

1 **Seed size and its rate of evolution correlate with species diversification across**
2 **angiosperms**

3

4 Short title: Seed size and angiosperm diversification

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20 **Abstract**

21

22 Species diversity varies greatly across the different taxonomic groups that comprise
23 the Tree of Life (ToL). This imbalance is particularly conspicuous within
24 angiosperms, but is largely unexplained. Seed mass is one trait that may help clarify
25 why some lineages diversify more than others because it confers adaptation to
26 different environments, which can subsequently influence speciation and extinction.
27 The rate at which seed mass changes across the angiosperm phylogeny may also be
28 linked to diversification by increasing reproductive isolation and allowing access to
29 novel ecological niches. However, the magnitude and direction of the association
30 between seed mass and diversification has not been assessed across the angiosperm
31 phylogeny. Here, we show that absolute seed size and the rate of change in seed size
32 are both associated with variation in diversification rates. Based on the largest
33 available angiosperm phylogenetic tree, we found that smaller-seeded plants had
34 higher rates of diversification, possibly due to improved colonisation potential. The
35 rate of phenotypic change in seed size was also strongly positively correlated with
36 speciation rates, providing rare, large-scale evidence that rapid morphological change
37 is associated with species divergence. Our study now reveals that variation in
38 morphological traits and, importantly, the rate at which they evolve can contribute to
39 explaining the extremely uneven distribution of diversity across the ToL.

40

41

42 **Introduction**

43 Angiosperms are one of the most species-rich clades on Earth and have dominated
44 terrestrial plant communities since the Late Cretaceous [1]. The astounding diversity

45 of flowering plants is distributed extremely unevenly across the ToL. Each of the five
46 most species-rich angiosperm families contains >10,000 species while more than 200
47 families contain <100 species each [2]. An enduring pursuit in evolutionary biology is
48 to explain this uneven distribution of biodiversity, not only in angiosperms, but also
49 across the whole ToL [3].

50

51 Biological traits offer one way to explain disparity in species diversification if they
52 confer adaptation to different environments. Seed mass is one such trait that is
53 particularly important for angiosperms because it integrates across many
54 characteristics of an individual's life history strategy [4]. Along with adult plant size,
55 seed mass affects survival, reproductive lifespan and dispersal [5]. These life history
56 characteristics contribute to fitness and adaptation, which are the ultimate
57 determinants of whether lineages diversify or go extinct [6]. In support of this idea,
58 seed mass has been shown to correlate negatively with diversification in the
59 Polygonaceae [7], but this has not been investigated across large taxonomic scales. As
60 seed mass varies over ten orders of magnitude in angiosperms, from the minute 1 μg
61 seeds of some orchids to the >18 kg seeds of the sea coconut (*Lodoicea maldivica*),
62 this huge variation may coincide with variation in species diversity. Generalising the
63 direction and magnitude of a link between seed mass and diversification across
64 taxonomic scales has, however, proved difficult. Some life history characteristics
65 encapsulated by seed mass are expected to promote speciation or extinction, while
66 others may simultaneously counteract such effects [8].

67

68 The rate of change in key biological traits, such as seed size, can be as important in
69 driving macroevolutionary dynamics as the absolute values of the traits themselves

70 [9]. This is because phenotypic divergence may cause reproductive isolation that
71 results in speciation [10]. Nevertheless, few empirical studies have detected a
72 correlation between rates of phenotypic evolution and lineage diversification
73 ([9,11,12] but see [13]). A correlation between the two may be expected where a trait
74 can change more rapidly in some species than others in response to selective pressures
75 (i.e. high “evolvability” [14]). This rapid change may enable greater access to new
76 ecological niches or quicker establishment of reproductive isolation, thereby
77 increasing the rate of speciation (λ) [15]. In the case of seed mass, the ability to switch
78 rapidly from small seeds with high dispersal ability to larger seeds with lower
79 dispersal ability might promote cycles of rapid colonisation and isolation or permit
80 adaptation to new dispersal vectors in novel environments. Rapid evolution of new
81 phenotypes may also allow individuals to escape harsh environmental conditions and
82 competitive interactions [16], thereby decreasing extinction rates (μ). The overall
83 outcome of these processes on net diversification ($r = \lambda - \mu$) will ultimately depend
84 upon which of these rates responds more strongly to phenotypic change.

85

86 Here, we show that both seed mass and its phenotypic rate of evolution correlate with
87 speciation and extinction across the angiosperm ToL. Our approach combined the
88 most comprehensive phylogenetic timetree available [17] with an unparalleled dataset
89 of seed mass measurements from over 30,000 angiosperm species [18]. We estimated
90 rates of speciation, extinction and seed size evolution across the phylogeny using
91 Bayesian, method-of-moments, and maximum likelihood analyses – each with
92 different assumptions regarding rate variation through time. We then tested whether
93 there were any links between rates of diversification and both seed size and its rate of
94 evolution. Additionally, we examined whether these links were consistent across

95 different methodologies and timescales.

