RESEARCH PAPER

Beneath the veil: plant growth form influences the strength of species richness–productivity relationships in forests

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ABSTRACT

Aim Species richness has been observed to increase with productivity at large spatial scales, though the strength of this relationship varies among functional groups. In forests, canopy trees shade understorey plants, and for this reason we hypothesize that species richness of canopy trees will depend on macroclimate, while species richness of shorter growth forms will additionally be affected by shading from the canopy. In this study we test for differences in species richness–productivity relationships (SRPRs) among growth forms (canopy trees, shrubs, herbaceous species) in small forest plots.

Location We analysed 231 plots ranging from 34.0° to 48.3° N latitude and from 75.0° to 124.2° W longitude in the United States.

Methods We analysed data collected by the USDA Forest Inventory and Analysis program for plant species richness partitioned into different growth forms, in small plots. We used actual evapotranspiration as a macroclimatic estimate of regional productivity and calculated the area of light-blocking tissue in the immediate area surrounding plots for an estimate of the intensity of local shading. We estimated and compared SRPRs for different partitions of the species richness dataset using generalized linear models and we incorporated the possible indirect effects of shading using a structural equation model.

Results Canopy tree species richness increased strongly with regional productivity, while local shading primarily explained the variation in herbaceous plant richness. Shrub species richness was related to both regional productivity and local shading.

Main conclusions The relationship between total forest plant species richness and productivity at large scales belies strong effects of local interactions. Counter to the pattern for overall richness, we found that understorey herbaceous plant species richness does not respond to regional productivity gradients, and instead is strongly influenced by canopy density, while shrub species richness is under multivariate control.

Keywords

Actual evapotranspiration, competition, growth form, species richness, structural equation modelling, temperate forests, USA.

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INTRODUCTION

Although a wide variety of factors influence patterns of species richness (reviewed in Rosenzweig, 1995, and Ricklefs, 2004), biologists have often debated which single factor has the greatest effect (Huston, 1994). Climate may play a large role (Currie, 1991; Storch *et al.*, 2005; Mönkkönen *et al.*, 2006). However, the exact form of the relationship between climate and species

richness varies among studies, scales and groups of species (reviewed in Waide *et al.*, 1999, and Mittelbach *et al.*, 2001). Furthermore, several mechanisms may contribute to climate–richness relationships, as well as their variation, including niche-based, abundance-based and evolutionary mechanisms (reviewed in Evans *et al.*, 2005).

At large geographical extents, species richness tends to increase monotonically with climatic variables that limit productivity (Hillebrand, 2004; Field *et al.*, 2009). Within functional groups, the form of the relationship is often consistent across biogeographical regions (Currie & Paquin, 1987). This might imply a general population-based mechanism that translates climate into richness through productivity (Francis & Currie, 2003). If certain species out-compete others for growth-limiting resources, they may drive the relationship between productivity and richness. For example, more competitive species may exclude others of the same guild in high-productivity environments, resulting in a hump-shaped species richness–productivity relationship (SRPR) (Tilman, 1982; Mittelbach *et al.*, 2001; Pärtel *et al.*, 2007).

While the role of competitive exclusion has received considerable theoretical attention and empirical support at small spatial scales, competition may influence SRPRs indirectly at larger scales. When dominant species consistently change the microclimate for other species in the community, SRPRs may vary between these groups. For plants, temperature, water and light limit rates of photosynthesis and therefore growth. Climate determines the availability of these resources to entire communities, and climatic indices explain regional variation in productivity (Stephenson, 1998). However, the majority of productivity in forest communities occurs in the canopy (Kira *et al.*, 1969). As plants in the canopy grow, they increasingly shade shorter plants, limiting understorey productivity (Weiner, 1990; Muller-Landau *et al.*, 2006). Because forest plants vary in height at maturity, asymmetric competition for light subordinates shorter plants to a less productive environment for most of their life cycle.

In view of the consequences of vertical stratification in forest communities, a careful dissection of the overall relationship between richness and productivity in forests may reveal considerable complexity (Grubb, 1987). To the extent that actual productivity mediates climate–richness relationships, we hypothesize that (1) canopy plant richness responds more strongly to regional estimates of total forest productivity than understorey plant richness does. Given that shading mediates differences in productivity among strata, we further hypothesize that (2) understorey plant species richness is lower under more closed canopies. Furthermore, because shorter plants mature in more deeply shaded strata, we hypothesize that (3) forest growth forms that are relatively shorter at maturity show weaker responses to regional variation in productivity regardless of actual height. Finally, given that many models predict richness for all plants based solely on climate, we hypothesize that (4) the net effect of climatic energy on forest plant species richness is similar for all growth forms when it includes both direct effects through total community productivity and indirect effects on short plants through shading.

