

Plant geography upon the basis of functional traits: an example from eastern North American trees

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Abstract. Plant geographers have sought for decades to describe and predict the geographic distribution of vegetation types on the basis of plant function and its relationship with the abiotic environment. Traditionally this has been accomplished using categorical representations such as plant functional types. Increasingly, plant functional ecologists have sought to refine categorical functional types via quantitative functional traits in order to understand the ecological implications of trade-offs in plant form and function. Fewer works have focused upon testing whether commonly measured functional traits enhance our understanding of plant biogeography broadly and the geographic distribution of vegetation types in particular. Here we combine a continental-scale forest inventory data set containing 18 111 plots with a plant functional trait data set to ask: (1) Is there a strong relationship between the abiotic environment and the distribution of functional trait values in forest inventory plots? And (2) can different Holdridge life zones be distinguished upon the basis of their functional trait distributions? The results show geographic patterns of functional trait distributions that are often strongly correlated with climate and also show that the Holdridge life zones in the study area can be differentiated using a combination of functional traits.

Key words: *functional ecology; Holdridge life zones; leaf percent nitrogen; maximum height; precipitation; seed mass; temperature; wood density.*

INTRODUCTION

The geographic distributions of species result from the interplay of historical contingency and species interactions with the abiotic and biotic environment. Plant geographers and plant ecologists have advocated a functional approach to studying the distribution and coexistence of plant species for over a century (e.g., Schimper 1898). This approach argues that by examining the function of a plant and the way that function relates to the environment, a mechanistic and predictive framework for studying the distribution and coexistence of species can be achieved. Thus, a major theme in plant ecology has been to quantify and define plant functional strategies (Grime 1977, Westoby et al. 2002). The concept of plant functional strategies is useful in that it compares the functional strategy of a species in relation to a global range of alternative strategies. Thus quantifying the plant traits that represent the functional strategies of each species in a community provides a refined insight into the geographic distribution of species (McGill et al. 2006).

Over the past decade attempts to identify the key axes or dimensions of plant function that confer their functional strategies have intensified and resulted in a

list of a limited number of plant traits, many of which are easily measurable, that can be used to quantitatively represent the functional strategies of plant species (Westoby et al. 2002). This widely recognized suite of plant functional traits has led to a number of initial broad-scale investigations into topics ranging from the evolution of plant functional traits (e.g., Moles et al. 2005, Swenson and Enquist 2007) to species coexistence in diverse tropical communities (e.g., Swenson and Enquist 2009).

Despite this progress, there remain several outstanding challenges that require the integration of large trait and plant occurrence data sets. One clear challenge has been to produce maps that depict the geographic distribution of continuous plant functional trait values. Such maps could be used to test ecological hypotheses, further our understanding of ecosystem function, and refine the next generation of global vegetation models (Reich 2005). A related challenge is to understand whether plant functional trait distributions within and across vegetation types or life zones can be predicted using the distribution of functional trait values found in a community. For example, are community functional trait distributions indicative of the Holdridge life zones (Holdridge 1979) in which they reside? If so, this would allow researchers to predict the functional composition of life zones across continents and how that composition may be altered by climatic shifts.

Manuscript received 22 September 2009; revised 14 January 2010; accepted 22 March 2010. Corresponding Editor: E. M. Bruna.

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The following study aims to address both of these challenges by combining a continental scale forest inventory data set with a functional trait data set. Specifically, here we merge these data sets to (1) map the spatial distribution of plant functional trait distributions in eastern North American tree communities at two spatial scales, (2) quantify the relationship between climate and community functional trait distributions, and (3) test whether the plant functional trait distribution in a community can predict the Holdridge life zone (Holdridge 1979) in which it is found. We use the widely known, often implemented and abiotically defined Holdridge life zone classification to provide an initial test of how well functional trait distributions can differentiate life zones on a continental scale.

