Disparity, Diversity, and Duplications in the Caryophyllales

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Summary

- The role whole genome duplication (WGD) plays in the history of lineages is actively debated. WGDs have been associated with advantages including superior colonization, various adaptations, and increased effective population size. However, the lack of a comprehensive mapping of WGDs within a major plant clade has led to uncertainty regarding the potential association of WGDs and higher diversification rates.
- Using seven chloroplast and nuclear ribosomal genes, we constructed a phylogeny of 5,036 species of Caryophyllales, representing nearly half of the extant species. We phylogenetically mapped putative WGDs as identified from analyses on transcriptomic and genomic data and analyzed these in conjunction with shifts in climatic niche and lineage diversification rate.
- Thirteen putative WGDs and twenty-seven diversification shifts could be mapped onto the phylogeny. Of these, four WGDs were concurrent with diversification shifts, with other diversification shifts occurring at more recent nodes than WGDs. Five WGDs were associated with shifts to colder climatic niches.
- While we find that many diversification shifts occur after WGDs it is difficult to consider diversification and duplication to be tightly correlated. Our findings suggest that duplications may often occur along with shifts in either diversification rate, climatic niche, or rate of evolution.

Keywords: Caryophyllales, duplications, climatic niche, diversification rates, phylogenomics

Introduction

Understanding the causes and correlates of diversification within flowering plants has been a central goal of evolutionary biologists. Genomic and transcriptomic data have reinvigorated hypotheses associating whole genome duplication (WGD) with lineage diversification rate increases (e.g., Levin, 1983; Levin 2002; Barker *et al.* 2009; Estep *et al.,* 2014; Soltis *et al.*, 2014; Edger *et al.* 2015; Puttick *et al.* 2015; Tank *et al.*, 2015; Barker *et al.* 2016; Huang *et al.* 2016; McKain *et al.* 2016; Laurent *et al.* 2017). It is not self-evident why WGDs would be associated with increases in lineage diversification. One hypothesis suggests that the additional genetic material provides a basis to generate new adaptations (Edger *et al.*, 2015), although this itself assumes a co-occurrence of adaptation and lineage proliferation (Levin, 1983). The

apparent lack of precise co-occurrence of adaptation and lineage proliferation has been explained by the potential of a lag model (Schranz *et al.* 2012; Tank *et al.* 2015) where diversification may follow WGD events. In the absence of overwhelming correlative signal, we are often unable to discern true ancient WGD events from aneuploidy without advanced genomic information such as synteny mapping (Dohm *et al.*, 2012). Because it is often difficult to distinguish the two, for simplicity we will define WGD broadly to include putative ancient WGD events (paleopolyploidy) and ancient aneuploidy events. WGD events are thought to be a common occurrence and have been associated with an estimated 15% of angiosperm speciation events (Wood *et al.*, 2009). However, whether speciation by WGD is correlated with higher diversification rates remains highly debated (Mayrose *et al.*, 2011; Estep *et al.* 2014; Soltis *et al.*, 2014; Tank *et al.*, 2015; Kellogg *et al.* 2016). Analyses based on recent WGD events have concluded that immediate extinction rates are higher for polyploid plants (Mayrose *et al.*, 2011; Arrigo and Barker, 2012). This may result from small initial population sizes and an increased dependence on selfing. Alternatively, despite the disadvantages of WGD, others have suggested that polyploids may be superior colonizers (Soltis and Soltis, 2000).

Indeed, extreme environments are associated with high levels of WGD, with up to 87% of species restricted to areas that were glaciated during the last ice age consisting of polyploids (Brochmann, 2004). However, in the example from Arctic plants, the high level of WGD has occurred post-glaciation representing a micro-evolutionary period whereas previous studies often focus at much deeper macro-evolutionary time scales (Mayrose *et al.*, 2011; Tank *et al.*, 2015; Soltis *et al.*, 2014). From the perspective of a short timescale, polyploidy has the disadvantages of higher error rates in mitosis (Storchová *et al.*, 2006) and masking of deleterious mutations allowing them to accumulate to higher frequencies in a population (Otto & Whitton, 2000). A suite of advantages however may also arise, including gain of asexuality (Miller *et al*. 2000) and varying effects of heterosis (Comai, 2005). The net role these advantages and disadvantages play on the macroevolutionary scale is difficult to determine from either the purely short-term or purely long-term time scales previously used.

The long-term consequence of WGD is a central question in macroevolution and comparative genomics. However, with a suite of advantages and disadvantages, much debate surrounds the importance and patterns of correlation of WGD (Comai 2005). While polyploidization events can cause instant speciation, there is no reason to assume that these

93 singular speciation events in themselves would influence large-scale diversification rate shifts
94 when considering lineage survivorship. Instead, there may be other factors, such as the increase
95 in genetic material, perhaps increasing genetic diversity or enabling adaptation, that cause long
96 term shifts in rates of diversification. Adaptations need not be associated with shifts in the tempo
97 of diversification and those adaptations and shifts in diversification may not co-occur on the
98 same branch (i.e., there may be a lag time; Donoghue 2005; Smith *et al.,* 2011, Schranz *et al.,*
99 2012; Donoghue & Sanderson 2015; Tank *et al.,* 2015; Dodsworth *et al.,* 2016). In the broader
100 context of plant evolution, there are several possible outcomes of WGD in relation to the
101 evolution and diversification of clades: 1) no relationship between WGD and speciation rate or
102 habitat shift/adaptation, 2) WGD coincides with an increase of speciation rate, with or without a
103 lag time, 3) WGD promotes dispersal and habitat shifts, which has mixed relationship with
104 speciation rate, and 4) a mixture (some association, some not), similar to the previous hypothesis
105 but without explicitly promoting dispersal or habitat shift or speciation (e.g., adaptation could be
106 more prominent than dispersal and habitat shift). Here, we contribute to this discussion on
107 diversification and WGDs with an in-depth examination of the intersection of diversification and
108 WGDs happening at a range of scales within the hyperdiverse Caryophyllales.
109 The Caryophyllales comprise ~12,500 species in 39 families (Thulin *et al.*, 2016; APG
110 IV: Chase *et al.*, 2016), representing approximately 6% of extant angiosperm species diversity.
111 The estimated crown age of Caryophyllales is approximately 67–121 millions of years ago
112 (mega-annum, Ma) (Bell *et al.*, 2010; Moore *et al.*, 2010). Species of the Caryophyllales exhibit
113 extreme life-history diversity, ranging from tropical trees to temperate annual herbs, and from
114 desert succulents (e.g., Cactaceae) to a diverse array of carnivorous plants (e.g., the sundews
115 *Drosera* and pitcher plants *Nepenthes*). Such extraordinary diversity makes Caryophyllales a
116 particularly useful system for investigating the relationship between WGD vs. diversification and
117 niche evolution. Our previous analyses using 62 transcriptomes representing 60 species across
118 the Caryophyllales identified 13 well-supported ancient WGD events (Yang *et al.*, 2015). We
119 have since nearly tripled the taxon sampling and assembled a data set comprising high-coverage
120 transcriptomes and genomes from 169 species across the Caryophyllales (Yang *et al.*,
121 submitted), providing even greater power for resolving the number and phylogenetic locations of
122 WGD events. Moreover, the growth in the number of plant taxa on GenBank that are represented
123 by traditional targeted sequences (e.g., *rbc*L*, mat*K*,* ITS, etc.) and the growth of publicly

124 available collections data (e.g., GBIF, iDigBio) provide excellent opportunities to apply
125 megaphylogeny and niche diversification approaches at fine scales in Caryophyllales.
126 By examining WGDs and diversification within the Caryophyllales, we present an
127 important example. Not only does the dataset examined have a high density of transcriptomic
128 sampling, the diversification of the bulk of Caryophyllales occurred during a time frame
129 intermediate to that of most published studies that have probed a link between WGD and
130 macroevolution. This time frame, between 10 and 100 Ma, is important for angiosperms as much
131 of the diversification that has led to the modern flora occurred during this period and most
132 modern angiosperm families appeared by this time. Discussion of speciation rate, niche shift, and
133 WGD would be flawed without accurate mappings of WGD events within this time scale. We
134 compiled a data set with extensive and precise mapping of WGD combined with a species-level
135 phylogeny. The megaphylogeny approach has been used extensively in the past to combine data
136 from many gene regions and across broad taxonomic groups to address evolutionary questions
137 (Smith *et al.*, 2009). Here, we use this approach to help inform analyses from phylogenomic
138 studies, and provide a broad context in which to examine these genomic phenomena. With half
139 of the species sampled, this represents one of the largest and most exhaustive studies of WGDs,
140 diversification rate, and adaptive shifts.
141
142 **Materials and Methods**
143 ***Sanger sequencing and assembly.*** —A total of 248 new *matK* sequences were included in this
144 study (Table 1). To generate these sequences, leaf samples were collected in silica in the field or
145 from cultivated material, or were collected from herbarium sheets. DNA was isolated using
146 either the Nucleon Phytopure kit (GE Healthcare Life Sciences, Pittsburgh, PA, USA), using the
147 0.1 g protocol and following manufacturer's instructions, or using the Doyle & Doyle (1987)
148 protocol, with the addition of 1% PVP-40. An approximately 950 bp region in the middle of the
149 *matK* gene was amplified and sequenced using custom-designed primers (Table 2). PCRs were
150 performed in 12.5 µL volumes with 0.5 µL of 5 mM primer for both primers, 5-20 ng of DNA
151 template, 0.1 µL of GoTaq (Promega, Madison, WI, USA), 6.25 µL of Failsafe Premix B
152 (Epicentre, Madison, WI, USA), and 4.7 µL of sterile, deionized water. Reactions were run on a
153 Bio-Rad PTC 200 thermocycler (Bio-Rad, Hercules, CA, USA) at Oberlin College. Individual
154 PCRs were cleaned in 16.5 µL reactions containing 10 U of Exonuclease I (Affymetrix,

155 ThermoFisher Scientific, Waltham, MA, USA), 2 U of shrimp alkaline phosphatase
156 (Affymetrix), 8 µL of PCR product, and 8.5 µL of sterile, deionized water. Sanger sequencing of
157 the resulting cleaned PCRs was conducted by Neogenomics (formerly SeqWright; Houston, TX,
158 USA) using an ABI 3730xl automated sequencer (Applied Biosystems, ThermoFisher
159 Scientific). The resulting forward and reverse sequences for each reaction were trimmed and *de*
160 *novo* assembled using default parameters of the Geneious assembler in Geneious versions 5-7
161 (Biomatters, Auckland, New Zealand).
162
163 ***Molecular Data for Phylogenetic Reconstruction.*** —Nucleotide data from the nuclear
164 ribosomal internal transcribed spacers (ITS) and *phyC* gene, and the plastid loci *matK*, *ndhF,*
165 *rbcL*, *trnH-psbA* spacer, and *trnL-trnF* spacer were used to reconstruct the phylogeny. These data
166 were gathered first using PHLAWD (Smith & Donoghue, 2008; Smith *et al.*, 2009) and then
167 curated and combined with newly sequenced *matK* data for 124 additional species. This yielded
168 the following sampling: ITS 2,969 species, *matK* 2,270 species, *ndhF* 417 species, *phyC* 172
169 species, *rbcL* 947 species, *trnH-psbA* 240 species, and *trnL-trnF* 1,996 species. We used *mat*K,
170 *rbc*L, and *ndh*F sequences from *Aextoxicon, Apium, Berberidopsis, Campanula, Clethra, Coffea,*
171 *Echinops, Helwingia, Ilex, Ipomoea, Lamium, Lonicera, Nyssa, Polysoma, Primula, Santalum,*
172 *Valeriana,* and *Viburnum* to represent outgroups.
173
174 ***Phylogenetic Reconstruction.*** —We conducted phylogenetic analyses with RAxML v7.2.8
175 (Stamatakis, 2014) using the full analysis command, -f a, which conducts a rapid bootstrap and
176 then a full maximum likelihood search. The combined bootstrap and maximum likelihood search
177 allows for a more thorough maximum likelihood analysis where the initial rapid bootstrap results
178 prime the maximum likelihood analysis. However, we did not use the rapid bootstrap trees from
179 this analysis and instead, we conducted a full bootstrap, generating the bootstrap dataset using
180 phyx (Brown *et al.*, 2017) and then conducting individual maximum likelihood runs on each
181 constructed bootstrap dataset. This allowed us to conduct SH-like approximate likelihood ratio
182 test (SH-aLRT; Guindon *et al.*, 2010) on the resulting bootstrap set. We conducted bootstraps
183 within gene regions and we retained the individual bootstrap alignments to conduct additional
184 analyses (i.e., bootstrapped alignments contained the same number of gene-specific sites as the
185 empirical alignment). On each of the resulting trees of the bootstrap and the maximum likelihood