96

97 **Results**

98 Our results point to a strong association between angiosperm diversification and rates
99 of seed size evolution irrespective of analytical method or timescale, with weaker
100 evidence for a link between macroevolutionary dynamics and absolute seed size. In
101 the first instance, we calculated rates of speciation (λ), extinction (μ) and seed size
102 evolution using Bayesian Analysis of Macroevolutionary Mixtures (BAMM) [19].
103 BAMM models rate heterogeneity through time and lineages, and accounts for
104 incomplete taxon sampling. We used a phylogenetic tree that contained 29,703
105 angiosperm species for the speciation/extinction analysis. The tree was subset to
106 13,577 species with seed size data for phenotypic evolution analysis. As expected,
107 given the high degree of taxonomic imbalance observed in the angiosperm phylogeny,
108 we found strong support for more than 500 shifts in the rates of diversification. There
109 was also marked heterogeneity in the rates of seed size evolution (Fig. 1), which
110 varied over three orders of magnitude (Fig. S1).

111

112 **Figure 1. Seed mass and macroevolutionary rates estimated with BAMM across**
113 **the angiosperm tree of life.** Phylogenetic tree of 13,577 species of flowering plants
114 with seed mass, rate of seed mass change, and speciation (λ), extinction (μ) and net
115 diversification (r) rates estimated by BAMM. Seed mass and rate data were
116 standardised to Z-scores so that variation could be directly compared. λ , μ and r were
117 calculated with a larger, 29,703-species tree.

118

119 We then estimated whether shifts in macroevolutionary dynamics (λ , μ and r)

120 estimated with BAMM were significantly correlated with absolute seed size and tip-
121 specific rates of seed size evolution by comparing the empirical correlations to a null
122 distribution generated using SStructured Rate Permutations on Phylogenies
123 (STRAPP), which is robust to phylogenetic pseudoreplication (see Methods for
124 details) [20]. We were able to link major differences in diversity across angiosperm
125 clades with both the present rate of phenotypic evolution and the absolute value of
126 trait itself. Specifically, increased speciation was associated with a faster rate of seed
127 size evolution (Spearman's $\rho = 0.55$, p-value < 0.0001 ; Fig. 2a). Increased extinction
128 rates were similarly associated with higher evolvability ($\rho = 0.44$, p-value < 0.0001 ;
129 Fig 2b), but given the weaker effect, the net outcome of $\lambda - \mu$ was that diversification
130 rates were positively correlated with phenotypic change ($\rho = 0.49$, p-value < 0.0001 ;
131 Fig. 2c). We also identified an association between seed size and both speciation ($\rho = -$
132 0.17 , p-value = 0.003 ; Fig. 2d), and extinction rates ($\rho = -0.17$, p-value = 0.003 , Fig.
133 2e). As the correlations with speciation and extinction were in the same direction and
134 of comparable magnitude, and estimates of extinction rates were relatively variable
135 (Fig. 2e), net diversification rates did not change with seed size ($\rho = -0.12$, p-value =
136 0.077 ; Fig. 2f). Generally, the observed correlations arose from many phenotypically
137 fast-evolving clades distributed across the phylogeny (Fig. S1) and were robust to
138 prior choice in the BAMM analyses (Fig. S2).

139

140 **Figure 2. Seed mass and seed mass rate of evolution correlate with**
141 **macroevolutionary dynamics estimated with BAMM.** Spearman correlations were
142 calculated between speciation (λ), extinction (μ), and net diversification (r) and each
143 of a) present-day rate of seed mass change and b) seed mass. Coloured lines are
144 correlations for one sample of the BAMM posterior distribution, bold line is the

145 median. The insets show the density plots of the absolute difference between the
146 observed and null correlation calculated across 1,000 structured permutations of the
147 evolutionary rates on the phylogenetic tree (myr = million years).

148

149 Given recent discussion on the reliability of BAMM for estimating diversification
150 rates ([21], but see [22]), we tested the robustness of our results by using alternative
151 methodologies to infer macroevolutionary dynamics across clades at different
152 timescales. Ten, 2 million year-wide time slices from the present up to 20 million
153 years ago were defined. These time slices were used to identify the most inclusive
154 monophyletic clades of ≥ 4 species in which we had estimated a $\geq 70\%$ probability of
155 recovering the correct crown age node of the clade (see Methods). For each resulting
156 clade in each time slice, we calculated diversification rates using a method-of-
157 moments estimator, which assumes rates are constant over time [23]. We also fitted a
158 series of time-dependent diversification models to each clade with RPANDA, which
159 uses a maximum likelihood approach to estimate speciation and extinction and allows
160 for incomplete taxon sampling [24] (see Table S1 for a summary of the best fitting
161 models for each time slice). Rates of seed size evolution were estimated within each
162 clade that also had ≥ 4 species with seed size data by fitting both Brownian motion
163 (BM) and early burst (EB) or accelerating decelerating [25] models of trait evolution.
164 Mirroring the BAMM results, we found a positive correlation between the rate of seed
165 size evolution and speciation rates that was consistent across time slices (Fig. 3a, Fig.
166 S3a). As expected given the weaker association between seed size and speciation
167 found in our BAMM analyses, correlations were generally weaker and non-significant
168 (Fig. 3b), except for one of the time slices (Fig. S3b).

169

170 **Figure 3. Seed mass and seed mass rate of evolution correlate with speciation in**
171 **the clade-based analysis.** Correlation of (a) rate of seed mass evolution and (b) seed
172 mass with speciation rate (λ) estimated using RPANDA in the clade-based analysis.
173 The strength of correlations is shown as PGLS slopes and were calculated using mean
174 clade-level seed mass across 10 time slices in our species-level phylogenetic tree. The
175 size of the circles represents the number of clades in each time slice plotted at the
176 median age of the time slice. Colour indicates the significance of the slope. A detailed
177 representation of the results in each time slice is given in figures S13 and S14.
178 Correlations calculated with speciation rates obtained with the method-of-moments
179 estimator are given in Fig. S3.

