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## Phylogenetic patterns and phenotypic profiles of the species of plants and mammals farmed for food

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1 **Phylogenetic patterns and phenotypic profiles of the species of plants and**  
2 **mammals farmed for food**

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49 **The origins of agriculture were key events in human history, during which people**  
50 **came to depend for their food upon small numbers of animal and plant species.**  
51 **However, the biological traits determining which species were domesticated for food**  
52 **provision and which were not, are unclear. Here, we investigate the phylogenetic**  
53 **distribution of livestock and crops, and compare their phenotypic traits with those of**  
54 **wild species. Our results indicate that phylogenetic clustering is modest for crop**  
55 **species but more intense for livestock. Domesticated species explore a reduced portion**  
56 **of the phenotypic space occupied by their wild counterparts and have particular traits**  
57 **in common. For example, herbaceous crops are globally characterized by traits**  
58 **including high leaf nitrogen concentration and tall canopies, which make them fast**  
59 **growing and proficient competitors. Livestock species are relatively large mammals**  
60 **with low basal metabolic rates, which indicate moderate to slow life histories. Our**  
61 **study therefore reveals ecological differences in domestication potential between**  
62 **plants and mammals. Domesticated plants belong to clades with traits advantageous**  
63 **in intensively-managed high-resource habitats whereas domesticated mammals are**  
64 **from clades adapted to moderately productive environments. Combining comparative**  
65 **phylogenetic methods with ecologically relevant traits has proven useful to unravel the**  
66 **causes and consequences of domestication.**

67

68 The plant and animal species domesticated for human food supply represent only a small  
69 fraction of global biodiversity. Of around 370,000 extant flowering plants<sup>1</sup>, only 1,000-  
70 2,000 have undergone some form of domestication for that purpose<sup>2-4</sup>. Similarly, humans  
71 have domesticated 20-31 species of mammals for food<sup>5,6</sup>, from ~ 5,400 species  
72 contemporary to late Paleolithic people<sup>7</sup>. The taxonomic distribution of species used for

73 farming seems non-random<sup>5,8</sup>, such that certain families include numerous domesticated  
74 species (*e.g.* grasses and legumes among flowering plants, and bovids and camelids among  
75 mammals), while many others contain none. An uneven phylogenetic distribution of the  
76 species that became domesticated would imply that certain combinations of phenotypic  
77 traits are more adaptive for husbandry, if these traits are phylogenetically conserved<sup>9</sup>.  
78 However, global comparative analyses between domesticates and wild relatives are rare<sup>10-12</sup>  
79 or consider taxonomically and/or geographically restricted groups of species<sup>13,14</sup>. Filling  
80 that gap would direct agricultural sciences towards the phylogenetic groups and traits that  
81 could be pursued for new food sources. Additionally, investigating such patterns at a global  
82 scale, while explicitly linking phylogenetic and trait distributions, would highlight the  
83 usefulness of the tools and concepts of evolutionary ecology to address questions at its  
84 interface with agricultural sciences and archaeology.

85         The phenotypes of current livestock and crops are the result of early domestication  
86 processes and millennia of unconscious and deliberate selection under farming<sup>15</sup>. Evolution  
87 under farming has caused the traits of domesticated species to change under shifting  
88 selective forces<sup>13</sup>. For example, local breeding preserves mutants that would otherwise be  
89 eliminated by natural selection and thereby offset the sampling effects of early farming<sup>4</sup>. In  
90 fact, diversifying selection has promoted remarkable variance in the size of crop seeds or in  
91 animal coat colors<sup>5,16</sup>. Conversely, directional selection for productivity has resulted in the  
92 convergence of a number of livestock and crop traits, *i.e.* the domestication  
93 syndrome<sup>5,9,17</sup> (but see <sup>18,19</sup>). Domestication syndrome traits include increased docility or  
94 reductions in brain size in livestock<sup>5,6,20</sup> and increased palatability or the loss of seed  
95 dispersal mechanisms in crop plants<sup>4,9</sup>.

96           Adaptations to the farming environment might also promote convergent evolution  
97 *via* natural selection<sup>13</sup>. For instance, evolution in high-resource croplands should select for  
98 suites of traits that enable fast resource acquisition and rapid canopy closure, according to  
99 trait-based ecology<sup>21</sup>. A few recent studies have partially supported this view, showing that  
100 several crop plants display traits indicative of high competitive ability<sup>14,22–24</sup>. Therefore, if  
101 directional and stabilizing selection are strong, the phenotypic diversity of domesticated  
102 species will be low, adding to early domestication bottlenecks. In contrast, diversifying  
103 selection, associated with centuries-long geographic expansion under farming, is expected  
104 to promote the widening of phenotypic spaces<sup>16</sup>. The net effects of the early filtering of  
105 wild species, of subsequent domestication processes, and of later crop and livestock  
106 evolution, on the phenotypic spaces explored by domesticated species remain unknown. In  
107 this paper, we show the results of the first broad-scale phylogenetic analyses addressing  
108 whether domesticates are a limited phylogenetic and phenotypic sample of wild plants and  
109 animals, and uncovering traits that distinguish domesticated species from wild species.

110           We used phylogenetic comparative methods to investigate the phylogenetic patterns  
111 of domestication events, and to ask whether domesticates are phenotypically distinct from  
112 their wild relatives. We did this by compiling and analyzing two large datasets. First, we  
113 compiled a database on the distribution of species domesticated for food across mammal  
114 and angiosperm families and genera. With that dataset we investigated evolutionary  
115 patterns of the relative abundance of domesticated species (proportion of all domesticated  
116 species within a given genus or family), and of domestication frequencies (proportion of all  
117 species in a genus or family that were domesticated) across mammal and angiosperm  
118 phylogenies. Second, we put together a large-scale database of three key phenotypic traits  
119 for farm mammals (size-corrected basal metabolic rate, adult body mass and neonate body



120 mass) and crop plants (leaf nitrogen content, plant canopy height and seed dry mass) across  
121 a broad sample of domesticated (23 mammals, 181 angiosperms) and wild species (885  
122 mammals, 2,943 angiosperms). Traits were selected based on their key functional relevance  
123 for resource-use-acquisition, life history and ecological strategies, both for domesticated  
124 and for wild species<sup>21,25–28</sup>. Using this second dataset, we compared the phenotypic spaces  
125 of domesticates to those of their wild relatives. We set out to address three questions: 1)  
126 How are food domesticates distributed across the phylogenies of mammals and  
127 angiosperms? 2) Do livestock and crop species have particular phenotypic profiles, when  
128 compared to their wild counterparts? And, if so, 3) Do the phenotypic traits of domesticated  
129 species fall within the trait space exhibited by wild species, or do they extend their  
130 phenotypic space beyond the boundaries set by wild plants and animals?

131

## 132 **Results**

133 Some families and genera contain more livestock or crop species than others. Livestock  
134 species were found in only ten families. In particular, Bovidae harbour ~40 % of  
135 domesticated species (Supplementary Table 1), and only 22 genera of mammals contain  
136 domesticated species (Supplementary Table 1). In contrast, crop species were distributed  
137 across 120 families and 453 genera of angiosperms (Supplementary Data 1). Fabaceae,  
138 *Solanum*, and Poaceae are examples of taxa yielding high proportions of crops. The  
139 abundances of domesticated species were far from randomly distributed across families and  
140 growth forms (plants) or dietary types (mammals), both for mammals and angiosperms  
141 (Supplementary Table 2). We next investigated whether the above deviations from a  
142 random distribution were phylogenetically structured.

143 In general, we found that the phylogenetic structure of domestication abundances  
144 and frequencies was modest for plants, though stronger for mammals. First, Local  
145 Indicators of Phylogenetic Affinity (LIPAs) indicated that ca. 90% of the plant families  
146 hosting domesticated species were randomly distributed with respect to the domestication  
147 status of their phylogenetic neighbourhood (Supplementary Data 2). Approximately 10% of  
148 angiosperm families departed from a non-significant LIPA score (Supplementary Data 2).  
149 However, such departure signalled over-dispersion (*i.e.* focal family surrounded by families  
150 without domesticated species more than the random expectation), rather than clustering  
151 (Supplementary Data 2). Interestingly, that ca. 10% of angiosperm families include  
152 Fabaceae, Poaceae, Rosaceae, Solanaceae or Asteraceae, which host crops of high  
153 agricultural relevance. For mammals, four (Suidae, Cervidae, Caviidae, and Cunilidae) out  
154 of ten families with domesticated species had at least one LIPA score indicating  
155 phylogenetic clustering, either for abundances or frequencies. Second, we investigated  
156 phylogenetic clustering at the scale of the whole phylogenetic tree. When two contrasting  
157 evolutionary models were compared (*i.e.* a Brownian motion model of evolution,  
158 representing strong phylogenetic structure, *vs.* a star phylogeny, representing full  
159 phylogenetic independence), phylogenetically independent models showed better fit to the  
160 data than Brownian motion models, both for mammals and angiosperms (Supplementary  
161 Tables 3 and 4). Finally, global phylogenetic clustering was investigated with a gradual  
162 approach (phylogenetic signal), which complemented the binary (non-phylo *vs* phylo)  
163 comparison of phylogenetic models above. The frequency of domestication events  
164 generally showed a phylogenetic signal (Figure 1 and Supplementary Figure 1, but see  
165 angiosperm families in Figure 1). Domestication abundance, instead, showed low or no  
166 phylogenetic signal in angiosperms, low signal in mammals at the family scale, and high

167 signal when mammals were examined separately for each dietary type (Figure 1 and  
168 Supplementary Figure 1).

169         The subset of domesticated species used for phenotypic space analyses covered a  
170 wide range of phylogenetic and geographic origins (Figure 2). In spite of this taxonomic  
171 and geographic diversity, domesticated species were distributed across a portion of the  
172 phenotypic space generally occupied by wild species, and rarely fell beyond the bounds set  
173 by wild mammals and plants (Figures 3 and 5; and Supplementary Tables 5 and 6, but see  
174 ruminant livestock in Figure 3). Livestock occupied a small subset of the phenotypic spaces  
175 of wild mammals (Figure 3 and Supplementary Table 5). Within the common phenotypic  
176 boundary occupied by wild and domesticated mammals, livestock species were, on average,  
177 larger as adults and gave birth to larger neonates, but had lower basal metabolic rates,  
178 compared to their wild counterparts (Figure 4 and Supplementary Tables 7 and 9). Those  
179 phenotypic biases were upheld when investigated separately for ruminants and non-  
180 ruminants, though domestic ruminants lied mostly outside the phenotypic boundaries of  
181 wild ruminants. In contrast, domesticated crops have been selected from a wide range of  
182 botanical diversity in the three focal traits (Figure 5 and Supplementary Table 6). An  
183 exception to that pattern is the small phenotypic space occupied by domesticated  
184 graminoids (grass-like monocot plants), in comparison with their wild analogues (Figure 5  
185 and Supplementary Table 6). However, although crops were phenotypically diverse, they  
186 occupied some regions of the phenotypic space more than others, which lead to phenotypic  
187 differentiation when compared to wild plants. Specifically, herbaceous crops, both  
188 graminoid and non-graminoid, were generally larger plants with larger seeds, and with  
189 leaves with higher nitrogen content, than their wild counterparts (Figure 6 and  
190 Supplementary Tables 8 and 10). Woody crops were more similar to wild woody plants,

191 though they consistently had larger seeds (Figure 6 and Supplementary Tables 8 and 10).  
192 The phenotypic departure of domesticated species from the trait medians of their wild  
193 counterparts was generally unrelated to the differences in geographic origin, climate at  
194 geographic origin, or antiquity of domestication of crop and livestock species  
195 (Supplementary Table 11).