METHODS

Vegetation surveys

Primary data were collected by the Forest Inventory and Analysis (FIA) Program, operated by the USDA Forest Service (Miles *et al.*, 2001). We used all of the FIA data that met our criteria (see below) and that had been released at the time of our data capture. FIA plots consist of four subplots, each with a radius of 7.32 m. In each subplot, foresters measured all rooted trees 12.7 cm or larger in diameter at 1.3 m height. Nested within the subplots were 12 1-m^2 vegetation diversity quadrats. During the summer growing season, trained botanists recorded each species of vascular plants whose foliage intersects quadrat boundaries projected into the canopy. We included all plots where: (1) the FIA identified at least 10 of the 12 quadrats as being 'forested', (2) geographical information provided by the FIA could be used to estimate total productivity, and (3) canopy measurements had been taken within 3 years of the vegetation diversity survey. This provided us with 231 plots ranging from 34.0°–48.3° N latitude and from 75.0°–124.2° W longitude (Fig. 1), including softwood-dominated, hardwood-dominated and mixed stands.

Our measures of local species richness were derived solely from the 12 1-m^2 vegetation diversity quadrats, hereafter collectively referred to as a site. For a partition of total richness based on actual height, we classified each observed plant into one of two vertical strata based on plant height data recorded by the FIA at the time of survey. The canopy stratum is more productive and includes plants with most foliage higher than 2 m (primarily large shrubs and mature canopy trees). The understorey stratum is less productive and includes observations with most foliage below 2 m (primarily herbaceous plants, subshrubs and canopy tree seedlings).

We also classified the plants into one of three growth form categories using growth form designations in the USDA PLANTS database (USDA, NRCS 2007). The first category, hereafter referred to as 'herbaceous,' included all species designated as an 'herb', 'forb' or 'graminoid'; these are non-woody species that typically grow to < 2 m in height. The second category, 'shrub', included all species designated as a 'shrub' or 'subshrub'; these are woody species that typically grow to 0.5–5 m in height. The third category, 'canopy tree', included species either designated only as 'tree' or having a maximum height that exceeds 15 m. Species listed as 'vine' (about 5% of total), were absent from about half of the sites. Rather than analysing this rare growth form separately, we assigned these observations to the herbaceous category if their growth form was listed as 'vine, herb/forb' or to the woody non-canopy category if their growth form was designated as 'vine, shrub/subshrub.' Around 15% of all observations were not identified to species and could not be assigned to a category using PLANTS. Of these, any observation identified by a growth from (e.g. unidentified forb) was placed in that category (i.e. herbaceous). Observations identified to genus were assigned to a category if that genus is predominately (> 90%) of a single growth form (e.g. *Carex* = herbaceous). We excluded the remaining observations (4.7% of total) from all of our analyses.
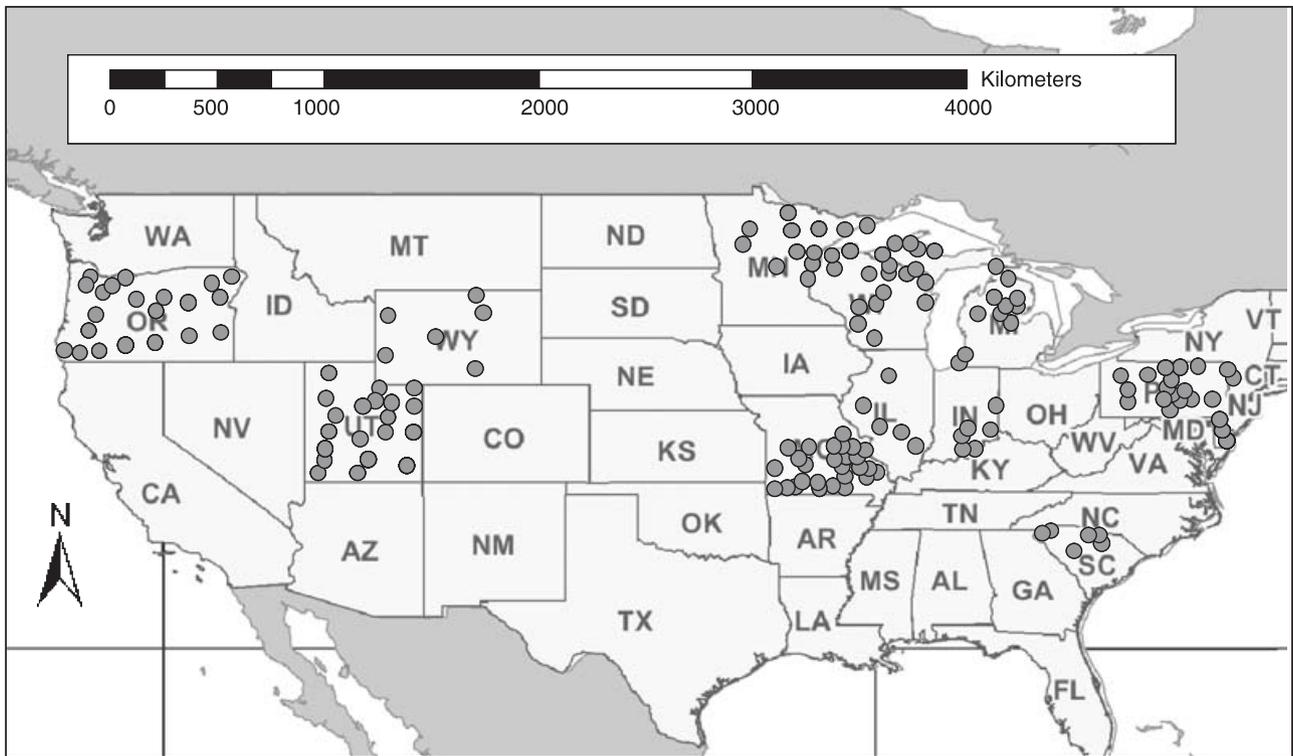
Figure 1 Map of site locations. Geographical coordinate system projected, WGS 1984 datum.