METHODS

Forest Inventory plot data

Geo-referenced occurrences of individual tree plots were taken from plot level data (i.e., no seedling plots) produced by the United States Department of Agriculture Forest Inventory and Analysis Program (FIA; FIA Database Description and User's Guide Version 3.0, *available online*).⁴ Each FIA plot consists of four circular subplots 1/24 acre (0.017 ha) in area where all stems five inches (12.7 cm) in diameter or greater are inventoried. Within each of the subplots is a 1/300 acre (0.001 ha) "microplot" that inventories all stems 1 inch (2.54 cm) in diameter or greater. This study utilized all tree stems from both the subplot and microplots. Data were taken from the 2006 inventory year, with the exception of Louisiana, which were taken from 2005. We used only plots east of 95° E (roughly the meridian from Houston, Texas to central Minnesota, USA). Further, we only used plots where all species in the plot could be assigned a species-level or generic-level trait mean for the four traits. Overall, this study utilized 18 111 individual FIA plots in 33 states containing 660 246 individual trees representing 88 genera, 247 species, and 35 additional species codes where the stem was only identified to the generic-level. The geographic locations of the FIA plots are "fuzzed" by the FIA to a location typically within 0.5 miles (0.8 km) of the actual location to protect the integrity of the plot. This fuzzing of coordinates is therefore of little consequence to studies on the spatial scales presented in this work.

Functional trait data

A series of four functional traits were selected for this study: maximum height, seed mass, leaf nitrogen content, and wood density. Leaf nitrogen content (leaf %N) was used to represent the leaf economics spectrum where plants fall along a continuum of low construction costs, high photosynthetic rates, high nutrient content and short leaf life spans to high construction costs, low

photosynthetic rates, low nutrient content, and long leaf life spans (Wright et al. 2004). Wood density was used to represent the wood economics spectrum (Chave et al. 2009) where a species falls along a continuum between high volumetric growth rates, low construction costs, and high mortality rates vs. low volumetric growth rates, high construction costs, and low mortality rates (Swenson and Enquist 2007, Chave et al. 2009). Maximum height was used to indicate the adult light niche (Moles et al. 2009) and seed mass was used to represent a trade-off between producing many small seeds per unit energy vs. producing a few large seeds per unit energy (Moles and Westoby 2006). These traits were selected as they provide coarse indicators of plant functional strategy, they represent multiple axes of functional differentiation as described above and because several studies have previously found strong linkages between these traits and the abiotic environment (e.g., Wright et al. 2004, Moles et al. 2005, Swenson and Enquist 2007). They were also selected because they are often quantified by plant functional ecologists making them more readily found in the literature than other plant traits. Despite the benefits of using these four traits, ideally other equally or more important plant traits and measurements of plant physiology (e.g., photosynthetic rate, hydraulic conductance), that are not as widely reported across the eastern United States tree flora, would be included in this study, but for the time being we are limited to this small list. Thus, we do not assert that the four traits utilized are necessarily the best traits for predicting the geographic distribution of vegetation types. Rather, they represent a portion of the best candidates for this purpose that also happen to be widely available in the literature.

The functional trait data for this study were gleaned from literature sources and large publicly available trait databases (Appendix A). When multiple trait values were reported for a species, a mean value was calculated and used for all subsequent analyses. All subspecies or varieties were assigned the mean trait value for the binomial. Thus, intra-specific variation in response to the environment was ignored in this study. The omission of this variation likely resulted in a bias towards weaker trait–climate relationships. Future work will be needed to either fill this data gap and/or to model in this potentially important information. Species-specific mean values were obtained for 100%, 82.6%, 98.8%, and 94.7% of the species for maximum height, leaf %N, seed mass, and wood density, respectively. When no species-specific values were available or when an individual stem was only identified to the generic level, we calculated the mean of the trait values reported for congeneric species. Previous studies have found little variance in congeneric trait values for some traits (seed mass, Moles et al. 2005; wood density, Swenson and Enquist 2007), but even for these traits congeneric means will hide detailed information that may be important (Hulshof and Swenson 2010). We do,

⁴ (<http://fia.fs.fed.us/>)

TABLE 1. The Pearson correlation coefficients for climatic variables and the four moments of the function trait distribution in the 18 111 U.S. Department of Agriculture Forest Inventory and Analysis Program (FIA) plots.