196

## 197 **Discussion**

198 Our results provide the first quantitative global test of the long-standing hypothesis that  
199 domestication events have a strong phylogenetic structure. We found only weak evidence  
200 for phylogenetic clustering in crops, but stronger evidence of such clustering in livestock  
201 species. Interestingly, the non-random phylogenetic distribution of species that became  
202 domesticated was associated with non-random phenotypic spaces of crops and farm  
203 mammals. Livestock species had moderate to low basal metabolic rates, gave birth to large  
204 offspring and were large adults. Herbaceous crops had high leaf nitrogen content (an  
205 indicator of photosynthetic rates), were large as adults, and produced large seeds. These  
206 results show that domesticated mammals and plants occupy specific portions of the spectra  
207 of phenotypic variation<sup>21,25–28</sup>. Despite such phenotypic differentiation, and in spite of  
208 substantial trait evolution during domestication<sup>16</sup>, domesticated species were rarely  
209 positioned outside the bounds of the phenotypic spaces set by the wild species of their kind,  
210 excluding ruminant livestock. These findings have important implications for  
211 understanding the potential of wild species for farming, the patterns of phenotypic  
212 convergence under domestication, and the adaptation of wild species to the environmental  
213 conditions of farming habitats<sup>13,18,20,29,30</sup>. In addition, we demonstrate that a macro-

214 evolutionary approach, scarcely embraced in the domestication literature, has the strong  
215 potential to advance this field.

216 Our analyses showed that domesticated mammals represent a small sub-sample of  
217 the total phenotypic variation displayed by wild animals. This was expected, since livestock  
218 species are a very small fraction of all contemporary mammals. More unexpectedly, farmed  
219 mammals had mid-to-low basal metabolic rates and were mid-to-large adults and neonates.  
220 These results portray domesticated mammals as moderate to slow life history strategists,  
221 *i.e.* species with intermediate body temperatures, with moderately long juvenile periods,  
222 giving birth to few but relatively large offspring, and living for reasonably long time spans,  
223 accordingly to the fast-slow life-history framework<sup>26,27</sup>. Low basal metabolic rates, which  
224 might entail slow relative growth rates<sup>31</sup>, are adaptive in unproductive and unpredictable  
225 environments in ruminants<sup>32</sup>, rodents<sup>33</sup> and mammals in general<sup>27,28</sup>. In addition, a  
226 moderate-slow lifestyle might genetically associate with behavioural traits that are critical  
227 to animal domestication, such as boldness, tameness, or sociality<sup>33-35</sup>, which remains to be  
228 investigated. Interestingly, many domesticated mammals evolved body size reduction after  
229 domestication<sup>29,36</sup>. This suggests that the moderate-slow lifestyle of livestock identified in  
230 our current work is largely the result of early selection of wild animals, rather than of  
231 further evolution under farming. In livestock species that show such body size reductions  
232 during domestication, decreases in sexual dimorphism were also reported, which, following  
233 Rensch's rule<sup>37</sup>, might account for their overall smaller adult size<sup>5,29,38</sup>. Further studies  
234 advancing this line of enquiry should consider the wild progenitors of livestock species,  
235 account for sexual dimorphism, and address species domesticated for purposes beyond food  
236 provision, which clearly display body size reduction after domestication (*e.g.* dogs or cats).

237 For crops, our results for non-woody plants are compatible with hypotheses positing  
238 that early human selection favoured traits advantageous in the fertile, disturbed habitats  
239 surrounding human settlements and early agricultural fields<sup>5,9,30</sup>. Herbaceous crops  
240 occupied only a portion of the phenotypic space of their wild counterparts, suggesting  
241 habitat filtering<sup>39</sup>. This is in line with previous case studies reporting that crops are a  
242 subsample of the phenotypic variation found in nature, and have not surpassed the  
243 biological limits observed for wild plants<sup>13,23,40,41</sup>, which suggests limitations of artificial  
244 selection to move phenotypes beyond what is observed in the wild. Additionally, the  
245 phenotypic profiles described here indicate that herbaceous crops are fast growing species  
246 (high leaf nitrogen content) and proficient competitors in resource abundant environments  
247 (tall plants and large seeds)<sup>21,25</sup>, which would suit the ecological requirements of early  
248 agricultural habitats<sup>42</sup>. Such phenotypic differentiation passed unnoticed in the previous  
249 literature addressing smaller sets of crops, where crop-specific contrasting results were  
250 commonly reported<sup>14,22-24,41</sup>. This highlights the relevance of a global approach and the  
251 usage of the comparative method in this field. Woody crops yielded large seeds but, in  
252 contrast to herbs, were neither tall species nor species with high nitrogen content in their  
253 leaves. Multiple explanations might account for such discrepancy between growth forms,  
254 including trade-offs in resource allocation to fruit tissue, to vegetative growth, and to the  
255 maintenance of woody tissues, the clonal mode of propagation common to woody crops, or  
256 crop uses<sup>4,9,18,43</sup>.

257 A direct comparison of the phenotypic spaces of plants and mammals yielded an  
258 additional relevant insight. In plants, metabolism and size are largely decoupled<sup>25</sup>. In  
259 contrast, the evolution of metabolic rates and body size are coordinated in mammals<sup>44</sup>. Our  
260 trait analyses were consistent with these patterns, both for wild and domesticated species

261 (Figures 3 and 5). The phenotypes of domesticates therefore evolve under different  
262 constraints in plants and mammals. As a consequence, we found wider combinations of  
263 traits and larger phenotypic spaces for crops than for livestock. Endothermy, design of the  
264 vascular system, and size-metabolism constraints might impede the simultaneous  
265 maximization of mass-specific growth rates and body size in mammals<sup>45</sup>, both of which are  
266 desirable traits for productive husbandry. Within these constraints, human selection for  
267 farming favoured animals with intermediate-high sizes, although at the cost of low  
268 metabolic rates, and thus probably modest relative growth rates. Breeding livestock that  
269 overcome size-metabolism constraints are therefore expected to be challenging. On the  
270 other hand, crop plants occupied a wider part of the tradeoff-free spectrum of metabolism  
271 (leaf nitrogen) vs. size (plant and seed sizes), in line with their wild counterparts. Plant  
272 modularity and nitrogen transfer among modules, which underpin such uncoupling between  
273 metabolism and size<sup>46</sup>, might thus promote the greater phenotypic diversity of crops than  
274 livestock mammals, even when considered within plant growth-forms. Breeding to  
275 simultaneously optimize variation in plant and organ sizes, and variation in metabolic rates,  
276 might be tradeoff-free in plants.

277 Finally, we highlight two limitations of the current work. First, trait data come from  
278 plants and animals sampled in their typical habitats, which are different among species, and  
279 are undoubtedly so among organisms living in farm vs wild habitats. Thus, the phenotypic  
280 patterns encountered here came from a mixture of genotypic and environmental drivers,  
281 whose relative importance is plainly indistinguishable for large scale macroecological  
282 studies. However, the few experiments that grew sets of crops and of their wild progenitors  
283 in common gardens, and phenotyped the types of traits that we measured here, tended to  
284 concur with our results, which suggests a strong genetic component at play<sup>22,40,47</sup>.

285 Therefore, it will be necessary to take these experimental approaches one step further in  
286 terms of number of species and phylogenetic breadth, both for wild and domesticated  
287 organisms. Second, we note that, for both domesticated and wild species, intraspecific  
288 variation was not considered here. Such variation, even if unmanageable to explore  
289 systematically at the macroevolutionary scale of the current study, might expand trait  
290 spaces greatly<sup>48</sup>. Leaf trait intraspecific variation in sunflower, wheat, maize and coffee was  
291 recently reported, and occupies a fair portion of wild phenospaces, though very rarely  
292 spreading outside wild boundaries<sup>40,49,50</sup>. We supplemented those leaf trait patterns  
293 available in the literature with *ad hoc* analyses for seed and plant sizes (Supplementary  
294 Figure 2). Similarly to leaf traits, intraspecific variation in size traits is constrained within  
295 wild envelopes in sunflower, soybean, and barley (Supplementary Figure 2). However,  
296 maize, as a crop species in which the seed-plant size centroid is outside the phenospace of  
297 its corresponding wild analogs (Figure 5), expands most of its intraspecific variation  
298 outside wild boundaries (Supplementary Figure 2). In our view, these analyses, and the  
299 available literature, are still too scant to reach solid solid conclusions on the role of  
300 intraspecific variation in trait differences between wild and domesticated organisms. Thus,  
301 investigating how and to what extent diversifying breeding of domesticates expands  
302 phenospaces is needed to bridge the macro- and the micro-evolutionary scales.

303 This study placed domesticates within their broader botanical and zoological  
304 context, which facilitates appreciation of the qualities and potentials of the species that  
305 support our food system, and could help in the search for suitable future domesticates.  
306 Suitable phenotypes among mammals include moderate-slow life histories, while fast  
307 growth traits and large size dominate among herbaceous crops. Further, the usage of a  
308 phylogenetic comparative approach, which was seldom embraced in the domestication



309 literature (but see<sup>12,14,51</sup>), provided unique insights, that are unattainable at smaller scales.  
310 Overall, our work indicates that certain phylogenetic clades and phenotypic profiles have  
311 been more exploited than others for provisioning human food, and that such filtering was  
312 based on strong, conscious or unconscious, early selection at human settlements. Future  
313 work should investigate biogeographic and historical determinants, disentangle genotypic  
314 from environmental drivers, and address the microevolutionary scale, of the broad  
315 phylogenetic and phenotypic patterns of differences between domesticated and wild kins  
316 revealed here.

317

## 318 **Methods**

319

### 320 **Study system**

321 We explored macroevolutionary patterns of the distributions of species domesticated for  
322 human food, and compared their phenotypic trait space occupancy with that of wild  
323 species. We included the broadest possible diversity of mammals and angiosperms farmed  
324 for human food provision, with distinct domestication histories and intensities,  
325 phylogenetic affinities, and phenotypic profiles (see Supplementary Table 1,  
326 Supplementary Data 1, and Figures 1-6).

327

### 328 **Collection of data on the distribution and abundance of angiosperms and mammals** 329 **farmed for food**

330 In order to assess patterns of distribution and abundance of food domesticates across  
331 phylogenies, we compiled the abundances and identities of domesticated species within  
332 mammals and angiosperms, at the family and genus levels. We aimed to build a

333 comprehensive working list of all putative species domesticated for food. Therefore we  
334 included all species for which farming could be substantiated, as an indicator of some  
335 degree, even if incipient, of domestication.

336 We used the literature to build a preliminary list of mammals farmed for food<sup>5,6,52,53</sup>.  
337 We excluded most anecdotal evidence of deer and antelopes farming, but for the sake of  
338 inclusivity we considered species like reindeer, sika deer, moose, bison, muskox or  
339 common eland, which are regularly farmed regionally, and thus should include incipiently  
340 domesticated populations. We also included recent incipient domesticated species for food  
341 like the African giant rat, or the South American paca. The set of mammals comprised 27  
342 domesticated species, distributed across 22 genera and 10 families. Taxonomy was checked  
343 using the *taxize* R package<sup>54</sup>.

