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Title

A targeted phylogenetic approach helps explain New World functional diversity patterns of two eudicot lineages.

Running title

New World eudicot functional diversity

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30 **Abstract**

31 *Aim:*

32 Large-scale functional diversity studies typically examine isolated traits, often without
33 phylogenetic context. Here, we integrate data from five life-history traits with phylogeny and
34 occurrence records to assess: (1) correlated latitudinal gradients of trait combinations; (2) which
35 traits show phylogenetic conservatism; (3) quantitative, clade-specific differences in trait
36 syndromes, illustrating the phylogenetic scale of observable variation in ecological strategies.

37 *Location:*

38 The Americas.

39 *Taxon:*

40 Ericales (Asterids) and Fabales (Rosids).

41 *Methods:*

42 We used publicly-available trait data sets on height, seed mass, wood density, leaf mass per area
43 (LMA), and growth form, an open-source phylogeny, and georeferenced occurrence records to
44 investigate functional diversity patterns. We employed phylogenetic generalized least squares
45 and phylogenetic principal components analyses (pPCA) to assess correlated trait evolution and
46 quantify the trait syndrome, respectively. We employed the InfoMap Ecoregions web app to
47 cluster species by bioregions. We used standard statistical tests and randomization simulations to
48 assess statistical significance of results.

49 *Results:*

50 Ericales and Fabales exhibited a biogeographically-consistent, phylogenetically-conserved trait
51 syndrome. Moving poleward, species exhibited progressively smaller trait values and more
52 herbaceous and shrubby growth forms (except for LMA, which showed no consistent pattern).
53 We quantified latitudinal variation in this trait syndrome using pPCA, and provide evidence for
54 correlated trait evolution.

55 *Main conclusions:*

56 We demonstrate a functional trait syndrome involving height, seed mass, wood density, and
57 growth form, but not LMA. Functional trait values showed consistent latitudinal patterns and
58 evidence of correlated evolution, suggesting an underlying ecological strategy. Further, the two
59 clades showed quantitative differences in the manifestation of this trait syndrome. Variation in
60 the syndrome was best observed among species from con-ordinal families. We interpret this trait

61 syndrome as a strategy of resource acquisition in which habitats with relatively greater soil
62 nutrient content and a shorter growing season favor shorter stature, lower seed mass and wood
63 density, and shrubby or herbaceous growth form.

64 65 **Keywords**

66 angiosperms, cold tolerance, Ericales, Fabales, functional diversity, latitudinal gradient, life-
67 history traits.

68 69 **Introduction**

70 Functional traits mediate numerous aspects of plant ecology (Grime, 2006), and there has
71 been extensive interest in categorizing the distributional patterns of functional trait values. Such
72 patterns represent the confluence of differing ecological strategies and interactions, selection
73 pressures, physiological constraints, abiotic filtering, and historical contingency (Reich et al.,
74 2003). Nevertheless, understanding the underlying biological reasons for the observed patterns
75 remains elusive. Strong latitudinal gradients in many life-history traits, sometimes assessed
76 across all angiosperms or seed plants, have given researchers a first glimpse into continental-
77 scale patterns of functional diversity (Moles et al., 2005; Moles et al., 2007, 2009; Swenson et
78 al., 2012), which might provide crucial insight into the integrated ecological strategies employed
79 by particular taxa (Grime, 2006).

80 Despite these advances, important gaps in our syntheses of these trait patterns remain
81 (Moles, 2018). Large-scale analyses of functional diversity often look at only a single trait
82 (Moles et al., 2005, 2007, 2009), or include phylogeny in only a limited context (Swenson et al.,
83 2012; Swenson & Weiser, 2010). However, ecological strategies might manifest in the
84 combination of traits a plant exhibits (Grime, 2006; Pierce et al., 2017), and functional trait
85 values will vary among different clades, and can be influenced by evolutionary history (e.g.
86 phylogenetic constraint). For example, although trees may be taller on average in the tropics,
87 what constitutes tall may vary among different lineages. Thus, one important and outstanding
88 question is the extent to which traditional functional traits show evidence of phylogenetic signal/
89 conservatism (Blomberg et al., 2003; Wiens et al., 2010). Indeed, phylogenetic niche
90 conservatism, in general, has been upheld as the primary driver of present-day distributional
91 patterns among New World trees (Segovia et al., 2020). Understanding the extent to which the

92 functional trait values which contribute to a plant's niche are conserved, therefore, has
93 significant implications for understanding modern biodiversity.

94 Another important consideration is the extent to which certain functional traits correlate,
95 or group together, potentially indicating an integrated strategy. In part, this is a practical concern,
96 since if two traits are tightly correlated, but only one of the pair is easily measured, then it may
97 suffice to measure only that trait for which data acquisition is simpler. However, biologically, it
98 might also be the case that a plant's ecological strategy is better understood in the context of
99 multiple traits and that phylogenetic niche conservatism might manifest as coordinated evolution
100 among multiple characters. Underpinning both the question of phylogenetic signal and
101 coordinated evolution of traits is the question of appropriate evolutionary scale: at what
102 phylogenetic scale is variation in ecological strategies observed?

103 To begin addressing these questions, we examined five life-history traits that relate to
104 ecological strategies and are linked to plant and ecosystem function: height, seed mass, wood
105 density, leaf mass per area (LMA), and growth form. Plant height is important for its relationship
106 to carbon sequestration (Conti & Díaz, 2013; Moles et al., 2009) and competition for light
107 (Moles & Leishman, 2008), as well as influencing habitat type available for animal species (e.g.
108 closed canopy forest vs. open woodland). Seed mass is one determinant of dispersal syndrome
109 (Muller-Landau, Wright, Calderón, Condit, & Hubbell, 2008; Westoby, Falster, Moles, Vesk, &
110 Wright, 2002) and contributes to fecundity-survival (Muller-Landau, 2010) and shade tolerance
111 trade-offs (Wright et al., 2010). Wood density provides mechanical support and forms a 'wood
112 economics spectrum' (Chave et al., 2009). Leaf traits relate directly to photosynthetic strategy
113 and the leaf economics spectrum (Wright et al., 2004; Wright et al., 2010). Leaf mass per area
114 (LMA) represents a fundamental part of a plant's carbon-investment strategy and has been
115 correlated with leaf lifespan in woody plants.

116 While previous work on continental-scale diversity patterns (Moles et al., 2007, 2009;
117 Swenson et al., 2012; Swenson & Weiser, 2010) has found a signal for latitudinal gradients for
118 several traits, the inclusion of phylogeny has been limited. On the other hand, studies that have
119 related functional trait patterns to phylogeny (Moles et al., 2005; Zanne et al., 2014) have
120 utilized very broad phylogenetic scales (the entire seed plant or angiosperm phylogeny; but see
121 Hawkins et al., 2014). These extremely broad studies may obscure the underlying biological
122 explanations for observed patterns. Here, we adopt a targeted approach that allows us to account

123 for individual histories of particular lineages and provides a clearer understanding of empirical
124 patterns.

125 We examine the geographic distribution of this suite of life-history traits across the
126 Americas within two angiosperm clades: Ericales (Asterids) and Fabales (Rosids). Ericales is a
127 large clade within the Asterids, containing 22 taxonomic families and comprised of ~12,000
128 known species (Stevens, 2001; APG IV, 2016). Although resolution of deep divergences remains
129 contentious, the clade likely began diversifying between 100-125 million years ago (MYA; cf.
130 Magallón, Sánchez-Reyes, & Gómez-Acevedo, 2019; Rose et al., 2018; Stevens, 2001),
131 providing not only ample opportunity for phenotypic diversification, but also for species to be
132 exposed to several changes in habitat types and climate regimes. Similarly, Fabales represents a
133 ~80-100 MYA clade (Li et al., 2015; Stevens, 2001; Wikström, Savolainen, & Chase, 2001) that
134 has diversified into numerous ecosystems across the globe. Additionally, Fabales are of
135 particular note for their involvement with nitrogen-fixing bacteria (Sprenst, 2009), of which the
136 Fabaceae contributes greatly to the global nitrogen cycle.

137 Both Ericales and Fabales are present throughout the Americas and contribute to the
138 structure and diversity of a wide range of ecosystems, including tropical rainforests, forest
139 understories, open habitats, and polar environments (Hedwall, Brunet, Nordin, & Bergh, 2013;
140 Moquet et al., 2017; Stevens, 2001; ter Steege et al., 2006). Therefore, we expected that each of
141 these two clades would show sufficient variation in functional trait values to address the question
142 of which traits show phylogenetic conservatism and evidence of correlated evolution.
143 Nevertheless, because these clades are relatively distantly related (separated by over 100 MY),
144 we expected clade-specific quantitative differences in the trait values characterizing each clade,
145 even if overall qualitative phenotypic patterns were similar.

146

147 **Methods**

148 *Phylogenies & species lists.*

149 We obtained species-level Ericales and Fabales phylogenies from the Smith and Brown
150 (2018) seed plant phylogeny, and left polytomies unresolved. Species lists from this phylogeny
151 were used to query trait and geographic occurrence record databases (see below). To investigate
152 the interaction between traits and biogeographic distribution, we pruned each larger phylogeny
153 (Ericales or Fabales) based on trait-data availability to create subtrees for each trait, yielding the

154 following species-by-trait coverage after data cleaning and processing (percent indicates fraction
155 of species for which trait data was available) . Growth form: 2362 (Ericales, 14.9%), 4052
156 (Fabales, 16.5%). Plant height: 558 (Ericales, 3.5%), 593 (Fabales, 2.4%). Seed mass: 412
157 (Ericales, 2.6%), 1014 (Fabales, 4.1%). Wood density: 314 (Ericales, 1.9%), 367 (Fabales,
158 2.4%). LMA: 451 (Ericales, 2.8%), 625 (Fabales, 2.6%).

159 We illustrated the correspondence between species' trait values and their farthest
160 latitudinal extent from the equator (see *Occurrence Records* below) with phylogenetic heatmaps
161 for which we painted ancestral state reconstructions on branches and latitudinal categories
162 surrounding each phylogeny. Phylogenies were visualized using the R statistical computing
163 environment (R Development Core Team. 2011) with 'GGTREE' (Yu, Smith, Zhu, Guan, &
164 Lam, 2017) and 'TREEIO' (Wang et al., 2020) packages; reconstructions were calculated with
165 'PHYTOOLS' (Revell, 2012).

