

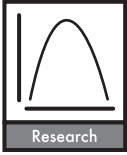
ECOGRAPHY

PATTERN AND DIVERSITY IN ECOLOGY



37

SEPTEMBER 2014, no. 9
ISSN 0906-7590



EDITOR'S
CHOICE

Ecography 37: 814–826, 2014

doi: 10.1111/ecog.00473

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Subject Editor: Dominique Gravel. Accepted 12 January 2014

Using trait and phylogenetic diversity to evaluate the generality of the stress-dominance hypothesis in eastern North American tree communities

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The stress-dominance hypothesis (SDH) is a model of community assembly predicting that the relative importance of environmental filtering increases and competition decreases along a gradient of increasing environmental stress. Tests of the SDH at limited spatial scales have thus far demonstrated equivocal support and no prior study has assessed the generality of the SDH at continental scales. We examined over 53 000 tree communities spanning the eastern United States to determine whether functional trait variation and phylogenetic diversity support the SDH for gradients of water and soil nutrient availability. This analysis incorporated two complementary datasets, those of the U.S. Forest Service Forest Inventory and Analysis National program and the Carolina Vegetation Survey, and was based on three ecologically important traits: leaf nitrogen, seed mass, and wood density. We found that mean trait values were weakly correlated with water and soil nutrient availability, but that trait diversity did not vary consistently along either gradient. This did not conform to trait variation expected under the SDH and instead suggested that environmental filters structure tree communities throughout both gradients, without evidence for an increased role of competition in less stressful environments. Phylogenetic diversity of communities was principally driven by the ratio of angiosperms to gymnosperms and therefore did not exhibit the pattern of variation along stress gradients expected under the SDH. We conclude that the SDH is not a general paradigm for all eastern North American tree communities, although it may operate in certain contexts.

Ecological communities are expected to be structured by a variety of stochastic and deterministic processes. Two deterministic processes thought to play a strong role in determining the coexistence of species in the same trophic level are interspecific competition and environmental filtering, where species are excluded from a community due to an inability to survive and reproduce in a given physical environment. General rules for predicting the relative importance of these processes in different contexts are still largely unresolved (HilleRisLambers et al. 2012). One compelling community assembly model predicts that environmental filtering will be more important in structuring communities in stressful environments, while competitive interactions will be more important in benign environments (depicted in Weiher and Keddy 1995). This hypothesis, which we refer to as the stress-dominance hypothesis (terminology adapted from Swenson and Enquist 2007), derives from the expectation that the importance of competition in plant communities declines with increasing environmental stress (Grime 1977) and is consistent with modern theory predicting that fitness

differences change along abiotic gradients (HilleRisLambers et al. 2012).

Testing the generality of the stress-dominance hypothesis (SDH) is difficult. The experiments required to identify competition and environmental filtering are infeasible in many types of communities (for example, among long-lived organisms) and rarely cover a sufficiently broad geographic extent to confirm that the hypothesis is generalizable. Large-scale observational studies provide a unique opportunity to evaluate the generality of the SDH because 1) the number of communities that can be analyzed may be several orders of magnitude larger than in traditional field studies, 2) large-scale studies tend to span broader environmental gradients related to the processes of interest, and 3) the occurrence of strong relationships amidst the ecological heterogeneity of a large observational data set provides more persuasive evidence of generality. Nevertheless, parsing ecological processes in a non-experimental setting is notoriously difficult, especially when making inferences from patterns of species diversity and community composition (Gotelli and Graves

1996). Ecologists are increasingly using information about species traits and phylogenetic relationships to strengthen observational pattern-based inference of the mechanisms of community assembly (Webb et al. 2002, Emerson and Gillespie 2008, Kraft et al. 2008, Cavender-Bares et al. 2009, Spasojevic and Suding 2012). The variation of certain traits within a community can indicate the relative strength of processes such as competition and environmental filtering since traits differentially mediate an organism's ability to use and obtain resources and to tolerate environmental stressors (Keddy 1992, Tilman 2004). Where trait information has been unavailable, the phylogenetic structure of communities has frequently been used as a proxy for functional structure (Bryant et al. 2008, Cadotte et al. 2008, Graham and Fine 2008).

Functional and phylogenetic diversity have recently been used to elucidate processes structuring a wide range of communities (Ricotta and Moretti 2011), and several studies have found patterns consistent with the SDH (Swenson and Enquist 2007, Kluge and Kessler 2011, Machac et al. 2011, Graham et al. 2012, Mason et al. 2012, Spasojevic and Suding 2012). However, most studies encompass a relatively small geographic extent and focus on a single community or habitat type. While this allows researchers to collect detailed data on traits within communities, it is unclear how general these findings are. Several major efforts to accumulate and coordinate extensive trait and phylogenetic information (e.g. Phylocom, Webb et al. 2008; TRY, Kattge et al. 2011) have expanded the potential geographic scope of trait-based ecology, leading to a number of recent studies of continental to global scale variation in traits, functional and phylogenetic diversity (Reich and Oleksyn 2004, Wright et al. 2004, Ordoñez et al. 2009, Safi et al. 2011, Huang et al. 2012, Swenson et al. 2012b). The next step is to use these broad-scale patterns to evaluate the generality of community-scale ecological theory. Doing so requires a dataset encompassing a wide variety of species, communities, and processes that influence these communities. It is uncertain if the inherent heterogeneity of such a dataset will obscure any general signals, or whether hypothesized 'rules', such as the SDH, are strong enough to be observed regardless (Lawton 1999).

Here we test whether patterns of phylogenetic and trait diversity in 53 439 tree communities in the eastern United States are consistent with shifts from environmental filtering to competition predicted by the SDH. In doing so, we assess the general applicability of this hypothesis to eastern North American forests and evaluate the utility of broad-scale trait diversity patterns for understanding processes that structure communities. By using a data set with a small spatial grain and large spatial extent we can examine whether community-level processes are general across continental to regional scales.

Phylogenetic diversity and multivariate metrics of functional diversity integrate over many different organismal attributes, and are potentially influenced by many different processes in addition to competition and environmental filtering, including dispersal limitation, positive interactions, and predation or parasitism (Cavender-Bares et al. 2009, Pavoine and Bonsall 2011, Spasojevic and Suding 2012). As such, examining functional diversity based on single traits

that are directly related to an organism's competitive or stress tolerance abilities may provide less ambiguous information about the importance of the two processes of interest (Weiher et al. 1998, Swenson and Enquist 2009, Spasojevic and Suding 2012). The expected response of a trait depends on the trait's ecological role (Fig. 1). In the context of the SDH, environmental filtering acts on traits that are important for stress tolerance, favoring convergence to an optimal trait value. This lowers within-community trait variation, which we refer to as 'trait diversity'. Competition can have opposite effects on traits related to niche differences versus traits related to competitive ability (Mayfield and Levine 2010). It is expected to increase the diversity of traits involved in resource partitioning, but lower the diversity of traits conferring competitive dominance by favoring convergence on the trait value that leads to greatest competitive ability (Kunstler et al. 2012). Competition can occur throughout forest development, and competitive pressures at different successional stages may select for different phenotypes (Huston and Smith 1987). Given that the majority of eastern U.S. forests are young (Pan et al. 2011) due to logging and extensive abandonment of agricultural lands in the last century (Abrams 1992, Smith et al. 2009), competitive processes operating at the early successional phases are most likely to dominate the trait distributions of current forests.

To assess whether the variation of phylogenetic and trait diversity in tree communities is consistent with the stress dominance hypothesis, we developed and tested a set of hypotheses (Table 1) for changes in community mean trait values, trait diversity, and phylogenetic diversity along two stress gradients (soil nutrient availability and water availability). Our hypotheses are based on competition favoring a fast-growth, low resource-use efficiency strategy in benign environments. However, this may not be realistic in older

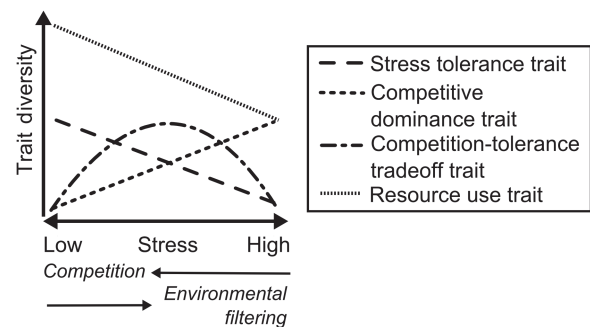


Figure 1. Expected shifts in trait diversity of different trait types under the stress-dominance hypothesis. Competition and environmental filtering can have different effects on the within-community dispersion of different types of traits. Consequently, if the relative strength of these processes varies along a stress gradient as predicted by the SDH, the diversity of different trait types will exhibit different correlations with particular environmental stressors. For example, traits related to niche differences (resource-use traits) are expected to exhibit high diversity in highly competitive environments due to limiting similarity, whereas traits conferring greater competitive ability will be filtered and exhibit low diversity. Traits mediating a tradeoff between competitive ability and stress-tolerance may be filtered at both ends of the gradient and reach maximum diversity in moderate environments.

Table 1. Expected shifts in phylogenetic diversity, trait values and trait diversity along a stress gradient under the stress-dominance hypothesis. Predictions assume that environmental filters dominate community assembly in stressful environments and that competitive filters dominate in benign environments. Solid blue lines depict expected shifts in the mean trait value across communities. Red dashed lines depict expected shifts in trait diversity across communities.

	Low stress (strong competition)	High stress (strong environmental filtering)	
Phylogenetic diversity *These expectations hold only when the phenotypes governing plants' environmental tolerances and niche relations are phylogenetically conserved, so that phylogenetic distance measures functional dissimilarity.	Phylogenetic diversity will be high due to competitive exclusion of species with similar phenotypes and the coexistence of phylogenetically dissimilar species.*	Phylogenetic diversity should be low in the most stressful environments because only certain clades have evolved the adaptations necessary to tolerate these conditions.*	
Seed mass Sources differ on how seed size should be affected by stress gradients because seed mass is typically thought to reflect a tradeoff between viability and dispersal (Kitajima 2007).	Large seeds are advantageous under strong competition (see references in Leishman et al. 2000). Therefore, mean seed mass will be high and seed mass diversity will be low due to competitive filtering.	Both small and large seeds can be advantageous in stressful environments (Leishman 2001, Moles and Westoby 2004). Seed mass diversity will be high.	
Leaf nitrogen content Leaf nitrogen content reflects a tradeoff between stress tolerance and competitive dominance (Wright et al. 2004)	Competition favors faster growth rates, leading to high leaf nitrogen content due to lower resource-use efficiency. Leaf nitrogen diversity will be low due to competitive filtering.	Stressful environments favor high resource use efficiency and should lead to low leaf nitrogen content. Leaf nitrogen diversity will be low due to environmental filtering.	
Wood density Wood density reflects a tradeoff between stress tolerance and competitive dominance (e.g. the wood economics spectrum; Chave et al. 2009).	Competition favors fast growth and consequently low wood density. Wood density diversity will be low due to competitive filtering.	Low water and nutrient availability in stressful environments favors high resource use efficiency and resistance to embolism, leading to high wood density (Hacke et al. 2001, Martínez-Cabrera et al. 2009). Since the xylem architecture of conifers allows them to persist in stressful conditions despite low wood density relative to angiosperms (Hacke et al. 2001), this increase in mean wood density may not be very pronounced. Wood density diversity will be high because high-density angiosperms co-occur with lower density conifers.	

forests where competitive exclusion has selected for trees with a shade-tolerant phenotype, or in disturbance regulated forests that do not follow a traditional successional trajectory. We considered three physiologically important traits that represent ecological trade-offs: seed mass, leaf nitrogen content, and wood density. Previous work has examined geographic variation in these traits (Swenson and Weiser 2010, Siefert et al. 2012) as well as temporal and spatial variation in phylogenetic diversity (Potter and Woodall 2012, Hawkins et al. 2014) in eastern U.S. forests, but has not evaluated whether this variation reflects changes in community assembly processes along environmental gradients.

Methods

Tree community data

This study was conducted using two complementary databases of vegetation plots in the eastern United States: the U.S. Forest Service Forest Inventory and Analysis National program (FIA; Gray et al. 2012) and the Carolina Vegetation Survey (CVS; Peet et al. 2012) (Fig. 2). We used data from FIA forest plots spanning all states east of the Great Plains (approximately 96°W longitude). The CVS data set is smaller in extent and contains plots in North Carolina, South Carolina, Georgia, and Florida. Although both programs

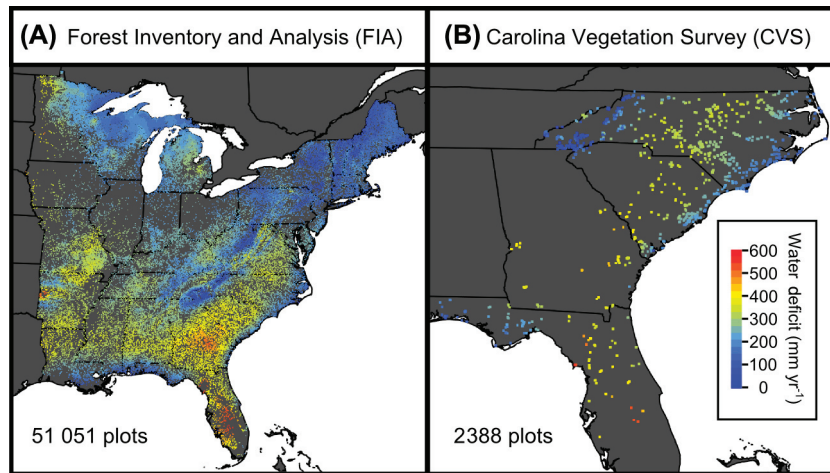


Figure 2. Geographic distribution of plots in the FIA and CVS datasets. Plots are colored by mean annual climatic water deficit.

measure all tree species occurring on plots of fairly equivalent size (FIA – 672 m²; CVS – 1000 m²), the two programs differ in their sampling ideology and methodology. The goal of the FIA program is to assess the state of United States forest land by surveying randomly located plots. In contrast, CVS aims to record naturally occurring plant communities in the southeastern U.S. and chooses plot locations that maximize homogeneity within plots and exclude potentially human-introduced elements. We used only the most recent survey data from each plot and excluded FIA plots with evidence of tree planting or cutting and CVS plots labeled as early successional plots. We conducted parallel analyses on the two datasets separately, since differences in sampling methodology may impact ecological inference. Criteria used to select plots and specific methods of plot sampling are described in Supplementary material Appendix 1. Our final data set consisted of 51 051 FIA plots sampled during 1997–2010 and 2388 CVS plots sampled during 1988–2010. Data available from the Dryad Digital Repository: < <http://dx.doi.org/10.5061/dryad.m5g7d> >.

Trait data

We compiled species-level mean trait data for 269 species for three traits from primary literature sources and publicly available trait databases (Supplementary material Appendix 2): seed mass (average mass of 1 seed, 0.055–16200 mg), wood density (oven dry mass divided by green volume, 0.24–0.89 g cm⁻³), and leaf nitrogen content as a percent of dry weight (0.32–3.54%). Both the CVS and FIA datasets contained some trees that were identified only to the genus level (26 taxa) as well as some species for which we were unable to obtain trait data (41 species: 20 missing all three traits, of which 15 are *Crataegus* species); for these cases, we used genus-level average trait values, calculated from the species that were present in our datasets (Supplementary material Appendix 2). Fourteen species retained missing values due to a lack of information at the genus level. Seed mass spanned five orders of magnitude and was therefore log₁₀-transformed prior to all calculations. We calculated the community-weighted mean trait values

for each trait in each plot by averaging the species-level trait values for all species present in the plot, weighted by their relative abundance (Garnier et al. 2004, Ricotta and Moretti 2011). For CVS, relative abundance was based on percent cover and for FIA, relative abundance was based on basal area.