186 tree, we conducted SH-aLRTs as implemented in RAxML. These analyses calculate support for
187 each edge while also finding the NNI-optimal topology. RAxML completed the likelihood
188 search for each of these bootstrap replicates, however the SH-aLRT analyses often resulted in an
189 improved maximum likelihood topology. The trees that resulted from the SH-aLRT, ML, and
190 bootstrap samples, were used for further analyses. Because several deep relationships within
191 Caryophyllales are hard to resolve without large amounts of molecular data that are unavailable
192 for most of the taxa included in this analysis (Yang *et al.*, 2015), for all phylogenetic analyses we
193 applied the following topological constraint: (Droseraceae, (*Microtea*, (Stegnospermataceae,
194 Limeaceae, (Lophiocarpaceae, (Barbeuiaceae, Aizoaceae))))) as per previous analysis
195 (Brockington *et al.*, 2009; Yang *et al.*, 2015).
196
197 ***Divergence Time Estimation.*** — Few tractable options for divergence time estimation exist for
198 datasets of the size presented here. We use the penalized likelihood approach (Sanderson, 2003)
199 as implemented in the program treePL (Smith & O'Meara, 2012), which can handle large-scale
200 phylogenies. The early fossil record of the Caryophyllales is sparse with only a few known
201 records (Friis *et al.*, 2011; Arakaki *et al.*, 2011): (1) fossil pollen has been ascribed to
202 Amaranthaceae (*Chenopodipollis*) from the Paleocene of Texas (Nichols & Traverse, 1971); (2)
203 a putative fossil infructescence from within the Phytolaccaceae in the Campanian has also been
204 reported (Cevallos-Ferriz *et al.*, 2008), but this phylogenetic position has been disputed (pers.
205 comm. S. Manchester) and hence we excluded it; (3) Jordan & Macphail (2003) describe a
206 middle to late Eocene inflorescence from the species *Caryophylloflora paleogenica,* ascribed to
207 Caryophyllaceae; (4) pollen from Argentina within the Nyctaginaceae has been reported from the
208 middle Eocene (Zetter *et al.*, 1999); and (5) fossil pollen and seeds of *Aldrovanda* (Degreef,
209 1997). The penalized likelihood method performs better when a calibration is used at the root.
210 For this calibration, and because there is no fossil record for the earliest Caryophyllales, we use a
211 secondary calibration from the comprehensive angiosperm divergence time analyses of Bell *et*
212 *al.* (2010). We attached several other secondary calibrations to major clades where fossils are not
213 available (Ocampo & Columbus 2010; Arakaki *et al.*, 2011; Schuster *et al.*, 2013; Valente *et al.*,
214 2013; see Supp. Table S1 for detail on placement and calibrations). We conducted a priming
215 analysis to determine the best optimization parameter values. We then performed a cross

216 validation analysis using the random cross validation setting to determine the optimal smoothing
217 parameter value.
218
219 ***Climate occupancy analyses.*** —We downloaded 6,592,700 georeferenced occurrences for the
220 Caryophyllales from GBIF (accessed on 6/1/2015; http://gbif.org). After removing samples
221 present in living collections, and therefore not necessarily representative of native climates, and
222 removing samples whose localities were over water, 6,009,552 samples remained. We extracted
223 bioclimatic values for each coordinate using the 2.5 arc-minute resolution data from WorldClim
224 (http://worldclim.org). We only included taxa that had at least three samples in these analyses to
225 reduce potential errors and to have the minimum number of samples required to calculate mean
226 and variance. The resulting overlap of the taxa represented in both the geographic and genetic
227 data was 2,843 taxa. We conducted principal component analyses (PCA) on these extracted
228 values. With both the bioclimatic values and the first two axes of the PCA, we conducted
229 ancestral state reconstruction analyses.
230 We also conducted contrast analyses and calculated Brownian motion rates of evolution
231 between sister clades (comparing duplicated lineages with their sisters) for mean annual
232 precipitation, mean annual temperature, and principal component axis 1. We calculated contrasts
233 using phylogenetic independent contrasts. We calculated Brownian motion rates on sister
234 lineages independently using the analytical solution for rate: $\sigma^2 = \frac{1}{n}\sum_{i=1}^{n}\frac{u_i^2}{V_i^2}$.
235
236 ***Diversification analyses.*** —To map diversification rate shifts, we conducted MEDUSA (Alfaro
237 *et al.*, 2009; Pennell *et al.*, 2014) analyses on the maximum likelihood tree and the bootstrap
238 trees. MEDUSA is far more computationally tractable than some other diversification estimation
239 methods. Furthermore, we required the ability to feasibly integrate over the phylogenetic
240 uncertainty within the phylogenetic dataset because of both the nature of the larger phylogenetic
241 dataset and the inherent biological uncertainty within the Caryophyllales. MEDUSA fits a birth-
242 death model of diversification (with parameters *r*: net diversification (birth - death), and ε:
243 relative extinction (death / birth)) before using stepwise AIC (Burnham & Anderson, 2002) to
244 identify shifts in rates of diversification. These complementary analyses accommodate
245 topological and branch length uncertainty. We employed a birth-death model for 97 chronograms
246 generated from nonparametric bootstrapping of the original matrix, inferring ML trees in

247 RAxML, and estimating divergence times in treePL using the temporal constraints described
248 above. We discarded three trees based on poor fossil placement resulting from phylogenetic
249 uncertainty causing fossil placements to conflict.
250
251 ***Whole Genome Duplication Identification.*** — To identify WGDs (procedure described below),
252 we generated a tree based on transcriptomic data. For this tree, we used 178 ingroup data sets
253 (175 transcriptomes, 3 genomes) representing 169 species in 27 families and 40 outgroup
254 genomes (Table S1-S2 in Yang et al. submitted). We mapped putative WGD events using
255 multiple strategies: gene tree topology, plotting synonymous distance, and chromosome counts
256 (Yang *et al.* 2015; Yang *et al.*, submitted). For gene tree topology analyses, we performed two
257 alternative strategies for mapping duplication events from gene trees to the species tree: mapping
258 to the most recent common ancestor (MRCA), or mapping to the species tree only when gene
259 tree and species tree topologies are compatible.
260 To conduct synonymous distance analyses, we performed the following procedure. For
261 all ingroup Caryophyllales transcriptome data sets, we calculated the distribution of paralog
262 synonymous distance following the same procedure as (Yang *et al.*, 2015). We reduced highly
263 similar peptide sequences with CD-HIT (-c 0.99 -n 5)(Li & Godzik 2006). We also carried out an
264 all-by-all BLASTP within each taxon using an E value cutoff of 10 and -max_target_seq set to
265 20. Resulting hits with pident < 20% or niden < 50 amino acids were removed. We removed
266 sequences with ten or more hits to avoid overrepresentation of gene families that experienced
267 multiple recent duplications. We used the remaining paralog pairs and their corresponding CDS
268 to calculate Ks values using the pipeline https://github.com/tanghaibao/bio-
269 pipeline/tree/master/synonymous_calculation (accessed November 29, 2014). The pipeline first
270 carries out pairwise protein alignment using default parameters in ClustalW (Larkin *et al.*, 2007),
271 back-translates the alignment to a codon alignment using PAL2NAL (Suyama *et al.*, 2006), and
272 calculates the synonymous substitution rate (Ks) using yn00 as part of the PAML package
273 (Yang, 2007), with Nei–Gojobori correction for multiple substitutions (Nei & Gojobori, 1986).
274 We obtained chromosome counts from the Chromosome Counts Database (CCDB;
275 http://ccdb.tau.ac.il accessed Oct 5, 2015). When multiple counts were reported from different
276 authors or different plants, we erred on the conservative estimate and recorded the lowest
277 number. For species that were not available in the database, we found counts from the literature

278 (e.g., Jepson eFlora http://ucjeps.berkeley.edu/eflora/ and Flora of North America
279 http://floranorthamerica.org) or by a consensus from species of the same genera.
280
281 **Results and Discussion**
282 ***Phylogenetic results.*** —Phylogenetic analyses showed strong support based on bootstrap and
283 SH-aLRT values for the monophyly of most Caryophyllales families (see Fig. S1). We found
284 strong support for the carnivorous clade including Droseraceae, Ancistrocladaceae,
285 Nepenthaceae, Drosophyllaceae, and Dioncophyllaceae. There was also strong support for this
286 clade as sister to a clade including Frankeniaceae, Tamaricaceae, Plumbaginaceae, and
287 Polygonaceae. However, relationships among the families showed more varied support. There
288 was weak support for the placement of other families relative to other early diverging
289 Caryophyllales (see Fig. S1). There was strong support for Caryophyllaceae sister to
290 Amaranthaceae. There was very weak support for Aizoaceae sister to
291 Phytolaccaceae+Nyctaginaceae. As with previously published analyses, there was no support for
292 the monophyly of Phytolaccaceae in the traditional sense (i.e., including Phytolaccaceae s.s.,
293 Petiveriaceae, and *Agdestis*; APG IV) and very weak support for the placement of Sarcobataceae.
294 There was also weak support for the relationships among Limeaceae, Molluginaceae, and the
295 Portulacineae. Many of these relationships have been found to be strongly supported but
296 conflicting in different analyses (Brockington *et al.*, 2009; Soltis *et al.*, 2011; Yang *et al.*, 2015;
297 Smith *et al.*, 2015; Walker *et al.*, 2017). Here, we focused less on the systematic resolution
298 within the Caryophyllales and instead examine the potential relationship of diversification and
299 climate occupancy shifts to WGDs. Therefore, we placed more emphasis on including more taxa
300 over that of more gene regions (i.e., transcriptomes) at the cost of more missing data. Confident
301 resolution of many of the systematic relationships will require genomic and transcriptomic
302 sampling, as well as more thorough taxon sampling (Yang *et al.*, submitted).
303
304 ***Climate occupancy reconstruction results.*** —We performed climate occupancy ancestral
305 reconstruction analyses on the phylogeny of 2,843 taxa that included taxa with at least three
306 sampled geographic coordinates (Figs. 1-3). We conducted these analyses for visualization and
307 for comparison with diversification and WGD results (see below). Results for individual
308 bioclimatic variables and principal components can be found in Figs. S2-S4. Bioclimatic variable

