Is dispersal mode a driver of diversification and geographical distribution in the tropical plant family Melastomataceae?

Marcelo Reginato[a,*], Thais N.C. Vasconcelos[b], Ricardo Kriebel[c], André Olmos Simões[d]

[a] *Departamento de Botânica, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil*
[b] *Laboratório de Sistemática Vegetal, Departamento de Botânica, Universidade de São Paulo, São Paulo, SP, Brazil*
[c] *Department of Botany, University of Wisconsin-Madison, Madison, WI, USA*
[d] *Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, SP, Brazil*

ABSTRACT

Species of plants with different life history strategies may differ in their seed dispersal mechanisms, impacting their distribution and diversification patterns. Shorter or longer distance dispersal is favored by different dispersal modes, facilitating (or constraining) population isolation, which can, in turn, impact speciation and species range sizes. While these associations are intuitive, few studies have explicitly tested these hypotheses for large clades of angiosperms. The plant family Melastomataceae is found on disparate habitats with different dispersal modes, representing a good model to address these questions. In this study, we reconstruct the phylogeny of Melastomataceae and gather data on their dispersal mode and range size to test the impact of dispersal mode on diversification and range size evolution. We found that abiotic dispersal is ancestral in the family, while biotic dispersal evolved multiple times. Species richness distribution is very similar across dispersal modes, although abiotically dispersed species tend to be relatively more diverse in seasonal environments. Range sizes across dispersal modes are not significantly different, although biotically dispersed species have slightly wider distributions. Model comparisons indicate that factors other than dispersal mode might have driven diversification heterogeneity. We did not find evidence for the role of dispersal mode driving diversification rates or range size in the Melastomataceae, suggesting a complex macroevolutionary scenario for this diverse angiosperm family. The bulk of changes to biotic dispersal coinciding with an increase in passerine diversification suggests a possible "past" key innovation in Melastomataceae. Future studies should investigate the role of other diversification drivers in the family and the relatively higher diversity of abiotically dispersed species in open habitats.

1. Introduction

The positive dependent relationship between angiosperms and animals has been well documented through various pollination and seed dispersal studies (Stebbins, 1970; Tiffney, 1984, 2004; Eriksson, 2014). While these ecological interactions occur at small temporal scales, they can have long term consequences in the evolutionary dynamics of plants. Species with different life history strategies can differ in their fruit morphology and seed dispersal mechanism, which can impact their distribution and diversification patterns through time (Howe and Smallwood, 1982; Givnish, 2010). Because plants are sessile, seed dispersal is their only means through which to expand their distribution ranges (Willson and Traveset, 2000). Shorter or longer distance dispersal is favored by different dispersal modes, facilitating (or constraining) population isolation which can, in turn, impact speciation and diversification.

Certain dispersal modes have been shown to be prevalent in particular habitats. For instance, while plants with dry, woody, and dehiscent capsules that rely on wind for seed dispersal are prevalent in open habitats, plants with fleshy fruits with seeds dispersed by animals predominate in forest habitats (Bolmgren and Eriksson, 2005; Givnish et al., 2005; Renner, 1989). Clades with fleshy and vertebrate dispersed fruits have been shown to have diversified faster than lineages with dry fruits and wind dispersed seeds, suggesting a positive effect of vertebrate dispersal on plant diversification (Smith, 2001; Givnish et al., 2009; Biffin et al., 2010; Lagomarsino et al., 2016; Matuszak et al., 2016). Furthermore, while dispersal by understory frugivorous birds is usually restricted to small geographic areas, occasional long-distance dispersal events can facilitate speciation by "rampant allopatry" (Givnish, 2010). On the other hand, when dry fruits bearing wind dispersed seeds are associated with mechanisms to improve dispersal (e.g., pappus), chances of allopatry are also augmented, often

increasing diversification rates (Beaulieu and Donoghue, 2013).

Apart from impacting speciation rates, dispersal mode may also influence species range sizes, which have been shown to have high variances (Sonkoly et al., 2017). In Fagaceae, for instance, biotically dispersed lineages have larger ranges and higher speciation rates (Larson-Johnson, 2016). In *Ephedra*, on the other hand, bird dispersal is associated with colonization of a broader set of habitats, while range sizes do not differ among dispersal syndromes (Loera et al., 2015). Apart from the effect of dispersal mode on diversification rates and range sizes, dispersal mode also varies across geographical (latitudinal and altitudinal) and climatic space (Chen et al., 2017; Lu et al., 2019). A better understanding of how dispersal mode impacts species distributions is essential to further understand how species might be able to adapt in the face of global climate change (Nogués-Bravo et al., 2014).

The Melastomataceae (Order Myrtales *sensu* APG; Chase et al., 2016) includes more than 5000 species (Clausing and Renner, 2001; Renner, 1993; Reginato et al., 2016), representing one of the most diverse plant families on Earth. Members of this family are common elements of tropical savannas, cloud forests, and rainforests (Renner, 1993). While pollination is predominantly performed by bees through buzz pollination, seed dispersal presents a more even distribution across different agents. As in other Myrtales, Melastomataceae seed dispersal is accomplished by both biotic and abiotic vectors (Renner, 1989; Conti et al., 1997). Most biotically dispersed species in the family have juicy berries with endozoochorous seeds embedded in pulp that are dispersed by frugivorous birds (e.g., Stiles and Rosselli, 1993; Loiselle and Blake, 1999; Kessler-Rios and Kattan, 2012). Furthermore, ants, bats, lizards, marmosets, howler monkeys, marsupials, rodents, tapirs, turtles, and fish act as additional dispersal agents (Goulding, 1983; Magnusson and Sanaiotti, 1987; Renner, 1989; De Figueiredo and Longatti, 1997; Hodgkison et al., 2003; Castro-Luna and Sosa, 2009; Lessa and Costa, 2010; Lima et al., 2013). Most abiotically dispersed species in the family have dry capsular fruits and small wind-dispersed seeds that can persist for many months, during which the seeds are gradually shaken out (Renner, 1989). Only a few small genera with capsular fruits are thought to be dispersed by water (Freire-Fierro, 2002; Pizo and Morellato, 2002; Goldenberg et al., 2015; Kriebel, 2016; Bacci et al., 2019).

Fleshy fruits have evolved multiple times within the family (Renner, 1993; Clausing et al., 2000), but the exact number of times remains an open question given the lack of a comprehensive phylogeny of the group. Although fruit type appears to show strong phylogenetic signal and has been widely used in tribal classifications of the family (de Candolle, 1828; Naudin, 1851; Triana, 1871; Cogniaux, 1891; Renner, 1993), closely related species (e.g., in *Aciotis*, *Melastoma*, *Otanthera* and *Pternandra*) can differ in fruit morphology and seed dispersal mechanism (Renner, 1993). Dispersal mode is thought to be associated with major radiations in the family (Renner, 1989). For instance, one can speculate that the strong imbalance in species-richness between the giant tribe Miconieae, which includes ca. 2000 species with bird dispersed fleshy berries, and its closest relatives with different dispersal modes may be linked to this trait. The size of the family, the diversity of dispersal modes with putatively multiple origins, and the high species richness in different habitats make Melastomes an ideal clade to address long standing questions about the possible relationship between dispersal mode, increased speciation and range evolution dynamics.

Here, we reconstruct the largest phylogeny of the Melastomataceae to date and gather data on the dispersal mode and range size for all 1684 species sampled (ca. 34% of the diversity of the family). We use this information to reconstruct dispersal mode ancestral states across the family, including the number and timing of transitions in order to test whether the evolution of dispersal mode fits an "early burst" scenario. The following hypotheses were also tested: 1) biotic seed dispersal positively affects net-diversification in the Melastomataceae; 2) biotic seed dispersal is correlated to large species range sizes within this plant family.

2. Material and methods

2.1. Molecular sampling

All sequences of Melastomataceae and its sister CAP clade (Crypteroniaceae + Alzateaceae + Pennaeaceae; Conti et al., 1997; Berger et al., 2016) available in GenBank were downloaded and divided into homologous markers based on their annotations. Sequence orientation, checking, and alignment were performed with the R package DECIPHER 2.4.0 (Wright, 2016), using the functions OrientNucleotides, AlignSeqs (iterations = 50, refinements = 50) and AdjustAlignment. Poorly aligned regions of each individual marker were removed using aliscore.pl with the -r option (Misof and Misof, 2009).

Sequence filtering was performed in R (R Core Team, 2018) with custom scripts (available in https://github.com/mreginato), using functions of the packages ape 4.1 (Paradis et al., 2004), phyloch 1.5.3 (Heibl, 2008), and in-house functions. Briefly, filtering consisted in removing sequences unidentified at the species level, updating their taxonomy, checking for consistency of metadata across different markers (species, voucher and isolate), removing duplicated sequences per species within markers, and removing markers with less than 100 sequences. The taxonomic database used to update the species names was downloaded from the MelNames website (Renner et al., 2007 onwards). In order to remove the duplicated sequences per marker, first the number of markers per voucher were tabulated, and then duplicated sequences of vouchers with fewer markers were removed. After this step, the sequences left of the same species, with the same or different accessions, were treated under the same terminal in the phylogenetic analyses. Sequence metadata, including the species name and GenBank accession are available at Supplementary Material Table S1. Alignment descriptors, including number of terminals, aligned base pairs, variable sites and missing data are available as Supplementary Material Table S2.

Further individual marker sequences and/or terminal filtering was performed through monophyly tests across gene trees and a rogue taxa analysis on the concatenated tree. Gene tree analyses were performed with RAxML 8.2.10 (Stamatakis, 2014) through the CIPRES Science Gateway portal (Miller et al., 2010). Phylogenetic inference was performed with maximum likelihood estimation plus 1000 rapid bootstraps (–f a) using the GTR + G model. The ML gene tree topology of each marker was checked for consistency with a priori defined groups using the R package MonoPhy 1.2 (Schwery and O'Meara, 2016). Species were assigned to a priori clades (Supplementary Material Table S1) corresponding to the tribal level (or informal equivalent) recovered on previous phylogenetic hypotheses published for the family, from which our molecular sampling was primarily based upon (Clausing and Renner, 2001; Fritsch et al., 2004; Michelangeli et al., 2004, 2011, 2013, 2014; Stone, 2006; Bécquer-Granados et al., 2008; Goldenberg et al., 2008, 2012, 2015; Martin et al., 2008; Amorim et al., 2009; Penneys et al., 2010; Reginato et al., 2010; Penneys, 2013; Kriebel et al., 2015; Majure et al., 2015; Kriebel, 2016; Reginato and Michelangeli, 2016; Rocha et al., 2016; Zeng et al., 2016; Veranso-Libalah et al., 2017; Bacci et al., 2019; Bochorny et al., 2019). Sequences causing monophyly problems (outliers) in each gene tree were flagged and removed from further analyses (Supplementary Material Table S3). These filtered alignments were concatenated and a preliminary phylogenetic analysis was performed as described for the individual gene trees. The resulting bootstrapped tree set was then used as input for a rogue taxon analysis conducted in RogueNaRok (Aberer et al., 2012), using a majority rule consensus tree and removing terminals with raw improvement greater than one (Supplementary Material Table S4).