166 To determine phylogenetic clustering (niche conservatism) of species within latitudinal
167 categories, we calculated the average phylogenetic distance among species found in each
168 category. To assess whether these average distances were more extreme than expected by
169 chance, we performed 1000 random draws of n taxa from the phylogeny and calculated the
170 average distance among them for each draw (where n equals the number of species in a
171 category). Observed phylogenetic distances were deemed significant if they were more extreme
172 than 95% of distances obtained from these simulations.

173 We used phylogenetic principal component analyses (pPCA) to quantify our trait
174 syndrome, calculated with 'PHYTOOLS' and visualized with 'PCA3D' (Weiner, 2015). pPCA
175 accounts for the covariance structure of the phylogeny during ordination (Polly, Lawing, Fabre,
176 & Goswami, 2013), allowing one to measure the degree of correlation among variables beyond
177 what is expected from Brownian motion. We performed pPCA on the subsets of taxa for which
178 complete trait data was available (86 Ericales, 220 Fabales species), though we did not include
179 growth form (categorical trait) in the ordination. For these subsets, correlated evolution among
180 traits was assessed by phylogenetic generalized least squares (PGLS), using the variance-
181 covariance matrix of the subtree as the expected correlation structure, in order to quantify the
182 degree of correlation between traits beyond what would be expected solely from a Brownian
183 motion model of trait evolution.

184

185 *Occurrence records.*

186 Ericales and Fabales georeferenced occurrence records across all American countries
187 were obtained from the Global Biodiversity Information Facility (GBIF; www.gbif.org) and
188 processed using the ‘COORDINATECLEANER’ package (Zizka et al., 2019) in R to remove suspect
189 coordinates, fossil records, and match taxa to country. Records were further processed by
190 removing those with fewer than two decimal precision (~1.1 km) and matching all names to
191 those from the Smith and Brown (2018) phylogeny. From these records, each species was
192 assigned a unique latitudinal category based on the farthest *absolute* distance it was found from
193 the equator. We required at least three records within a category in order to assign a species to it.
194 Categories were: beyond 60° (polar); between 60° and 50° (hemi-boreal); between 50° and 40°
195 (temperate); between 40° and 20° (subtropical); between 20° and 0° (tropical). Results were
196 robust to changes in the boundaries of these latitudinal categories (data not shown).

197 Latitudinal gradients were visualized with ‘GGPLOT2’ (Wickham, 2016) in R. Trait
198 disparity maps were constructed as follows. For each clade and trait, we calculated standardized
199 effect size as $SES = (X - \bar{X}) / \sigma_x$, where X denotes species’ trait value, \bar{X} the mean clade-wide trait
200 value (Supplemental Figure S1), and σ_x is the standard deviation of the trait distribution. We
201 calculated the average SES found within a 0.5 degree grid cell in order to visualize ‘hot spots’
202 where trait values differ significantly from the overall clade average. Positive (negative) values
203 indicate grid cells with average trait values much larger (smaller) than the clade-wide average.
204 Scores are in units of standard deviations and can be interpreted as a Z-score. American terrain
205 maps were obtained from stamen maps (Stamen Design, under CC BY 3.0. Data
206 by OpenStreetMap, under CC BY SA) via the ‘GGMAP’ API (Kahle & Wickham, 2013).

207
208 *Trait and climate data.*

209 Trait data were obtained from the TRY Plant Trait Database (Kattge et al., 2020), by
210 querying all traits related to plant height, seed mass, wood density, LMA, and growth form for
211 our Ericales and Fabales species lists. Trait data were converted to standard units (seed mass—
212 mg; height—m; wood density—g/cm³; LMA—mg/mm²; growth form—unitless, see below),
213 entries flagged with risk factor >4 by TRY removed, and remaining trait values averaged for
214 each species. We log-transformed all traits, except growth form, prior to analyses. Growth form,

215 instead, was coded numerically as: 0—herbaceous, 0.5—shrub/ climber; 1—tree; *NA*—other;
216 however, we did not use such values as ordinated points.

217 We downloaded 30-sec climate data from worldclim.org (Fick & Hijmans, 2017)
218 describing mean annual temperature (MAT), precipitation (MAP), and elevation (ELV) of the
219 Americas. We then extracted MAT, MAP, and ELV values for each species' location using the
220 'RASTER' package in R, and calculated the minimum MAT, MAP, and maximum ELV for each
221 species across all of its sites.

222

223 *Bioregion mapping and trait distributions.*

224 For those species with complete functional trait information, we used their georeferenced
225 occurrence records to cluster species by biogeographical regions (bioregions), using the Infomap
226 Bioregions web application (<https://bioregions.mapequation.org>). Briefly, this algorithm takes
227 species' point occurrences as input and uses an information-theoretic clustering algorithm,
228 Infomap (Edler et al., 2016; Rosvall & Bergstrom, 2008), to form a bipartite network mapping
229 species to different bioregions. Rather than binning species by latitudinal-extrema, this approach
230 allowed the entirety of species' ranges to define potentially biologically-relevant geographical
231 boundaries that might separate groups of species using different ecological strategies. Parameters
232 used for clustering each clade by bioregion are given in Supplemental Table S1. To examine the
233 relationship between functional traits and the bioregions identified by the Infomap algorithm, we
234 calculated mean and standard error of functional trait values for all species assigned to each
235 bioregion.

236

237 **Results**

238 *Correspondence between geography & traits.*

239 From an initial set of 1,854,067 GBIF records, data cleaning methods yielded a final set
240 of 1,170,770 records (~63% retained). Among these, we observed a strong relationship between
241 species' latitudinal category and most life-history trait values (Figures 1), LMA being an
242 exception (Figure S2). Both Ericales and Fabales occurring at more extreme latitudes (particularly
243 beyond 50° from the equator) exhibited a high-latitude trait syndrome characterized by the
244 production of smaller seeds, shorter stature, lower wood density, being herbaceous or shrubby,
245 and lower LMA. The converse was generally true for taxa confined to within 20° of the equator.

246 Production of larger seeds, higher wood density and stature, and tree growth form typified the
247 lower-latitude manifestation of this trait syndrome.

248 Quantitatively, we found a latitudinal gradient in trait values for each trait and clade
249 (Figure 1), with the exception of LMA (Figure S2), which showed a comparatively modest trend.
250 Although both clades showed a graded tendency toward lower trait values at progressively
251 higher latitudes, the quantitative trait values within each latitudinal category differed between
252 Fabales and Ericales. For example, for both groups, species at polar latitudes were significantly
253 shorter than those at tropical latitudes ($p < 0.05$); however, at polar latitudes Fabales species were
254 significantly taller than Ericales species ($p < 0.05$; see Discussion). We also note that Fabales
255 tended to produce larger seeds, on average, than Ericales (Figure S1). Further, there was a strong
256 drop in median Fabales wood density at polar latitudes, which was not present for Ericales. To
257 some extent, these clade-specific differences might be attributable to differences in how Fabales
258 and Ericales are distributed with regards to temperature, precipitation, and elevation (Figure S3).

259 We found variation in the intensity of trait disparity for each clade and trait, using a
260 standardized effect size metric (see Methods; Figure 2). In general, for both clades, grid cells at
261 higher (lower) latitudes show average trait values that were significantly lower (higher) than the
262 within-clade average. Clade-specific differences in the extent of relative trait disparity were also
263 apparent. For example, while both groups had lower average wood density at polar latitudes,
264 Fabales species at polar latitudes showed significantly lower wood density compared to Ericales
265 taxa ($p < 0.05$), and Ericales taxa had a higher proportion of shrub taxa in polar regions than
266 Fabales.

267
268 *Correspondence between traits, phylogeny, and geography.*

269 Species demonstrated phylogenetically-conserved life-history trait values (Figure 3). In
270 addition to showing conserved *individual* trait values, clades within each lineage also showed
271 conserved *suites* of trait values. For example, Sapotaceae (Ericales) tended to be tall trees with
272 large seeds and higher wood density, while *Trifolium* (Fabales) tended to be shorter statured,
273 herbaceous or with lower wood density, and produce smaller seeds. Overall, congeneric species
274 were similar in their functional trait values, indicating that within-genus comparisons would
275 generally not provide observable variation in the functional traits we examined here. However,
276 comparisons of con-ordinal species from differing families (e.g. comparing Sapotaceae,

277 Ericaceae, and Primulaceae) permitted observable variation in functional trait values, indicating
278 that this phylogenetic scale is better suited for this trait syndrome. Comparisons made by
279 grouping Ericales and Fabales together, however, could obscure the ability to see variation in this
280 syndrome (see Discussion).

281 In general, there was also phylogenetic conservatism of latitudinal categories (colored
282 bars surrounding phylogenies in Figure 3; Figure 4). Species tended to be significantly more
283 closely related to species in the same latitudinal category (i.e. diagonal elements in Figure 4 tend
284 to have lower values than other elements in the same row or column). Additionally, species
285 inhabiting polar latitudes tended to be more closely related to each other than to species in other
286 categories (i.e. the average polar-polar phylogenetic distance is usually among the smallest
287 values in each table). Overall, therefore, taxa showed phylogenetically-conserved life-history
288 trait syndromes, which corresponded to the latitudinal-extrema at which the species are found.
289 LMA was an exception to this trend, however; this trait showed little connection to phylogeny or
290 latitudinal extrema.

291 Although data from both Ericales and Fabales was consistent with these trends, there
292 were notable differences between the two clades in terms of how trait values and latitudinal
293 extrema were distributed along their respective phylogenies. For example, although both clades
294 had similar fractions of tropical species sampled for plant height (Figure S5 for proportion of
295 species in each latitudinal category), tropical Fabales typically were clustered in the phylogeny,
296 whereas tropical Ericales were distributed throughout multiple clades. The overall effect was that
297 Ericales trait syndromes generally corresponded to Linnaean families, whereas the Fabales did
298 not fall as easily into typical family or tribe categories (see Discussion).