We estimated species richness as the number of remaining taxa. We used average richness at sites surveyed more than once.

Climatic variables

Privacy regulations prevent publication of precise geographical information for FIA sites. For an estimate of the influence of climate on total forest productivity, we mapped the geographical centroids of each county that contained a site onto a continental-scale actual evapotranspiration (AET) dataset (Shuttleworth–Wallace estimation) with a grid size of 0.5° × 0.5° compiled by Vörösmarty *et al.* (1998), using ArcGIS v9.1 (ESRI Inc.). AET estimates the amount of water that leaves the soil during the course of a year, based on climate and land cover. This index reflects climatic limitations on overall plant growth within a region. Because the average county size is smaller than the grid size of the climate dataset, we considered this to be a reasonably accurate regional estimate of total community productivity.

For a local estimate of the intensity of shading at each site, we analysed canopy data collected as part of the same program from the four 7.32-m radius subplots surrounding the vegetation diversity quadrats at each site. For each tree we calculated the area of its light-blocking tissue by multiplying crown density (the proportion of a tree's canopy that blocks light as viewed from below) by crown area (the area of the ellipse formed by perpendicular crown diameters). We summed across all trees for an index of local canopy density (CD) measured in square metres of light-blocking tissue. This measure is very similar to canopy cover, a common method for quantifying the intensity of local

shading (Jennings *et al.*, 1999). We only included sites where crown measurements were made for more than 80% of the trees in the subplots.

Statistical analyses

We used generalized linear models (GLMs) to characterize univariate SRPRs for the various partitions of forest richness. While count data from small sites should follow a Poisson distribution, the observed spatial clustering of sites (Fig. 1) may increase dispersion beyond the Poisson (McCullagh & Nelder, 1989), resulting in artificially small standard error estimates for parameters. Negative binomial regression accounts for this effect by modelling extra sources of variation, including spatial random effects, with an overdispersion parameter (Venables & Ripley, 1999). The approach performs similarly to alternatives that explicitly model spatial error structure (Gschlößl & Czado, 2006). Initial model comparisons confirmed overdispersion, so only negative binomial results are shown. Both stratum and growth form were coded as categorical variables with two and three levels respectively. For each partition (total richness, total richness by stratum, total richness by growth form, understorey richness and understorey richness by growth form) we tested reduced through second-order models with interactions. We selected among models for each partition using Akaike's information criterion (Akaike, 1974) and the Bayes information criterion (Schwarz, 1978). When these criteria selected simplified models or different full models, we used likelihood ratio tests to compare them. We used type-3 likelihood analyses to test
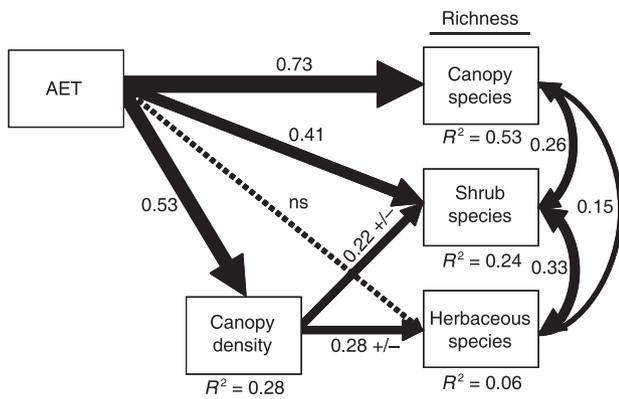
Figure 2 Structural equation model relating richness of different growth form categories based on relative height at maturity to total climate-based productivity measured by actual evapotranspiration (AET) including the indirect effect of shading as measured by canopy density (CD). Unidirectional arrows indicate a priori direct effects. Bidirectional arrows indicate correlated errors. Arrow size is approximately proportional to the magnitude of the path coefficient. The path coefficients marked with '+/–' indicate that the effect of CD on short growth form species richness is nonlinear.

significance of variables as main effects in best-fit models and we used custom linear contrasts to test for different SRPRs among different growth forms. We fit all models using SAS v. 9.0 PROC GENMOD (SAS Institute).