Filtered alignments were then submitted to DNA model partitioning performed with partitionFinder2 (Lanfear et al., 2016). A greedy search was used to check whether or not different markers could be treated in the same partition under the GTR + G model. The best partitioning

scheme recovered in this step was used in all further phylogenetic analyses. The best partitioning included eight partitions as follows: (i) *accD-psaI*, *psbK-psbI* and *trnS-trnG*; (ii) *atpB-rbcL*, *matK*, *ndhF* and *trnL*; (iii) *atpF-atpH* and *rpl16*; (iv) nrETS; (v) nrITS; (vi) *psbA-trnH*; (vii) *rbcL*; and, (viii) *waxy*.

2.2. Sparse tree inference

In order to assure convergence, a thinned sampled phylogenetic inference with divergence times estimation was performed in BEAST 2.5.0 (Bouckaert et al., 2014). Filtered alignments were randomly sampled to include species from all a priori assigned clades (tribal level), where a maximum of 50 species per clade was allowed. This thinned concatenated alignment was then used for the sparse tree inference with model and partitioning schemes previously recovered, molecular clock prior set to the lognormal uncorrelated, and tree prior set to the birth and death model. Two fossil and two secondary calibrations were used to time-calibrate the tree. Two lognormally distributed priors were set at the crown of Melastomataceae (m = 1; s = 1; offset = 56; based on "*Melastomites montanensis*", a 56–59 My old leaf fossil from Brown, 1962) and at the crown of Rhexieae (m = 1; s = 1; offset = 20; based on 23–20 My old seed fossils from Collinson and Pingen, 1992). Additionally, two normally distributed priors were set at the crown of the CAP clade (mean = 52.7; sigma = 6) and at the crown of CAP + Melastomataceae (mean = 90; sigma = 4.5), both priors were based on the 95% HPD recovered in a previous wider analyses of Myrtales (Berger et al., 2016). Two independent analyses of 200 million generations each, sampling every 10,000 generations were performed. Convergence was assessed in Tracer 1.5 (Rambaut and Drummond, 2007), and runs were considered satisfactory with ESS values greater than 200. The stable posterior distributions of the independent runs were combined using LogCombiner 2.5.0 and summarized (maximum clade credibility, common ancestor heights) using TreeAnnotator 2.5.0 (Bouckaert et al., 2014). The maximum credibility tree topology was checked for consistency with the a priori defined groups. No monophyly issues were identified.

2.3. Final tree inference

A constrained partitioned maximum likelihood analysis was performed in RAxML 8.2.10, using the sparse tree inference topology as a binary constraint tree (maximum credibility tree) along with 1000 rapid bootstraps (-q -f a -k -r). The ML tree was then time-scaled using secondary calibrations with penalized likelihood (Sanderson, 2002) implemented in treePL (Smith and O'Meara, 2012). The smoothing parameter was determined using the random subsample and replicate cross-validation approach (Smith and O'Meara, 2012). Ages for all a priori defined groups (95% HPD) were extracted from the maximum clade credibility tree from the sparse sampled data set and applied as minimum and maximum age constraints in the secondary calibrations. To account for uncertainty in divergence time estimation, we also repeated this analysis over the 1000 bootstrapped trees. The results were summarized onto the time-scaled ML tree with TreeAnnotator 2.5.0 (Bouckaert et al., 2014).

2.4. Compilation of distribution data

Records of all Melastomataceae were downloaded from the GBIF data portal (GBIF, 2018). Records belonging to all species sampled in our phylogenetic hypothesis were filtered in R (R Core Team, 2018) with custom scripts (available under request from the first author), and functions from the packages maptools (Bivand and Lewin-Koh, 2013), raster (Hijmans, 2016), rgeos (Bivand and Rundel, 2013), and sp (Pebesma and Bivand, 2005). The taxonomy of the records was updated with the same Melnet database downloaded for the Genbank sequence filtering. Records were filtered in several ways in order to flag both

coordinate misplacements and putative taxonomic misidentifications. Briefly, coordinate filtering consisted in removing records with invalid coordinates, from countries where the Melastomataceae is not known to occur (e.g., European countries), from non-terrestrial areas, collected before 1970, with less than four decimals, with coordinates intersecting country centroids, and inconsistent coordinates. In order to identify outliers with putative misidentifications, records were intersected with the map of ecoregions of the world (Olson et al., 2001) and with the climatic layers of WorldClim 2 (30″ spatial resolution; Fick and Hijmans, 2017). The data was tabulated for each species and species with records across more than one realm were excluded (i.e., the minority realm). Following the boxplot rule, outliers were identified regarding the presence across different ecoregions, geographic distance, and climatic variables. Records flagged as outliers in more than one test were excluded. Finally, species reported as invasive were excluded from the distributional dataset. The invasive species list was based on two online databases: Invasive and Exotic Species of North America (2018), and Global Invasive Species Database (2018), with a few additions of known widely cultivated species, i.e., *Tibouchina heteromalla* (D.Don) Cogn., *Heterotis rotundifolia* (Sm.) Jacq-Fél. and *Medinilla magnifica* Lindl.

2.5. Range size estimation

Range sizes were estimated for all species based on their filtered records and climatic niche models. The latter were estimated in Maxent 3.3.3 (Phillips and Dudík, 2008) based on the 19 climatic variables from the WorldClim 2 (30″ spatial resolution; Fick and Hijmans, 2017). In order to reduce the effect of biased species occurrence, the data set was spatially thinned with the R package spThin 0.1.0 (Aiello-Lammens et al., 2014) prior to species distribution modeling. Only points with a minimum distance of 10 km apart from each other were kept. For each species, a mask was generated with a circular buffer of 1000 km of diameter around its known distribution, where the immediate area around the known localities were excluded from the background with a buffer of 100 km in diameter around each known point. Climatic layers were cropped and masked using the individual species masks. All 10,000 random pseudo-absence points were sampled in the masked area for modeling. Default parameters were applied, and models were trained based on the presence only records (75% training and 25% testing). Models with AUC greater than 0.85 were projected and their thresholds (kappa, sum of the sensitivity and specificity, equal sensitivity and specificity, and sensitivity) were estimated. The projected model was binarized using the mean of all thresholds and transformed into polygons. The resulting polygons were intersected with the known occurrences. Polygons that did not intersect any known point were excluded from the final range. For species with models with AUC lower than 0.85, a different procedure was applied as follows: create a buffer of 30 km surrounding the known point localities, crop the buffered range using the occurrences elevational range (plus a buffer of 200 m), and intersect the cropped range to known localities (removing non-intersecting polygons). Both procedures were performed in R with functions from the packages maptools (Bivand and Lewin-Koh, 2013), raster (Hijmans, 2016), rgeos (Bivand and Rundel, 2013), and sp (Pebesma and Bivand, 2005). The resulting polygons were used to build richness maps (stacked polygons) of all sampled species, and biotically/abiotically dispersed species separately. A richness map depicting the difference of biotically/abiotically dispersed species corrected by the total number of species in each state was also generated.

The resulting polygons were used to estimate the distributional range size of each species (polygon) in km^2 with the R package raster. In order to test whether there are significant differences of range size across dispersal modes, a simulation based phylogenetic analysis of variance (Garland et al., 1993) was performed with the phyloANOVA function implemented in the R package phytools 0.7 (Revell, 2012) with 1000 simulations.

2.6. Dispersal mode

Most biotic dispersed species in the family present juicy berries, ranging in size from five to ca. 35 mm in diameter, derived from inferior ovaries with endozoochorous seeds embedded in pulp (Renner, 1989). Less frequently, fleshy fruits may have a dry exocarp tearing open irregularly to expose a dark red, fleshy placentae in which the seeds remain embedded (e.g., in *Melastoma*; Clausing et al., 2000), while in others the hypanthium but not the ovary wall becomes fleshy and there is no pulp surrounding the seeds (e.g., in *Pternandra*; Renner, 1989; Renner, 1993). Most abiotic dispersed species in the family are wind-dispersed bearing dry capsular fruits and small seeds. Additionally, small herbaceous understory species with broadly conical capsules (e.g., in *Salpinga*, *Monolena*, and *Bertolonia*) may also have their seeds dispersed ballistically by raindrops (Renner, 1989; Bacci et al., 2019). A morphological matrix of dispersal mode (abiotic vs. biotic) was compiled for all species sampled in our phylogeny. Biotic dispersed species included plants with fleshy fruits (berries and capsules with fleshy placentae), while abiotic dispersal included the remaining species with dry capsules, dispersed by wind or water. Coding was determined based on the taxonomic literature of Melastomataceae and its sister CAP clade (Van Beusekom-Osinga and Van Beusekom, 1975; Maxwell, 1981; Dahlgren and Thorne, 1984; Graham, 1984; Renner, 1993; Meyer, 2001; Freire-Fierro, 2002). The morphological matrix is available at Supplementary Material Table S5.

2.7. Morphological evolution

To reconstruct dispersal mode evolution on the phylogeny of Melastomataceae, two models of character evolution ("ER" - Equal Rates and "ARD" - All Rates Different) were first evaluated using the fitDiscrete function of the R package geiger 2.0 (Harmon et al., 2008). The best model was selected using the Akaike Information Criterion (AIC) and used for stochastic character mapping (Huelsenbeck et al., 2003; Bollback, 2006). Stochastic mapping was implemented in the R package phytools (Revell, 2012), where 1000 stochastic maps were generated and summarized using the functions make.simmap and describe.simmap (Revell, 2012). The results were summarized and plotted on the phylogeny using the R package ape (Paradis et al., 2004). We also aimed to test whether or not the dispersal mode evolution across the family could be described by an "early burst" model. This model predicts that when lineages first enter a new adaptive zone, morphological evolution is initially rapid, and as the ecological space becomes filled, the rate of morphological evolution slows down (Harmon et al., 2010). Model fit comparisons across five tree transformations reflecting different scenarios of tempo and mode of morphological evolution were performed with fitDiscrete (Harmon et al., 2008). Comparisons included the null (no transformation), early burst (Blomberg et al., 2003), lambda, punctional, time-dependent, and white-noise (non-phylogenetic) models.