299
300 *Categorizing trait syndromes.*

301 Although not every species was represented for every trait (see Methods), by examining
302 multiple traits across each plant clade, the correspondence between phylogeny and functional
303 trait values suggested clades could be categorized by trait syndromes (Figure 5a,b). In general,
304 the phylogenies showed that clusters of species exhibited shared suite of traits, indicating
305 phylogenetic conservatism of this functional trait syndrome. LMA is an exception to this pattern,
306 appearing instead as a ‘barcode’ pattern with very little relationship to phylogeny (Figure 5a,b).
307 This trait syndrome was quantified using phylogenetic principal components analysis (pPCA);

308 Figure 6). For both clades, the first two principal components (PCs) accounted for over 88% of
309 the total variance, though we include the first three here ($>95\%$ variance explained; Figure 6).
310 For Fabales, tropical and subtropical species clustered separately from temperate and boreal
311 species, and this separation is visible in all 3 PCs, suggesting two broad trait patterns at the
312 transition from tropical to temperate latitudes. For Ericales, there was greater separation between
313 temperate taxa and those found in boreal latitudes (3 groups). Thus, the manifestation of the trait
314 syndrome differs between these two clades (see Discussion).

315 We also examined the evidence for correlated evolution of functional trait values. We
316 illustrated this graphically in Figure 5c,d, where phylogenies are mapped onto the trait space of
317 each pairwise trait combination. For many trait combinations, there was a visually apparent
318 correlation between the traits examined. Further, we utilized PGLS to ask whether or not these
319 correlations were significant *beyond* what we would expect under a Brownian motion model of
320 trait evolution (p-values in lower right corner of each plot). Most, but not all, PGLS correlations
321 were found to be significant. LMA, in particular, did not show evidence of correlated evolution.
322 Our results suggest that clades possess a shared suite of functional trait values that may have
323 evolved in a correlated manner, though greater coverage of these functional traits would help
324 strengthen this claim.

325
326 *Bioregion mapping and trait distributions.*

327 In addition to latitudinal categories, for those species with complete functional trait
328 information, we also allowed species' ranges to define biogeographical clusters (see Methods),
329 which in turn might be expected to use different functional-trait strategies. For both clades, we
330 obtained a similar number of clusters (Ericales: 11; Fabales: 10), and clusters converged on
331 similar geographic regions (Figure S6). When measuring average trait values among all species
332 assigned to each cluster, we found that clusters tended to exhibit consistent trait patterns (e.g. all
333 low or all high trait values, excepting LMA, as in above analyses; insets of Figure S6).
334 Additionally, geographically adjacent regions tended to exhibit similar trait values. Seed mass,
335 however, showed an abrupt transition dividing tropical clusters (large average seed mass) from
336 extra-tropical (low average seed mass) ones. Both trait data limitations and sparse sampling from
337 certain regions (e.g. southern South America) influenced the biogeographical clusters obtainable

338 in this analysis and enhanced data collection should continuously update and refine the clusters
339 thus identified.

340

341 **Discussion**

342 Our results provide evidence among New World Ericales and Fabales of a latitudinally-
343 graded (Figures 1-2) and phylogenetically-conserved (Figures 3-5) functional-trait syndrome
344 involving height, seed mass, wood density, and growth form, but not LMA. Moving poleward,
345 species tend to exhibit progressively shorter stature, smaller seeds, lower wood density, and
346 become predominantly herbaceous or shrubby. pPCA for those taxa with complete trait data
347 suggest that this trait syndrome can be classified based on the clustering of species into separate
348 groups in trait-space (Figure 6). Additionally, the comparative analyses provide evidence that the
349 life-history traits involved in this syndrome may have evolved in a correlated manner (Figure
350 5c,d).

351 Our results also highlight quantitative, clade-specific, differences in the manifestation of
352 this syndrome, illustrating the need for targeted phylogenetic approaches and examining
353 potential patterns at different phylogenetic scales. While previous studies have made strides in
354 examining broad intersections of ecological function and plant traits, they have typically
355 incorporated phylogeny in a limited sense (e.g. Swenson et al., 2012), or used an extremely
356 broad phylogenetic scale (e.g. Zanne et al., 2014). However, just as ecological studies have
357 gained appreciation for the appropriate choice of spatial scale in study design, choice of
358 phylogenetic scale can also be an important decision. To observe variation in the trait syndrome
359 we describe here required looking beyond the level of congeners, which, for those traits we
360 examined, tended to have very similar trait values, and our results suggest that comparisons of
361 species sampled from con-ordinal families provided the best scale at which this trait syndrome
362 could be quantified.

363 The importance of scale can be illustrated by examining seed mass measurements. If
364 Fabales and Ericales seed mass measurements are lumped together, latitudinal differences among
365 species whose ranges extend to temperate, boreal, and polar areas are largely obscured due to the
366 statistically significant differences in average seed mass between the two groups (Figure S1).
367 There are also clade-specific differences in plant height among taxa within the same latitudinal
368 category. For example, among polar-latitude species, Fabales are significantly taller than Ericales

369 ($p < 0.05$, Figure 1, compare blue boxes), but at temperate latitudes, the situation is reversed and
370 Ericales are taller ($p < 0.05$, Figure 1, compare green boxes). In Figure S3, we show that, at polar
371 latitudes Ericales occur at sites with lower average temperature and higher average elevation
372 than Fabales. In contrast, in temperate regions, Ericales tend to occur at sites with lower average
373 elevation and higher average precipitation. These differences in how taxa are distributed
374 according to smaller-scale climatic factors might help explain some of the clade-specific
375 differences in the manifestation of the trait syndrome described here, particularly height and seed
376 mass. We also note that other trait syndromes might be best observed at quite different
377 phylogenetic scales. For instance, the disparity in traits relating to chemical defense against
378 herbivory among co-occurring congeneric species of *Inga* is known to be quite high (Sedio,
379 Parker, McMahon, & Wright, 2018). Thus, careful and study-specific choice of phylogenetic
380 scale can be important in teasing out processes of interest.

381 Unlike Ericales (Asterids), Fabales (Rosids) are part of the nitrogen-fixing clade (Friis,
382 Crane, & Pedersen, 2011), and form root nodules in association with Rhizobia bacteria to fix
383 atmospheric nitrogen. Further, in higher-latitude environments, Fabales tend to preferentially
384 produce indeterminate nodules, whereas determinate nodules are utilized more in tropical forests
385 (Sprent, 2009). Thus, Fabales taxa show a distinct high-latitude nitrogen-fixing phenotype. It is
386 possible that such differences in the nitrogen-fixation mode also contribute to differences in how
387 these two clades manifest this trait syndrome and how they are arrayed along elevational and
388 precipitation gradients, particularly at higher latitudes, where nitrogen may be more limiting
389 (Reich & Oleksyn, 2004).

390 Although we focused on latitudinal categories for species, we also clustered species into
391 bioregions using the InfoMap algorithm (see Methods; Figure S6; Edler et al., 2016). That both
392 Ericales and Fabales species clustered into a similar number of roughly geographically-
393 convergent bioregions could suggest these regions represent areas with distinct ecological
394 strategies. Indeed, the functional trait values for height, seed mass, and wood density within each
395 bioregion tended to coincide with the presence of the functional trait syndrome we describe here,
396 and LMA showed little relationship with any of the bioregions. Geographically-proximate
397 bioregions tended to have similar trait values, suggesting that clustering species by bioregions
398 supplemented rather than supplanted the latitudinally-based analyses, and that both methods of
399 organizing species illustrate the occurrence of a similar trait syndrome. Clade-specific

400 differences were also apparent in the bioregions analysis. Most notably, tropical Ericales were
401 divided into two bioregions, whereas tropical Fabales formed a single, large cluster.

402 The manifestation of this trait syndrome, occurring under a variety of geographically-
403 based delimiting methods, could have originated under a variety of scenarios. For instance, this
404 trait syndrome may represent a resource acquisition strategy whose manifestation is primarily
405 influenced by soil nutrient availability and growing season length (i.e. the time in which
406 available nutrients can be utilized). In particular, we note that, at higher latitudes, the
407 manifestation of this trait syndrome is qualitatively similar to the suite of traits associated with
408 ‘pioneer,’ or early successional-stage, tropical species (e.g. smaller stature, lower seed mass,
409 LMA, and wood density; Wright et al., 2010). ‘Pioneer,’ here, refers to those plants that colonize
410 disturbed patches or gaps first and display enhanced growth rates under favorable conditions. In
411 tropical soils, nutrient availability is generally lower than at higher absolute latitudes (Reich &
412 Oleksyn, 2004). Treefall gaps can help to unlock some of these nutrients and make them
413 available for early colonizers employing a resource-acquisitive strategy. As succession proceeds,
414 plant growth within the gap again sequesters those nutrients and the manifestation of the
415 resource-acquisition strategy changes, typically characterized by taller stature trees with larger
416 seeds and higher wood density.

417 At higher latitudes, soil nutrients are relatively more abundant than in tropical soils
418 (Reich & Oleksyn, 2004), and recent glaciation cycles have further helped to enhance deposition
419 of these nutrients (Chadwick et al., 1999; Van Andel, 1994). However, also at progressively
420 higher latitudes, the incident angle of light changes, resulting in a shorter effective growing
421 season for plants. This, in turn, limits the time over which plants can utilize these available
422 nutrients, and might favor a more resource-acquisitive strategy in these areas as well. The effects
423 of light seasonality are latitudinally-graded and would predate the onset of global cooling in the
424 Eocene (Graham, 2011). Additionally, temperature seasonality imposes limits on growing-season
425 length at higher latitudes, favoring a more resource-acquisitive strategy as well.

426 The manifestation of the trait syndrome we describe, and its similarity to a tropical
427 pioneer species strategy, might, therefore, be explained as a strategy to deal with both light and
428 temperature seasonality in a relatively nutrient-rich environment with a short growing season.
429 This trait syndrome could have arisen in several different ways. For example, it may have
430 originated through the dispersal of tropical pioneer lineages preadapted to have a more resource-

431 acquisitive strategy. Or it might have arisen independently at higher latitudes in response to light
432 seasonality prior to the onset of global cooling, when the flora at such latitudes consisted of both
433 boreal and tropical elements (e.g. boreotropical forests; Dick & Pennington, 2019; Graham,
434 2011). Under this hypothesis, lineages found in colder environments might represent longer-
435 lasting endemics of past, non-analogous biomes, whose ecological strategies for addressing light
436 seasonality became advantageous for temperature seasonality as well. Since light seasonality
437 predates global cooling, and a similar trait syndrome occurs among tropical pioneers, where
438 cold-tolerance is not a factor, it may be that the higher-latitude trait syndrome we observe is not a
439 direct cold adaptation *per se*. Further work investigating timing of shifts in trait values with the
440 biogeographic history of lineages undergoing those shifts would be invaluable to tease apart
441 these scenarios or discover alternative explanations.

