Actual Evapotranspiration (AET) and Tree Species Richness in the Eastern U.S.A.

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ABSTRACT: *Although many studies confirm that competition and disturbance play important roles in determining tree diversity locally, climatic constraints become increasingly important at broader geographic scales. We evaluate the extent that annual actual evapotranspiration (AET) might account for observed variation in tree diversity across the entire eastern U.S. and within 24 Level III ecoregions designated by the Environmental Protection Agency. To estimate tree diversity, we extracted data from a total of 87,137 Forest Inventory and Analysis (FIA) survey plots. For each 1000 km^2 cell with ≥15 plots, logarithmic functions were derived to predict the number of species encountered per hectare (equivalent to 17 fixed-radius plots). Across the region, tree diversity exhibited a humped-shaped pattern with AET (r^2=0.49, P < 0.0001). Stratifying ecoregions by AET, which increases from north to south, winter temperature emerged as a significant variable where AET averaged <800 mm.yr^{-1}, whereas summer temperature accounted for much of the variation where AET was between 800 to 950 mm.yr^{-1}. In ecoregions with AET>1100 mm.yr^{-1}, significant variation in tree diversity was associated with seasonal differences in precipitation. We conclude that across the eastern U.S., AET provides a reasonable prediction of regional variation in tree diversity, especially where AET is < 800 mm.yr^{-1}.*

KEY WORDS: AET, AET stratification, tree species richness; tree diversity, level III ecoregions, FIA database, environmental variables of species diversity; the eastern US.

Introduction

It appears more and more likely that species diversity will be significantly reduced in response to changing climatic conditions over the coming decades. This possibility has lead to increased effort to correlate current biodiversity with climate. At the continental scale, the variable most frequently correlated with biodiversity is actual evapotranspiration (AET), which expresses the annual balance between precipitation and latent heat exchange. AET is also considered a surrogate for net primary production because of a close relationship between production and climatic factors (Lieth 1975). In reference to trees, diversity

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In: McWilliams, Will; Moisen, Gretchen; Czaplewski, Ray, comps. 2009. 2008 Forest Inventory and Analysis (FIA) Symposium; October 21-23, 2008: Park City, UT. Proc. RMRS-P-56CD. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 1 CD.

generally increases from cold, dry conditions with low AET to warm, moist tropical environments with high AET (Currie and Paquin 1987, Latham and Ricklafs 1993, Davies et al. 2004). Other environmental variables often associated with variation in biodiversity include potential evapotranspiration and rainfall (Hawkins et al. 2003).

Within regions, physiographic variation and historical factors explain much of the residual variation not account for by AET (Whittaker and Field 2000, Caley and Schluter 1997, Currie et al. 1999, Huston 1999, Whittaker et al. 2001, Sarr et al. 2005). In the United States, the portion east of the Mississippi River contains the largest spatial variation in tree diversity, whether analyzed from species range maps (Currie and Paquin 1987), ecoregions (Waring et al. 2006) or counties (Iverson and Prasad 2001). Studies of tree diversity that rely on range maps have the disadvantage of not being responsive to future climatic limitations. Range maps also overlay areas where the environment may limit a species' presence. As a result, environmental correlations are likely to differ from those based on extensive field surveys (Hurlbert and White 2005).

In the United States, we are fortunate that the federal government has supported and continues to support intensive ground surveys of forested areas throughout the eastern U.S. as part of the Federal Inventory and Analysis (FIA) program (http://fia.fs.fed.us/tools-data/default.asp). Sampling in the western United States is less intensive than in the eastern portion of the country, and to date, most data have been acquired only within variable-radius plots instead of the more robust fixed-radius sampling design. The availability of both fixed- and variable-area plots in the eastern U.S. permits a correlation to be established between the two types of sample plots to provide estimates of tree species present per hectare (described below).