2.8. Diversification rates

Heterogeneity in diversification rates along the phylogeny resulting from our final tree inference were detected and quantified with BAMM 2.5.0 (Rabosky, 2014). Markov chains were run for 50,000,000 generations, sampling every 10,000 generations (burnin of 10%), with a conservative maximum number of expected shifts (1). The outgroup was pruned out of the tree and appropriate priors were estimated beforehand with the R package BAMMtools 2.17 (Rabosky et al., 2014). Sampling fractions of each major clade/tribe (Table 1) were included in the analysis to account for incomplete taxon sampling. The output was checked for convergence (ESS values were estimated and runs considered satisfactory with values greater than 200) and summarized with BAMMtools. The maximum shift credibility configuration is presented.

2.9. Trait dependent diversification rates

In order to test whether or not diversification rates are associated with a particular dispersal mode, Binary State Speciation and Extinction (BiSSE) models were compared (Maddison et al., 2007). The comparisons also included a null model of trait-independent diversification (CID2) with similar complexity to the BiSSE model (Beaulieu and O'Meara, 2016). Sampling fractions following Table 1 were included for all models (abiotic = 0.25; biotic = 0.39). Model comparison was performed with the R package hisse 1.9.6 (Beaulieu and O'Meara, 2016). Posterior distributions of the parameters (speciation, extinction, and transition rates) were estimated under the BiSSE model with the R package diversitree 0.9 (FitzJohn, 2012). The distributions were based on 10,000 generations with a 10% burnin.

3. Results

3.1. Phylogeny and dispersal mode

The phylogenetic hypothesis included 1684 species of Melastomataceae (Fig. 2A, Supplementary File 1), corresponding to ~34% of the 5159 accepted species and 90% of the accepted genera (154 out of 171) in the family. Among the sampled species, 576 have abiotic dispersal (ca. 26% of abiotic dispersed species in the family), while 1108 have biotic dispersal (ca. 39%). Summary statistics of the data set analyzed in this study, including information on sampling, range size, and divergence time estimation by major clade is presented in Table 1.

3.2. Geographical distribution of dispersal mode

Overall, biotically and abiotically dispersed taxa show a similar distribution of species richness with higher/lower diversity across the same regions (Fig. 1C–D). High richness of both dispersal modes is found in the Neotropics, including Central America, the Andes, western Amazon, highlands of Guyana, and eastern Brazil. Nonetheless, some regions show a biased distribution towards one dispersal mode when corrected by total richness (Fig. 1B). The strongest bias towards abiotically dispersed species is observed in the central Brazilian plateau (the "Campos Rupestres" region). Additional areas with a relatively higher amount of abiotically dispersed species included the United States, savannas of Venezuela, Bolivia, Paraguay, and eastern Asia. Regions including relatively more species with biotic dispersal include most of the above-mentioned species-rich areas, especially along the Neotropical forests. On the other hand, the regions with bias towards abiotic dispersal tend to present lower species-richness in general, except from the central Brazilian region. Although biotically dispersed species show slightly wider distributions, a comparison of distributional range sizes across the different dispersal modes revealed no significant differences (p-value = 0.86) between dispersal modes (Fig. 2B).

3.3. Dispersal mode evolution

The best fitting model for dispersal mode evolution was estimated to be the all rates different (AIC = 196.7) against the equal rates (AIC = 206.5). A summary of stochastic mapping of ancestral states estimates of abiotic/biotic dispersal along the Melastomataceae phylogeny are presented in Fig. 2A (see Supplementary Fig. S1 for the ancestral estimates including the outgroup). Ancestral states for the whole family and throughout the backbone are estimated as having had abiotic mode of dispersal. An asymmetry in the transitions between dispersal mode is observed (Fig. 2C). More changes from abiotic to biotic dispersal were recovered (median = 18), while the opposite scenario is less frequent (median = 3). When comparing different tree transformations, the best fitting model recovered was the scenario with no transformation ("none", Table 2), indicating rate constancy of fruit

Table 1

Descriptive statistics of the data set analyzed in this study, including information on sampling, geographical distribution and results of geographical range size and divergence times estimation. Descriptors are provided by major clade in the Melastomataceae. Sampling information includes the estimated number of accepted species ("Spp"); number of sampled species ("Sampled"); predominant dispersal mode (and its relative presence in the clade – "Dispersal"); median and bounds of the estimated geographical range size in Km^2 ("Range size"); distribution across the world realms ("Distribution"), where AA = Australasia, AT = Afrotropic, IM = Indomalaya, NA = Nearctic, NT = Neotropic, and PA = Palearctic; estimated crown ("Age (crown)") and stem ("Age (stem)") mean ages and 95% HPD. Both estimated ages are based on the sparse phylogenetic analysis.

	Tribe	spp	Sampled (%)	Fruit type (%)	Range size	Distribution	Age (crown)	Age (stem)
1	Olisbeoideae	524	131 (25%)	biotic (100%)	36,184 [264, 1,542,126]	AA, AT, IM, NT	31.31 [20.12, 44.92]	63.43 [56.14, 77.3]
2	Kibessieae	17	5 (29%)	biotic (100%)	60,592 [31,495, 71,447]	AA, IM	9.87 [4.37, 16.67]	58.93 [47.33, 72.04]
3	Astronieae	145	11 (8%)	abiotic (100%)	739 [152, 8163]	AA, IM	7.95 [4.73, 12.12]	23.6 [12.87, 36.07]
4	Henrietteeae	93	29 (31%)	biotic (100%)	185,459 [347, 3,316,373]	NT	12.92 [8.4, 17.41]	23.6 [12.87, 36.07]
5	Bertolonieae	23	4 (17%)	abiotic (100%)	71,471 [41,640, 118,953]	NT	11.57 [4.64, 20.29]	42.15 [34.41, 50.27]
6	Trioleneae	42	6 (14%)	abiotic (100%)	79,866 [13,999, 350,177]	NT	22.05 [12.37, 32.36]	37.87 [29.94, 45.14]
7	Sonerileae	528	67 (13%)	abiotic (73%)	15,469 [154, 466,498]	AA, AT, IM, NT, PA	25.36 [18.79, 33.07]	36.45 [28.6, 43.61]
8	Cyphostyleae	22	10 (45%)	abiotic (100%)	13,754 [245, 258,914]	NT	14.15 [7.12, 21.48]	33.2 [24.66, 41.51]
9	Dissochaeteae	38	8 (21%)	biotic (100%)	22,431 [611, 311,790]	AA, IM	28.51 [19, 37.27]	30.7 [21.19, 40.33]
10	Blakeeae	191	79 (41%)	biotic (100%)	21,377 [88, 773,121]	NT	6.45 [3.73, 9.54]	30.7 [21.19, 40.33]
11	Cambessedesieae	68	24 (35%)	abiotic (100%)	39,031 [4772, 744,967]	NT	26.61 [18.79, 34.77]	36.09 [29.46, 42.68]
12	Rhexieae	18	14 (78%)	abiotic (100%)	222,428 [2365, 823,935]	NA	22.15 [20.13, 25.04]	28.11 [23.6, 33.49]
13	Microlicieae	223	28 (13%)	abiotic (100%)	71,557 [1272, 1,889,001]	NT	15.99 [9.3, 22.66]	30.01 [24.87, 35.5]
14	Marcetieae	139	81 (58%)	abiotic (93%)	149,403 [90, 2,077,284]	NT	26.26 [20.99, 32.09]	31.08 [26.01, 36.88]
15	Melastomateae	697	254 (36%)	abiotic (94%)	69,794 [122, 2,856,884]	AA, AT, IM, NT, PA	24.92 [19.24, 30.41]	31.08 [26.01, 36.88]
16	Merianieae	311	71 (23%)	abiotic (100%)	63,238 [214, 1,121,418]	NT	21.36 [15.34, 28.47]	27.12 [18.23, 38.38]
17	Eriocnemeae	6	4 (67%)	abiotic (100%)	28,681 [2662, 48,778]	NT	8.16 [3.84, 12.5]	13.25 [8.91, 18.81]
18	Miconieae	1961	856 (44%)	biotic (100%)	84,795 [29, 3,380,824]	NT	11.25 [7.36, 15.8]	13.25 [8.91, 18.81]

evolution throughout the tree. Nonetheless, although not significant, a slight tendency to an "early burst" scenario is observed in the evolution of dispersal mode, given the relatively higher number of changes earlier in the history of the group (Fig. 2D) and the second-best fit model ("EB", Table 2).

3.4. Diversification analyses

The maximum credibility shift set included a total of 26 net-

diversification shifts across the family. A phylorate plot depicting net-diversification rates of this scenario is provided in Fig. 3. Thirteen shifts are located on biotically dispersed clades and 13 on abiotically dispersed clades. From those, two shifts are observed in the Paleotropics (Olisbeoideae), two in the Indomalayan region (Astronieae and Sonerileae), and all remaining shifts are observed in Neotropical groups (Henrietteeae, Cyphostyleae, Blakeeae, Marcetieae, Microlicieae, Melastomateae, Merianieae and Miconieae).

The mean value of the posterior distribution of net-diversification in
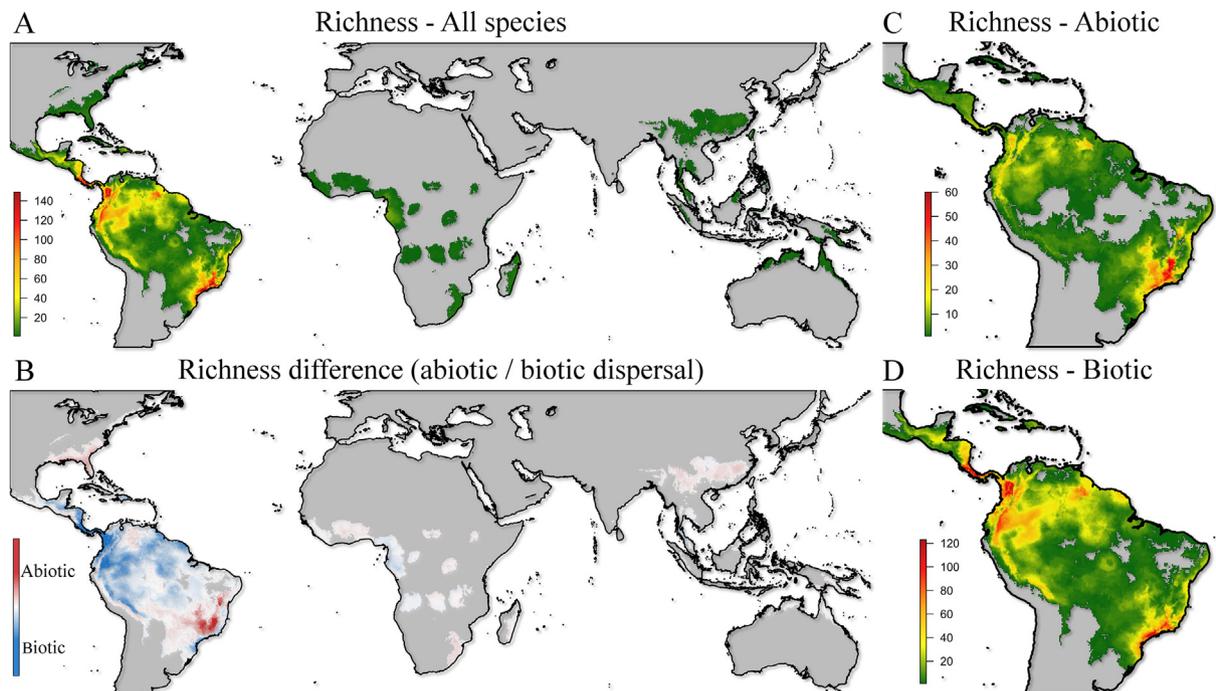