344 For plants, we compiled a list of all putative domesticated species from the  
345 literature<sup>2,4,18,55</sup>. From that list, we extracted taxa for which cultivation could be  
346 demonstrated, and filtered that extract by species used for human food or forage. We  
347 include forage species because human food supply depends on livestock feeding, and a  
348 substantial part of the agricultural land is devoted to that usage. To assign usage for food or  
349 forage we primarily used two studies<sup>2,56</sup>, supplemented with <http://www.pfaf.org> and with  
350 other sources when needed. Plant taxonomy was standardized using the *Taxonstand* R  
351 package<sup>57</sup>, synonymous names were cleaned, and binomials were attributed to families  
352 using The Plant List (<http://www.theplantlist.org/>). Thirty-five species were taxonomically  
353 unresolved, and their provisional binomials were used. Our final 944 species list should  
354 include the vast majority of angiosperms known to have been cultivated for human food.  
355 The species of our list belonged to 453 genera and 120 angiosperm families.

356 Domesticated mammals were grouped into two dietary types, *i.e.* ruminants and  
357 non-ruminants, based on the MammalDIET database<sup>58</sup>, and on information at  
358 <http://www.ultimateungulate.com/ungulates.html> - Ruminantia. The ruminant category also  
359 included pseudo-ruminants, *i.e.* Camelidae and Hippopotamidae. Domesticated plants were  
360 grouped by growth form into herbaceous, graminoids (Poaceae, Cyperaceae and  
361 Juncaceae), and woody plants (shrubs, trees, woody vines and tree-like species). Growth  
362 forms were assigned using the TRY database<sup>59</sup>, the Global Woodiness Database<sup>60</sup>, and were  
363 supplemented species-wise with primary literature when not available in those sources.

364

### 365 **Selection and compilation of phenotypic traits**

366 We selected a set of three traits for mammals and three traits for angiosperms that are  
367 functionally analogous. Selection of traits used the following criteria: 1) previous evidence  
368 of domestication effects on those traits<sup>14,22,29,30,36</sup>; 2) functional relevance for basic  
369 metabolism, resource-use, competition and reproductive strategies; and 3) availability of  
370 data, both for domesticated and for wild species. By functional analogy, the selected traits  
371 can be grouped into: 1) plant canopy height (m) and mammal adult body mass (g) as  
372 proxies for adult size and competitive ability for resources<sup>61,62</sup>; 2) leaf nitrogen content (mg  
373 N mg<sup>-1</sup>), and size-corrected mammalian basal metabolic rate (ml O<sub>2</sub> h<sup>-1</sup> g<sup>-1</sup>) as proxies of  
374 photosynthetic and metabolic rate, respectively<sup>26,63</sup>; and 3) seed dry mass (mg) and neonate  
375 body mass (g) as proxies for offspring size and likelihood of survival<sup>64,65</sup>.

376 The two trait datasets were assembled separately for mammals and angiosperms.  
377 The dataset on mammal traits was compiled from the PanTHERIA database for adult and  
378 neonate body mass<sup>66</sup>, and from<sup>67</sup> for basal metabolic rate (supplemented with PanTHERIA  
379 if basal metabolic rate was unavailable at<sup>67</sup>). The dataset on mammal traits comprised 480

380 species, including 23 domesticated species (see Supplementary Table 1 for the identity of  
381 domesticated species). For domesticated plants, trait data were not available for all 944  
382 crops species. Thus, we started by retrieving data from the 203 species list of domesticated  
383 plants published in Meyer et al.<sup>18</sup>, which was built to maximize crop diversity. This helped  
384 to avoid biases in growth form, taxonomy, or agricultural relevance. That list of crop taxa  
385 was further supplemented, again using criteria to maximize diversity and filtering by the  
386 availability of trait data. Then, data for wild angiosperms were added. Overall, the sources  
387 for angiosperm trait data were: 1) the TRY database<sup>59</sup> (<https://www.try-db.org>, accessed  
388 2016-11-13; 2) literature searches for wild species incompletely recorded or not present in  
389 the TRY database; 3) literature searches for trait data of crop species, which are mostly  
390 absent from TRY<sup>68</sup>; 4) our own data already collected on crops and other wild species (see  
391 Data availability section). The final angiosperm trait dataset comprised 3,124 species,  
392 including 181 domesticated species (see Supplementary Data 1 for the identity of  
393 domesticated species).

394 Plant species names were standardized using the *Taxonstand* R package<sup>57</sup>, and were  
395 attributed to families according to The Plant List (<http://www.theplantlist.org/>). A majority  
396 of crop binomials are synonymous to the wild genotypes of their wild progenitors.  
397 Therefore, to decide whether a given observation of a crop related binomial was attributable  
398 to a crop or a synonymous wild species we used the following criteria. First, we looked for  
399 explicit statements in the original publication or database on whether the studied taxa were  
400 crop or wild. If uncertain, an observation was assigned to “wild” if the study was  
401 observational and was conducted under natural field conditions, or if the seeds for an  
402 experiment were collected from wild stocks. In contrast, an observation was assigned to

403 “crop” if the seeds came from commercial companies, cultivars or varieties or if studies had  
404 been conducted in an agricultural setting, and no explicit mention to wild status was found.

405

#### 406 **Data handling prior to analyses**

407 Our angiosperm dataset had 1.51 % missing data (leaf nitrogen 1.70 %, plant height 1.27%,  
408 and seed mass 1.58 %). Since several plots and analyses involved the joint use of two or  
409 more traits, we adopted a multiple imputation approach to deal with missing data, following  
410 recommended procedures<sup>69,70</sup>. We generated ten complete datasets using the Predictive  
411 Mean Matching method (PMM) of the *MICE* package<sup>71</sup>. Phylogenetic relatedness (built as  
412 described below) was incorporated into the imputation procedure as phylogenetic  
413 orthogonal eigenvectors<sup>72</sup>. Results reported in the main body of the paper are from  
414 averaged imputed data of those ten complete datasets. A dataset without imputed data, and  
415 thus with a slightly reduced sample size, was used to test for robustness and sensitivity to  
416 our data handling procedures. The results of sensitivity analyses were consistent with those  
417 shown in the main text (Supplementary Note, and Supplementary Tables 12-14). The  
418 mammalian traits dataset lacked basal metabolic rate data for six species, which were  
419 estimated using the phylogenetically-corrected allometric scaling of adult body mass to  
420 basal metabolic rate available at <sup>67</sup> ( $BMR = 2.382m^{0.729}$ ). All continuous variables were  
421 log-transformed prior to analyses. An exception was seed mass, which was log-generalized  
422 transformed because a few crops do not yield seeds (*Musa acuminata*, *Vaccinium*  
423 *corymbosum* and *Allium sativum*). This latter procedure is recommended when data contain  
424 zeros, and the smallest positive value is not close to one.

425

#### 426 **Macroevolutionary patterns in the abundance and frequency of food domesticates**

427 We performed separate analyses on the relative abundance of domesticated species, and  
428 domestication frequency, at the family and genus levels. Relative abundance, at family and  
429 genus level, was calculated as the number of domesticated species in a particular family or  
430 genus divided by the total number of domesticated species. Because this metric does not  
431 account for species richness within clades, we also calculated a domestication frequency  
432 metric as the number of domesticated species in a focal family or genus per total number of  
433 species in that same family or genus. These two metrics inform about different features of  
434 the distribution of domesticated species. Species richness at family and genus level, needed  
435 to compute domestication frequencies, was retrieved from lists of accepted names from  
436 Wilson and Reeder (2005) for mammals, and from The Plant List v1.1  
437 (<http://www.theplantlist.org/>), making use of the *taxonlookup* R package  
438 (<https://github.com/traitecoevo/taxonlookup>), for plants.

439 Phylogenetic hypotheses were built at the family and genus levels for mammals and  
440 for angiosperms separately. Mammal phylogenies were based on Bininda-Emonds et al's<sup>73</sup>  
441 megaphylogeny as a backbone. The mammalian family-level tree included 142 families  
442 (91% of total mammalian families), while the genus-level tree included 498 genera (39.6 %  
443 of total mammalian genera). Seventy-two genera were ruminants and 337 were non-  
444 ruminant herbivores (<http://tolweb.org>). Angiosperm phylogenies were based on the  
445 PhytoPhylo megaphylogeny<sup>60,74</sup>. The angiosperm family-level tree included 404 families  
446 (97% of total angiosperm families), while the genus-level tree included 7,233 genera (ca.  
447 56 % of total angiosperm genera) (<http://www.theplantlist.org/>). All families, and all but  
448 seven genera with domesticated species, were present in the megaphylogeny. Those seven  
449 genera (*Gigantochloa*, *Nopalea*, *Parmentiera*, *Polianthes*, *Sphenostylis*, *Stizolobium*, and  
450 *Vitellaria*) were bound to the PhytoPhylo megaphylogeny based on published phylogenies

451 of their respective families. The genus level tree included 2,745 genera of herbs, 421 of  
452 graminoids, 3,500 of woody plants and 567 genera hosting both herbs and woody plants.  
453 Genera containing herbs and woody plants were included in both of their respective growth  
454 form analyses. Angiosperm phylogenies were fully resolved, but mammalian phylogenies  
455 contained some internal polytomies (12 % of nodes in the family-level tree, 24 % in  
456 ruminants and 38 % in non-ruminant herbivores). Therefore, analyses were run across 100  
457 randomly resolved family and genus-level mammalian trees.

458 To assess whether the abundance and frequency of domestication are randomly  
459 distributed across mammal and angiosperm families and genera, we performed four  
460 complementary analyses. First, we conducted randomisation analyses to test whether the  
461 distribution of the abundances of domesticated species per family, and of the frequencies of  
462 domestication events, differed from random expectations. Observed kurtosis and skewness  
463 of the distribution of abundances were compared to that of 1,000 randomised distributions  
464 at each respective level. Second, we computed Local Indicators of Phylogenetic  
465 Association (LIPA) based on Local Moran's  $I$ <sup>75</sup>, to detect families surrounded by  
466 phylogenetic neighbourhoods with similar or distinctive (positive or negative  
467 autocorrelation, respectively) relative abundances of domesticated species or domestication  
468 frequencies. For each LIPA score, statistical significance was assigned by performing non-  
469 parametric two-sided tests with 999 randomisations. For mammals, LIPAs were averaged  
470 across the 100 randomly resolved trees. Third, we calculated the phylogenetic signal of the  
471 relative abundances of domesticated species, and of the frequencies of domestication, at the  
472 genus and family levels, and separately for mammals and angiosperms. Provided that our  
473 data followed either zero-inflated log-normal (abundances), or binomial (frequencies),  
474 distributions, we did not calculate standard Pagel's  $\lambda$  or Blomberg's  $K$  metrics, which are

475 meant for continuous data with normal or log-normal distributions. Instead, we computed  
476 phylogenetic signal as the phylogenetic heritability parameter ( $\lambda$ ) of phylogenetic mixed  
477 models (PMMs), where our metrics of domestication were the response, an intercept was  
478 set as the sole fixed-effects predictor, and inverse matrices of the phylogenetic distances  
479 matrices were the covariance structure terms<sup>76,77</sup>. PMMs allow the specification of family  
480 distributions of data deviating from Gaussian. The lambda parameter of such models,  
481 specified without meaningful fixed-effect predictors, and without additional covariance  
482 structures in the random term, is the phylogenetic signal of the response variable,  
483 analogously to a null Phylogenetic Generalized Least Square (PGLS) model<sup>76</sup>. Fourth, we  
484 fitted and compared two evolutionary models to test whether relative abundances and  
485 domestication frequencies were phylogenetically structured or phylogenetically  
486 independent. We used a Brownian motion (BM) model to approximate neutral drift  
487 evolution or randomly fluctuating selection<sup>78</sup>. Under BM, relative abundances and  
488 frequencies evolve as a random walk through trait space along the branches of the  
489 phylogeny, and thus represents strong phylogenetic structuring. BM was compared to a  
490 non-phylogenetic model (a star phylogeny), which was used to approximate a phylogenetic  
491 independent distribution. To compare both models we used the bias-corrected Akaike  
492 Information Criterion ( $AIC_c$ ), and calculated the difference between the  $AIC_c$  of the best  
493 (smallest  $AIC_c$ ) and the alternative model<sup>79</sup>. In addition, for each model we calculated the  
494  $AIC_c$  weights ( $AIC_c$ -w), with a high  $AIC_c$ -w indicating a low relative  $AIC_c$  for that model  
495 and hence higher support<sup>79</sup>. For mammals, all parameters were averaged across 100  
496 randomly resolved trees and the percentage of preferred models was calculated.  
497 Phylogenetic signals were computed using the *MCMCglmm* function of the R package  
498 *MCMCglmm*<sup>80</sup>, setting family distribution as zero inflated poisson for domestication



499 abundances, and as binomial for frequencies of domestication. Evolutionary model fitting  
500 was performed with the *FitContinuous* function of the R package *geiger*<sup>81</sup>. Local Moran's *I*  
501 was calculated using the *lipaMoran* function of the R package *phylosignal*<sup>75</sup>.