Because the eastern U.S. is a region where rainfall is generally sufficient and evenly distributed throughout the year, reasonable estimates of AET may be made without requiring detailed information on available soil moisture or canopy leaf area index, as would be required to calculate AET in the more arid portions of the western U.S. (Churkina et al. 1999). Based on the literature, we hypothesize that different patterns will emerge between AET and tree diversity depending on the scale of analysis, and on how a region is stratified in reference to AET. Specifically, we expect a humped-shaped relation with AET and tree diversity across the entire region, as resulted from a similar analysis in the northwestern portion of the country (Swenson and Waring 2006). If that is the case, we would expect positive, neutral, or negative relationships between tree diversity and AET as AET increase from north to south. Where a clear relationship between tree diversity and AET is lacking, other environmental factors may emerge as significant, such as winter or summer temperature and precipitation, soil water storage, and topographic relief. If a common set of variables can explain variation in tree diversity across a set of climatically comparable ecoregions, we

should achieve a better understanding of the impact of climatic change on tree species diversity.

Methods

The study covers all forested areas in 31 states in the eastern U. S. For across region analysis, we evaluate the relationship between nine environmental variables and tree richness recorded on all 1000 km^2 (31.6 km x 31.6 km) cells with 15 or more FIA survey plots. A total of 24 ecoregions delineated by the Environmental Protection Agencies' Level III classification (<http://www.epa.gov/wed/pages/ecoregions/ecoregions.htm>) qualified for within ecoregion analysis with at least 20 such cells within each ecoregion (Table 1). Analyses were not conducted at finer scale because the geographic locations of sampling plots are imprecise to maintain privacy of information acquired on private lands (McRoberts et al. 2005 http://ncrs2.fs.fed.us/4801/fiadb/fiadb_documentation/Perturbing-Swapping.pdf).

TABLE 1: The 24 ecoregions recognized by the EPA level III classification and number of qualified 1000 km^2 cells (N)

Code	Name	N
35	South Central Plains	84
39	Ozark Highlands	90
45	Piedmont	156
49	Northern Minnesota Wetlands	22
50	Northern Lakes and Forests	198
51	North Central Hardwood Forests	64
52	Driftless Area	36
56	Southern Michigan/Northern Indiana Drift Plains	23
58	Northeastern Highlands	109
59	Northeastern Coastal Zone	31
60	Northern Appalachian Plateau and Uplands	27
62	North Central Appalachians	28
63	Middle Atlantic Coastal Plain	70
65	Southeastern Plains	310
66	Blue Ridge	46
67	Ridge and Valley	93
68	Southwestern Appalachians	37
69	Central Appalachians	64
70	Western Allegheny Plateau	71
71	Interior Plateau	52
72	Interior River Valleys and Hills	46
75	Southern Coastal Plain	107
82	Laurentian Plain and Hills	42
83	Eastern Great Lakes and Hudson Lowlands	28

Species diversity

One lesson learned from previous studies is that there are advantages, especially when the sample size is small, if comparable areas are sampled (Whittaker et al. 2001, Sarr et al. 2005). In the study, we estimate species

diversity (richness) per hectare. This was a challenge because the largest data sets acquired by the FIA surveys used variable radius plots, where the sampling area varies as a function of prism angle size and the diameter and distance of trees from a central point (Alerich et al. 2004). Moreover, the choice of prism size varied, even within states. Although the sampled area can be estimated from mean tree diameter, large variations around the mean result in questionable estimates of species richness per unit area if made directly from variable radius plot data.

Fortunately, over the last seven years, the FIA surveys have introduced a standard fixed-radius plot layout, where four 7.3 m (24 ft.) radius subplots cover a total of 0.0675 ha (1/6 of an acre) (USDA, Forest Service 2004). However, fixed-radius plots are only available for a limited number of states thus far and the sampling density of fixed-radius plots is sparse compared to variable-radius plots. To utilize the more extensive variable-radius plot data, we compared the two independent estimates of species richness where both sets of samples were available.