442 Our ability to describe the correlated evolution among this collection of (rather than
443 individual) traits was limited significantly by data availability. In particular, wood density
444 measurements were primarily for tropical tree species, and the extreme southern latitudes of
445 South America and regions of the Amazon basin suffered from relatively poor species sampling.
446 Given the destructive and labor-intensive methodology required for obtaining wood density, it is
447 perhaps unsurprising this trait would be limiting. However, greater sampling of temperate and
448 boreal wood densities for angiosperm species would have greatly enhanced our dataset. We
449 suggest that as an avenue for further data collection, along with greater species sampling at
450 extreme southern latitudes for Ericales and Fabales.

451
452 *Conclusion*

453 We suggest the tendency for a biogeographically-consistent and phylogenetically-
454 conserved functional trait syndrome involving height, seed mass, wood density, and growth form
455 (and excluding LMA) among Ericales (Asterids) and Fabales (Rosids) New World taxa. By
456 focusing on specific lineages, we are able to illustrate that variation in this trait syndrome is best
457 observed by sampling species from con-ordinal families. Quantitative differences in the
458 manifestation of this trait syndrome among Ericales and Fabales taxa occurring in similar regions
459 highlight the importance of matching phylogenetic scale with the research question(s) and pose
460 potential new research avenues. We interpret the manifestation of this trait syndrome at higher
461 latitudes as a resource-acquisitive strategy adapted to relatively high soil nutrient content coupled

462 with a short growing season, a situation somewhat analogous to that faced by gap specialists in
463 tropical forest communities which exhibit a similar suite of traits.

464

465

466

467 **Figure legends**

468

469 Figure 1. Latitudinal gradients for each clade (Ericales, *left panels*; Fabales, *right panels*) and
470 functional trait (height, seed mass, wood density, growth form). For both clades, taxa confined to
471 tropical latitudes show significantly higher trait values than those which reach polar latitudes
472 ($p < 0.05$ in all cases), and there is a tendency for a graded increase in trait values with decreasing
473 distance from the equator. This trend is interpreted as a trait syndrome since it manifests across
474 multiple traits. We omit LMA here because it did not show a strong latitudinal gradient (see
475 Figure S2 for LMA results), though tropical taxa still possess higher median LMA values than
476 polar ones. Differences between Fabales and Ericales are discernible, indicating quantitative
477 differences in the manifestation of this trait syndrome (see Discussion). (*Boxplots indicate*
478 *median values. Growth form is plotted using average values (points) and standard deviations*
479 *(lines) because this trait was treated differently than others in the analyses (see Methods).)*

480

481 Figure 2. Geographic heatmaps showing the extent of trait disparity for each clade (Ericales, *left*
482 *panels*; Fabales, *right panels*) and functional trait (height, seed mass, wood density, growth
483 form). LMA is omitted because it did not show a strong latitudinal gradient (see Figure S2).
484 Except for growth form, grid cell colors indicate the extent to which the average trait value in
485 that grid cell differs from the overall average across the entire clade (standard deviation units,
486 e.g. z-score; see Methods), with red (purple) grid cells indicating values much lower (higher)
487 than the average. For growth form, grid cells are colored by the most common (modal) growth
488 habit in that cell (blue: tree; green: shrub; red: herbaceous). In general, South American tropics
489 have trait values higher than the average and are dominated by trees (though many more Fabales
490 are herbs here), while polar latitudes have trait values lower than the average and a greater
491 proportion of herbs (though many more Ericales are shrubs here). Maps for the same trait share a

492 common legend, however, maps of different traits do not and so colors are not directly
493 comparable between different traits.

494

495

496 Figure 3. Phylogenetic conservatism of functional trait values and latitudinal extrema for
497 Ericales (*left column*) and Fabales (*right column*). Species names are colored according to
498 observed trait values. Colors along phylogenetic branches depict the ancestral state
499 reconstruction for each functional trait, with warmer (cooler) colors indicating larger (smaller)
500 trait values. Colored bars surrounding each phylogeny illustrate the assigned latitudinal category.
501 Bar colors are as in Figure 1: polar (blue), hemiboreal (cyan), temperate (green), subtropical
502 (yellow), tropical (red). In order to maintain readability, for traits with data available for more
503 than 500 species, only a random sample of 500 tips are included in this figure (see Figure S4 for
504 phylogenies without any tips excluded). However, for all analyses, we included all species. For
505 traits other than LMA, trait values are conserved, with closely related species having similar trait
506 values. Species also tend to show conservation of latitudinal category, meaning that similarly
507 colored bars around each phylogeny tend to be grouped together. Further, clades within each
508 lineage tend to show conserved suites of traits when one looks across multiple traits within each
509 column. The distribution of both functional trait values and of latitudinal category differs
510 noticeably between Ericales and Fabales. Although similar fractions of each clade are
511 represented in each latitudinal category (Figure S5), extra-tropical Fabales taxa cluster together
512 in one portion of the phylogeny, whereas they are distributed throughout the Ericales phylogeny.

513

514

515 Figure 4. Mean pairwise phylogenetic distances (MPD) among taxa within each latitudinal
516 category, for Ericales (*top row*) and Fabales (*bottom row*). Matrices are symmetrical, and we
517 show only the lower triangle of each. Darker (lighter) color indicates smaller (larger)
518 phylogenetic distances, indicating species are more (less) closely related on average. In general,
519 species in the same latitudinal category tend to be more closely related (i.e. the diagonal
520 elements are usually darker color than other elements in the same row/column), and polar species
521 tend to be more closely related to each other than any other combination (i.e. the polar-polar
522 element is usually one of the smallest values in the table). More generally, species outside of the

523 tropics tend to be more closely related to each other than to tropical or subtropical species (the
524 converse is also true). Most values were statistically significant (see Methods). ($p < 0.001$, #; $p <$
525 0.05 , *; not significant, NS.)

526

527

528 Figure 5. *Top panels*: Phylogenetic heatmaps for (a) Ericales and (b) Fabales taxa for which
529 complete trait information is available, indicating a conserved trait syndrome. The first column
530 of trait values (*Lat.*) corresponds to the latitudinal extrema (colors are as in Figures 1 and 3). For
531 functional traits, we include height (*HT*), seed mass (*SD*), wood density (*WD*), and *LMA* here
532 because these traits were used in tests of correlated evolution (bottom panels) and phylogenetic
533 principal components analysis (pPCA, Figure 6). Growth form was excluded in those analyses
534 because it is not an ordinated trait. Colors for each trait are as in the ancestral state
535 reconstructions of Figure 3, and bottom panels of this same figure. In general, but with the
536 exception of *LMA*, species tend to show blocks of trait values consistent with a trait syndrome.
537 This trait syndrome corresponds well to species' assigned latitudinal category.

538 *Bottom panels*: Tests for correlated evolution among those functional traits depicted in top panels
539 for Ericales (c) and Fabales (d) taxa. The grids show correlations of each pairwise trait
540 combination, with the phylogeny mapped onto the two-dimensional trait space. Along the
541 diagonal of the grid, we plot ancestral state reconstructions for each trait on the phylogenies
542 shown in (a) and (b) above. With the exception of *LMA*, correlations between traits are
543 discernible. We utilized phylogenetic generalized least squares (PGLS) to determine if
544 correlations were significant *beyond* what would be expected under a Brownian motion model of
545 trait evolution (p-values indicated in lower right corners of each plot). Correlations with *LMA*
546 were generally not significant, whereas other correlations were. Though relatively few species
547 have sufficient trait data to allow for these comparative methods, this is consistent with
548 correlated evolution of these traits—thus indicating that the relative trait values defining the
549 syndrome we describe here might have evolved in concert.

550

551

552 Figure 6. Phylogenetic principal components analysis (pPCA) among height, seed mass, wood
553 density, and *LMA*, for Ericales and Fabales taxa (as indicated by arrows in the plot). Growth

554 form was excluded in the ordination because it is not an ordinated trait. For both clades, the first
555 two principal components capture >88% of the total variance, but we include the first three
556 components here (>92% total variance). Small points indicate individual species, while larger
557 circles indicate centroids of each group. The groups are colored based on latitudinal category
558 (colors are as in Figure 1). For both Ericales and Fabales, species within different latitudinal
559 categories cluster separately in the composite trait space. This is consistent with the latitudinally-
560 graded multi-trait syndrome we describe here. However, there are differences between the two
561 clades. Fabales shows two main clusters, with tropical and subtropical species clustering
562 separately from temperate, hemiboreal, and polar ones. Ericales, however, shows greater
563 separation between temperate and hemiboreal/polar taxa (three clusters). Thus, the manifestation
564 of the trait syndrome differs between these two groups.

565

566 **Data availability statement**

567

568 Species lists, subtrees, and trait tables are available for download from Dryad Digital Repository:
569 < <https://doi.org/10.5061/dryad.wdbrv15mg> > (Figueroa & Smith, 2020).

570

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572

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744 **Biosketch**

745

746 **Hector Figueroa** endeavors to understand how historical contingency and physiological
747 constraint drive current patterns of phenotypic distribution. Leveraging a background in
748 biochemistry and physiology, he asks community assembly questions bridging ecology and
749 evolutionary biology. By incorporating phylogeny and natural history into ecological hypotheses,
750 questions of coexistence and biodiversity can be framed in biologically-meaningful ways. His
751 current research focuses on the distribution of angiosperm life-history traits across the Americas
752 in relation to survival in extreme environments, such as polar climates, alpine summits, and arid
753 deserts.

754

755 **Stephen A. Smith** aims to better understand the evolution of innovation and complexity in
756 plants and how those changes intersect with molecular evolution. This often requires working
757 with new data types as well as the development of new approaches and techniques. Currently, his
758 research focuses on the evolution of several large eudicot lineages and how movements into new
759 environments correspond to morphological and genomic changes.