309 1 (mean annual temperature, Fig. 1) showed that there are several strong phylogenetic patterns of
310 clades with preferences for colder or warmer regions. For example, Polygonaceae,
311 Caryophyllaceae, and Montiaceae each are dominated by taxa with preferences for cold
312 environments, although each also contains early-diverging taxa with preferences to warm
313 environments. In contrast, taxa inhabiting warm environments predominate in Cactaceae,
314 Amaranthaceae, Aizoaceae, the carnivorous clade (Droseraceae, Drosophyllaceae,
315 Nepenthaceae, Ancistrocladaceae, Dioncophyllaceae), and the phytolaccoid clade
316 (Nyctaginaceae, Phytolaccaceae, Petiveriaceae, Sarcobataceae, and *Agdestis*). Bioclimatic
317 variable 12 (mean annual precipitation) showed a relatively consistent pattern of relatively dry to
318 intermediately wet clades throughout the group. Indeed, only a few clades inhabiting wet
319 ecosystems (in this case, the wet tropics) exist in the Caryophyllales, specifically small groups
320 within the carnivorous clade, the phytolaccoids, early-diverging Polygonaceae, and other small
321 groups throughout the Caryophyllales. The principal component loadings are presented in Fig. 2
322 and Fig. S5. Principal component 1, PCA1, showed significant differentiation throughout the
323 Caryophyllales, as for example, early-diverging Polygonaceae vs the rest of Polygonaceae, early
324 diverging Caryophyllaceae vs the rest of Caryophyllaceae, phytolaccoids vs Aizoaceae, and
325 Portulacineae + relatives vs Cactaceae, to mention a few. These results generally reflect the
326 extensive ecological diversification throughout the group. They also reflect significant
327 diversification in the temperate regions of the world especially within the Caryophyllaceae and
328 Polygonaceae contrasted with extensive diversification in the succulent lineages (especially
329 Aizoaceae and Cactaceae) found in relatively dry and warm environments.
330
331 ***Diversification.*** —Significant shifts in diversification were detected in most major clades (Table
332 4, Fig. 1). The results from diversification analyses on the maximum likelihood tree and
333 bootstrap tree set were generally congruent with each other. However, there were discrepancies
334 (Fig. 1). The bootstrap set recovered many shifts in Polygonaceae, the carnivorous clade,
335 Caryophyllaceae, some shifts within Cactaceae, phytolaccoids, and Amaranthaceae.
336 Disagreements on the existence and placement of shifts are primarily within Portulacineae,
337 Aizoaceae, and Amaranthaceae. Overall, MEDUSA detected 27 increases in diversification rate
338 using the ML tree and 16 increases using the bootstrap trees. Given the relative lack of support of
339 some of the branches in the phylogeny, we find the MEDUSA results on the set of bootstrapped

340 trees to be the most conservative while the ML results are suggestive but not definitive of
341 diversification shifts.
342
343 ***Duplications, diversification, and climate occupancy.*** —WGD analyses showed thirteen
344 putative WGDs that can be mapped to clades (i.e., involve more than 1 taxon in the dataset;
345 Table 3 and Figs. 1-3). Many of these were found in early diverging lineages as opposed to
346 nested deep within families, though there are WGDs identified in *Amaranthus* and *Claytonia*.
347 We also found evidence of nested WGDs as within the phytolaccoids and Portulacineae. In
348 addition to these deeper WGDs, there were several more recent WGDs that were present in Ks
349 plots but could not be mapped to a clade (Yang *et al.*, submitted). By sampling more extensively,
350 Yang *et al.* (submitted) and Walker *et al.* (2017) found additional WGD events within the
351 Caryophyllales. We will surely find additional WGDs events in other lineages as more effort is
352 placed on denser taxon sampling using genomes and transcriptomes. We did not explore WGDs
353 that could only be mapped to terminal branches as we could not verify these phylogenetically.
354 Further discussion of specific results related to the WGDs themselves can be found in Yang et al.
355 (submitted) and Walker et al. (2017).
356 To better examine whether WGDs coincide with diversification rate shifts, increases and
357 decreases, or notable changes in climate tolerance, we mapped WGDs onto the large phylogenies
358 and summarized the number of species and climate occupancy information for each clade
359 (Tables 3-4, Figs. 1-3). Some WGD events were associated with synchronous diversification
360 events. For example, within Nyctaginaceae, a WGD event occurs on the same branch (leading to
361 Tribe Nyctagineae; Douglas & Spellenberg, 2010) as an increase in diversification rate in both
362 the ML tree and the bootstrapped dataset (Fig. 1, dup:1 div:n). These events were also associated
363 with a shift in life history and niche from an ancestral woody habit in the tropics to the largely
364 herbaceous, arid-adapted temperate Nyctagineae. This was also the case for *Amaranthus* (Fig. 1,
365 dup:5 div:x). Other coincident diversification and WGD events in the Droseraceae and
366 Nepenthaceae were only supported by the ML tree. Although these correlated events may, in
367 fact, be accurate, we will reserve more comments for when these are more confidently resolved.
368 Other than these simultaneous shifts and one diversification shift at the base of the MRCA of
369 Nyctaginaceae+Cactaceae, all other shifts in diversification occured more recently than WGD
370 events. Several authors have suggested that this lagging pattern may be common at the broader

371 angiosperm scale (Schranz *et al.* 2015, Tank *et al.* 2015), though the expected distance of the
372 diversification shift from the WGD event was not specified (this is discussed more below). In the
373 results presented here, some diversification events occur shortly after the WGD event, such as
374 within the Amaranthaceae (dup: 6) and Portulacineae (dup: 4). For others, it is difficult to
375 determine whether the diversification events that occur after the WGD events are significantly
376 close to the WGD to warrant suggestion of an association (e.g., dup: 7, dup: 10, dup: 8). More
377 description of a model that would generate a null expectation would be necessary to determine
378 what is "close enough" (see discussion below).
379 Many of the other inferred lineage diversification rate shifts are associated with very
380 recent, rapid radiations within genera such as those documented within *Commicarpus*
381 (Nyctaginaceae), *Dianthus* (Caryophyllaceae), *Cerastium* (Caryophyllaceae), *Arenaria*
382 (Caryophyllaceae), and *Salicornia* (Amaranthaceae), to name a few (Table 4). Although
383 polyploids were reported in these clades, we were unable to pinpoint the phylogenetic location of
384 any WGD with our current taxon sampling (e.g., *Dianthus*; Carolin, 1954; Weiss *et al.* 2002).
385 Increased sampling of transcriptomes and genomes will shed more light in these areas. While we
386 only find a few WGDs that coincide well with diversification rate shifts, it is important to note
387 that the uncertainty in the phylogenies makes it difficult to map anything but the strongest
388 diversification signals. This discrepancy can be seen in the difference between the number of
389 events supported by the ML analyses and those supported by the bootstrap analyses. It is possible
390 that additional sequence data will improve phylogenetic resolution and confidence, and that
391 consequently additional diversification events will emerge.
392 Equally interesting to the few WGD events associated directly with diversification are the
393 WGD events associated with general shifts in climate tolerance. WGDs in the Polygonaceae,
394 Caryophyllaceae, Montiaceae, and the Tribe Nyctagineae appear to be associated with movement
395 into colder environments (Figs. 1-2 and Figs. S2-S3). Species arising after the WGD within the
396 Amaranthaceae occupy wetter environments than the sister clade. The WGDs within the
397 carnivorous plants were also associated with shifts in environment as Nepenthaceae are found in
398 very wet environments and the Droseraceae are found in somewhat drier environments, at least
399 comparatively. However, in these cases, perhaps the development of the wide array of
400 morphologies associated with carnivory, apart from *Drosophyllum*, is more obviously associated
401 with the WGD (Walker *et al.*, 2017).

402 While these qualitative assessments suggest potential correlations of shift in the climate
403 occupied and WGDs, more specific and direct comparisons are necessary to quantify the extent
404 of the shifts. For many of the clades experiencing WGD, a direct comparison with a sister clade
405 is difficult because the sister may consist of a single species, another clade with WGD, or
406 another complication. For example, there are WGDs at the base of both Polygonaceae and
407 Plumbaginaceae as well as Nepenthaceae and Droseraceae. However, we made direct
408 comparison of five duplicated lineages (see Fig. 3) in both means (i.e., character contrasts
409 between sister clades) and variances (rate of Brownian motion) of climatic variables. In each
410 case, the duplicated lineage occupied a colder mean annual temperature. This was also the case
411 with the nested WGDs of Portulacineae and the Tribe Nyctagineae. Of course, we are not
412 suggesting that all WGDs are associated with a shift to a colder climate. While such a pattern
413 may exist in some groups such as Caryophyllaceae, we emphasize the observation that there is a
414 shift in the climate occupied rather than the direction of the shift. Mean annual precipitation is
415 not as clear with some clades occupying a higher precipitation and some occupying lower
416 precipitation. Perhaps the best summary of climatic niche is the principal components of all the
417 climatic variables. Here, while the shift in units is less easily interpreted, duplicated clades
418 occupied different niches than sister lineages. This supports the hypothesis that WGD events are
419 associated with adaptations. Here, many of these adaptations are associated with shifts in
420 climatic niches. This necessitates further examination in other angiosperm clades to investigate
421 how general these results are.
422 The rates of niche evolution show more complicated patterns. While some clades, such as
423 the Portulacineae, showed significant increase in a rate of niche evolution as compared to the
424 sister clade (e.g., MAT), no clear pattern emerged across all comparisons. There were other
425 shifts in rate such as with MAT and MAP in the Nyctaginaceae and Montiaceae, but these were
426 not as strong as the pattern of climate occupancy itself discussed above.
427 With each of these patterns presented here, it is important to consider them in the context
428 of uncertainty, both inherent in the biological processes that generate the phylogeny and in the
429 analyses associated with large scale datasets. These large phylogenies and datasets allow for
430 more thorough examination of the clades, but uncertainty makes precise mapping of weaker
431 signals difficult. As mentioned above, both the mapping of diversification events and
432 duplications demonstrate this. Furthermore, the comparisons of the sister clades for climatic

433 niche analyses assumes accurate identification of sister lineages. Increasing taxon sampling may
434 help, but additional sequence data and specimen data for phylogenetic analyses, WGD mapping
435 analyses, and climate niche characterization will surely improve our precision in these
436 investigations.
437 What emerges from these analyses of WGD, diversification, and climate occupancy? It
438 would appear as though, perhaps not unexpectedly, the patterns are complex and mixed. Some
439 WGD are associated directly with diversification events, some WGD are associated with shifts in
440 climate tolerance, some WGD are coincident with shifts in rates of niche evolution, and still
441 other WGD are associated with known adaptations (carnivory, habit shifts associated with
442 montane habitats, etc.). Some diversification shifts follow WGD events. However, it is unclear
443 whether these events are linked or correlated and, if so, if they are correlated more with
444 diversification than an additional adaptation or other evolutionary pattern or process. As data
445 increase in these groups and as confidence increases in the phylogenetic relationships as well as
446 the placement of both diversification and WGD events, we will be able to better address these
447 questions. However, at least for the Caryophyllales, it does not appear as though diversification
448 is tightly linked with WGD. Instead, for the clades that can be tested, we find shifts in climate
449 occupancy correspond well to WGD.
450
451 ***Suggestions for moving forward.*** —WGD are almost certainly one of the dominant processes
452 that contribute to major evolutionary events within plant lineages. This may be in the form of
453 increased diversification, development of novel traits, adaptation to new environments, and many
454 other events (e.g., Schubert and Vu, 2016; Clavijo *et al.* 2017). However, for several reasons,
455 these events (i.e., WGD and other evolutionary events) may not occur simultaneously. In fact,
456 there may be little to no expectation for the events to occur simultaneously (e.g., Donoghue,
457 2005; Schranz *et al.* 2012; Donoghue & Sanderson, 2015; Tank *et al.*, 2015; Dodsworth *et al.*
458 2016). In any case, more precise expectations and null models need to be developed to allow for
459 reasonable tests of the correlations among these events. For example, there may be shifts in
460 diversification that follow a WGD, but is it close enough, or frequent enough to infer that the two
461 events are related? Is correlation possible or identifiable if, as is expected, intervening lineages
462 have gone extinct? These questions would benefit from simulation studies where the true
463 correlation pattern is known. Furthermore, more precise connections should be made to the

464 biology of speciation and genome WGDs to better determine why, specifically, WGDs would be
465 expected to correspond with any diversification pattern instead of adaptations, which may or may
466 not correspond with increases or decreases in speciation. While still challenging, investigating
467 the fate of and patterns of selection within individual genes (e.g., subfunctionalization and
468 neofunctionalization) may shed light into the genomic basis of post-WGD and possibly allow for
469 more concrete expectations for diversification. With the availability of genomes and
470 transcriptomes, this is now beginning to become a possibility (e.g., Brockington *et al.*, 2015,
471 Walker *et al.*, 2017). Only when these suggestions are linked to more specific biological
472 hypotheses will we be able to better understand the ultimate impact of WGD in plant evolution.
473

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487 **Author contributions**

488 S.A.S., J.F.W., Y.Y., M.J.M., and S.F.B. designed research. C.P.D, R. B., N.L., and N.A.D.
489 collected data. S.A.S., J.W.B., and Y.Y. analyzed the data. S.A.S. led the writing. All authors
490 read and contributed to the manuscript.
491

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688

689 **Tables**

690 **Table 1** Voucher information and GenBank accession numbers for newly reported plastid *matK*
691 sequences. Families follow APG IV (Angiosperm Phylogeny Group, 2016).

