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Supporting Online Material for

Individuals and the Variation Needed for High Species Diversity in Forest Trees

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Supplement material (on-line)

METHODS

Theoretical development

Consider a population of species s where each individual i competes with n_{is} neighbors of species s' , for a total of $n_i = \sum_s n_{is}$ neighbors. The ‘size’ of the interaction neighborhood is described by a kernel \mathbf{K}_i , a symmetric $n_i \times n_i$ matrix, elements of which could decline with distance from individual i . Several kernels \mathbf{K}_i were used for the analysis, all yielding similar results. For the examples shown in the main text, the kernel is uniform with radius 20 m for growth and 100 m for fecundity, representing approximate areas of influence for competition for resources and recruitment sites, respectively. For the examples shown in this supplement, the kernel is expanded to include the entire stand. These examples bound realistic assumptions of interaction neighborhoods and they yield the same qualitative results. Assume a Gaussian distribution of demographic rates for individual i , g_{is} , and its n_{is} neighbors of species s' , $\mathbf{g}_{is'} = [g_{i1}, \dots, g_{in_{s'}}]$, where the demographic rates are expressed in terms of departures from each species mean values (Fig. S1). The demographic rates analyzed here are ln growth and ln fecundity, the latter restricted to reproductively mature individuals. If individual i responds to environmental variation like its competitors, then competition is increased when the environment favors high growth or fecundity of both i and its neighbors. This tendency to respond like competitors can be expressed as a correlation R_{is} and by a covariance S_{is} . There is multivariate normal distribution for ln growth rate or ln fecundity for i and its neighbors of species s' ,

$$N_{1+n_{is'}} \left([g_{is}, \mathbf{g}_{is'}]^T, \mathbf{S}_i \right)$$

with covariance matrix \mathbf{S}_i (see below). The tendency of i to respond like neighbors is described by a conditional distribution having expectation

$$g_{is} \equiv E[g_{is} | \mathbf{g}_{is'}] = S_{is'} S_{s's}^{-1} \mathbf{g}_{is'} \quad \text{S1}$$

where $S_{is'}$ is the length $n_{s'}$ vector of covariances between i and neighbors of species s' , and $S_{s's}$ is the covariance matrix for the s' neighbors. These covariances can incorporate not only the empirical covariances from growth or fecundity data, but also the size of the interaction neighborhood. For example, in the partitioned $(1 + n_{s'}) \times (1 + n_{s'})$ covariance matrix

$$\mathbf{S}_i = \begin{bmatrix} S_{ii} & S_{is'} \\ S_{s'i} & S_{s's'} \end{bmatrix} \circ \mathbf{K}_i \quad \text{S2}$$

the submatrices are estimates for the variance for i , a scalar S_{ii} , the row and column vectors of covariances between i and each of its $n_{s'}$ neighbors $S_{is'} = S_{s'i}^T$, and the covariance for neighbors $S_{s's'}$. The Hadamard product of covariance matrix \mathbf{S}_i and kernel matrix \mathbf{K}_i is positive definite and thus a valid covariance matrix. However, the kernel is not required, in which case all individuals in the population are taken to be neighbors of equal influence.

Now consider the relative strength of competition from individuals of the same species $s = 1$ and from a different species $s = 2$. Individual i experiences greater competition from its own species when it responds to the environment more like others of its own species $g_{iA} > g_{iB}$, or

$$S_{i1} S_{11}^{-1} \mathbf{g}_1 > S_{i2} S_{22}^{-1} \mathbf{g}_2 \quad \text{S3}$$

For a standardized growth deviation of magnitude, say, one standard deviation,

$\mathbf{g}_1 = \sqrt{\text{diag}(S_{11})} \equiv S_1$ and $\mathbf{g}_2 = \sqrt{\text{diag}(S_{22})} \equiv S_2$ this becomes

$$S_{i1}S_{11}^{-1}S_1 > S_{i2}S_{22}^{-1}S_2$$

where S_1 and S_2 are the lengths $n_1 - 1$ and n_2 vectors of standard deviations. For a single competitor of species 1 or 2 this growth inequality is

$$R_{i1} > R_{i2}$$

where R_{i1} and R_{i2} are correlations between i and competitors of the two species. Thus, the general result reduces to the intuitive relationship between correlations--an individual experiences stronger competition from its own species when it has a high correlation with its own species relative to the other species.