Phylogeny

We constructed a phylogeny for each data set using the Phylomatic online software ver. 2 (Webb et al. 2008), which provides a dendrogram resolved to the genus level based on the Angiosperm Phylogeny Group III (Stevens 2012). Branch lengths were assigned using the BladJ function of the Phylocom software, which assigned nodal ages down to the family-level based on (Wikström et al. 2001). Where node ages were unavailable, the software split known distances evenly between ageless nodes and branch tips occurring between or after known nodes. The Phylomatic online software provided the topology for gymnosperms, although no nodal ages were available so branch lengths were split evenly between each node in the gymnosperm clade. Similar phylogenies have been useful in evaluating ecological hypotheses about the phylogenetic relationships among species in communities (Cavender-Bares et al. 2006, Kembel and Hubbell 2006, Kraft and Ackerly 2010).

Trait and phylogenetic diversity

We measured trait and phylogenetic diversity using the abundance-weighted mean pairwise distance among species in a plot (MPD; Clarke and Warwick 1998, Webb 2000). This is equivalent to Rao's quadratic entropy (Botta-Dukát 2005) which has been shown to discriminate between community assembly processes in simulated data (Mouchet et al. 2010) and empirical data (Ricotta and Moretti 2011). MPD is suitable for this analysis because it is mathematically independent of richness and robust to imbalanced phylogenies when detecting overdispersed and clustered community assembly processes (Vellend et al. 2011).

For trait diversity, traits were standardized by their mean and standard deviations across species and then distances among species were computed as the Euclidean distance between these values. Species with missing trait values were omitted from calculations involving the missing trait (affecting 728 plots, but with only 2.3% of the total cover in these plots omitted). For phylogenetic diversity, the distance between species is the total branch length between them on the phylogeny. Calculations were performed in R ver. 2.14.0 (R Core Team) using the FD (Laliberté and Shipley 2011) and *picante* (Kembel et al. 2010) packages.

Inference of environmental filtering and competition is usually based on the deviation (z-score) of a community's functional diversity from the diversity value expected under a null model that simulates random assembly (Cornwell et al. 2006, Mouillot et al. 2007, Swenson and Enquist 2007). In addition, z-scores allow diversity to be compared among communities that differ in species number, since MPD can be correlated with species richness due to sampling effects (Weiher 2011). We generated trait diversity null distributions for each plot by randomly shuffling trait values across the entire species pool in each data set 1000 times and recalculating trait diversity each time (Swenson and Weiser 2010). We then calculated trait diversity z-scores by subtracting the mean of the null distribution from the observed trait diversity and dividing by the standard deviation of the null distribution. Plots falling in the 95th or higher percentile of the null distribution were considered 'overdispersed', exhibiting higher diversity than expected by random assembly, and plots in the 5th or lower percentile were considered 'underdispersed', exhibiting lower diversity than expected under random assembly (Swenson et al. 2012a). A similar model was used to generate null distributions of phylogenetic diversity for each plot, except in this case, species were shuffled across the tips of the phylogeny. Because our phylogeny had an unbalanced, decelerating topology resulting from the initial gymnosperm-angiosperm bifurcation, we also calculated MPD using only angiosperm taxa in order to examine potential inconsistencies. We also evaluated the mean nearest taxon distance (MNTD) which may be less sensitive to the angiosperm-gymnosperm split (Supplementary material Appendix 3). Because unconstrained null models can be biased toward identifying underdispersion (de Bello et al. 2012), we also calculated z-scores using null models in which the species at each site were randomly drawn from the set of species with environmental niches spanning the environmental conditions found at that site. Results based on this constrained null model were qualitatively similar and are addressed in the Discussion section.

Environmental data and models

We chose to examine two of the most important environmental variables known to structure plant communities worldwide: soil nutrient availability and water availability (Archibold 1995). To represent water stress, we used average annual climatic water deficit (D) (Stephenson 1990), defined as the difference between potential evapotranspiration (PET) and actual evapotranspiration (AET) over a

calendar year. D is an effective measure of overall water stress to plants because it represents the potential additional evaporative demand not met by available water based on energy input and precipitation (Stephenson 1998, Lutz et al. 2010). It has also been shown to better correlate with tree distributions than water supply measures, such as annual precipitation (Piedallu et al. 2013). We calculated D for each plot by intersecting plot geographic coordinates with 30-arc-second resolution maps of long-term average annual PET and AET (CGIAR-CSI's Global Aridity and PET Database and Global High-Resolution Soil-Water Balance database, (Trabucco and Zomer 2009, 2010)), which were generated using WorldClim temperature and precipitation data (Hijmans et al. 2005) under the Hargreaves model. Thirty-one plots (27 FIA, 6 CVS) were excluded as probable outliers and 118 CVS plots were excluded from D models due to missing geographic coordinates. A subset of FIA plots (44 394 plots) were classified as 'xeric' or 'mesic' within the FIA database according to topographic position and water availability as perceived by the survey crew. We used these classes as a local-scale alternate measure of water stress and used a Mann-Whitney U-test to compare mean trait values and trait diversity between these two groups of plots.

Soil nutrient availability was calculated for CVS plots using principle components analysis (PCA) of 23 soil characteristics measured at each plot (Supplementary material Appendix 1). Correlations of individual soil variables with the first principle component indicated that it represents a gradient from acidic, low nutrient, stressful conditions to benign high nutrient, basic conditions (Pee et al. 2014). We were unable to calculate soil nutrient availability for 301 CVS plots due to missing data. We did not calculate soil nutrient availability for FIA plots because only a small subset had associated soil data.

We tested for monotonic relationships between mean trait values and the two stress gradients by fitting two models: a simple linear regression and a power function of the form $y = ax^b$ using non-linear least-squares (chosen over linear regression on log-transformed data so that models could be compared using AIC). We used the same models to test for a monotonic relationship between PD and the stress gradients. However, for trait diversity we had hypothesized hump-shaped relationships so we also tested a linear model with a quadratic term. Models of trait and phylogenetic diversity used z-scores as the response variable. All models were fit in R ver. 2.14. The model with the lowest AIC is reported, unless the difference in AIC was less than 2, in which case the simpler model was used (Supplementary material Appendix 4, Table A4.1). Because of the large number of plots included in the analysis, all slopes differed from zero with $p < 0.001$, so we only report relationships explaining at least 5% of the total variation ($r^2 > 0.05$).

Results

Phylogenetic diversity

CVS phylogenetic diversity (PD) was negatively correlated with soil nutrient availability ($r = -0.44$; Fig. 3), the

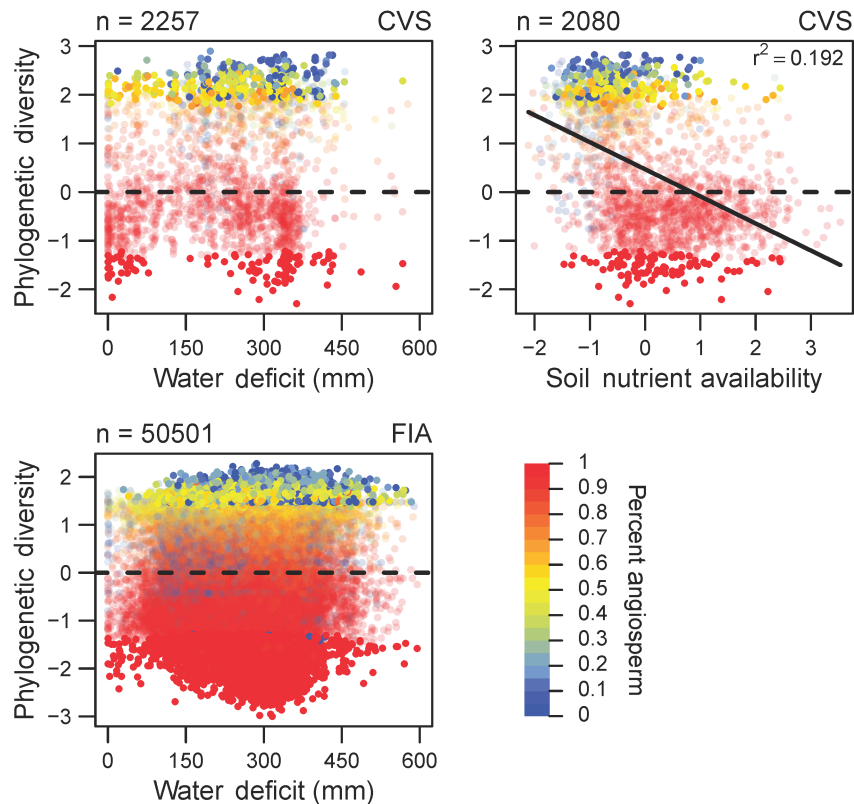


Figure 3. Phylogenetic diversity in CVS and FIA plots along water deficit and soil nutrient availability gradients. Phylogenetic diversity is measured as the mean pair-wise phylogenetic distance between taxa in a community. Positive z-score values indicate higher diversity and negative values indicate lower diversity relative to a null model of random community assembly with respect to phylogenetic relationships. Opaque points are above the 95th or below the 5th percentile of the null distribution and points are colored by the proportion of the community that is comprised of angiosperm taxa. Regression lines are shown for relationships with $r^2 > 0.05$. Horizontal bands of color indicate that phylogenetic diversity of a community is largely driven by the relative abundance of gymnosperms versus angiosperms in a community which results from the deep initial split between these clades.

opposite of our prediction that fertile sites should exhibit phylogenetic overdispersion due to stronger competition and weak environmental filtering. PD was not correlated with water deficit in either data set (Table 2). For both CVS and FIA, PD was strongly influenced by the presence of gymnosperms, increasing as the proportion of gymnosperms in the community increased (Fig. 3). PD changed dramatically when only angiosperm taxa were included in the analysis, eliminating the previously observed negative correlation between soil nutrient availability and PD (Supplementary material Appendix 3, Fig. A3.2). Other diversity metrics performed similarly (Supplementary material Appendix 3).

Community-weighted mean trait values

Mean leaf nitrogen content and wood density responded as predicted to the stress gradients. However mean seed mass increased with environmental stress, the opposite of our initial hypothesis (Fig. 4 and 5, Table 2). Most relationships were weak, explaining less than 10% of the total variation in mean trait values. The strongest relationship was in CVS plots between mean leaf nitrogen and soil nutrient availability ($r^2 = 0.38$), where leaf nitrogen content initially increased with soil nutrient availability and reached a plateau at high levels (Fig. 5). Other model results are in Table 2.

Analysis of mean traits using the local-scale xeric-mesic categorization yielded trends consistent with the water deficit models. Xeric sites had significantly higher wood density and seed mass and lower leaf nitrogen content than mesic sites (Supplementary material Appendix 5, Fig. A5.1).

Trait diversity

Trait diversity showed no clear relationship ($r^2 < 0.05$) with either stress gradient, with two exceptions (Fig. 4, 5). We found a moderately weak, negative relationship between seed mass diversity and water deficit in CVS plots ($r^2 = 0.09$). We also detected a weak quadratic relationship between wood density diversity and soil nutrient availability (Fig. 5) with diversity reaching a minimum in the middle of the gradient. Trait diversity was higher in xeric than in mesic FIA plots for seed mass and wood density ($p < 0.001$), however, these differences were small (Supplementary material Appendix 5, Fig. A5.1) and may not be biologically meaningful.

We found very little overdispersion of trait diversity in CVS and FIA plots (Table 3) and this may have decreased our ability to detect the hypothesized shifts in trait diversity along stress gradients. Although in several cases peak diversity appears to occur in the middle of the stress gradient (Fig. 4, 5), permutation tests revealed that the distribution

Table 2. Models relating mean traits, trait diversity and phylogenetic diversity to water and soil nutrient availability. Models in bold highlight AIC supported models explaining at least 5% of the variation. r^2 for non-linear power models were calculated using the residual sum of squares (deviance) according to $1 - (SS_{\text{residual}}/SS_{\text{total}})$ (Kvålseth 1985). The estimate reported is the slope parameter for linear models, the quadratic parameter for quadratic models, and the exponential parameter for power models. N is the number of plots used in each model.

Predictor	Response	Dataset	Form	r^2	Estimate	Std. Err.	t	p	N
Water deficit	Seed mass	FIA	linear	0.10	3.54E-03	4.68E-05	75.6	0.00E+00	51023
		CVS	linear	0.03	7.27E-04	9.24E-05	7.9	5.76E-15	2264
	Wood density	FIA	linear	0.07	2.38E-04	3.77E-06	63.2	0.00E+00	51023
		CVS	linear	0.08	1.53E-04	1.06E-05	14.5	2.31E-45	2264
	Nitrogen %	FIA	linear	0.01	-3.49E-04	1.61E-05	-21.6	1.95E-103	51023
		CVS	linear	0.09	-9.99E-04	6.63E-05	-15.1	5.96E-49	2264
	Seed mass diversity	FIA	quadratic	0.01	-8.95E-06	3.61E-07	-24.8	2.79E-135	50501
		CVS	quadratic	0.09	3.35E-06	1.33E-06	2.5	1.18E-02	2256
	Wood density diversity	FIA	quadratic	0.02	-1.43E-06	2.66E-07	-5.4	7.99E-08	50501
		CVS	quadratic	0.03	4.61E-06	9.17E-07	5.0	5.39E-07	2256
Nitrogen % diversity	FIA	quadratic	0.02	2.00E-06	2.66E-07	7.5	5.34E-14	50501	
	CVS	linear	0.02	9.65E-04	1.27E-04	7.6	5.53E-14	2257	
Phylogenetic diversity	FIA	power	0.00	5.78E-01	2.61E-01	2.2	2.67E-02	50501	
	CVS	power	0.02	3.41E-01	8.58E-02	4.0	7.15E-05	2257	
Soil nutrient availability	Seed mass	CVS	power	0.00	-3.16E-02	1.21E-02	-2.6	9.18E-03	2087
	Wood density	CVS	power	0.07	-6.88E-02	5.32E-03	-12.9	7.77E-37	2087
	Nitrogen %	CVS	power	0.38	3.53E-01	1.04E-02	34.1	1.40E-202	2087
	Seed mass diversity	CVS	quadratic	0.03	-1.49E-01	1.92E-02	-7.7	1.61E-14	2079
	Wood density diversity	CVS	quadratic	0.05	8.77E-02	1.29E-02	6.8	1.20E-11	2079
	Nitrogen % diversity	CVS	quadratic	0.04	9.11E-02	1.36E-02	6.7	2.51E-11	2080
	Phylogenetic diversity	CVS	linear	0.19	-5.57E-01	2.51E-02	-22.2	3.34E-98	2080

of overdispersed plots along the stress gradient did not differ from the distribution of non-overdispersed plots. Overdispersed plots appear to occur in the middle of the gradient simply because most plots occur in the middle of the gradient.

Discussion

Phylogenetic diversity

Our analysis of phylogenetic diversity clearly demonstrates the importance of taxonomic scale for interpreting phylogenetic overdispersion. Analyzing communities containing both angiosperms and gymnosperms necessitates a deep initial bifurcation in any phylogeny which leads to phylogenetic diversity being chiefly driven by the ratio of angiosperm and gymnosperm taxa. Because these two groups are not as functionally and ecologically distinct as this bifurcation would imply, phylogenetic diversity is a poor proxy for functional diversity. This dependence of phylogenetic diversity on taxonomic breadth of the phylogeny is well-known (Cavender-Bares et al. 2006, Vellend et al. 2011), and our work suggests that measures of phylogenetic diversity are difficult to interpret in a functional context when a community includes both angiosperms and gymnosperms. However, we chose not to interpret phylogenetic diversity from only the angiosperm portion of the community because doing so eliminates a functionally non-random subset and could mis-represent the process of community assembly.

