



Foundation Species Across a Latitudinal Gradient in China

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46 *Abstract.* Foundation species structure forest communities and ecosystems but are dif-
47 ficult to identify without long-term observations or experiments. We used statistical criteria—
48 outliers from size-frequency distributions and scale-dependent negative effects on alpha di-
49 versity and positive effects on beta diversity—to identify candidate foundation woody plant
50 species in 12 large forest-dynamics plots spanning 26 degrees of latitude in China. We
51 used these data to: [1] identify candidate foundation species in Chinese forests; [2] test
52 the hypothesis—based on observations of a mid-latitude peak in functional trait diversity
53 and high local species richness but few numerically dominant species in tropical forests—
54 that foundation woody plant species are more frequent in temperate than tropical or boreal
55 forests; and [3] compare these results with data from the Americas to suggest candidate foun-
56 dation genera in Northern Hemisphere forests. Using the most stringent criteria, only two
57 species of *Acer*, the canopy tree *Acer ukurunduense* and the shrubby treelet *Acer barbinerve*,
58 were identified in temperate plots as candidate foundation species. Using more relaxed crite-
59 ria, we identified four times more candidate foundation species in temperate plots (including
60 species of *Acer*, *Pinus*, *Juglans*, *Padus*, *Tilia*, *Fraxinus*, *Prunus*, *Taxus*, *Ulmus*, and *Corlyus*)
61 than in (sub)tropical plots (the treelets or shrubs *Aporosa yunnanensis*, *Ficus hispida*, *Bras-*
62 *saiopsis glomerulata*, and *Orophea laui*). Species diversity of co-occurring woody species was
63 negatively associated with basal area of candidate foundation species more frequently at 5-
64 and 10-m spatial grains (scale) than at a 20-m grain. Conversely, Bray-Curtis dissimilarity
65 was positively associated with basal area of candidate foundation species more frequently at
66 5-m than at 10- or 20-m grains. Both stringent and relaxed criteria supported the hypothesis
67 that foundation species are more common in mid-latitude temperate forests. Comparisons of
68 candidate foundation species in Chinese and North American forests suggest that *Acer* be
69 investigated further as a foundation tree genus.

70 *Keywords:* *Beta diversity; biodiversity; China; CForBio; codispersion analysis; forest dy-*
71 *namic plots; ForestGEO; latitudinal gradient.*

Introduction

A foundation species is a single species (or a group of functionally similar taxa) that dominates an assemblage numerically and in overall size (e.g., mass or area occupied), determines the diversity of associated taxa through non-trophic interactions, and modulates fluxes of nutrients and energy at multiple control points in the ecosystem it defines (Ellison 2019). Because foundation species are common and abundant, they generally receive less attention from conservation biologists, conservation professionals, or natural-resource managers who emphasize the study, management or protection of rare, threatened, or endangered species (Gaston and Fuller 2007, 2008). However, protecting foundation species before they decline to non-functional levels can maintain habitat integrity and potentially protect associated rare species at lower cost and less effort (Ellison and Degrassi 2017, Degrassi et al. 2019).

Identifying foundation species is difficult because it can take many years—often decades—to collect enough data to distinguish foundation species from other species that also are common, abundant, or dominant (*sensu* Grime 1987) but lack “foundational” characteristics (Baiser et al. 2013, Ellison 2014, 2019). Rather than investigating one common or dominant species at a time in myriad ecosystems, Ellison and his colleagues have worked with data from individual and multiple large forest dynamics plots within the ForestGEO network¹ (Anderson-Teixeira et al. 2015) to develop statistical criteria that can suggest which tree species might merit further attention as candidate foundation species in forests (Buckley et al. 2016a,b, Case et al. 2016, Ellison et al. 2019). Specifically, Ellison et al. (2019) proposed two statistical criteria for candidate foundation tree species: they would be outliers from the expected “reverse-J” size-frequency distribution, and negatively associated with the total abundance, alpha diversity of associated woody species at local spatial scales *and* a positive association between its size or abundance and species turnover (beta diversity) (where diversity is computed as Hill numbers: Chao et al. 2014). These two criteria are described in more detail in the Methods section.

¹<https://www.ForestGEO.si.edu/>

98 We emphasize that the application of these criteria to identify candidate foundation
99 species leads to the hypothesis that a particular taxon may be a foundation species, not
100 that it is one. Asserting that a species is a foundation species requires additional obser-
101 vational and, ideally, experimental evidence (Ellison 2014, 2019). Indeed, we derived these
102 two statistical criteria after more than a decade of observational and experimental studies
103 of *Tsuga canadensis*-dominated forests in New England, USA that lend strong support for
104 the hypothesis that *T. canadensis* is a foundation species (Orwig et al. 2013, Ellison 2014).
105 These criteria subsequently were applied to five additional ForestGEO plots in the western
106 hemisphere (Buckley et al. 2016b, Ellison et al. 2019) with encouraging results. Here, we ap-
107 ply these criteria to 12 large forest dynamics plots in China that range from cold-temperate
108 forests to tropical rain forests. These plots are all part of the Chinese Forest Biodiversity
109 Monitoring Network (CForBio)²; eight of these plots also are part of the ForestGEO network.

110 Foundation tree species have been identified most frequently in mid-latitude, temperate
111 forests (Schweitzer et al. 2004, Whitham et al. 2006, Ellison 2014, Tomback et al. 2016) and
112 low-diversity or mono-dominant tropical forests (Ellison et al. 2005). Ellison et al. (2005)
113 and Ellison et al. (2019) hypothesized that foundation tree species would be less likely in
114 species-rich tropical forests because few species numerically dominate many tropical forests.
115 We note that this observation and the derived hypothesis about the occurrence of foundation
116 species in tropical forests are scale-dependent. For example, Draper et al. (2019) found in
117 a regional-scale analysis that <1% of the tree species in 207 0.025–1-ha plots in Western
118 Amazonia accounted for 50% of the individuals, driving beta-diversity patterns across the
119 region. In larger tropical forest plots, such as those in the ForestGEO network used here, it is
120 rare for any single species to account for >20% of the individuals. The diversity criterion we
121 use includes both species richness and beta diversity, and, with the addition of codispersion
122 analysis (Buckley et al. 2016a,b, Case et al. 2016, Ellison et al. 2019), also identifies scale-
123 dependency in the effects of candidate foundation species on diversity of associated species.

²<http://www.cfbiodiv.org>

124 At the same time, the mid-latitude peak in functional-trait diversity of trees (Lamanna
125 et al. 2014) extends this hypothesis to suggest that foundation tree species should be less
126 common in cold-temperate or boreal forests at high latitudes (or at high elevations in lower
127 latitudes) than in mid-latitude, temperate forests (Ellison et al. 2019). In some of these
128 colder systems, tussock- or cushion-forming perennial plants replace trees as foundation
129 species (e.g., Ellison and Degrassi 2017, Elumeeva et al. 2017). Although we do not explicitly
130 address functional-trait diversity in this paper, we did include cold-temperate CForBio plots
131 in our analysis to screen for candidate foundation species in colder forests.

132 In addition to being the largest synthetic analysis of foundation species in forest ecosys-
133 tems to date, there are two fundamentally new contributions of this work. First, we explicitly
134 test the hypothesis that foundation tree species should be uncommon or absent in species-
135 rich subtropical and tropical forests. Second, the application of our statistical criteria yield
136 new insights into ecological patterns and processes not only for China, but also concern-
137 ing similarities between the floras of East Asia and Eastern North America (Tiffney 1985,
138 Pennington et al. 2004).

