

Foundation species across a latitudinal gradient in China

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Citation: Qiao, X., J. Zhang Z. Wang, Y. Xu, T. Zhou, X. Mi, M. Cao, W. Ye, G. Jin, Z. Hao, X. Wang, X. Wang, S. Tian, X. Li, W. Xiang, Y. Liu, Y. Shao, K. Xu, W. Sang, F. Zeng, H. Ren, M. Jiang, and A. M. Ellison. 2021. Foundation species across a latitudinal gradient in China. *Ecology*. 102(2):e03234. 10.1002/ecy.3234

Abstract. Foundation species structure forest communities and ecosystems but are difficult to identify without long-term observations or experiments. We used statistical criteria—outliers from size-frequency distributions and scale-dependent negative effects on alpha diversity and positive effects on beta diversity—to identify candidate foundation woody plant species in 12 large forest-dynamics plots spanning 26 degrees of latitude in China. We used these data (1) to identify candidate foundation species in Chinese forests, (2) to test the hypothesis—based on observations of a midlatitude peak in functional trait diversity and high local species richness but few numerically dominant species in tropical forests—that foundation woody plant species are more frequent in temperate than tropical or boreal forests, and (3) to compare these results with data from the Americas to suggest candidate foundation genera in northern hemisphere forests. Using the most stringent criteria, only two species of *Acer*, the canopy tree *Acer ukurunduense* and the shrubby treelet *Acer barbinerve*, were identified in temperate plots as candidate foundation species. Using more relaxed criteria, we identified four times more candidate foundation species in temperate plots (including species of *Acer*, *Pinus*, *Juglans*, *Padus*, *Tilia*, *Fraxinus*, *Prunus*, *Taxus*, *Ulmus*, and *Corlyus*) than in (sub)tropical plots (the treelets or shrubs *Aporosa yunnanensis*, *Ficus hispida*, *Brassaiopsis glomerulata*, and *Orophea laui*). Species diversity of co-occurring woody species was negatively associated with basal area of candidate foundation species more frequently at 5- and 10-m spatial grains (scale) than at a 20-m grain. Conversely, Bray-Curtis dissimilarity was positively associated with basal area of candidate foundation species more frequently at 5-m than at 10- or 20-m grains. Both stringent and relaxed criteria supported the hypothesis that foundation species are more common in mid-latitude temperate forests. Comparisons of candidate foundation species in Chinese and North American forests suggest that *Acer* be investigated further as a foundation tree genus.

Key words: beta diversity; biodiversity; China; CForBio; codispersion analysis; forest-dynamics plots; ForestGEO; latitudinal gradient.

Manuscript received 23 March 2020; revised 10 August 2020; accepted 14 September 2020. Corresponding Editor: Maria Uriarte.

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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 nontrophic 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 nonfunctional levels can maintain habitat integrity and potentially protect associated rare species at lower cost and less effort (Ellison and Deggrasi 2017, Deggrasi 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 network²⁰ (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 (Case et al. 2016, Buckley et al. 2016a, b, Ellison et al. 2019). Specifically, Ellison et al. (2019) proposed two statistical criteria for candidate foundation tree species: (1) they would be outliers from the expected reverse-J size-frequency distribution; and (2) their size or abundance would be negatively associated with the total abundance and alpha diversity of associated woody species at local spatial scales but positively associated with 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.

We emphasize that the application of these criteria to identify candidate foundation species leads to the hypothesis that a particular taxon may be a foundation species, not that it is one. Asserting that a species is a foundation species requires additional observational and, ideally, experimental evidence (Ellison 2014, 2019). Indeed, we derived these two statistical criteria after more than a decade of observational and experimental studies of *Tsuga canadensis*-dominated forests in New England, United States that lend strong support for the hypothesis that *T. canadensis* is a

foundation species (Orwig et al. 2013, Ellison 2014). These criteria subsequently were applied to five additional ForestGEO plots in the western hemisphere (Buckley et al. 2016b, Ellison et al. 2019) with encouraging results. Here, we apply these criteria to 12 large forest dynamics plots in China that range from cold-temperate forests to tropical rain forests. These plots are all part of the Chinese Forest Biodiversity Monitoring Network (CForBio); eight of these plots also are part of the ForestGEO network.

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

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

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

²⁰<https://www.ForestGEO.si.edu/>

METHODS

Forest dynamics plots in China

We used data from 12 of the 17 CForBio plots in our exploration of candidate foundation species in Chinese forests (Fig. 1, Table 1; Appendix S1). These plots (acronym in parentheses and Appendix S1) span >26 degrees of latitude and include the 9-ha broad-leaved Korean pine mixed forest plot at Liangshui in the Xiaoxing'an Mountains of Heilongjiang Province (LS); the 25-ha *Taxus cuspidata*-dominated forest in the Muling Nature Reserve, also in Heilongjiang Province (MLG); the 25-ha deciduous broad-leaved Korean pine mixed forest plot on Changbai Mountain in Jilin Province (CB); the 20-ha warm-temperate deciduous broad-leaved forest plot on Dongling Mountain in Beijing (DL); the 25-ha subtropical evergreen broad-leaved forest plot on Tiantong Mountain in Zhejiang Province (TT); the 25-ha mid-subtropical mountain evergreen and deciduous broad-leaved mixed forest plot on Badagong Mountain in Hunan province (BDG); the 24-ha subtropical evergreen broad-leaved forest plot on Gutian Mountain in Zhejiang Province (GT); the 20-ha lower subtropical evergreen broad-leaved forest plot on Dinghu Mountain in Guangdong Province (DH); the 25-ha cold-temperate spruce-fir forest plot on Yulong Snow Mountain in Yunnan Province (YLXS); the 25-ha karst evergreen and deciduous broad-leaved mixed forest plot at Mulun in the Guangxi Zhuang Autonomous Region (ML); the 15-ha karst seasonal rainforest plot at Nonggang, also in the Guangxi Zhuang Autonomous Region (NG); and the 20-ha tropical forest plot at Xishuangbanna in Yunnan Province (XSBN).