Mean trait values

Weak shifts in community-weighted mean trait values along the two stress gradients provide some evidence that

filters act to shape tree communities along these gradients. Sites with high water deficit, where potential evaporative demand is much higher than water availability, tended to have species with lower nitrogen content in their leaves, denser wood, and larger seeds. From the SDH, we predicted all but the last relationship, hypothesizing that higher stress environments with lower resource availability favor plants with higher resource-use efficiency, whereas if low stress environments are structured by competition, plants with lower resource-use efficiency, but faster growth will be favored.

The strongest relationship we observed was between soil nutrient availability and leaf nitrogen content, which is consistent with previous studies (Ordoñez et al. 2009). Because we observe a response in literature-based species-level mean traits, our analysis provides evidence of an environmental filter rather than a plastic response of individuals to local conditions or soil enrichment by decomposition of high nitrogen-content leaf litter. The decrease in leaf nitrogen content with increasing water stress that we observed in CVS plots was consistent with our hypothesis that greater resource use efficiency would be promoted in stressful environments. This is contrary to studies showing increased leaf nitrogen in arid environments, as an adaptation to prevent water loss by allowing stomata to remain closed for longer periods of time (Wright et al. 2001, 2005). However, these studies included sites which were more arid than the climate of eastern North America.

Among the three traits we examined, seed mass showed the least response to both stress gradients. This may reflect the fact that seed mass is tied to dispersal strategy (Leishman 2001, Kitajima 2007), which we do not expect to be strongly influenced by either of the two stress gradients. The notable positive relationship between seed mass and water deficit runs counter to our initial prediction that large seeds would

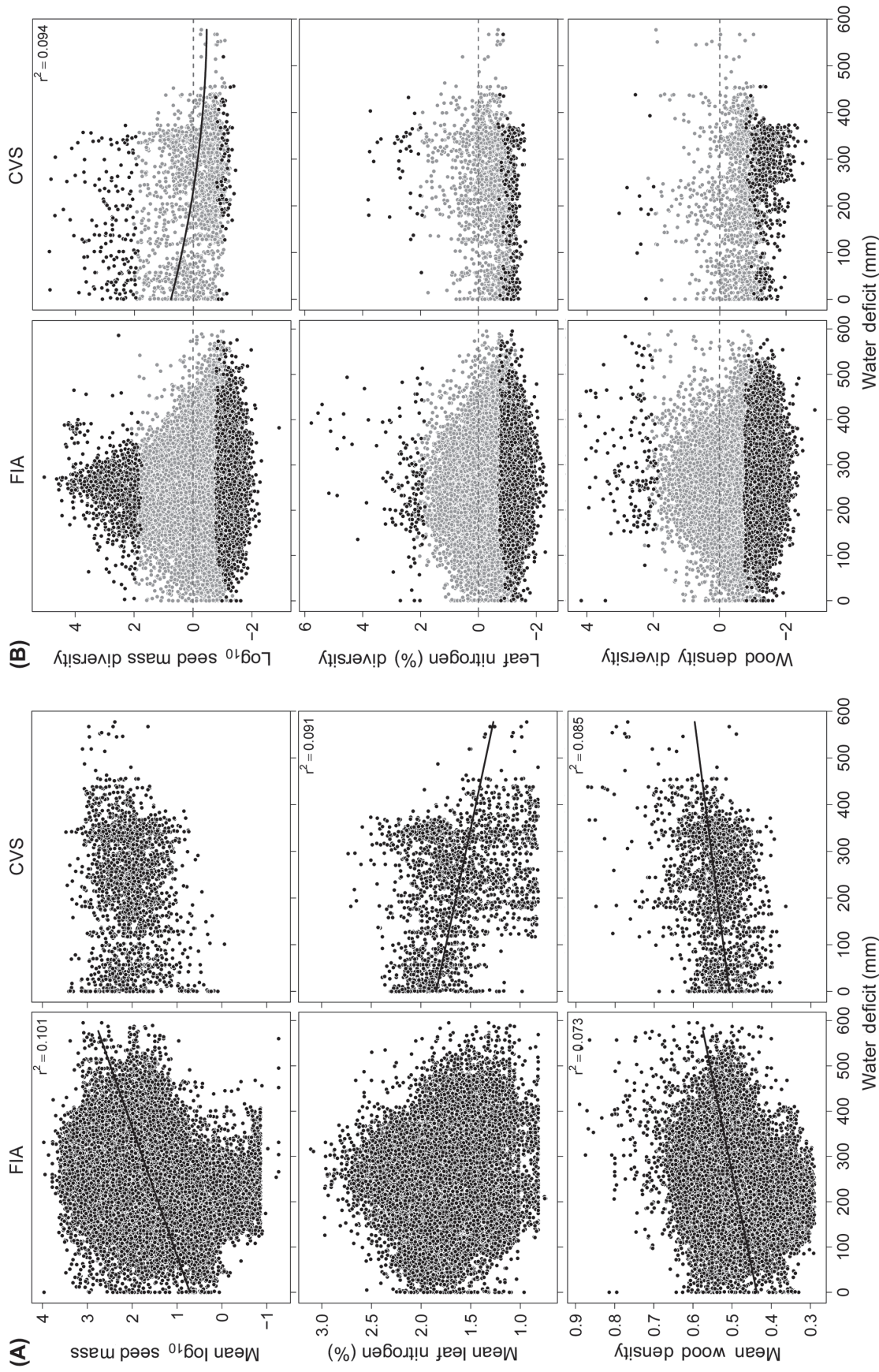


Figure 4. Effect of water stress on community-weighted mean trait values and trait diversity in FIA and CVS plots. Water deficit is plotted on the x-axis with higher water deficit corresponding to higher water stress. Panel (A) shows mean trait values while panel (B) shows trait diversity z-scores. Positive z-score values indicate high diversity and negative values indicate low diversity compared to a null model of random community assembly with respect to traits. Black points are above the 95th or below the 5th percentile of the null distribution, whereas grey points are between these percentiles. Lines show the best fit models and only included if $r^2 > 0.05$ (Table 2 and Supplementary material Appendix 4, Table A4.1).

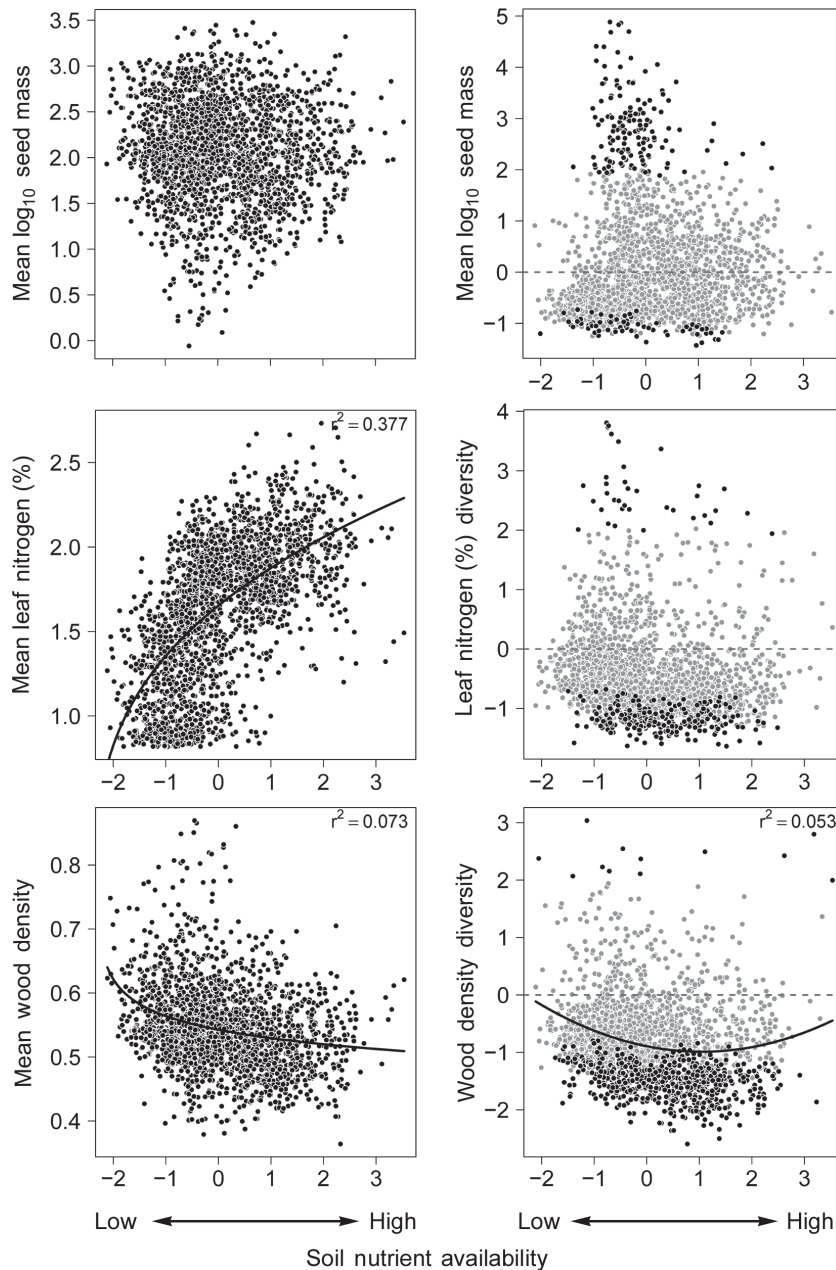


Figure 5. Effect of soil nutrient availability on community-weighted mean trait values and trait diversity in CVS plots. The x-axis is the first principle component of a PCA of 23 soil variables and represents a soil nutrient availability gradient ranging from acidic, stressful conditions (negative values) to basic, benign conditions (positive values). The first column shows mean trait values and the second column shows trait diversity z-scores, as described in Fig. 4. Black points are above the 95th or below the 5th percentile of the null distribution, whereas grey points are between these percentiles. Lines show the best-fit models and are only included if $r^2 > 0.05$ (Table 2 and Supplementary material Appendix 4, Table A4.1).

be competitively superior in low stress environments. Instead it seems to support experimental evidence that large seeds are advantageous in drier soil because they confer greater seedling survival (see references in Leishman et al. 2000). Given the slight trend toward lower seed mass diversity at higher water deficit, our data suggest that the relationship between seed mass and water availability may be driven by filtering for larger seeds at drier sites. We find no evidence for competitive filters on seed mass in benign environments.

The observed shifts in mean trait values differ from those reported previously in Forest Inventory and Analysis plots, in which annual precipitation was positively correlated with seed mass and wood density and negatively correlated with leaf nitrogen content (Swenson and Weiser 2010). This apparent disagreement can be resolved by recognizing that annual precipitation measures water supply whereas water deficit measures evaporative demand. In fact, annual precipitation and water deficit were weakly positively correlated along our stress gradient ($r = 0.20$),

Table 3. Proportion of FIA and CVS plots with significantly overdispersed or underdispersed trait diversity. Overdispersed plots have trait diversity above the 95th percentile of the null distribution, underdispersed plots are below the 5th percentile, and random plots are between the 5th and 95th percentiles. More plots are underdispersed than overdispersed, but in general most plots have a level of trait diversity that does not differ from random assembly.

	% Overdispersed	% Random	% Underdispersed
FIA wood density diversity	1.33	75.42	23.25
CVS wood density diversity	0.93	70.41	28.67
FIA leaf nitrogen diversity	1.35	82.69	15.96
CVS leaf nitrogen diversity	2.03	85.82	12.15
FIA seed mass diversity	3.18	81.71	15.10
CVS seed mass diversity	7.95	88.43	3.62

with highest water deficit occurring in locations with moderate annual precipitation.

Trait diversity

Trait diversity did not notably respond to either of the stress gradients we examined. This can be interpreted in several ways: 1) our data set did not encompass a wide enough environmental range to capture both stressful and benign conditions, 2) the traits we examined are not influenced by the environmental gradients measured, 3) the species-level mean trait values we used masked local trait–environment relationships, 4) our metrics did not accurately capture existing trait convergence or divergence, or 5) our hypotheses about processes structuring tree communities along stress gradients are not generally true across eastern North America.

It is unlikely our dataset failed to encompass a viable stress gradient or that the traits we examined were not influenced by it, because we do observe shifts in mean trait values along both environmental gradients, as have others (Wright et al. 2005, Swenson and Weiser 2010). Combined with the significant trait underdispersion that we observe in many plots, this suggests that both gradients encompass conditions stressful enough to impose filters (albeit weak) on community membership.

It is possible that our metrics did not accurately capture existing patterns of trait diversity, either by ignoring intraspecific variation or by our choice of diversity metric and null model. Using species-level mean traits may have masked local mechanisms whereby trait plasticity among individuals allows coexistence through niche partitioning (Clark 2010, Burns and Strauss 2012). Several studies have found trait divergence in local communities when accounting for intraspecific trait variation (Jung et al. 2010, de Bello et al. 2011, Paine et al. 2011). The necessity of including intraspecific trait variation in large-scale studies has been debated, since for many traits, variation between species is usually greater than variation within species when enough species are included. This is likely true for the three traits we

measured (Leishman et al. 2000, Sungpalee et al. 2009, Albert et al. 2010, Auger and Shipley 2013). However, a study examining community-scale processes, regardless of spatial extent, may still need to account for local variation in traits (Albert et al. 2011).

The trait-diversity z-scores that we analyzed are known to be susceptible to the formulation of the null model (Mouchet et al. 2010, de Bello 2012). Unconstrained null models like ours are biased toward detecting underdispersion because regional species pools may differ in their trait distributions. Our null model implicitly assumed that any species could colonize any site. If certain geographic areas do not contain species with trait values covering the entire range of trait values found in the total species pool, then our null model would bias sites in those areas toward underdispersion. However, we checked the range of trait values that occurred within equal-area grid cells across our study region and found no geographic bias in these trait ranges. Unconstrained null models are also biased toward underdispersion because environmental filters operate prior to biotic interactions so that observed communities will typically have lower trait diversity than expected of a community randomly assembled from species across different environments or habitats (de Bello et al. 2012). One solution is to attempt to remove abiotic environmental filters by comparing communities to a null expectation acquired only from species that could potentially tolerate a site's environment (Peres-Neto et al. 2001, de Bello et al. 2012). While this approach does not allow us to compare the relative influence of environmental filtering and competition, which is crucial for testing the SDH, we wanted to affirm that the underdispersion and lack of systematic variation that we observed was not an artifact of an unconstrained null model. We re-calculated trait diversity z-scores for CVS plots and a subset of southeastern FIA plots using environmentally constrained null models that only permitted shuffling of species among sites that fell within species' environmental niches. Although this resulted in a small increase in the number of plots exhibiting trait diversity overdispersion, there was no change in the lack of observed relationships between trait diversity and environmental gradients (Supplementary material Appendix 6). Analytical approaches that separate the effects of competition from environmental filtering (de Bello et al. 2012) are especially useful when these processes are predicted to filter traits toward similar values. In our case, competitive and environmental filters were expected to select for different trait values.

The overall lack of plots exhibiting trait overdispersion limited our ability to discern shifts in trait diversity along the gradients. Yet, the pervasiveness of trait diversity underdispersion may be ecologically meaningful. Several other studies have found consistent underdispersion in plant communities along environmental gradients. De Bello et al. (2009) attributed underdispersion in specific leaf area throughout a moisture gradient to environmental filtering. Savage and Cavender-Bares (2012) also found that environmental filtering was important for willow tree communities along the length of a hydrologic gradient, with trees at the dry end exhibiting traits associated with drought tolerance and trees at the wet end exhibiting traits

associated with flooding tolerance. The persistent underdispersion in our forest plots may indicate a role for environmental filtering across many habitats. Our results do imply that, at this large spatial extent, competition is unlikely to strongly influence tree community trait structure, since we found no evidence of competitive filtering along either stress gradient. The relationships between community mean leaf nitrogen and wood density could have been driven principally by environmental filtering at the stressful end of the gradient even without competition occurring in benign environments. Additionally, we did not observe the predicted shift in mean seed mass, which relied on competitive filters acting at the benign end of the gradient. Instead, we observed a pattern consistent with environmental filtering for larger seeds in dry environments.