139 Methods

140 *Forest dynamics plots in China*

141 We used data from 12 of the 17 CForBio plots in our exploration of candidate foundation
142 species in Chinese forests (Fig. 1, Table 1, Appendix S1). These plots span >26 degrees of
143 latitude and include: the 9-ha broad-leaved Korean pine mixed forest plot at Liangshui in
144 the Xiaoxing'an Mountains of Heilongjiang Province; the 25-ha *Taxus cuspidata*-dominated
145 forest in the Muling Nature Reserve, also in Heilongjiang Province; the 25-ha deciduous
146 broad-leaved Korean pine mixed forest plot on Changbai Mountain in Jilin Province; the
147 20-ha warm-temperate deciduous broad-leaved forest plot on Dongling Mountain in Bei-
148 jing; the 25-ha subtropical evergreen broad-leaved forest plot on Tiantong Mountain in Zhe-
149 jiang Province; the 25-ha mid-subtropical mountain evergreen and deciduous broad-leaved

150 mixed forest plot on Badagong Mountain in Hunan province; the 24-ha subtropical evergreen
151 broad-leaved forest plot on Gutian Mountain in Zhejiang Province; 20-ha lower subtropical
152 evergreen broad-leaved forest plot on Dinghu Mountain in Guangdong Province; the 25-ha
153 cold-temperate spruce-fir forest plot on Yulong Snow Mountain in Yunnan Province; the 25-
154 ha karst evergreen and deciduous broad-leaved mixed forest plot at Mulun in the Guangxi
155 Zhuang Autonomous Region; the 15-ha karst seasonal rain-forest plot at Nonggang, also in
156 the Guangxi Zhuang Autonomous Region; and the 20-ha tropical forest plot at Xishuang-
157 banna in Yunnan Province.

158 [Table 1 about here]

159 [Figure 1 about here]

160 *Tree census and measurement*

161 Standard ForestGEO procedures (Condit 1995) are used to collect data across all CForBio
162 plots. All woody stems (free-standing trees, “shrubs” [including multi-stemmed subcanopy
163 trees], and lianas) at least 1 cm in diameter at breast height (“DBH”; stem diameter measured
164 1.3 m above the ground level) were tagged, measured, identified to species, and mapped. In
165 all of the plots, the individuals have been censused every 5 years (initial census years in these
166 12 plots varied between 2004 and 2014; Table 1); we used the first census data from each
167 plot in our analysis. In all the analysis, we used only the main stem of each individuals (i.e.,
168 smaller stems of multi-stemmed individuals were excluded from the analyses).

169 *The outlier criterion for identifying candidate foundation species*

170 The first criterion is that candidate foundation tree species are outliers from the expected
171 “reverse-J” size-frequency distribution observed in virtually all assemblages of co-occurring
172 species (Loehle 2006). For woody species, we use the size-frequency distribution of mean
173 DBH plotted against the number of individual. The departure from expected size-frequency
174 relationships reflects the abundance of foundation species and their relatively large sizes that

175 lead to their disproportionate influence on overall community structure (Ellison et al. 2019).

176 We refer to this criterion as the “outlier criterion”.

177 In a previous paper (e.g., Ellison et al. 2019), identification of these outliers was done
178 qualitatively (“by eye”). Here we identified outliers quantitatively. After centering and stan-
179 dardizing the values of DBH and number of individuals, we fit a quantile reciprocal function
180 to the data ($y = (1.1 \times 10^{-4})x$; quantile = 0.975) and considered the outliers to be any species
181 above the fitted line. This initial screen revealed 1–22 candidate foundation tree species in
182 each of the 12 forest dynamics plots (Fig. 2). The largest number of candidate species oc-
183 curred in DLS and the fewest were in XSBN. To avoid missing other possible candidate
184 foundation species, we also included in our first cut any species with importance values (IV
185 = relative abundance + relative density + relative basal area) greater than those of any
186 outliers in each plot. Species that were outliers on the size-frequency plots usually had high
187 importance values, but including the latter did expand our initial pool of candidate species
188 to up to 26 species per plot (Appendix S2: Table S1). Four plots still had very few candidate
189 species (BDG with 4, ML [5], NG [4], and XSBN [1]), so for those plots, we brought the total
190 of assessed species up to 10/plot by including additional species with high IVs.

191 [Figure 2 about here]

192 *The diversity criterion for identifying candidate foundation species*

193 The second criterion (the “diversity criterion”) is that the size or abundance of candidate
194 foundation species should be negatively associated with the total abundance, three measures
195 of alpha diversity (species richness, Shannon diversity, Inverse Simpson Diversity) of asso-
196 ciated woody species at local (small) spatial scales *and* a positive association between its
197 size or abundance and species turnover (beta diversity) across large forest plots or stands
198 (Ellison et al. 2019). The three measures of alpha diversity either treat all species identically
199 (species richness), down-weight rare species (Shannon diversity), or down-weight common
200 species (inverse Simpson diversity) within subplots. The negative spatial association between

201 the size or abundance of foundation tree species with local diversity of co-occurring woody
202 species results simply from the foundation species occupying most of the available space in
203 a standard 20 × 20-m (0.04-ha) forest plot (or, in fact, any relatively small plot).

204 In contrast, the positive spatial association between the size or abundance of a foundation
205 tree species with beta diversity results from it creating patchy assemblages at landscape
206 scales. For example, forest stands dominated by foundation species such as *Tsuga canadensis*
207 in eastern North America or *Pseudotsuga menziesii* in western North America manifest
208 themselves as distinctive patches on the landscape. Similarly, species that dominate small
209 plots (< 1 ha in area) can drive beta diversity in tropical Amazonian forests (Draper et al.
210 2019). When these foundation or dominant species decline or are selectively harvested, the
211 landscape is homogenized and beta diversity declines. Indeed, Ellison et al. (2019) suggested
212 that the preservation of landscape diversity may be the most important reason to protect
213 and manage foundation tree species before they decline or disappear.

214 **Forest structure and species diversity indices**

215 For each plot, we calculated the total basal area, mean basal area, and total number of
216 individuals of each of the candidate foundation tree and shrub species (Table S1) within
217 contiguous 5 × 5, 10 × 10, and 20 × 20-m subplots. For species other than the candidate
218 foundation species, we calculated their total abundance, species richness, Shannon and in-
219 verse Simpson diversity indices (as Hill numbers: Chao et al. 2014) and mean Bray-Curtis
220 dissimilarity (overall methods as in Ellison et al. 2019). The `diversity()` and `vegdist()`
221 functions in the `vegan` package (Oksanen et al. 2018) of the R software system (R Core Team
222 2019) were used for calculating each diversity metric.

223 **Codispersion analysis**

224 The associations between size or abundance of candidate foundation species and mea-
225 sures of alpha or beta diversity also should be consistent (isotropic) across the plots when

226 calculated at a given spatial grain (*a.k.a.* spatial scale) and at most (ideally all) spatial lags
227 (Buckley et al. 2016a, Ellison et al. 2019). We estimated effects of foundation species on di-
228 versity of associated species at different spatial grains (5×5 , 10×10 , and 20×20 -m subplots)
229 using codispersion analysis (Buckley et al. 2016a, Ellison et al. 2019). Codispersion can iden-
230 tify and describe anisotropic spatial patterns (i.e., different expected values when measured
231 in different directions) of co-occurring variables for given spatial lags and directions (Cuevas
232 et al. 2013). The codispersion coefficient ranges from -1 to 1 , with positive values indicating
233 a positive spatial association and negative values indicating a negative spatial association for
234 a given spatial lag and direction. These values can be visualized with a codispersion graph
235 (Vallejos et al. 2015; see also Buckley et al. 2016a).

236 Although we computed codispersion patterns using mean basal area, total basal area, and
237 total abundance of candidate foundation species, we focus our presentation on the codisper-
238 sion between the total basal area of the candidate foundation species and associated woody
239 plant diversity at different spatial grains (i.e., in the differently-sized contiguous subplots)
240 in each of the 12 forest dynamics plots; qualitatively similar patterns were observed when
241 using mean basal area or total numbers of individuals of candidate foundation species. For
242 each candidate foundation tree species, we first computed the observed codispersion coeffi-
243 cient between its total basal area and abundance, alpha, and beta diversity of the associated
244 woody species in the subplots. The maximum spatial lag examined for each plot ranged from
245 the length of the subplot to one-fourth of the length of the shortest side of each forest plot,
246 which ensured adequate sample sizes for reliable estimation of codispersion coefficients at
247 the largest spatial lag (Buckley et al. 2016a).