Analysis

The model used to estimate demographic rates is described in ref [S1](#) (see also Supplementary Material for that article and [S2](#)). This hierarchical Bayes model allows for variation and uncertainty at the parameter, process, and data stages. Each component of the model is independently evaluated, including diameter growth ([S3](#) – [S6](#)), survival ([S1](#), [S7](#), [S8](#)), and maturation, fecundity and dispersal ([S9](#), [S10](#)). The process model assumes individuals are immature when small, growth occurs each year, and, with increasing size, trees make the transition to maturity, after which reproduction can occur. Each year new growth accumulates with an associated risk of death and probability of maturation. Data include censuses of tree diameter, canopy, survival, and reproductive status, increment cores, and seed traps. Specific modeling details are discussed in the references cited here. The current model departs from refs [S1](#), [S2](#) only in that here crown areas are taken directly from the estimates of ref [S3](#) and not imputed as described in refs [S1](#), [S2](#).

Estimates from the model include parameter values and latent states, the demographic rates used to evaluate the extent to which individuals respond like others of the same and different species. The covariance/correlation estimates presented here are taken from growth and fecundity estimates over years for each individual tree on 11 plots, ranging from 0.64 to 5 ha in area (Table S1). The plots span a range of environmental conditions (Table S1), with species distributed among plots as summarized in Table S3 and species codes provided in Table S2. A full description of data and models is contained in ref [S1](#). Figure S2 shows estimates of fecundity and diameter growth for 200 individuals of *Liriodendron tulipifera* selected at random from all 11 plots (lines are not visible when all individuals are plotted), varying in light availability (line thicknesses in Figure S2). These are the posterior mean estimates, available for every year and every individual.

The correlations between individuals are taken over time, within neighborhoods of a size relevant for competition and recruitment. The covariance matrix \mathbf{S}_i was constructed for each individual, by evaluating the covariance structure with all individuals of all other species within its neighborhood, defined by the kernel \mathbf{K}_i (eqn S2). This was done on a species-by-species basis on each of the 11 plots. Thus, there are values for the deviation g_{is} , each conditioned on individuals of every species that occurs within the neighborhood of i . For species that respond like i , the deviation g_{is} is positive, and vice versa. For N_s total individuals of species s , each having an average neighborhood size of $\langle n_i \rangle$, there are $\langle n_i \rangle^{N_s}$ calculations, each involving a matrix inversion (eqn S3). The means and credible intervals plotted in Figure 1A of the main

text show 95% of the variation across all individuals of two species. Figure S3 illustrates how this figure is constructed, at the level of individual stands.

In Figure S3 the growth rates for each individual of the species *Liriodendron tulipifera* and three dominant competitors are shown. Within each stand, the correlations between growth rates of all pairs of individuals are evaluated. In Figure 1 of the main text the neighborhood is 20 m in radius. In Figure S3 the neighborhood is taken to be the entire stand, having area given in Table S1. We use the full stand here to highlight the general pattern reported in the text is not dependent on the assumption that neighborhoods are small. There is thus one correlation coefficient for each pair of individuals. Correlations between individuals of the same species are the basis for red and black histograms on the right-hand side of Figure S3. Correlations between individuals of the different species are the basis for the brown histograms in the same figure. The histograms for comparisons between individuals of a different species are shifted to the left of those for the same species, because they respond to environmental variation more like others of their own species. The vertical dashed lines indicate the mean correlation for each species.

