in palms on an oceanic island. *Nature* **441**: 210–213.

Schlessman MA, Vary LB, Munzinger J, Lowry PP. 2014. Incidence, correlates, and origins of dioecy in the island flora of New Caledonia. *International Journal of Plant Sciences* **175**: 271–286.

Tucker CM, Cadotte MW, Carvalho SB, *et al.* 2017. A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews of the Cambridge Philosophical Society* **92**: 698–715.

Vamosi JC, Vamosi SM. 2004. The role of diversification in causing the correlates of dioecy. *Evolution* **58**: 723–731.

Vamosi JC, Vamosi SM. 2005. Present day risk of extinction may exacerbate the lower species richness of dioecious clades. *Diversity and Distributions* **11**: 25–32.

Vamosi SM, Mazer SJ, Cornejo F. 2008. Breeding systems and seed size in a neotropical flora: testing evolutionary hypotheses. *Ecology* **89**: 2461–2472.

Vamosi JC, Magallón S, Mayrose I, Otto SP, Sauquet H. 2018. Macroevolutionary patterns of flowering plant speciation and extinction. *Annual Review of Plant Biology* **69**: 685–706.

Webb CJ, Lloyd DG, Delph LF. 1999. Gender dimorphism in indigenous New Zealand seed plants. *New Zealand Journal of Botany* **37**: 119–130.

Weigelt P, Kissling WD, Kisel Y, *et al.* 2015. Global patterns and drivers of phylogenetic structure in island floras. *Scientific Reports* **5**: 12213.

Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* **33**: 125–159.

Zhang Q, Onstein RE, Little SA, Sauquet H. 2019. Estimating divergence times and ancestral breeding systems in Ficus and Moraceae. *Annals of Botany* **123**: 191–204.

Zona S, Henderson A. 1989. A review of animal-mediated seed dispersal of palms. *Selbyana* **11**: 6–21.