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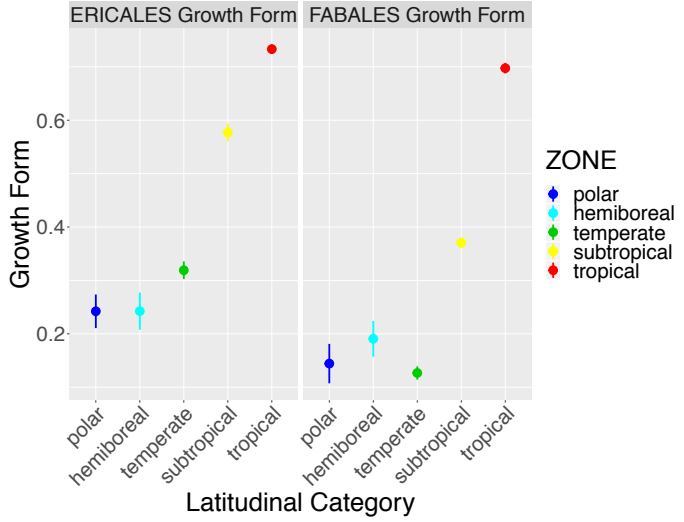
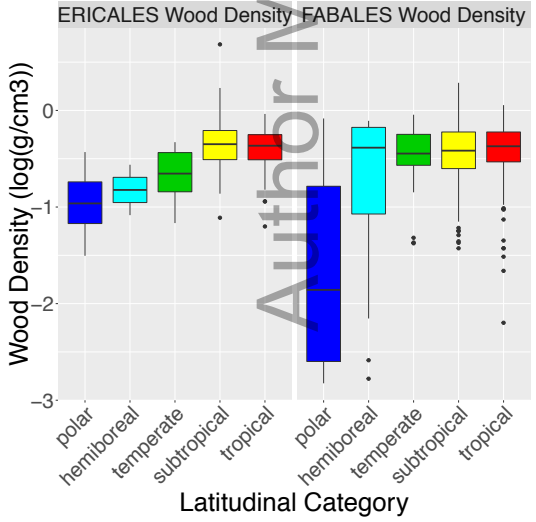
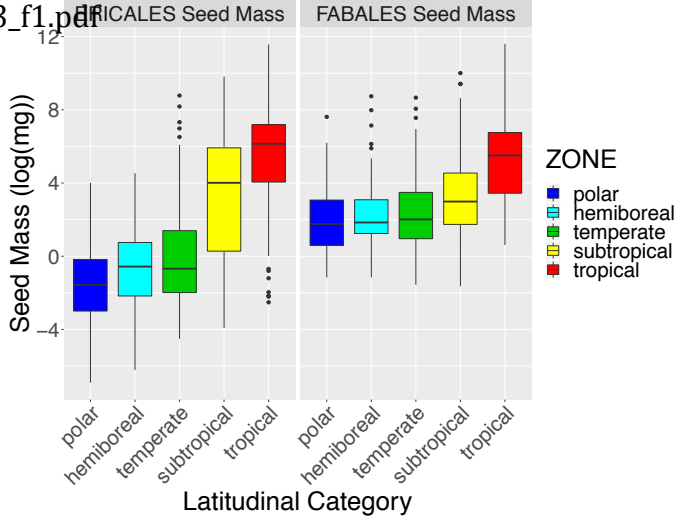
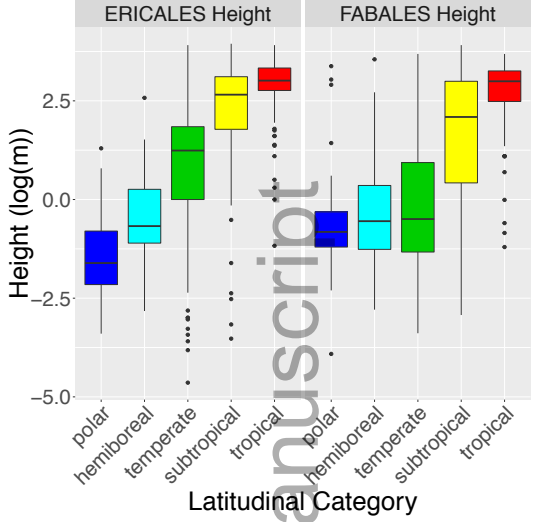
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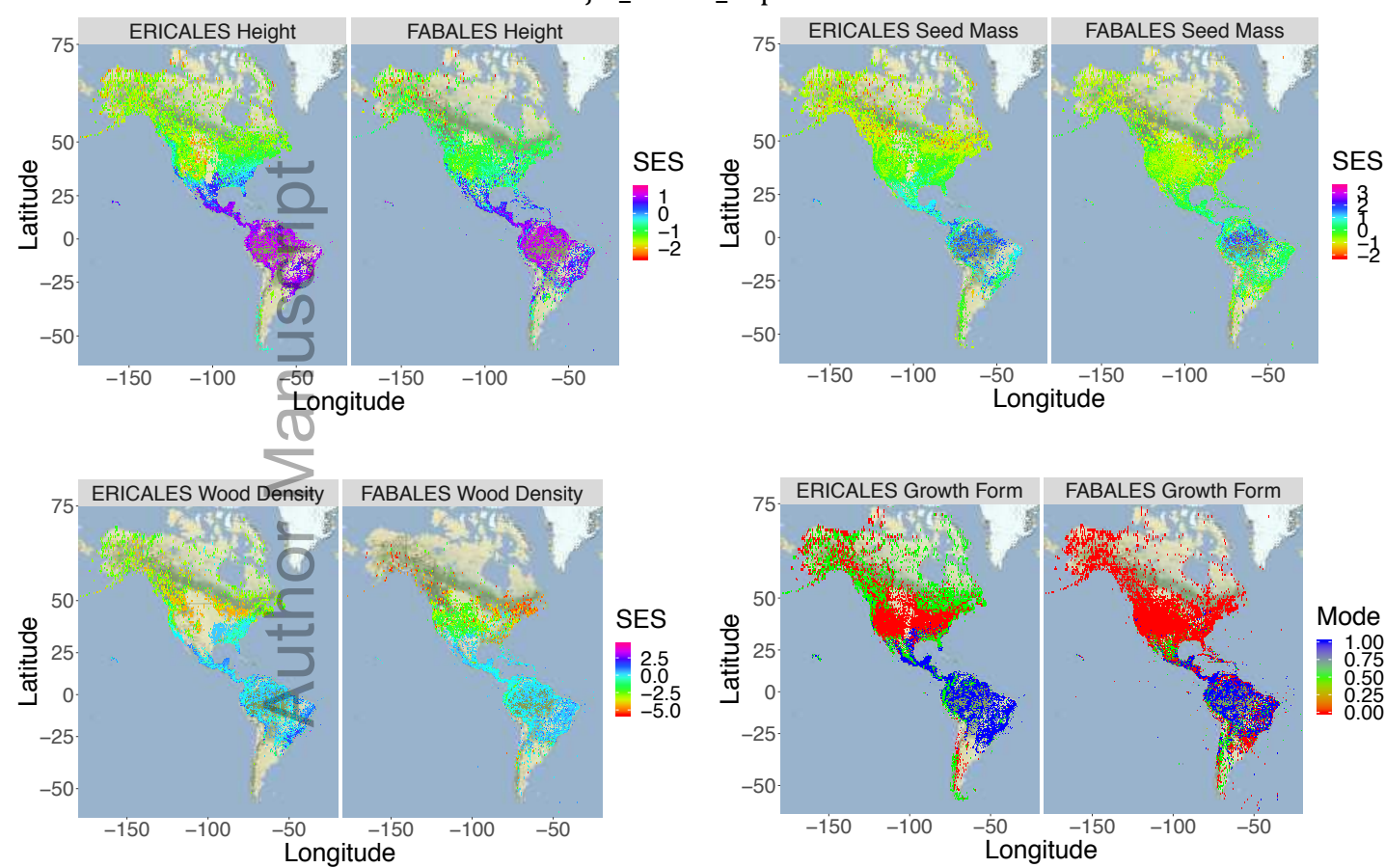
762 **Author contributions**

763 H.F. conceived of the study and analyzed the data. H.F. and S.A.S. collected some of the data.

764 H.F. wrote the first draft of the manuscript. H.F. and S.A.S. contributed to editing and revising

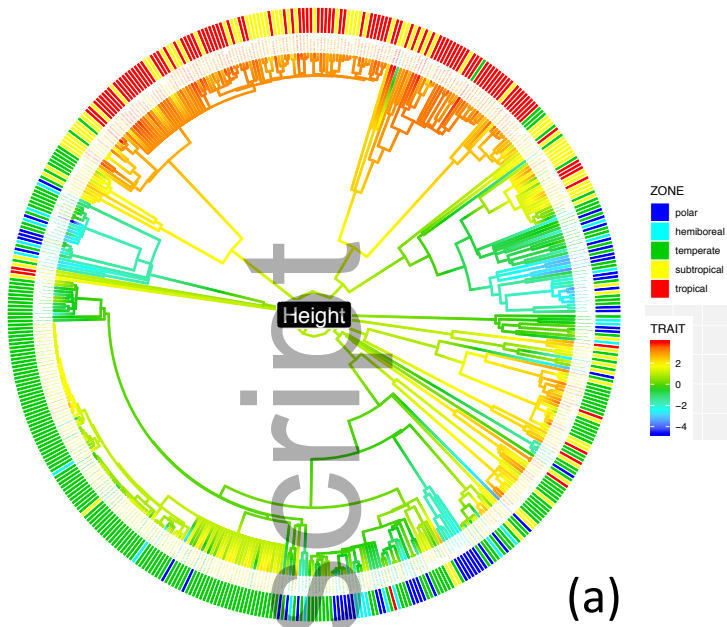
765 the final version of the manuscript.