Tree census and measurement

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

The outlier criterion for identifying candidate foundation species

The first criterion is that candidate foundation tree species are outliers from the expected reverse-J size-frequency distribution observed in virtually all assemblages of co-occurring species (Loehle 2006). For woody

species, we use the size-frequency distribution of mean dbh plotted against the number of individuals. The departure from expected size-frequency relationships reflects the abundance of foundation species and their relatively large sizes that lead to their disproportionate influence on overall community structure (Ellison et al. 2019). We refer to this criterion as the outlier criterion.

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

The diversity criterion for identifying candidate foundation species

The second criterion (the diversity criterion) is that the size or abundance of candidate foundation species should be negatively associated with the total abundance and three measures of alpha diversity (species richness, Shannon diversity, and inverse Simpson diversity) of associated woody species at local (small) spatial scales, and positively associated with species turnover (beta diversity) across large forest plots or stands (Ellison et al. 2019). The three measures of alpha diversity either treat all species identically (species richness), downweight rare species (Shannon diversity), or downweight common species (inverse Simpson diversity) within subplots. The negative spatial association between the size or abundance of foundation tree species with local diversity of co-occurring woody species results simply from the foundation species occupying most of the available space in a standard 20 × 20 m (0.04-ha) forest plot (or, in fact, any relatively small plot).

In contrast, the positive spatial association between the size or abundance of a foundation tree species with beta diversity results from it creating patchy assemblages at landscape scales. For example, forest stands dominated by foundation species such as *T. canadensis* in eastern North America or *Pseudotsuga menziesii* in

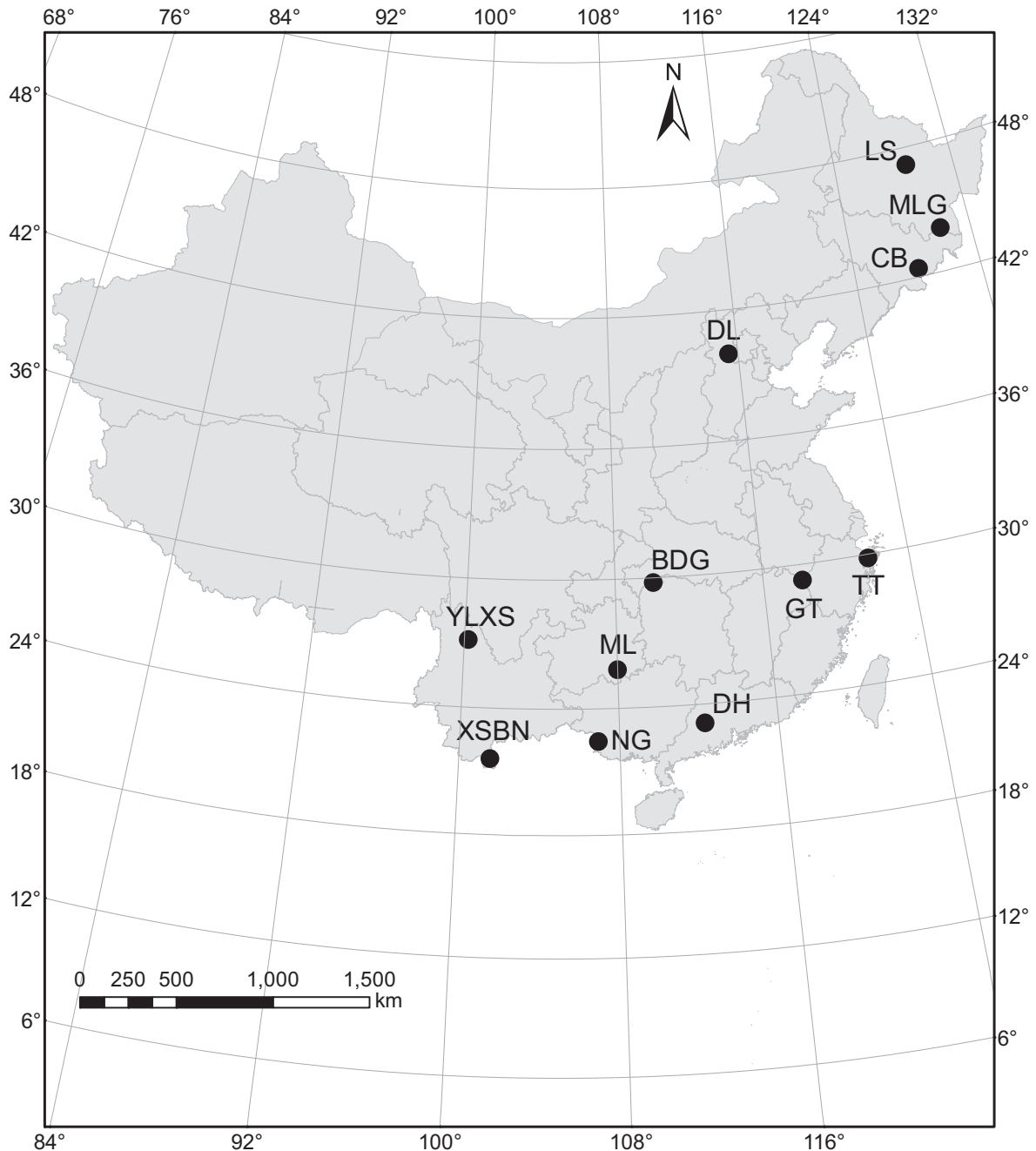


FIG. 1. Locations of the CForBio plots from where the data used in this paper were collected. See Table 1 for geographic data and Table 1 and Appendix S1 for site abbreviations and detailed descriptions of each plot.

western North America manifest themselves as distinctive patches on the landscape. Similarly, species that dominate small plots (<1 ha in area) can drive beta diversity in tropical Amazonian forests (Draper et al. 2019). When these foundation or dominant species decline or are selectively harvested, the landscape is homogenized and beta diversity declines. Indeed, Ellison et al. (2019) suggested that the preservation of landscape

diversity may be the most important reason to protect and manage foundation tree species before they decline or disappear.