180

181 We also found limited evidence that other traits that co-vary with seed size (Tables S2,
182 S3) better explained our results. If our results were explained by seed size being a
183 proxy of some other phenotypic trait that ultimately influenced speciation, we would
184 expect this other phenotypic trait to be strongly correlated with seed size. We would
185 also expect a significantly stronger correlation of speciation with both this trait and its
186 rate of evolution when compared to seed size and its rate of evolution. By comparing
187 the effects of genome size, life cycle, plant height and woodiness across a subset of
188 1,007 species in our dataset, we found that only the distinction between woody and
189 herbaceous and annual and perennial species were more strongly correlated with
190 macroevolutionary dynamics than absolute seed size. The rate of phenotypic evolution
191 of all the continuous traits (genome size, seed size and plant height) was strongly and
192 similarly correlated with speciation (Fig. S4, Table S4). Importantly, however, neither
193 the rate of evolution nor the absolute values of both genome size and plant height
194 were more strongly associated with speciation than seed size or its rate of evolution

195 (Fig. S4). These results therefore suggest that the correlation between
196 macroevolutionary dynamics and both seed size and its rate of evolution is not simply
197 mediated by other phenotypic traits.

198

199 **Discussion**

200 Our study supports the ideas that variation in seed mass and, particularly, its rate of
201 evolution can help explain disparity in diversification across the angiosperm
202 phylogeny by playing a central role in plant life history. As we show with our clade-
203 based analysis, our results are repeatable across many methodologies, varying
204 timescales and are not restricted to a particular taxonomic rank (Figs 2, 3).

205

206 The robust association of high rates of phenotypic change with lineage diversification
207 has recently been observed in other taxonomic groups [9,26], but never across the
208 whole of the angiosperm ToL as we find here. Accelerated morphological evolution
209 may allow radiating lineages to occupy more complex adaptive landscapes [27].
210 Species with greater rate of change in their seed mass (i.e., higher evolvability) could
211 also shift between adaptive peaks or develop reproductive barriers more rapidly.
212 Alternatively, the theory of punctuated equilibria [28], whereby morphological
213 changes can arise from the speciation process, might also explain the connection of
214 phenotypic evolution with species divergence. However, current methods do not allow
215 us to distinguish whether speciation is responding to morphological change or vice
216 versa when reconstructing 250 million years of evolutionary history [9].

217

218 Seed mass itself will also co-vary with dispersal ability and environmental tolerance
219 in ways that can change speciation. For example, we found that smaller-seeded genera

220 had faster speciation rates. This may be because smaller-seeded genera generally
221 disperse over larger distances [29], which can promote speciation by creating isolated
222 populations [30]. However, the relationship between dispersal and speciation is highly
223 context dependent. The permeability of a landscape to dispersal determines the
224 dispersal distances that may promote species divergence. For example, long distance
225 dispersal may be needed for isolation to occur in continuous habitats but be less
226 effective in highly fragmented landscapes [31]. Therefore, the weak correlation that
227 we observed between seed size and diversification might reflect contradicting patterns
228 operating in different angiosperm clades. Dispersal syndromes may also modify the
229 effect of seed size on speciation. For instance, species with larger seeds are generally
230 associated with biotic dispersal that distributes seeds over greater distances than wind
231 or gravity dispersal [5]. However, broad-scale predictions for the effects of dispersal
232 syndromes on diversification may be inaccurate, since the former depend on
233 landscape connectivity [8] and can sometimes be inconsistent, e.g. a wind-dispersed
234 seed might be transported by an animal. Detailed contextual data will be necessary to
235 expand upon the mechanisms underlying our findings in specific regions and clades.

236

237 Although seed mass is associated with other traits that can affect diversification, there
238 is little evidence that these better explain our observed correlations or that seed size is
239 a mere proxy for one of these other traits. For example, genome size positively
240 correlates with seed mass [32], and faster rates of genome size evolution have been
241 linked to increased speciation in angiosperms [12]. Shorter, smaller-seeded plants also
242 tend to have faster life cycles, which may accelerate mutation rates [33,34] and
243 promote diversification [35]. But unlike other traits [12], both absolute seed size as
244 well as its rate of change were correlated with speciation. Thus, although other traits

245 surely influence diversification [36], we argue that our results generally reflect the
246 role of seed size as a trait that integrates across multiple aspects of life history
247 characteristics in ways that can predictably influence plant macroevolutionary
248 dynamics (Fig. S5).

249

250 Our analyses build upon the largest available phylogenetic timetree for angiosperms
251 in ways that do not consider topological and branch length uncertainty. Similar to
252 other megaphylogenies, the low sampling fraction (approximately 10% of described
253 flowering plants) and limited number of phylogenetic markers (a maximum of seven),
254 which were employed in constructing our phylogeny [17], may affect the inference of
255 macroevolutionary estimates [37,38]. In any case, we believe our results, particularly
256 the strong correlation between the rate of seed size evolution and speciation rates may
257 reflect general patterns on how biodiversity is generated across angiosperms. Detailed
258 studies in well-sampled clades can expand upon our findings and reveal different
259 relationships operating in particular groups of organisms.

