

PREDICTING TREE DIVERSITY ACROSS THE UNITED STATES AS A FUNCTION OF MODELED GROSS PRIMARY PRODUCTION

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Abstract. At the regional and continental scale, ecologists have theorized that spatial variation in biodiversity can be interpreted as a response to differences in climate. To test this theory we assumed that ecological constraints associated with current climatic conditions (2000–2004) might best be correlated with tree richness if expressed through satellite-derived measures of gross primary production (GPP), rather than the more commonly used, but less consistently derived, net primary production. To evaluate current patterns in tree diversity across the contiguous United States we acquired information on tree composition from the USDA Forest Service's Forest Inventory and Analysis program that represented more than 174 000 survey plots. We selected 2693 cells of 1000 km² within which a sufficient number of plots were available to estimate tree richness per hectare. Our estimates of forest productivity varied from simple vegetation indices indicative of the fraction of light intercepted by canopies at 16-d intervals, a product from the MODIS (Moderate Resolution Imaging Spectro-radiometer), to 8- and 10-d GPP products derived with minimal climatic data (MODIS) and SPOT-Vegetation (Système Pour l'Observation de la Terre), to 3-PGS (Physiological Principles Predicting Growth with Satellites), which requires both climate and soil data. Across the contiguous United States, modeled predictions of gross productivity accounted for between 51% and 77% of the recorded spatial variation in tree diversity, which ranged from 2 to 67 species per hectare. When the analyses were concentrated within nine broadly defined ecoregions, predictive relations largely disappeared. Only 3-PGS predictions fit a theorized unimodal function by being able to distinguish highly productive forests in the Pacific Northwest that support lower than expected tree diversity. Other models predicted a continuous steep rise in tree diversity with increasing productivity, and did so with generally better or nearly equal precision with fewer data requirements.

Key words: 3-PGS; gross primary production; Moderate Resolution Imaging Spectroradiometer; remote sensing, process-based models; Système Pour l'Observation de la Terre; tree species richness; USDA, Forest Inventory and Analysis.

INTRODUCTION

Over the last few decades, ecologists have expanded their effort to predict biological diversity as a function of climate at both the regional (Currie and Paquin 1987, O'Brien, 1998, Hawkins et al. 2003, Venevsky and Veneskaia 2003) and global scale (Latham and Ricklefs 1993, Gaston 2000, Kleidon and Mooney 2000). This expanded interest is justified on the basis of accelerated extinction and the expectation that a major reconfiguration of vegetation patterns will occur during this century (Iverson and Prasad 2001).

The paleobotanical record provides evidence that a changing climate obliterates major associations and causes new ones to be formed (Axelrod et al. 1991). For this reason, most analyses dealing with climatically

driven changes in vegetation have relied on range maps of individual species rather than that of plant associations. Many range maps, however, fail to recognize conversion of land to other uses and ignore gaps caused by mountainous terrain. In the United States we have an alternative to range maps: systematic surveys of forest composition are available through the USDA Forest Service's Forest Inventory and Analysis (FIA) program (*available online*).⁵ These FIA surveys are periodically repeated, providing a basis for evaluating spatial changes in species composition and diversity over time.

Although there is considerable debate about the extent that causal relationships associated with competition and disturbance apply over a range of spatial scales (O'Brien 1998, Huston 1999, Whittaker and Field 2000), there is a consensus that historical factors must be recognized to explain differences in the pool of species present in different areas that today share similar

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⁵ (<http://ncrs2.fs.fed.us/4801/fiadb/>)

TABLE 1. Data requirements for models used to derive estimates of forest productivity across the United States.

Model	Satellite data	Climate data	Light-use efficiency	Soils data
MODIS NDVI, EVI MODIS GPP	NDVI, EVI MODIS fPAR	temperature, radiation, and vapor pressure deficit	biome-defined maximum ϵ	
SPOT GPP	fPAR derived from SPOT and NOAA AVHRR NDVI data	temperature dependency factor, radiation, fertilization factor, and climate efficiency	ϵ fixed for all vegetation types	
3-PGS	MODIS fPAR	temperature, radiation, vapor pressure deficit, frost, and precipitation	fertility index from soil nitrogen	soil water balance

Notes: Models are arranged with complexity increasing from top to bottom rows and are identified in detail in *Materials and methods*. Measurements are: GPP, gross primary production; NDVI and EVI, normalized difference vegetation and the enhanced vegetation indices; fPAR, fraction of photosynthetically active radiation absorbed by vegetation; and ϵ , maximum canopy radiation use efficiency (g C/MJ absorbed PAR).

climates (Qian and Ricklefs 2000). In addition, there should be some consideration of disturbance and fragmentation of the landscape, although these factors are generally dwarfed by the overriding influence of climate on species distributions (see review by Sarr et al. [2005]).