Overall, trait diversity showed some support for the first part of the SDH, environmental filtering along stress gradients, but no support for predictions based on the importance of competition. This may be because plant traits are poor indicators of competition among trees. Traits in local tree communities result from competition integrated over the entire lifespan of the trees and reflect selective mortality at several stages of forest development. Competition for light at the establishment phase may favor traits associated with rapid growth, whereas long-term population-scale competition in closed-canopy forests selects for shade-tolerance and higher resource-use efficiency (Huston and Smith 1987). Using trait data to make inferences about competition in forests may prove most feasible when analyses are restricted to a narrowly defined successional stage. An alternative interpretation of our results is that many tree communities are assembled stochastically with respect to the traits we measured, which would be supported by the lack of trait under or overdispersion observed in the majority of plots. It is possible that examining other traits would yield different results and support the existence of competitive filters in less stressful environments.

Generality of the stress-dominance hypothesis

The stress-dominance hypothesis appears logically simple: communities in stressful environments should be structured by environmental filters, whereas competition should be of relatively greater importance in less stressful environments. However, we detected no strong evidence to support this hypothesis in either of the two datasets examined. One benefit of utilizing two distinct datasets was that we were able to qualitatively evaluate whether differences in sampling ideology and methodology influenced our ability to detect processes structuring communities. We expected that the greater within-site heterogeneity present in the FIA plots relative to the CVS plots would result in stronger trait–environment relationships in the CVS dataset. However, both datasets were equally able to detect relationships between traits and water deficit and, when present, these relationships were congruent. From either dataset, we would conclude that the best interpretation of the weak shifts in trait values and unresponsiveness of trait diversity to environmental gradient is that the SDH is not a general paradigm for eastern North American tree

communities, although it may operate in more restricted subsets.

The broad geographic extent and large number of communities in our analysis spanned a variety of climates, habitat types, successional stages, and disturbance regimes. This heterogeneity of environmental contexts is a necessary condition for testing the generality of a theory in community ecology, but it also could have obscured patterns resulting from the SDH if this hypothesis only applies under certain circumstances. The majority of the plots that we analyzed were embedded in a human-modified landscape and occurred at a range of successional stages. This may have masked trait–environment relationships, given that the importance of dispersal limitation, abiotic filters, and biotic interactions are known to shift throughout forest succession as are the traits that are affected by these processes (Prach et al. 1997, Douma et al. 2012, Kröber et al. 2012 and references therein). Additionally, the SDH may not apply across forests experiencing different levels of disturbance, since disturbance-related filters on tree traits can vary across disturbance regimes (Loehle 2000). Future studies could assess whether SDH-related trait variation is more evident when restricting analyses to particular ecological contexts. Given the contingent nature of many ecological systems, this approach could aid the search for general principles in a time of increasing data availability and integration.

Acknowledgements – This work resulted from a Dimensions of Biodiversity Distributed Graduate Seminar at the Univ. of North Carolina at Chapel Hill and we thank the participants for compiling the trait data and initiating the idea for project: K. Becraft, C. Fieseler, C. Hakkenberg, C. Mitchell, C. Payne, K. Peck, D. Tarasi, and C. Urbanowicz. We also thank the entire DBDGS community for their support. This project would not be possible without the individuals who collected the FIA and CVS data and made it available. Special thanks to Robert Peet and Nathan Swenson for the use of their data and to four reviewers and the subject editor whose comments significantly improved the manuscript. This work was funded by NSF grant #DEB-1050680 to the Univ. of Washington (J. Parrish and S. Andelman, PIs) through a subcontract to the Univ. of North Carolina at Chapel Hill (AHH, C. Mitchell and R. Peet, PIs). All authors contributed equally to this research.

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Supplementary material (Appendix ECOG-00473 at <www.oikosoffice.lu.se/appendix>). Appendix 1–6.

Ecography

ECOG-00473

Coyle, J. R., Halliday, F. W., Lopez, B. E., Palmquist, K. A., Wilfahrt, P. A. and Hurlbert, A. H. 2014. Using trait and phylogenetic diversity to evaluate the generality of the stress-dominance hypothesis in eastern North American tree communities. – *Ecography* doi: 10.1111/ecog.00473

Supplementary material

Appendix 1. Detailed methods of data compilation, collection, and analysis

To assemble forest plot data sets from the Forest Inventory & Analysis Program (FIA) and Carolina Vegetation Survey (CVS) databases, we compiled all plots designated as forest or woodland, defined by greater than 10% cover of trees, consistent with definitions used by several national agencies (e.g. U.S. National Vegetation Classification, U.S.F.G.D.C. 2008; The U.S. Forest Service Inventory and Analysis Program, Gray et al. 2012). FIA plots with evidence of human disturbance or silvicultural treatment and CVS plots classified as “successional” were excluded from the analysis, as were plots not sampled according to the standard plot layout described below. In cases where a plot was surveyed more than once, we used the most recent survey.

CVS plots used in this analysis were 1000 m² in area. The presence of all vascular plant species was recorded within each plot and each species was assigned a cover class value (Peet et al. 1998). Additionally, all woody stems greater than breast height (1.37 m) were identified to species and tallied into diameter classes. A list of tree species for each plot was generated by removing all species classified as shrubs or herbs using growth form classifications reported in Radford et al. 1968; the USDA PLANTS Database, (USDA NRCS 2011), and Weakley 2012. Taxa recorded to subspecies or variety were combined (abundances summed) to the species level. Taxa that were hybrids between two species were combined with the parent species that had the highest abundance in the plot. If neither parent was present, the hybrid was assigned arbitrarily to one of the parent species. Ambiguous taxa and unknown taxa were removed from the data set. Some plots contained trees identified only to the genus level. These taxa were retained and assigned average trait values for the genus and added to the phylogeny at the genus node with a branch length equal to other species within that genus. Thereafter, percent cover was

calculated for each species in each plot using the midpoint of ten visually estimated cover classes (trace, 0-1%, 1-2%, 2-5%, 5-10%, 10-25%, 25-50%, 50-75%, 75-95%, 95-100%).

CVS plots in Florida (FL) and Georgia (GA) do not adequately represent all forest types present in these states and were mostly located in long-leaf pine (*Pinus palustris* L mill.) savannas. To ensure that including only this community type at the most arid end of the water deficit gradient did not bias our results, we conducted a series of sensitivity analyses excluding these plots. First, we examined the distribution of traits of species occurring in FL and GA plots to determine whether inclusion of these species may have altered our inference from null models. Only three species occurred exclusively in FL and GA plots (*Pinus clausa*, *Quercus chapmannii*, and *Q. myrtifolia*) and these species did not have trait values outside the range of the trait distribution all other species in the CVS data set (Figure A1.1). Second, we re-fit all of the regression models excluding plots in FL and GA, but doing so did not qualitatively alter any of the observed relationships between stress gradients and trait values, trait diversity, or phylogenetic diversity (Figures A1.2-3). Based on these analyses we decided to retain FL and GA plots in the final analysis.

Plots in the FIA dataset consisted of four circular subplots, 7.32 m in radius in which all trees greater than 12.7 cm at diameter at breast height (1.37 m; DBH) were identified and measured. Trees smaller than 12.7 cm were measured on four 2.07 m radius microplots nested within these subplots. To account for differences in sampling area, all species abundances for individuals less than 12.7 cm DBH were multiplied by a scaling factor. Seedlings (any tree shorter than breast height) were also counted in the microplots, but in some cases abundances greater than 6 individuals were not recorded. For these plots we estimated seedling abundance based on the average seedling abundance for each species from other plots in the dataset. A list

of tree species for each plot was generated directly from the tree and seedling records for each plot. We removed ambiguously assigned and unidentified species. Some FIA seedlings were only identified to genus and if a tree in that genus was present in the plot, genus-level seedlings were assumed to be that species. If no other tree was in the same genus, the seedling was assigned a genus-level name. Trees and seedlings with genus-level identification were assigned trait and phylogenetic diversity values using the same method as in the CVS database. Thereafter, we calculated basal area for each species on each plot, assuming that each seedling contributed 0.25 cm^2 to basal area.

For FIA taxa not identified to species, we calculated genus-level trait values by averaging species-level traits from both the FIA and CVS datasets. For CVS taxa not identified to species, we calculated genus-level trait values using only species that were in the CVS database. These genus-level averages were also used for 30 species that were missing trait data (Table A1.1). Species for which we could find no data at the genus level were left with no data for that trait (Table A1.1). All 240 species in the FIA data set have complete trait information, while of the 211 species in the CVS data set, 4 species were missing data for seed mass, 9 for leaf nitrogen, and 15 for wood density. In addition to missing trait information, we were not able to calculate mean pairwise phylogenetic distance for several plots because they had only one functionally distinct species. Thus, 522 FIA plots and 8 CVS plots were excluded from analyses involving phylogenetic or trait diversity.

We calculated water deficit (D) for each plot by intersecting plot geographic coordinates with 30-arc-second resolution maps of long-term average annual PET and AET. However, estimates of D for FIA plots may be slightly inaccurate for two reasons. First, most FIA plot geographic coordinates are fuzzed within 0.5 miles and up to 1.0 miles. Second, 20% of plots on

private land are swapped with other private land plots that have similar plot characteristics and which are in the same county (average county area: 576 mi², largest county: 6,829 mi²).

However, because of the relatively small spatial extent of fuzzing and the autocorrelations inherent in modeled spatial environmental data, we do not believe that this introduces any significant errors into the conclusions we draw. Twenty-seven FIA plots and six CVS plots had D values much larger than 600 and were concentrated around a small point in central Florida. Since these values were likely anomalies, we excluded them from analyses involving D. In addition, we were unable to calculate D for 118 CVS plots that were missing geographic coordinates and these plots were also excluded from analyses involving D.

For CVS plots, we examined trait diversity, phylogenetic diversity and mean trait values along a soil nutrient availability gradient in addition to along D. During the time of sampling, soil samples were collected in each CVS plot from the A horizon (top 10 cm) and analyzed for texture (sand, silt, clay %), exchangeable cations (Ca, Mg, K, Na in ppm), extractable micro-nutrients (Al, Fe, Mn, Cu, B in ppm), percent of base saturation for Ca, Mg, K, Na, and H, estimated N release, soluble S, easily extractable P, percent organic matter, percent base saturation, total cation exchange capacity (meq/100g), pH, and bulk density (g/cc)(Peet et al. 1998). Extractions were carried out using the Mehlich III method (Mehlich 1984) and percent organic matter was determined by loss on ignition. Texture analysis employed the Bouyoucos hydrometer method (Patrick 1958).

We used principle components analysis (PCA) to extract a soil nutrient availability axis from the raw CVS soil data (PCA1, variation explained = 0.32). Before analysis, 9 of the 23 soil variables (Ca, Mg, Fe, Al, K, Na, Mn in ppm, soluble S, and easily extractable P))% were log₁₀ transformed to normalize the data and give less weight to outliers. PCA1 was varimax rotated to

maximize the correlation between PCA1 and individual soil variables within the PCA. Base saturation (0.81), log Ca ppm (0.89) log Mg ppm (0.84) loaded strongly on PCA1, indicating PCA1 represents a soil nutrient availability axis ranging from acidic, stressful conditions to basic, benign conditions (Peet et al. 2013).

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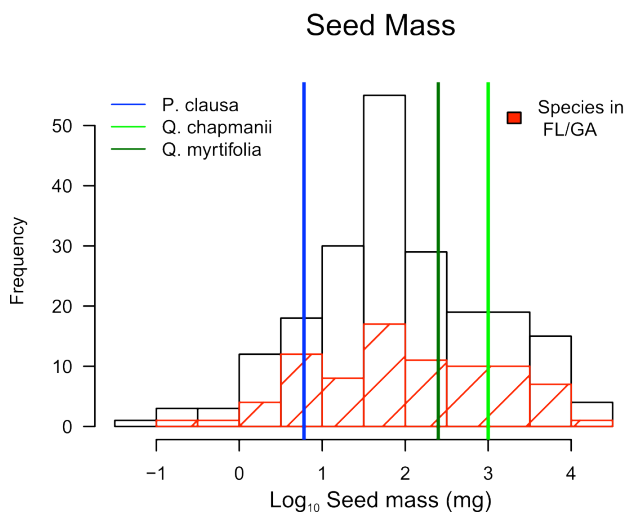
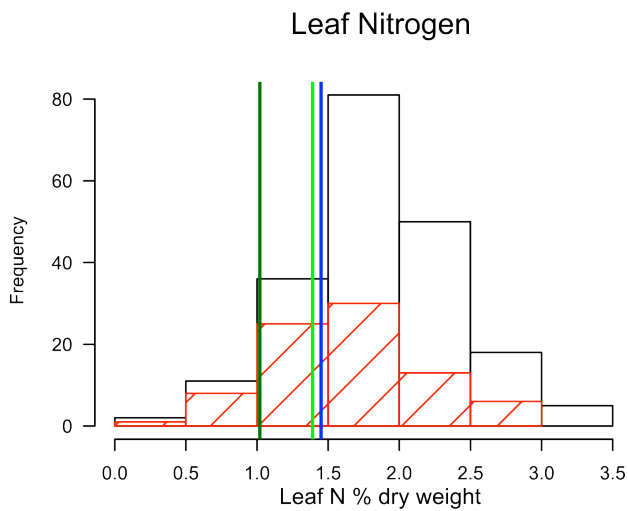
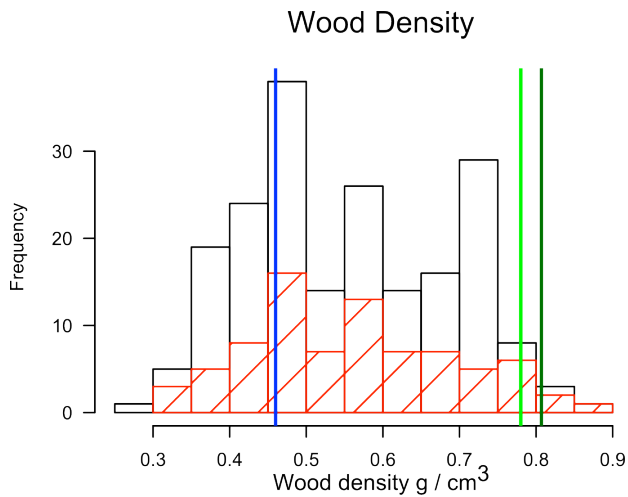


Figure A1.1 Trait distributions of species in all CVS plots versus CVS plots in Florida and Georgia. Histograms in black show the distributions of traits of species in all CVS plots while histograms in red show the distributions of traits for species found in Florida and Georgia CVS plots. Three species were found exclusively in FL and GA plots and their trait values are indicated by vertical lines in blue (*Pinus clausa*), light green (*Quercus chapmanii*) and dark green (*Quercus myrtifolia*).