260

261 The approach applied here can help to unravel the processes responsible for
262 generating large-scale asymmetries in biodiversity. It also offers the potential to test
263 how widely-varying traits and their rate of morphological evolution influence other
264 aspects of the evolution and adaptation of flowering plants (e.g. [17]). Clade-specific
265 exceptions arising from local interactions with non-focal traits [39] and specific
266 spatio-temporal contexts will undoubtedly interact with broad-scale
267 macroevolutionary patterns and may modulate the effects of seed mass on
268 diversification. Regardless, our results show that seed size and its rate of evolution
269 correlate with speciation and extinction across the flowering plants. This finding may

270 help to explain why some clades are much more species-rich than others and points to
271 the role of rapid morphological evolution in generating greater levels of diversity.

272

273 **Materials and methods**

274 *Seed mass and phylogenetic dataset*

275 Seed mass data for 31,932 species were obtained from the Royal Botanic Gardens
276 Kew Seed Information Database [18]. Species names were standardised with The
277 Plant List (TPL) nomenclature [2] and cleaned using the *Taxonstand* R package [40].
278 Further processing was performed with the *taxonlookup* R package [41], which is a
279 complete genus-family-order mapping for vascular plants that draws from TPL, the
280 Angiosperm Phylogeny website [42] and a higher-level manually-curated taxonomic
281 lookup [17].

282

283 We used the most comprehensive phylogenetic tree for land plants [17,43] that
284 comprises 31,389 species. Taxonomic information for our phylogenetic tree was run
285 through *Taxonstand* and *taxonlookup* as described above to prune it down to
286 angiosperms. The final phylogenetic tree contained 29,703 angiosperm species
287 belonging to 353 plant families (following APG IV, Fig.S6).

288

289 *Diversification and phenotypic evolution analyses*

290 Speciation, extinction and net diversification rates were estimated across the 29,703
291 species tree using BAMM version 2.5.0 [19]. BAMM models shifts in
292 macroevolutionary regimes across a phylogenetic tree using reversible-jump Markov
293 chain Monte Carlo (rjMCMC) sampling. The size of the tree precluded a single
294 analysis from readily converging. Therefore, we divided our initial tree into clades of

295 ≤ 6000 species. This resulted in six monophyletic clades and one additional clade that
296 contained the backbone of the tree (i.e., one representative of the six monophyletic
297 clades) plus the remaining, unassigned species (Fig. S7). We then ran BAMB
298 speciation/extinction analyses for each of the seven clades (six monophyletic clades
299 plus the backbone set). Initial prior settings were calculated with the *setBAMBpriors*
300 function in *BAMBtools* [44], and the *expectedNumberOfShifts* parameter was set at
301 50. Following [12], we incorporated non-random incomplete sampling information by
302 calculating the proportion of species sampled inside each family and estimated the
303 backbone sampling as the overall proportion of sampled species. *Taxonlookup* was
304 used as a reference for these calculations. Analyses were run for 150 million
305 generations and convergence was verified by plotting chain traces and ensuring that
306 the effective sample sizes of all relevant parameters exceeded 200. The first 100
307 million generations were discarded as burn-in. The resulting event files for all seven
308 analyses were combined into a single event file, effectively generating one BAMB
309 result set that was then analysed following standard procedure. This clade-level
310 analysis allowed for diversification rate estimation with the most complete dataset that
311 was available. The resulting rate estimates results were strongly correlated with
312 estimates from a single speciation/extinction analysis using the 13,577 species that
313 were present in our seed size database (Fig. S8; $r = 0.92$, $p\text{-value} < 0.001$).

314

315 Rates of seed size evolution were also estimated with BAMB using the phylogenetic
316 tree of the 13,577 species that were present in our seed size database. Initial priors
317 were calculated as above and analyses were run for 300 million generations. The
318 initial 30 million generations were discarded as burn-in. We analysed BAMB prior
319 sensitivity following recent concerns ([45], but see [22]) by re-running both the

320 diversification and the trait evolution analyses for the 13,577 species dataset with
321 different settings for the *expectedNumberOfShifts* parameter of either 25, 50, 100 or
322 250. These analyses confirmed a low prior sensitivity for the posterior of the number
323 of expected rate shifts (Fig. S2).

324

325 Finally, we obtained clade-based measures of diversification and seed size evolution
326 across the species-level tree. Clades were defined as non-overlapping monophyletic
327 groupings of four or more species and their ages were defined using a series of 2-
328 million year wide time slices from the present up to 20 myr ago (see Fig. S13 for the
329 number of clades in each time slice). For each clade, we estimated its sampling
330 fraction by weighting the genus-specific sampling fractions (i.e., the number of
331 congeneric species in the 13,577 species tree divided by the total number of described
332 species for that genus) with the number of species from each genus present in the
333 clade. A minimum clade-specific sampling fraction of 0.3 was used for inclusion in
334 our analyses, ensuring that the crown sampling probability for each clade was at least
335 0.7 (the actual median clade crown sampling probabilities for the time slices ranged
336 between 0.90 and 0.96). Crown ages for the selected clades were then used to estimate
337 net diversification rates using the method-of-moments estimator [23]. Following
338 standard practice [46,47], we assumed three values of relative extinction fraction, $\epsilon =$
339 0, 0.5 and 0.9. Different values did not affect our conclusions (results not shown);
340 therefore we present the results of the intermediate extinction fraction ($\epsilon = 0.5$). We
341 also used RPANDA to fit a series diversification models that estimated time-
342 dependent rates for each clade. We fitted six different models of diversification: (i)
343 pure birth model with constant λ (speciation rate); (ii) pure birth model with
344 exponential λ ; (iii) birth-death model with constant λ and μ (extinction); (iv) birth-

345 death model with exponential λ and constant μ ; (v) birth-death model with constant λ
346 and exponential μ ; and (vi) birth-death model with exponential λ and exponential μ .
347 We then used AIC-based model selection to select the best fitting model and obtain
348 the corresponding macroevolutionary parameters. Finally, we estimated the rates of
349 seed size evolution by fitting BM and EB models of evolution to the seed size data
350 within each clade using *fitContinuous* from the *geiger* R package [48]. We performed
351 AIC-based model selection to find the best fitting model of trait evolution. More than
352 99.7% of the clades showed a higher support for the BM model. Additionally, to
353 account for possible biases when analysing clades with many non-congeneric species,
354 we confirmed the results of our clade-based analysis by considering clades that only
355 contained congeneric species (Fig. S9).