The large number of comparisons must be summarized. Figure 2 of the text was constructed as follows. For the example in Figure S3, the average correlations between individuals of the same species (vertical red and black lines) lie to the right of those for individuals of different species (vertical brown lines). For these comparisons, the average intra-specific correlations are higher than the interspecific correlations. *Liriodendron* would then be compared to the remaining species, recording for each comparison whether mean correlations were higher for intra- vs inter-specific comparisons. Figure 2 of the text shows the fraction of cases where such comparisons were higher for intra-specific comparisons, being taken over each tree, $\langle g_{is} - g_{is'} \rangle \forall (s' \neq s)$, and summarized for each pair-wise species combination (s, s'). We further calculated the mean correlation between individual i and others of the same and of different species in its neighborhood. As with growth deviations (eqn S1), the average of the differences in correlation between individuals of the same species vs other species is included in Figure 2. The vertical axis in Figure 2 shows the fraction of comparisons where individuals respond more like their own species than for individuals of a different species.

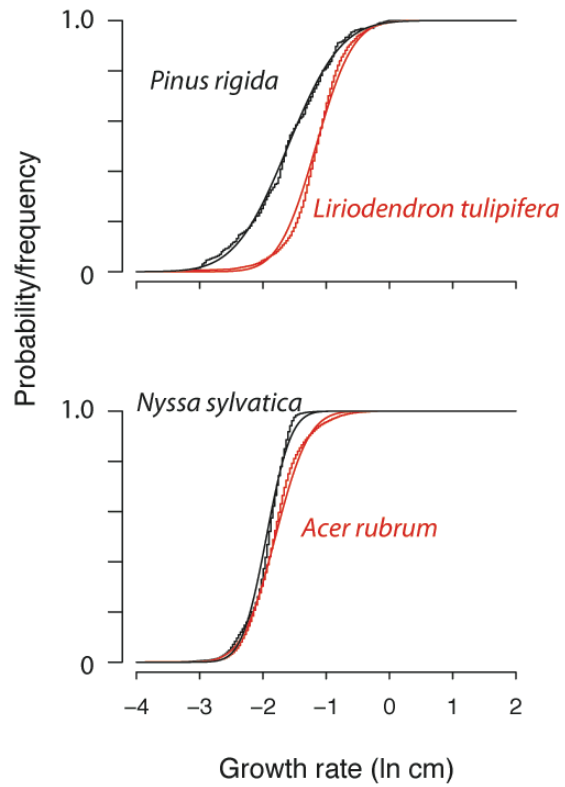


Figure S1. Cumulative frequency distributions of log growth rate (step curves) compared with Gaussian cumulative distribution functions (smooth curves) for examples in this Supplement (above) and in the main text (below).