248 Statistical significance of the codispersion coefficients was determined using null model
249 analysis (Buckley et al. 2016b, Ellison et al. 2019). Codispersion coefficients for all spatial lags
250 and directions were computed for co-occurrence matrices randomized using a toroidal-shift
251 null model, which maintains the autocorrelation structure of the species and spatial patterns
252 caused by underlying environmental gradients while shifting the associated woody species in

253 random directions and distances (Buckley et al. 2016b, Ellison et al. 2019). For each candidate
254 foundation species in each plot, we ran 199 randomizations; significance was determined
255 based on empirical 95% confidence bounds. Calculation of codispersion coefficients and all
256 randomizations were done using custom C and R code written by Ronny Vallejos and Hannah
257 Buckley, respectively.

258 *Data and code availability*

259 Each of the CForBio plots were established at different times and are scheduled to be (or
260 already have been) censused every five years. To maximize comparability among datasets, we
261 used data collected at the first census for each plot (Table 1). Data for individual plots are
262 available from the PIs of each plot; their contact information is provided in the individual plot
263 descriptions in Appendix S1. R code for all analyses is available from the Environmental Data
264 Initiative (DOI: <https://doi.org/10.6073/pasta/5adc884142cee1c856dfacd32858a3ab>).

265 **Results**

266 *Candidate foundation species in the CForBio plots*

267 Only two candidate foundation species in one plot (MLG) and at one spatial grain (5-
268 m) satisfied both the outlier *and* diversity criteria for all diversity measures for candidate
269 foundation species (Table 2). These two species were the shrub *Acer barbinerve* (Appendix
270 S2: Figs. S1, S2) and the congeneric tree *Acer ukurunduense* (Appendix S2: Figs. S3, S4).

271 More species were considered as candidate foundation species when we retained the out-
272 lier criterion (Fig. 2) but relaxed the diversity criterion to require only a positive spatial
273 relationship between the size of the candidate foundation species and beta diversity *and* a
274 negative spatial relationship between the size of the candidate foundation species and at least
275 one of the alpha-diversity measures (species indicated with an asterisk [*] in Table 2). These
276 additional candidate foundation species included two additional *Acer* species, tree or treelet
277 species in the genera *Pinus*, *Taxus*, *Fraxinus*, *Quercus*, *Juglans*, *Syringa*, *Prunus*, *Ulmus*,

278 *Aporosa*, and *Tilia*, and one shrub (*Corylus mandshurica*). However, whether we applied
279 the stringent or relaxed diversity criterion, all but three of the candidate foundation species
280 occurred in plots with cool- or cold-temperate climates. The exceptions were the trees *Pinus*
281 *massoniana* and *Quercus serrata* at GT and *Aporosa yunnanensis* at DH; all three of these
282 species occurred in the subtropical evergreen broad-leaved forest plots.

283 A few of our initial candidate species that had high importance values but were not
284 outliers from the expected size-frequency distributions (unstarred species in Table S1) did
285 partially meet the diversity criterion in both temperate and tropical plots (Table 2). These
286 included *Prunus padus* at CB, *Brassaiopsis glomerulata* at ML, *Ficus hispida* at NG, and
287 *Orophea laui* at XSBN.

288 *Scale-dependence of candidate foundation species*

289 More candidate foundation species—including all species that met at least one of the
290 two criteria—were identified at smaller spatial grains: 16 species at the 5-m grain, 12 at the
291 10-m grain, and seven at the 20-m grain (Table 2). This pattern applied both among and
292 within the plots. Average codispersion between total basal area of the candidate foundation
293 species and Bray-Curtis dissimilarity increased significantly with spatial grain (Fig. 3; raw
294 data in Table S2) but was not anisotropic (Appendix S2: Figs. S1, S3). In contrast, average
295 codispersion between total basal area of the candidate foundation species and measures of
296 alpha diversity, while generally negative, were more variable and not scale-dependent (Fig.
297 3; raw data in Table S2).

298 [Figure 3 about here]

299 *Candidate foundation species across a latitudinal gradient*

300 The median number of candidate foundation species in the four temperate plots was five,
301 but was ≤ 1 for the the eight subtropical and tropical plots (Table 2). Both the number of
302 woody species in each plot that were outliers from the expected size-frequency distribution

303 and the number of candidate foundation species increased with increasing latitude (Fig.
304 4A, C; slopes = 0.6 and 0.2 species/degree of latitude, respectively; $P < 0.01$). As expected,
305 within-plot species richness declined significantly with latitude (slope = -10.2 species/degree
306 of latitude; $P < 0.01$), but this relationship was unrelated to the latitudinal pattern in either
307 the number of outliers or the number of candidate foundation species. The relationship
308 between the number of outliers and species richness was negative (Fig. 4B; $P < 0.01$) and
309 there was no significant relationship between the number of candidate foundation species
310 and within-plot species richness (Fig. 4D; $P = 0.10$).

311 [Figure 4 about here]

312 Spatial association (expressed as codispersion) within each plot between candidate foun-
313 dation species and total abundance, mean alpha diversities, and mean beta diversity of asso-
314 ciated woody species on average did not vary with latitude at any spatial grain (Fig. 5; raw
315 data in Appendix S2: Table S2). Quantile regression (to account for potential extreme effects
316 of foundation species) yielded similar results. There were no observed latitudinal patterns in
317 effects of candidate foundation species except for a slight strengthening of the negative effect
318 of candidate foundation species on associated woody species richness and total abundance
319 at the 5-m grain (Fig. 5; $P = 0.03$ and 0.04 respectively). When understory shrubs and
320 multi-stemmed subcanopy trees were excluded from the analysis, there only were negative
321 relationships between latitude and spatial association of richness at 5-m and 10-m grains
322 (Fig. 6; $P = 0.02$ and 0.04 respectively).

323 [Figure 5 about here]

324 [Figure 6 about here]

325 Discussion

326 We applied two statistical criteria (Ellison et al. 2019) to screen 12 CForBio Forest Dy-
327 namic plots in China for candidate foundation species. These 12 plots ranged from 47 to 21

328 °N latitude, represented conifer-dominated, broad-leaved deciduous, subtropical, and tropi-
329 cal forests (Table 1), and included two forest types referred to by particular species (“Korean
330 pine” mixed forests at Liangshi and Changbai Mountain, and the “*Taxus cuspidata*” mixed
331 coniferous forest at Muling). Such eponyms do suggest traditional or cultural-based knowl-
332 edge of foundation (or other “important”) species (Ellison et al. 2005, Ellison 2019). Whereas
333 both Korean pine (*Pinus koraiensis*) and *Taxus cuspidata* were identified as candidate foun-
334 dation species (Table 2), they were only candidates in the Muling *Taxus cuspidata*-dominated
335 forest plot, not in either of the “Korean pine” mixed forests. We also found a strong lati-
336 tudinal gradient, unrelated to the expected (and observed) underlying latitudinal gradient
337 in woody plant species richness, in the number of candidate foundation species, which were
338 more frequent in temperate than in tropical forest plots (Fig. 4). Where they occurred, can-
339 didate foundation species had comparable effects at all latitudes (Figs. 5, 6), suggesting that
340 foundation species effects more likely reflect specific combinations of traits and interspecific
341 effects rather than being manifestations of “neutral” (sensu Hubbell 2001) processes (Ellison
342 et al. 2019).