Family	Taxon	Voucher specimen (Herbarium acronym)	Collection locality	NCBI accession number
Achatocarpaceae	*Achatocarpus gracilis* H.Walter	Silvia H. Salas Morales et al. 5608 (TEX)	Mexico: Oaxaca	KY952292
Achatocarpaceae	*Phaulothamnus spinescens* A.Gray	Michael J. Moore et al. 976 (OC)	United States: Texas	KY952477
Achatocarpaceae	*Phaulothamnus spinescens* A.Gray	William R. Carr 27176 (TEX)	United States: Texas	KY952478
Amaranthaceae	*Allenrolfea occidentalis* (S.Watson) Kuntze	Michael J. Moore 474 (OC)	United States: Texas	KY952314
Amaranthaceae	*Alternanthera caracasana* Kunth	Michael J. Moore 1808 (OC)	United States: Texas	KY952319
Amaranthaceae	*Amaranthus cruentus* L.	Michael J. Moore 356 (OC)	United States: Ohio (cultivated)	KY952320
Amaranthaceae	*Amaranthus* sp.	Michael J. Moore 1801 (OC)	United States: Texas	KY952321
Amaranthaceae	*Amaranthus* sp.	Michael J. Moore 2186 (OC)	United States: Ohio	KY952322
Amaranthaceae	*Amaranthus* sp.	Michael J. Moore 2187 (OC)	United States: Illinois	KY952323
Amaranthaceae	*Atriplex prosopidum* I.M.Johnst.	Hilda Flores Olvera et al. 1658 (MEXU)	Mexico: Coahuila	KY952340
Amaranthaceae	*Atriplex* sp.	Michael J. Moore 1689 (OC)	United States: Texas	KY952338
Amaranthaceae	*Atriplex* sp.	Michael J. Moore 1699 (OC)	United States: Texas	KY952339
Amaranthaceae	*Celosia argentea* L. var. *plumosa*	Michael J. Moore 359 (OC)	United States: Ohio (cultivated)	KY952359
Amaranthaceae	*Charpentiera ovata* Gaudich. var. *ovata*	Flora K. Samis 7 (Lyon Arboretum living collection, accession 2011.0034)	United States: Hawaii	KY952360
Amaranthaceae	*Charpentiera tomentosa* Sohmer var. *maakuaensis* Sohmer	Flora K. Samis 6 (Lyon Arboretum living collection, accession 88.0141)	United States: Hawaii	KY952361
Amaranthaceae	*Chenopodium album* L.	Michael J. Moore 344 (OC)	United States: Ohio	KY952362
Amaranthaceae	*Gossypianthus lanuginosus* (Poir.) Moq.	Michael J. Moore 1807 (OC)	United States: Texas	KY952408
Amaranthaceae	*Guilleminea densa*	Michael J. Moore et	Mexico:	KY952412

	(Humb. & Bonpl. ex Schult.) Moq.	al. 2445 (OC)	Chihuahua	
Amaranthaceae	*Kali tragus* (L.) Scop.	Michael J. Moore 453 (OC)	United States: Texas	KY952506
Amaranthaceae	*Nototrichium divaricatum* D.H.Lorence	Flora K. Samis 3 (Lyon Arboretum living collection, accession 96.0036 #3)	United States: Hawaii	KY952468
Amaranthaceae	*Nototrichium humile* Hillebr.	Flora K. Samis 2 (Lyon Arboretum living collection, accession 2001-0254)	United States: Hawaii	KY952469
Amaranthaceae	*Suaeda jacoensis* I.M.Johnst.	Hilda Flores Olvera et al. 1662 (MEXU)	Mexico: Coahuila	KY952514
Amaranthaceae	*Suaeda jacoensis* I.M.Johnst.	Michael J. Moore et al. 2617 (OC)	Mexico: Nuevo Leon	KY952515
Amaranthaceae	*Suaeda mexicana* (Standl.) Standl.	Hilda Flores Olvera et al. 1654 (MEXU)	Mexico: Coahuila	KY952516
Amaranthaceae	*Tidestromia lanuginosa* (Nutt.) Standl.	Michael J. Moore 1128 (OC)	United States: Texas	KY952521
Amaranthaceae	*Zuckia brandegeei* (A.Gray) S.L.Welsh & Stutz var. *plummeri* (Stutz & S.C.Sand.) Dorn	Joseph L. M. Charboneau 9672 (RM)	United States: Colorado	KY952528
Cactaceae	*Leuenbergeria quisqueyana* (Alain) Lodé	Flora K. Samis 11 (Lyon Arboretum living collection, accession 2000.0281)	United States: Hawaii	KY952473
Caryophyllaceae	*Moehringia macrophylla* (Hook.) Fenzl	Arianna Goodman 1 (OC)	United States: Oregon	KY952464
Caryophyllaceae	*Paronychia lundellorum* Torr. & A.Gray	William R. Carr 17607 (MEXU)	United States: Texas	KY952472
Caryophyllaceae	*Saponaria officinalis* L.	Michael J. Moore et al. 1819 (OC)	United States: Indiana	KY952507
Caryophyllaceae	*Schiedea kaalae* Wawra	Flora K. Samis 5 (Lyon Arboretum living collection, accession 92.0513)	United States: Hawaii	KY952509
Caryophyllaceae	*Spergularia salina* J.Presl & C.Presl	Michael J. Moore 1693 (OC)	United States: Texas	KY952512
Didiereaceae	*Alluaudia ascendens* (Drake) Drake	Michael J. Moore 1645	United States (cultivated)	KY952318
Dioncophyllaceae	*Triphyophyllum peltatum* (Hutch. & Dalziel) Airy Shaw	Carel C. H. Jongkind et al. 7136 (WAG)	Liberia	KY952524
Droseraceae	*Drosera burmannii* Vahl cv. Pilliga Red	Michael J. Moore 1814 (OC)	United States (cultivated)	KY952400
Droseraceae	*Drosera peltata* Thunb.	Michael J. Moore	Australia:	KY952401

		1817 (OC)	Tasmania (cultivated)	
Droseraceae	*Drosera regia* Stephens	Michael J. Moore 1812 (OC)	United States (cultivated)	KY952402
Drosophyllaceae	*Drosophyllum lusitanicum* (L.) Link	Michael J. Moore 1816 (OC)	United States (cultivated)	KY952403
Frankeniaceae	*Frankenia gypsophila* I.M.Johnst.	Michael J. Moore et al. 1880 (OC)	Mexico: Nuevo Leon	KY952406
Microteaceae	*Microtea debilis* Sw.	Manuel Rimachi 11128 (TEX)	Peru: Loreto	KY952415
Montiaceae	*Claytonia sibirica* L.	Arianna Goodman 2 (OC)	United States: Oregon	KY952363
Montiaceae	*Phemeranthus parviflorus* (Nutt.) Kiger	Michael J. Moore et al. 2214 (OC)	United States: New Mexico	KY952479
Nyctaginaceae	*Abronia angustifolia* Greene	Michael J. Moore et al. 2063 (OC)	Mexico: Coahuila	KY952281
Nyctaginaceae	*Abronia angustifolia* Greene	Michael J. Moore et al. 896 (OC)	United States: New Mexico	KY952282
Nyctaginaceae	*Abronia bigelovii* Heimerl	Michael J. Moore et al. 704 (OC)	United States: New Mexico	KY952283
Nyctaginaceae	*Abronia elliptica* A.Nelson	Norman A. Douglas 2039 (DUKE)	United States: Arizona	KY952284
Nyctaginaceae	*Abronia fragrans* Nutt. ex Hook.	Billie L. Turner 20-22 (SRSC)	United States: Texas	KY952285
Nyctaginaceae	*Abronia fragrans* Nutt. ex Hook.	Glenn Kroh et al. 3021 (TEX)	United States: Texas	KY952286
Nyctaginaceae	*Abronia macrocarpa* L.A.Galloway	Steve L. Orzell et al. 6492 (TEX)	United States: Texas	KY952287
Nyctaginaceae	*Abronia mellifera* Douglas ex Hook.	N. Elizabeth Saunders BP 19 (SIU)	United States: Wyoming	KY952288
Nyctaginaceae	*Abronia mellifera* Douglas ex Hook.	N. Elizabeth Saunders BP 20 (SIU)	United States: Wyoming	KY952289
Nyctaginaceae	*Abronia nana* S.Watson var. *nana*	Robert C. Sivinski et al. 3108 (NMC)	United States: Arizona	KY952290
Nyctaginaceae	*Abronia umbellata* Lam.	N. Elizabeth Saunders LU 45 (SIU)	United States: California	KY952291
Nyctaginaceae	*Acleisanthes acutifolia* Standl.	James Henrickson et al. 22916 (TEX)	Mexico: Coahuila	KY952293
Nyctaginaceae	*Acleisanthes angustifolia* (Torr.) R.A.Levin	Michael J. Moore 460 (OC)	United States: Texas	KY952294
Nyctaginaceae	*Acleisanthes* cf. *purpusiana* (Heimerl) R.A.Levin	James Henrickson 23026 (TEX)	Mexico: Coahuila	KY952309
Nyctaginaceae	*Acleisanthes chenopodioides* (A.Gray) R.A.Levin	Michael J. Moore et al. 733 (OC)	United States: Texas	KY952295