502

### 503 **Comparative analyses of phenotypic trait space occupancy of wild and domesticated** 504 **species**

505 New sets of phylogenetic trees were built at the species level for those mammals and  
506 angiosperms included in our traits datasets. The mammal phylogeny for the 480 species  
507 with trait data was built from Bininda-Emonds et al's<sup>73</sup> megaphylogeny using Phylomatic  
508 v.3<sup>82</sup> (<http://phylodiversity.net/phyloomatic/pmws>). The angiosperm phylogeny for the 3,124  
509 species with trait data was based on the PhytoPhylo megaphylogeny<sup>60,74</sup>, and was built  
510 using scenario three of the R package *S.PhyloMaker*<sup>74</sup>. To account for phylogenetic  
511 uncertainty (20.3 % of unresolved nodes for mammals and 15.3 % for angiosperms), all  
512 analyses were performed on 100 randomly resolved trees by using the *multi2di* function of  
513 the *ape* R package<sup>83</sup>.

514 To visualize the phenotypic spaces explored by wild and domesticated species we  
515 used bivariate phenospaces. Additionally, we used convex hulls to draw the minimum  
516 convex envelope for each pair of traits, domestication status and growth form or dietary  
517 type<sup>84</sup>. In addition, for each growth form or dietary type, we calculated the area and volume  
518 of each three-traits convex hull. To test for significant differentiation in trait space between  
519 domesticated and wild species, we performed phylogenetic-corrected MANOVAs and  
520 ANOVAs, separately for each growth form or dietary type. Convex hull calculations were  
521 performed using function *convhulln* of the R package *geometry*<sup>85</sup>. Phylogenetic  
522 MANOVAs/ANOVAs were run with the function *aov.phylo* in the R package *geiger*<sup>81</sup>. See

523 Supplementary Methods for tests on whether the phenotypic departure of domesticated  
 524 species from the trait medians of their wild counterparts was related to differences between  
 525 domesticates in geographic origin, climate at geographic origin, or antiquity of  
 526 domestication. All analyses of the paper were conducted in R v3.4.3<sup>86</sup>.

527

### 528 **Data availability**

529 All phenotypic traits of mammalian species included in this study are available from the  
 530 literature (see Methods section). For plants, most data are available from the database  
 531 TRY<sup>59</sup> (<https://www.try-db.org>), and all original sources of TRY data are listed in  
 532 Supplementary References 1. All references for data not included in TRY are available in  
 533 the Supplementary References 2. Unpublished data owned by R.M. and J.M.B. are  
 534 available from Supplementary Data 3. Unpublished data from the University of Sheffield  
 535 database of weed functional attributes can be requested from G.J. Lists of livestock and  
 536 crop taxa are available at Supplementary Table 1 and Supplementary Data 1, respectively.  
 537 Phylogenetic trees used in this study are available from Supplementary Data 4. Data on  
 538 geography and climate at domestication sites are available as Supplementary Data 5.

539

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541

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747

#### 748 **Author contributions**

749 R.M. and J.M.B. designed the study and compiled the data, R.M., J.M.B., J. C-L. and  
750 M.M.T. performed statistical analyses. R.M. and J.M.B. wrote a first draft of the paper.  
751 M.M.T., G.J., C.P.O. and C.V. extensively revised drafts. All authors contributed to the  
752 writing of, and approved, the final version.

753

#### 754 **Competing interests**

755 The authors declare no competing financial interests.

756

757 **FIGURE LEGENDS**

758 **Figure 1. Distribution of the abundance of food domesticates and frequency of**  
759 **domestication events across mammalian and angiosperm families.** Length of blue bars  
760 are relative abundance of domesticated species (proportion of all domesticated species that  
761 are found within a given family), and of domestication frequencies (proportion of all  
762 species in a family that were domesticated). Raw data can be found in Supplementary Table  
763 1 and Supplementary Data 1, and family identities in the phylogeny can be browsed online  
764 in the high resolution version of the Figure. Colors of tree edges correspond to  
765 domestication abundances or frequencies, according to a gradient of increasing rates from  
766 zero (red) to one (blue). Within each phylogeny, the inset indicates the posterior mode of  
767 the phylogenetic signal ( $\lambda$ ), together with its 95% credible interval.

768

769 **Figure 2: Phylogeographic distribution of the putative place of origin of food**  
770 **domesticates included in phenotypic space analyses.** Locations in the map are medians  
771 of GBIF coordinate records for the putative wild progenitor of each domesticate. Data were  
772 retrievable for 168 wild progenitors of crops, out of 181 crop species, and for all of the 23  
773 wild progenitors of mammal domesticates. Insets: Mantel test statistics for the correlation  
774 between phylogenetic and geographic distance matrices. See Supplementary Methods for  
775 further details.

776

777 **Figure 3. Phenospace occupancy of livestock and wild mammals.** Separate plots  
778 are shown for all mammals, ruminants, and non-ruminant herbivores. Grey dots and red  
779 dots are wild and domesticated mammals, respectively. Black and red polygons are convex  
780 hulls for wild and domesticated mammals, respectively. Numbers in the insets are % of



781 convex hull area of domesticates outside the wild boundary (light red), of domesticates  
782 inside the wild boundary (strong red-grey), and of wild space occupied by domesticates  
783 (grey).

784

785 **Figure 4. Phenotypic differentiation between livestock and wild mammals.** Separate  
786 panels are shown for all mammals, non-ruminants, and ruminants. Asterisks indicate  
787 statistically significant differences at  $\text{phy-P} \leq 0.05$  between domestication statuses  
788 according to phylogenetic Anovas (Supplementary Table 7). Center line, median; box  
789 limits, upper and lower quartiles; whiskers, lowest/highest datum still within  $1.5 \times \text{IQR}$ ;  
790 points, data exceeding whisker bounds.

791

792 **Figure 5. Phenospace occupancy of crops and wild angiosperms.** Separate plots are  
793 shown for all angiosperms and for each growth form (*i.e.* herbaceous, graminoids and  
794 woody). Grey dots and red dots are wild and domesticated angiosperms, respectively. Black  
795 and red polygons are convex hulls for wild and domesticated angiosperms, respectively.  
796 Numbers in the insets are % of convex hull area of domesticates outside the wild boundary  
797 (light red), of domesticates inside the wild boundary (strong red-grey), and of wild space  
798 occupied by domesticates (grey).