Statistic	Precipitation				Temperature			
	Annual	Wettest month	Driest month	Seasonality	Mean annual	Maximum	Minimum	Seasonality
Maximum height								
Mean	0.26*	0.16*	0.28*	-0.25*	0.27*	0.26*	0.28*	-0.25*
Variance	0.06	0.05	0.05	-0.03	0.09	0.12*	0.08	-0.06
Skew	-0.14*	-0.06	-0.17*	0.17*	-0.09	-0.11*	-0.09	0.09
Kurtosis	0.18*	0.06	0.25*	-0.26*	0.11*	0.11*	0.12*	-0.13*
Leaf nitrogen								
Mean	-0.32*	-0.40*	-0.19*	0.02	-0.31*	-0.23*	-0.32*	0.36*
Variance	-0.02	-0.05	0.02	-0.04	-0.07	-0.12*	-0.05	0.01
Skew	0.06	0.01	0.10*	-0.09	0.07	0.09	0.07	-0.06
Kurtosis	0.21*	0.12*	0.25*	-0.23*	0.15*	0.11*	0.16*	-0.19*
Seed mass								
Mean	0.40*	0.30*	0.39*	-0.36*	0.51*	0.53*	0.51*	-0.46*
Variance	-0.16*	-0.17*	-0.12*	0.09	-0.17*	-0.12*	-0.18*	0.20*
Skew	-0.01	-0.01	-0.01	0.02	0.03	0.03	0.02	-0.01
Kurtosis	0.11*	0.02	0.18*	-0.20*	0.03	0.02	0.05	-0.07
Wood density								
Mean	0.40*	0.31*	0.38*	-0.33*	0.48*	0.48*	0.48*	-0.44*
Variance	-0.06	-0.02	-0.05	0.06	-0.09	-0.13*	-0.07	0.02
Skew	0.15*	0.22*	0.05	0.06	0.21*	0.18*	0.19*	-0.19*
Kurtosis	0.12*	0.04	0.18*	-0.20*	0.10*	0.10*	0.11*	-0.10*

* $P < 0.05$.

however, point out that those species for which species-level trait values were unavailable usually represented the rarest species in the database generally occurring in less than 50 plots and in low abundance. A full list of the trait data sources utilized for this study is provided in Appendix A.

Analyses

In each of the 18 111 FIA plots we generated a community trait distribution for each functional trait. This was done using both presence-absence weighting (i.e., equal weighting of the species) and abundance weighting where abundance was defined as the number of individual stems in the FIA plot. From these presence-absence weighted and abundance weighted distributions we determined the four moments of the trait distribution for each trait and we quantified the correlation between the first four moments of the trait distribution (i.e., mean, variance, skew, and kurtosis) in plots and eight climatic variables: mean annual temperature, maximum temperature, minimum temperature, temperature seasonality (standard deviation of monthly mean temperature), annual precipitation, precipitation in the wettest month, precipitation in the driest month, and precipitation seasonality (coefficient of variation in the monthly precipitation level). Specifically, for each FIA plot, we extracted the climatic values for that plot and calculated the four moments of the trait distribution for each trait. Next, we quantified the correlation between the moments of the distribution and the climatic variables using a Pearson's correlation coefficient.

We reduced the degrees of freedom in each of the above analyses because of the spatial autocorrelation present in the data set. The corrected degrees of freedom were determined by using the macroecological software SAM (Rangel et al. 2006). Climatic data were obtained from the WorldClim database using a map resolution of 2.5 arc-minutes (Hijmans et al. 2005).

We tested the ability of each of the moments of the plot-level trait distribution to predict its Holdridge life zone (Holdridge 1979) by assigning each plot to one of the five Holdridge life zone categories found in the study region: boreal wet forest (Bwf), cool temperate moist forest (CtMf), cool temperate wet forest (CtWf), subtropical moist forest (SMf), and warm temperate moist forest (WtMf). We used the widely accepted Holdridge life zone classification over other existing classification systems (Merriam 1889, Rivas-Martinez 1981) as it is perhaps the most widely used abiotically based system in North America. Future work can explore the predictability of other classifications systems. We used ANOVA (with post hoc pairwise Tukey tests) to compare the moments of the plot trait distributions in the five Holdridge life zones. As there was likely substantial spatial autocorrelation in the plot trait distributions, we estimated the mean of the moments of the trait distributions of plots in each life zone based on a spatial generalized least squares model. The GLS model used a simultaneous autoregression to estimate the mean. To examine the scale dependence of the above at a coarser spatial scale, we binned all plots into $1^\circ \times 1^\circ$ grid cells and repeated the analyses.