FIA plot data were downloaded from the FIADB website, http://fiatools.fs.fed.us/fiadb-downloads/fiadb3.html, of USDA Forest Service. In this data set, plots are identified by their locations as provided by the database, and were then grouped as they occurred in 1000 km^2 cells. All cells containing ≥15 FIA plots were included because an asymptote in species numbers is approached with that sample size, and by setting a higher minimum, the number of qualified cells would be reduced significantly. For each cell with both sets of plots (fixed- and variable-radius), logarithmic functions of species richness with increasing number of plots were calculated and compared. To smooth the curves, we first listed plots of each set in a cell by number of species in ascending order, then in descending order, before randomly reordering the sequence twice. The average species richness values from the four summarizations were used for each 1000 km^2 cell. We standardized the estimates for 17 fixed-radius plots, equivalent to one hectare, based on the cell-specific slope and intercept of the logarithmic function of species number vs. plots number. We generally attained an excellent fit between species richness and increasing plot areas for each 1000 km^2 cell with an $R^2 > 0.95$. The results from variable radius plots were compared with that of fixed radius plots and the relationship statistically assessed.

Environmental variables

Nine environmental variables were selected to correlate with species richness patterns. These included two climatic indices: AET and mean annual precipitation (PPT); two soil properties: soil organic matter content (OM) and soil water holding capacity (SW); and five topographic descriptors: average % slope (SL), range in % slopes (RSL), average elevation (EL), range in elevation (REL), and the length of major roads (LR).

The USGS (2002) provides a GIS Database (http://webgis.wr.usgs.gov/globalgis/), where annual AET, representing the difference between precipitation and latent heat loss, is calculated for the U.S. based on equations developed by Prentice et al. (1993). The equations are applied at monthly time steps and the values then summed for the year. This formulation differs from the more data demanding Penman-Monteith equation by not requiring information on canopy leaf area, and stomatal response to evaporative demand and limitations of soil water. AET values were acquired using ArcGIS/ArcInfo software for all qualified 1000 km^2 cells by averaging values extracted from the 1 x 1 km resolution data. The values of PPT were acquired similarly. Data of SL, RSL, SW, and OM were calculated from the USDA STATSGO database (1994) at a scale of 1:250000. Before intersecting with the soil data layers, each 1000 km^2 cell was further divided into 49 equally spaced cells to capture the spatial variations of each variable. Within each 1000km^2 cell, the 49 smaller cells were then either summed, averaged or the range calculated, depending on the variable. Elevation data at a scale of 1:250000 were downloaded form USGS GeoData website (http://edc.usgs.gov/products/elevation/dem.html) and the values of average elevation and elevation ranges for each 1000 km^2 cell were summarized as with the soil data. Total length of major roads was calculated for each 1000 km^2 cell in GIS using ArcGIS/ArcInfo by overlaying the cells with the road map provided by the USGS Global GIS Database.

Statistical Analysis

Across the entire region, a stepwise regression analysis with all nine abiotic variables was first performed using all qualified 1000 km^2 cells. A variable was included if significant at $P < 0.001$. We then repeated the process separately for each of the 24 defined ecoregions. Finally, we stratified ecoregions by AET and assessed tree richness correlations in reference to differences in seasonal temperature and precipitation.

Results

Species richness

We found that the number of species from the two FIA inventories, fixed and variable radius plots, was significantly and positively related ($R^2 = 0.74$, $P < 0.0001$) when standardized to 17 plots (Figure 1). The slope of the linear function was 0.97 when the intercept was set to 0. With the relationship established between fixed- and variable-radius plots illustrated in Figure 1, we were able to convert estimates of species richness derived from variable-radius plots to richness per hectare (equivalent to 17 fixed-radius plots).

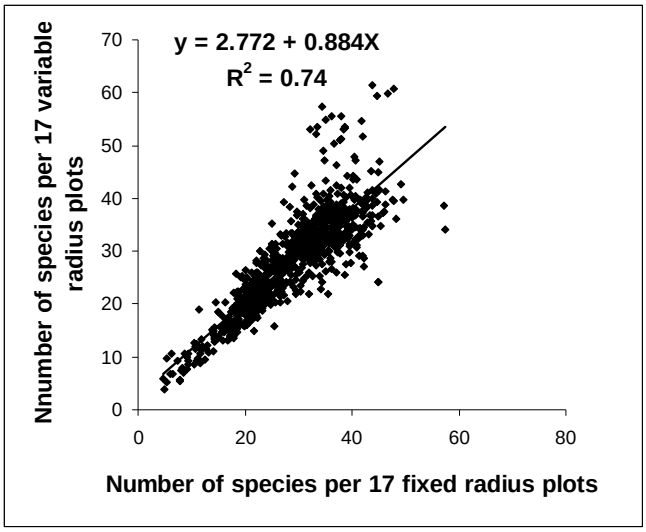

FIGURE 1: The relationship between number of species per 17 variable radius plots and number of species per 17 fixed radius plots (R^2 = 0.74). When the intercept was set to 0, the slope of the linear function is 0.97, which demonstrates that estimates of species richness from the two independent FIA inventories are equivalent.