Forest structure and species diversity indices

For each plot, we calculated the total basal area, mean basal area, and total number of individuals of each of

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 is the site abbreviation given in Methods and Appendix S1.

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	3,282	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

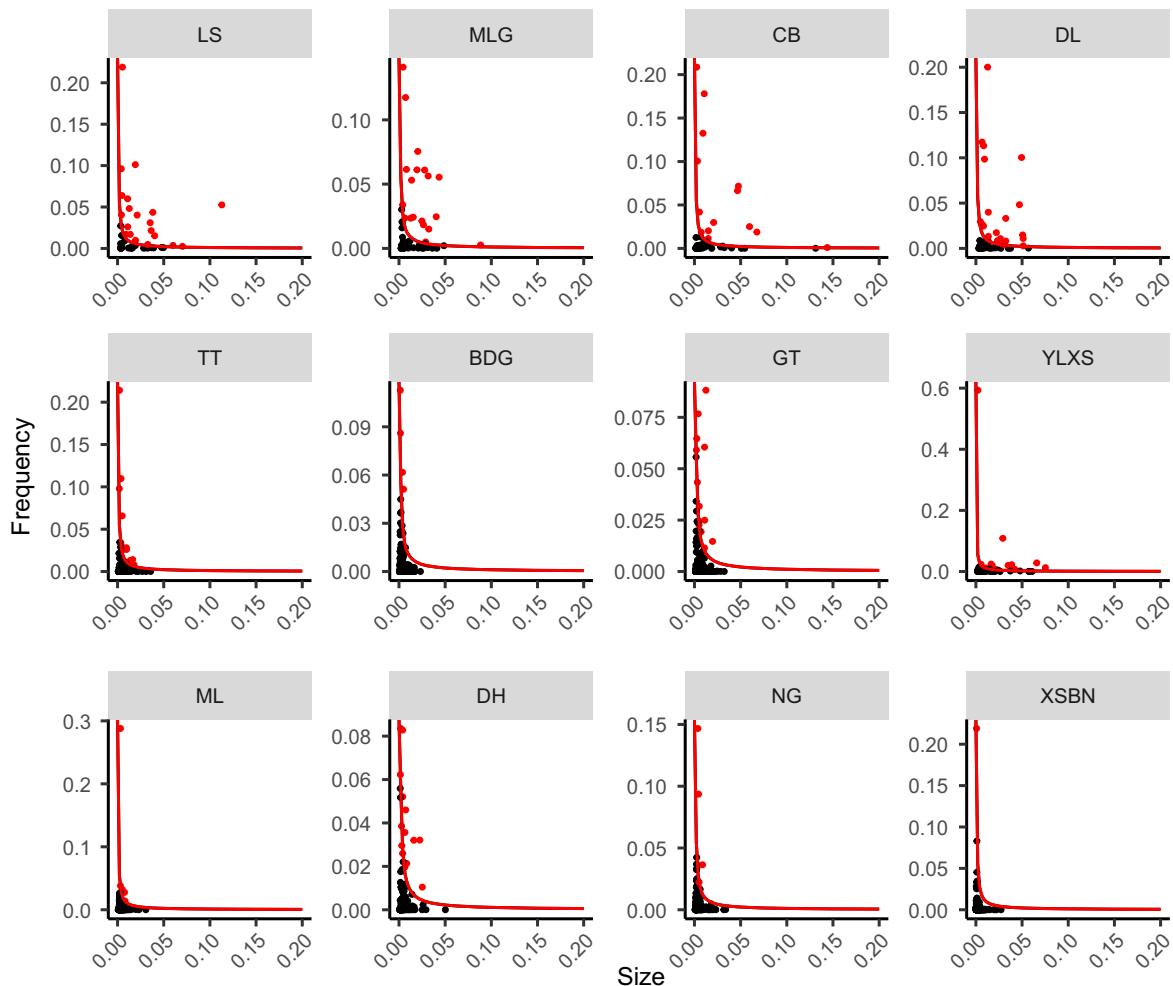


FIG. 2. Size (diameter at breast height [dbh]) -frequency distributions of the species in each plot. Species falling outside of the reverse-J boundary (0.0975 th quantile of the quantile reciprocal function $y = (1.1 \times 10^{-4})x$; red line) were placed in the first set of candidate foundation species (Appendix S2: Table S1). Plots are ordered left to right and top to bottom by latitude. Plot abbreviations as in Methods, Table 1, and Appendix S1

the candidate foundation tree and shrub species (Appendix S2: Table S1) within contiguous 5×5 , 10×10 , and 20×20 -m subplots. For species other than the candidate foundation species, we calculated their total abundance, species richness, Shannon and inverse Simpson diversity indices (as Hill numbers: Chao et al. 2014) and mean Bray-Curtis dissimilarity (overall methods as in Ellison et al. 2019). The diversity() and vegdist() functions in the vegan package (Oksanen et al. 2018) of the R software system (R Development Core Team 2019) were used for calculating each diversity metric.

Codispersion analysis

The associations between size or abundance of candidate foundation species and measures of alpha or beta diversity also should be consistent (isotropic) across the plots when calculated at a given spatial grain (also known as spatial scale) and at most (ideally all) spatial lags (Buckley et al. 2016a, Ellison et al. 2019). We estimated effects of foundation species on diversity of associated species at different spatial grains (5×5 , 10×10 , and 20×20 -m subplots) using codispersion analysis (Buckley et al. 2016a, Ellison et al. 2019). Codispersion can identify and describe anisotropic spatial patterns (i.e., different expected values when measured in different directions) of co-occurring variables for given spatial lags and directions (Cuevas et al. 2013). The codispersion coefficient ranges from -1 to 1 , with positive values indicating a positive spatial association and negative values indicating a negative spatial association for a given spatial lag and direction. These values can be visualized with a codispersion graph (Vallejos et al. 2015; see also Buckley et al. 2016a).