799

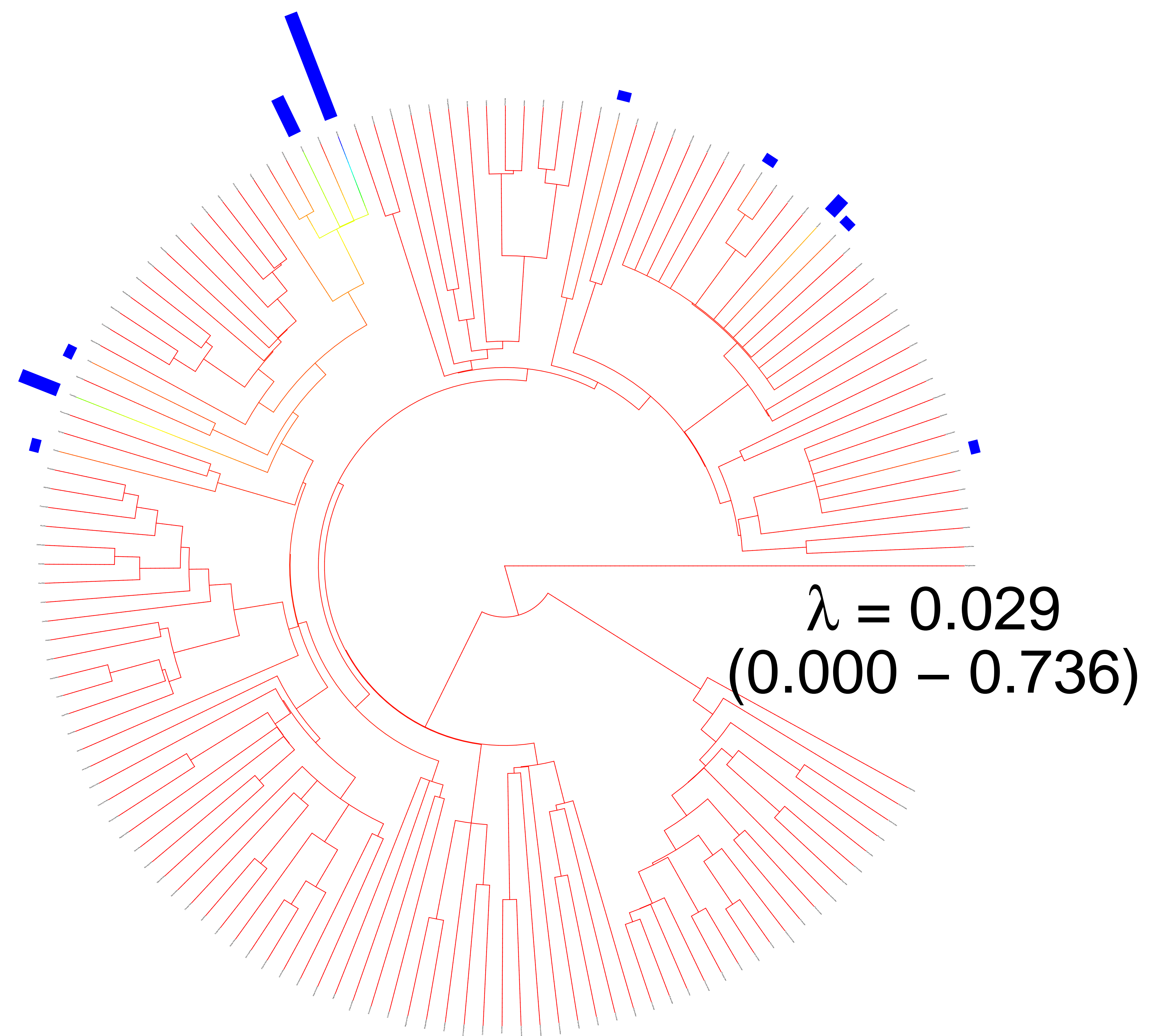
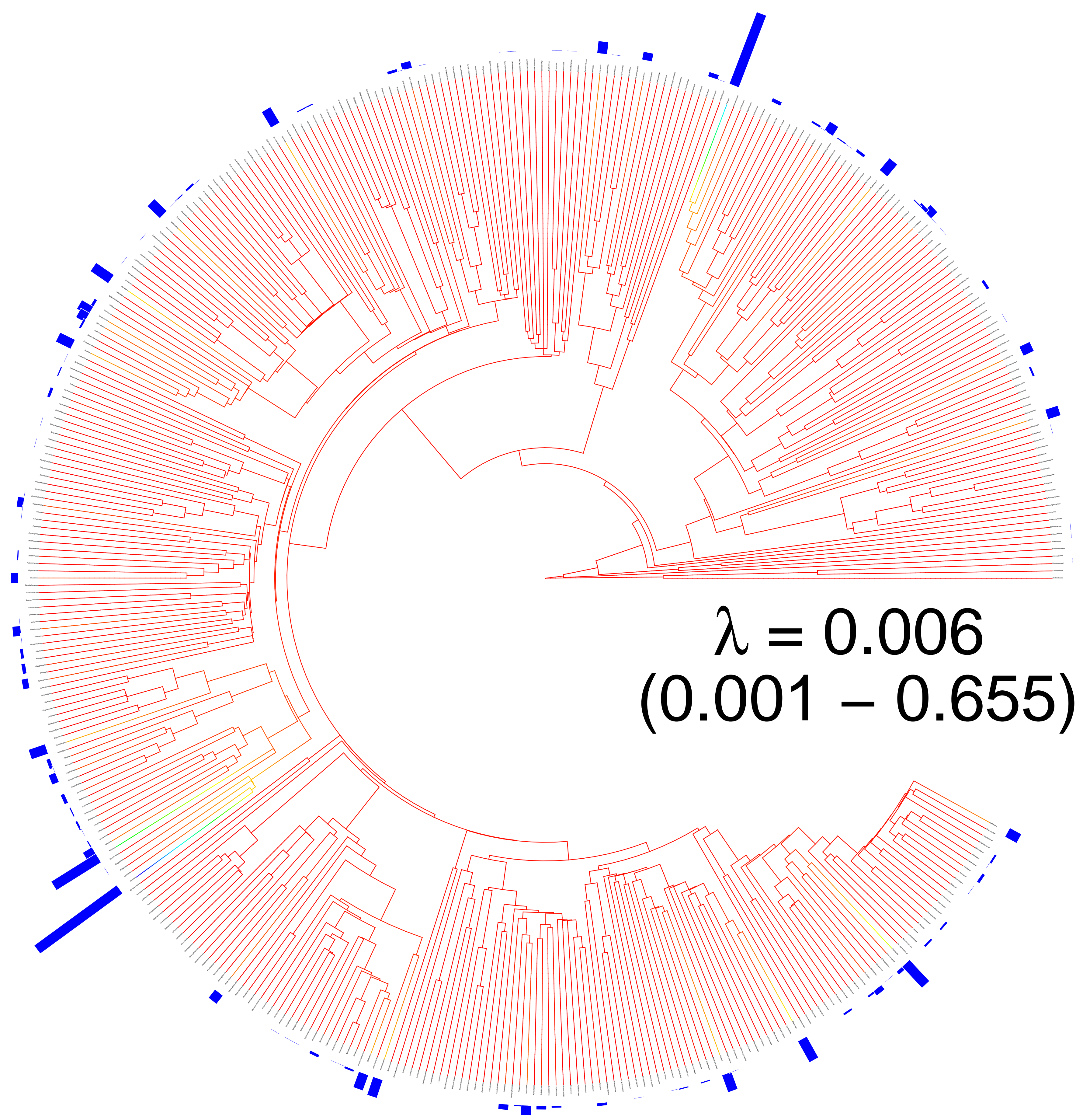
800 **Figure 6. Phenotypic differentiation between crops and wild angiosperms.** Separate  
801 plots are shown for all angiosperms and each growth form (*i.e.* herbaceous, graminoids and  
802 woody). Asterisks indicate statistically significant differences at  $\text{phy-P} \leq 0.05$  between  
803 domestication statuses according to phylogenetic Anovas (Table 2). Center line, median;

- 804 box limits, upper and lower quartiles; whiskers, lowest/highest datum still within  $1.5 \cdot \text{IQR}$ ;
- 805 points, data exceeding whisker bounds.

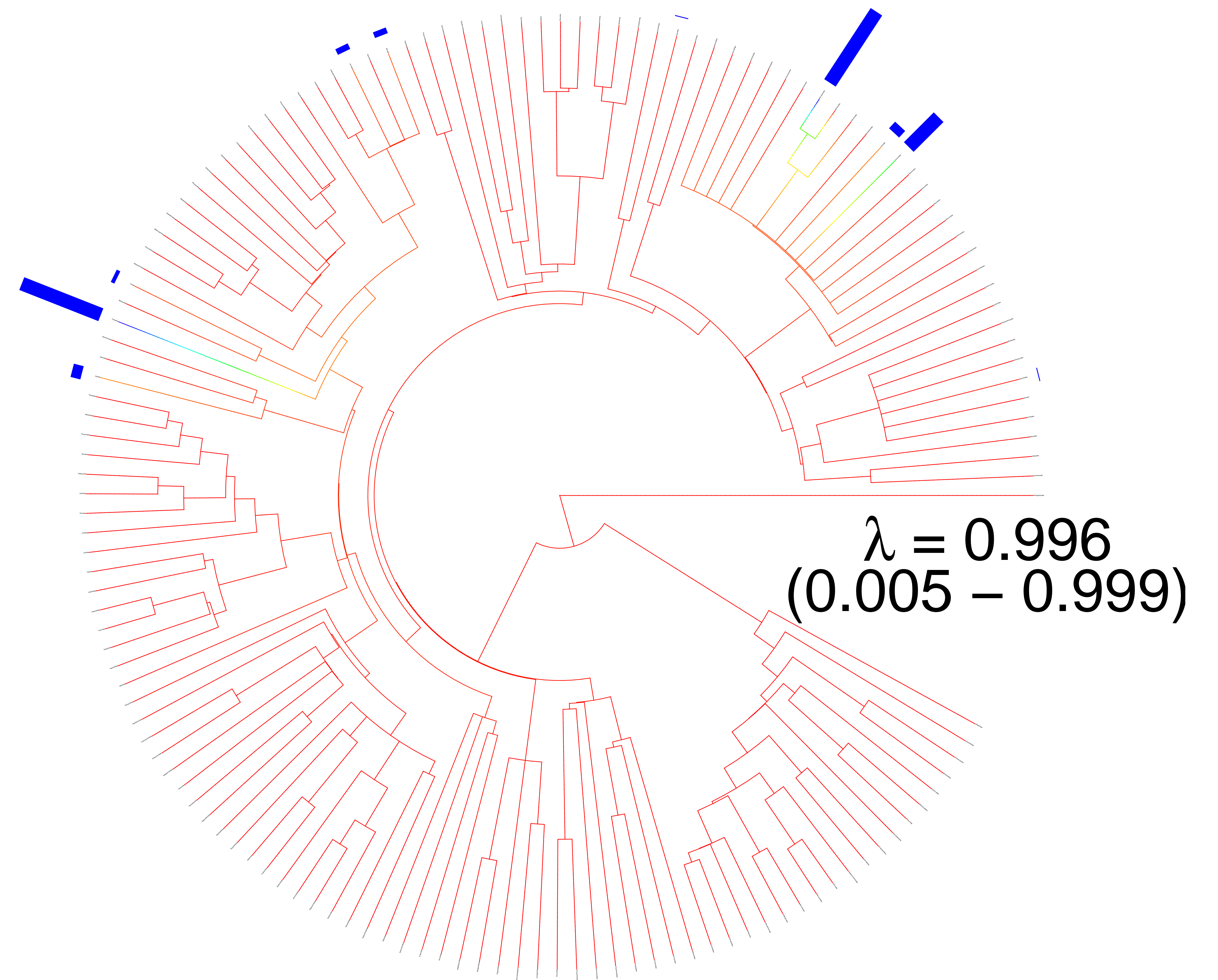
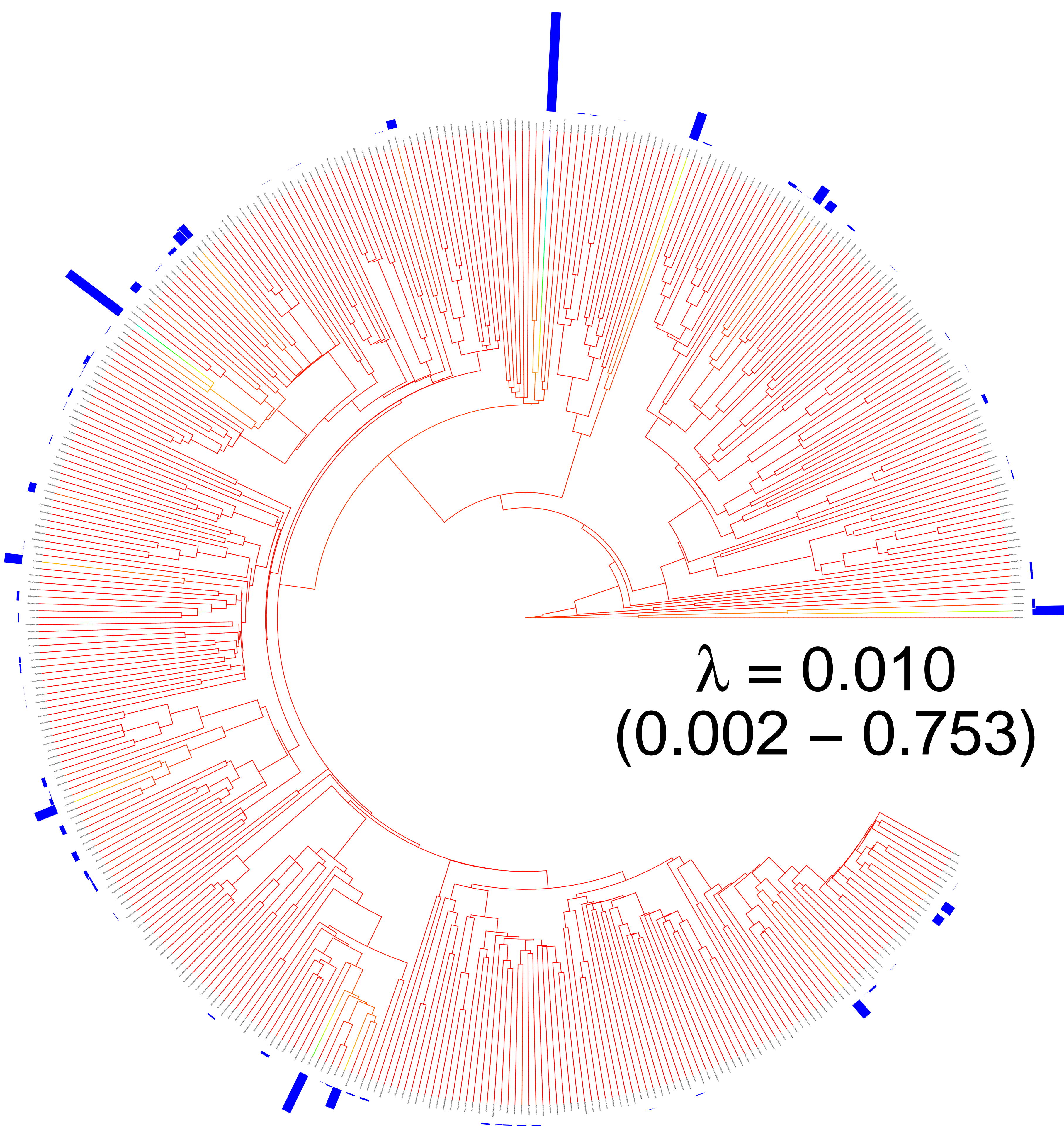
# ANGIOSPERMS