Spatial variation of tree species richness in the eastern U.S. indicates that areas with the highest richness are located in central portion with heterogeneous topography and a favorable climate. Species richness decreases significantly in all directions (Figure 2).

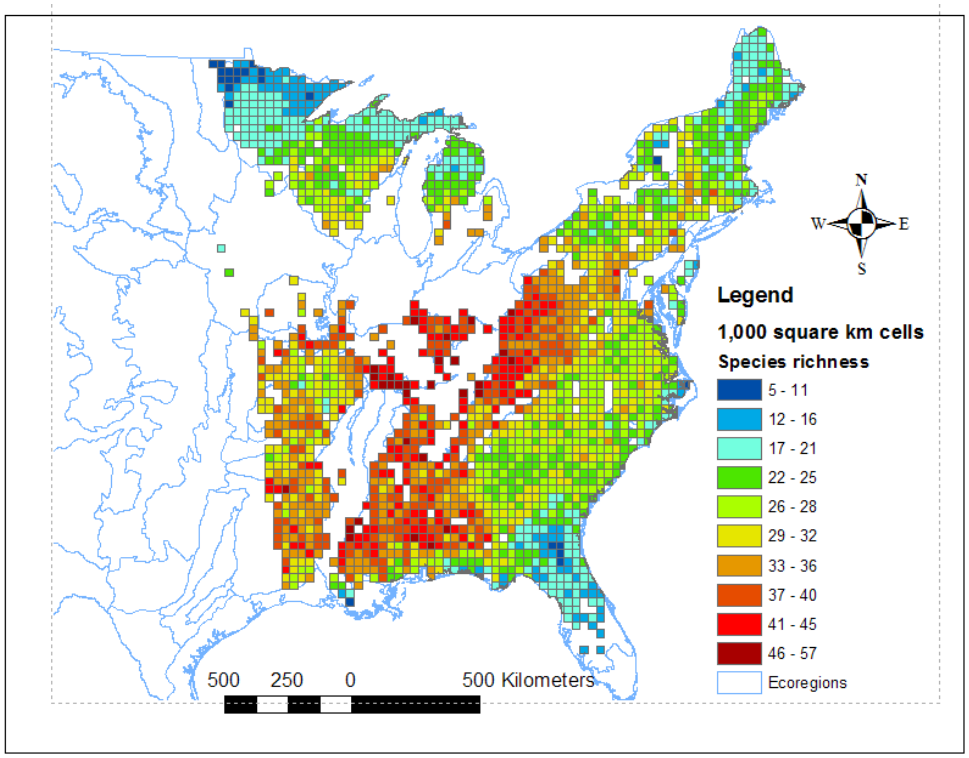

FIGURE 2: Spatial variations of tree species richness estimated for qualified 1000 km cells with ≥15 FIA survey plots. The highest number of species occurs in the central portion of the region where the climate is moderate and the topography heterogeneous.

Across ecoregions

Across all ecoregions, AET was the sole variable accounting for significant variation in species richness ($R^2 = 0.41$, $P < 0.0001$). We found that a 3rd order polynomial equation gave a better fit to the data, raising the R^2 to 49% (Figure. 3). Species richness increases significantly as AET increases to about 950 mm. yr^{-1}, flattens out between 950 - 1100 mm. yr^{-1} before decreasing. Separation of AET values by ecoregions demonstrates that the ecoregions with intermediate AET (950 – 1100), such as ecoregions 65 (Southeastern Plains), 69 (Central Appalachians), 71 (Interior Plateau), and 72 (Interior River Valleys and Hills), have the highest species richness, while ecoregion 75 (Southern Coastal Plain) with very high AET values (1214 mm. yr^{-1}) exhibits much lower species richness, equivalent to values recorded in ecoregion 58 (Northeastern Highlands) with very low AET (700 mm. yr^{-1}).