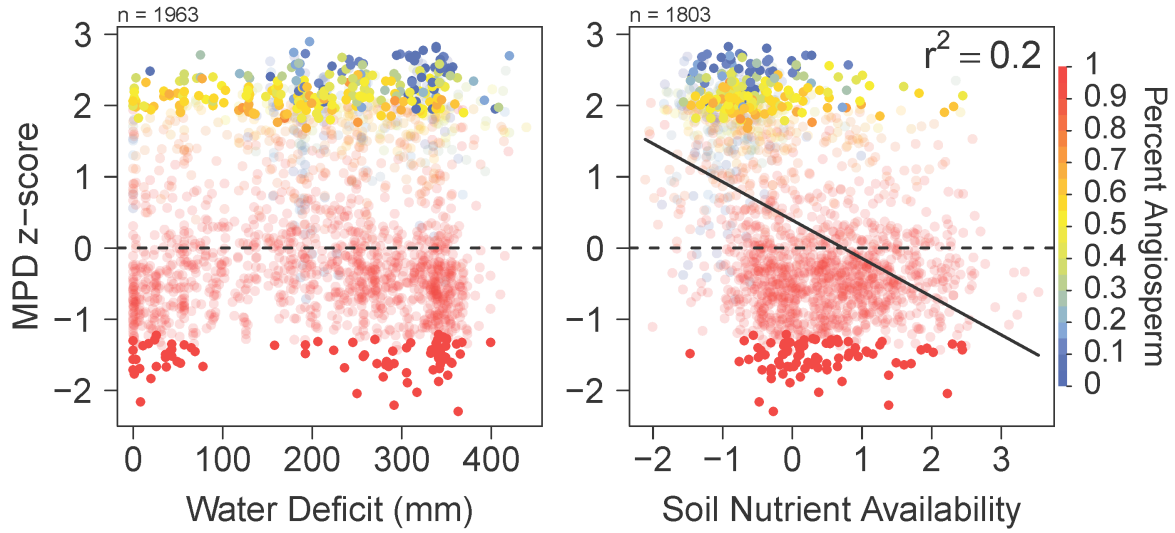


Figure A1.2. Relationship between phylogenetic diversity and stress gradients in CVS plots not located in Florida or Georgia. Removing CVS plots located in FL and GA does not change the relationship (compare to Figure 3).

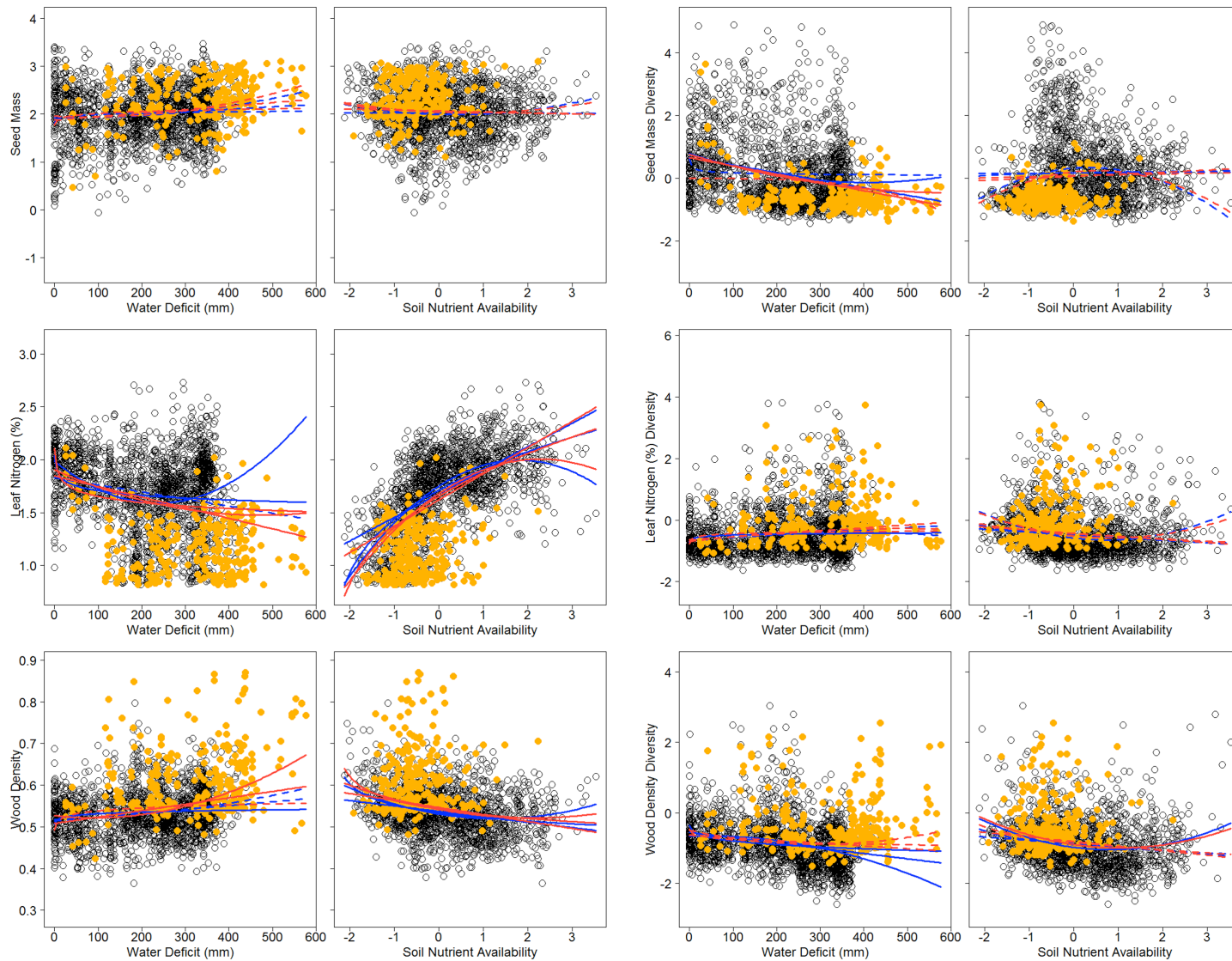


Figure A1.3. Relationships between stress gradients and mean traits and trait diversity in CVS plots when plots in Florida and Georgia are excluded. Points in yellow are plots in FL and GA. Red lines show linear, quadratic, and power models fit to all plots. Blue lines show models fit to plots that are not in FL or GA. Dashed lines indicate $r^2 < 0.05$, while solid lines indicate $r^2 \geq 0.05$. Models appear to be mostly unaffected by the exclusion of FL and GA plots, especially away from the ends of the gradients where most plots occur.

Appendix 2. Trait Data

Data for the following species were obtained from Nathan Swenson (Swenson and Weiser 2010).

Trait data for other species are in Tables A2.1-3.

Seed mass (23 species).

Acer leucoderme, *Amelanchier arborea*, *Bursera simaruba*, *Carya carolinae-septentrionalis*,
Carya ovalis, *Carya pallida*, *Carya texana*, *Castanea pumila*, *Crataegus mollis*, *Ficus aurea*,
Juniperus coahuilensis, *Laguncularia racemosa*, *Malus angustifolia*, *Planera aquatica*,
Populus nigra, *Quercus margaretta*, *Quercus margarettiae*, *Quercus minima*, *Quercus*
oglethorpensis, *Quercus prinoides*, *Quercus similis*, *Salix sepulcralis*, *Vernicia fordii*

Wood density (88 species):

Abies fraseri, *Acer barbatum*, *Acer floridanum*, *Acer leucoderme*, *Acer rubrum*, *Acer*
spicatum, *Aesculus glabra*, *Aesculus sylvatica*, *Albizia julibrissin*, *Amelanchier arborea*,
Annona glabra, *Asimina triloba*, *Avicennia germinans*, *Bursera simaruba*, *Carya alba*,
Carya carolinae-septentrionalis, *Carya ovalis*, *Carya pallida*, *Carya texana*, *Castanea*
mollissima, *Castanea pumila*, *Cladrastis kentukea*, *Conocarpus erectus*, *Cotinus obovatus*,
Crataegus crus-galli, *Crataegus mollis*, *Ficus aurea*, *Fraxinus caroliniana*, *Fraxinus*
quadrangulata, *Ginkgo biloba*, *Gleditsia aquatica*, *Gordonia lasianthus*, *Gymnocladus*
dioicus, *Halesia diptera*, *Juniperus ashei*, *Juniperus coahuilensis*, *Juniperus deppeana*,
Laguncularia racemosa, *Magnolia macrophylla*, *Magnolia tripetala*, *Malus angustifolia*,
Malus coronaria, *Malus ioensis*, *Melaleuca quinquenervia*, *Morus rubra*, *Nyssa biflora*,
Nyssa ogeche, *Osmanthus americanus*, *Persea borbonia*, *Picea engelmannii*, *Picea pungens*,
Pinus ponderosa, *Planera aquatica*, *Populus heterophylla*, *Populus nigra*, *Prunus*
americana, *Prunus nigra*, *Prunus persica*, *Prunus virginiana*, *Quercus ellipsoidalis*, *Quercus*

ilicifolia, Quercus imbricaria, Quercus marilandica, Quercus minima, Quercus montana, Quercus muehlenbergii, Quercus oglethorpensis, Quercus pagoda, Quercus prinoides, Quercus prinus, Quercus similis, Quercus sinuata, Rhizophora mangle, Sabal palmetto, Salix amygdaloides, Salix bebbiana, Salix caroliniana, Salix sepulcralis, Sideroxylon lanuginosum, Sorbus americana, Swietenia mahagoni, Syzygium cumini, Taxodium ascendens, Triadica sebifera, Tsuga caroliniana, Ulmus serotina, Ulmus thomasi, Vernicia fordii

Leaf nitrogen content (91 species):

Abies fraseri, Acer barbatum, Acer floridanum, Acer leucoderme, Acer nigrum, Acer rubrum, Aesculus flava, Ailanthus altissima, Albizia julibrissin, Annona glabra, Avicennia germinans, Bursera simaruba, Carya alba, Carya aquatica, Carya carolinae-septentrionalis, Carya laciniosa, Carya myristiciformis, Carya ovalis, Carya pallida, Castanea mollissima, Castanea pumila, Celtis laevigata, Conocarpus erectus, Cotinus obovatus, Crataegus crus-galli, Crataegus mollis, Ficus aurea, Fraxinus caroliniana, Fraxinus profunda, Fraxinus quadrangulata, Ginkgo biloba, Gleditsia aquatica, Gordonia lasianthus, Gymnocladus dioicus, Halesia carolina, Halesia diptera, Juniperus ashei, Juniperus coahuilensis, Juniperus deppeana, Laguncularia racemosa, Maclura pomifera, Magnolia acuminata, Magnolia tripetala, Magnolia virginiana, Malus angustifolia, Malus ioensis, Melaleuca quinquenervia, Melia azedarach, Nyssa aquatica, Nyssa biflora, Nyssa ogeche, Paulownia tomentosa, Picea engelmannii, Pinus clausa, Pinus glabra, Pinus ponderosa, Pinus pungens, Pinus serotina, Pinus virginiana, Planera aquatica, Populus nigra, Prunus americana, Prunus nigra, Prunus persica, Quercus bicolor, Quercus imbricaria, Quercus lyrata, Quercus margaretta, Quercus margarettiae, Quercus minima, Quercus muehlenbergii,

Quercus oglethorpensis, *Quercus phellos*, *Quercus prinoides*, *Quercus similis*, *Quercus sinuata*, *Rhizophora mangle*, *Sabal palmetto*, *Salix amygdaloides*, *Salix caroliniana*, *Salix sepulcralis*, *Sideroxylon lanuginosum*, *Swietenia mahagoni*, *Triadica sebifera*, *Tsuga caroliniana*, *Ulmus alata*, *Ulmus crassifolia*, *Ulmus pumila*, *Ulmus serotina*, *Ulmus thomasi*, *Vernicia fordii*

Table A2.1. Seed mass values and data sources. Seed mass is measured as the average mass of one seed in mg. Values used in the analysis of FIA and CVS data are listed separately because we calculated different genus-level average trait values for each data set. A dash indicates that a taxon did not occur in the data set. Data sources are in Table A2.4 and ‘derived’ indicates that the value is from a genus-level average or, for hybrids, an average of the two parent taxa.

Taxon	FIA	CVS	Data Source
Abies	7.52	-	derived
Abies balsamea	7.58	-	6
Abies fraseri	7.46	7.46	6
Acer	-	72.46	derived
Acer barbatum	64.80	-	6
Acer floridanum	-	64.80	6
Acer negundo	39.93	39.93	6
Acer nigrum	64.52	64.52	6
Acer pensylvanicum	39.93	39.93	6
Acer platanoides	171.82	-	6
Acer rubrum	19.96	19.96	6
Acer saccharinum	281.73	281.73	6
Acer saccharum	69.36	69.36	6
Acer spicatum	19.96	19.96	6
Aesculus	11173.38	-	derived
Aesculus flava	16199.73	16199.73	6
Aesculus glabra	7820.56	-	6
Aesculus pavia	4346.66	4346.66	4
Aesculus sylvatica	11339.81	11339.81	6
Ailanthus altissima	30.98	30.98	6
Albizia julibrissin	41.24	41.24	6

Alnus glutinosa	1.40	-	6
Amelanchier	5.54	36.32	derived
Amelanchier arborea	5.68	-	6
Amelanchier laevis	-	67.10	4
Amelanchier sanguinea	5.40	-	7
Annona glabra	229.00	-	4
Aralia spinosa	-	3.46	6
Asimina	-	650.78	derived
Asimina triloba	650.78	650.78	6
Avicennia germinans	10120.00	-	5
Betula	0.67	0.98	derived
Betula alleghaniensis	1.02	1.02	6
Betula lenta	0.70	0.70	6
Betula nigra	1.21	1.21	6
Betula papyrifera	0.33	-	6
Betula populifolia	0.11	-	6
Carpinus caroliniana	12.96	12.96	6
Carya	4761.23	5014.34	derived
Carya alba	6213.59	6213.59	6
Carya aquatica	2267.96	2267.96	6
Carya cordiformis	2907.64	2907.64	6
Carya glabra	2267.96	2267.96	6
Carya illinoensis	3489.17	-	6
Carya laciniosa	15119.75	15119.75	6
Carya myristiciformis	3658.00	3658.00	6
Carya ovata	4724.92	4724.92	6
Castanea dentata	4535.92	4535.92	6
Castanea mollissima	6047.90	-	7
Catalpa	22.15	-	derived
Catalpa bignonioides	22.15	22.15	6
Catalpa speciosa	22.15	22.15	6
Celtis	108.36	108.36	derived
Celtis laevigata	206.18	206.18	6
Celtis occidentalis	10.55	10.55	6
Celtis tenuifolia	-	108.36	derived
Cercis canadensis	25.20	25.20	6
Chamaecyparis thyoides	0.99	0.99	6
Chionanthus virginicus	-	252.00	6
Cinnamomum camphora	108.00	-	4
Cladrastis kentukea	37.80	37.80	6
Conocarpus erectus	3.30	-	4
Cornus	-	78.97	derived
Cornus alternifolia	-	56.70	6

Cornus florida	101.25	101.25	6
Cotinus obovatus	8.95	-	4
Crataegus	90.52	36.29	derived
Crataegus [collina + punctata]	-	101.80	derived
Crataegus aestivalis	-	22.68	6
Crataegus alleghaniensis	-	22.68	6
Crataegus aprica	-	36.29	derived
Crataegus berberifolia	-	36.29	derived
Crataegus crus-galli	90.72	90.72	6
Crataegus flava	-	36.29	derived
Crataegus intricata	-	36.29	derived
Crataegus iracunda	-	36.29	derived
Crataegus lacrimata	-	36.29	derived
Crataegus macrosperma	-	36.29	derived
Crataegus margaretta	-	36.29	derived
Crataegus marshallii	-	22.68	6
Crataegus phaenopyrum	-	53.47	4
Crataegus pruinosa	-	50.43	4
Crataegus pulcherrima	-	36.29	derived
Crataegus schuettei	-	36.29	derived
Crataegus spathulata	-	36.29	derived
Crataegus viridis	-	22.68	6
Diospyros	262.90	-	derived
Diospyros virginiana	377.99	377.99	6
Elaeagnus	-	87.91	derived
Elaeagnus angustifolia	87.91	87.91	6
Fagus grandifolia	283.50	283.50	6
Frangula caroliniana	-	171.47	4
Fraxinus	69.29	74.44	derived
Fraxinus americana	45.36	45.36	6
Fraxinus caroliniana	78.97	78.97	6
Fraxinus nigra	46.62	-	6
Fraxinus pennsylvanica	31.68	31.68	6
Fraxinus profunda	141.75	141.75	6
Fraxinus quadrangulata	71.40	-	4
Ginkgo biloba	1522.00	-	4
Gleditsia	156.60	-	derived
Gleditsia aquatica	151.20	151.20	6
Gleditsia triacanthos	162.00	162.00	6
Gordonia lasianthus	3.36	3.36	6
Gymnocladus dioicus	1972.14	-	6
Halesia	292.95	-	derived
Halesia carolina	283.50	283.50	6