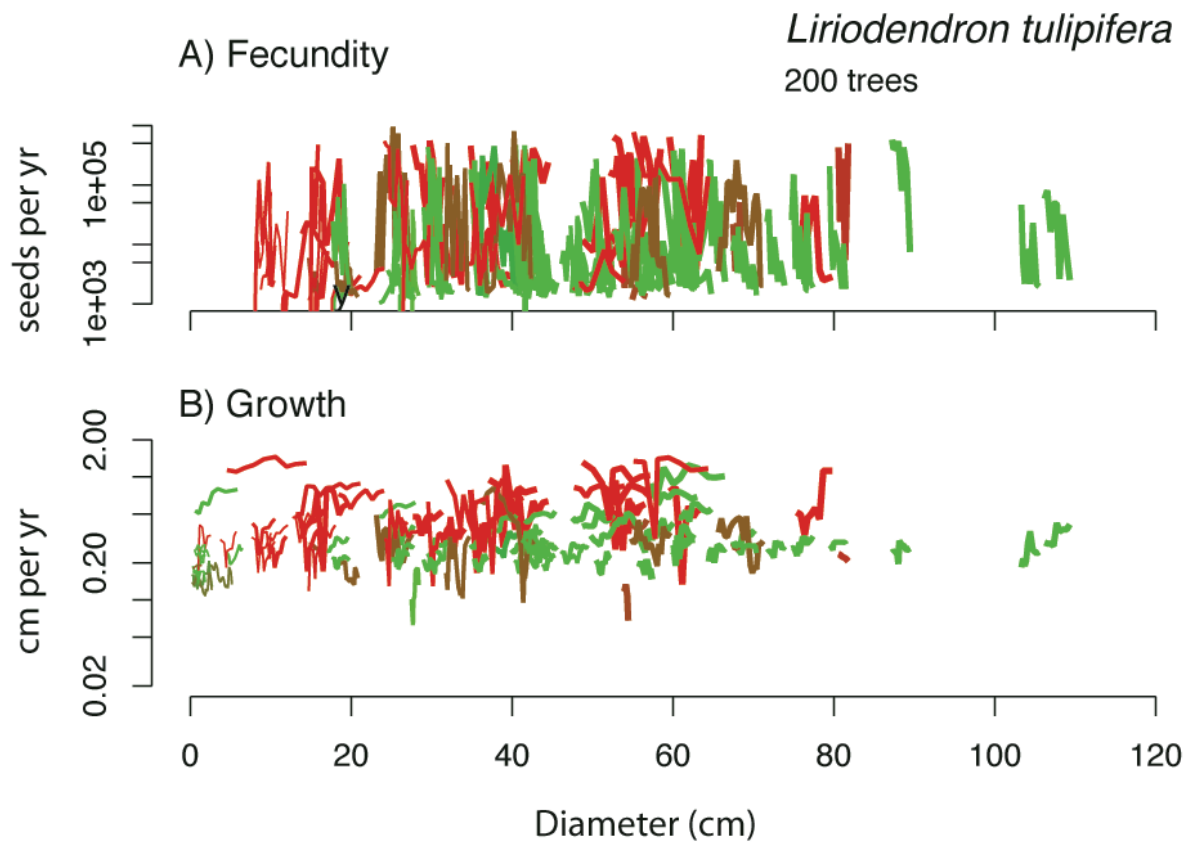


Figure S2. Example showing fecundity (A) and growth rate (B) for 200 *Liriodendron* trees. Each line indicates the estimates of growth and fecundity of an individual plotted against its diameter. Colors indicate plots ranging from high elevation (1410 m a.s.l.) in green to intermediate in brown to low elevation (780 m a.s.l.) in red. Line thickness indicates relative canopy exposure, those with thick lines having most access to light. Correlations between these individual year-to-year rates are basis for calculations in this analysis.