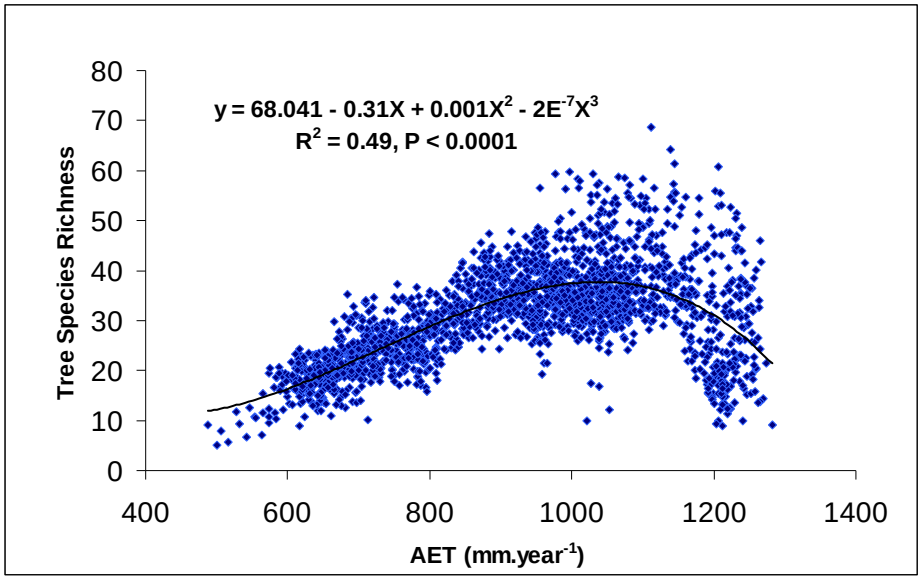

FIGURE 3: The polynomial relationship between AET and species richness across ecoregions in the eastern US. Species richness increases as AET increases to about 950 mm. yr^{-1}, plateaus from 950 mm. yr^{-1} to about 1100 mm. yr^{-1} before decreasing as AET continue to increase above 1100 mm. yr^{-1} .

Within ecoregions

The detailed analyses show that where AET is low in the northern tier of ecoreigons (i.e., < 800 mm.yr^{-1}), winter temperature is important with a few exceptions (Table 2). In ecoregions with AET between 800 – 950 mm.yr^{-1}, summer temperature is generally important. In ecoregions with AET > 1100 mm. yr^{-1}, 26% to 42% of variations in species richness were accounted for by seasonal precipitation. Only between 950 – 1100 mm.yr^{-1}, did neither AET, seasonal temperature nor precipitation account for a significant amount of variation in species richness (Table 2).

TABLE 2: Results of analysis of individual ecoregions where the most important climatic variable is identified. The variables include winter temperature (WT), summer temperature (ST), winter precipitation (WP), and summer precipitation (SP). N is the number of qualified cells within an ecoregion. Ecoregions are listed in ascending order of average annual AET ($mm.yr^{-1}$) to reflect the shift in importance of other variables as AET increases. N/A indicates that no climatic variable was found significant in an ecoregion.

Ecoregion Code	N	Average annual AET	Standard deviation of AET	R^2 with AET function	Best climatic variables	R^2 of the climatic function
49	22	603	41.9	0.36	WT	0.34
82	42	659	41.0	N/A	N/A	N/A
50	198	666	37.2	0.24	ST	0.34
58	109	700	61.2	0.31	WT	0.29
51	64	702	54.4	0.21	WT	0.37
56	23	705	37.4	0.66	ST	0.77
83	28	734	35.0	0.32	N/A	N/A
60	27	778	19.1	0.18	WT	0.42
59	31	782	16.0	N/A	WP	0.40*
52	36	791	15.9	0.22	WT	0.30
62	28	806	14.6	0.24	ST	0.37
70	71	883	33.2	0.22	ST	0.49
67	93	909	83.3	N/A	N/A	N/A
72	46	916	27.0	0.22	SP	0.46
69	64	917	44.6	0.63	ST	0.41
71	52	951	39.0	N/A	N/A	N/A
39	90	960	25.2	N/A	N/A	N/A
66	46	969	60.7	N/A	N/A	N/A
68	37	1016	27.9	N/A	N/A	N/A
45	156	1027	67.0	N/A	N/A	N/A
63	70	1065	77.9	N/A	N/A	N/A
35	84	1079	55.7	N/A	N/A	N/A
65	310	1121	85.7	N/A	SP	0.42*
75	107	1214	26.4	N/A	WP	0.26

* This is an R^2 of a negative relationship.