Halesia diptera	302.39	-	6
Halesia tetraptera	-	283.50	derived
Ilex	-	10.54	derived
Ilex cassine	-	2.70	3
Ilex decidua	-	9.30	4
Ilex montana	-	12.73	4
Ilex opaca	15.95	15.95	6
Ilex vomitoria	-	12.00	6
Juglans	13229.78	-	derived
Juglans cinerea	15119.75	15119.75	6
Juglans nigra	11339.81	11339.81	6
Juniperus	63.29	-	derived
Juniperus ashei	42.90	-	4
Juniperus deppeana	177.62	-	4
Juniperus virginiana	10.40	10.40	6
Larix	1.55	-	derived
Larix laricina	1.55	-	6
Liquidambar styraciflua	5.53	5.53	6
Liriodendron tulipifera	32.40	32.40	6
Maclura pomifera	64.80	-	6
Magnolia	124.17	-	derived
Magnolia [tripetala + virginiana]	-	161.70	derived
Magnolia acuminata	83.23	83.23	6
Magnolia fraseri	99.69	99.69	6
Magnolia grandiflora	70.87	70.87	6
Magnolia macrophylla	167.80	167.80	4
Magnolia tripetala	263.16	263.16	4
Magnolia virginiana	60.24	60.24	6
Malus	21.76	25.09	derived
Malus coronaria	32.85	32.85	4
Malus ioensis	15.12	-	7
Melaleuca quinquenervia	0.22	-	4
Melia azedarach	348.00	348.00	4
Morus	2.22	1.62	derived
Morus alba	1.93	1.93	6
Morus nigra	3.40	-	4
Morus rubra	1.32	1.32	6
Nyssa	-	422.99	derived
Nyssa aquatica	944.98	944.98	6
Nyssa biflora	189.00	189.00	6
Nyssa ogeche	368.77	-	6
Nyssa sylvatica	135.00	135.00	6

Osmanthus americanus	-	n.d.	no data
Ostrya virginiana	15.12	15.12	6
Oxydendrum arboreum	0.12	0.12	6
Paulownia tomentosa	0.16	0.16	6
Persea	216.00	-	derived
Persea borbonia	216.00	216.00	6
Persea palustris	-	216.00	derived
Picea abies	7.09	-	6
Picea engelmannii	3.36	-	7
Picea glauca	2.43	-	6
Picea mariana	1.12	-	6
Picea pungens	4.28	-	6
Picea rubens	3.24	3.24	6
Pinus	-	22.05	derived
Pinus banksiana	3.46	-	6
Pinus clausa	6.03	6.03	6
Pinus echinata	9.45	9.45	6
Pinus elliotii	31.33	31.33	6
Pinus glabra	9.78	9.78	6
Pinus nigra	17.39	-	6
Pinus palustris	106.98	106.98	6
Pinus ponderosa	37.80	-	6
Pinus pungens	13.26	13.26	6
Pinus resinosa	8.70	-	6
Pinus rigida	7.31	7.31	6
Pinus serotina	8.34	8.34	6
Pinus strobus	16.77	16.77	6
Pinus sylvestris	6.41	-	6
Pinus taeda	24.65	24.65	6
Pinus virginiana	8.70	8.70	6
Platanus occidentalis	2.36	2.36	6
Populus	3.21	-	derived
Populus balsamifera	0.24	-	4
Populus deltoides	1.07	1.07	6
Populus grandidentata	0.15	-	6
Populus heterophylla	2.98	2.98	6
Populus tremuloides	0.14	-	6
Prunus	495.61	195.93	derived
Prunus alleghaniensis	153.78	-	4
Prunus americana	521.37	521.37	6
Prunus angustifolia	-	441.70	4
Prunus avium	187.00	-	4
Prunus caroliniana	-	358.00	2

Prunus injucunda	-	181.44	6
Prunus nigra	93.04	93.04	6
Prunus pensylvanica	31.94	31.94	6
Prunus persica	2792.00	-	4
Prunus serotina	94.50	94.50	6
Prunus umbellata	-	195.93	derived
Prunus virginiana	91.25	91.25	6
Pseudotsuga menziesii	10.78	-	6
Ptelea trifoliata	-	37.80	6
Pyrus calleryana	-	12.90	4
Quercus	2115.43	1693.84	derived
Quercus "waccamawensis"	-	1693.84	derived
Quercus alba	3543.69	3543.69	6
Quercus arkansana	-	1693.84	derived
Quercus austrina	-	1330.00	1
Quercus bicolor	3779.94	-	6
Quercus chapmanii	-	1000.00	1
Quercus coccinea	1930.18	1930.18	6
Quercus ellipsoidalis	1557.93	-	4
Quercus falcata	839.99	839.99	6
Quercus geminata	-	640.00	1
Quercus hemisphaerica	-	740.00	1
Quercus ilicifolia	648.49	648.49	4
Quercus imbricaria	1092.99	1092.99	6
Quercus incana	1000.00	1000.00	4
Quercus laevis	1148.34	1148.34	6
Quercus laurifolia	809.99	809.99	6
Quercus lyrata	3239.95	3239.95	6
Quercus macrocarpa	6047.90	-	6
Quercus marilandica	647.99	647.99	6
Quercus michauxii	5336.38	5336.38	6
Quercus montana	-	4535.92	6
Quercus muehlenbergii	1133.98	1133.98	6
Quercus myrtifolia	-	250.00	1
Quercus nigra	1148.34	1148.34	6
Quercus pagoda	782.06	782.06	6
Quercus palustris	1106.32	1106.32	6
Quercus phellos	981.80	981.80	6
Quercus prinus	4535.92	-	6
Quercus rubra	3628.74	3628.74	6
Quercus shumardii	4535.92	4535.92	6
Quercus sinuata	1567.00	-	4
Quercus stellata	1193.66	1193.66	6

Quercus texana	4785.00	-	4
Quercus velutina	1851.40	1851.40	6
Quercus virginiana	1288.61	1288.61	6
Rhizophora mangle	10100.00	-	4
Robinia	-	18.90	derived
Robinia pseudoacacia	18.90	18.90	6
Sabal palmetto	270.80	270.80	6
Salix	0.14	-	derived
Salix alba	0.12	-	4
Salix amygdaloides	0.17	-	6
Salix bebbiana	0.18	-	4
Salix caroliniana	0.05	0.05	6
Salix nigra	0.18	0.18	6
Salix pyrifolia	0.14	-	derived
Sassafras albidum	90.72	90.72	6
Sideroxylon lanuginosum	79.56	79.56	4
Sideroxylon lycioides	-	90.72	6
Sideroxylon salicifolium	79.56	-	derived
Sideroxylon tenax	-	85.14	derived
Sorbus	16.36	-	derived
Sorbus americana	2.83	2.83	6
Sorbus decora	29.88	-	7
Staphylea	-	56.61	4
Staphylea trifolia	-	41.53	4
Stewartia ovata	-	n.d.	no data
Styphnolobium japonicum	-	118.10	4
Styrax grandifolius	-	56.30	4
Swietenia mahagoni	62.48	-	6
Symplocos tinctoria	-	n.d.	no data
Syzygium cumini	113.40	-	6
Taxodium ascendens	90.72	90.72	6
Taxodium distichum	87.23	87.23	6
Thuja occidentalis	1.31	-	6
Tilia	95.19	95.19	derived
Tilia americana	95.19	95.19	6
Triadica sebifera	133.00	133.00	4
Tsuga	3.85	-	derived
Tsuga canadensis	2.42	2.42	6
Tsuga caroliniana	5.27	5.27	6
Ulmus	14.73	7.18	derived
Ulmus alata	4.07	4.07	6
Ulmus americana	6.40	6.40	6
Ulmus crassifolia	6.77	-	6

Ulmus pumila	6.98	-	6
Ulmus rubra	11.06	11.06	6
Ulmus serotina	3.04	-	6
Ulmus thomasii	64.80	-	6
Vaccinium arboreum	-	1.24	4
Zanthoxylum clava-herculis	-	28.50	4

Table A2.2. Wood density values and data sources. Wood density is measured as the oven dry mass divided by green volume in g/cm^3 . Values used in the analysis of FIA and CVS data are listed separately because we calculated different genus-level average trait values for each data set. A dash indicates that a taxon did not occur in the data set. Data sources are in Table A2.4 and ‘derived’ indicates that the value is from a genus-level average or, for hybrids, an average of the two parent taxa.

Taxon	FIA	CVS	Data Source
Abies	0.42	-	derived
Abies balsamea	0.33	-	1
Acer	-	0.49	derived
Acer negundo	0.42	0.42	1
Acer nigrum	0.52	0.52	1
Acer pensylvanicum	0.44	0.44	1
Acer platanoides	0.53	-	1
Acer rubrum	-	0.49	1
Acer saccharinum	0.44	0.44	1
Acer saccharum	0.56	0.56	1
Aesculus	0.36	-	derived
Aesculus flava	0.35	0.35	1
Aesculus pavia	0.36	0.37	derived
Ailanthus altissima	0.46	0.46	1
Alnus glutinosa	0.42	-	1
Amelanchier	0.76	0.76	derived
Amelanchier arborea	-	0.76	derived
Amelanchier laevis	-	0.76	derived
Amelanchier sanguinea	0.76	-	derived
Aralia spinosa	-	-	1
Asimina	-	0.38	derived
Betula	0.51	0.55	derived
Betula alleghaniensis	0.55	0.55	1
Betula lenta	0.60	0.60	1
Betula nigra	0.49	0.49	1
Betula papyrifera	0.48	-	1
Betula populifolia	0.45	-	1

Carpinus caroliniana	0.58	0.58	1
Carya	0.66	0.67	derived
Carya aquatica	0.61	0.61	1
Carya cordiformis	0.60	0.60	1
Carya glabra	0.66	0.66	1
Carya illinoensis	0.60	-	1
Carya laciniosa	0.62	0.62	1
Carya myristiciformis	0.56	0.56	1
Carya ovata	0.64	0.64	1
Castanea dentata	0.40	0.40	1
Catalpa	0.37	-	derived
Catalpa bignonioides	0.36	0.36	1
Catalpa speciosa	0.38	0.38	1
Celtis	0.48	0.48	derived
Celtis laevigata	0.47	0.47	1
Celtis occidentalis	0.49	0.49	1
Celtis tenuifolia	-	0.48	derived
Cercis canadensis	0.65	0.65	1
Chamaecyparis thyoides	0.31	0.31	1
Chionanthus virginicus	-	n.d.	no data
Cinnamomum camphora	0.62	-	1
Cornus	-	0.64	derived
Cornus alternifolia	-	0.64	derived
Cornus florida	0.64	0.64	1
Crataegus	0.72	0.72	derived
Crataegus [collina + punctata]	-	0.72	derived
Crataegus aestivalis	-	0.72	derived
Crataegus alleghaniensis	-	0.72	derived
Crataegus aprica	-	0.72	derived
Crataegus berberifolia	-	0.72	derived
Crataegus flava	-	0.72	derived
Crataegus intricata	-	0.72	derived
Crataegus iracunda	-	0.72	derived
Crataegus lacrimata	-	0.72	derived
Crataegus macrosperma	-	0.72	derived
Crataegus margaretta	-	0.72	derived
Crataegus marshallii	-	0.72	derived
Crataegus phaenopyrum	-	0.72	derived
Crataegus pruinosa	-	0.72	derived
Crataegus pulcherrima	-	0.72	derived
Crataegus schuettei	-	0.72	derived
Crataegus spathulata	-	0.72	derived
Crataegus viridis	-	0.72	derived
Diospyros	0.67	-	derived
Diospyros virginiana	0.67	0.67	1
Elaeagnus	-	0.46	derived
Elaeagnus angustifolia	0.46	0.46	1
Fagus grandifolia	0.56	0.56	1
Frangula caroliniana	-	n.d.	no data
Fraxinus	0.51	0.51	derived

Fraxinus americana	0.55	0.55	1
Fraxinus nigra	0.45	-	1
Fraxinus pennsylvanica	0.53	0.53	1
Fraxinus profunda	0.48	0.48	1
Gleditsia	0.66	-	derived
Gleditsia triacanthos	0.60	0.60	1
Halesia	0.42	-	derived
Halesia carolina	0.42	0.42	1
Halesia tetraptera	-	0.42	derived
Ilex	-	0.50	derived
Ilex cassine	-	0.50	derived
Ilex decidua	-	0.50	derived
Ilex montana	-	0.50	derived
Ilex opaca	0.50	0.50	1
Ilex vomitoria	-	0.50	derived
Juglans	0.44	-	derived
Juglans cinerea	0.36	0.36	1
Juglans nigra	0.51	0.51	1
Juniperus	0.54	-	derived
Juniperus virginiana	0.44	0.44	1
Larix	0.49	-	derived
Larix laricina	0.49	-	1
Liquidambar styraciflua	0.46	0.46	1
Liriodendron tulipifera	0.40	0.40	1
Maclura pomifera	0.76	-	1
Magnolia	0.42	-	derived
Magnolia [tripetala + virginiana]	-	0.43	derived
Magnolia acuminata	0.44	0.44	1
Magnolia fraseri	0.40	0.40	1
Magnolia grandiflora	0.37	0.37	1
Magnolia virginiana	0.42	0.42	1
Malus	0.71	0.67	derived
Melia azedarach	0.38	0.38	1
Morus	0.59	0.59	derived
Morus alba	0.59	0.59	1
Morus nigra	0.59	-	derived
Nyssa	-	0.48	derived
Nyssa aquatica	0.46	0.46	1
Nyssa sylvatica	0.46	0.46	1
Ostrya virginiana	0.63	0.63	1
Oxydendrum arboreum	0.50	0.50	1
Paulownia tomentosa	0.28	0.28	1
Persea	0.64	-	derived
Persea palustris	-	0.64	derived
Picea abies	0.37	-	1
Picea glauca	0.33	-	1
Picea mariana	0.38	-	1
Picea rubens	0.37	0.37	1
Pinus	-	0.47	derived
Pinus banksiana	0.40	-	1

Pinus clausa	0.46	0.46	1
Pinus echinata	0.47	0.47	1
Pinus elliotii	0.54	0.54	1
Pinus glabra	0.41	0.41	1
Pinus nigra	0.42	-	1
Pinus palustris	0.54	0.54	1
Pinus pungens	0.49	0.49	1
Pinus resinosa	0.41	-	1
Pinus rigida	0.47	0.47	1
Pinus serotina	0.51	0.51	1
Pinus strobus	0.34	0.34	1
Pinus sylvestris	0.39	-	1
Pinus taeda	0.47	0.47	1
Pinus virginiana	0.45	0.45	1
Platanus occidentalis	0.46	0.46	1
Populus	0.34	-	derived
Populus balsamifera	0.31	-	1
Populus deltoides	0.37	0.37	1
Populus grandidentata	0.36	-	1
Populus tremuloides	0.35	-	1
Prunus	0.45	0.45	derived
Prunus alleghaniensis	0.45	-	derived
Prunus angustifolia	-	0.45	derived
Prunus avium	0.47	-	1
Prunus caroliniana	-	0.45	derived
Prunus injucunda	-	0.45	derived
Prunus pensylvanica	0.36	0.36	1
Prunus serotina	0.47	0.47	1
Prunus umbellata	-	0.45	derived
Pseudotsuga menziesii	0.43	-	1
Ptelea trifoliata	-	n.d.	no data
Pyrus calleryana	-	n.d.	no data
Quercus	0.65	0.66	derived
Quercus "waccamawensis"	-	0.66	derived
Quercus alba	0.60	0.60	1
Quercus arkansana	-	0.66	derived
Quercus austrina	-	0.75	1
Quercus bicolor	0.66	-	1
Quercus chapmanii	-	0.78	1
Quercus coccinea	0.60	0.60	1
Quercus falcata	0.52	0.52	1
Quercus geminata	-	0.87	1
Quercus hemisphaerica	-	0.69	1
Quercus incana	0.71	0.71	1
Quercus laevis	0.64	0.64	1
Quercus laurifolia	0.56	0.56	1
Quercus lyrata	0.57	0.57	1
Quercus macrocarpa	0.58	-	1
Quercus margaretta	-	0.76	1
Quercus margarettiae	0.76	-	1