343 *Candidate foundation species are more common in temperate latitudes*

344 Foundation species in forests control species diversity locally within forest stands and at
345 landscape and larger scales by creating habitat for associated flora (e.g., epiphylls, epiphytes,
346 vines, lianas) and modifying soil structure and composition (e.g., Ellison et al. 2005, Brantley
347 et al. 2013, Baiser et al. 2013, Vallejos et al. 2018, Degrassi et al. 2019, Ellison 2019). Forest
348 foundation species frequently are common and abundant large trees (e.g., Schweitzer et al.
349 2004, Ellison et al. 2005, Whitham et al. 2006, Tomback et al. 2016, Ellison et al. 2019), but
350 understory shrubs and subcanopy trees also can have foundational characteristics (Kane et al.
351 2011, Ellison and Degrassi 2017, Ellison et al. 2019). Ellison et al. (2005) hypothesized that
352 foundation species would be more likely in temperate forests because of their relatively low
353 species richness and more frequent dominance by one or a small number of taxa. In contrast,

354 most tropical forests should lack foundation species as they generally are speciose and are
355 dominated less frequently by a small number of taxa. Our data supported this hypothesis:
356 candidate foundation species in the CForBio plots were more common at higher latitudes
357 than in the tropics (Fig. 4; Ellison et al. 2019).

358 The increased likelihood of candidate foundation species in temperate forests may also
359 reflect three other, related processes. First, deterministic “niche” processes may be more
360 prevalent in temperate forests than in tropical ones, where neutral dynamics predominate
361 (Gravel et al. 2006, Qiao et al. 2015). Second, functional-trait diversity of trees peaks at mid-
362 latitudes (Lamanna et al. 2014). Because foundation species have unique sets of traits, there
363 may be only one or a few species with all the relevant traits in species-poor temperate forests,
364 whereas higher functional redundancy in speciose tropical forests may lead to no one species
365 being “singled out” by foundational characteristics. Finally, foundation species control the
366 diversity of associated taxa primarily through non-trophic effects (Baiser et al. 2013) but
367 trophic interactions are more important in structuring tropical forests than temperate ones
368 (e.g., Janzen 1970, Connell 1971, Roslin et al. 2017, Longo et al. 2018).

369 We hypothesize that tropical forests dominated by a one or a few closely-related species,
370 such as coastal mangrove forests dominated by *Rhizophora* spp. (Tomlinson 1995) and mon-
371 odominant tropical lowland forests dominated by species of Dipterocarpaceae in southeast
372 Asia or species of Leguminosae (subfamily Caesalpinioideae) in Africa and the Neotropics
373 (Torti et al. 2001, van der Velden et al. 2014, Hall et al. 2020) may be structured by founda-
374 tion species (Ellison et al. 2005). Indeed, *Gilbertiodendron dewevrei* in the Ituri ForestGEO
375 plot in the Democratic Republic of Congo (Makana et al. 2004a,b) has functional character-
376 istics similar to *Tsuga canadensis* in northeastern US forests. *Gilbertiodendron* casts deep
377 shade; produces leaf litter that decomposes very slowly, creating a dense and deep litter
378 layer; creates soils with $\approx 30\%$ of the available nitrogen (ammonium + nitrate) relative to
379 nearby mixed forests; and has a depauperate (albeit not unique) fauna of leaf-litter ants and
380 mites (Torti et al. 2001).

381 At XSBN, the dipterocarp *Parashorea chinensis* occurs in monodominant patches (van der
382 Velden et al. 2014), has a high importance value (Appendix S2: Table S1), but did not end
383 up in our winnowed list of candidate foundation species (Table 2). This was because in our
384 analyses, as in those of van der Velden et al. (2014), diversity of associated woody species
385 did not differ between 20 × 20-m subplots dominated by *P. chinensis* and adjacent mixed
386 stands. This does not mean that *P. chinensis* could not have foundational characteristics in
387 any forest, just that it does not currently act as a foundation species in this CForBio plot.
388 Foundational characteristics may be apparent only at later successional stages or in mature
389 forest stands (Ellison et al. 2014, 2019). van der Velden et al. (2014) suggest that the *P.*
390 *chinensis* patches at XSBN may represent remnants of old-growth forest in a matrix of a
391 forest historically modified by shifting cultivation, in which case we may now be observing
392 a ruined foundation.

393 Mycorrhizal associations may contribute to foundational effects of particular tree species.
394 Trees associated with ectomycorrhizae may have weaker negative density-dependence among
395 conspecifics than trees associated with arbuscular-mycorrhizae (Bennett et al. 2017, John-
396 son et al. 2018, Chen et al. 2019). Experiments in the GT plot investigating different effects
397 of pathogenic and mutualistic fungi on community structure found increased abundance
398 of pathogenic fungi increased negative density-dependent interactions among conspecifics
399 whereas increased abundance of mutualistic fungi decreased density-dependent interactions
400 among conspecifics (Chen et al. 2019). The two candidate foundation species in GT (*Pi-*
401 *nus massoniana* and *Quercus serrata*) are abundant and associated with mutualistic fungi.
402 Analysis of species distribution and diversity associated with potential foundation species
403 in Southeast Asian forests dominated by Dipterocarpaceae (ectomycorrhizal), such as the
404 ForestGEO 50-ha Pasoh plot in Malaysia (Kochummen et al. 1991, Ashton et al. 2003) ver-
405 sus others lacking abundant dipterocarps, such as the 30-ha ForestGEO Mo Singto plot in
406 Thailand (Brockelman et al. 2011) or the 2-ha plot in Aluoi, Vietnam (Nguyen et al. 2016)

407 would provide useful comparisons with the analyses of the CForBio plots—especially the
408 20-ha Xishuangbanna plot—presented here.

409 Conversely, the mid-latitude peak in functional-trait diversity of trees (Lamanna et al.
410 2014) led Ellison et al. (2019) to hypothesize that foundation tree species should be less
411 common in boreal forests at high latitudes or at high elevations in lower latitudes than
412 in more temperate ones. Our data showing no candidate foundation species at the high-
413 elevation but low-latitude Yulong Snow Mountain plot support this hypothesis (Table 2).
414 In other high-elevation and high-latitude boreal ecosystems, foundation species tend to be
415 low-growing perennial, cushion- or tussock-forming plants (e.g., Ellison and Deggrasi 2017,
416 Elumeeva et al. 2017).

417 *Foundation species effects are scale-dependent at landscape, not local scales*

418 Ellison (2019) argued that foundation species increase “patchiness” (beta diversity) at
419 landscape scales, and that this effect of foundation species is of paramount importance when
420 considering whether and how to conserve or otherwise manage them (see also Ellison et al.
421 2019). Across the 12 CForBio plots, we observed an increase in the strength of foundation
422 species effects on beta diversity, expressed as a significant increase in codispersion between
423 the candidate foundation species and compositional dissimilarity of associated species at
424 increasingly larger spatial grain (Fig. 3). At the 20-m grain, the magnitude of the codispersion
425 coefficient approached that of many of the candidate foundation species in ForestGEO plots
426 in the Americas (0.25–0.35; Fig. 3), but still less than the very strong effects of *T. canadensis*
427 in northeastern US forests (Ellison et al. 2019).

428 Conversely, although foundation species can provide habitat for associated species, thus
429 increasing their local diversity, the opposite pattern and magnitude of effects has been found
430 when analyzing only associated woody plant species in forest dynamic plots (Buckley et al.
431 2016a, Ellison et al. 2019) because foundation species occupy most of the available space. In
432 the CForBio plots, codispersion similarly was negative between candidate foundation species

433 and alpha diversity of associated woody plants (Figs. S1–S3), but this relationship did not
434 vary significantly with spatial grain (Fig. 3). Additional data on faunal groups (e.g., Sackett
435 et al. 2011, Record et al. 2018) or non-woody plants (e.g., Ellison et al. 2016) could provide a
436 test of whether these candidate foundation species have a positive effect on other associated
437 species that are not competing for space with canopy or subcanopy trees (e.g. Schowalter
438 1994, Ruchty et al. 2001, Ellison 2018).