Nyctaginaceae	*Acleisanthes crassifolia* A.Gray	Michael J. Moore et al. 569 (OC)	United States: Texas	KY952296
Nyctaginaceae	*Acleisanthes diffusa* (A.Gray) R.A.Levin var. *diffusa*	Michael J. Moore et al. 624 (OC)	United States: Texas	KY952297
Nyctaginaceae	*Acleisanthes lanceolata* (Wooton) R.A.Levin var. *lanceolata*	Michael J. Moore et al. 870 (OC)	United States: New Mexico	KY952298
Nyctaginaceae	*Acleisanthes lanceolata* (Wooton) R.A.Levin var. *lanceolata*	Michael J. Moore et al. 903 (OC)	United States: Texas	KY952299
Nyctaginaceae	*Acleisanthes lanceolata* (Wooton) R.A.Levin var. *megaphylla* (B.A.Fowler & B.L.Turner) Spellenb. & J.Poole	Alfred T. Richardson 1666 (TEX)	Mexico: Chihuahua	KY952300
Nyctaginaceae	*Acleisanthes longiflora* A.Gray	Michael J. Moore 435 (OC)	United States: Texas	KY952301
Nyctaginaceae	*Acleisanthes longiflora* A.Gray	Michael J. Moore et al. 571 (OC)	United States: Texas	KY952302
Nyctaginaceae	*Acleisanthes nana* I.M.Johnst.	Jackie Smith et al. 798 (TEX)	Mexico: San Luis Potosi	KY952303
Nyctaginaceae	*Acleisanthes obtusa* (Choisy) Standl.	Michael J. Moore et al. 984 (OC)	United States: Texas	KY952304
Nyctaginaceae	*Acleisanthes palmeri* (Hemsley) R.A.Levin	George S. Hinton 28620 (TEX)	MexicoNuevo Leon	KY952305
Nyctaginaceae	*Acleisanthes parvifolia* (Torr.) R.A.Levin	Michael J. Moore 452 (OC)	United States: Texas	KY952306
Nyctaginaceae	*Acleisanthes purpusiana* (Heimerl) R.A.Levin	James Henrickson 22709 (TEX)	Mexico: Coahuila	KY952307
Nyctaginaceae	*Acleisanthes purpusiana* (Heimerl) R.A.Levin	Billie L. Turner 6205 (TEX)	Mexico: Coahuila	KY952308
Nyctaginaceae	*Acleisanthes undulata* (B.A.Fowler & B.L.Turner) R.A.Levin	James Henrickson 23195 (TEX)	Mexico: Coahuila	KY952310
Nyctaginaceae	*Acleisanthes wrightii* (A.Gray) Benth. & Hook.	Michael J. Moore et al. 620 (OC)	United States: Texas	KY952311
Nyctaginaceae	*Allionia choisyi* Standl.	Norman A. Douglas 2187 (DUKE)	Mexico: Coahuila	KY952315
Nyctaginaceae	*Allionia incarnata* L.	Michael J. Moore et al. 1352 (OC)	Mexico: Nuevo Leon	KY952316
Nyctaginaceae	*Allionia* sp.	Michael J. Moore 424 (OC)	United States: Texas	KY952317
Nyctaginaceae	*Andradea floribunda* Allemão	André M. Amorim 2294 (NY)	Brazil	KY952324
Nyctaginaceae	*Andradea floribunda* Allemão	Jacquelyn Ann Kallunki 701 (NY)	Brazil	KY952325
Nyctaginaceae	*Anulocaulis annulatus*	Richard W.	United States:	KY952326

	(Coville) Standl.	Spellenberg 3162 (NMC)	California	
Nyctaginaceae	*Anulocaulis eriosolenus* (A.Gray) Standl.	James Henrickson et al. 23103 (TEX)	Mexico: Coahuila	KY952327
Nyctaginaceae	*Anulocaulis eriosolenus* (A.Gray) Standl.	Michael J. Moore et al. 611 (OC)	United States: Texas	KY952328
Nyctaginaceae	*Anulocaulis hintoniorum* B.L.Turner	Patricia Hernández Ledesma 52 (MEXU)	Mexico: Coahuila	KY952329
Nyctaginaceae	*Anulocaulis leiosolenus* (Torr.) Standl. var. *gypsogenus* (Waterf.) Spellenb. & T.Wootten	Michael J. Moore 402 (OC)	United States: New Mexico	KY952330
Nyctaginaceae	*Anulocaulis leiosolenus* (Torr.) Standl. var. *howardii* Spellenb. & T.Wootten	Thomas Wootten et al. s.n. (NMC)	United States: New Mexico	KY952331
Nyctaginaceae	*Anulocaulis leiosolenus* (Torr.) Standl. var. *lasianthus* I.M.Johnston	Michael J. Moore et al. 610 (OC)	United States: Texas	KY952332
Nyctaginaceae	*Anulocaulis leiosolenus* (Torr.) Standl. var. *leiosolenus*	Michael J. Moore 493 (OC)	United States: Texas	KY952333
Nyctaginaceae	*Anulocaulis leiosolenus* (Torr.) Standl. var. *leiosolenus*	Michael J. Moore et al. 825 (OC)	United States: Nevada	KY952334
Nyctaginaceae	*Anulocaulis leiosolenus* (Torr.) Standl. var. *leiosolenus*	Michael J. Moore et al. 853 (OC)	United States: Arizona	KY952335
Nyctaginaceae	*Anulocaulis reflexus* I.M.Johnst.	Michael J. Moore et al. 242 (TEX)	Mexico: Chihuahua	KY952336
Nyctaginaceae	*Anulocaulis reflexus* I.M.Johnst.	Michael J. Moore 483 (OC)	United States: Texas	KY952337
Nyctaginaceae	*Boerhavia anisophylla* Torr.	Norman A. Douglas 2194 (DUKE)	Mexico: Durango	KY952341
Nyctaginaceae	*Boerhavia ciliata* Brandegee	Norman A. Douglas 2145 (DUKE)	United States: Texas	KY952342
Nyctaginaceae	*Boerhavia coccinea* Mill.	Michael J. Moore 366 (OC)	United States: New Mexico	KY952343
Nyctaginaceae	*Boerhavia coulteri* (Hook.f.) S.Watson var. *palmeri* (S.Watson) Spellenb.	Richard W. Spellenberg 13273 (NMC)	United States: Arizona	KY952344
Nyctaginaceae	*Boerhavia dominii* Meikle & Hewson	H. Smyth 42 (NY)	Australia: South Australia	KY952345
Nyctaginaceae	*Boerhavia gracillima* Heimerl	Richard W. Spellenberg 12447 (NMC)	United States: Texas	KY952347
Nyctaginaceae	*Boerhavia intermedia* M.E.Jones	Richard W. Spellenberg 13279	United States: Arizona	KY952348

		(NMC)		
Nyctaginaceae	*Boerhavia lateriflora* Standl.	Norman A. Douglas 2161 (DUKE)	Mexico: Sonora	KY952349
Nyctaginaceae	*Boerhavia linearifolia* A.Gray	Michael J. Moore et al. 581 (OC)	United States: Texas	KY952350
Nyctaginaceae	*Boerhavia purpurascens* A.Gray	Richard W. Spellenberg 13261 (NMC)	United States: Arizona	KY952351
Nyctaginaceae	*Boerhavia repens* L.	J. S. Rose 2	United States: Hawaii	KY952352
Nyctaginaceae	*Boerhavia repens* L.	Richard W. Spellenberg 7183 (NMC)	Yemen: Sana	KY952353
Nyctaginaceae	*Boerhavia* sp.	Erin Tripp et al. 4090 (OC)	Namibia	KY952346
Nyctaginaceae	*Boerhavia torreyana* (S.Watson) Standl.	Michael J. Moore et al. 633 (OC)	United States: Texas	KY952354
Nyctaginaceae	*Bougainvillea campanulata* Heimerl	Michael Nee 51257 (TEX)	Bolivia: Santa Cruz	KY952355
Nyctaginaceae	*Bougainvillea glabra* Choisy	Michael J. Moore 538 (OC)	United States: Ohio (cultivated)	KY952356
Nyctaginaceae	*Bougainvillea spinosa* (Cav.) Heimerl	J. Saunders et al. 3371 (TEX)	Argentina: San Juan	KY952357
Nyctaginaceae	*Bougainvillea stipitata* Griseb.	Michael Nee 50723 (TEX)	Bolivia: Santa Cruz	KY952358
Nyctaginaceae	*Colignonia glomerata* Griseb.	Michael Nee 52523 (NY)	Bolivia	KY952364
Nyctaginaceae	*Colignonia scandens* Benth.	Martin Grantham 63 (SFBG living collection, accession 1996-0202)	Ecuador	KY952365
Nyctaginaceae	*Commicarpus ambiguus* Meikle	Mats Thulin 11015 (UPS)	Somalia: Sanaag	KY952366
Nyctaginaceae	*Commicarpus arabicus* Meikle	Mats Thulin et al. 9294 (UPS)	Yemen: Taizz	KY952367
Nyctaginaceae	*Commicarpus arabicus* Meikle	Richard W. Spellenberg 7217 (NMC)	Yemen: Ibb	KY952368
Nyctaginaceae	*Commicarpus arabicus* Meikle	Richard W. Spellenberg 7297 (NMC)	Yemen: Ibb	KY952369
Nyctaginaceae	*Commicarpus australis* (Meikle) Govaerts	Richard W. Spellenberg et al. 9469 (NMC)	Australia: Western Australia	KY952370
Nyctaginaceae	*Commicarpus boissieri* (Heimerl) Cufod.	Mats Thulin 11423 (UPS)	Oman: Dhofar	KY952371
Nyctaginaceae	*Commicarpus boissieri* (Heimerl) Cufod.	Carl J. Rothfels et al. 4331	Oman: Ash Sharqiyah	KY952373
Nyctaginaceae	*Commicarpus*	Patricia Hernández	Mexico: Baja	KY952372

	brandegeei Standl.	Ledesma 55 (MEXU)	California Sur	
Nyctaginaceae	*Commicarpus coctoris* N.A.Harriman	Richard W. Spellenberg et al. 12883 (NMC)	Mexico: Oaxaca	KY952374
Nyctaginaceae	*Commicarpus commersonii* (Baill.) Cavaco	Mats Thulin et al. 11836 (UPS)	Madagascar: Toliara	KY952380
Nyctaginaceae	*Commicarpus decipiens* Meikle	Erin Tripp et al. 4127 (NMC)	Namibia	KY952375
Nyctaginaceae	*Commicarpus grandiflorus* (A.Rich.) Standl.	Mats Thulin et al. 9311 (UPS)	Yemen: Taizz	KY952376
Nyctaginaceae	*Commicarpus greenwayi* Meikle	Mats Thulin 606 (UPS)	Tanzania: Iringa	KY952377
Nyctaginaceae	*Commicarpus helenae* (Roem. & Schult.) Meikle	Richard W. Spellenberg et al. 7504 (NMC)	Yemen: Dhamar	KY952378
Nyctaginaceae	*Commicarpus hiranensis* Thulin	Mats Thulin et al. 11225 (UPS)	Ethiopia: Harerge	KY952379
Nyctaginaceae	*Commicarpus mistus* Thulin	Mats Thulin et al. 9786 (UPS)	Yemen: Mahrah	KY952381
Nyctaginaceae	*Commicarpus parviflorus* Thulin	Mats Thulin 6318 (UPS)	Somalia: Banaadir	KY952382
Nyctaginaceae	*Commicarpus pedunculosus* (A.Rich.) Cufod.	Mats Thulin 1301 (UPS)	Ethiopia: Arussi	KY952383
Nyctaginaceae	*Commicarpus plumbagineus* (Cav.) Standl.	Mats Thulin 10747 (UPS)	Somalia: Togdheer	KY952384
Nyctaginaceae	*Commicarpus plumbagineus* (Cav.) Standl.	Mats Thulin et al. 11330 (UPS)	Ethiopia: Harerge	KY952385
Nyctaginaceae	*Commicarpus plumbagineus* (Cav.) Standl.	Richard W. Spellenberg et al. 7374 (NMC)	Yemen: Ta'izz	KY952386
Nyctaginaceae	*Commicarpus praetermissus* N.A.Harriman	Richard W. Spellenberg et al. 12905 (NMC)	Mexico: Michoacán	KY952387
Nyctaginaceae	*Commicarpus reniformis* (Chiov.) Cufod.	Mats Thulin 4200 (UPS)	Somalia: Sool	KY952388
Nyctaginaceae	*Commicarpus reniformis* (Chiov.) Cufod.	Mats Thulin et al. 8337 (UPS)	Yemen: Hadramaut	KY952389
Nyctaginaceae	*Commicarpus scandens* (L.) Standl.	Michael J. Moore 1127 (OC)	United States: Texas	KY952390
Nyctaginaceae	*Commicarpus scandens* (L.) Standl.	Richard W. Spellenberg et al. 12887 (NMC)	Mexico: Puebla	KY952391
Nyctaginaceae	*Commicarpus sinuatus* Meikle	Mats Thulin 10737 (UPS)	Somalia: Woqooyi Galbeed	KY952392