356

357 *Correlation of diversification and trait evolution*

358 All rate variables were log-transformed for the correlation analyses. Following [20]
359 we treated seed mass evolutionary rates at the tips of the tree as character states and
360 used STRAPP to test for multiple associations between these present-day rates and
361 BAMM-estimated diversification dynamics. We similarly analysed the correlation of
362 absolute seed mass and speciation/extinction dynamics. STRAPP compares the
363 correlation between a focal trait and a macroevolutionary parameter (λ , μ or r) to a
364 null distribution of correlations. The null correlations are generated by permuting the
365 evolutionary rates in the tips of the phylogenetic tree while maintaining the location of
366 rate shift events in the phylogeny. In each case, we calculated the absolute difference
367 between the observed correlation of the macroevolutionary rate and the trait state and
368 the null correlation obtained by the structured permutations across 5000 samples from
369 the BAMM posterior (for an example of the observed correlation in one of the

370 samples in the posterior, see Fig. S10). The reported p-value was the proportion of
371 replicates where the null correlation coefficient was greater than the observed
372 correlation. We found a low type I error associated with our STRAPP correlation
373 analysis (p-value = 0.094, Fig. S11). We also investigated the correlation between the
374 mean speciation and mean phenotypic rates across all the branches in the tree using an
375 ordinary least squares regression (Fig. S12). We note however, that this regression
376 does not correct for phylogenetic dependence in the branch estimates, despite
377 suggesting something about patterns across the whole evolutionary history of the
378 angiosperms.

379

380 For the clade-based analyses, we estimated the correlation between speciation rates
381 (measured as λ at present time for the RPANDA analyses) and each of seed size rate
382 of evolution and phylogenetically-corrected mean seed size (i.e., trait value at the root
383 node of the clade under a BM). Correlations were estimated using phylogenetic
384 generalised least square (PGLS) as implemented in the R package *caper* [49] (Fig.
385 S13, Fig. S14). Similar results as presented in the main text were obtained when
386 analysing net diversification instead of speciation rates (Fig. S15). Finally, we
387 similarly analysed the correlation between speciation and each of seed size and its rate
388 of change when selecting only clades consisting of congeneric species. Again, this
389 analysis resulted in a similar pattern as the one presented in the main text (Fig. S9).

390

391 *Diversification dynamics and other phenotypic traits*

392 Seed mass is central to a network of inter-correlated traits associated with plant life
393 history that can impact diversification. Some of these traits are genome size or plant
394 C-value (measured as picograms of DNA per haploid nucleus), plant height, life cycle

395 and woodiness. We compared the correlation between macroevolutionary parameters
396 (λ , μ , r) and each of seed mass, seed mass rate of evolution, C-value (i.e., genome
397 size), plant height, life cycle and woodiness across a dataset of 1,007 angiosperm
398 species for which all phenotypic traits could be assembled. Genome content and life
399 cycle data were downloaded from the Plant DNA C-values database [50]. Woodiness
400 data were obtained from [17,51]. Plant height data was obtained from the TRY
401 database [52]. The rates of phenotypic evolution for the continuous traits (seed size,
402 plant height and C-value) were calculated as the phenotypic rate inferred at the tips of
403 the tree in our main BAMM analysis (see above). Surprisingly, mean seed mass did
404 not differ between the 214 strictly annual and 793 perennial plants when accounting
405 for phylogenetic relationships using a phylogenetic ANOVA (Fig. S16, phylANOVA:
406 p -value = 0.308, significance assessed with 1,000 random simulations with *phytools*
407 [53]). In this reduced dataset, we ran STRAPP correlations for each focal trait with the
408 diversification parameters calculated from our main BAMM analysis. We then
409 calculated the absolute differences in the observed and the null correlations between
410 the macroevolutionary parameters and seed mass, C-value, “annuality” (a binary
411 variable specifying whether the species was strictly annual or not), plant height,
412 woodiness (a binary variable specifying whether the species was herbaceous or
413 woody) and the rates of seed size evolution, genome size evolution and plant height
414 evolution. As expected, all phenotypic traits and their rates of evolution were
415 correlated with each other (Fig S5).

416

417 *Code availability*

418 Scripts used to carry out the analysis described in the paper and generate the figures
419 will be deposited in Github (<https://github.com/javierigea/XXXX>) upon acceptance.

420

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427

428 **Author contributions**

429 J.I and A.S.T.P conceived the study. J.I. and E.F.M. performed the analysis. J.I. and
430 A.J.T interpreted the analysis and wrote the manuscript. All authors edited the
431 manuscript.