Fig. 1. Distribution maps of sampled species in the Melastomataceae. **A.** Richness map of all species included in this study (n = 1684). **B.** Relative richness corrected by total richness of abiotically dispersed species minus biotically dispersed species; red colors indicate regions with relatively more abiotically dispersed species, blue indicates relatively more biotically dispersed species, and white regions have similar relative richness of both dispersal modes. **C.** Detail of abiotically dispersed species richness in the Neotropical region. **D.** Detail of biotically dispersed species richness in the Neotropical region. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
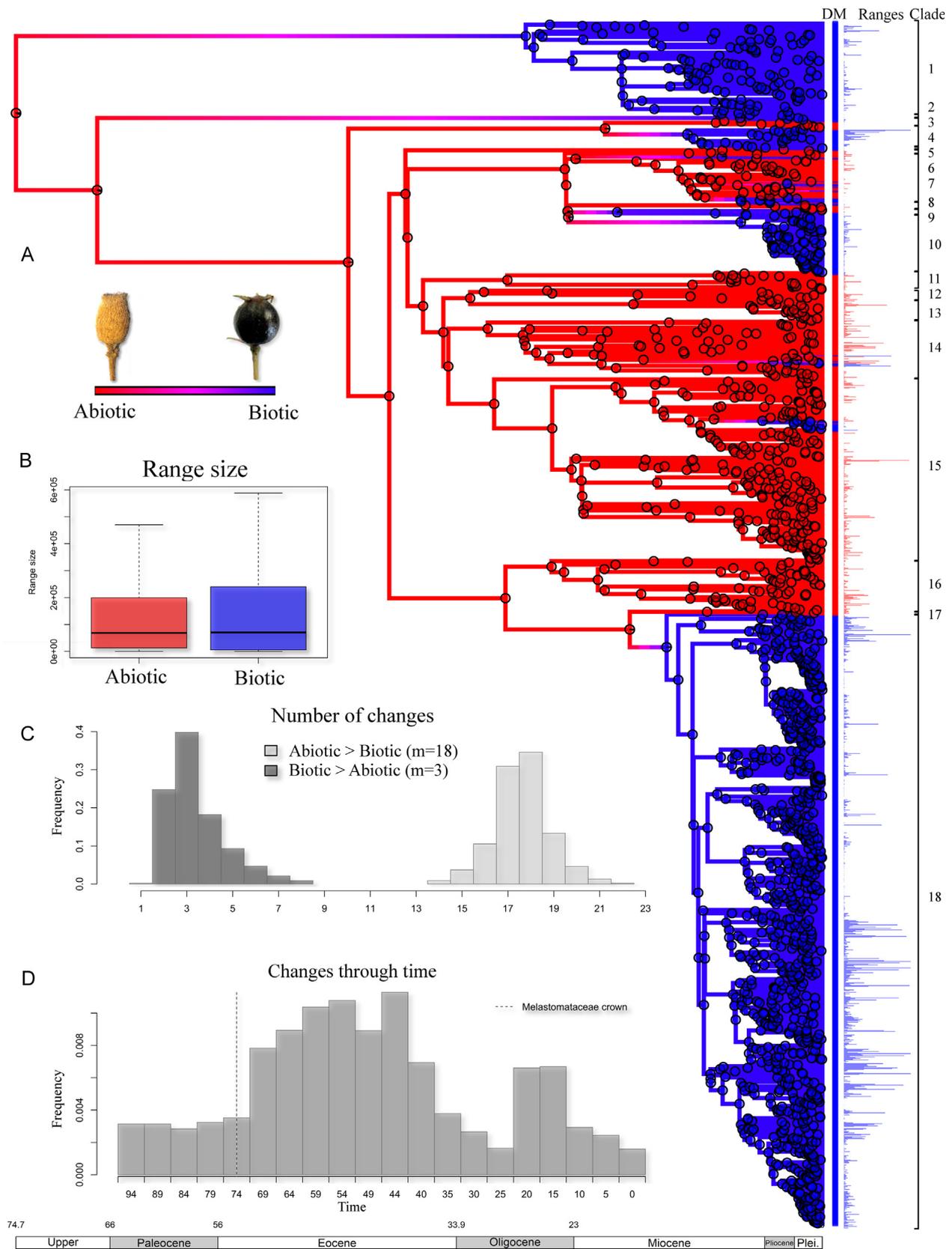
(caption on next page)

biotically dispersed lineages is higher than in abiotically dispersed lineages under the full BiSSE model, with similar speciation rates across dispersal modes and higher extinction rates in abiotic dispersed lineages (Fig. 3B–D). The transition rate from the abiotic to the biotic state is slightly higher than in the opposite direction (Fig. 3E). Nonetheless, a trait-independent diversification model allowing rate variation across the phylogeny (CID-2) presents a better fit than the trait-dependent scenario (BiSSE), indicating that factors other than dispersal

Fig. 2. **A**. Summary of stochastic mapping of ancestral state estimates of abiotic/biotic dispersal mode across the Melastomataceae (density map), pies at the nodes represent the probability of each state (red = abiotic; blue = biotic). Colored bars next to the tree (right) represent the distribution range sizes of each terminal (red = abiotic dispersal, blue = biotic dispersal). Clade = major clades are indicated with within bracts, numbering corresponds to the first column of Table 1. The outgroup (CAP clade) is not shown in this figure (see Supplementary Fig. S1 for the full ancestral estimates including the outgroup). **B**. Boxplot of distributional range size across dispersal modes. **C**. Histogram of transition number (lighter gray = abiotic to biotic; darker gray = biotic to abiotic) across all 1000 stochastic maps. **D**. Histogram of number of changes trough time corrected by branch length across all 1000 stochastic maps. **D**. Density map summarizing the stochastic mapping of ancestral state estimates (red = dry; blue = fleshy). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Model fit of dispersal mode evolution (biotic/abiotic) across models with different tree transformations. None = rate constancy through time; EB = Early-burst model of Blomberg et al. (2003); lambda = Pagel (1991); kappa = punctuational model of Pagel (1999); delta = time-dependent model of Pagel (1999); white = white-noise (non-phylogenetic) model.

Model	lnL	k	AIC	AICc
None	− 96.3425	2	196.685	196.692
EB	− 95.8884	3	197.7767	197.7907
Lambda	− 96.3425	3	198.685	198.699
Kappa	− 96.3425	3	198.685	198.699
Delta	− 96.2537	3	198.5074	198.5215
White	− 1086.63	1	2175.258	2175.26

mode may have influenced the diversification rate heterogeneity across the Melastomataceae phylogeny (Table 3).

4. Discussion

4.1. Independent origins of biotic dispersal in Melastomataceae

The most comprehensive phylogeny of Melastomataceae assembled to date confirmed that abiotic dispersal is the ancestral condition in the family, with biotic dispersal evolving multiple times independently (Renner, 1993; Clausing et al., 2000). Our analyses estimated that biotic dispersal evolved at least 18 times independently across the family, with three reversions to abiotic dispersal, indicating a strong asymmetry in the transitions between modes. It has been suggested that the exceptional evolutionary flexibility of Melastomataceae fruits, and associated dispersal modes, may stem from the structure of myrtalean flowers in which hypanthium and ovary tissues are both involved in fruit construction (Clausing et al., 2000). Such flower architecture would allow different degrees of tissue fusion, thickening, hardening, and/or disintegration, facilitating the development of different fruit types regarding form and function (Clausing et al., 2000). Asymmetrical change in dispersal mode is likely to be a more general pattern across angiosperms. Changes to biotic dispersal have been demonstrated to be favored in the large monocot clade (Givnish et al., 2005), as well as in some other eudicot lineages (Givnish, 1999; Smith, 2001; Sytsma et al., 2002; Lagomarsino et al., 2016).

Our model comparisons indicated rate constancy of dispersal mode change along the history of the Melastomataceae. Nonetheless, although not significant, a tendency towards an "early burst" scenario is observed in the evolution of dispersal mode, where most changes happened early in the history of the family and are usually associated and fixed within major clades. It has been suggested that early shifts from anemochory to zoochory in the Melastomataceae might be associated with their success in the understory of closed forests, where animal dispersal is more advantageous than wind dispersal (Renner, 1989). Our results indicated that dispersal mode change might have contributed to successful invasions of new habitats throughout the history of the family; but these changes predominate in the early history of the group.

Our results agree with the observation that the small-seeded melastome berry appears to have evolved primarily in association with masher-type frugivores such as tanagers, with the later addition of

other bird families such as the manakins that swallow entire fruits (Stiles and Rosselli, 1993). In fact, frugivorous birds are most diverse in the Neotropics (Kissling et al., 2009), where the mega diverse biotically dispersed tribe Miconieae and some other biotically dispersed tribes (e.g., Blakeeae, Henrietteae) are endemic. The speciation dynamics of birds suggests that there was an increase in net diversification rates leading to extant lineages that started about 50 Mya (Jetz et al., 2012; Oliveros et al., 2019). This increase in speciation coincides with the age of the bulk of changes to biotic dispersal detected in the Melastomataceae. Furthermore, increases in diversification rate found in the passerine super radiation around 15–20 Mya match the other shifts to biotic dispersal in Melastomataceae which occurred ~15 Mya. Although this evidence is circumstantial, the timing of speciation of extant bird clades and the melastomes they eat suggest a link between the two, even if "diffuse" as previously suggested (Stiles and Rosselli, 1993). A correspondence of the timing of diversification in biotically dispersed plant clades with the increase in bird diversification at around 50 Mya was also documented for mistletoes (Liu et al., 2018). Future work including frugivory related traits such as fruit size may help to understand if additional shifts in diversification rates observed within biotically dispersed lineages like Miconieae resulted from selection for smaller fruits, as found in the palms (Onstein et al., 2017).