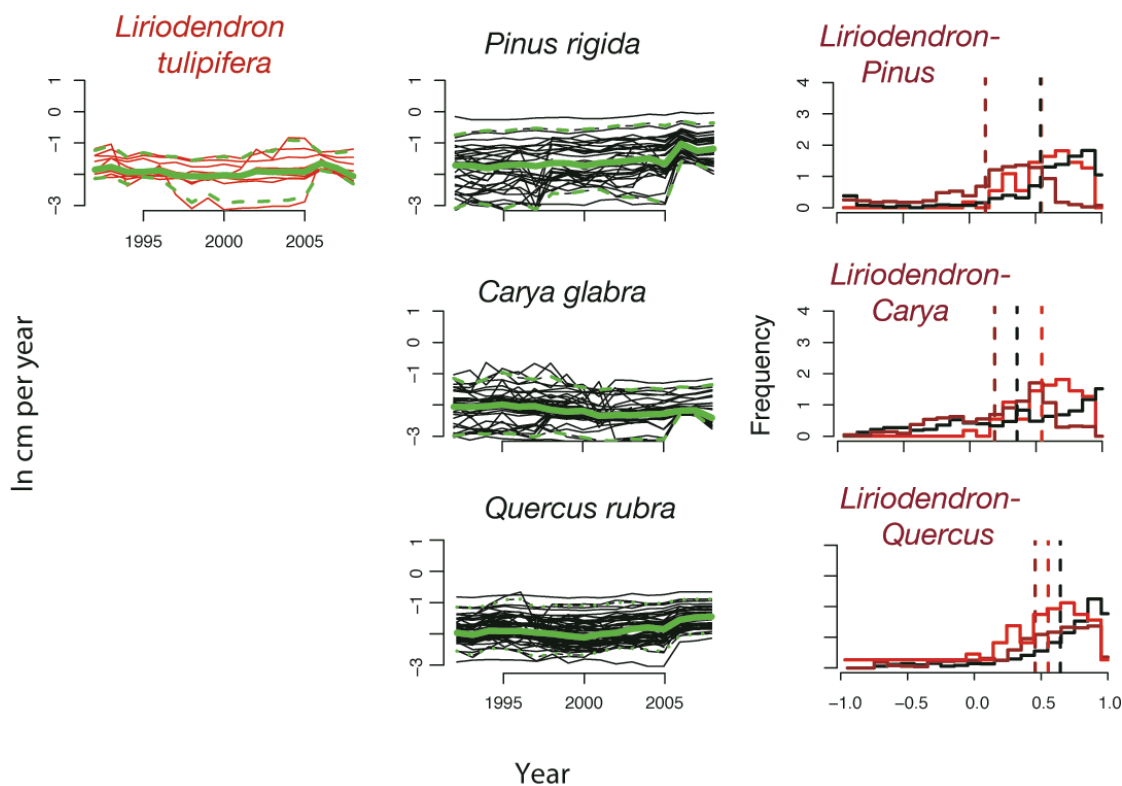


Figure S3. Relationships used for the analysis for the example of *Liriodendron tulipifera* and three dominant competitors on the first plot, C1. Shown at left are growth rates for individuals of *Liriodendron* and three species with which it co-occurs, *Pinus rigida*, *Quercus rubra* and *Carya glabra*. Means (green solid) and 95% (green dashed) lines summarize species-level trends, but individuals vary widely. Still, correlations between individuals of the same species tend to be higher than those of different species, shown by histograms of all pairwise correlations between *Liriodendron* and these three species at right. Vertical dashed lines show mean correlations within (red and black) and between (brown) species. These mean correlations are tabulated in Figure 2 of the text.

Table S1. Study sites, including location, climate, and parent material.

Province	Blue Ridge (Coweeta Hydrologic Lab)							Transition (Mars Hill)		Piedmont (Duke Forest)	
mean annual T	12.7°C							11.6°C		14.6°C	
Mean annual P	1780 - 2500 mm (low to high elevation)							1020 mm		1210 mm	
Litho-tectonic	Blue Ridge Belt									Triassic Basin	
Plot	C1	C2	C3	C4	C5	CL	CU	MP	MF	DB	DH
Elev (m)	780	820	870	1110	1410	1030	1140	710	770	155	170
Lat, Long	35°03' N, 83°27' W							35°49'N, 82°32'W		35°58'N, 79°5'W	
First yr	1992	1992	1992	1992	1992	2000	2000	2004	2004	2000	1999
Area (ha)	0.64	0.64	0.64	0.64	0.64	2.75	1.45	0.5	0.5	4.11	2.40

Table S2. Species codes used in Table S3.

Code	Species
acru	<i>Acer rubrum</i>
acsa	<i>Acer saccharum</i>
acpe	<i>Acer pensylvanicum</i>
acba	<i>Acer barbatum</i>
acun	<i>Acer unknown</i>
beal	<i>Betula alleghaniensis</i>
bele	<i>Betula lenta</i>
beun	<i>Betula unknown</i>
caca	<i>Carpinus caroliniana</i>
cagl	<i>Carya glabra</i>
caov	<i>Carya ovata</i>
cato	<i>Carya tomentosa</i>
caun	<i>Carya unknown</i>
ceca	<i>Cercis canadensis</i>
cofl	<i>Cornus florida</i>
fram	<i>Fraxinus americana</i>
ilde	<i>Ilex decidua</i>
ilop	<i>Ilex opaca</i>
list	<i>Liquidambar styraciflua</i>
litu	<i>Liriodendron tulipifera</i>
nysy	<i>Nyssa sylvatica</i>
oxar	<i>Oxydendron arboreum</i>
piri	<i>Pinus rigida</i>
pist	<i>Pinus strobus</i>
pita	<i>Pinus taeda</i>
piec	<i>Pinus echinata</i>
pivi	<i>Pinus virginiana</i>
qual	<i>Quercus alba</i>
quco	<i>Quercus coccinea</i>

qufa	<i>Quercus falcata</i>
quma	<i>Quercus marilandica</i>
quph	<i>Quercus phellos</i>
qupr	<i>Quercus montana</i>
quru	<i>Quercus rubra</i>
qust	<i>Quercus stellata</i>
quve	<i>Quercus velutina</i>
quun	<i>Quercus unknown</i>
rops	<i>Robinia pseudoacacia</i>
tiam	<i>Tilia americana</i>
tsca	<i>Tsuga canadensis</i>
ulal	<i>Ulmus alata</i>
ulam	<i>Ulmus americana</i>
ulru	<i>Ulmus rubra</i>
ulun	<i>Ulmus unknown</i>

Table S3. Basal area (m^2ha^{-1}) of species included in this analysis, ranked by weighted average against plot elevation.