Figure 4 presents the most important variables selected by stepwise regression for each ecoregion. None of the nine environmental variables accounted for a significant amount of variation in species richness in those ecoregions designated in white. The relative importance of variables shifts with location. Soil water holding capacity is significant in the southern and southwestern portion of the eastern U.S. while AET is dominant in the north. Precipitation is important in the northeastern coastal regions (negative relationships) and in the northwest (positive relationships). Topographic heterogeneity accounts for a significant amount of variation in the central part of the region. In 18 out of the 24 ecoregions, environmental factors account for 17% to 66% of variation in species richness. These factors are generally weak predictors in the south (R^2s are between 0.17-0.4) but become stronger in the more centrally located ecoregions (R^2s are between 0.58 - 0.66) where topography is most varied and species richness highest.

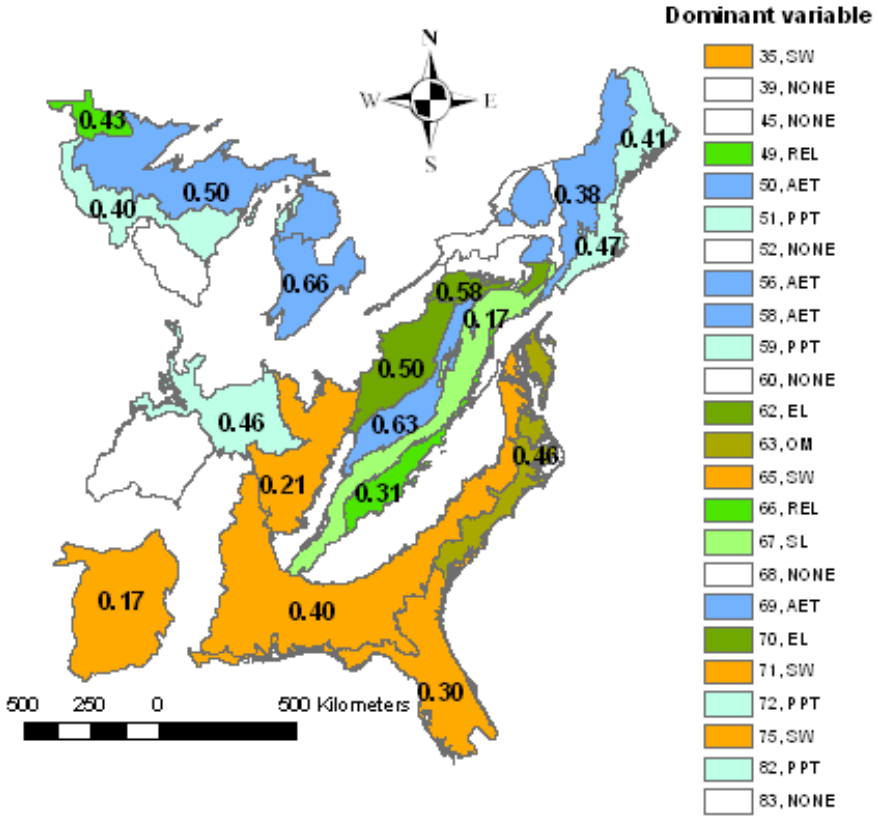

FIGURE 4: Distribution of dominant environmental variables influencing species richness within ecoregions in the eastern US. Ecoregions are color coded to reflect similar variables and labeled with R^2 values of the relationship between the dominant variable and species richness. In general, soil water holding capacity has significant predicting power in the south and southwest, AET is dominant in the north, and topographic heterogeneity account for a significant amount of variation in species richness in the central part of the region.