4.2. Dispersal mode in relation to habitat

Dispersal mode plasticity in the Melastomataceae, underlined by fruit diversity and flower architecture, can also be related to habitat pressure, given the association between dispersal mode (abiotic and biotic) and vegetation type (open and closed; Renner, 1989; Clausing et al., 2000). It has been suggested that biotically dispersed Melastomataceae are more diverse in closed habitats (e.g., in lowland and montane forests), whereas abiotically dispersed clades are richest in open habitats (mainly savannas; Renner, 1989). Nonetheless, our results suggest that species richness distribution is very similar across dispersal modes, with higher and lower diversity of both modes found across the same geographical areas. In the Neotropics, where our sampling is more robust, a gradient of richness is observed in both dispersal modes, with greater diversity in tropical montane areas (e.g., Andes, Central America, Guyana, and eastern Brazil) and western Amazon, all of which are characterized mainly by forested habitats. This pattern further supports the observation that species richness distribution of biotic dispersed Melastomataceae in the Neotropics closely follows the distribution of its major consumers: manakins and tanagers (Stiles and Rosselli, 1993). On the other hand, we also found absolute richness of abiotically dispersed species following the same pattern (Fig. 1C–D). Species richness distribution of Melastomataceae in the Neotropics, regardless of the dispersal mode, fits the "Andean-centered" pattern, as previously suggested by Gentry (1982).

Despite similar richness across the same regions in both dispersal modes, a bias towards one mode is observed when the data is corrected by richness (Fig. 1B), corroborating earlier expectations (e.g., "open habitat/abiotic dispersal and closed habitat/biotic dispersal"; Renner, 1989). Interestingly, the strongest bias towards abiotically dispersed species is observed in the central Brazilian plateau (the "Campos Rupestres" region). These seasonally dry areas with infertile soils provide little nutrient for plant growth, leading to trade-offs in investment that
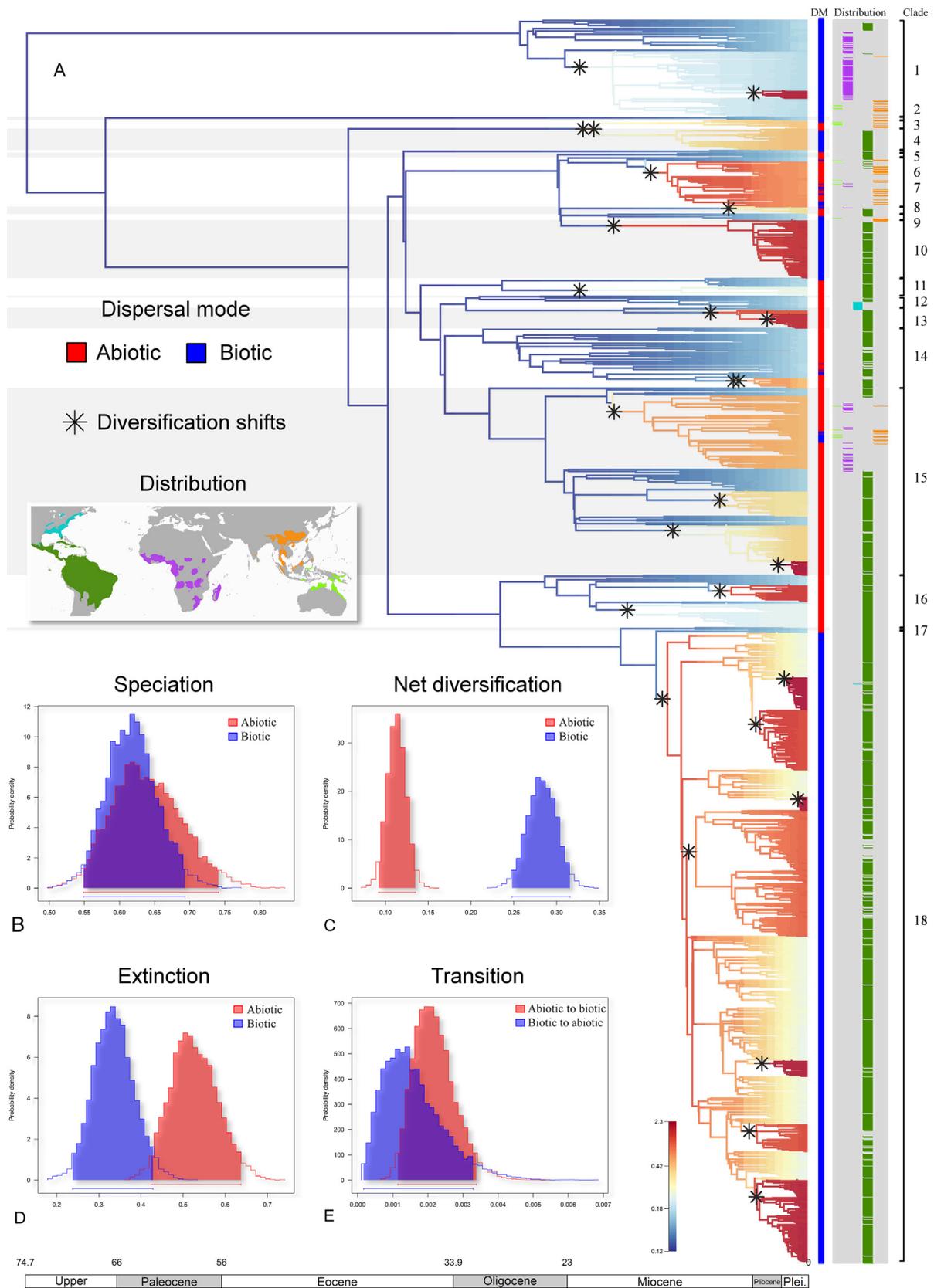
Fig. 3. A. Phylorate plot with net-diversification rates depicted along the branches including the maximum credibility shift set configuration of Melastomataceae (BAMM analysis). Warm colors indicate higher net-diversification rates and significant shifts on net-diversification are indicated by asterisks. Next to the phylorate (right) are indicated: DM = dispersal mode (red = abiotic; blue = biotic); Distribution = distribution across biogeographical realms (colors following the map); Clade = major clades are indicated with within bracts, numbering corresponds to the first column of Table 1. **B–E**. Posterior distributions of parameters estimate from the BiSSE analysis. **B**. Speciation. **C**. Net-diversification. **D**. Extinction. **E**. Transition rates between states (abiotic to biotic; biotic to abiotic). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3

Summary of the best models (based on AIC) of trait-dependent diversification (BiSSE) and the null trait-independent model (CID2). ΔAIC values show comparisons of all models against the best-fit model (CID2). For dispersal mode (biotic/abiotic).

Model	k	Loglik	AIC	ΔAIC
BiSSE (equivalent)	6	− 4402.4	8816.9	757.8
BiSSE (equal speciation)	5	− 4403.8	8817.7	758.6
BiSSE (equal extinction)	5	− 4416.6	8843.3	784.2
CID2 (null model)	12	− 4017.5	8059.1	0.0

allow less resources to be allocated for fleshy fruits production. This nutrient paucity may explain the low incidence of biotically dispersed fruits and frugivorous animals in species-rich ecosystems (Givnish, 2010; Conceição et al., 2016). These biases show that, even though species richness for both modes is higher in forested areas, different kinds of environment may restrict the survival of lineages with different dispersal modes, creating gradients of species-richness.

These results are in agreement with the expectation that a higher proportion of endozoochory (indicated by the proportion of fleshy-fruited species) will be observed in areas with greater precipitation and lower precipitation seasonality (Chen et al., 2017). Those findings are also consistent with the observation that some non-fleshy fruits need consistent or sufficient dryness to release their seeds (Correa et al., 2015; Chen et al., 2017). In fact, the same pattern is also observed in other related Myrtales. Myrtaceae, the largest family in the order (ca. 6000 species), has a similar overall pattern of distribution and species-richness among different dispersal strategies. Large abiotically dispersed groups (e.g., Eucalypteae and Chamelaucieae) have biased species-richness towards open and dry areas in Australia, while fleshy-fruited lineages (e.g., Myrteae and Syzygieae) are particularly diverse in the humid forests of South America and Southeast Asia (Biffin et al., 2010).

4.3. Hypothesis 1: Biotic seed dispersal is correlated to large species range sizes within the Melastomataceae

Dispersal strategy has a major impact on energy investment in fruits and seed type, as well as on rates of pre-dispersal seed predation and seed dispersal distances (Chen et al., 2017). Among Melastomataceae, many of the most successful pioneer species are bird dispersed. For example, the Neotropical *Miconia calvescens* and *Clidemia hirta* have become invasive in several places across the globe (Renner, 1989; Murphy et al., 2008). Additionally, biotic dispersal is associated with wider geographical ranges in other angiosperms (Larson-Johnson, 2016). However, our comparison of range sizes across dispersal modes showed no significant differences between range size and dispersal mode, with biotically dispersed species having slightly wider distributions. This result can be explained by the fact that range size can be influenced by several other aspects of plant biology rather than only dispersal mode, such as pollination, apomixis, and other ecological factors. Data on reproductive biology across the family is still scarce, precluding integrated analyses on dispersal mode and reproductive biology.

4.4. Hypothesis 2: Biotic dispersal increases net-diversification in the Melastomataceae

While some studies suggest that biotic and abiotic dispersal can lead to micro-endemism when combined to different habitat types (Smith, 2001; Givnish et al., 2009; Biffin et al., 2010; Givnish, 2010; Lagomarsino et al., 2016), others emphasize the capacity of both biotic (Larson-Johnson, 2016) and abiotic modes (Beaulieu and Donoghue, 2013) in producing wide ranges. The possibility of altering distribution range has also been used as an argument to justify faster diversification

rates, where increased chances of population isolation would lead to frequent allopatry, accelerating speciation rates. In this context, differences in diversification would be expected across different dispersal modes if the relationship among dispersal, range size, speciation, and extinction risk are strongly tied within a given plant lineage (Vamosi and Vamosi, 2012; Larson-Johnson, 2016). These associations, however, are not corroborated by our results with the Melastomataceae. We tested if increased diversification is dependent on dispersal mode, which would suggest that biotic dispersal might represent a key innovation.

Nevertheless, our model comparisons indicated that factors other than dispersal mode might have driven the diversification heterogeneity observed across the family. In fact, when the number of diversification shifts is taken into account, a balanced scenario regarding dispersal mode is observed in the family (13 shifts in clades of each dispersal mode). Even though there are some net-diversification shifts coinciding with changes from abiotic to biotic dispersal, such as in the Neotropical Henrietteae, Blakeeae, and Miconieae (clades 4, 10 and 18 in Fig. 3), there are also several shifts that do not coincide with transitions in dispersal mode, including shifts within the biotically dispersed Miconieae and all shifts in abiotically dispersed lineages. Furthermore, the higher net-diversification observed in biotically dispersed lineages is possibly biased by the major radiation within Melastomataceae (the Neotropical Miconieae including ca. 35% of the species in the family).