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

Statistical significance of the codispersion coefficients was determined using null-model analysis (Buckley et al. 2016b, Ellison et al. 2019). Codispersion coefficients for all spatial lags and directions were computed for co-occurrence matrices randomized using a toroidal-shift null

model, which maintains the autocorrelation structure of the species and spatial patterns caused by underlying environmental gradients while shifting the associated woody species in random directions and distances (Buckley et al. 2016b, Ellison et al. 2019). For each candidate foundation species in each plot, we ran 199 randomizations; significance was determined based on empirical 95% confidence bounds. Calculation of codispersion coefficients and all randomizations were done using custom C and R code written by Ronny Vallejos and Hannah Buckley, respectively.

Data and code availability

Each of the CForBio plots were established at different times and are scheduled to be (or already have been) censused every 5 yr. To maximize comparability among data sets, we used data collected at the first census for each plot (Table 1). Data for individual plots are available from the Principal Investigators of each plot; their contact information is provided in the individual plot descriptions in Appendix S1. R code for all analyses is available from the Environmental Data Initiative.²¹

RESULTS

Candidate foundation species in the CForBio plots

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

More species were considered as candidate foundation species when we retained the outlier criterion (Fig. 2) but relaxed the diversity criterion to require only a positive spatial relationship between the size of the candidate foundation species and beta diversity and a negative spatial relationship between the size of the candidate foundation species and at least one of the alpha-diversity measures (species indicated with an asterisk [*] in Table 2). These additional candidate foundation species included two additional *Acer* species and tree or treelet species in the genera *Pinus*, *Taxus*, *Fraxinus*, *Quercus*, *Juglans*, *Syringa*, *Prunus*, *Ulmus*, *Aporosa*, and *Tilia*, and one shrub (*Corylus mandshurica*). However, whether we applied the stringent or relaxed diversity criterion, all but three of the candidate foundation species occurred in plots with cool- or cold-temperate climates. The exceptions were the trees *Pinus massoniana* and *Quercus serrata* at GT and *Aporosa yunnanensis* at DH; all three of these species occurred in the subtropical evergreen broad-leaved forest plots.

²¹ <https://doi.org/10.6073/pasta/5adc884142cee1c856dfac32858a3ab>

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 BDG, TT, or YLXS plots at any spatial grain.

Plot	Spatial grain		
	5 m	10 m	20 m
LS	* <i>Acer ukurunduense</i>	* <i>Acer ukurunduense</i>	–
	* <i>Corylus mandshurica</i> ⁺	–	–
	* <i>Fraxinus mandshurica</i>	–	–
	* <i>Prunus padus</i>	* <i>Prunus padus</i>	* <i>Prunus padus</i>
MLG	* <i>Acer barbinerve</i> ⁺	* <i>Acer barbinerve</i> ⁺	–
	* <i>Acer tegmentosum</i>	–	–
	* <i>Acer ukurunduense</i>	–	–
	* <i>Corylus mandshurica</i> ⁺	–	–
	–	* <i>Pinus koraiensis</i>	* <i>Pinus koraiensis</i>
	* <i>Taxus cuspidata</i>	–	–
	* <i>Tilia amurensis</i>	* <i>Tilia amurensis</i>	* <i>Tilia amurensis</i>
CB	* <i>Acer barbinerve</i> ⁺	–	–
	* <i>Acer pseudosieboldianum</i>	* <i>Acer pseudosieboldianum</i>	–
	* <i>Acer tegmentosum</i>	–	–
	* <i>Corylus mandshurica</i> ⁺	* <i>Corylus mandshurica</i> ⁺	–
	* <i>Syringa reticulata</i> var. <i>amurensis</i> ⁺	* <i>Syringa reticulata</i> var. <i>amurensis</i> ⁺	–
DL	<i>Prunus padus</i>	<i>Prunus padus</i>	<i>Prunus padus</i>
	* <i>Juglans mandshurica</i>	–	–
TT	* <i>Ulmus laciniata</i>	* <i>Ulmus laciniata</i>	–
	–	–	–
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>

A few of our initial candidate species that had high importance values but were not outliers from the expected size-frequency distributions (unstarred species in Appendix S2: Table S1) did partially meet the diversity criterion in both temperate and tropical plots (Table 2). These included *Prunus padus* at CB, *Brassaiopsis glomerulata* at ML, *Ficus hispida* at NG, and *Orophea laui* at XSBN.

Scale-dependence of candidate foundation species

More candidate foundation species—including all species that met at least one of the two criteria—were identified at smaller spatial grains: 16 species at the 5-m grain, 12 at the 10-m grain, and 7 at the 20-m grain (Table 2). This pattern applied both among and within the plots. Average codispersion between total basal area

of the candidate foundation species and Bray-Curtis dissimilarity increased significantly with spatial grain (Fig. 3; raw data in Appendix S2: Table S2) but was not anisotropic (Appendix S2: Figs. S1, S3). In contrast, average codispersion between total basal area of the candidate foundation species and measures of alpha diversity, while generally negative, was more variable and not scale dependent (Fig. 3; raw data in Appendix S2: Table S2).