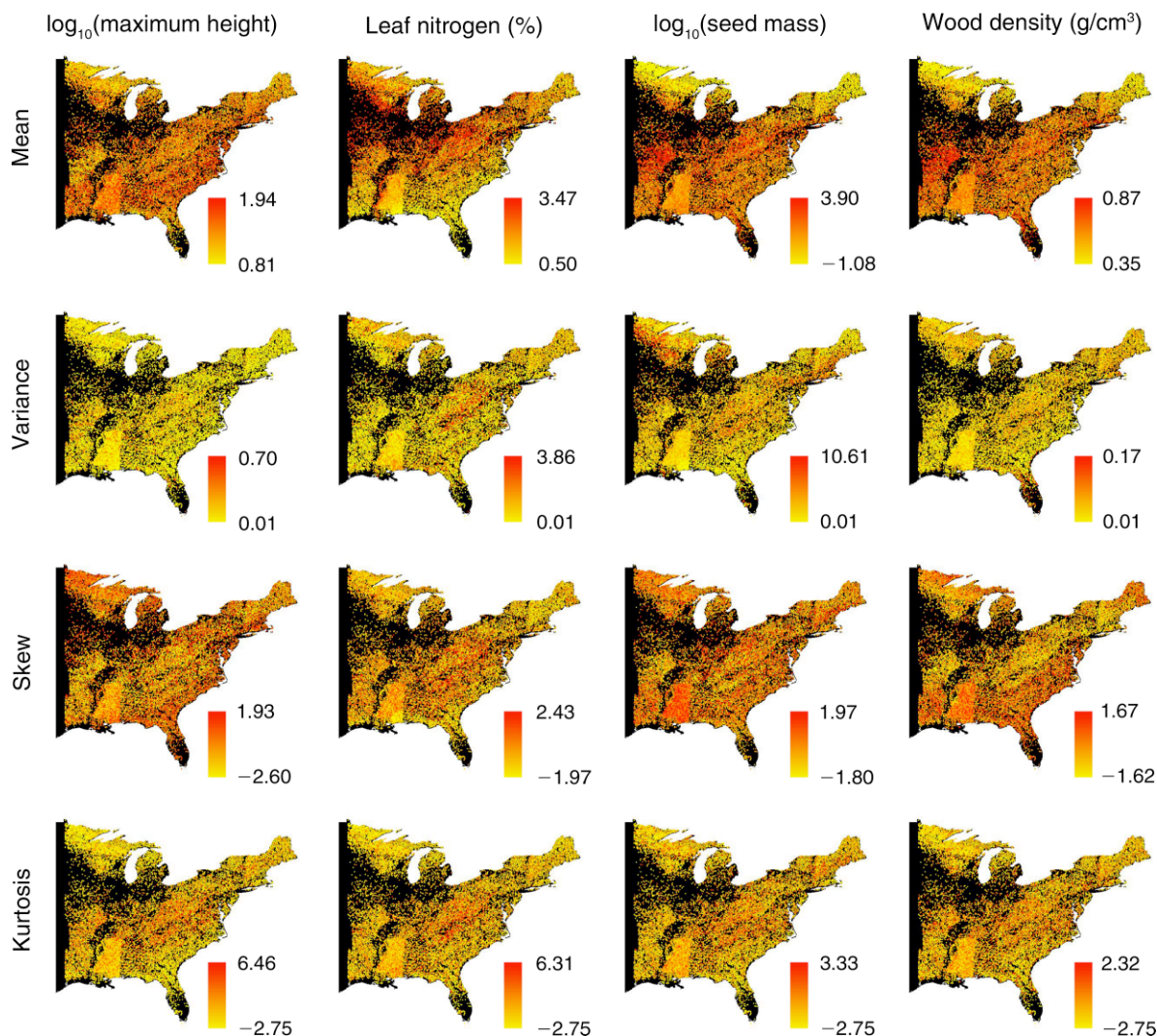


FIG. 1. Maps of the mean, variance, skew, and kurtosis of the presence–absence weighted functional trait distributions in 18 111 individual U.S. Department of Agriculture Forest Inventory and Analysis Program (FIA) plots in eastern North America. Black areas are areas where no data are available.