Discussion

Our hypothesis was not rejected. Different patterns emerge between AET and tree species richness depending on how a region is stratified in reference to AET. Our findings on the relationship between species richness and AET across ecoregions generally support those of other studies conducted at a similar scale (Charles et al. 2001, O'Brien 1993). It is generally acknowledged that AET is closely related to productivity (Lieth 1975, Law et al. 2002). The results of this study are consistent therefore with analyses of FIA survey data in the western U.S. where high species diversity was associated with intermediate levels of productivity and decreased at higher or lower values (Waring et al 2002, Swenson and Waring 2006).

A positive response of species richness to AET is generally expected at lower values of AET, as also observed in reference to Net Primary Production (NPP). At intermediate values of AET or NPP, the relationship is insensitive but in this range tree richness is generally the highest. As values of AET increases further the relation becomes negative. In our study, as in others, neither AET nor

probably productivity accounted for all the observed variation in tree richness; different variables become important depending on the location. For example, we found that winter temperature accounted for a significant amount of variations (29 - 42%) in species richness in the northern tier of ecoregions. Ecoregions 50, 56, and 83 were exceptions, possibly because of deep snow accumulates in the vicinity of large unfrozen lakes during the winter, which may protect more sensitive tree species. In the ecoregions with AET between 800 - 950 mm. yr^{-1}, species richness increased as summer temperature increased. As expected, no significant relationship between AET and specie richness was observed in ecoregions with AET between 950 - 1100 mm. yr^{-1}, where species richness peaked. We interpret the decrease in species richness for the areas with AET > 1100 mm. yr^{-1} as a likely result of a few fast-growing species dominating and restricting light available for other species (Safford et al. 2001, Waring et al. 2002, Swenson and Waring 2006, Hooper and Dukes 2004, Grime 2001).

Within ecoregions, we found that AET was a significant factor in 12 of the 15 ecoregions with AET less than 950 cm. yr^{-1} (Table 2). The variations in species richness and its environmental variables in ecoregion 59, 67 and 82 were considered as special cases. Based on the EPA's description of ecoregion 67, topographic variation is extreme, where high mountains and deep valleys occur over relatively short distances (ftp://ftp.epa.gov/wed/ecoregions/us/useco_desc.doc). As a result, the standard deviation of AET was much higher (84 mm. yr^{-1}) than in other ecoregions (Table 2). With a minimum cell size of 1000 km^2, we expect the full variation in climatic conditions were not captured. Ecoregions 59 and 82 were special cases because, although both are highly forested regions, they had many large lakes that may ameliorate water stress but, with increasing precipitation, foster cloudiness, reducing the amount of light absorbed by the forest canopy, while increasing competition on species adapted to shaded conditions. In ecoregions with AET > 1100 mm. yr^{-1} (i.e. ecoregions 65 and 75) species richness was positively associated to soil water holding capacity (Figure 4). This positive relationship may be a result of large areas of coarse textured soils dominated by pine-oak forests. The explanatory power of soil water holding capacity was between 30 - 40%. The detailed analysis indicated that winter precipitation accounted for 26% of the variation in species richness in ecoregion 75 whereas summer precipitation was negatively related to species richness in ecoregion 65 ($R^2 = 0.42$) (Table 2). A possible explanation of these inverse relationships is that winter precipitation might promote species richness in ecoregion 75 if soil moisture were limiting in the spring whereas summer precipitation might increase productivity and, competition leading to reduced species richness in ecoregion 65.

For this detailed environmental analysis within and across ecoregions we took advantage of both variable- and fixed-radius FIA sampling. As a result of cross-comparison between the two data sets, we have confidence in our ability to utilize variable-area data sets in the western U.S. where fixed-radius sampling is as yet limited. The detailed analysis also indicates that in the search for general responses between environmental variables (or productivity) that the EPA

ecoregion classification level III may be too refined and that a broader stratification may be warranted. Future studies will test this assumption.

Acknowledgement

This study was supported by the National Aeronautics and Space Administration (NASA Grant NNG04GK26G) as part of the Biodiversity and Ecological Forecasting program. We thank Drs. Nicholas Coops and Joanne Nightingale for their helpful suggestions and editing.

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