Although our results did not find a significant, or exclusive, association between dispersal mode and general macroevolutionary patterns in this clade, speciation rates were shown to be similar across dispersal modes, while extinction rates are more pronounced in abiotically dispersed lineages. These results should be taken with caution though, given the low power to estimate extinction rates in analyses of this nature (Rabosky, 2010, 2014). Nonetheless, these results provide information on extinction risk that have practical implications for conservation. Extinction risk is closely tied to species richness and range size across angiosperm clades, where those with relatively small ranges show the highest risk of losing a significant proportion of their species (Gaston and Fuller, 2009; Vamosi and Vamosi, 2012). In the Melastomataceae, the similar range sizes observed across the dispersal modes indicate that range size alone cannot explain the apparently higher extinction rate in abiotically dispersed lineages. In the Melastomataceae lineages with abiotic dispersal are likely to have a lower frequency of apomictic species and more specialized (showy) flowers than biotically dispersed lineages in general (e.g., in Marcetieae, Melastomateae, Merianieae, Microlicieae, Rhexieae) (Goldenberg and Shepherd, 1998). Species with more specialized flowers and a lower range of pollinators are thought to be linked to higher extinction risk through chance processes than generalists (Stang et al., 2007), or to species with an additional asexual reproductive path. In this scenario, higher extinction rates would not be directly linked to the presence of abiotic dispersal itself, but to other traits that are possibly associated to it in the evolution of these lineages. This hypothesis remains to be tested in future studies.

On the other hand, comprehensive analyses conducted on a phylogenetic framework have suggested that extinction risk in plants cannot be explained by correlations with simple biological traits, and that young and fast-evolving plant lineages would be at higher risk (Davies et al., 2011). Interestingly, some studies have also found that species restricted to environments with limited resources, would be more vulnerable to extinction, due to the inherently limited growth rates imposed by evolutionary adaptations to stress tolerance (Leão et al., 2014). This would be the case in open environments such as rocky outcrops, scrub vegetation, and savannas, where a relatively higher number of abiotic lineages are observed (Leão et al. 2014).

These results indicate a complex scenario of macroevolutionary dynamics for this diverse clade of angiosperms, where patterns are somehow smoothened by the complexity of different stories. Such a

scenario is concordant with diversification resulting from the evolution of multiple causal agents across the phylogeny, instead of a single key innovation (here biotic dispersal) to explain extant melastome diversity in the same framework suggested across angiosperms (Donoghue and Sanderson, 2015). For instance, key characters such as growth form, generation time, floral morphology, pollinators, reproductive biology, and especially, habitat preference also show variation within the family. In this sense, it is possible that biotic dispersal might lead to higher diversification, but only under some circumstances (e.g., in closed habitats), and in selected lineages.

5. Conclusions

Here, we have demonstrated that changes from abiotic to biotic dispersal mode were favored during the history of Melastomataceae. Most changes have occurred early in the history of this clade and were likely associated with passerine radiations. Although there is no support for the hypothesis that biotic dispersal is as key innovation in this group, it is plausible that biotic dispersal might have represented a key innovation in the past.

Like other angiosperms, most of the diversification shifts in the Melastomataceae were recovered in Neotropical clades (85% of the shifts). Although it is likely that most diversification shifts happened within Neotropical lineages, this scenario might be less asymmetrical, given the more intensive sampling of Neotropical lineages and reduced sampling of Southeast Asian clades (Table 1). Shifts in net-diversification across the family are located in clades with heterogeneous distribution, ecology, and morphological features. It is possible that several of these diversification shifts will have specific combinations of causes underlying them. Thus, preventing general single causes to emerge as explanations to account for the highly heterogeneity of macroevolutionary dynamics observed in the entire clade.

Declaration of Competing Interest

None.

Acknowledgements

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2020.106815.

References

Aberer, A.J., Krompass, D., Stamatakis, A., 2012. Pruning rogue taxa improves phylogenetic accuracy: an efficient algorithm and webservice. Syst. Bio. 62 (1), 162–166.

Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B., Anderson, R.P., 2014. spThin: Functions for Spatial Thinning of Species Occurrence Records for Use in Ecological Models. R package version 0.1.0 [online]. Available from https://CRAN.R-project.org/package=spThin.

Amorim, A.M., Goldenberg, R., Michelangeli, F.A., 2009. A new species of *Physeterostemon* (Melastomataceae) from Bahia, Brazil, with notes on the phylogeny of the genus. Syst. Bot. 34 (2), 324–329.

Bacci, L.F., Michelangeli, F.A., Goldenberg, R., 2019. Revisiting the classification of Melastomataceae: implications for habit and fruit evolution. Bot. J. Linn. Soc. 190 (1), 1–24.

Beaulieu, J.M., Donoghue, M.J., 2013. Fruit evolution and diversification in campanulid angiosperms. Evolution 67 (11), 3132–3144.

Beaulieu, J.M., O'Meara, B.C., 2016. Detecting hidden diversification shifts in models of trait-dependent speciation and extinction. Syst. Bio. 65 (4), 583–601.

Bécquer-Granados, E.R., Neubig, K.M., Judd, W.S., Michelangeli, F.A., Abbott, J.R., Penneys, D.S., 2008. Preliminary molecular phylogenetic studies in *Pachyanthus* (Miconieae, Melastomataceae). Botanical Rev. 74 (1), 37–52.

Berger, B.A., Kriebel, R., Spalink, D., Sytsma, K.J., 2016. Divergence times, historical biogeography, and shifts in speciation rates of Myrtales. Mol. Phylogenet. Evol. 95, 116–136.

Biffin, E., Lucas, E., Craven, L., Costa, I.R., Harrington, M., Crisp, M.D., 2010. Evolution of exceptional species richness amongst lineages of fleshy-fruited Myrtaceae. Ann. Bot. 106 (1), 79–93.

Bivand, R., Lewin-Koh, N., 2013. maptools: Tools for reading and handling spatial objects. R package version 0.8-27. http://CRAN.R-project.org/package=maptools.

Bivand, R., Rundel, C., 2013. Rgeos: Interface to Geometry Engine - Open Source (GEOS). R package version 0.3-2. http://CRAN.R-project.org/package=rgeos.

Blomberg, S.P., Garland Jr., T., Ives, A.R., 2003. Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. Evolution 57 (4), 717–745.

Bochorny, T., Michelangeli, F.A., Almeda, F., Goldenberg, R., 2019. Phylogenetics, morphology and circumscription of Cambessedesieae: a new Neotropical tribe of Melastomataceae. Bot. J. Linn. Soc. 190 (3), 281–302.

Bollback, J.P., 2006. Stochastic character mapping of discrete traits on phylogenies. BMC Bioinform. 7 (1), 88.

Bolmgren, K., Eriksson, O., 2005. Fleshy fruits – origins, niche shifts, and diversification. Oikos 109 (2), 255–272.

Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.H., Xie, D., Suchard, M.A., Rambaut, A., Drummond, A.J., 2014. BEAST 2: a software platform for bayesian evolutionary analysis. PLOS Comput. Biol. 10 (4), e1003537.

Brown, R.W., 1962. Paleocene flora of the Rocky Mountains and great Plains. Vol. 375. US Government Printing Office.

de Candolle, A.P., 1828. Melastomaceae. Prodromus Systematis Naturalis Regni Vegetabilis 3, 99–202.

Castro-Luna, A.A., Sosa, V.J., 2009. Consumption of *Conostegia xalapensis* fruits and seed dispersal of *Coussapoa oligocephala* by the nectarivorous bat *Hylonycteris underwoodi* Thomas, 1903 (Chiroptera: Phyllostomidae). Stud. Neotrop. Fauna Environ. 44 (3), 137–139.

Chase, M.W., Christenhusz, M.J.M., Fay, M.F., Byng, J.W., Judd, W.S., Soltis, D.E., Mabberley, D.J., Sennikov, A.N., Soltis, P.S., Stevens, P.F., 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Bot. J. Linn. Soc. 181 (1), 1–20.

Chen, S.C., Cornwell, W.K., Zhang, H.X., Moles, A.T., 2017. Plants show more flesh in the tropics: variation in fruit type along latitudinal and climatic gradients. Ecography 40 (4), 531–538.

Clausing, G., Meyer, K., Renner, S.S., 2000. Correlations among fruit traits and evolution of different fruits within Melastomataceae. Bot. J. Linn. Soc. 133 (3), 303–326.

Clausing, G., Renner, S.S., 2001. Molecular phylogenetics of Melastomataceae and Memecylaceae: implications for character evolution. Am. J. Bot. 88 (3), 486–498.

Cogniaux, A., 1891. Melastomaceae. In: Candolle, A.P. de, Candolle, C.P. de (Eds), Monographiae Phanerogamarum. G. Masson, Paris, v. 7, 1–1256.

Collinson, M.E., Pingen, M., 1992. Seeds of the Melastomataceae from the Miocene of Central Europe. In: Kovar-Eder, J. (Ed.), Palaeovegetational development in Europe. Museum of Natural History, Vienna, Austria, pp. 129–139.

Conceição, A.A., Rapini, A., Carmo, F.F., Brito, J.C., Silva, G.A., Neves, S.P., Jacobi, C.M., 2016. Rupestrian grassland vegetation, diversity, and origin. Pp. 105–127 in G. W. Fernandes, ed. Ecology and conservation of mountaintop grasslands in Brazil. Springer, Cham.

Conti, E., Litt, A., Wilson, P.G., Graham, S.A., Briggs, B.G., Johnson, L.A.S., Sytsma, K.J., 1997. Interfamilial relationships in Myrtales: molecular phylogeny and patterns of morphological evolution. Syst. Bot. 22, 629–647.

Correa, D.F., Álvarez, E., Stevenson, P.R., 2015. Plant dispersal systems in Neotropical forests: availability of dispersal agents or availability of resources for constructing zoochorous fruits? Glob. Ecol. Biogeogr. 24 (2), 203–214.

Dahlgren, R., Thorne, R.F., 1984. The order Myrtales: circumscription, variation, and relationships. Ann. Missouri Bot. Gard. 71, 633–699.

Davies, T.J., Smith, G.F., Bellstedt, D.U., Boatwright, J.S., Bytebier, B., Cowling, R.M., Forest, F., Harmon, L.J., Muasya, A.M., Schrire, B.D., Steenkamp, Y., 2011. Extinction risk and diversification are linked in a plant biodiversity hotspot. PLOS Biol. 9 (5), e1000620.