432

433

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- 594

595

596 **Supporting Information captions**

597

598 **Fig. S1.** Phylogenetic tree of 13,577 angiosperm species with branch colours
599 indicating the rate of seed mass evolution estimated with BAMM. Branches were
600 scaled by speciation rate as determined by a BAMM analysis on a larger 19,703 tree.

601

602 **Fig. S2.** Prior and posterior distribution of the number of rate shifts in BAMM for a)
603 the speciation/extinction and b) phenotypic evolution analyses for
604 *expectedNumberOfShifts* = 25, 50 and 100 and 250. The analyses in the main text
605 were carried out with *expectedNumberOfShifts* = 50 for both speciation/extinction and
606 phenotypic evolution analyses.

607

608 **Fig. S3.** Seed mass and its rate of evolution are associated with speciation in the
609 clade-based analyses. (a) PGLS slope of the relationship between speciation rate (λ)
610 from the method-of-moments estimator and the rate of seed mass evolution across 10
611 time slices. Circles are scaled to the number of clades in each time slice while colour
612 indicates the significance of the slope. (b) PGLS slope of the relationship between
613 speciation rate and mean clade seed mass. For a detailed representation of the results
614 in each time slice, see figure S14 and S15.

615

616 **Fig. S4.** STRAPP correlations of diversification and phenotypic traits for 1,007
617 angiosperm species. The distribution of the absolute difference in the observed
618 correlation minus the null correlation is plotted for each trait. The coloured dotted
619 lines indicate the mean of that distribution, and the black dotted line indicates 0; a

620 distribution with mean = 0 would show no association between a focal trait and
621 macroevolutionary dynamics. STRAPP correlation of seed size (shown in red), C-
622 value (shown in yellow), life cycle (shown in light green), woodiness (shown in dark
623 green), height (shown in blue), seed size rate (shown in dark blue), C-value rate
624 (shown in purple); and height rate (shown in pink) with a) speciation rate (λ), b)
625 extinction rate (μ), and c) net diversification rate (r).

626

627 **Fig. S5.** Proposed effects of seed mass and other life history traits on diversification
628 (solid lines). Dashed lines indicate correlations between life history traits. Numbers
629 indicate reference where the link is proposed.

630

631 **Fig. S6.** Phylogenetic tree of 353 angiosperm families with representatives in our
632 analyses. The red bars indicate the levels of sampling for each family.

633

634 **Figure S7.** Angiosperm phylogenetic tree collapsed to monophyletic clades of ≤ 6000
635 species. The name of one representative species per clade is shown, and the numbers
636 in parentheses indicate the number of species included in each clade. The BAMM
637 analyses were carried out for six monophyletic clades (shown in red, yellow, green,
638 blue, dark blue and pink) and one “backbone” analysis with the remaining clades
639 (shown in grey) and one representative of each of the six monophyletic clades.

640

641 **Fig. S8.** Comparison of the speciation rates at the tip of the tree obtained with the
642 complete Zanne tree (29,703 species) and the seed size filtered tree (13,577 species).
643 The dotted line represents the 1:1 reference line.

644

645 **Figure S9.** Correlation of speciation with seed mass and seed mass rate of evolution
646 in the clade-based analysis only considering congeneric species. (a) PGLS slope of the
647 relationship of speciation rate - estimated with the method-of-moments estimator -
648 with mean clade seed mass across 10 time slices. The size of the circles represents the
649 number of clades in each time slice while the colour indicates the significance of the
650 slope. (b) PGLS slope of the relationship of speciation rate and the rate of seed mass
651 evolution.

652

653 **Fig. S10.** Correlation between speciation rate and rate of seed size evolution in a
654 random sample of the BAMM posterior. The dotted line represents the Spearman
655 correlation ($\rho = 0.47$, p-value < 0.001)

656

657 **Fig. S11.** Type I error analysis. We estimated the type I error rate of our analysis by
658 simulating neutral traits on the angiosperm phylogenetic tree. We performed 1,000
659 simulations and then ran 1,000 STRAPP tests with each simulated dataset. We
660 estimated the corresponding p-values for the association between traits and
661 diversification and calculated the type I error as the proportion of datasets where a
662 significant association (p-value < 0.05) was detected.

663

664 **Fig. S12.** Correlation of mean speciation and mean phenotypic rates across all the
665 branches of the angiosperm phylogenetic tree. The dotted line is the ordinary least
666 squares regression ($R^2 = 0.31$, p-value < 0.001)

667

668 **Fig. S13.** Correlations between clade rate of seed size evolution and speciation rate
669 (estimated with RPANDA) across time slices from: (a) 0 to 2 million years (myr); (b)

670 2 to 4 myr; (c) 4 to 6 myr; (d) 6 to 8 myr; (e) 8 to 10 myr; (f) 10 to 12 myr; (g) 12 to
671 14 myr; (h) 14 to 16 myr; (i) 16 to 18 myr; and (j) 18 to 20 myr. The degrees of
672 freedom (df) are equivalent to the number of clades minus one.

673

674 **Fig. S14.** Correlations between mean clade seed mass and speciation rate (estimated
675 with RPANDA) across time slices from: (a) 0 to 2 million years (myr); (b) 2 to 4 myr;
676 (c) 4 to 6 myr; (d) 6 to 8 myr; (e) 8 to 10 myr; (f) 10 to 12 myr; (g) 12 to 14 myr; (h)
677 14 to 16 myr; (i) 16 to 18 myr; and (j) 18 to 20 myr. The degrees of freedom (df) are
678 equivalent to the number of clades minus one.