439 *Acer as a candidate foundation genus*

440 In this study, four species of *Acer* were candidate foundation species among the three
441 cold-temperate plots in China (Liangshui, Muling, and Changbai: Table 2). Among these, *A.*
442 *ukurunduense* and *A. barbinerve* were the only two of all our candidate foundation species
443 that met the most stringent criteria for consideration. In a comparable study across a lat-
444 itudinal gradient in the Americas, *A. circinatum* was identified as a candidate foundation
445 species in the the Wind River ForestGEO plot in Washington State, USA (Ellison et al.
446 2019). We hypothesize that in many forests throughout the Northern Hemisphere, that *Acer*
447 not only can be a dominant genus in terms of abundance or total basal area, but that it may
448 function as a foundation genus, akin to *Quercus* in the Tyson ForestGEO plot in central
449 North America (Ellison et al. 2019).

450 *Acer* species often are common and abundant in temperate deciduous broad-leaved, conif-
451 erous, and mixed forests throughout the Holarctic (Braun 1938, 1955, Tiffney 1985, Penning-
452 ton et al. 2004), and in subtropical montane forests in China (Xu 1996). *Acer* includes >150
453 species (WFO (World Flora Online) 2020), at least 99 of which (including 61 endemics)
454 occur in China (Xu et al. 2008) and more than a dozen are found in North America (Alden
455 1995). *Acer* species generally are shade tolerant, (i.e., they can regenerate and grow under
456 closed canopies) and have relatively high seedling and sapling survival rates (Tanaka et al.
457 2008). Some more shade-intolerant (“photophilous”) early-successional *Acer* species create

458 conditions that facilitate restoration of both later successional forests and their associated
459 animal assemblages (Zhang et al. 2010).

460 There are several forests named after *Acer* species in China, including the *Acer mono-*
461 *Tilia amurensis-T. mandshurica* temperate broad-leaved deciduous forest, the *Schima superba-*
462 *Acer caudatum-Toxicodendron succedaneum* eastern subtropical forest, and the *Cyclobal-*
463 *anopsis multinervis-Castanopsis eyrel var. caudata-Liquidambar acalycina-Acer sinense* for-
464 est in southwest China (Wu 1995). *Acer* also are considered primary “companion” species in
465 Chinese *Quercus* and mixed broad-leaved-Korean pine forests where multiple *Acer* species
466 co-occur. For example, six–seven additional *Acer* species were recorded with the three can-
467 didate foundation *Acer* species in the two broad-leaved-Korean pine mixed forests plots (LS,
468 CB). The nine *Acer* species in the CB plot account for >46% of the total stems (Zhang et al.
469 2010).

470 In North American forests, *Acer* species also define several forest types, including “Sugar
471 Maple” (i.e., *A. saccharum*), “Beech-Maple”, “Sugar Maple –Beech–Yellow Birch”, “Sugar
472 Maple–Basswood”, “Red Maple” (i.e., *A. rubrum*), and “Silver Maple–American Elm” (i.e.,
473 *A. saccharinum*) (Braun 1938, 1955, Eyre 1980). In forests of the Pacific Northwest of North
474 America, the subcanopy treelet *A. circinatum* not only grows rapidly, has high biomass,
475 and forms broad canopies that suppress other species (Lutz and Halpern 2006, Halpern and
476 Lutz 2013), which causes it to have negative codispersion with other woody taxa (Ellison
477 et al. 2019), but it also supports a high diversity of epiphytes (Ruchty et al. 2001). An-
478 other North American species, *A. saccharinum*, dominates floodplain forests on well-drained
479 alluvial soils in the eastern U.S. (Gabriel 1990). Although Vankat (1990) subsumed “Silver
480 Maple–American Elm” forests within a “Mixed Hardwood Wetland Forest” type and consid-
481 ered *A. saccharinum* to be only a minor component of these forests, this species historically
482 was a significant constituent of at least some primary forests in the upper Midwestern U.S.
483 and Canada (Cho and Boerner 1995, Simard and Bouchard 1996, Guyon and Battaglia 2018),
484 supports unique assemblages of birds (Yetter et al. 1999, Knutson et al. 2005, Kirsch and

485 Wellik 2017), and, among woody species, contributes substantially to carbon fixation in tidal
486 wetlands (Milligan et al. 2019). *Acer saccharinum* may be similar to other North American
487 (candidate) foundation species whose effects are most pronounced at different successional
488 stages (Ellison et al. 2014, 2019). However, we know of no large plots in either “Silver Maple–
489 American Elm” or “Mixed Hardwood Wetland” forests from which we could derive data to
490 test whether *A. saccharinum* meets our statistical criteria for candidate foundation species.
491 Whereas it may be premature to establish large forest dynamics plots in floodplains in ei-
492 ther the temperate zone or the tropics, or in tropical coastal habitats with low tree diversity,
493 comparable data could be used to test more general ideas about the foundational importance
494 of particular genera, such as *Acer* or *Rhizophora*, in forested wetlands worldwide.

495 In conclusion, candidate foundation species were more common in temperate forests than
496 in tropical forests, likely reflecting lower tree species diversity and a greater importance of
497 non-trophic and “niche” effects in the temperate zone. Foundation species effects on alpha
498 (within subplot) diversity were invariant with spatial grain, but foundation species effects
499 on beta diversity increased with increasing spatial grain. These results suggest it may be
500 possible to use statistical criteria to identify, manage, and protect foundation forest species
501 before they are no longer functionally relevant in forests around the world.

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513 **Author contributions**

514 XQ and AME conceptualized and designed the study and wrote the manuscript; XQ and
515 all other authors except AME collected the data at the individual CForBio plots. All authors
516 contributed critically to the drafts and gave final approval for publication.

517 **Conflict of interest**

518 The authors declare no conflicts of interest.

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Table 1: Geographic data for CForBio forest dynamics plots studied here. Latitude and longitude are in °N and °E, respectively; elevation is in meters above sea level (m a.s.l.); area is in hectares (ha), and census year is the year of the first census of the plot.

Plot	Province	Latitude	Longitude	Elevation	Vegetation type	Area (ha)	Census Year
LS	Heilongjiang	47.18	128.88	467	Broad-leaved Korean pine mixed forest	9	2010
MLG	Heilongjiang	43.95	130.07	720	<i>Taxus cuspidata</i> -dominated mixed coniferous forest	25	2014
CB	Jilin	42.38	128.08	802	Deciduous broad-leaved Korean pine mixed forest	25	2004
DL	Beijing	39.96	115.43	1395	Deciduous broad-leaved forest	20	2010
TT	Zhejiang	29.80	121.80	454	subtropical evergreen broad-leaved forest	20	2009
BDG	Hunan	29.77	110.09	1412	Mid-subtropical mountain evergreen and deciduous broad-leaved mixed forest	25	2011
GT	Zhejiang	29.25	118.12	581	subtropical evergreen broad-leaved forest	24	2005
YLXS	Yunnan	27.14	100.22	3282	Cool-temperate spruce-fir forest	25	2014
ML	Guangxi	25.80	108.00	550	Karst evergreen and deciduous broad-leaved mixed forest	25	2014
DH	Guangdong	23.10	112.32	350	lower subtropical evergreen broad-leaved forest	20	2005
NG	Guangxi	22.45	106.95	260	Karst seasonal rain forest	15	2011
XSBN	Yunnan	21.61	101.57	789	Tropical rain forest	20	2007

Table 2: A winnowed list of candidate foundation tree and shrub species (the latter indicated by a plus sign [+]) at three different spatial grains (i.e., subplot size) in 12 Chinese forest dynamics plots. Plots are ordered by latitude, and within each plot, candidate foundation species are ordered alphabetically. The two *Acer* species in **bold type** satisfied all aspects of both the outlier and the diversity criteria for candidate foundation species at the given spatial grain. The starred (*) species satisfied the outlier criterion (Fig. 2) and partially satisfied the diversity criterion at the given spatial grain: a positive spatial relationship between candidate foundation species size and beta diversity, and a negative spatial relationship between candidate foundation species size and at least one measure of alpha diversity. The remaining species did not satisfy the outlier criterion but did meet some aspects of the diversity criterion. No species met either foundation species criterion in the BDGS, TTS and YLXS plots at any spatial grain.