RESULTS

The mean and variance of the presence–absence weighted and abundance weighted trait distributions in the 18 111 FIA plots were highly correlated, while the skew and kurtosis of these distributions correlated very little (Appendix B). There was little to no scale dependence in results between the two spatial scales examined here. Plot-level and 1° by 1° grid cell trait-climate correlations gave similar results (Appendices C and D). Therefore, for the remainder of the article we will only discuss the presence–absence weighted results at the plot level, but all results are available in appendices.

The mean of the community trait distributions for all four traits were significantly correlated with the temperature and precipitation variables utilized in this study (Table 1). Conversely, the variance and skew of the

community trait distributions were generally uncorrelated with the climate. The kurtosis of the community trait distributions was generally positively correlated with temperature and precipitation levels, but negatively correlated with temperature and precipitation seasonality. In other words, the community trait distribution was, on average, more peaked in warm, wet and aseasonal environments (Table 1, Fig. 1, and Appendices E–G).

A central goal of this work was to determine whether community functional trait distributions could be used to differentiate Holdridge life zones. The results from the ANOVA show that for each trait at least one Holdridge life zone contained forest plots that had a significantly different mean of their trait distributions than those recorded in forest plots in other life zones (maximum height, $F_{4,18106} = 3.21$, $P < 0.05$; leaf %N,