De Figueiredo, R.A., Longatti, C.A., 1997. Ecological aspects of the dispersal of a *Melastomataceae* by marmosets and howler monkeys (Primates: Platyrrhini) in a semideciduous forest of Southeastern Brazil. Rev. Ecol-Terre Vie 52 (1), 3–8.

Donoghue, M.J., Sanderson, M.J., 2015. Confluence, synnovation, and depauperons in plant diversification. New Phytol. 207 (2), 260–274.

Eriksson, O., 2014. Evolution of angiosperm seed disperser mutualisms: the timing of origins and their consequences for coevolutionary interactions between angiosperms and frugivores. Biol. Rev. Camb. Philos. Soc. 91 (1), 168–186.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37 (12), 4302–4315.

FitzJohn, R.G., 2012. Diversitree: comparative phylogenetic analyses of diversification in R. Methods Ecol. Evol. 3 (6), 1084–1092.

Freire-Fierro, A., 2002. Monograph of *Aciotis* (Melastomataceae). Syst. Bot. Monogr. 62, 1–99.

Fritsch, P.W., Almeda, F., Renner, S.S., Martins, A.B., Cruz, B.C., 2004. Phylogeny and circumscription of the near-endemic Brazilian tribe Microlicieae (Melastomataceae). Am. J. Bot. 91 (7), 1105–1114.

Garland, T., Dickerman, A.W., Janis, C.M., Jones, J.A., 1993. Phylogenetic analysis of covariance by computer simulation. Syst. Bio. 42 (3), 265–292.

Gaston, K.J., Fuller, R.A., 2009. The sizes of species' geographic ranges. J. Appl. Eco. 46 (1), 1–9.

GBIF, 2018. GBIF Occurrence. Downloaded at https://doi.org/10.15468/dl.4ppbzv.

Gentry, A.H., 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? Ann. Missouri Bot. Gard. 69 (3), 557–593.

Givnish, T.J., 1999. Adaptive radiation, dispersal, and diversification of the Hawaiian lobeliads. In: Kato, M. (Ed.), The Biology of Biodiversity. Springer Verlag, Tokyo, pp. 67–90.

Givnish, T.J., 2010. Ecology of plant speciation. Taxon 59 (5), 1326–1366.

Givnish, T.J., Millam, K.C., Theim, T.T., Mast, A.R., Patterson, T.B., Hipp, A.L., Henss, J.M., Smith, J.F., Wood, K.R., Sytsma, K.J., 2009. Origin, adaptive radiation, and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). Proc. R. Soc. B 276 (1656), 407–416.

Givnish, T.J., Pires, J.C., Graham, S.W., McPherson, M.A., Prince, L.M., Patterson, T.B., Rai, H.S., Roalson, E.H., Evans, T.M., Hahn, W.J., Millam, K.C., Meerow, A.W., Molvray, M., Kores, P.J., O'Brien, H.E., Hall, J.C., Kress, W.J., Sytsma, K.J., 2005. Repeated evolution of net venation and fleshy fruits among monocots in shaded habitats confirms a priori predictions: evidence from an *ndhF* phylogeny. Proc. R. Soc. B 272 (1571), 1481–1490.

Goldenberg, R., Penneys, D.S., Almeda, F., Judd, W.S., Michelangeli, F.A., 2008. Phylogeny of *Miconia* (Melastomataceae): patterns of stamen diversification in a megadiverse neotropical genus. Int. J. Plant Sci. 169 (7), 963–979.

Goldenberg, R., de Fraga, C.N., Fontana, A.P., Nicolas, A.N., Michelangeli, F.A., 2012. Taxonomy and phylogeny of *Merianthera* (Melastomataceae). Taxon 61 (5), 1040–1056.

Goldenberg, R., Almeda, F., Sosa, K., Ribeiro, R.C., Michelangeli, F.A., 2015. Rupestrea: a new Brazilian genus of Melastomataceae, with anomalous seeds and dry indehiscent fruits. Syst. Bot. 40 (2), 561–571.

Goldenberg, R., Shepherd, G.J., 1998. Studies on the reproductive biology of Melastomataceae in "cerrado" vegetation. Plant Syst. Evol. 211 (1–2), 13–29.

Goulding, M., 1983. The role of fishes in seed dispersal and plant distribution in Amazonian floodplain ecosystems. Sonderbd. Naturwiss. Ver. Hamburg 7, 271–283.

Graham, S.A., 1984. Alzateaceae, a new family of Myrtales in the American tropics. Ann. Missouri Bot. Gard. 71, 757–779.

Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E., Challenger, W., 2008. GEIGER: investigating evolutionary radiations. Bioinformatics 24 (1), 129–131.

Harmon, L.J., Losos, J.B., Jonathan Davies, T., Gillespie, R.G., Gittleman, J.L., Bryan Jennings, W., Kozak, K.H., McPeek, M.A., Moreno-Roark, F., Near, T.J., Purvis, A., 2010. Early bursts of body size and shape evolution are rare in comparative data. Evolution 64 (8), 2385–2396.

Heibl, C., 2008. PHYLOCH: R language tree plotting tools and interfaces to diverse phylogenetic software packages. Avaliable online at: http://www.christophheibl.de/Rpackages.html.

Hijmans, R.J., 2016. raster: Geographic Data Analysis and Modeling. R package version 2.5-8. https://CRAN.R-project.org/package=raster.

Hodgkison, R., Balding, S.T., Zubaid, A., Kunz, T.H., 2003. Fruit bats (Chiroptera: Pteropodidae) as seed dispersers and pollinators in a lowland Malaysian rain forest. Biotropica 35 (4), 491–502.

Howe, H.F., Smallwood, J., 1982. Ecology of seed dispersal. Ann. Rev. Ecol. Syst. 13 (1), 201–228.

Huelsenbeck, J.P., Neilsen, R., Bollback, J.P., 2003. Stochastic mapping of morphological characters. Syst. Biol. 52 (2), 131–138.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K., Mooers, A.O., 2012. The global diversity of birds in space and time. Nature 491 (7424), 444–448.

Kessler-Rios, M.M., Kattan, G.H., 2012. Fruits of Melastomataceae: phenology in Andean forest and role as a food resource for birds. J. Trop. Ecol. 28 (1), 11–21.

Kissling, W.D., Böhning-Gaese, K., Jetz, W., 2009. The global distribution of frugivory in birds. Glob. Ecol. Biogeogr. 18 (2), 150–162.

Kriebel, R., Michelangeli, F.A., Kelly, L.M., 2015. Discovery of unusual anatomical and continuous characters in the evolutionary history of *Conostegia* (Miconieae: Melastomataceae). Mol. Phylogenet. Evol. 82, 289–313.

Kriebel, R., 2016. Phylogenetic placement of the monotypic genus Schwackaea (Melastomeae: Melastomataceae) and the evolution of its unique fruit. Int. J. Plant Sci. 177 (5), 440–448.

Lagomarsino, L.P., Condamine, F., Mulch, A., Antonelli, A., Davis, C., 2016. The abiotic and biotic drivers of rapid diversification in Andean bellflowers (Campanulaceae). New Phytol. 210 (4), 1430–1442.

Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T., Calcott, B., 2016. PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Mol. Biol. Evol. 34 (3), 772–773.

Larson-Johnson, K., 2016. Phylogenetic investigation of the complex evolutionary history of dispersal mode and diversification rates across living and fossil Fagales. New Phytol. 209 (1), 418–435.

Leão, T.C., Fonseca, C.R., Peres, C.A., Tabarelli, M., 2014. Predicting extinction risk of Brazilian Atlantic Forest angiosperms. Conserv. Biol. 28 (5), 1349–1359.

Lessa, L.G., Costa, F.N., 2010. Diet and seed dispersal by five marsupials (Didelphimorphia: Didelphidae) in a Brazilian cerrado reserve. Mamm. Biol. 75 (1), 10–16.

Lima, M.H.C., Oliveira, E., Silveira, F., 2013. Interactions between ants and non-myrmecochorous fruits in *Miconia* (Melastomataceae) in a neotropical savanna. Biotropica 45 (2), 217–223.

Liu, B., Le, C.T., Barrette, R.L., Nickrent, D.L., Chen, Z., Lu, L., Vidal-Russell, R., 2018. Historical biogeography of Loranthaceae (Santalales): Diversification agrees with emergence of tropical forests and radiation of songbirds. Mol. Phylogenet. Evol. 124, 199–212.

Loera, I., Ickert-Bond, S., Sosa, V., 2015. Ecological consequences of contrasting dispersal syndromes in New World Ephedra: higher rates of niche evolution related to dispersal ability. Ecography 38 (12), 1187–1199.

Loiselle, B.A., Blake, J.G., 1999. Dispersal of melastome seeds by fruit-eating birds of tropical forest understory. Ecology 80 (1), 330–336.

Lu, L., Fritsch, P.W., Matzke, N.J., Wang, H., Kron, K.A., Li, D.Z., Wiens, J.J., 2019. Why is

fruit colour so variable? Phylogenetic analyses reveal relationships between fruit-colour evolution, biogeography and diversification. Glob. Ecol. Biogeogr., https://doi.org/10.1111/geb.12900.

Maddison, W.P., Midford, P.E., Otto, S.P., 2007. Estimating a binary character's effect on speciation and extinction. Syst. Biol. 56 (5), 701–710.

Magnusson, W., Sanaiotti, T., 1987. Dispersal of *Miconia* seeds by the rat *Bolomys lasiurus*. J. Trop. Ecol. 3 (3), 277–278.

Majure, L.C., Neubig, K.M., Skean, J.D., Bécquer, E.R., Judd, W.S., 2015. Evolution of the Sandpaper clade (Miconieae, Melastomataceae). Int. J. Plant Sci. 176 (7), 607–626.

Martin, C.V., Little, D.P., Goldenberg, R., Michelangeli, F.A., 2008. A phylogenetic evaluation of *Leandra* (Miconieae, Melastomataceae): a polyphyletic genus where the seeds tell the story, not the petals. Cladistics 24 (3), 315–327.

Matuszak, S., Favre, A., Schnitzler, J., Muellner-Riehl, A.N., 2016. Key innovations and climatic niche divergence as drivers of diversification in subtropical Gentianinae (Gentianaceae) in southeastern and eastern Asia. Am. J. Bot. 103 (5), 899–911.

Maxwell, J.F., 1981. Revision of the genus *Pternandra* (Melastomataceae). Gard. Bull. (Singapore) 34, 1–90.

Meyer, K., 2001. Revision of the Southeast Asian genus *Melastoma*. Blumea 46 (2), 351–398.

Michelangeli, F.A., Penneys, D.S., Giza, J., Soltis, D., Hils, M.H., Skean, J.D., 2004. A preliminary phylogeny of the tribe Miconieae (Melastomataceae) based on nrITS sequence data and its implications on inflorescence position. Taxon 53 (2), 279–290.