Multivariate analyses including both the direct effect of climate and its indirect effect on short plants through shading were conducted using structural equation modelling (SEM) (Grace, 2006) and the software MPLUS (Muthén & Muthén, Los Angeles, CA). The steps in the SEM analysis were as follows: first, an initial model was developed with the architecture shown in Fig. 2, with canopy tree richness, shrub richness and herbaceous richness as functions of AET, while including the mediator variable, CD, as a predictor of Shrub and Herbaceous richness. Second, a maximum-likelihood solution procedure was implemented in MPLUS that allowed for nonlinear effects of predictors on responses (using polynomial terms) (Grace, 2006, Chapter 7, pp. 192–195). Third, chi-square tests were used to evaluate the fit of data to the model. Fourth, individual parameters were tested for significance using single-degree of freedom chi-square tests for increasingly restricted models (where path coefficients having low z-values were set to zero). Fifth, for paths where multiple polynomial terms were significant, composite variables (modelled as zero-error latent variables) were used to capture the combined effects of the nonlinearity (Grace & Bollen, 2008). The result of these procedures was used to provide both an evaluation of the consistency of the data with the initial model and to provide a set of standardized parameter estimates that are comparable among linear and nonlinear pathways. The resulting path coefficients for directed paths (the single-headed arrows in Fig. 2; similar to regression coefficients) can be interpreted as measures of the degree of sensitivity of responses to predictors in terms of standard deviation units, while for non-directed paths (double-

headed arrows in Fig. 2), they represent the standardized residual correlations that do not imply directionality.

We examined the spatial structure of standardized residuals from each model using ARCGIS v9.1 (ESRI Inc.) We visually inspected maps for associations between extreme values (more than 2 SD from the predicted value) and biogeographical patterns. We also calculated spatial autocorrelation in the residuals using the global Moran's I statistic.

RESULTS

Overall, we found a positive relationship between vascular plant species richness and regional gradients in AET (Fig. 3a). The SRPR for the whole forest community showed no higher-order curvature beyond the simple exponential relationship fitted by the GLM (Table 1).

When total richness was partitioned into two vertical strata, the strength of the SRPR depended on the height of the plants (AET × stratum interaction, DF = 1, $\chi^2 = 12.8$, $P = 0.0004$; AET^2 × stratum interaction, DF = 1, $\chi^2 = 7.44$, $P = 0.0064$; Fig. 3b). Species richness of plants of height greater than 2 m increased with AET at a decelerating rate, while AET did not explain a significant amount of variation in richness among plants less than 2 m high (understorey AET, DF = 1, $\chi^2 = 0.86$, $P = 0.35$; understorey AET^2, DF = 1, $\chi^2 = 0.03$, $P = 0.85$).

Among plants in the understorey stratum, a model with CD fitted the data better than a model with AET (Table 1). Across the sampling area, richness of plants in the understorey was hump-shaped with respect to CD (Fig. 4), with low richness under both relatively open and relatively closed canopies.

When partitioning total richness into growth forms, the strength of the correlation between richness and total productivity depended on relative height at maturity (AET × growth form interaction, DF = 2, $\chi^2 = 36.9$, $P < 0.0001$; AET^2 × growth form interaction, DF = 2, $\chi^2 = 22.9$, $P < 0.0001$; Fig. 3c). Canopy tree species showed a positive decelerating relationship, while shrub species showed a weakly accelerating relationship. AET did not explain variation in herbaceous plant richness (herbaceous AET, DF = 1, $\chi^2 = 1.47$, $P = 0.23$; herbaceous AET^2, DF = 1, $\chi^2 = 1.31$, $P = 0.25$). SRPRs differed significantly among all pairs of growth forms (herbaceous versus shrub SRPR, DF = 2, $\chi^2 = 16.29$, $P = 0.0003$; herbaceous versus canopy tree SRPR, DF = 2, $\chi^2 = 112.71$, $P < 0.0001$; shrub versus canopy tree SRPR, DF = 2, $\chi^2 = 72.03$, $P < 0.0001$).