Candidate foundation species across a latitudinal gradient

The median number of candidate foundation species in the four temperate plots was five, but was less than or equal to 1 for the the eight subtropical and tropical plots (Table 1). Both the number of woody species in each plot that were outliers from the expected size-frequency

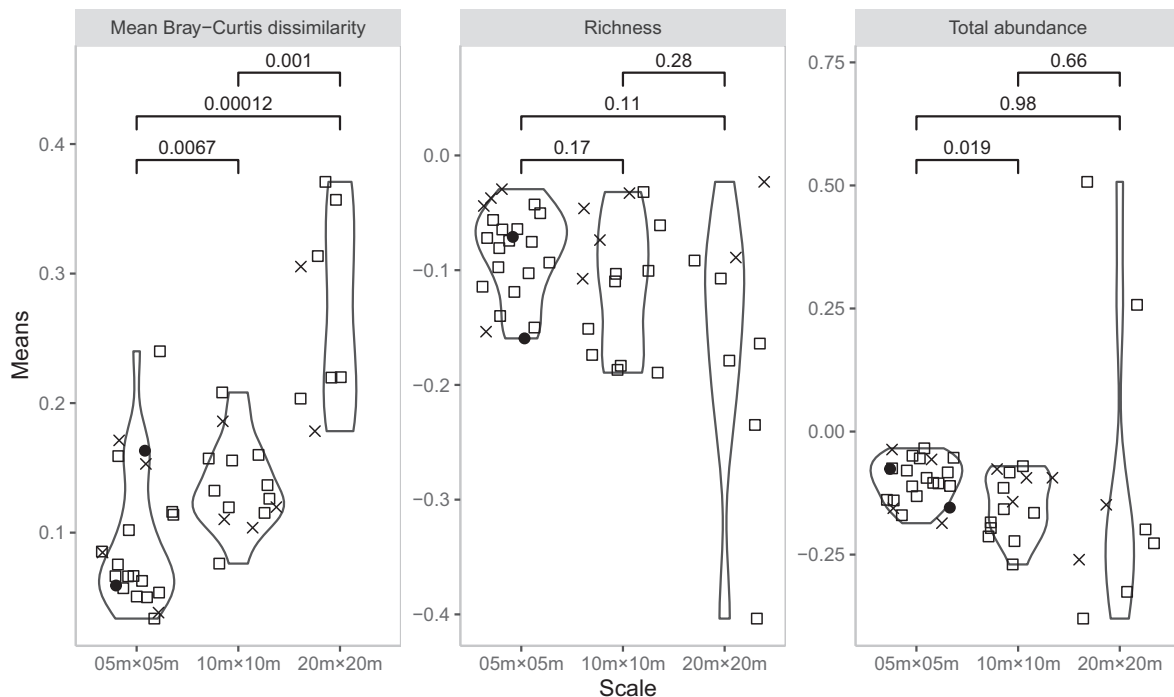


FIG. 3. Distribution of average codispersion observed between total basal area of candidate foundation species and Bray-Curtis dissimilarity, species richness, and total abundance of associated woody plant species in contiguous 5 × 5, 10 × 10, and 20 × 20-m subplots in the 12 CForBio plots. Points indicate mean codispersion values for each candidate foundation species listed in Appendix S2: 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.

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

Spatial association (expressed as codispersion) within each plot between candidate foundation species and total abundance, mean alpha diversities, and mean beta diversity of associated woody species on average did not vary with latitude at any spatial grain (Fig. 5; raw data in Appendix S2: Table S2). Quantile regression (to account for potential extreme effects of foundation species) yielded similar results. There were no observed latitudinal patterns in effects of candidate foundation species except for a slight strengthening of the negative effect of candidate foundation species on associated woody species richness and total abundance at the 5-m grain (Fig. 5; $P = 0.03$ and 0.04, respectively). When

understory shrubs and multitemmed subcanopy trees were excluded from the analysis, there only were negative relationships between latitude and spatial association of richness at 5-m and 10-m grains (Fig. 6; $P = 0.02$ and 0.04, respectively).

DISCUSSION

We applied two statistical criteria (Ellison et al. 2019) to screen 12 CForBio Forest Dynamic plots in China for candidate foundation species. These 12 plots ranged from 47 to 21° N latitude, represented conifer-dominated, broad-leaved deciduous, subtropical, and tropical forests (Table 1), and included two forest types referred to by particular species (Korean pine mixed forests at Liangshi and Changbai Mountain, and the *Taxus cuspidata* mixed coniferous forest at Muling). Such eponyms do suggest traditional or cultural-based knowledge of foundation (or other important) species (Ellison et al. 2005, 2019). Whereas both Korean pine (*Pinus koraiensis*) and *Taxus cuspidata* were identified as candidate foundation species (Table 2), they were only candidates in the Muling *T. cuspidata*-dominated forest plot, not in either of the Korean pine mixed forests. We also found a strong latitudinal gradient, unrelated to the expected (and observed) underlying latitudinal gradient in woody