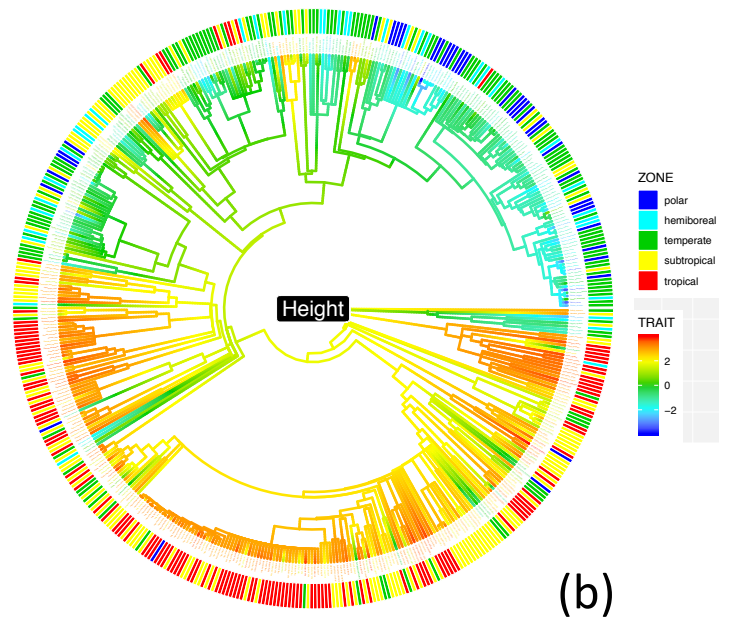


ERICALES

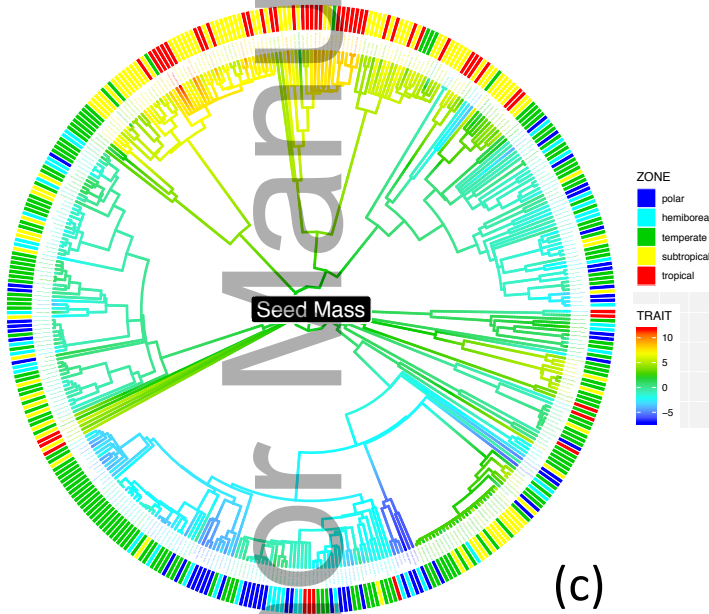
FABALES



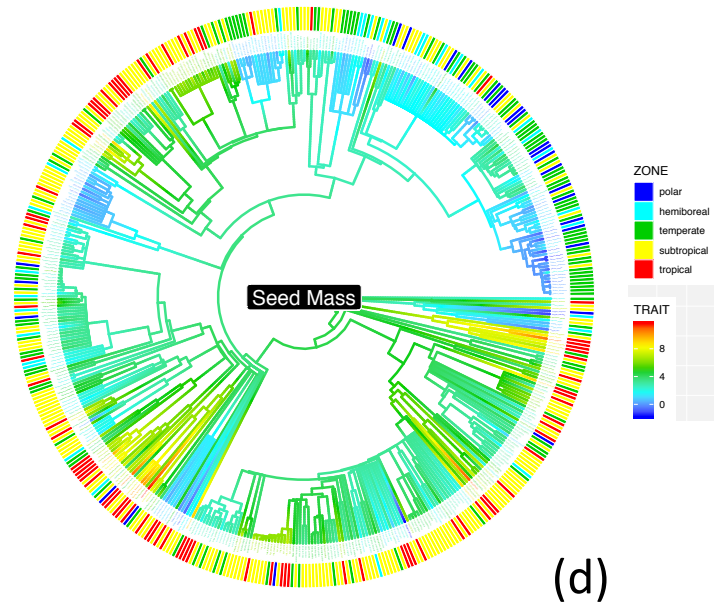
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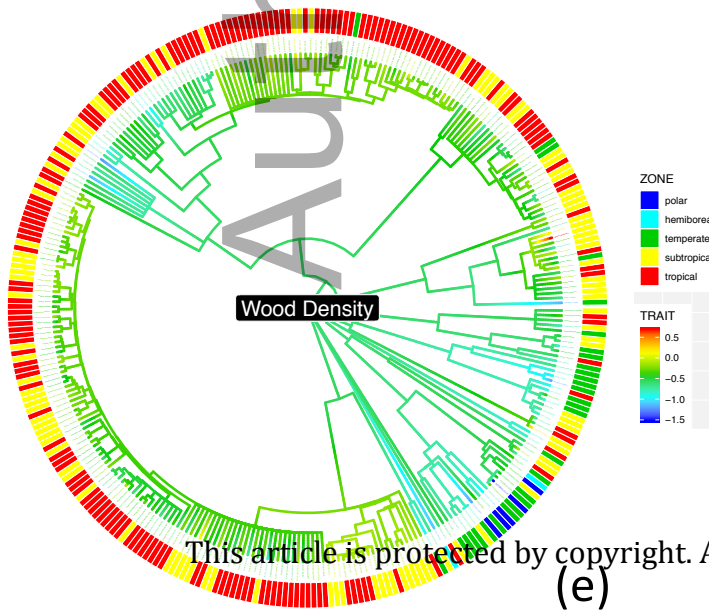
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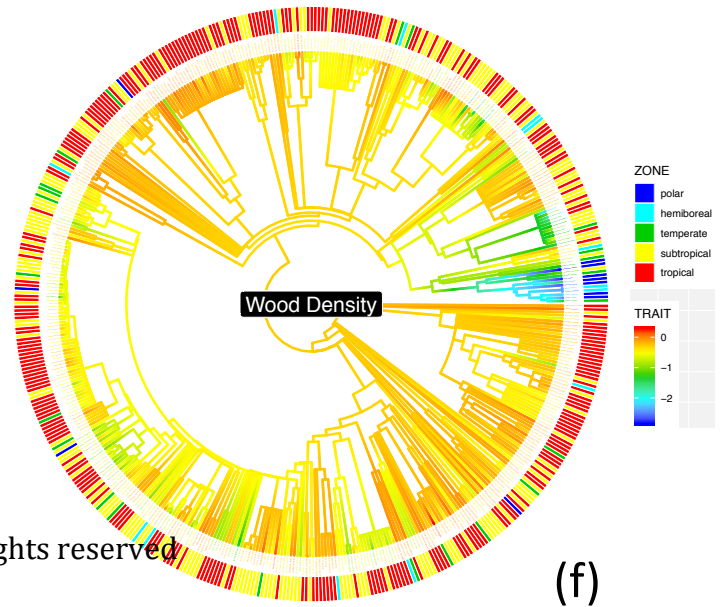
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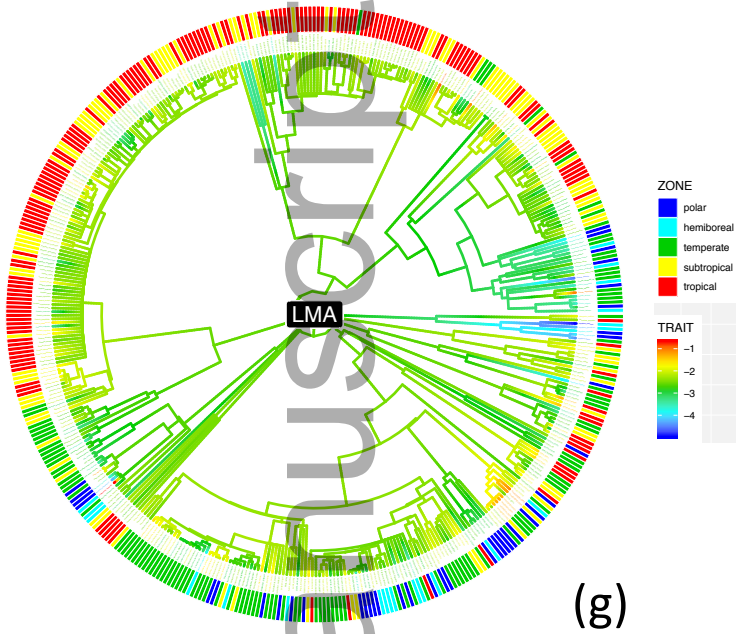
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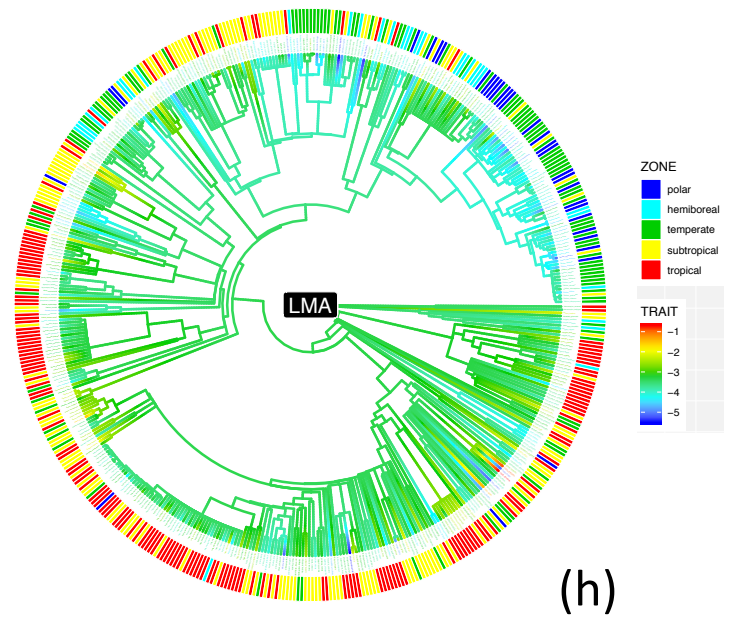
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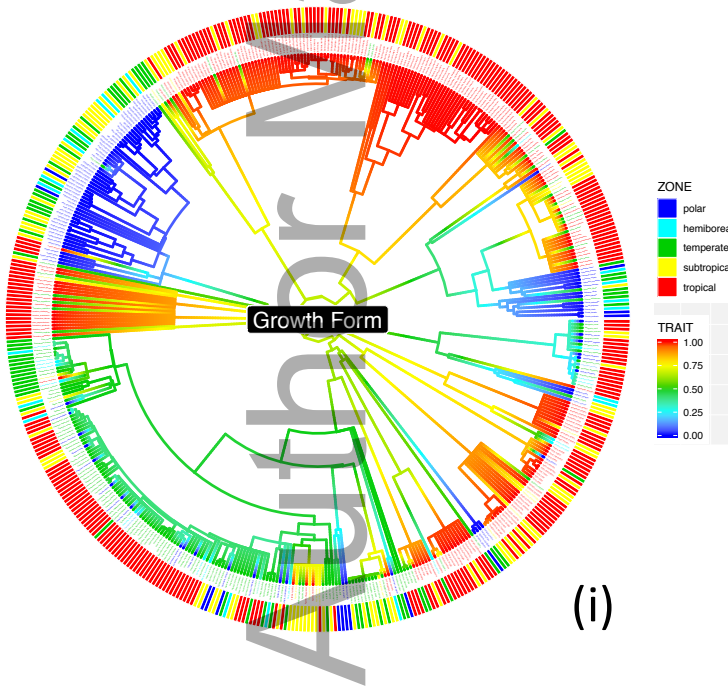
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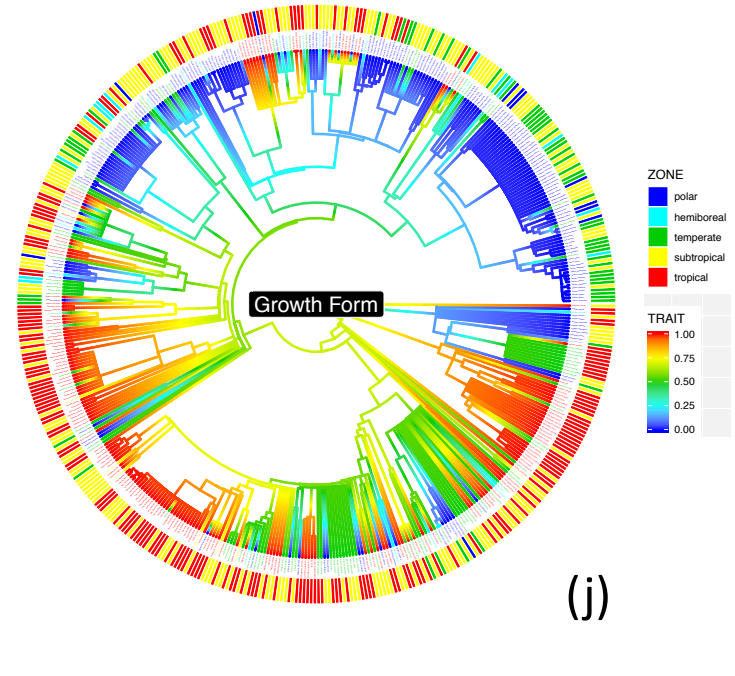
(g)