# MAMMALS

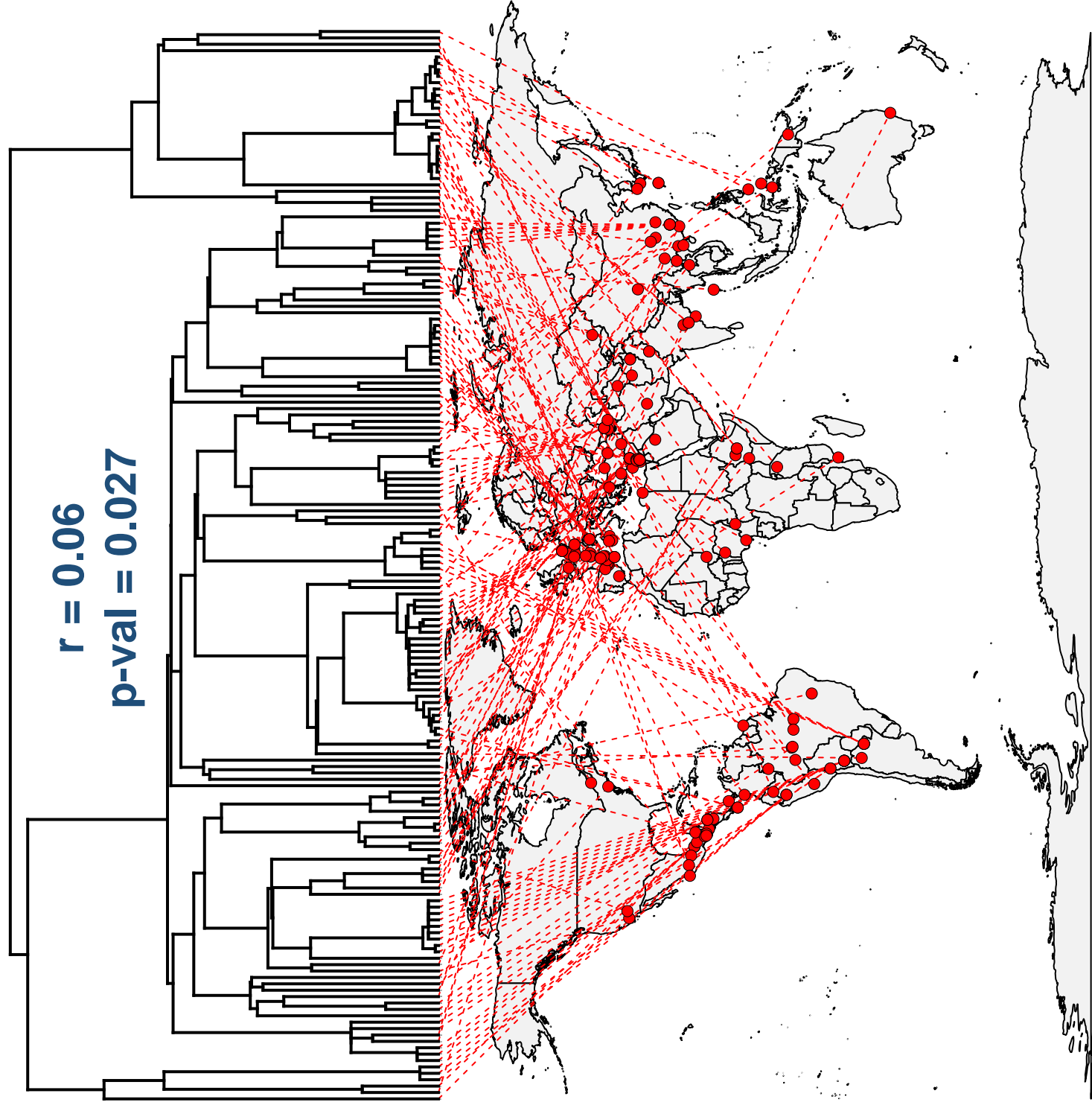
ABUNDANCE OF DOMESTICATES



DOMESTICATION FREQUENCY



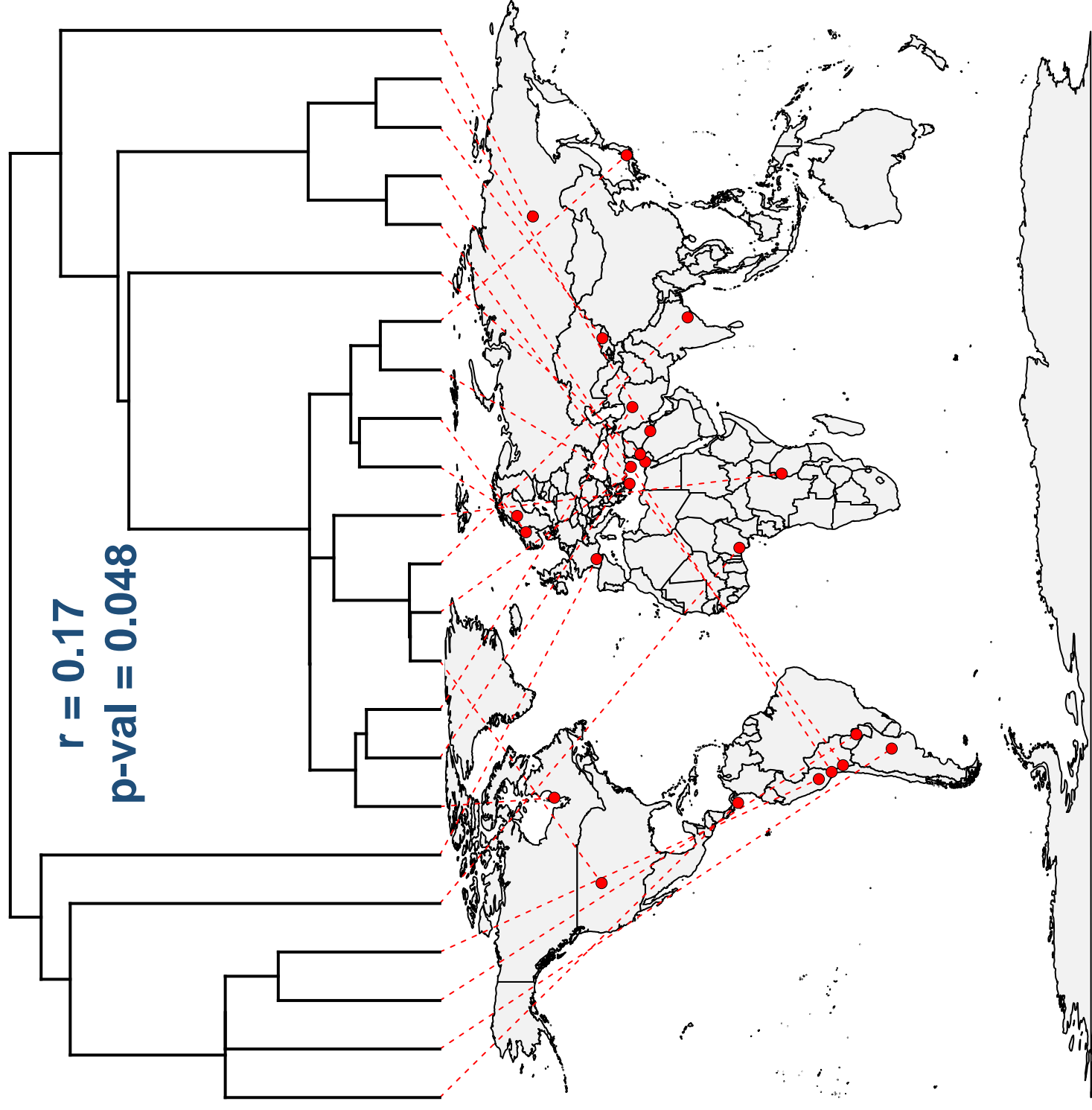
# ANGIOSPERMS



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$p\text{-val} = 0.027$

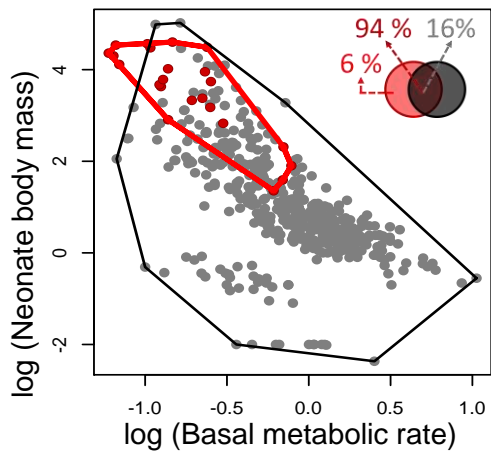
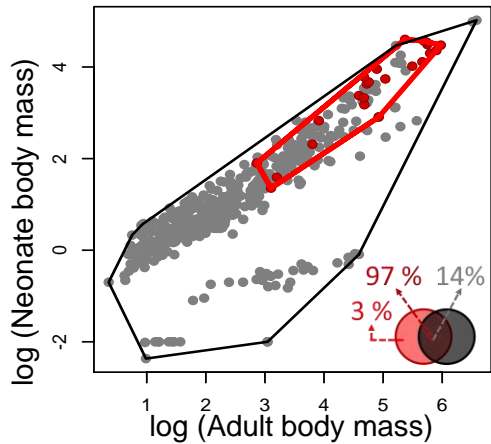
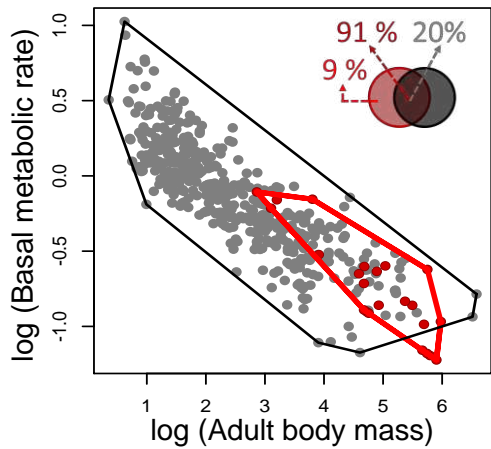
# MAMMALS