Nyctaginaceae	*Commicarpus sinuatus* Meikle	Richard W. Spellenberg 7144 (NMC)	Yemen: Sana'a	KY952393
Nyctaginaceae	*Commicarpus sinuatus* Meikle	Richard W. Spellenberg 7506 (NMC)	Yemen: Dhamar	KY952394
Nyctaginaceae	*Commicarpus squarrosus* (Heimerl) Standl. var. *squarrosus*	Erin Tripp et al. 4049 (NMC)	Namibia	KY952395
Nyctaginaceae	*Commicarpus stenocarpus* (Chiov.) Cufod.	Mats Thulin et al. 8062 (UPS)	Yemen: Hadramaut	KY952396
Nyctaginaceae	*Cuscatlania vulcanicola* Standl.	José L. Linares 12938 (MEXU)	El Salvador: Sonsonate	KY952397
Nyctaginaceae	*Cuscatlania vulcanicola* Standl.	José L. Linares 13440 (MEXU)	El Salvador: Sonsonate	KY952398
Nyctaginaceae	*Cyphomeris gypsophiloides* (M.Martens & Galeotti) Standl.	Michael J. Moore et al. 582 (OC)	United States: Texas	KY952399
Nyctaginaceae	*Grajalesia fasciculata* (Standl.) Miranda	José L. Linares 13416 (MEXU)	El Salvador: Sonsonate	KY952409
Nyctaginaceae	*Guapira discolor* (Spreng.) Little	Richard W. Spellenberg 13294 (NMC)	United States: Florida	KY952410
Nyctaginaceae	*Guapira eggersiana* (Heimerl) Lundell	Scott A. Mori 25542/40 (NY)	French Guiana	KY952411
Nyctaginaceae	*Mirabilis albida* (Walter) Heimerl	Norman A. Douglas 2035 (DUKE)	United States: Arizona	KY952416
Nyctaginaceae	*Mirabilis albida* (Walter) Heimerl	William R. Carr 11075 (TEX)	United States: Texas	KY952417
Nyctaginaceae	*Mirabilis alipes* (S.Watson) Pilz	Arnold Tiehm 13461 (TEX)	United States: Nevada	KY952418
Nyctaginaceae	*Mirabilis bigelovii* A.Gray var. *retrorsa* (A. Heller) Munz	James D. Morefield et al. 3780 (TEX)	United States: California	KY952419
Nyctaginaceae	*Mirabilis* cf. *glabrifolia* (Ortega) I.M.Johnst.	Michael J. Moore et al. 1244 (OC)	Mexico: San Luis Potosi	KY952428
Nyctaginaceae	*Mirabilis* cf. *nesomii* B.L.Turner	George S. Hinton 25567 (TEX)	Mexico: Nuevo Leon	KY952449
Nyctaginaceae	*Mirabilis coccinea* (Torr.) Benth. & Hook.f.	Norman A. Douglas 2133 (DUKE)	United States: Arizona	KY952420
Nyctaginaceae	*Mirabilis coccinea* (Torr.) Benth. & Hook.f.	Steven P. McLaughlin et al. 9354 (ARIZ)	United States: Arizona	KY952421
Nyctaginaceae	*Mirabilis comata* (Small) Standl.	Norman A. Douglas 2084 (DUKE)	United States: Arizona	KY952422
Nyctaginaceae	*Mirabilis decumbens* (Nutt.) Daniels	Richard W. Spellenberg et al. 4073 (TEX)	Mexico: Zacatecas	KY952423

Nyctaginaceae	*Mirabilis donahooiana* Le Duc	Alice Le Duc et al. 247 (TEX)	Mexico: Michoacán	KY952424
Nyctaginaceae	*Mirabilis exserta* Brandegee	Pedro Tenorio 10586 (MEXU)	Mexico	KY952425
Nyctaginaceae	*Mirabilis gigantea* (Standl.) Shinners	J. Quayle et al. 752 (TEX)	United States: Texas	KY952426
Nyctaginaceae	*Mirabilis glabra* (S.Watson) Standl.	Michael J. Moore et al. 674 (OC)	United States: New Mexico	KY952446
Nyctaginaceae	*Mirabilis glabrifolia* (Ortega) I.M.Johnst.	Guy Nesom et al. 7654 (TEX)	Mexico: Coahuila	KY952427
Nyctaginaceae	*Mirabilis glabrifolia* (Ortega) I.M.Johnst.	Michael J. Moore et al. 1325 (OC)	Mexico: Nuevo Leon	KY952429
Nyctaginaceae	*Mirabilis gracilis* (Standl.) LeDuc	Alice Le Duc et al. 71 (TEX)	Mexico: Jalisco	KY952430
Nyctaginaceae	*Mirabilis grandiflora* (Standl.) Standl.	EDL 1863 (MEXU)	Mexico	KY952431
Nyctaginaceae	*Mirabilis greenei* S.Watson	George E. Pilz 998 (TEX)	United States: California	KY952432
Nyctaginaceae	*Mirabilis himalaica* (Edgew.) Heimerl var. *chinensis* Heimerl	D. E. Boufford et al. 32449 (F)	China: Xizang (Tibet)	KY952433
Nyctaginaceae	*Mirabilis himalaica* (Edgew.) Heimerl var. *chinensis* Heimerl	D. E. Boufford et al. 41198 (F)	China: Xizang (Tibet)	KY952434
Nyctaginaceae	*Mirabilis himalaica* (Edgew.) Heimerl var. *chinensis* Heimerl	D. E. Boufford et al. 41435 (F)	China: Xizang (Tibet)	KY952435
Nyctaginaceae	*Mirabilis hintoniorum* Le Duc	Patricia Hernández Ledesma 118 (MEXU)	Mexico: Michoacán	KY952436
Nyctaginaceae	*Mirabilis jalapa* L.	Michael J. Moore s.n.	United States (cultivated)	KY952437
Nyctaginaceae	*Mirabilis laevis* (Benth.) Curran	Andrew C. Sanders et al. 29410 (TEX)	United States: California	KY952438
Nyctaginaceae	*Mirabilis latifolia* (A.Gray) Diggs, Lipscomb & O'Kennon	Victor L. Cory 24549 (GH)	United States: Texas	KY952439
Nyctaginaceae	*Mirabilis linearis* (Pursh) Heimerl	Billie L. Turner 21-854 (TEX)	United States: Texas	KY952440
Nyctaginaceae	*Mirabilis linearis* (Pursh) Heimerl var. *decipiens* (Standl.) S.L.Welsh	Michael J. Moore et al. 1984 (OC)	Mexico: Coahuila	KY952441
Nyctaginaceae	*Mirabilis longiflora* L.	Michael J. Moore et al. 1230 (OC)	Mexico: San Luis Potosi	KY952442
Nyctaginaceae	*Mirabilis longiflora* L. var. *wrightiana* (A.Gray ex Britton & Kearney) Kearney & Peebles	Alice Le Duc 185 (TEX)	United States: New Mexico	KY952443
Nyctaginaceae	*Mirabilis melanotricha*	Michael J. Moore et	Mexico: San	KY952444

	(Standl.) Spellenb.	al. 1191 (OC)	Luis Potosi	
Nyctaginaceae	*Mirabilis melanotricha* (Standl.) Spellenb.	Norman A. Douglas 2067 (DUKE)	United States: New Mexico	KY952445
Nyctaginaceae	*Mirabilis multiflora* (Torr.) A.Gray	Michael J. Moore 1110 (OC)	United States: Texas	KY952447
Nyctaginaceae	*Mirabilis multiflora* (Torr.) A.Gray	Norman A. Douglas 2037 (DUKE)	United States: Arizona	KY952448
Nyctaginaceae	*Mirabilis nesomii* B.L.Turner	Michael J. Moore et al. 2179 (NMC)	Mexico: Nuevo Leon	KY952450
Nyctaginaceae	*Mirabilis nesomii* B.L.Turner	Michael J. Moore et al. 2643 (NMC)	Mexico: Nuevo Leon	KY952451
Nyctaginaceae	*Mirabilis nyctaginea* (Michx.) MacMill.	William R. Carr 14590 (TEX)	United States: Texas	KY952452
Nyctaginaceae	*Mirabilis oligantha* (Standl.) Standl.	José L. Panero 2816 (MEXU)	Mexico: Baja California	KY952453
Nyctaginaceae	*Mirabilis oxybaphoides* (A.Gray) A.Gray	George S. Hinton 25572 (TEX)	Mexico: Nuevo Leon	KY952454
Nyctaginaceae	*Mirabilis polonii* Le Duc	Alice Le Duc 259 (MEXU)	Mexico: Nuevo Leon	KY952455
Nyctaginaceae	*Mirabilis pringlei* Weath.	Alice Le Duc et al. 63 (TEX)	Mexico: Jalisco	KY952456
Nyctaginaceae	*Mirabilis pudica* Barneby	Arnold Tiehm 10971 (TEX)	United States: Nevada	KY952457
Nyctaginaceae	*Mirabilis texensis* (J.M.Coult.) B.L.Turner	Billie L. Turner 22-417 (TEX)	United States: Texas	KY952458
Nyctaginaceae	*Mirabilis triflora* Benth.	Ramón Cuevas G. et al. 3415 (MEXU)	Mexico: Jalisco	KY952459
Nyctaginaceae	*Mirabilis urbani* Heimerl	Mark Fishbein et al. 5107 (MEXU)	Mexico: Michoacan	KY952460
Nyctaginaceae	*Mirabilis violacea* (L.) Heimerl	Patricia Hernández Ledesma 63 (MEXU)	Mexico: Distrito Federal	KY952461
Nyctaginaceae	*Mirabilis viscosa* Cav.	Michael J. Moore et al. 1824 (NMC)	Mexico: San Luis Potosi	KY952462
Nyctaginaceae	*Mirabilis viscosa* Cav.	Patricia Hernández Ledesma 13 (MEXU)	Mexico	KY952463
Nyctaginaceae	*Neea belizensis* Donn.Sm.	Cyrus L. Lundell 17692 (TEX)	Guatemala: Petén	KY952465
Nyctaginaceae	*Neea cauliflora* Poepp. & Endl.	Schanke S15106 (NY)	Peru	KY952466
Nyctaginaceae	*Neea psychotrioides* Donn.Sm.	Robert L. Wilbur 63654	Costa Rica: Heredia	KY952467
Nyctaginaceae	*Nyctaginia capitata* Choisy	Michael J. Moore et al. 617 (OC)	United States: Texas	KY952470
Nyctaginaceae	*Okenia hypogaea* Schltdl. & Cham.	Thomas R. Van Devender et al. 92-1069 (NMC)	Mexico: Sonora	KY952471
Nyctaginaceae	*Pisonia aculeata* L.	C. Martínez 1209 (TEX)	Mexico: Oaxaca	KY952483
Nyctaginaceae	*Pisonia brunoniana*	J. S. Rose 3	United States:	KY952484