(h)



(i)



(j)

ERICALES Height					
	<i>polar</i>	<i>hemiboreal</i>	<i>temperate</i>	<i>subtropical</i>	<i>tropical</i>
<i>polar</i>	0.674 _e				
<i>hemiboreal</i>	0.700 _e	0.695 _e			
<i>temperate</i>	0.670 _e	0.685 _e	0.589 _e		
<i>subtropical</i>	0.874 _e	0.888 _e	0.871 _e	0.732 _e	
<i>tropical</i>	0.902 _e	0.912 _e	0.893 _e	0.705 _e	0.620 _e

ERICALES Seed Mass					
	<i>polar</i>	<i>hemiboreal</i>	<i>temperate</i>	<i>subtropical</i>	<i>tropical</i>
<i>polar</i>	0.686 _e				
<i>hemiboreal</i>	0.726 _e	0.726 _e			
<i>temperate</i>	0.742 _e	0.757 _e	0.761 _e		
<i>subtropical</i>	0.838 _e	0.838 _e	0.833 _e	0.777 _e	
<i>tropical</i>	0.873 _e	0.882 _e	0.874 _e	0.808 _e	0.766 _e

ERICALES Wood Density					
	<i>polar</i>	<i>hemiboreal</i>	<i>temperate</i>	<i>subtropical</i>	<i>tropical</i>
<i>polar</i>	0.277 _e				
<i>hemiboreal</i>	0.344 _{ns}	0.476 _{ns}			
<i>temperate</i>	0.710 _{ns}	0.836 _e	0.793 _e		
<i>subtropical</i>	0.938 _e	0.944 _e	0.916 _e	0.730 _e	
<i>tropical</i>	0.951 _e	0.951 _e	0.925 _e	0.711 _e	0.641 _e

ERICALES LMA					
	<i>polar</i>	<i>hemiboreal</i>	<i>temperate</i>	<i>subtropical</i>	<i>tropical</i>
<i>polar</i>	0.650 _e				
<i>hemiboreal</i>	0.671 _e	0.664 _e			
<i>temperate</i>	0.690 _e	0.699 _e	0.692 _e		
<i>subtropical</i>	0.860 _e	0.862 _e	0.845 _e	0.751 _e	
<i>tropical</i>	0.897 _e	0.899 _e	0.875 _e	0.734 _e	0.676 _e

ERICALES Growth Form					
	<i>polar</i>	<i>hemiboreal</i>	<i>temperate</i>	<i>subtropical</i>	<i>tropical</i>
<i>polar</i>	0.679 _e				
<i>hemiboreal</i>	0.707 _e	0.704 _e			
<i>temperate</i>	0.735 _e	0.728 _e	0.729 _e		
<i>subtropical</i>	0.807 _e	0.804 _e	0.808 _e	0.819 _e	
<i>tropical</i>	0.804 _e	0.817 _{ns}	0.829 _e	0.838 _e	0.811 _e

FABALES Height					
	<i>polar</i>	<i>hemiboreal</i>	<i>temperate</i>	<i>subtropical</i>	<i>tropical</i>
<i>polar</i>	0.436 _e				
<i>hemiboreal</i>	0.533 _e	0.571 _e			
<i>temperate</i>	0.547 _e	0.597 _e	0.593 _e		
<i>subtropical</i>	0.692 _e	0.711 _e	0.690 _e	0.669 _{ns}	
<i>tropical</i>	0.750 _e	0.766 _e	0.733 _e	0.658 _e	0.595 _e

FABALES Seed Mass					
	<i>polar</i>	<i>hemiboreal</i>	<i>temperate</i>	<i>subtropical</i>	<i>tropical</i>
<i>polar</i>	0.462 _e				
<i>hemiboreal</i>	0.551 _e	0.590 _e			
<i>temperate</i>	0.549 _e	0.597 _e	0.591 _e		
<i>subtropical</i>	0.674 _e	0.687 _e	0.673 _e	0.670 _e	
<i>tropical</i>	0.710 _e	0.715 _e	0.703 _e	0.692 _e	0.698 _e

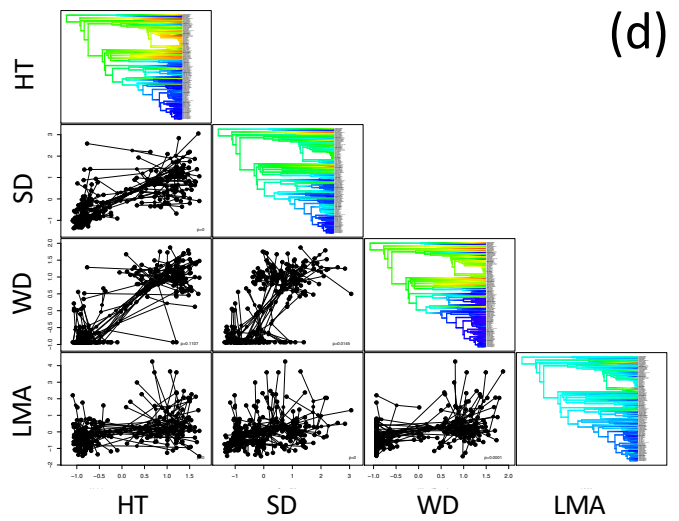
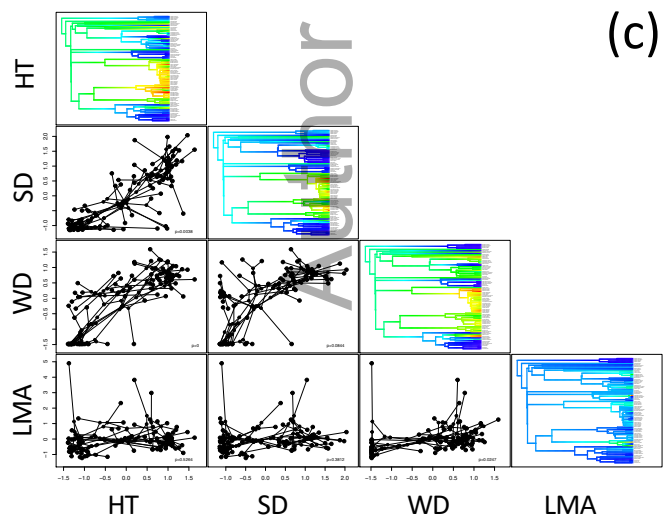
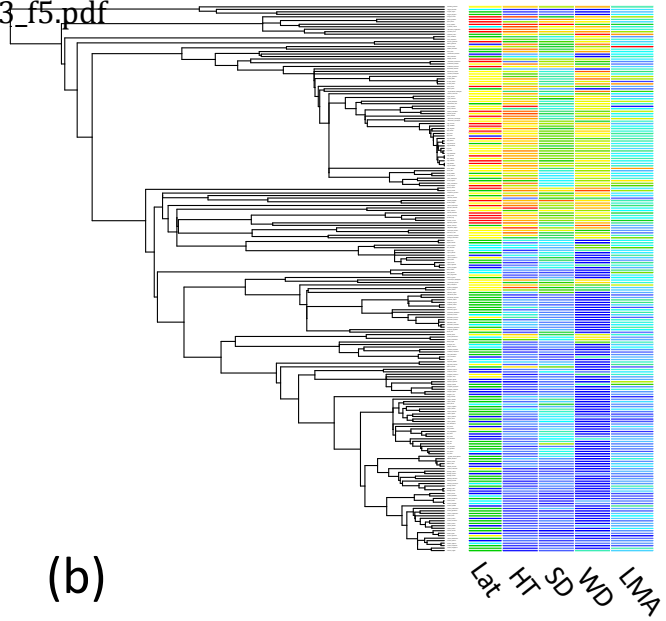
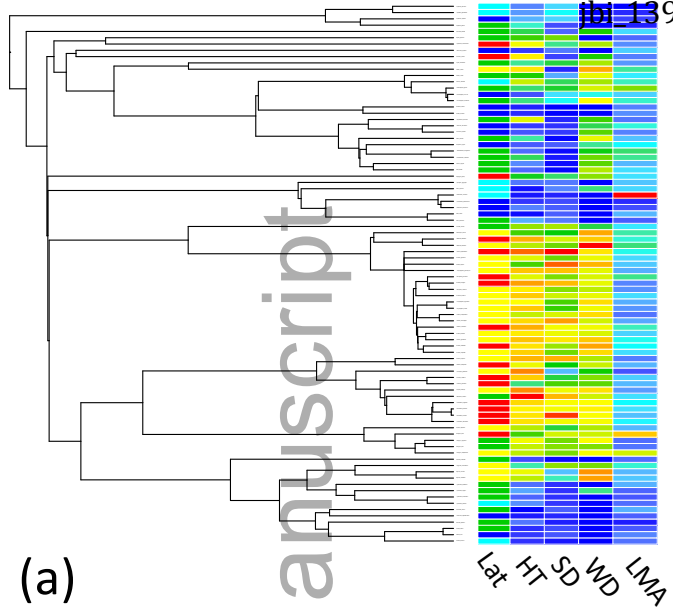
FABALES Wood Density					
	<i>polar</i>	<i>hemiboreal</i>	<i>temperate</i>	<i>subtropical</i>	<i>tropical</i>
<i>polar</i>	0.527 _e				
<i>hemiboreal</i>	0.655 _e	0.655 _e			
<i>temperate</i>	0.709 _{ns}	0.713 _{ns}	0.646 _e		
<i>subtropical</i>	0.727 _e	0.718 _e	0.664 _e	0.658 _e	
<i>tropical</i>	0.742 _e	0.735 _e	0.706 _e	0.702 _{ns}	0.717 _e