Michelangeli, F.A., Nicolas, A., Morales-Puentes, M.E., David, H., 2011. Phylogenetic relationships of *Allomaieta, Alloneuron, Cyphostyla,* and *Wurdastom* (Melastomataceae) and the resurrection of the tribe Cyphostyleae. Int. J. Plant Sci. 172 (9), 1165–1178.

Michelangeli, F.A., Guimaraes, P.J.F., Penneys, D.S., Almeda, F., Kriebel, R., 2013. Phylogenetic relationships and distribution of new world Melastomeae (Melastomataceae). Bot. J. Linn. Soc. 171 (1), 38–60.

Michelangeli, F.A., Ulloa, C.U., Sosa, K., 2014. *Quipuanthus*, a new genus of Melastomataceae from the foothills of the Andes in Ecuador and Peru. Syst. Bot. 39 (2), 533–540.

Miller, M.A., Pfeiffer, W., Schwartz, T., 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA, pp. 1–8.

Misof, B., Misof, K., 2009. A Monte Carlo approach successfully identifies randomness in multiple sequence alignments: a more objective means of data exclusion. Syst. Biol. 58 (1), 21–34.

Murphy, H.T., Hardesty, B.D., Fletcher, C.S., Metcalfe, D.J., Westcott, D.A., Brooks, S.J., 2008. Predicting dispersal and recruitment of *Miconia calvescens* (Melastomataceae) in Australian tropical rainforests. Bio. Invasions 10 (6), 925–936.

Naudin, C., 1851. Melastomacearum monographicae descriptionis. Annales des Sciences Naturelles, Botanique, Ser. 3 (18), 86–154.

Nogués-Bravo, D., Pulido, F., Bastos, M., Diniz-Filho, J.A.F., Garcia-Valdés, R., Kollmann, J., Svenning, J.-C., Valladares, F., Zavala, M.A., 2014. Phenotypic correlates of potential range size and range filling in European trees. Perspect. Plant Ecol. Evol. Syst. 16 (5), 219–227.

Oliveros, C.H., Field, D.J., Ksepka, D.T., Barker, F.K., Aleixo, A., Andersen, M.J., Alström, P., Benz, B.W., Braun, E.L., Braun, M.J., Bravo, G.A., Brumfield, R.T., Chesser, R.T., Claramunt, S., Cracraft, J., Cuervo, A.M., Derryberry, E.P., Glenn, T.C., Harvey, M.G., Hosner, P.A., Joseph, L., Kimball, R., Mack, A.L., Miskelly, C.M., Peterson, A.T., Robbins, M.B., Sheldon, F.H., Silveira, L.F., Smith, B.T., White, N.D., Moyle, R.G., Faircloth, B.C., 2019. Earth history and the passerine superradiation. Proc. Natl. Acad. Sci. USA 116 (16), 7916–7925.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. Terrestrial ecoregions of the world: a new map of life on Earth. Bioscience 51 (11), 933–938.

Onstein, R.E., Baker, W.J., Couvreur, T.L., Faurby, S., Svenning, J.-C., Kissling, W.D., 2017. Frugivory-related traits promote speciation of tropical palms. Nat. Ecol. Evol. 1 (12), 1903–1911.

Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20 (2), 289–290.

Pebesma, E.J., Bivand, R., 2005. Classes and methods for spatial data in R. R News 5 (2), http://cran.r-project.org/doc/Rnews/.

Penneys, D.S., Michelangeli, F.A., Judd, W.S., Almeda, F., 2010. Henrietteeae (Melastomataceae): a new neotropical berry-fruited tribe. Syst. Bot. 35 (4), 783–800.

Penneys, D.S., 2013. Preliminary phylogeny of the Astronieae (Melastomataceae) based on nuclear and plastid DNA sequence data, with comments on the Philippine endemic genus, Astrocalyx. Philippine J. Sci. 142, 159–168.

Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31 (2), 161–175.

Pizo, M.A., Morellato, L.P., 2002. A new rain-operated seed dispersal mechanism in *Bertolonia mosenii* (Melastomataceae), a Neotropical rainforest herb. Am. J. Bot. 89 (1), 169–171.

R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing. http://www.R-project.org/ (accessed 10 Jun 2018).

Rabosky, D.L., 2010. Extinction rates should not be estimated from molecular phylogenies. Evolut.: Int. J. Org. Evolut. 64 (6), 1816–1824.

Rabosky, D.L., 2014. Automatic detection of key innovations, rate shifts, and diversity dependence on phylogenetic trees. PLoS ONE 9 (2), e89543.

Rabosky, D.L., Grundler, M., Anderson, C., Title, P., Shi, J.J., Brown, J.W., Huang, H., Larson, J.G., 2014. BAMM tools: an R package for the analysis of evolutionary dynamics on phylogenetic trees. Methods Ecol. Evol. 5 (7), 701–707.

Rambaut, A., Drummond, A.J., 2007. Tracer. Available from: http://www.beast.bio.ed.ac.uk/Tracer.

Reginato, M., Michelangeli, F.A., Goldenberg, R., 2010. Phylogeny of *Pleiochiton* (Melastomataceae, Miconieae): total evidence. Bot. J. Linn. Soc. 162 (3), 423–434.

Reginato, M., Michelangeli, F.A., 2016. Untangling the phylogeny of *Leandra* s. str. (Melastomataceae, Miconieae). Mol. Phylogenet. Evol. 96, 17–32.

Reginato, M., Neubig, K.M., Majure, L.C., Michelangeli, F.A., 2016. The first complete plastid genomes of Melastomataceae are highly structurally conserved. PeerJ 4, e2715.

Renner, S.S., 1989. A survey of reproductive biology in Neotropical Melastomataceae and Memecylaceae. Ann. Mo. Bot. Gard. 76, 496–518.

Renner, S.S., 1993. Phylogeny and classification of the Melastomataceae and Memecylaceae. Nordic J. Bot. 13 (5), 519–540.

Renner, S.S., Triebel, D., Almeda, F., Stone, D., Ulloa, C., Michelangeli, F.A., Goldenberg, R., Mendoza, H., 2007 onwards. MELnames: a database with names of Melastomataceae. http://www.melastomataceae.net.

Revell, L.J., 2012. phytools: An R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. 3 (2), 217–223.

Rocha, M.J.R., Batista, J.A., Guimarães, P.J., Michelangeli, F.A., 2016. Phylogenetic relationships in the Marcetia alliance (Melastomeae, Melastomataceae) and implications for generic circumscription. Bot. J. Linn. Soc. 181 (4), 585–609.

Sanderson, M.J., 2002. Estimating absolute rates of molecular evolution and divergence times: a penalized likelihood approach. Mol. Biol. Evol. 19 (1), 101–109.

Schwery, O., O'Meara, B.C., 2016. MonoPhy: a simple R package to find and visualize monophyly issues. PeerJ Compute Sci. 2, e56.

Smith, J.F., 2001. High species diversity in fleshy-fruited tropical understory plants. Am. Nat. 157 (6), 646–653.

Smith, S.A., O'Meara, B.C., 2012. treePL: divergence time estimation using penalized likelihood for large phylogenies. Bioinformatics 28 (20), 2689–2690.

Sonkoly, J., Deák, B., Valkó, O., Molnár, V.A., Tóthmérész, B., Török, P., 2017. Do large-seeded herbs have a small range size? The seed mass-distribution range trade-off hypothesis. Ecol. Evol. 7 (24), 11204–11212.

Stamatakis, A., 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30 (9), 1312–1313.

Stang, M., Klinkhamer, P.G., Van der Meijden, E., 2007. Asymmetric specialization and extinction risk in plant–flower visitor webs: a matter of morphology or abundance? Oecologia 151 (3), 442–453.

Stebbins, G.L., 1970. Adaptive radiation of reproductive characteristics in angiosperms, I: pollination mechanisms. Annu. Rev. Ecol. Syst. 1 (1), 307–326.

Stiles, F.G., Rosselli, L., 1993. Consumption of fruits of the Melastomataceae by birds: how diffuse is coevolution? Vegetatio 107 (1), 57–73.

Stone, R.D., 2006. Phylogeny of major lineages in Melastomataceae, subfamily Olisbeoideae: utility of nuclear glyceraldehyde 3-phosphate dehydrogenase (GapC) gene sequences. Syst. Bot. 31 (1), 107–121.

Sytsma, K.J., Morawetz, J., Pires, J.C., Nepokroeff, M., Conti, E., Zjhra, M., Hall, J.C., Chase, M.W., 2002. Urticalean rosids: circumscription, rosid ancestry, and phylogenetics based on *rbcL*, *trnL-F*, and *ndhF* sequences. Am. J. Bot. 89 (9), 1531–1546.

Tiffney, B.H., 1984. Seed size, dispersal syndromes, and the rise of the angiosperms: evidence and hypothesis. Ann. Missouri Bot. Gard. 71 (2), 551–576.

Tiffney, B.H., 2004. Vertebrate dispersal of seed plants through time. Annu. Rev. Ecol. Evol. Syst. 35, 1–29.

Triana, J., 1871. Les Mélastomacées. Trans. Linnean Soc. London 28, 1–188.

Vamosi, S.M., Vamosi, J.C., 2012. Perspective: Causes and consequences of range size variation: the influence of traits, speciation, and extinction. Front. Biogeogr. 4 (4), 168–177.

Van Beusekom-Osinga, R.J., Van Beusekom, C.F., 1975. Delimitation and subdivision of the Crypteroniaceae (Myrtales). Blumea 22 (2), 255–266.

Veranso-Libalah, M.C., Stone, R.D., Fongod, A.G., Couvreur, T.L., Kadereit, G., 2017. Phylogeny and systematics of African Melastomateae (Melastomataceae). Taxon 66 (3), 584–614.

Willson, M.F., Traveset, A., 2000. The ecology of seed dispersal. In: Fenner, M. (Ed.), The Ecology of Regeneration in Plant Communities. CABI Publishing, Oxon, UK, pp. 85–110.

Wright, E.S., 2016. Using DECIPHER v2.0 to Analyze Big Biological Sequence Data in R. R J. 8(1), 352–359.

Zeng, S.J., Zou, L.H., Wang, P., Hong, W.J., Zhang, G.Q., Chen, L.J., Zhuang, X.Y., 2016. Preliminary phylogeny of *Fordiophyton* (Melastomataceae), with the description of two new species. Phytotaxa 247 (1), 45–61.

Web References

Invasive and Exotic Species of North America, 2018. http://www.invasives.org (accessed May 2018).

Global Invasive Species Database, 2018. http://www.iucngisd.org/gisd (accessed May 2018).