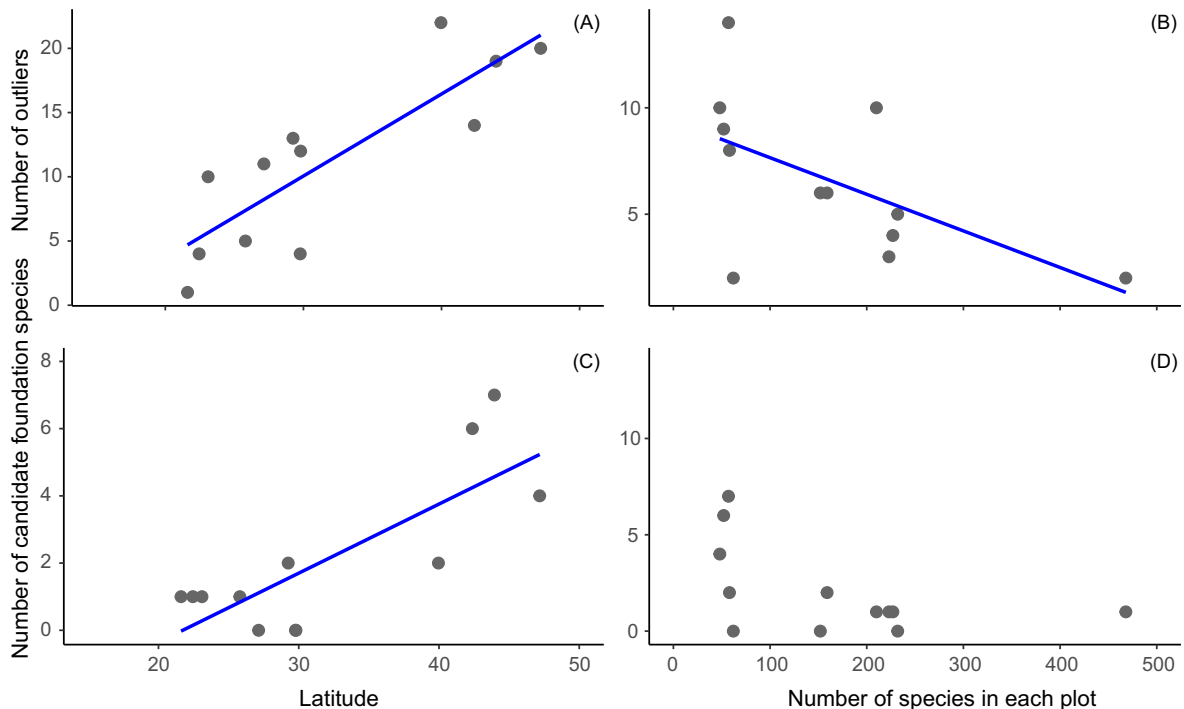


FIG. 4. Number of outliers from the expected size-frequency distribution (Fig. 2) and number of candidate foundation species (Table 2) as a function of latitude (A, C) or plot-level species richness (B, D). See main text for regression statistics.

plant species richness, in the number of candidate foundation species, which were more frequent in temperate than in tropical forest plots (Fig. 4). Where they occurred, candidate foundation species had comparable effects at all latitudes (Figs. 5, 6), suggesting that foundation species effects more likely reflect specific combinations of traits and interspecific effects rather than being manifestations of neutral (*sensu* Hubbell 2001) processes (Ellison et al. 2019).

Candidate foundation species are more common in temperate latitudes

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

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

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

We hypothesize that tropical forests dominated by one or a few closely related species, such as coastal mangrove

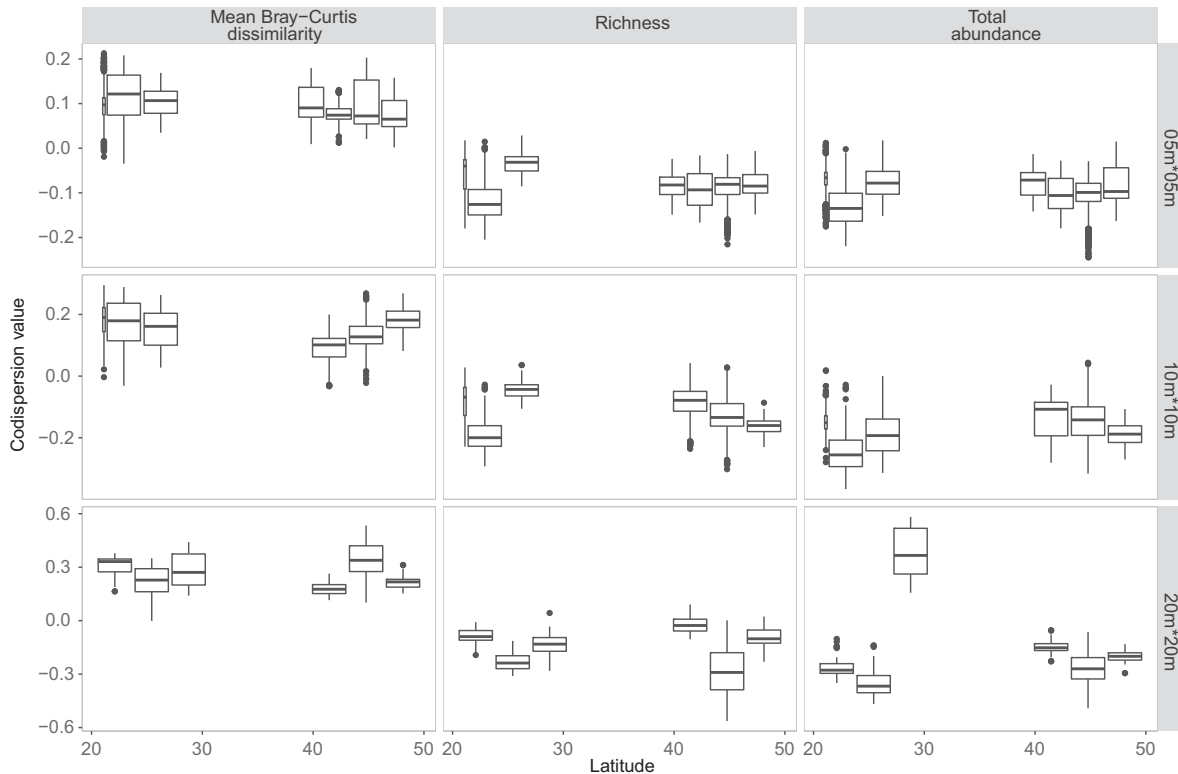


FIG. 5. Relationship between latitude and codispersion between candidate foundation species (canopy trees and understory trees and shrubs) and three measures of associated woody-plant diversity at different spatial grains. Box plots illustrate median, upper and lower quartiles, and individual points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

forests dominated by *Rhizophora* spp. (Tomlinson 1995) and monodominant tropical lowland forests dominated by species of Dipterocarpaceae in southeast Asia or species of Leguminosae (subfamily Caesalpinioideae) in Africa and the Neotropics (Torti et al. 2001, van der Velden et al. 2014, Hall et al. 2020) may be structured by foundation species (Ellison et al. 2005). Indeed, *Gilbertiodendron dewevrei* in the Ituri ForestGEO plot in the Democratic Republic of Congo (Makana et al. 2004a, 2004b) has functional characteristics similar to *T. canadensis* in northeastern U.S. forests. *Gilbertiodendron* casts deep shade; produces leaf litter that decomposes very slowly, creating a dense and deep litter layer; creates soils with $\approx 30\%$ of the available nitrogen (ammonium + nitrate) relative to nearby mixed forests; and has a depauperate (albeit not unique) fauna of leaf-litter ants and mites (Torti et al. 2001).