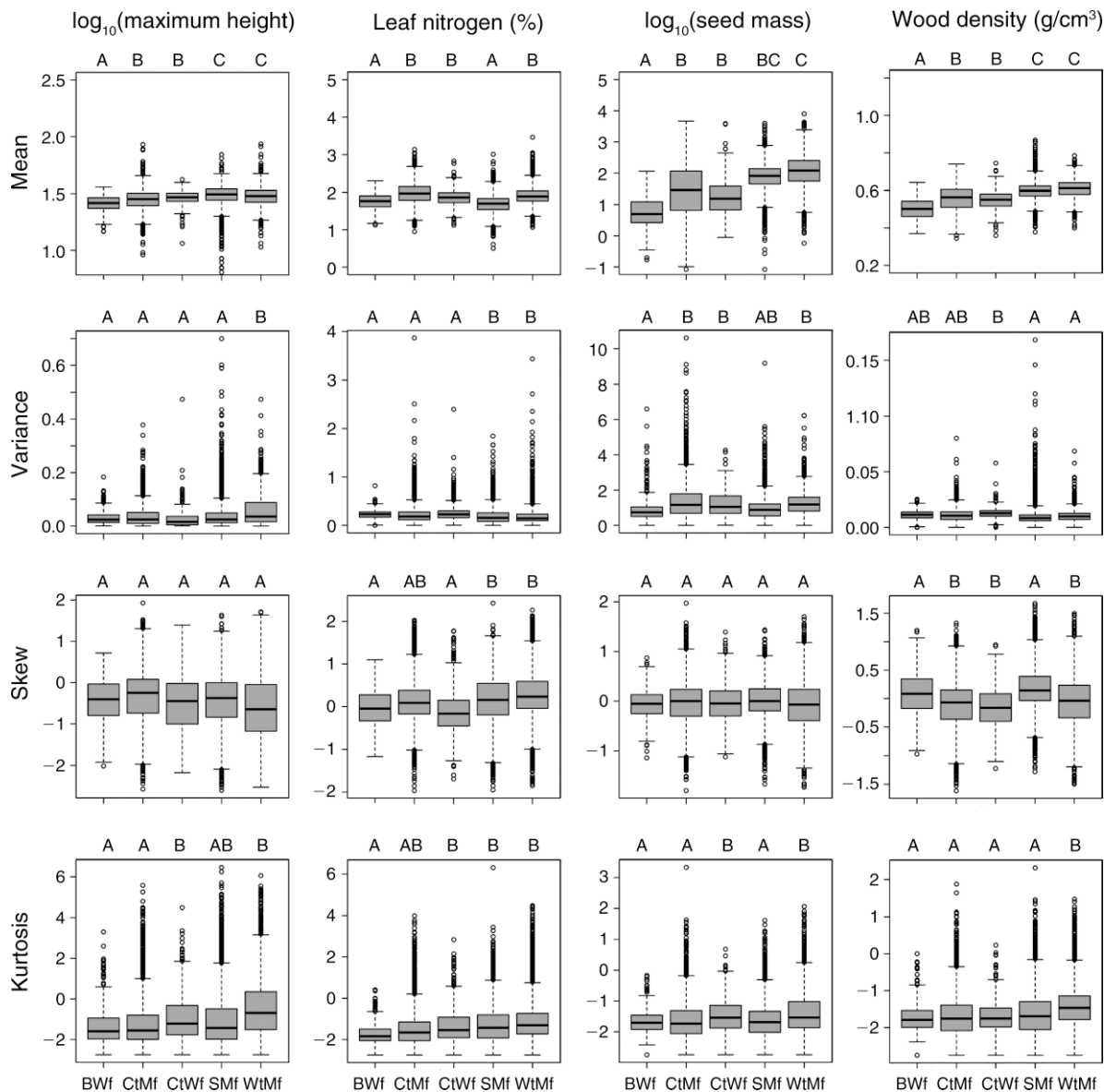


FIG. 2. A comparison of the moments of the functional trait distributions in FIA plots in the five Holdridge life zones in the study area. If the letters above two boxplots are the same, then the moments were statistically undistinguishable using an ANOVA followed by a Tukey test. Abbreviations are: BWF, boreal wet forest; CtMf, cool temperate moist forest; CtWf, cool temperate wet forest; SMf, subtropical moist forest; WtMf, warm temperate moist forest. Boxplots were made in R, and components are: top of the box, upper hinge; midline of box, median; bottom of box, lower hinge; bars, 1.5 times length of box (1.5 times the H-spread); dots, values that are greater or less than 1.5 times the H-spread of the distribution, plus the upper or lower hinge.

$F_{4,18106} = 3.24$, $P < 0.05$; seed mass, $F_{4,18106} = 6.21$, $P < 0.05$; wood density, $F_{4,18106} = 5.05$, $P < 0.05$; Fig. 2). This was also true for the community trait distribution variance (maximum height, $F_{4,18106} = 2.97$, $P < 0.05$; leaf %N, $F_{4,18106} = 3.01$, $P < 0.05$; seed mass, $F_{4,18106} = 3.96$, $P < 0.05$; wood density, $F_{4,18106} = 3.02$, $P < 0.05$), skew (maximum height, $F_{4,18106} = 3.91$, $P < 0.05$; leaf %N, $F_{4,18106} = 5.94$, $P < 0.05$; seed mass, $F_{4,18106} = 3.17$, $P < 0.05$; wood density, $F_{4,18106} = 6.15$, $P < 0.05$) and kurtosis (maximum height, $F_{4,18106} = 4.02$, $P < 0.05$; leaf %N, $F_{4,18106} = 3.99$, $P < 0.05$; seed mass, $F_{4,18106} = 4.11$,

$P < 0.05$; wood density, $F_{4,18106} = 4.18$, $P < 0.05$; Fig. 2 and Appendices H–J). When weighting the community trait distribution using abundance, there was no significant difference in the kurtosis of the trait distributions across Holdridge life zones (Appendices H and J).

The boreal wet forest life zone could be distinguished from all other life zones using their mean maximum height, seed mass and wood density, but its mean leaf %N was indistinguishable from that of the subtropical moist forest (see Fig. 2). The cool temperate moist forest

and the cool temperate wet forest could be distinguished from all other forests using mean maximum height or wood density, but they could not be distinguished from one another using the mean of any trait distribution. The subtropical moist forest could be distinguished from all other life zones using a combination of traits, but not with any single trait. Similarly, the wet tropical moist forest could be distinguished from all other life zones using a combination of traits, but not with any single trait (Fig. 2).

DISCUSSION

The results show that the mean trait value of eastern North American forest communities is generally correlated with the climate variables studied (Table 1). The reported relationships between community trait distribution means and climate on continental scales suggests that functional traits may be good indicators of vegetation types and life zones. Further it supports the notion that these traits may be used to predict vegetation shifts in response to climatic changes through space or time. Contrary to the mean of the trait distribution, the variance and skew of the community trait distribution were generally poorly correlated with the climatic variables studied. This suggests that other variables not quantified (i.e., physiography, soil type, biotic interactions, and disturbance history) may be important determinants of these moments of the functional trait distribution in eastern North American tree communities. Biotic interactions in particular may play a large role in determining the variance in community trait distributions. Last, the kurtosis of the functional trait distributions was often slightly, but positively correlated with temperature and precipitation and negatively correlated with seasonality using presence-absence weighting suggested a more peaked distribution in the southeastern United States. Thus it appears that in the more species rich and climatically benign southeastern United State forests species pack more tightly into a constrained functional trait space. Future, more detailed, tests that incorporate null models will be needed to clearly address this possibility and its implications in a community ecology context.