The differences among SRPRs for growth forms in the total community were similar to the differences among growth forms for SRPRs for plants in the understorey stratum (understorey AET × growth form interaction, DF = 2, $\chi^2 = 26.9$, $P < 0.0001$; understorey AET^2 × growth form interaction DF = 2, $\chi^2 = 16.1$, $P < 0.0001$; see Table S1 in Supporting Information). Canopy tree seedlings showed a positive decelerating relationship and small shrubs showed a weakly accelerating relationship, while herbaceous species again showed no relationship (herbaceous AET, DF = 1, $\chi^2 = 1.30$, $P = 0.25$; herbaceous AET^2, DF = 1, $\chi^2 = 1.17$, $P = 0.28$). SRPRs for growth forms in the understorey differed significantly in all pair-wise comparisons (understorey

Table 1 Generalized linear model comparisons for five partitions of the species richness dataset. Stratum (S) and growth form (GF) are categorical variables used to partition total forest richness as described in the text. Actual evapotranspiration (AET) and canopy density (CD) are estimates of regional productivity and the local effects of shading, respectively. All models include intercept and overdispersion parameters and were fitted using negative binomial error structure and a log link. Lowest Bayes information criterion (BIC) and Akaike information criterion (AIC) scores are in bold. Best-fit models are highlighted with an asterisk.

Partition		Model	n	Parameters	Log likelihood	BIC	AIC	Models	Likelihood ratio test Value	P
Total richness	1*	AET	231	3	18,781	**−37,545**	**−37,556**			
	2	AET AET^2	231	4	18,781	−37,540	−37,554	1 vs 2	0.39	0.533
Total richness by stratum (S)	1	S	462	3	16,401	−32,783	−32,795			
	2	S AET	462	4	16,433	−32,841	−32,857			
	3	S AET S × AET	462	5	16,444	**−32,858**	−32,879			
	4	S AET AET^2	462	5	16,434	−32,837	−32,858			
	5*	S AET AET^2 S × AET S × AET^2	462	7	16,450	−32,857	**−32,886**	5 vs 3	11.63	0.003
Total richness by growth form (GF)	1	GF	693	4	11,390	−22,753	−22,771			
	2	GF AET	693	5	11,434	−22,834	−22,857			
	3	GF AET AET^2	693	6	11,434	−22,828	−22,856			
	4	GF AET GF × AET	693	7	11,482	−22,919	−22,951			
	5*	GF AET GF × AET AET^2 GF × AET^2	693	10	11,495	**−22,925**	**−22,970**			
Understorey richness	1	AET	231	3	16,221	−32,426	−32,437			
	2	AET AET^2	231	4	16,221	−32,421	−32,435			
	3	CD	231	3	16,215	-32,413	−32,423			
	4*	CD CD^2	231	4	16,231	**−32,440**	**−32,453**			
Understorey richness by growth form (GF)	1	GF	693	4	10,067	−20,107	−20,125			
	2	GF AET	693	5	10,104	−20,175	−20,198			
	3	GF CD	693	5	10,075	−20,118	−20,140			
	4	GF AET AET^2	693	6	10,104	−20,169	−20,196			
	5	GF CD CD^2	693	6	10,107	−20,175	−20,202			
	6	GF AET AET × GF	693	7	10,152	**−20,257**	−20,289			
	7	GF CD CD × GF	693	7	10,088	−20,130	−20,162			
	8*	GF AET AET^2 GF × AET GF × AET^2	693	10	10,160	−20,255	**−20,300**	8 vs 6	17.03	0.001
	9	GF CD CD^2 GF × CD GF × CD^2	693	10	10,128	−20,191	−20,236			

herbaceous versus shrub SRPR, DF = 2, $\chi^2 = 13.95$, $P = 0.0009$; understorey herbaceous versus canopy tree SRPR, DF = 2, $\chi^2 = 104.99$, $P < 0.0001$; understorey canopy tree versus shrub SRPR, DF = 2, $\chi^2 = 67.12$, $P < 0.0001$).

A model of understorey richness that allowed different SRPRs for each growth form fit the data better than a model that allowed different reactions to CD among growth forms (Table 1). In the understorey, the relationship between CD and richness did vary among growth forms (Table S1). Canopy tree seedling richness tended to increase more with CD, and was more strongly peaked, compared with herbaceous plants and small shrubs (understorey herbaceous versus shrub CD relationship, DF = 2, $\chi^2 = 0.26$, $P = 0.8796$; understorey herbaceous versus canopy tree CD relationship, DF = 2, $\chi^2 = 36.68$, $P < 0.0001$; understorey shrub versus canopy tree CD relationship, DF = 2, $\chi^2 = 31.69$, $P < 0.0001$).

While incorporating the influence of CD explained additional variation in understorey plant species richness, it did not account for the variation in SRPRs among growth forms in our structural equation model. SEM analyses showed that the data were consistent with the initial model, with $\chi^2 = 0.021$ (DF = 1) and $P = 0.88$ (note that non-significant P-values indicate no significant deviations between model and data). The z-value (maximum likelihood equivalent of a t-value) for the path from AET to herbaceous richness was low, suggesting that the coefficient for this path might be indistinguishable from zero. With the coefficient for that path fixed to a value of 0, the model chi-square was 1.299 (DF = 2) and $P = 0.52$, confirming that this pathway is not necessary for an adequate description of the covariance structure of the data. Both first- and second-order moments of CD influenced shrub richness, as well as herbaceous richness, indicating that these were nonlinear pathways.