At XSBN, the dipterocarp *Parashorea chinensis* occurs in monodominant patches (van der Velden et al. 2014), has a high importance value (Appendix S2: Table S1), but did not end up in our winnowed list of candidate foundation species (Table 2). This was because in our analyses, as in those of van der Velden et al. (2014), diversity of associated woody species did not differ between 20×20 -m subplots dominated by *P. chinensis*

and adjacent mixed stands. This does not mean that *P. chinensis* could not have foundational characteristics in any forest, just that it does not currently act as a foundation species in this CForBio plot. Foundational characteristics may be apparent only at later successional stages or in mature forest stands (Ellison et al. 2014, 2019). van der Velden et al. (2014) suggest that the *P. chinensis* patches at XSBN may represent remnants of old-growth forest in a matrix of a forest historically modified by shifting cultivation, in which case we may now be observing a ruined foundation.

Mycorrhizal associations may contribute to foundational effects of particular tree species. Trees associated with ectomycorrhizae may have weaker negative density dependence among conspecifics than trees associated with arbuscular mycorrhizae (Bennett et al. 2017, Johnson et al. 2018, Chen et al. 2019). Experiments in the GT plot investigating different effects of pathogenic and mutualistic fungi on community structure found increased abundance of pathogenic fungi increased negative density-dependent interactions among conspecifics, whereas increased abundance of mutualistic fungi decreased density-dependent interactions among conspecifics (Chen et al. 2019). The two candidate foundation species in GT (*P. massoniana* and *Q. serrata*) are

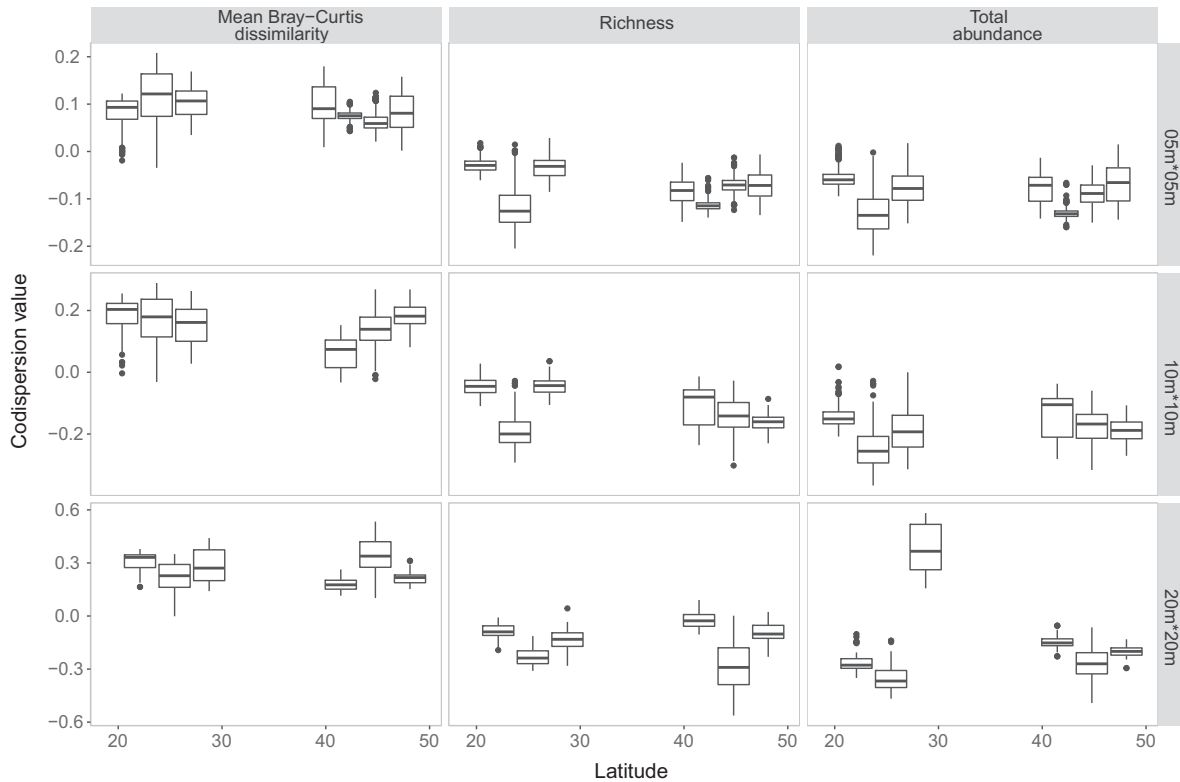


FIG. 6. Relationship between latitude and codispersion between candidate foundation canopy tree species and three measures of associated woody-plant diversity at different spatial grains. Box plots illustrate median, upper and lower quartiles, and individual points outside of the upper and lower deciles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

abundant and associated with mutualistic fungi. Analysis of species distribution and diversity associated with potential foundation species in Southeast Asian forests dominated by Dipterocarpaceae (ectomycorrhizal), such as the ForestGEO 50-ha Pasoh plot in Malaysia (Kochummen et al. 1991, Ashton et al. 2003) versus others lacking abundant dipterocarps, such as the 30-ha ForestGEO Mo Singto plot in Thailand (Brockelman et al. 2011) or the 2-ha plot in Aluoi, Vietnam (Nguyen et al. 2016) would provide useful comparisons with the analyses of the CForBio plots—especially the 20-ha Xishuangbanna plot—presented here.

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

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

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

Conversely, although foundation species can provide habitat for associated species, thus increasing their local diversity, the opposite pattern and magnitude of effects has been found when analyzing only associated woody plant species in forest dynamic plots (Buckley et al. 2016a, Ellison et al. 2019), because foundation species

occupy most of the available space. In the CForBio plots, codispersion similarly was negative between candidate foundation species and alpha diversity of associated woody plants (Appendix S2: Figs. S1–S3), but this relationship did not vary significantly with spatial grain (Fig. 3). Additional data on faunal groups (e.g., Sackett et al. 2011, Record et al. 2018) or nonwoody plants (e.g., Ellison et al. 2016) could provide a test of whether these candidate foundation species have a positive effect on other associated species that are not competing for space with canopy or subcanopy trees (e.g., Schowalter 1994, Ruchty et al. 2001, Ellison 2018).