Plot	Spatial grain		
	5 m	10 m	20 m
LS	* <i>Acer ukurunduense</i> * <i>Corylus mandshurica</i> ⁺ * <i>Fraxinus mandshurica</i> * <i>Prunus padus</i>	* <i>Acer ukurunduense</i> — — * <i>Prunus padus</i>	— — — * <i>Prunus padus</i>
MLG	* <i>Acer barbinerve</i> ⁺ * <i>Acer tegmentosum</i> * <i>Acer ukurunduense</i> * <i>Corylus mandshurica</i> ⁺ — * <i>Taxus cuspidata</i> * <i>Tilia amurensis</i>	* <i>Acer barbinerve</i> ⁺ — — — * <i>Pinus koraiensis</i> * <i>Tilia amurensis</i>	— — — — * <i>Pinus koraiensis</i> * <i>Tilia amurensis</i>
CB	* <i>Acer barbinerve</i> ⁺ * <i>Acer pseudosieboldianum</i> * <i>Acer tegmentosum</i> * <i>Corylus mandshurica</i> ⁺ * <i>Syringa reticulata</i> var. <i>amurensis</i> ⁺ <i>Prunus padus</i>	— * <i>Acer pseudosieboldianum</i> — * <i>Corylus mandshurica</i> ⁺ * <i>Syringa reticulata</i> var. <i>amurensis</i> ⁺ <i>Prunus padus</i>	— — — — — <i>Prunus padus</i>
DL	* <i>Juglans mandshurica</i> * <i>Ulmus laciniata</i>	— * <i>Ulmus laciniata</i>	— —
TT	—	—	—
BDG	—	—	—
GT	—	—	* <i>Pinus massoniana</i> * <i>Quercus serrata</i>
YLXS	—	—	—
ML	<i>Brassaiopsis glomerulata</i>	<i>Brassaiopsis glomerulata</i>	—
DH	* <i>Aporosa yunnanensis</i>	* <i>Aporosa yunnanensis</i>	* <i>Aporosa yunnanensis</i>
NG	<i>Ficus hispida</i> ⁺	<i>Ficus hispida</i> ⁺	—
XSBN	<i>Orophea laui</i>	<i>Orophea laui</i>	<i>Orophea laui</i>

Figure Legends

Figure 1. Locations of the CForBio plots from where the data used in this paper were collected. See Table 1 for geographic data and site abbreviations, and Appendix S1 for detailed descriptions of each plot.

Figure 2. Size (DBH)-frequency distributions of the species in each plot. Species falling outside of the “reverse-J” boundary (0.0975^{th} quantile of the quantile reciprocal function $y = (1.1 \times 10Y - 4)x$; red line) were placed in the first set of candidate foundation species (Table S1). Plots are ordered left-to-right and top-to-bottom by latitude. Plot abbreviations as in Table 1.

Figure 3. Distribution of average codispersion observed between total basal area of candidate foundation species and Bray-Curtis dissimilarity, species richness, and total abundance of associated woody plant species in contiguous 5×5 -, 10×10 -, and 20×20 -m subplots in the twelve CForBio plots. Points indicate mean codispersion values for each candidate foundation species listed in Table S1; solid points indicate the two candidate foundation species in the genus *Acer* that met both the outlier *and* diversity criterion for all indices; hollow squares indicate candidate species that met the outlier criterion and the relaxed diversity criterion; and crosses indicate the remaining candidate foundation species that met only the relaxed diversity criterion. Points are jittered within categories. *P* values for comparisons between groups are shown at the top of each panel.

Figure 4. Number of outliers from the expected size-frequency distribution (Fig. 2) and number of candidate foundation species (Table 2) as a function of latitude (**A**, **C**) or plot-level species richness (**B**, **D**). See main text for regression statistics.

Figure 5. Relationship between latitude and codispersion between candidate foundation species (canopy trees and understory trees and shrubs) and three measures of associated woody-plant diversity at different spatial grains. Box plots illustrate median, upper and lower quartiles, and individual points outside of the upper and lower deciles of average

785 codispersion at each latitude where candidate foundation species occurred (Table 2). Box
786 width is proportional to sample size.

787 Figure 6. Relationship between latitude and codispersion between candidate foundation
788 canopy tree species and three measures of associated woody-plant diversity at different spatial
789 grains. Box plots illustrate median, upper and lower quartiles, and individual points outside
790 of the upper and lower deciles of average codispersion at each latitude where candidate
791 foundation species occurred (Table 2). Box width is proportional to sample size.