SEM results are shown in Fig. 2. Influences of AET on richness declined dramatically with decreasing position in the canopy. Also, CD itself increased with increasing AET and was found to be important only for richness of growth forms that mature in the understorey. The responses of shrub richness and herbaceous richness to canopy density were both nonlinear in multivariate space (which is what is represented in the SEM), consistent with what was observed in univariate space (Fig. 4). Residual
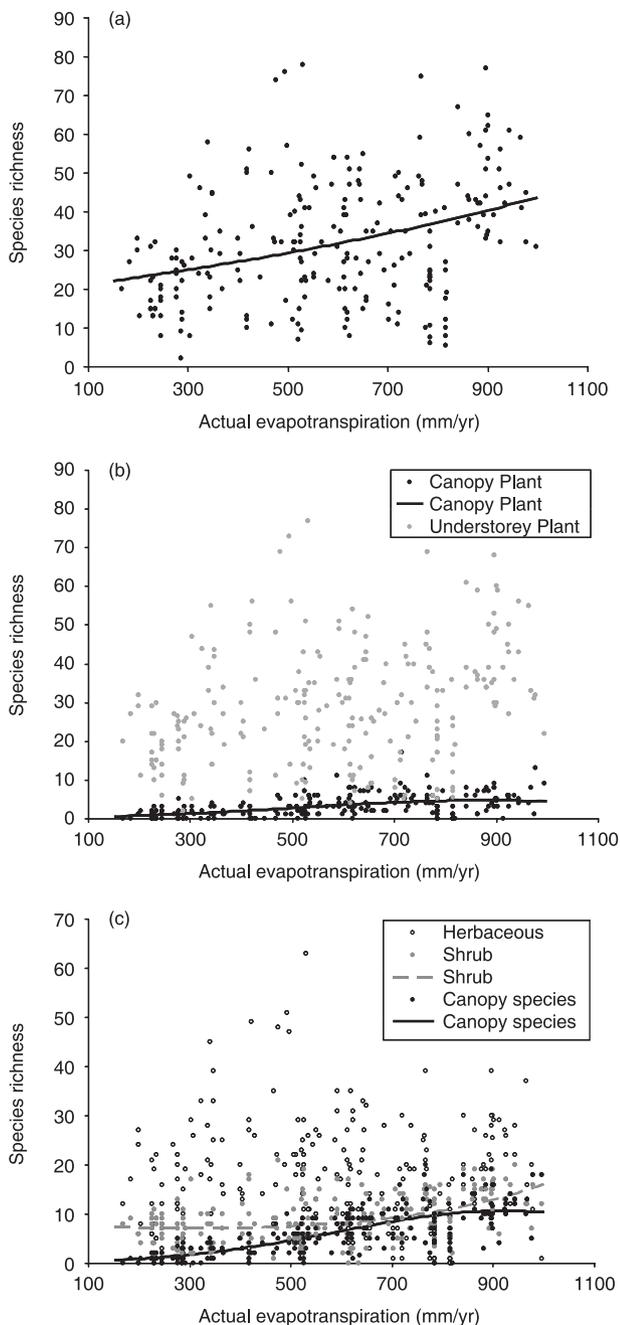
Figure 4 Species richness of plants less than 2 m high is hump-shaped with respect to local canopy density (CD) [understorey CD^2, DF = 1, χ^2 = 36.40, P < 0.0001; richness = exp(2.869 + 0.00368 × CD − 0.0000049 × CD^2)].

forms. The total effects of AET (including both direct and indirect pathways) on the three richness groups were as follows: canopy trees = 0.73, subcanopy trees/shrubs = 0.53, herbaceous species = 0.15.

The spatial distributions of residuals from the models tend to differ for each growth form (see Figure S1 in Supporting Information). Extreme residuals did not occur at the extremes of the AET gradient, nor were they clustered in any particular biogeographical region. In all cases residuals show weak but significant spatial clustering (global Moran's *I* ranging from 0.05−0.18, P < 0.01). In every model that contrasted different groups within the community, spatial autocorrelation was stronger for smaller plants (Table S2).

DISCUSSION

Consistent with previous studies conducted across broad geographical extents (Mittelbach *et al.*, 2001), we found that the richness of all vascular plants combined increased monotonically with a regional climatic estimate of productivity (Fig. 3a). However, when we separated the forest into strata based on height, we found that AET only explained variation in richness for plants taller than 2 m (Fig. 3b), despite understorey plants being almost nine times as species rich (Table S3). This result is consistent with our first hypothesis that tall plants, which are responsible for most productivity in forests, dominated the species richness–productivity relationship for the entire forest community.