	Endl.		Hawaii	
Nyctaginaceae	*Pisonia capitata* (S.Watson) Standl.	Ana L. Reina Guerrero et al. 2000-193 (NMC)	Mexico: Sonora	KY952485
Nyctaginaceae	*Pisonia capitata* (S.Watson) Standl.	Thomas R. Van Devender et al. 2003-17 (TEX)	United States: Arizona	KY952486
Nyctaginaceae	*Pisonia macranthocarpa* (Donn.Sm.) Donn.Sm.	Dennis E. Breedlove et al. 30361 (TEX)	Mexico: Chiapas	KY952487
Nyctaginaceae	*Pisonia sandwicensis* Hillebr.	Flora K. Samis 1 (Lyon Arboretum living collection)	United States: Hawaii	KY952488
Nyctaginaceae	*Pisonia sylvatica* Standl.	José L. Linares 13403 (MEXU)	El Salvador: Sonsonate	KY952489
Nyctaginaceae	*Pisonia umbellifera* (J.R.Forst. & G.Forst.) Seem.	Flora K. Samis 12 (Lyon Arboretum living collection, accession 68.0453)	United States: Hawaii	KY952490
Nyctaginaceae	*Pisonia zapallo* Griseb.	Israel G. Vargas et al. 2001 (TEX)	Bolivia: Santa Cruz	KY952491
Nyctaginaceae	*Pisoniella arborescens* (Lag. & Rodr.) Standl.	Alice Le Duc et al. 231 (NMC)	Mexico: Oaxaca	KY952492
Nyctaginaceae	*Pisoniella arborescens* (Lag. & Rodr.) Standl.	William R. Anderson 13522 (NY)	Mexico: Oaxaca	KY952493
Nyctaginaceae	*Ramisia brasiliensis* Oliv.	Jomar G. Jardim 1507 (NY)	Brazil	KY952495
Nyctaginaceae	*Reichenbachia hirsuta* Spreng.	Michael Nee 47813 (NY)	Bolivia	KY952496
Nyctaginaceae	*Reichenbachia paraguayensis* (D.Parodi) Dugand & Daniel	Maria Maguidaura Hatschbach 49218 (NY)	Brazil	KY952497
Nyctaginaceae	*Salpianthus arenarius* Bonpl.	Richard W. Spellenberg 12903 (NMC)	Mexico: Michoacán	KY952503
Nyctaginaceae	*Salpianthus macrodontus* Standl.	Thomas R. Van Devender et al. 91-894 (NMC)	Mexico: Sonora	KY952504
Nyctaginaceae	*Salpianthus purpurascens* (Cav. ex Lag.) Hook. & Arn.	Richard W. Spellenberg et al. 12885 (NMC)	Mexico: Oaxaca	KY952505
Nyctaginaceae	*Tripterocalyx carneus* (Greene) L.A.Galloway	Norman A. Douglas 2060 (DUKE)	United States: New Mexico	KY952525
Nyctaginaceae	*Tripterocalyx crux-maltae* (Kellogg) Standl.	Arnold Tiehm et al. 12213 (TEX)	United States: Nevada	KY952526
Nyctaginaceae	*Tripterocalyx micranthus* (Torr.) Hook.	B. MacLeod et al. 751 (TEX)	United States: Colorado	KY952527
Phytolaccaceae	*Agdestis clematidea* Moc. & Sessé ex DC.	George S. Hinton 25023 (TEX)	Mexico: Tamaulipas	KY952313

Phytolaccaceae	*Gallesia integrifolia* (Spreng.) Harms	Michael Nee et al. 50072 (TEX)	Bolivia: Santa Cruz	KY952407
Phytolaccaceae	*Hilleria latifolia* (Lam.) H.Walter	Michael Nee 33807 (TEX)	Bolivia: Santa Cruz	KY952413
Phytolaccaceae	*Petiveria alliacea* L.	Lucas C. Majure 4132 (FLAS)	United States: Florida	KY952476
Phytolaccaceae	*Phytolacca americana* L.	Michael J. Moore 342 (OC)	United States: Ohio	KY952480
Phytolaccaceae	*Phytolacca icosandra* L.	Mark H. Mayfield et al. 1001 (TEX)	Mexico: Guerrero	KY952481
Phytolaccaceae	*Phytolacca octandra* L.	Juan A. Encina et al. 1545 (TEX)	Mexico: Nuevo Leon	KY952482
Phytolaccaceae	*Rivina humilis* L.	Michael J. Moore 1129 (OC)	United States: Texas	KY952499
Phytolaccaceae	*Seguieria aculeata* Jacq.	Elsa Zardini et al. 22101 (TEX)	Paraguay	KY952510
Phytolaccaceae	*Seguieria paraguariensis* Morong	Michael Nee 48735 (TEX)	Bolivia: Santa Cruz	KY952511
Phytolaccaceae	*Trichostigma octandrum* (L.) H.Walter	Michael Nee 47094 (TEX)	Bolivia: Santa Cruz	KY952522
Phytolaccaceae	*Trichostigma peruvianum* (Moq.) H.Walter	Flora K. Samis 10 (Lyon Arboretum living collection, accession 94.0377)	United States: Hawaii	KY952523
Plumbaginaceae	*Aegialitis annulata* R.Br.	Christopher T. Martine 4043 (OC)	Australia: Western Australia	KY952312
Plumbaginaceae	*Limonium limbatum* Small	Michael J. Moore et al. 694 (OC)	United States: New Mexico	KY952414
Plumbaginaceae	*Plumbago scandens* L.	Michael J. Moore et al. 1828 (OC)	Mexico: San Luis Potosi	KY952494
Polygonaceae	*Eriogonum longifolium* Nutt. var. *longifolium*	Michael J. Moore 1796 (OC)	United States: Texas	KY952404
Polygonaceae	*Eriogonum rotundifolium* Benth.	Michael J. Moore 1769 (OC)	United States: New Mexico	KY952405
Polygonaceae	*Persicaria odorata* LaLlave	Flora K. Samis 9 (Lyon Arboretum living collection, accession 88.0439)	United States: Hawaii	KY952475
Polygonaceae	*Persicaria* sp.	Michael J. Moore 1177	United States: Ohio	KY952474
Polygonaceae	*Reynoutria japonica* (Houtt.) Ronse Decr.	Michael J. Moore 2188 (OC)	United States: Ohio	KY952498
Polygonaceae	*Rumex albescens* Hillebr.	Flora K. Samis 4 (Lyon Arboretum living collection, accession 2008-0119)	United States: Hawaii	KY952500
Polygonaceae	*Rumex* sp.	Michael J. Moore 1800 (OC)	United States: Texas	KY952501
Polygonaceae	*Rumex* sp.	Michael J. Moore	United States:	KY952502

		1805 (OC)	Texas	
Sarcobataceae	*Sarcobatus vermiculatus* (Hook.) Torr.	Michael J. Moore et al. 813 (OC)	United States: Utah	KY952508
Stegnospermataceae	*Stegnosperma cubense* A.Rich.	Silvia H. Salas Morales 2649 (NY)	Mexico: Oaxaca	KY952513
Talinaceae	*Talinum* cf. *aurantiacum* Engelm.	Michael J. Moore et al. 1985 (OC)	Mexico: Coahuila	KY952517
Talinaceae	*Talinum fruticosum* (L.) Juss.	Flora K. Samis 8 (Lyon Arboretum living collection, accession 2012.0008)	United States: Hawaii	KY952518
Talinaceae	*Talinum paniculatum* (Jacq.) Gaertn.	Michael J. Moore 1789 (OC)	United States (cultivated)	KY952520
Talinaceae	*Talinum* sp.	Michael J. Moore et al. 1974 (MEXU)	Mexico: Coahuila	KY952519

692

693 **Table 2** List of primers used to amplify the *matK* sequences newly reported here. Within each
694 primer name, the number indicates the approximate position of the primer in nucleotides
695 downstream from the start of *matK*.

696

Primer name	Sequence (5'→3')	Notes
matK.300F.Car	TTG CAG TCA TTG TGG AAA TTC C	works broadly across most of Caryophyllales, but generally fails in Caryophyllaceae and Frankeniaceae
matK.1350R.Car	GCC AAA GTT CTA GCA CAA GAA AG	works broadly across most of Caryophyllales
matK.210F.Car	TTC GGC TAA TGA TTC TCA CCA A	designed specifically for Caryophyllaceae
matK.1345R.Car	GAG CCA AAG TTC TAG CAC AAG AA	designed specifically for Caryophyllaceae
matK.1355R.Car	TGT GTT TAC GAG CTA AAG TTC TAG	designed specifically for Caryophyllaceae
matK.300F.Fra	TCG CTG TCT TTG CTG AAA TTC C	designed specifically for Frankeniaceae

697

698 **Table 3** Summary of WGD events at identified clades with distance to diversification shift and
699 climate occupancy information. Numbers correspond to those in Figs. 1 and 2.

#	**Putative WGD**	**Distance to diversification shift in nodes ML(BS)**	**Subtending species (sister)**	**Mean annual temp °C (sister)**	**Mean annual precip mm (sister)**
1	Tribe Nyctagineae within the Nyctaginaceae	0 (0)	123 (40)	17.49 (20.08)	482.9 (997.08)
2	Phytolaccoid clade	6 (6)	182 (407)	19.64 (18.36)	1007.58 (452.47)

3	*Claytonia*	NA	38 (15)	5.28 (7.25)	790.5 (970.36)
4	Portulacineae	1 (1)	1600 (38)	16.19 (19.35)	699.87 (736.42)
5	*Amaranthus*	0 (0)	28 (1)	16.27 (27.09)	797.74 (117.63)
6	Tribe Gomphrenoideae within Amaranthaceae	7 (7)	172 (41)	17.91 (16.65)	871.95 (1289.5)
7	in Caryophyllaceae (Alsinoideae + Caryophylloideae sensu Greenberg and Donoghue 2011)	9 (9)	793 (13)	11.44 (12.06)	761.43 (720.00)
8	Polygonaceae	13 (13)	670 (70)	16.3. (16.89)	1084.17 (794.28)
9	Plumbaginaceae	NA	70 (670)	16.89 (16.3)	794.28 (1084.17)
10	Droseraceae	8 (NA)	67 (108)	16.3 (19.08)	1280.57 (1491.72)
11	Nepenthaceae	4 (NA)	89 (19)	22.52 (20.05)	2170.5 (1611.63)
12	Ancistrocladaceae	0 (NA)	15 (3)	24.17 (25.6)	1899.13 (2882.4)
13	Tamaricaceae	NA	19 (3)	14.09 (16.21)	568.32 (469.61)