679

680 **Fig. S15.** Correlation of (a) rate of seed mass evolution and (b) seed mass with net
681 diversification rate (r) estimated using RPANDA in the clade-based analysis. The
682 strength of correlations is shown as PGLS slopes and was calculated using mean
683 clade-level seed mass across 10 time slices. The size of the circles represents the
684 number of clades in each time slice while the colour indicates the significance of the
685 slope.

686

687 **Fig. S16.** Mean genus seed mass of strict annual ($n = 214$) and perennial ($n = 793$)
688 genera. No significant difference between the means of the two groups was found
689 when accounting for phylogeny (phylANOVA: p -value = 0.308, significance assessed
690 with 1,000 random simulations).

691

692 **Fig. S17.** Correlations between clade rate of seed size evolution and speciation rate
693 (estimated with the method-of-moments estimator) across time slices from: (a) 0 to 2
694 million years (myr); (b) 2 to 4 myr; (c) 4 to 6 myr; (d) 6 to 8 myr; (e) 8 to 10 myr; (f)

695 10 to 12 myr; (g) 12 to 14 myr; (h) 14 to 16 myr; (i) 16 to 18 myr; and (j) 18 to 20
696 myr.

697

698 **Fig. S18.** Correlations between mean clade seed mass and speciation rate (estimated
699 with the method-of-moments estimator) across time slices from: (a) 0 to 2 million
700 years (myr); (b) 2 to 4 myr; (c) 4 to 6 myr; (d) 6 to 8 myr; (e) 8 to 10 myr; (f) 10 to 12
701 myr; (g) 12 to 14 myr; (h) 14 to 16 myr; (i) 16 to 18 myr; and (j) 18 to 20 myr.

702

703 **Table S1.** RPANDA diversification models for the clade-based analyses. For each 2-
704 million year (myr) time slice, we counted the number of clades where the best-fitting
705 model was either i) birth-death model with constant λ (speciation) and μ (extinction)
706 (λ .cst. μ .cst); pure birth model with constant λ (λ .cst. μ 0); pure birth
707 model with exponential λ (λ .exp. μ 0); birth-death model with exponential λ
708 and constant μ (λ .exp. μ .cst); birth-death model with exponential λ and
709 exponential μ (λ .exp. μ .exp); or birth-death model with constant λ and
710 exponential μ (λ .cst. μ .exp).

711 **Table S2.** Correlations of seed size and other phenotypic traits. Trait values were
712 obtained from a 1,007 species tree where all species had data for seed size, C-value
713 and plant height. The values are the slopes of the PGLS regressions and asterisks
714 denote statistically significant correlations (p-value < 0.05).

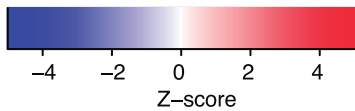
715

716 **Table S3.** Correlations of seed size rate of evolution and other phenotypic rates of
717 evolution. Rate values were obtained from a 1,007 species tree where all species had
718 data for seed size, C-value and plant height. The values are the slopes of the PGLS
719 regressions and asterisks denote statistically significant correlations (p-value < 0.05).

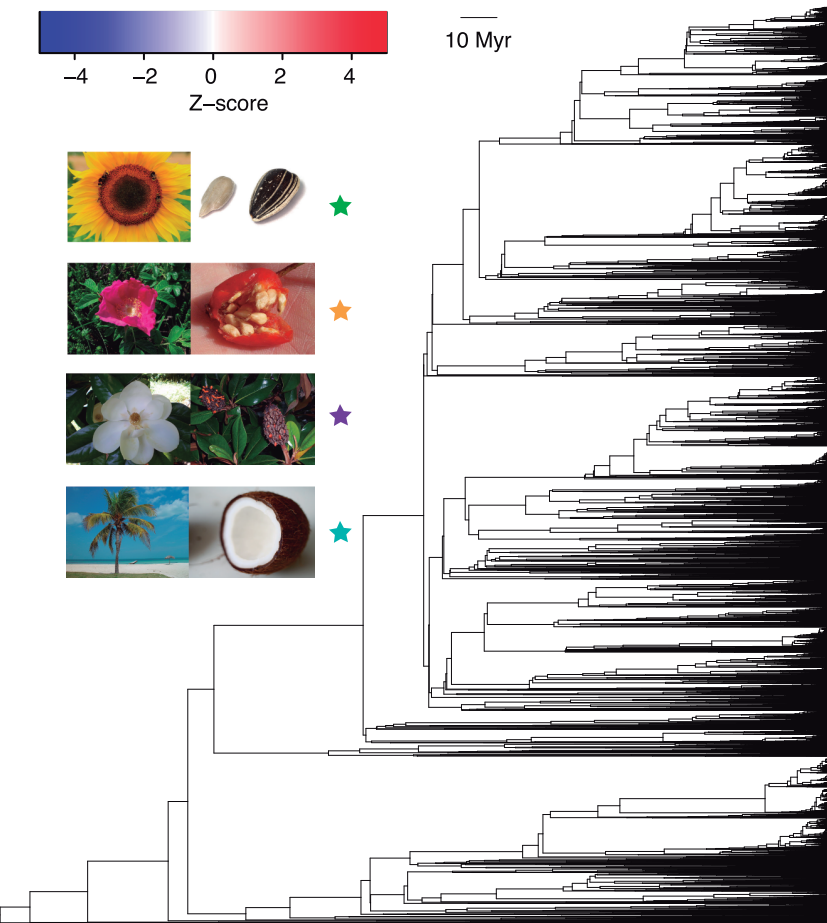
720

721 **Table S4.** STRAPP correlations (*rho*) for 1,007 species of angiosperms with seed size,
722 genome size (i.e., C-value), life cycle, height, woodiness data and rates of seed size,
723 C-value and height evolution. Significant correlation are shown in bold and p-values
724 are shown in parentheses.