Species richness of plants in the understorey is better explained by a local estimate of the amount of light-blocking tissue in the canopy (Table 1). Consistent with our second hypothesis, understorey richness was low under relatively closed canopies. However, richness was also low under relatively open canopies (Fig. 4). This hump-shaped relationship is commonly observed in studies at relatively small scales (Mittelbach *et al.*, 2001). Recent work has shown that in herbaceous plant communities, clonal species may dominate high-productivity environments, increasing the prevalence of hump-shaped SRPRs, while this trait is less common

Figure 3 Estimated species richness–productivity relationships for various partitions of vascular plant species richness. (a) Total richness increases monotonically with actual evapotranspiration (AET) [AET, DF = 1, χ^2 = 29.95, P < 0.0001; richness = exp(2.946 + 0.00079 × AET)]. (b) The strength of the species richness–productivity relationship (SRPR) increases with relative height. Plants in the canopy show a positive decelerating relationship, while plants in the understorey show no response. (c) The strength of the species richness–productivity relationship increases with relative height at maturity of the growth form.

correlations among richness values were significant for all pairwise cases, though they varied from modest (0.33) to weak (0.15) in strength, suggesting that some unmodelled factor(s) may weakly affect the species richness of plants across growth
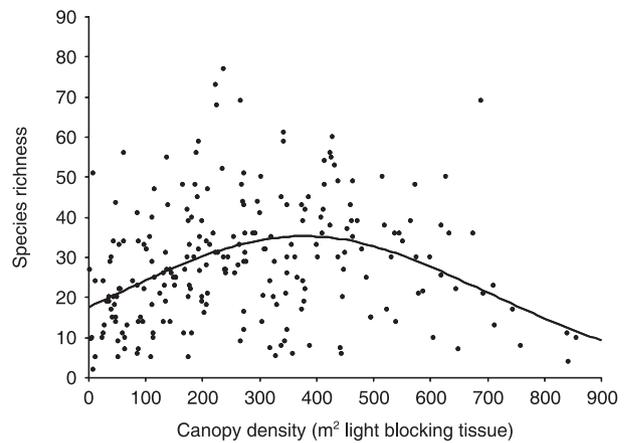
among woody growth forms, resulting in more monotonic SRPRs (Laanisto *et al.*, 2008). This difference in life history may contribute to variation in SRPRs among growth forms across habitat types. However, in our sampled forests, the shape of this relationship varied more strongly between canopy and subcanopy species rather than between woody and herbaceous species. Forests with open canopies may not have more productive understories. Rather, we suspect that the hump-shaped relationship between richness and canopy density results from a combination of mechanisms including higher microsite heterogeneity in light availability (Tilman & Pacala, 1993), and/or different times since canopy-disrupting disturbance (Connell, 1978), both of which could lead to higher probabilities of coexistence (and thus higher richness) under canopies that have intermediate density.

In addition to actual height, relative height at maturity influenced the strength of SRPRs (Fig. 3c). Consistent with our third hypothesis, canopy trees, which mature in the most productive stratum, exhibited a highly significant increase in richness with AET, shrubs exhibited a marginally significant increase, and herbaceous plant richness was not correlated with estimates of regional productivity. These differences remained when comparing herbaceous plant richness to small shrubs and canopy tree seedlings in the understorey (Table S1). The disparity was so pronounced that while CD provided the best model for cumulative understorey richness, when partitioned into separate growth forms AET provided a better model (Table 1). Thus, our findings strongly imply that growth form is an important trait that affects how species richness relates to productivity.

A SEM that includes the direct effect of climate on community productivity and the indirect effect of shading confirms that canopies are denser in more productive forests and that understorey richness relates to canopy density. The SEM also shows that regional estimates of total productivity have a stronger direct effect on species richness of taller growth forms, and that the indirect effect of competition for light is stronger for growth forms that are smaller. However, even after allowing for residual covariance in richness among growth forms, the ability of the model to explain richness patterns for canopy trees was much greater ($r^2 = 0.53$) than its ability to explain patterns for shrubs ($r^2 = 0.24$) and herbaceous species ($r^2 = 0.06$). This result is inconsistent with predictions from our fourth hypothesis and suggests that the mechanisms responsible for the maintenance of species richness below canopy trees are not as simple as an indirect consequence of asymmetric competition for light.

There are several likely reasons, both methodological and biological, for why our productivity model explained the majority of variation in richness for canopy trees but very little for herbaceous plants. We cannot exclude biogeographical influences on species richness. However, extreme data points show no obvious association with geography, so that regional biogeographical influences are unlikely to drive the patterns we observed. Furthermore, conventional models may overstate the significance of regression parameters when applied to spatially clustered data. This effect is associated with spatial autocorrelation among residuals. Our negative binomial model corrects for the influence of spatial error structure on significance statements

by including an overdispersion parameter. Therefore, the auto-correlation among our residuals reflects part of the correction for spatial data, rather than this problem of spatial data.