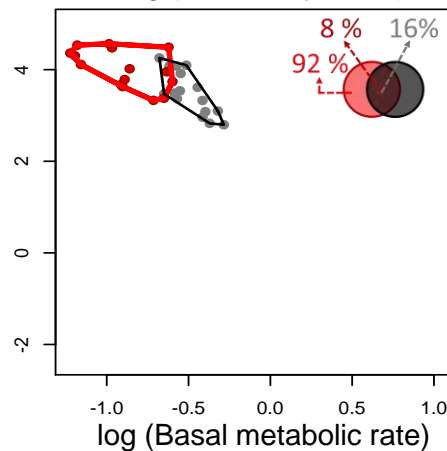
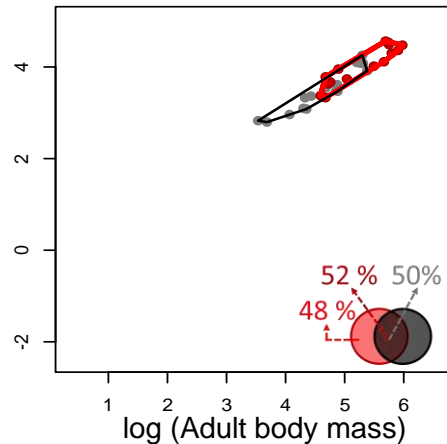
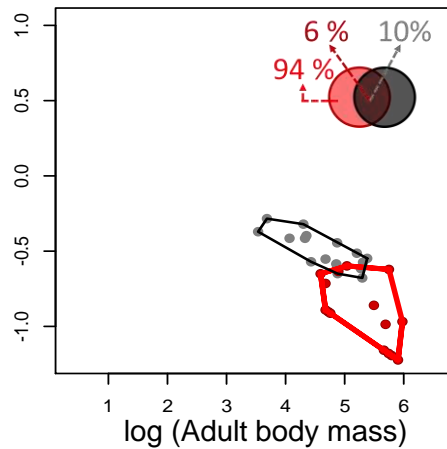
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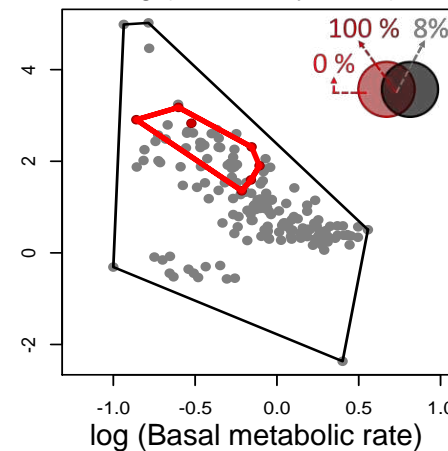
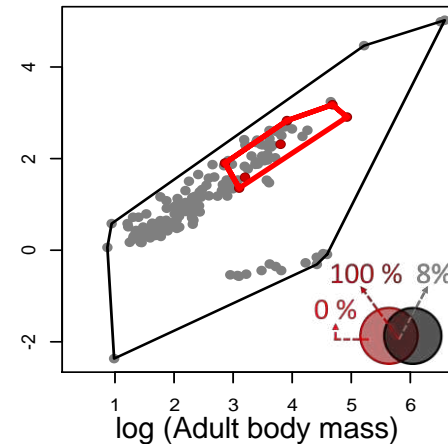
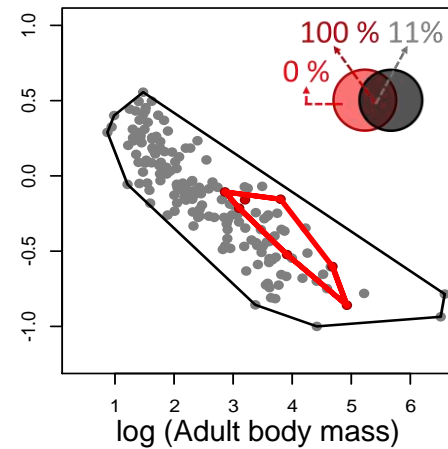
### All mammals

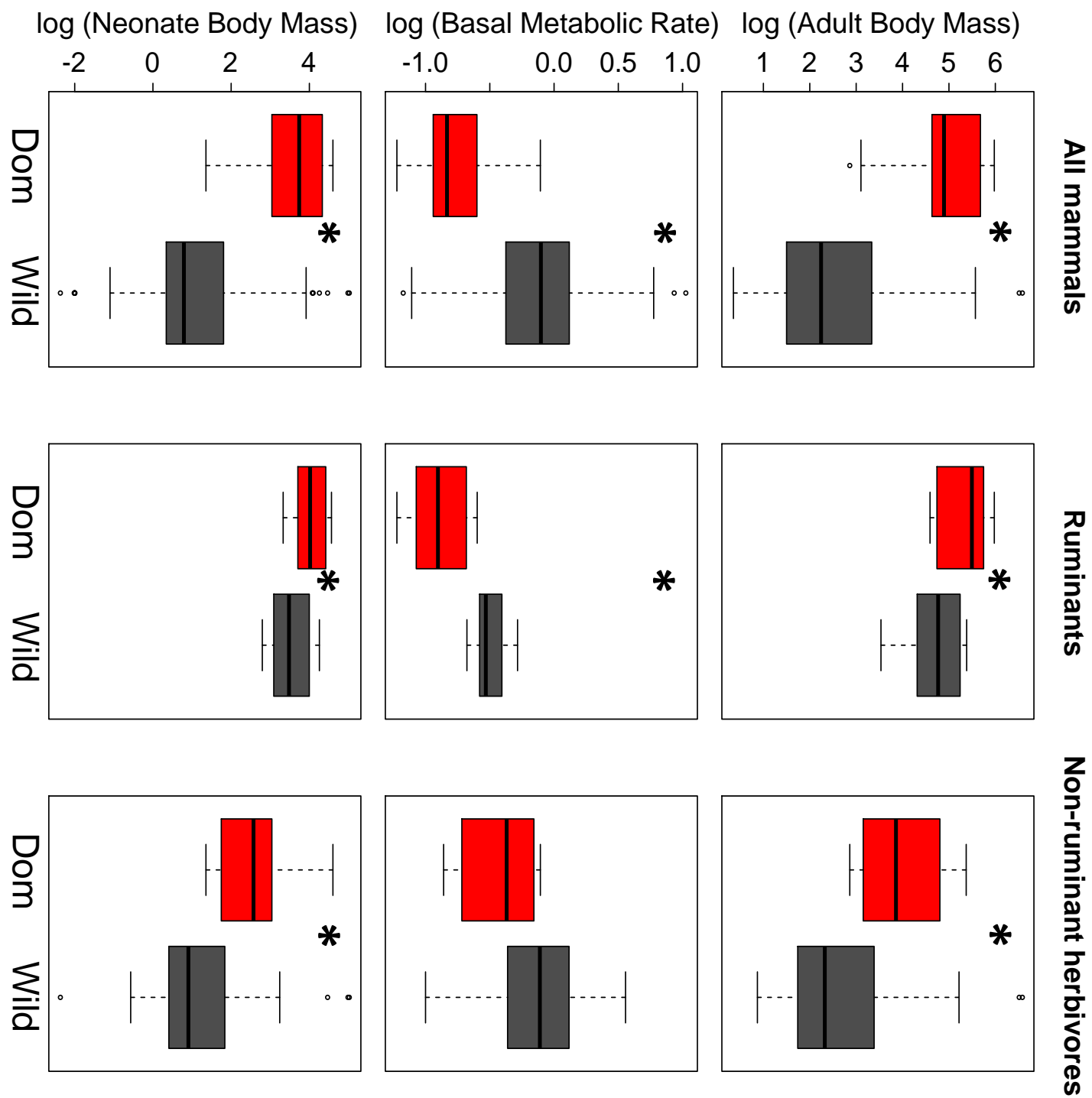


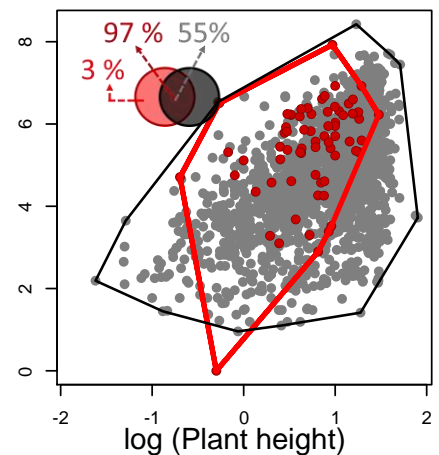
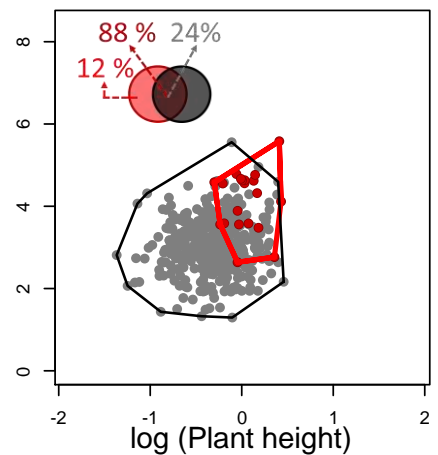
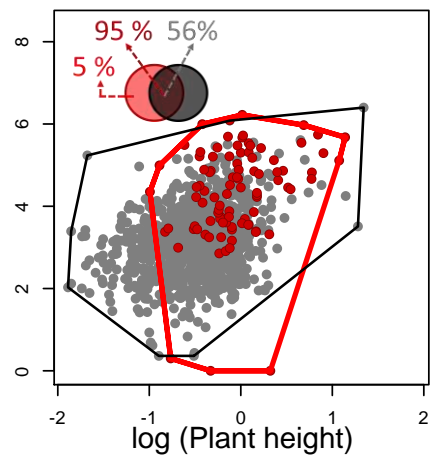
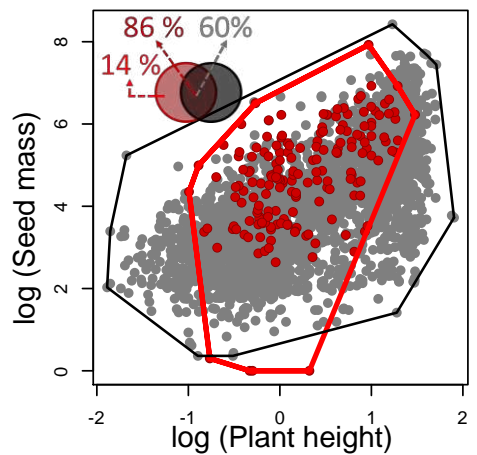
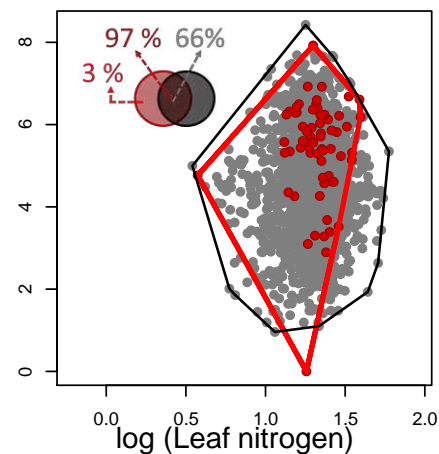
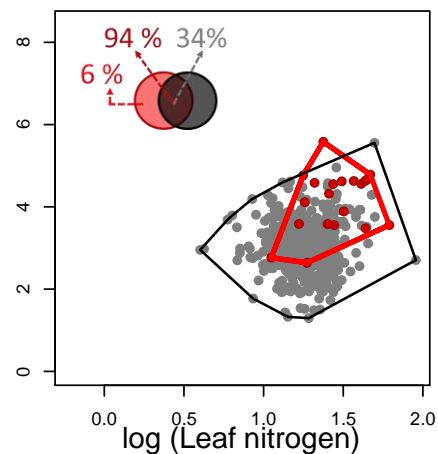
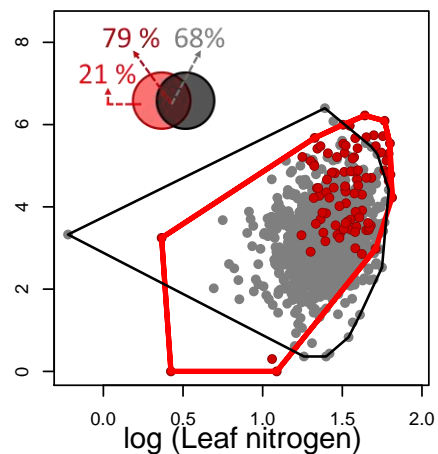
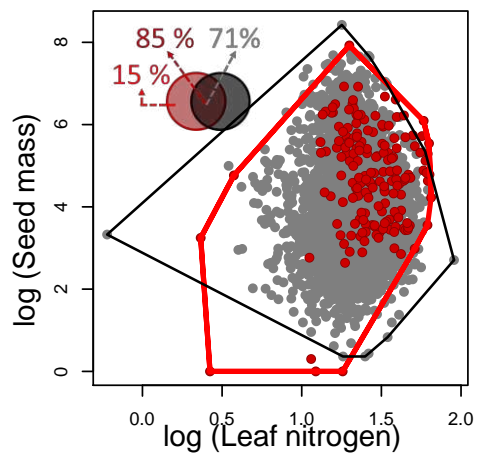
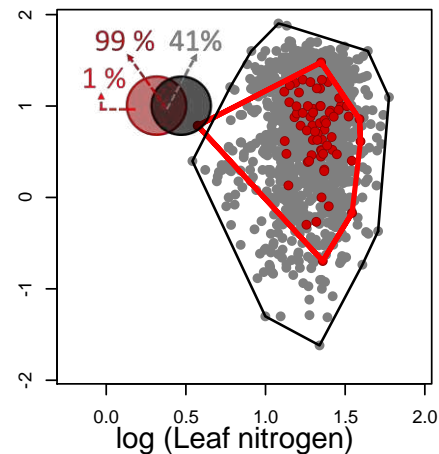
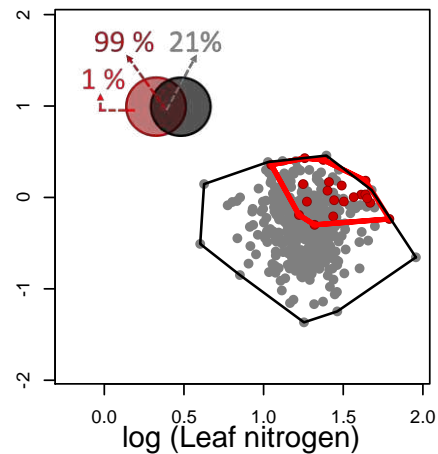
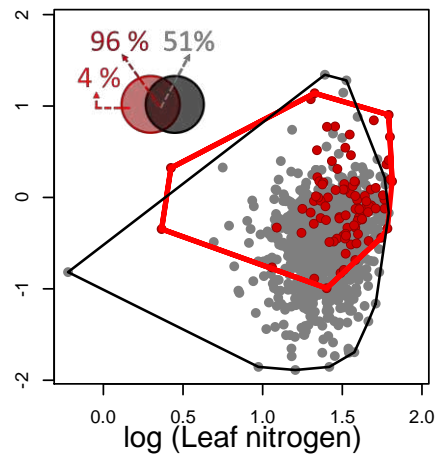
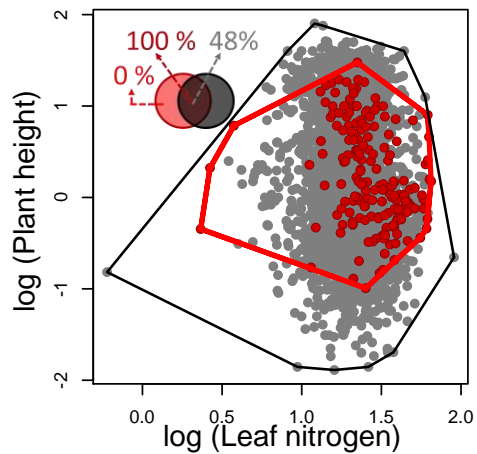
### Ruminants