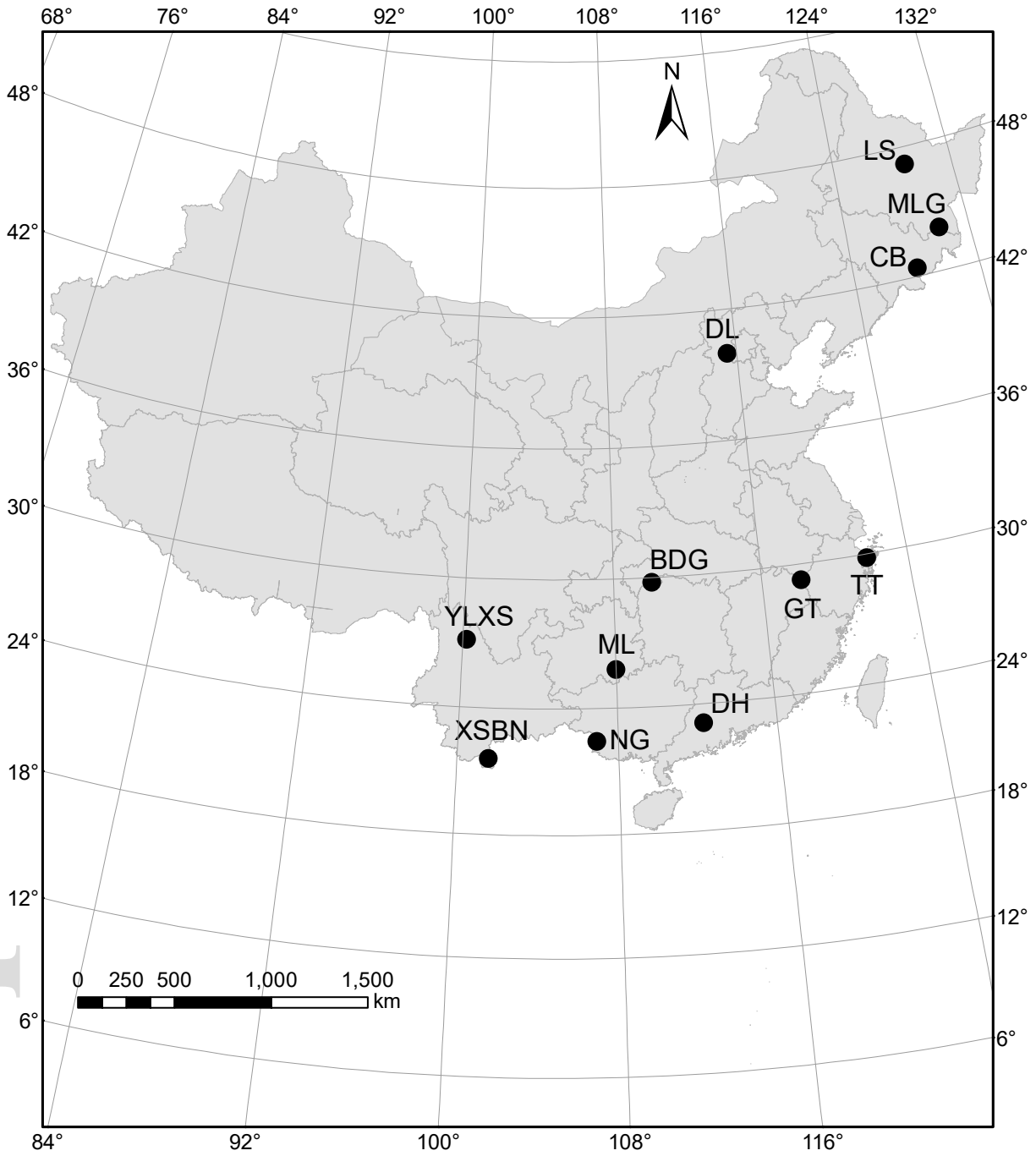


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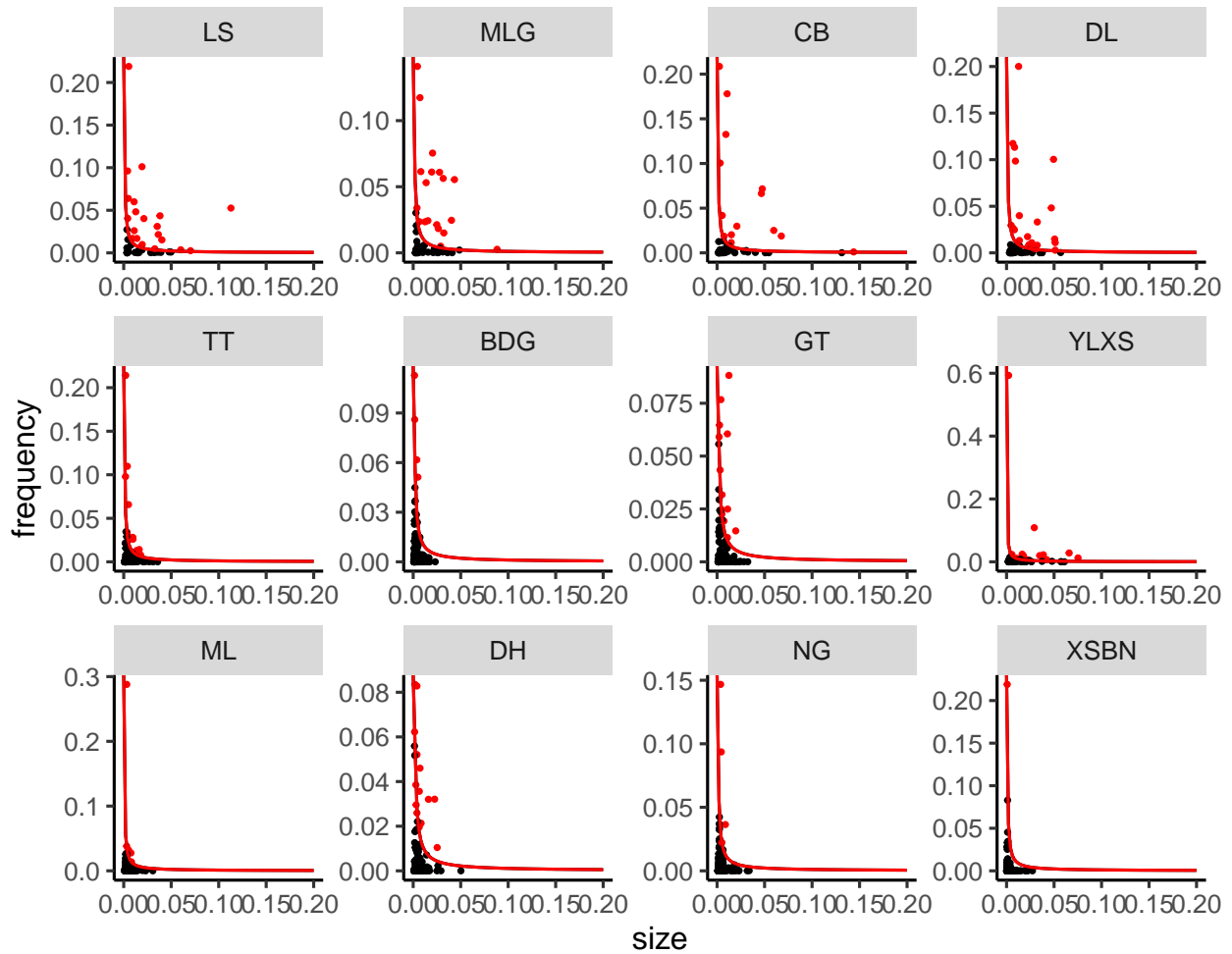


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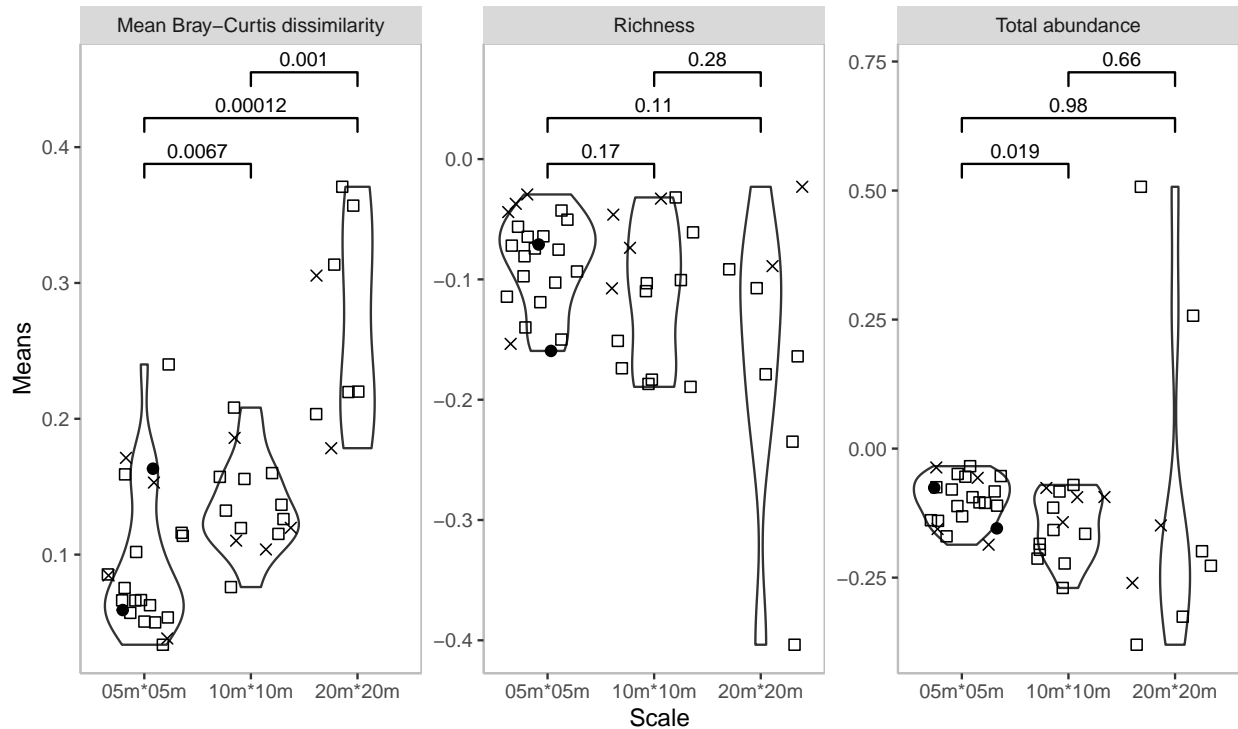


Figure 3: Distribution of average codispersion observed between total basal area of candidate foundation species and Bray-Curtis dissimilarity, species richness, and total abundance of associated woody plant species in contiguous 5×5 -, 10×10 -, and 20×20 -m subplots in the twelve CForBio plots. Points indicate mean codispersion values for each candidate foundation species listed in Table S1; solid points indicate the two candidate foundation species in the genus *Acer* that met both the outlier *and* diversity criterion for all indices; hollow squares indicate candidate species that met the outlier criterion and the relaxed diversity criterion; and crosses indicate the remaining candidate foundation species that met only the relaxed diversity criterion. Points are jittered within categories. *P* values for comparisons between groups are shown at the top of each panel.