	Piedmont		Transition		Blue Ridge						
Plot	DH	DB	MF	MP	C1	C2	C3	CL	C4	CU	C5
meters	165	170	720	730	780	820	870	1030	1110	1140	1410
ulru	0.31	0	0	0	0	0	0	0	0	0	0
quph	3.8	0.36	0	0	0	0	0	0	0	0	0
qust	2.74	0.5	0	0	0	0	0	0	0	0	0
acba	0.14	0.04	0	0	0	0	0	0	0	0	0
ulam	0.28	0.09	0	0	0	0	0	0	0	0	0
ulal	1.17	0.72	0	0	0	0	0	0	0	0	0
pita	12.84	14.34	0	0	0	0	0	0	0	0	0
qufa	0.58	0.7	0	0	0	0	0	0	0	0	0
list	4.26	5.29	0	0	0	0	0	0	0	0	0
pivi	0.03	0.21	0	0	0	0	0	0	0	0	0
ceca	0.02	0.18	0	0	0	0	0	0	0	0	0
piec	0.03	1.38	0	0	0	0	0	0	0	0	0
caca	0.27	0.07	0.01	0.02	0	0	0	0	0	0	0
cato	0.18	1.53	0	0	0	0	0	0.33	0	0.03	0
caov	0.64	0	0	0	0	0	0.31	0	0	0	0
qual	2.57	4.89	11.64	1.69	0.61	0	0	0	0	0	0.23
cofl	0.31	0.79	0.11	0.67	0.32	0.92	0.39	0.27	0.14	0.06	0.01
pist	0	0	2.37	0.83	0.03	0.03	0	0	0	0	0
fagr	0	0.01	5.77	1.14	0.07	0.01	0	0	0	0	0.41
piri	0	0	0	0	5.33	0	0	0	0	0	0
fram	1.9	0.8	0.02	1.41	0	0	0.07	0.04	0.76	0	2.36
quve	0	0.56	1.69	1.08	1.7	1.8	1.7	0.1	0.25	0.63	0
litu	1.15	3.75	3.05	1.75	0.13	7.83	1.08	13.12	0.05	0.05	0
cagl	0.66	0.72	0.13	0.7	1.59	3.83	3.87	0.74	1.43	0.11	0.13

acru	2.71	3.36	3.86	2.24	4.48	6.14	6.11	9.42	8.44	11.19	0.26
nysy	0.82	0.37	0.66	1.14	1.03	0.85	4.35	1.58	3.22	2.96	0
quco	0	0	4.23	0.34	2.77	2.87	0.14	2.38	1.82	3.57	0
qumo	0	0	1.11	20.17	5.8	4.6	14.77	6.68	11.69	11.06	0
rops	0	0.06	0	0	1.13	1.31	0.43	0.97	0.57	0.72	0
oxar	0	0.37	1.34	1.69	2.53	1.06	4.21	1.07	4.38	4.27	0
tsca	0	0	0	0	0.04	0.77	0.11	1.56	0.97	0.28	0.21
quru	0	0.68	0.39	1.98	2.88	1.3	3.98	6.42	6.21	2.7	7.31
bele	0	0	0	0	0.06	2.56	0.43	0.16	0.13	0.01	7.03
acpe	0	0	0	0	0.02	0.38	0.15	0.19	0.37	0.05	1.7
acsa	0	0	0	0.02	0	0.33	0	0.11	0	0	1.74
tiam	0	0	0	0	0	0.37	0	0	0	0	6.8
beal	0	0	0	0	0	0.05	0.08	0	0	0	9.89
Total	37.4	41.8	36.4	36.9	30.5	37	42.2	45.1	40.5	37.7	38.1

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