FABALES LMA					
	<i>polar</i>	<i>hemiboreal</i>	<i>temperate</i>	<i>subtropical</i>	<i>tropical</i>
<i>polar</i>	0.411 _e				
<i>hemiboreal</i>	0.550 _e	0.611 _e			
<i>temperate</i>	0.554 _e	0.624 _e	0.613 _e		
<i>subtropical</i>	0.713 _e	0.731 _e	0.712 _e	0.683 _e	
<i>tropical</i>	0.760 _e	0.768 _e	0.748 _e	0.693 _e	0.676 _e

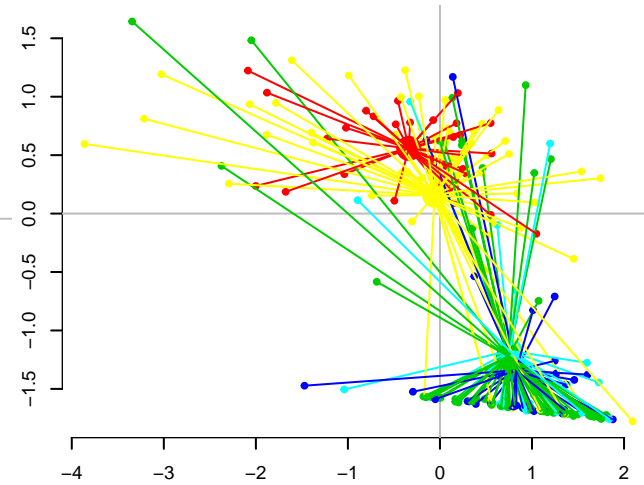
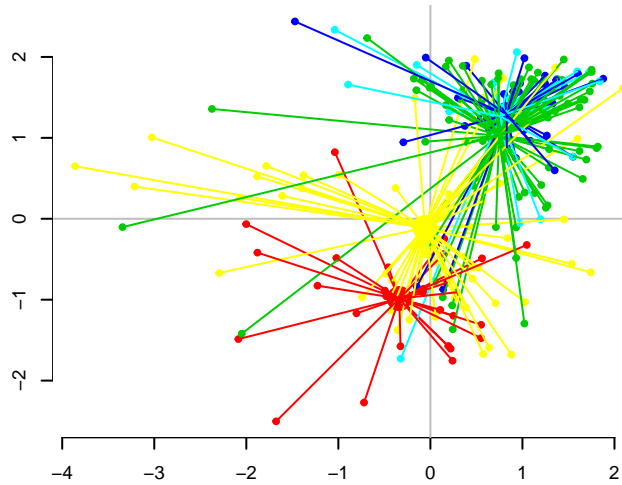
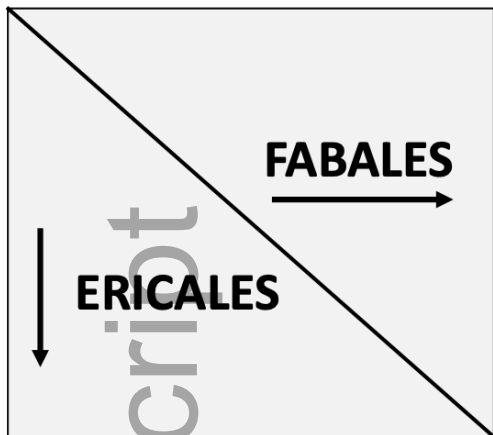
FABALES Growth Form					
	<i>polar</i>	<i>hemiboreal</i>	<i>temperate</i>	<i>subtropical</i>	<i>tropical</i>
<i>polar</i>	0.487 _e				
<i>hemiboreal</i>	0.590 _e	0.641 _e			
<i>temperate</i>	0.545 _e	0.613 _e	0.573 _e		
<i>subtropical</i>	0.668 _e	0.695 _e	0.671 _e	0.685 _e	
<i>tropical</i>	0.742 _e	0.750 _e	0.737 _e	0.720 _e	0.725 _e

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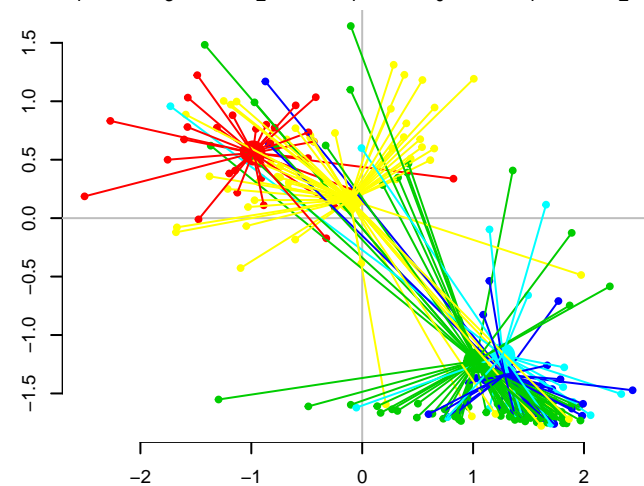
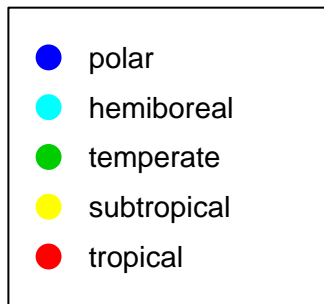
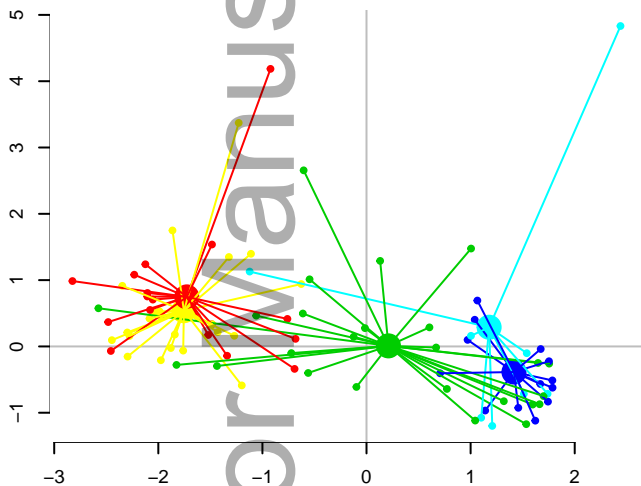
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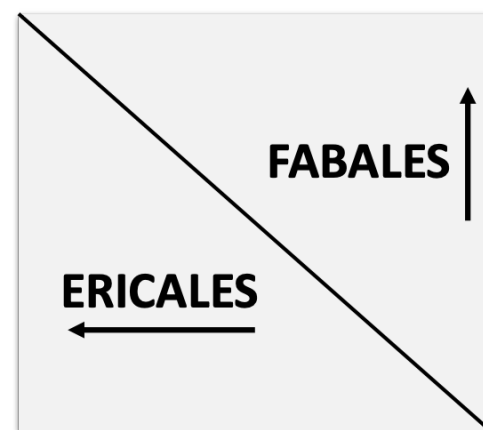
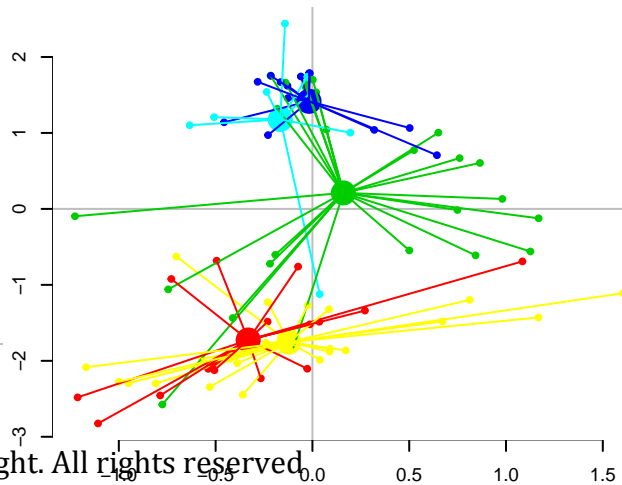
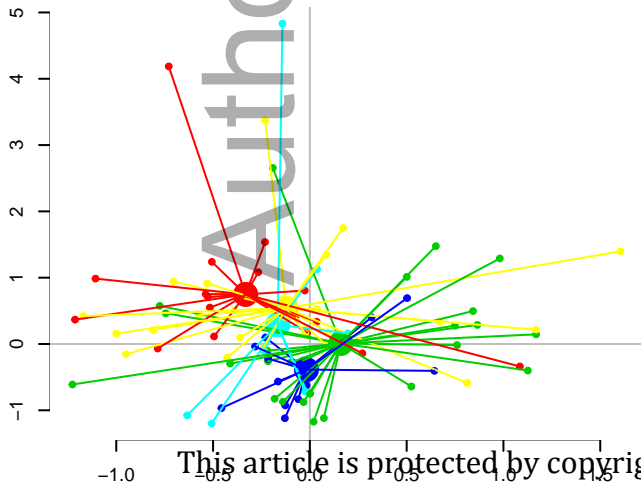
PCA 1



PCA 2



PCA 3



PCA 1

PCA 2

PCA 3