A total of five Holdridge life zones were included in this study of which none had a distinctive community trait distribution for all traits. That said, all life zones could be distinguished from one another by comparing the mean of two or more trait distributions (Fig. 2). The only exception was the two cool temperate life zones where they could only be differentiated based upon the kurtosis of their maximum height and seed mass distributions. In general, maximum height and wood density appear to be the most predictive traits used in this study.

Ultimately, for the traits and the forests studied, it appears that a combination of functional traits or multiple moments of community trait distributions will

be required to predict the forest type or life zone in which a community resides. This leads to two issues that must be addressed in future work, one operational and one conceptual. Operationally, it could be that the traits utilized in this study are simply the “wrong” set of traits and alternative traits that are less often or more difficult to measure will be much better predictors. Thus, more plant traits will need to be gathered and tested to determine what, if any, traits will be the best predictors of plant species and vegetation types. Conceptually, given that a combination of functional traits was required in this study to distinguish some life zones, the question of whether atomizing functional types or strategies via quantitative functional traits has reduced our predictive ability. On the one hand, continuous functional traits are clearly advantageous when compared to categorical functional types because they allow for quantitative predictions and modeling of plant function. On the other hand, a single emergent functional type or strategy of a species could likely arise from multiple different combinations of functional traits (Marks and Lechowicz 2006). Thus future work must address whether generating quantitative multivariate representations of functional types and strategies or the emergent functional type or strategy itself are of the most value to plant geography. We argue that the quantitative property of functional traits will lead to a more predictive and robust plant geography, but it will require a multivariate perspective and an appreciation of how multiple different trait combinations may lead to the same functional type or strategy.

ACKNOWLEDGMENTS

N. G. Swenson was supported by an NSF Postdoctoral Fellowship in Bioinformatics while conducting this work. M. D. Weiser was supported the U.S. Department of Energy (DOE-DE-FG02-08ER64510) and NASA Research Opportunities in Space and Earth Science (08-BIODIV-52).

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APPENDIX A

A list describing the literature sources and online databases from where the functional trait data were obtained (*Ecological Archives* A091-158-A1).

APPENDIX B

The results of a regression through the origin where the moments of the trait distribution of plots and grid cells calculated using presence-absence weighting are regressed on the mean trait values calculated using abundance weighting (*Ecological Archives* A091-158-A2).

APPENDIX C

The Pearson correlation coefficients for precipitation variables and the moments of the trait distribution in plots and 1° grid cells (*Ecological Archives* A091-158-A3).

APPENDIX D

The Pearson correlation coefficients for temperature variables and the moments of the trait distribution in plots and 1° grid cells (*Ecological Archives* A091-158-A4).

APPENDIX E

Maps of the moments of the trait distributions using abundance weighting in the FIA plots in eastern North America (*Ecological Archives* A091-158-A5).

APPENDIX F

Maps of the moments of the trait distributions using presence-absence weighting in the FIA plots in 1° × 1° grid cells in eastern North America (*Ecological Archives* A091-158-A6).

APPENDIX G

Maps of the moments of the trait distributions using abundance weighting in the FIA plots in 1° × 1° degree grid cells in eastern North America (*Ecological Archives* A091-158-A7).

APPENDIX H

The moments of the trait distribution in FIA plots weighted by abundance in the five Holdridge life zones in the study area (*Ecological Archives* A091-158-A8).

APPENDIX I

The moments of the trait distribution in FIA plots in 1° grid cells weighted by presence-absence in the five Holdridge life zones in the study area (*Ecological Archives* A091-158-A9).

APPENDIX J

The moments of the trait distribution in FIA plots in 1° grid cells weighted by abundance in the five Holdridge life zones in the study area (*Ecological Archives* A091-158-A10).