Acer as a candidate foundation genus

In this study, four species of *Acer* were candidate foundation species among the three cold-temperate plots in China (Liangshui, Muling, and Changbai; Table 2). Among these, *A. ukurunduense* and *A. barbinerve* were the only two of all our candidate foundation species that met the most stringent criteria for consideration. In a comparable study across a latitudinal gradient in the Americas, *A. circinatum* was identified as a candidate foundation species in the the Wind River ForestGEO plot in Washington, United States (Ellison et al. 2019). We hypothesize that in many forests throughout the northern hemisphere, *Acer* not only can be a dominant genus in terms of abundance or total basal area, but may function as a foundation genus, akin to *Quercus* in the Tyson ForestGEO plot in central North America (Ellison et al. 2019).

Acer species often are common and abundant in temperate deciduous broad-leaved, coniferous, and mixed forests throughout the Holarctic (Braun 1938, 1955, Tiffney 1985, Pennington et al. 2004), and in subtropical montane forests in China (Xu 1996). *Acer* includes >150 species (World Flora Online [WFO] 2020), at least 99 of which (including 61 endemics) occur in China (Xu et al. 2008) and more than a dozen are found in North America (Alden 1995). *Acer* species generally are shade tolerant (i.e., they can regenerate and grow under closed canopies) and have relatively high seedling and sapling survival rates (Tanaka et al. 2008). Some more shade-intolerant (photophilous) early-successional *Acer* species create conditions that facilitate restoration of both later successional forests and their associated animal assemblages (Zhang et al. 2010).

There are several forests named after *Acer* species in China, including the *Acer mono-Tilia amurensis-T. mandshurica* temperate broad-leaved deciduous forest, the *Schima superba-Acer caudatum-Toxicodendron succedaneum* eastern subtropical forest, and the *Cyclobalanopsis multinervis-Castanopsis eyrel* var. *caudata-Liquidambar acalycina-Acer sinense* forest in southwest China (Wu 1995). *Acer* also are considered primary companion species in Chinese *Quercus* and mixed broad-leaved Korean pine forests where multiple *Acer* species co-occur. For example, 6–7 additional *Acer*

species were recorded with the three candidate foundation *Acer* species in the two broad-leaved Korean pine mixed forests plots (LS, CB). The nine *Acer* species in the CB plot account for >46% of the total stems (Zhang et al. 2010).

In North American forests, *Acer* species also define several forest types, including sugar maple (i.e., *A. saccharum*), beech-maple, sugar maple–beech–yellow birch, sugar maple–basswood, red maple (i.e., *A. rubrum*), and silver maple–American elm (i.e., *A. saccharinum*) (Braun 1938, 1955, Eyre 1980). In forests of the Pacific Northwest of North America, the subcanopy treelet *A. circinatum* not only grows rapidly, has high biomass, and forms broad canopies that suppress other species (Lutz and Halpern 2006, Halpern and Lutz 2013), which causes it to have negative codispersion with other woody taxa (Ellison et al. 2019), but it also supports a high diversity of epiphytes (Ruchty et al. 2001). Another North American species, *A. saccharinum*, dominates floodplain forests on well-drained alluvial soils in the eastern United States (Gabriel 1990). Although Vankat (1990) subsumed silver maple–American elm forests within a mixed hardwood wetland forest type and considered *A. saccharinum* to be only a minor component of these forests, this species historically was a significant constituent of at least some primary forests in the upper midwestern United States and Canada (Cho and Boerner 1995, Simard and Bouchard 1996, Guyon and Battaglia 2018), supports unique assemblages of birds (Yetter et al. 1999, Knutson et al. 2005, Kirsch and Wellik 2017), and, among woody species, contributes substantially to carbon fixation in tidal wetlands (Milligan et al. 2019). *Acer saccharinum* may be similar to other North American (candidate) foundation species whose effects are most pronounced at different successional stages (Ellison et al. 2014, 2019). However, we know of no large plots in either silver maple–American elm or mixed hardwood wetland forests from which we could derive data to test whether *A. saccharinum* meets our statistical criteria for candidate foundation species. Whereas it may be premature to establish large forest dynamics plots in floodplains in either the temperate zone or the tropics, or in tropical coastal habitats with low tree diversity, comparable data could be used to test more general ideas about the foundational importance of particular genera, such as *Acer* or *Rhizophora*, in forested wetlands worldwide.

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

ACKNOWLEDGMENTS

This study was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB31000000), the National Natural Science Foundation of China (31670441, 31740551, 31270562, 31660130, 31760131), the National Key Research and Development Program of China (2016YFC0502405), the Guangxi Key Research and Development Program (AB17129009), Natural Science Foundation of Heilongjiang (CN) (QC2018025), and the Harvard Forest. We acknowledge the Chinese Forest Biodiversity Monitoring Network (CForBio) for installing and supporting the forest dynamic plots in China, and all the field technicians and students who have helped census the plots. Audrey Barker Plotkin, Brian Hall, Helen Murphy, Dave Orwig, Neil Pederson, Jonathan Thompson, and two anonymous reviewers provided constructive comments and feedback on early versions of the manuscript. The authors declare no conflicts of interest. XQ and AME conceptualized and designed the study and wrote the manuscript; XQ and all other authors except AME collected the data at the individual CForBio plots. All authors contributed critically to the drafts and gave final approval for publication.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3234/supinfo>

DATA AVAILABILITY

Code for all analyses is available from the Environmental Data Initiative. <https://doi.org/10.6073/pasta/5adc884142cee1c856dfa32858a3ab>