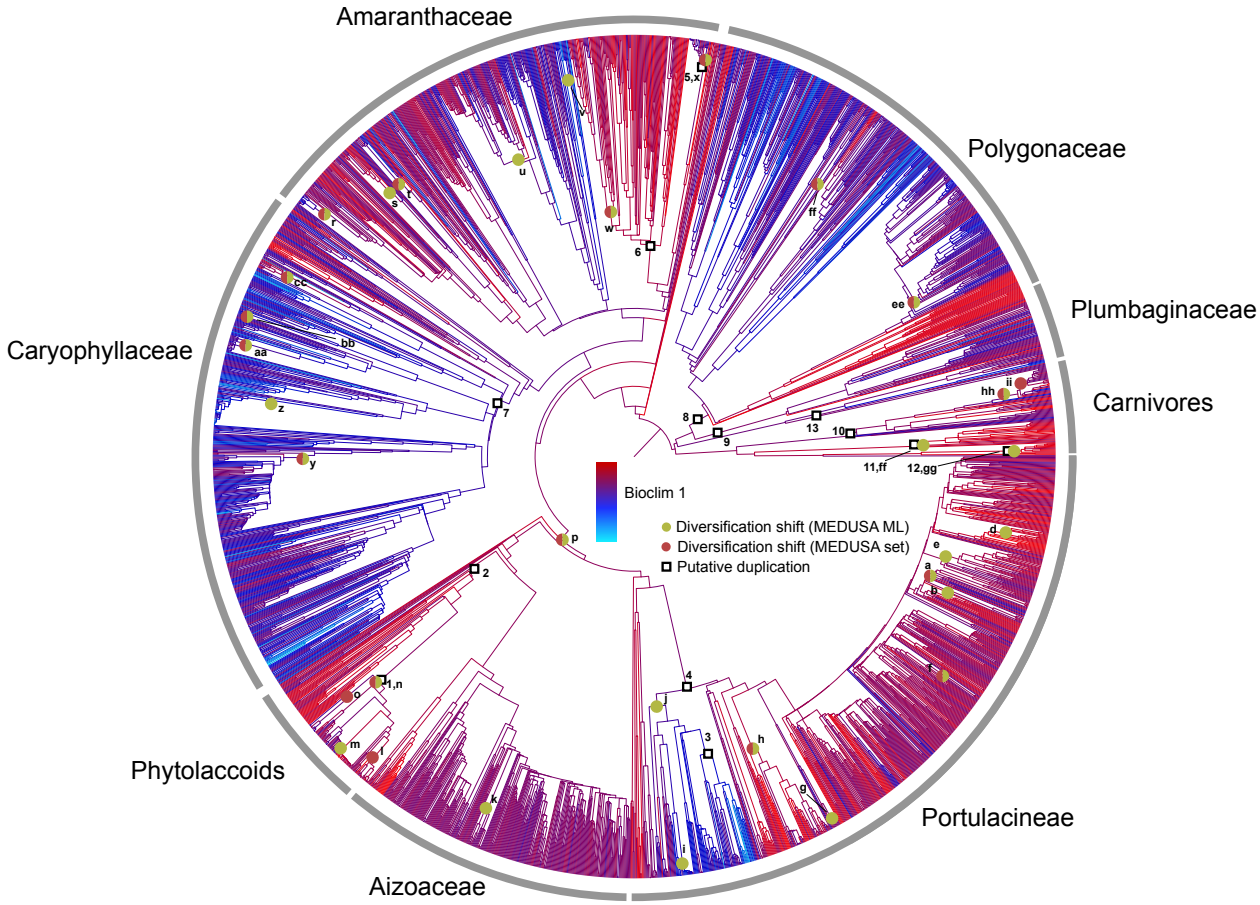
700

701

Table 4 Summary of diversification shifts. Letters correspond to those in Figs. 1 and 2.

#	Family	Diversification shift	Mean shift (ML)	Mean shift (BS)
a	Cactaceae	*Echinops*	1.7957	2.2008
b	Cactaceae	within *Gymnocalycium*	6.9152	
c	Cactaceae	*Gymnocalycium*	-0.001	0.0555
d	Cactaceae	*Hylocereus*+*Selenicereus*	0.1175	
e	Cactaceae	*Rhipsalis*+*Schlumbergera*+*Echinocereus*+relatives	0.0514	
f	Cactaceae	*Stenocactus*	-0.057	-0.019
g	Anacampserotaceae	*Anacampseros*	0.2624	
h	Portulacaceae	*Portulaca*	0.0427	0.0447
i	Montiaceae	*Montiopsis*	0.9418	
j	Montiaceae	Montiaceae	0.0325	
k	Aizoaceae	*Drosanthemum*+*Delosperma*+*Hereroa*+relatives	0.1469	
l	Nyctaginaceae	*Boerhavia*		0.0747
m	Nyctaginaceae	*Commicarpus*	0.9642	
n	Nyctaginaceae	Tribe Nyctagineae	0.0484	0.0485
o	Nyctaginaceae	*Abronia*		-0.084
p	Nyctag.+Aizo+Cact.+relatives	Nyctag.+Aizo+Cact.+relatives	0.0168	0.019
r	Amaranthaceae	*Salicornia*	0.2732	0.1649
s	Amaranthaceae	*Suaeda* clade 1	0.1027	
t	Amaranthaceae	*Suaeda* clade 2	-0.036	-0.028
u	Amaranthaceae	*Atriplex*	0.0384	
v	Amaranthaceae	*Corispermum*	0.1186	
w	Amaranthaceae	*Froelichia*+*Gomphrena*+relatives	0.0217	0.0132
x	Amaranthaceae	*Amaranthus*	0.335	0.2049
y	Caryophyllaceae	*Dianthus*	0.0662	0.0409
z	Caryophyllaceae	*Cerastium*	0.7137	
aa	Caryophyllaceae	*Arenaria*	0.4606	0.425
bb	Caryophyllaceae	*Moehringia*	1.0971	0.995
cc	Caryophyllaceae	*Schiedea*	0.2339	0.2767
dd	Polygonaceae	*Fagopyrum*	-0.04	-0.034
ee	Polygonaceae	*Eriogonum*+relatives	0.0432	0.0364
ff	Nepenthaceae	within *Nepenthes*	0.042	
gg	Ancistrocladaceae	*Ancistrocladus*	0.1426	
hh	Droseraceae	within *Drosera 1*	0.2237	0.2076
ii	Droseraceae	within *Drosera 2*		0.1622

705 **Figures**



706

707 **Fig. 1** Chronogram of the Caryophyllales with putative WGD mapped along with identified
708 diversification shifts. Diversification analyses were performed on the maximum likelihood tree
709 (ML) as well as the bootstrap tree set (set) and those shifts that were identified in both groups are
710 shown. The branches are colored based on Bioclim variable 1 (Mean Annual Temperature).
711

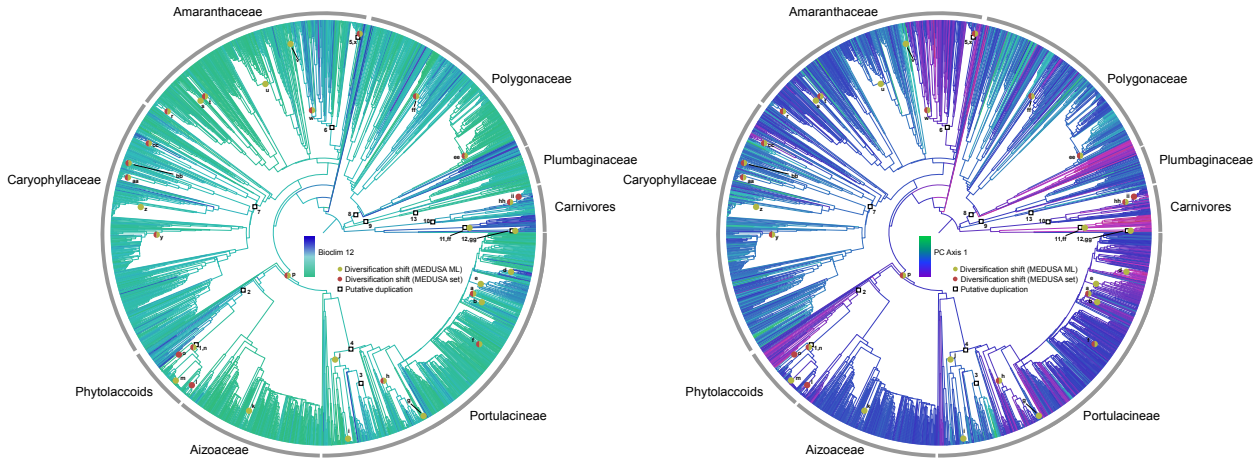


Fig. 2 The chronograms and mapping of diversification and WGD are as in Fig. 1 (see caption for details). A) The branches are colored based on Bioclim variable 12 (Mean Annual Precipitation), and B) based on the principal component analyses (PCA) axis 1.

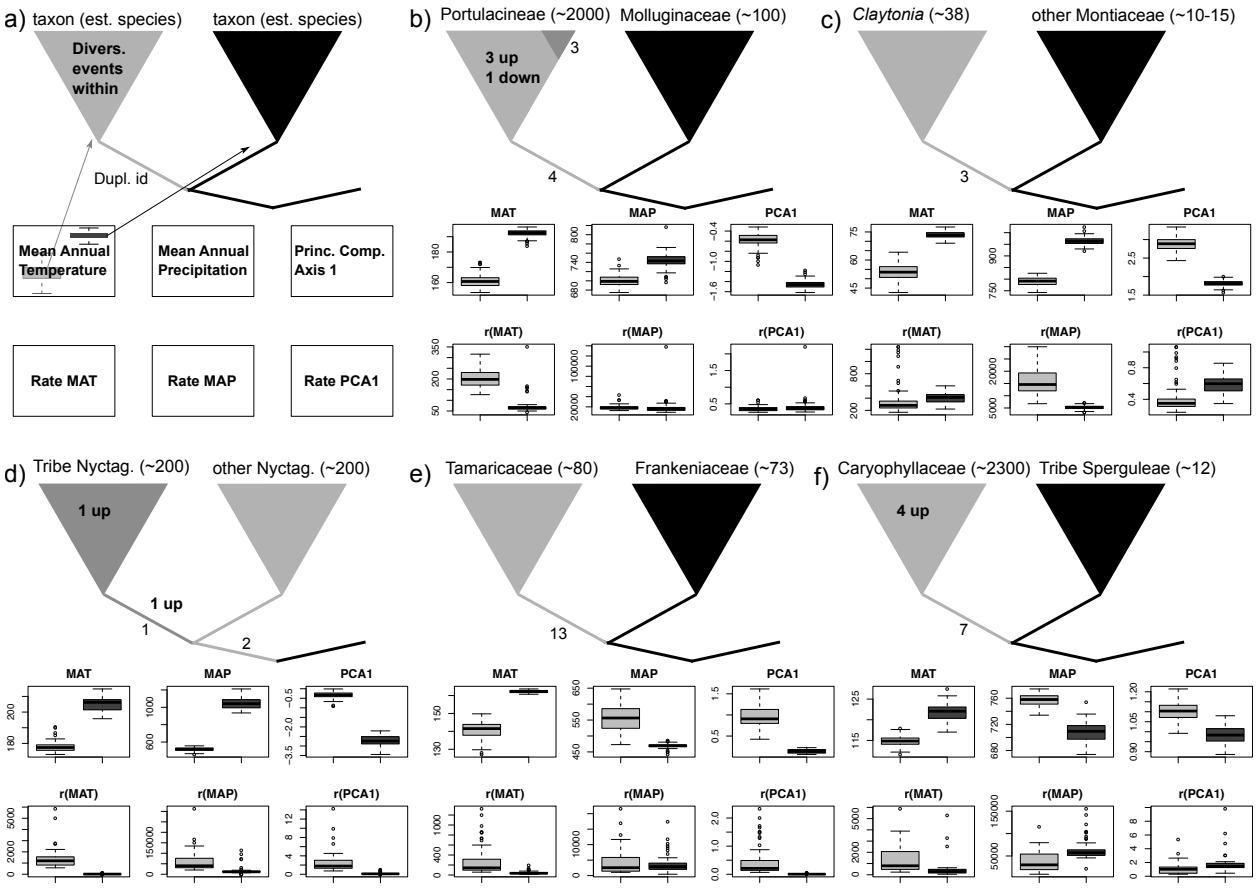


Fig. 3 Summary of WGD events, with numbers corresponding to those in Table 3, climatic variables, and diversification shifts. Numbers along branches denote WGD, with the numbers corresponding to those in Fig. 1 and Table 3. Numbers inside clades denote the number of diversification rate shifts. Estimated species numbers are listed beside clade names. Box plots show the values estimated (ancestral values are listed in the top rows, rates in the bottom rows) for both the left and right clades across bootstrap samples. Clades shaded grey denote a WGD. b), c), and d) have nested WGD.

Supporting Information

726 **Fig. S1** The cladogram with support mapped for the bootstrap replicates described in the
727 methods.
728 **Fig. S2** The chronograms and mapping of temperature variables (bioclimatic variables 13-19)
729 that are not presented in Fig. 1.
730 **Fig. S3** The chronograms and mapping of precipitation variables (bioclimatic variables 13-19)
731 that are not presented in Fig. 2.
732 **Fig. S4** The chronograms and mapping of PCA axis 2 on the broader Caryophyllales.
733 **Fig. S5** Principal component loadings for bioclimatic variables.