Furthermore, the sampling unit of this dataset is extremely small compared with many other macroecological studies. Stochastic effects may obscure the strength of SRPR observed. These effects should be strongest for the least abundant categories. However, the least abundant categories in this dataset (canopy trees) exhibit the strongest SRPRs (Table S3), suggesting that the differences we observe among growth forms are conservative.

In addition to the spatial configuration and sampling methodology, the time frame of sampling may influence the results. By including all vascular plants during the summer, this dataset focuses on competition for light when total productivity peaks, but excludes seasonality. Productivity varies seasonally, as does canopy density and understorey community composition in temperate forests. As such, seasonal variation may provide additional mechanisms that influence understorey richness. For instance, forests with deciduous canopies may show more seasonal variation in understorey community composition than forests with evergreen canopies if the phenologies of understorey species are adapted to avoid shade (Frank and Inouye, 1994).

Different responses to regional energy gradients among growth forms may also reflect biological differences among the groups of species. Among these, differences in lifespan (e.g. Richerson & Lum, 1980) and sensitivity to edaphic heterogeneity (e.g. Cornwell & Grubb, 2003; Grace & Keeley, 2006) may contribute. Both of these factors could weaken the response of short-lived, sensitive herbaceous plants to regional productivity, and contribute to the residual covariation we observed between herb and shrub species richness.

The inability of local canopy density to account for different SRPRs among growth forms suggests that mechanisms contributing to these differences are likely to be mediated at greater spatial or temporal scales where evolutionary processes could play a role (Harrison & Grace, 2007; Zobel & Pärtel, 2008). Differences among growth forms could reflect different evolutionary histories, if forest tree lineages tend to originate in the tropics (Wiens & Donoghue, 2004) while terrestrial herb lineages are predominately temperate (Guo & Ricklefs, 2000). Alternatively, if productivity directly influences speciation rate at large scales (Rohde, 1992), then canopy tree richness should increase more than herbaceous plant richness towards the tropics given that forest canopies are more productive than forest understories (Evans *et al.*, 2005).

Both evolutionary histories and evolutionary rates hypotheses predict that the proportion of canopy tree species in forest communities will increase towards the tropics, but neither predicts that terrestrial herbaceous richness will remain constant. Lavers and Field (2006) present a conceptual model that does. In their model, the physical environment limits plant growth, which influences the structural complexity of different habitats, such as forest canopy strata. Structurally complex habitats include a greater set of resource combinations that may provision a more diverse community through evolutionary time. If successive vertical strata in forests collectively deplete light and water resources to a baseline necessary for diversification, then diversity

in the lowest minimally productivity stratum may be similar across latitudes, while the proportion of total diversity represented by plants that diversified in that stratum (e.g. terrestrial herbaceous plants) decreases with increasing overall productivity. We observe both of these patterns in North American temperate forests. Two recent reviews of plot-based plant inventories suggest that these patterns extend into the tropics. Among 13 inventories of terrestrial herbaceous species richness from around the tropics, Costa (2004) reported only one study with greater species richness (74; Poulsen, 1996) than the maximum observed in our temperate dataset (63). In their study of global seed mass patterns Moles *et al.* (2007) report a dramatic decrease in the proportion of herbaceous plant species richness from the poles to the tropics. Our study together with these highlights a new latitudinal pattern that supports the Lavers and Field (2006) model in suggesting that evolution contributes to differences in large-extent richness patterns among growth forms and that forest herb communities share basic similarities.

In conclusion, we find that the mechanisms that contribute to species richness are likely to affect different functional groups of plant species in complex ways that are not obvious from composite patterns. In our study, herbaceous species made up over half of the species observed, and yet they statistically contribute nothing to the relationship between total forest richness and productivity, even after accounting for the indirect effects of productivity through shading. Differences among growth forms may have been invisible to other studies (e.g. Francis & Currie, 2003; see also Bhattarai & Vetaas, 2003; Pärtel *et al.*, 2007), in part because the most commonly applied forest survey methodologies have a minimum size that effectively excludes shrubs and herbs (e.g. Condit, 1998; Phillips *et al.*, 2003). As such, our results emphasize the importance of comparing interacting groups of species simultaneously in order to develop a comprehensive understanding how patterns of species richness relate to environmental gradients.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Maps of standardized residuals from the final structural equation model for each response with global autocorrelation coefficients (Moran's *I*).

Table S1. Generalized linear model results for three partitions of the species richness datasets.

Table S2. Global autocorrelation coefficients (Moran's *I*) for all responses in each best-fit model.

Table S3. Number of observations and taxa per plot in categories as described in the text (mean ± SE).

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