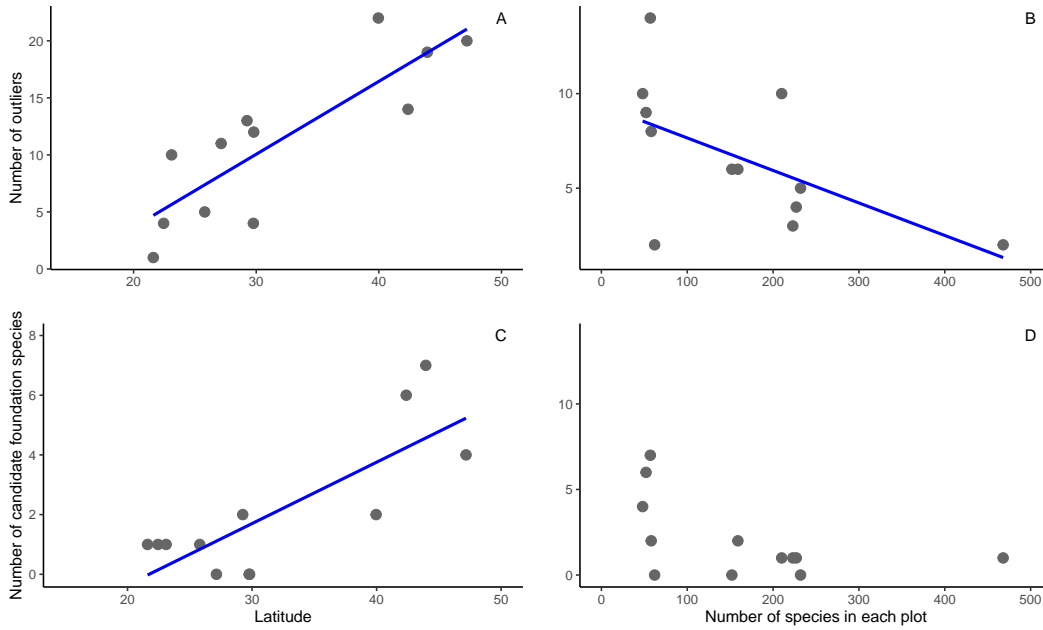


Figure 4: Number of outliers from the expected size-frequency distribution (Fig. 2) and number of candidate foundation species (Table 2) as a function of latitude (A, C) or plot-level species richness (B, D). See main text for regression statistics.

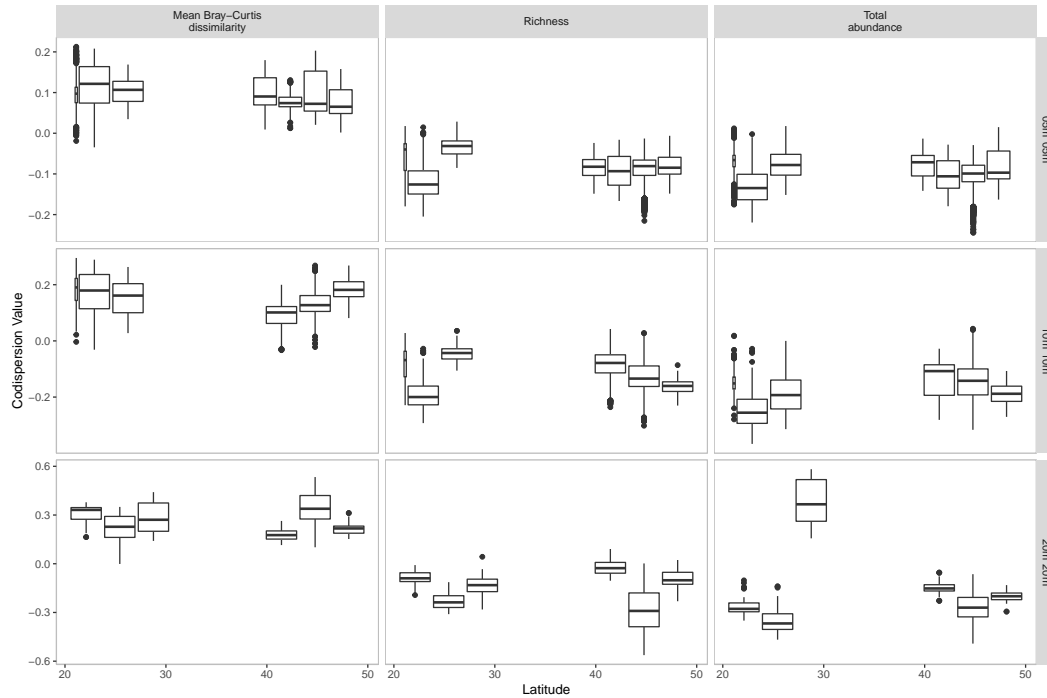


Figure 5: Relationship between latitude and codispersion between candidate foundation species (canopy trees and understory trees and shrubs) and three measures of associated woody-plant diversity at different spatial grains. Box plots illustrate median, upper and lower quartiles, and individual points outside of the upper and lower deciles of average codispersion at each latitude where candidate foundation species occurred (Table 2). Box width is proportional to sample size.

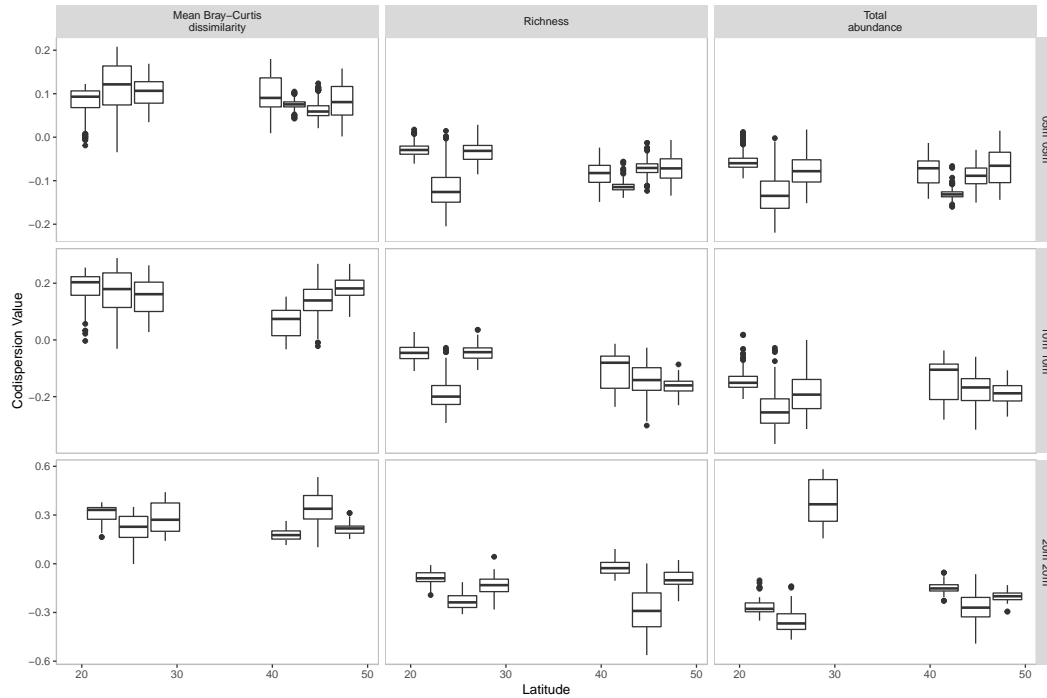


Figure 6: Relationship between latitude and codispersion between candidate foundation canopy tree species and three measures of associated woody-plant diversity at different spatial grains. Box plots illustrate median, upper and lower quartiles, and individual points outside of the upper and lower deciles of average codispersion at each latitude where candidate foundation species occurred (Table 2). Box width is proportional to sample size.