### Non-ruminant herbivores





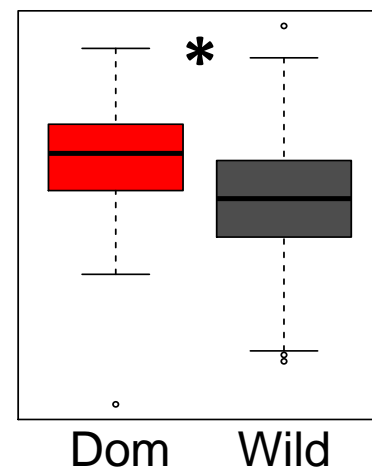
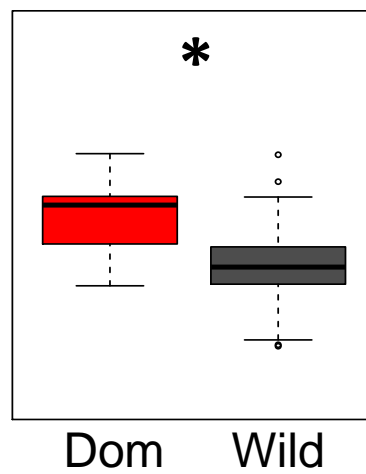
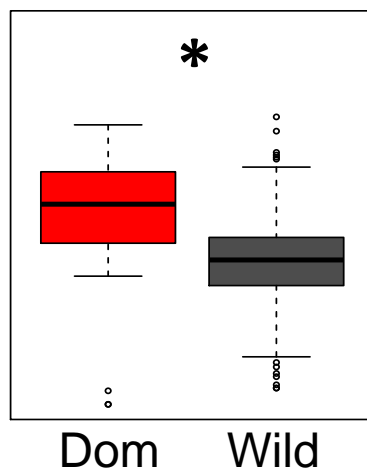
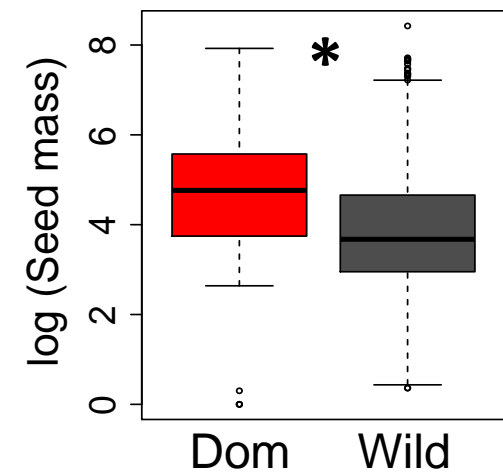
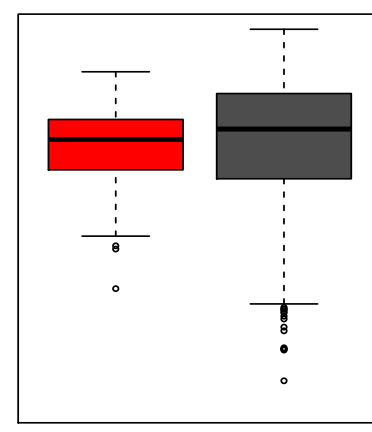
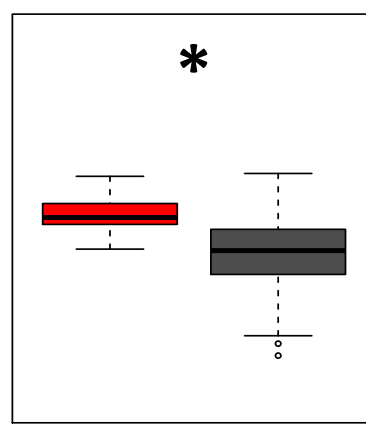
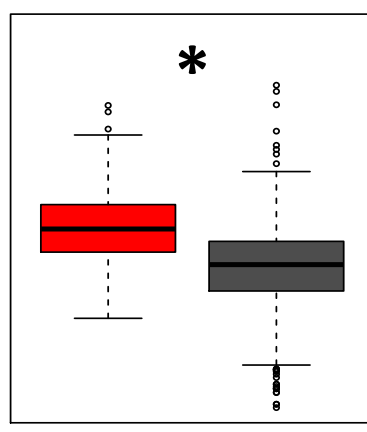
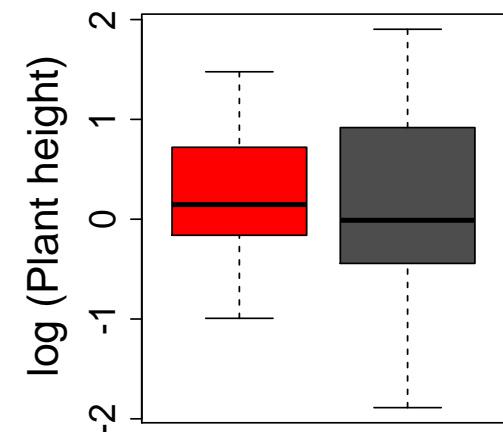
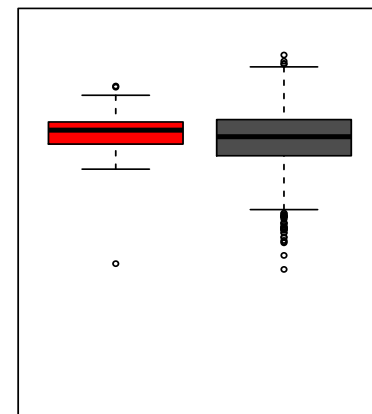
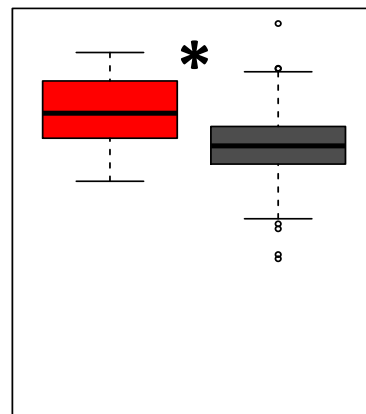
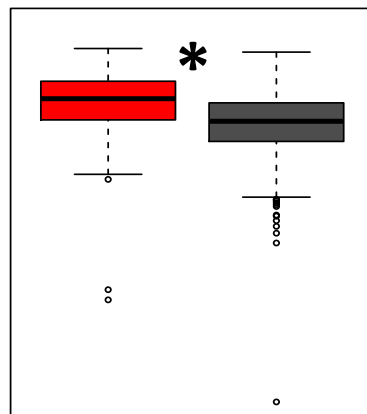
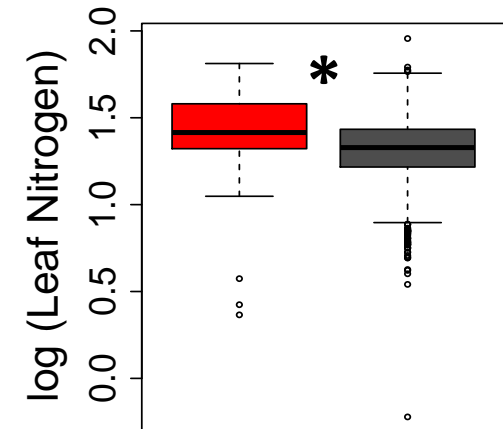
**All angiosperms****Herbaceous****Graminoids****Woody**

All angiosperms

Herbaceous

Graminoids

Woody



Dom

Wild

Dom

Wild

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Wild

Dom

Wild