Quercus michauxii	0.60	0.60	1
Quercus myrtifolia	-	0.81	1
Quercus nigra	0.56	0.56	1
Quercus palustris	0.58	0.58	1
Quercus phellos	0.56	0.56	1
Quercus rubra	0.56	0.56	1
Quercus shumardii	0.64	0.64	1
Quercus stellata	0.60	0.60	1
Quercus texana	0.64	-	derived
Quercus velutina	0.56	0.56	1
Quercus virginiana	0.80	0.80	1
Robinia	-	0.66	derived
Robinia pseudoacacia	0.66	0.66	1
Salix	0.35	-	derived
Salix alba	0.28	-	1
Salix nigra	0.36	0.36	1
Salix pyrifolia	0.35	-	derived
Sassafras albidum	0.42	0.42	1
Sideroxylon lycioides	-	0.67	derived
Sideroxylon salicifolium	0.81	-	derived
Sideroxylon tenax	-	0.67	derived
Sorbus	0.54	-	derived
Sorbus decora	0.54	-	derived
Staphylea	-	n.d.	no data
Staphylea trifolia	-	n.d.	no data
Stewartia ovata	-	n.d.	no data
Styphnolobium japonicum	-	n.d.	no data
Styrax grandifolius	-	n.d.	no data
Symplocos tinctoria	-	n.d.	no data
Taxodium distichum	0.42	0.42	1
Thuja occidentalis	0.29	-	1
Tilia	0.32	0.32	derived
Tilia americana	0.32	0.32	1
Tsuga	0.38	-	derived
Tsuga canadensis	0.38	0.38	1
Ulmus	0.57	0.51	derived
Ulmus alata	0.60	0.60	1
Ulmus americana	0.46	0.46	1
Ulmus crassifolia	0.64	-	3
Ulmus pumila	0.55	-	1
Ulmus rubra	0.48	0.48	1
Vaccinium arboreum	-	n.d.	no data
Zanthoxylum clava-herculis	-	n.d.	no data

Table A2.3. Leaf nitrogen values and data sources. Leaf nitrogen content is measured as the percent of dry leaf weight. Values used in the analysis of FIA and CVS data are listed separately because we calculated different genus-level average trait values for each data set. A

dash indicates that a taxon did not occur in the data set. Data sources are in Table A2.4 and

‘derived’ indicates that the value is from a genus-level average or, for hybrids, an average of the two parent taxa.

Taxon	FIA	CVS	Data Source
Abies	1.43	-	derived
Abies balsamea	1.29	-	33
Acer	-	2.11	derived
Acer negundo	2.50	2.50	37
Acer pensylvanicum	1.90	1.90	37
Acer platanoides	1.62	-	37
Acer rubrum	-	1.84	37
Acer saccharinum	2.60	2.60	25
Acer saccharum	1.85	1.85	37
Acer spicatum	2.49	2.49	33
Aesculus	2.11	-	derived
Aesculus glabra	2.08	-	22
Aesculus pavia	2.11	2.02	derived
Aesculus sylvatica	1.90	1.90	10
Alnus glutinosa	3.54	-	37
Amelanchier	1.80	1.80	derived
Amelanchier arborea	1.80	1.80	8
Amelanchier laevis	-	1.80	derived
Amelanchier sanguinea	1.80	-	derived
Aralia spinosa	-	n.d.	no data
Asimina	-	3.50	derived
Asimina triloba	3.50	3.50	1
Betula	2.09	2.18	derived
Betula alleghaniensis	2.20	2.20	20
Betula lenta	2.05	2.05	33
Betula nigra	2.28	2.28	37
Betula papyrifera	2.20	-	37
Betula populifolia	1.74	-	37
Carpinus caroliniana	2.00	2.00	37
Carya	2.05	2.03	derived
Carya cordiformis	2.60	2.60	37
Carya glabra	1.66	1.66	37
Carya illinoensis	2.05	-	33
Carya ovata	1.98	1.98	37
Carya texana	2.19	-	derived
Castanea dentata	2.59	2.59	37
Catalpa	1.73	-	derived
Catalpa bignonioides	1.60	1.60	5
Catalpa speciosa	1.85	1.85	26
Celtis	2.39	2.39	derived
Celtis occidentalis	2.39	2.39	37
Celtis tenuifolia	-	2.39	derived
Cercis canadensis	1.92	1.92	34

Chamaecyparis thyoides	0.74	0.74	23
Chionanthus virginicus	-	1.76	37
Cinnamomum camphora	1.60	-	25
Cladrastis kentukea	1.50	1.50	13
Cornus	-	1.55	derived
Cornus alternifolia	-	1.70	37
Cornus florida	1.40	1.40	37
Crataegus	1.73	1.73	derived
Crataegus [collina + punctata]	-	1.73	derived
Crataegus aestivalis	-	1.73	derived
Crataegus alleghaniensis	-	1.73	derived
Crataegus aprica	-	1.73	derived
Crataegus berberifolia	-	1.73	derived
Crataegus flava	-	1.73	derived
Crataegus intricata	-	1.73	derived
Crataegus iracunda	-	1.73	derived
Crataegus lacrimata	-	1.73	derived
Crataegus macrosperma	-	1.73	derived
Crataegus margaretta	-	1.73	derived
Crataegus marshallii	-	1.73	derived
Crataegus phaenopyrum	-	1.73	derived
Crataegus pruinosa	-	1.73	derived
Crataegus pulcherrima	-	1.73	derived
Crataegus schuettei	-	1.73	derived
Crataegus spathulata	-	1.73	derived
Crataegus viridis	-	1.73	derived
Diospyros	2.82	-	derived
Diospyros virginiana	2.82	2.82	22
Elaeagnus	-	3.30	derived
Elaeagnus angustifolia	3.30	3.30	7
Fagus grandifolia	2.30	2.30	20
Frangula caroliniana	-	n.d.	no data
Fraxinus	2.12	2.03	derived
Fraxinus americana	2.10	2.10	37
Fraxinus nigra	2.10	-	37
Fraxinus pennsylvanica	1.80	1.80	37
Gleditsia	2.75	-	derived
Gleditsia triacanthos	2.80	2.80	25
Halesia	1.98	-	derived
Halesia tetraptera	-	1.98	derived
Ilex	-	0.90	derived
Ilex cassine	-	0.73	35
Ilex decidua	-	0.90	derived
Ilex montana	-	1.30	5
Ilex opaca	1.12	1.12	37
Ilex vomitoria	-	0.45	17
Juglans	2.78	-	derived
Juglans cinerea	2.60	2.60	37
Juglans nigra	2.96	2.96	26
Juniperus	2.25	-	derived

Juniperus virginiana	1.64	1.64	26
Larix	2.01	-	derived
Larix laricina	2.01	-	33
Liquidambar styraciflua	1.45	1.45	37
Liriodendron tulipifera	2.13	2.13	37
Magnolia	1.32	-	derived
Magnolia [tripetala + virginiana]	-	1.04	derived
Magnolia fraseri	2.29	2.29	37
Magnolia grandiflora	1.34	1.34	37
Magnolia macrophylla	2.04	2.04	22
Malus	1.62	1.62	derived
Malus coronaria	1.62	1.62	33
Morus	2.17	2.17	derived
Morus alba	2.03	2.03	37
Morus nigra	2.17	-	derived
Morus rubra	2.31	2.31	26
Nyssa	-	1.78	derived
Nyssa sylvatica	1.84	1.84	37
Osmanthus americanus	-	0.80	4
Ostrya virginiana	2.20	2.20	37
Oxydendrum arboreum	1.86	1.86	37
Persea	1.64	-	derived
Persea borbonia	1.64	1.64	37
Persea palustris	-	1.64	derived
Picea abies	1.19	-	37
Picea glauca	1.20	-	37
Picea mariana	1.02	-	37
Picea pungens	1.33	-	24
Picea rubens	1.10	1.10	20
Pinus	-	1.24	derived
Pinus banksiana	1.24	-	26
Pinus echinata	1.07	1.07	15
Pinus elliotii	1.11	1.11	19
Pinus nigra	1.18	-	37
Pinus palustris	0.82	0.82	37
Pinus resinosa	1.17	-	26
Pinus rigida	1.16	1.16	37
Pinus strobus	1.35	1.35	37
Pinus sylvestris	1.39	-	26
Pinus taeda	1.50	1.50	27
Platanus occidentalis	2.07	2.07	22
Populus	1.91	-	derived
Populus balsamifera	1.90	-	37
Populus deltoides	2.36	2.36	26
Populus grandidentata	2.50	-	37
Populus heterophylla	2.40	2.40	37
Populus tremuloides	1.94	-	37
Prunus	2.50	2.17	derived
Prunus alleghaniensis	2.50	-	derived
Prunus angustifolia	-	0.32	17

Prunus avium	1.80	-	15
Prunus caroliniana	-	1.25	4
Prunus injucunda	-	2.17	derived
Prunus pensylvanica	2.40	2.40	37
Prunus serotina	2.68	2.68	37
Prunus umbellata	-	2.17	derived
Prunus virginiana	2.80	2.80	37
Pseudotsuga menziesii	1.08	-	37
Ptelea trifoliata	-	n.d.	no data
Pyrus calleryana	-	1.95	24
Quercus	1.63	1.59	derived
Quercus "waccamawensis"	-	1.59	derived
Quercus alba	2.20	2.20	37
Quercus arkansana	-	1.59	derived
Quercus austrina	-	1.94	37
Quercus chapmanii	-	1.39	37
Quercus coccinea	1.73	1.73	37
Quercus ellipsoidalis	2.10	-	26
Quercus falcata	1.47	1.47	37
Quercus geminata	-	0.87	37
Quercus hemisphaerica	-	1.69	11
Quercus ilicifolia	1.40	1.40	33
Quercus incana	0.95	0.95	37
Quercus laevis	1.53	1.53	37
Quercus laurifolia	1.32	1.32	37
Quercus macrocarpa	2.36	-	37
Quercus marilandica	1.38	1.38	15
Quercus michauxii	1.59	1.59	33
Quercus montana	-	1.50	37
Quercus myrtifolia	-	1.02	37
Quercus nigra	1.29	1.29	37
Quercus pagoda	1.44	1.44	33
Quercus palustris	2.33	2.33	22
Quercus prinus	1.50	-	37
Quercus rubra	2.01	2.01	37
Quercus shumardii	1.68	1.68	37
Quercus stellata	1.73	1.73	37
Quercus texana	0.99	-	13
Quercus velutina	1.38	1.38	37
Quercus virginiana	1.32	1.32	37
Robinia	-	2.97	derived
Robinia pseudoacacia	2.97	2.97	37
Salix	1.99	-	derived
Salix alba	1.64	-	6
Salix bebbiana	1.67	-	21
Salix nigra	2.50	2.50	37
Salix pyrifolia	1.99	-	derived
Sassafras albidum	1.90	1.90	8
Sideroxylon lycioides	-	2.44	derived
Sideroxylon salicifolium	2.44	-	derived

Sideroxylon tenax	-	2.44	derived
Sorbus	2.60	-	derived
Sorbus americana	2.60	2.60	33
Sorbus decora	2.60	-	derived
Staphylea	-	n.d.	no data
Staphylea trifolia	-	n.d.	no data
Stewartia ovata	-	n.d.	no data
Styphnolobium japonicum	-	1.60	13
Styrax grandifolius	-	n.d.	no data
Symplocos tinctoria	-	2.40	8
Syzygium cumini	2.01	-	37
Taxodium ascendens	1.06	1.06	2
Taxodium distichum	1.19	1.19	37
Thuja occidentalis	1.28	-	26
Tilia	2.88	2.88	derived
Tilia americana	2.88	2.88	37
Tsuga	0.99	-	derived
Tsuga canadensis	0.99	0.99	37
Ulmus	2.17	2.18	derived
Ulmus americana	2.00	2.00	37
Ulmus rubra	2.50	2.50	37
Vaccinium arboreum	-	1.21	37
Zanthoxylum clava-herculis	-	n.d.	no data

Table A2.4. Sources of trait data.

Seed Mass	
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Density	
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Leaf Nitrogen

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Appendix 3. Analyses of alternative phylogenetic diversity metrics and distances.

Our analyses of phylogenetic diversity (PD) of communities along water deficit and soil nutrient availability gradients indicated that PD, as measured by the mean pair-wise phylogenetic distance (MPD) between the taxa in a community, was strongly influenced by the relative proportion of angiosperm and gymnosperm taxa. Therefore, for the CVS data set, we also evaluated the mean nearest taxon distance (MNTD; Webb 2000) which may be less sensitive to the angiosperm-gymnosperm split. Since the distance between any angiosperm species and any gymnosperm species was more than 80% greater than the largest distance between any two angiosperm species, we also calculated PD metrics on a log-transformed distance matrix to attempt to ameliorate the effects of the angiosperm-gymnosperm bifurcation.

All metrics were strongly influenced by the relative proportion of angiosperm and gymnosperm taxa and using different metrics did not qualitatively influence the relationships between PD and the two stress gradients (Figure A3.1). For all metrics, using log-transformed distances weakened correlations between PD and the stress gradients, but did not alter the direction of these relationships.

We also calculated MPD only among the angiosperm taxa in each plot to determine whether changes in PD within a taxonomically restricted subset of each community exhibited patterns consistent with the stress-dominance hypothesis. Patterns of PD along stress gradients were different among angiosperms than among all taxa in the community (Figure A3.2).