725

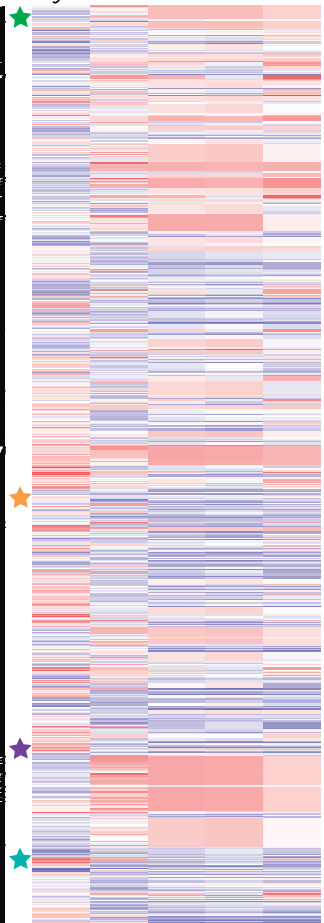


10 Myr



seed mass
seed mass evolution

λ μ r

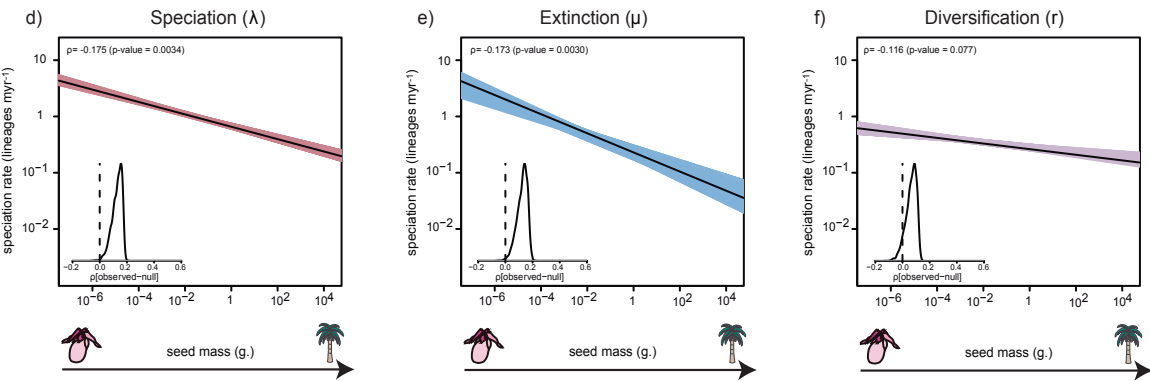
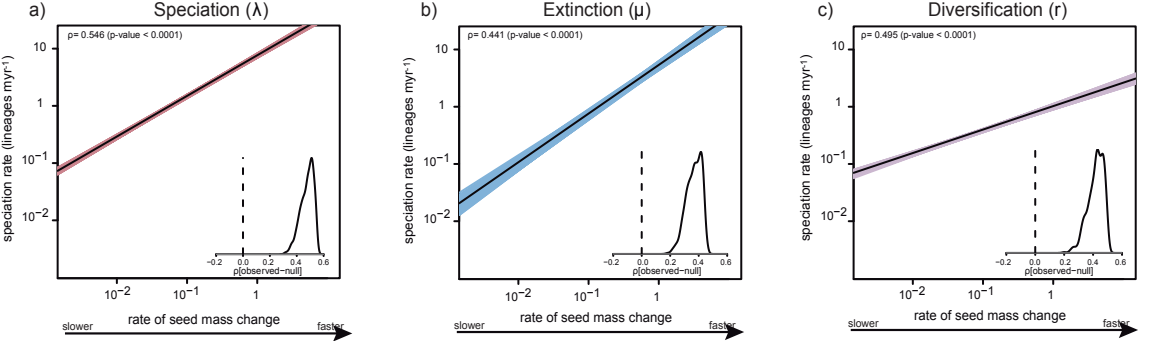


Asterids

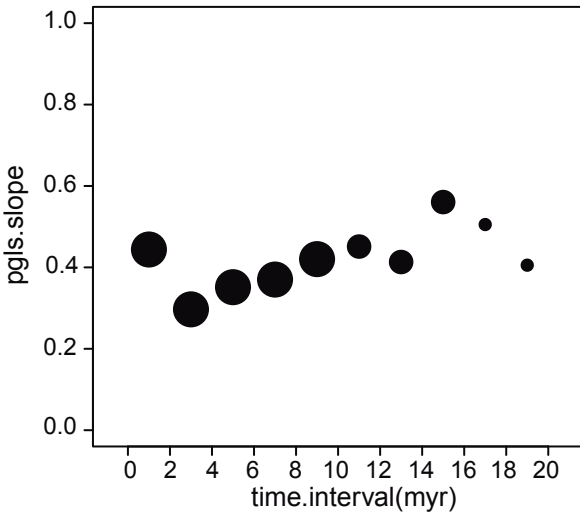
Rosids

Magnoliids

Monocots



a) Speciation ~ rate of seed mass change



b) Speciation ~ seed mass