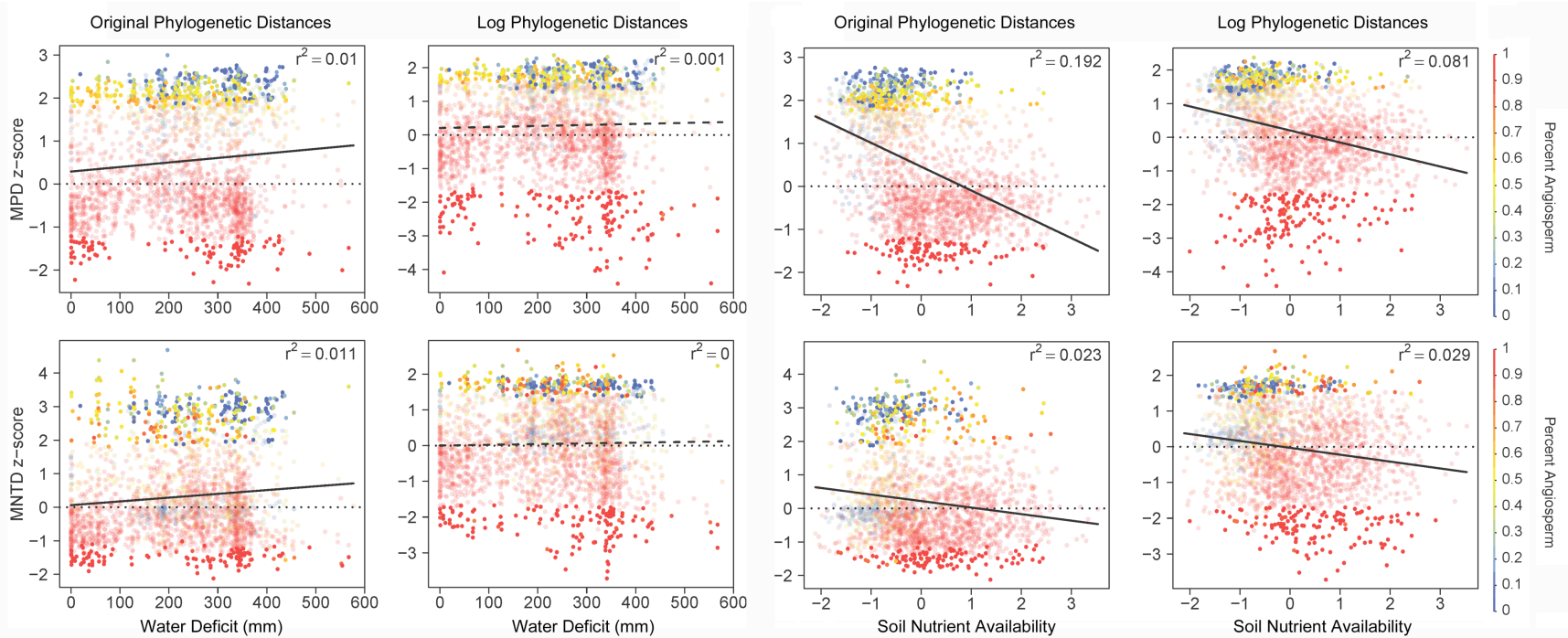


Figure A3.1. Effect of using different phylogenetic diversity metrics and phylogenetic distances on the relationship between stress gradients and phylogenetic diversity in CVS plots. Mean pair-wise phylogenetic distance (MPD) and mean nearest taxon distance (MNTD) were calculated from the original distances between taxa from the phylogeny as well as from log-transformed distances. The z-scores of these metrics are plotted on the y-axis against the two stress gradients, climatic water deficit and soil nutrient availability. Positive z-score values indicate higher diversity and negative values indicate lower diversity relative to a null model of random community assembly with respect to phylogenetic relationships. Opaque points are above the 95th or below the 5th

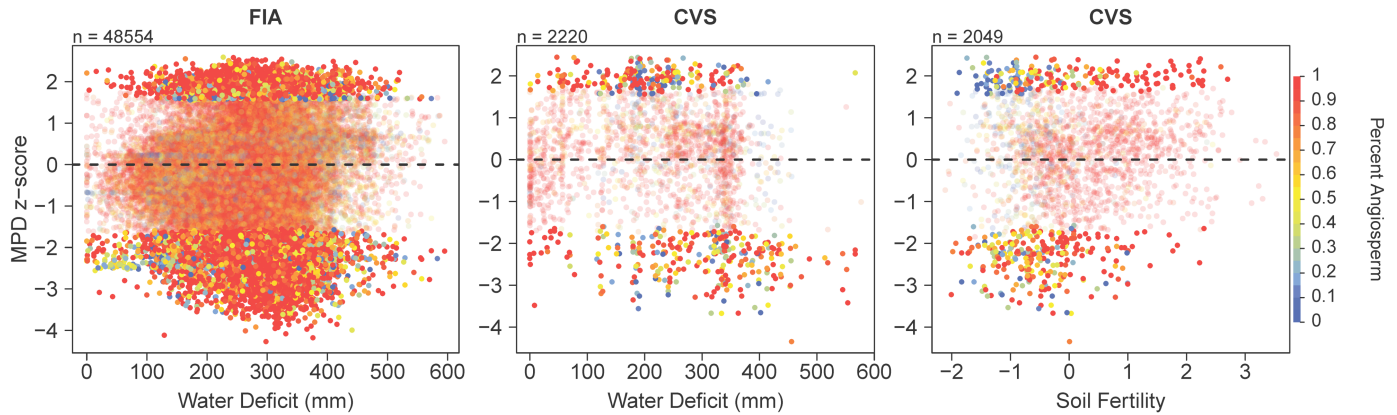


Figure A3.2. Phylogenetic diversity (MPD-mean pairwise distance) for angiosperm taxa occurring in FIA and CVS plots along stress gradients. Axes and points are as described in Figure A3.1. Plotting angiosperms only eliminated the previously observed negative correlation between phylogenetic diversity and soil nutrient availability in the CVS plots, suggesting phylogenetic diversity is being driven primarily by the deep basal split between angiosperms and gymnosperms on the phylogeny. Points are still colored by percent angiosperm abundance for visual reference of plots that contain gymnosperms.

Appendix 4. Model selection table showing AIC values for all models.

Table A4.1. AIC values of models between seed mass, leaf nitrogen, and wood density mean trait and trait diversity values and water deficit and soil nutrient availability. Linear and power models were fit to all combinations of mean trait, trait diversity, and environmental stress variables, while quadratic models were fit to only those combinations where a unimodal peak was hypothesized. Values in bold indicate the model chosen for inference.

Predictor	Response	Dataset	Linear	Power	Quadratic
Water deficit	Seed mass	FIA	132778.8	133033.9	
		CVS	3597.7	3623.0	
	Wood density	FIA	-124392.9	123120.2	
		CVS	-6203.0	-6088.9	
	Nitrogen %	FIA	24041.5	24419.1	
		CVS	2096.3	2113.2	
	Seed mass diversity	FIA	123193.5	123207.6	122582.7
		CVS	6446.6	6630.3	6442.3
	Wood density diversity	FIA	91701.8	91906.9	91675.0
		CVS	4789.2	4793.5	4766.1
	Nitrogen % diversity	FIA	91738.4	91742.1	91683.8
		CVS	5026.9	5053.9	5025.8
	PD	FIA	157861.2	157850.6	157024.5
		CVS	7452.6	7430.8	7418.5
Soil nutrient availability	Seed mass	CVS	3276.6	3272.8	
	Wood density	CVS	-5659.0	-5673.4	
	Nitrogen %	CVS	1281.4	1220.6	
	Seed mass diversity	CVS	6153.5	6155.2	6096.4
	Wood density diversity	CVS	4465.3	4451.6	4421.2
	Nitrogen % diversity	CVS	4691.6	4684.7	4649.0
	PD	CVS	6416.5	6608.1	6348.9

Appendix 5. Comparison of community-weighted mean trait values and trait diversity between xeric and mesic FIA plots.

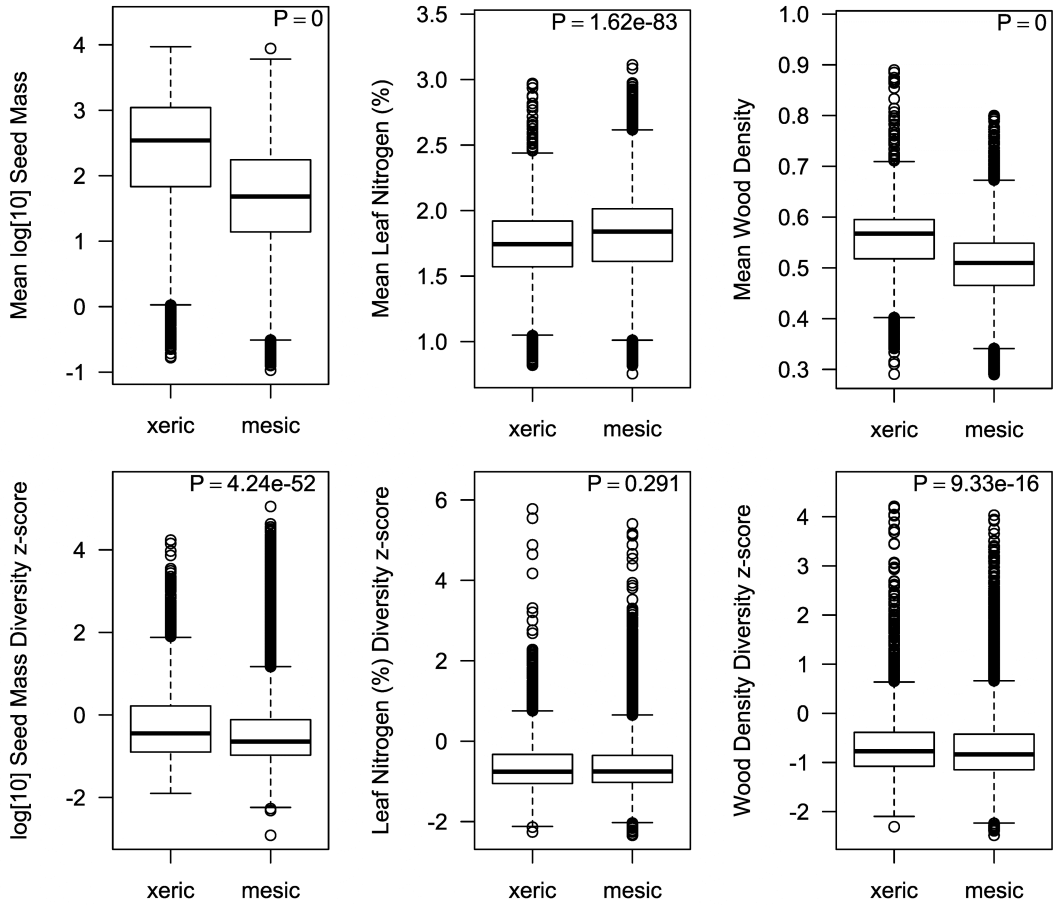


Figure A5.1. Boxplots of community-weighted mean trait values and trait diversity between xeric and mesic FIA plots. P-values in the upper right corner of panels test whether group means are different using a Mann-Whitney U test. Xeric plots have higher wood density, higher seed mass and lower leaf nitrogen content than mesic plots. There are only slight differences in trait diversity between xeric and mesic plots.

Appendix 6. Environmentally constrained null models

Using a subset of the FIA data (8,426 plots in North Carolina, South Carolina, Georgia, and Florida) and the entire CVS data set, we recalculated trait diversity z-scores using environmentally constrained null models. For the CVS data set, we defined environmental niches for each species as the range of water deficit (D) and soil fertility values within which each species was observed to occur in our data set. When shuffling species across sites in the null model, only species whose niches matched the environmental conditions at each site were permitted to occur. For the FIA data we used five environmental variables to define species niches (D, minimum temperature, annual precipitation, precipitation during the driest 3-month period, and the xeric-mesic-hydric site classification assigned by the FIA survey crew), where the three additional variables were derived from WorldClim 10 arc-minute bioclimatic variables (<http://www.worldclim.org/current>).

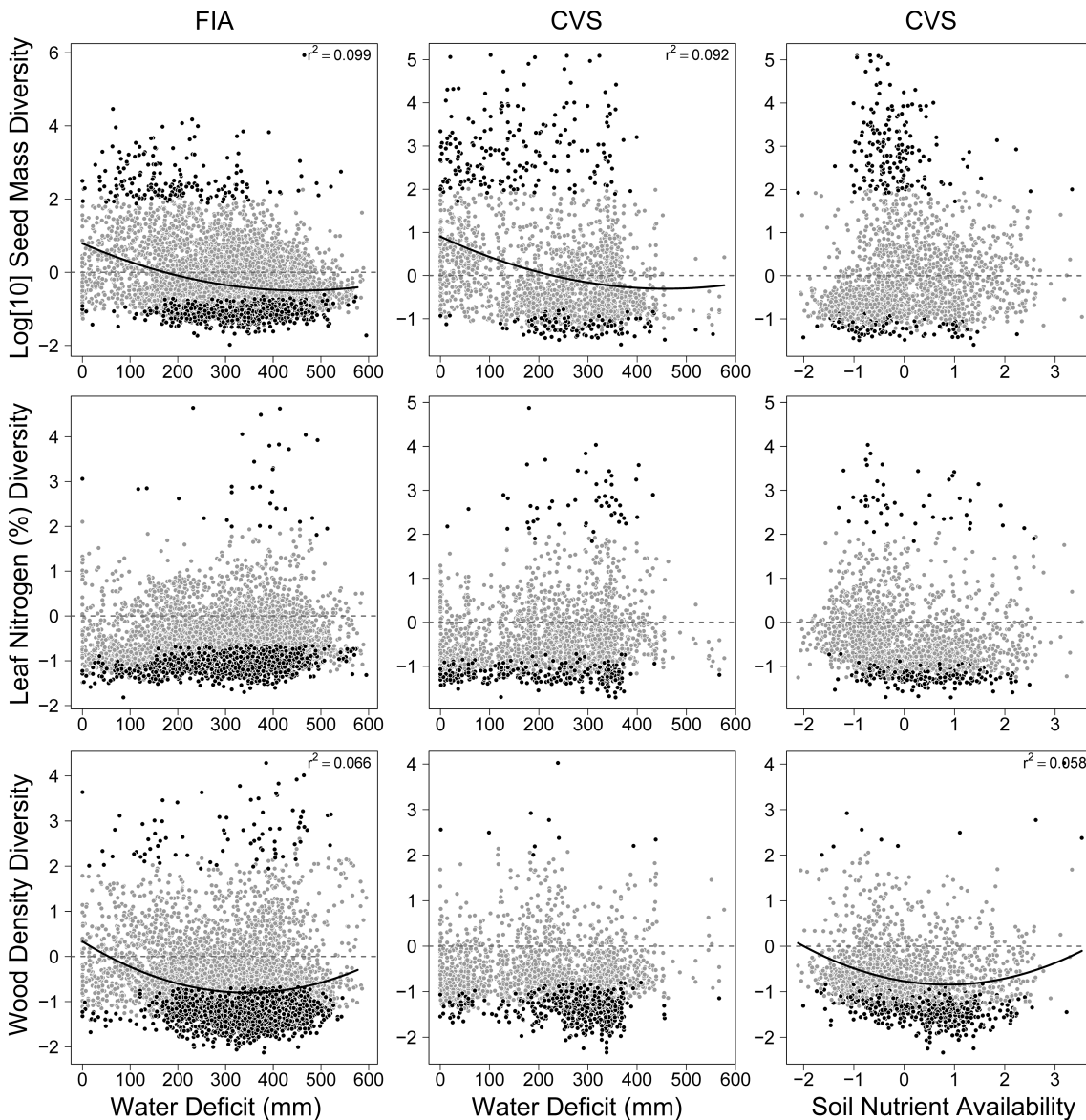
Using environmentally constrained null models generally decreased the number of underdispersed plots observed, but did not alter the lack of relationships between environmental variables and trait diversity.

Table A6.1. Change in the proportion of CVS and FIA plots with significantly overdispersed and underdispersed trait diversity when using an environmentally constrained null model compared to an unconstrained null model. Overdispersed plots have trait diversity above the 95th percentile of the null distribution, underdispersed plots are below the 5th percentile, and random plots are between the 5th and 95th percentiles.

	Overdispersed %		Random %		Underdispersed %	
	Original	Constrained	Original	Constrained	Original	Constrained
FIA Wood density diversity	0.9	1.0	61.3	70.5	37.8	28.5

CVS Wood density diversity	0.5	0.4	70.9	77.3	28.6	22.3
FIA Leaf nitrogen diversity	0.5	0.4	78.9	86.7	20.6	12.9
CVS Leaf nitrogen diversity	1.7	2.3	86.4	85.4	11.9	12.3
FIA Seed mass diversity	1.3	2.3	82.6	89.3	16.1	8.4
CVS Seed mass diversity	7.5	9.0	88.9	85.8	3.6	5.2

Figure A6.1. Relationship between trait diversity and environmental variables under constrained null models. Compare to Figures 4 and 5. Note that FIA data in this figure only contains plots from four states.



percentile of the null distribution and points are colored by the proportion of the community that is comprised of angiosperm taxa.

Solid regression lines are shown for relationships with $r^2 > 0.05$, whereas dashed lines indicate $r^2 \geq 0.05$.