The climatic variables most often associated with species distributions include annual means of temperature, precipitation, and potential (or actual) evaporation. Ideally, seasonal variation in temperature and precipitation patterns should be taken into account. To accommodate more refined climatic analyses, many ecologists have chosen to model annual net primary production (NPP), as it serves as a good biological expression of climatic constraints on growth and correlates well with species diversity (Hawkins et al. 2003).

Unfortunately, there are few places where NPP is measured directly. Usually NPP is modeled as a function of climatic (and sometimes soil) variables. In recent decades, the modeling of NPP has taken into account seasonal and interannual variation in climate using process-based growth models (see reviews by Landsberg [2003] and Nightingale et al. [2004]). These types of models allow one to recognize which climatic factor most constrains productivity across regions and continents (e.g., Nemani et al. 2003).

Although process-based models differ substantially in how respiration is calculated and growth is allocated, they generally estimate photosynthesis in a fairly consistent manner. For this reason, we favor generating spatial estimates of gross primary production (GPP) rather than NPP (Swenson and Waring 2006). Satellites orbiting the Earth since the 1960s provide a means of estimating seasonal and interannual variation in vegetation cover (Skole and Tucker 1993, Mildrexler et al. 2007). It is through this technology that changes in the length of the growing season have been documented (Schwartz et al. 2002). In general, GPP increases with a lengthening of the growing season, the less harsh the dormant season, and the more fertile the soil. Seasonal drought and infertile soils limit GPP, not only because photosynthetic capacity and activity are reduced, but also because fewer leaves are produced to intercept

sunlight with an increasing proportion of NPP allocated below ground. In recent years satellite coverage has greatly improved in spatial and spectral resolution (Running et al. 2004). As a result, GPP estimates derived from models with different data requirements are readily available for comparison.

Here we take advantage of satellite-derived information on spatial variation in climate and forest cover, along with ground-based surveys of forest composition, to evaluate the extent that tree diversity can be predicted across the continuous United States with three different models and two simple satellite-derived "greenness" indices. In a previous paper, we reported that variation in growing season greenness could account for between 60% and 80% of the observed variation in tree richness across 65 partially forested ecoregions, with the higher value attained by excluding ecoregions with <50% forest cover (Waring et al. 2006). In this paper we evaluate the extent to which different models of gross productivity account for variation in tree richness at two spatial scales: all currently forested areas in the contiguous United States, and within nine broadly defined ecoregions, in which one might expect to encounter sufficient variation to yield significant relationships between GPP and tree diversity.

MATERIALS AND METHODS

The models used to estimate gross primary production (GPP) for this study represent a range in data requirements (Table 1). The simplest model used 16-day MODIS (Moderate Resolution Imaging Spectroradiometer) vegetation indices including the normalized difference vegetation index and the enhanced vegetation index (NDVI and EVI, respectively) as surrogates for productivity (Goward and Dye 1987, Waring et al. 2006). We also evaluated the 8-day MODIS and 10-day SPOT-Vegetation (Système Pour l'Observation de la Terre) products that predict GPP based on the radiation use efficiency (RUE) concept of Monteith (1972, 1977). Both GPP products require a satellite-derived estimate of the fraction of photosynthetically active radiation absorbed by vegetation (fPAR), and an independent estimate of maximum canopy radiation use efficiency (ϵ), as well as three climatic variables (i.e., solar

radiation, temperature, and vapor pressure deficit) that further restrict gas exchange. The SPOT GPP product includes a fertilization factor to account for a presumed increase in carbon assimilation associated with elevated CO₂ concentrations since the industrial revolution (Veroustraete et al. 2002), as well as a simple climate efficiency factor derived from Mc Cree (1972). The most complex model, 3-PGS (Physiological Principles Predicting Growth with Satellites), applies a similar RUE-based approach but demands additional climate data (frost days and precipitation) as well as estimates of soil water holding capacity and fertility to estimate GPP.

GPP data

SPOT GPP annual product.—We derived annual GPP estimates from SPOT NPP products by taking into account carbon losses via autotrophic respiration, R_a (Eq. 1a); the latter variable was assumed to be a simple linear function of mean daily temperature (Eq. 1b; Goward and Dye 1987). We recognize that an exponential relationship between air temperature and respiration is more commonly assumed, but this is just one of the differences among models associated with calculating NPP.

The stated formal calculation of GPP for the SPOT model (Eq. 1c) is based on the Monteith-RUE approach and requires information on fPAR, derived from SPOT and the National Oceanic and Atmospheric Administration (NOAA) Advanced Very High Resolution Radiometer (AVHRR), and daily incoming solar radiation and mean daily air temperature (Sabbe and Veroustraete 2000). Ten-day integrated global SPOT-Vegetation NPP surfaces were acquired for the five-year period (January 2000–December 2004). We used average monthly temperature data to calculate respiration (R_a). Annual averaged GPP was calculated by summing values for each 10-d period in sequential years:

$$\text{NPP} = \text{GPP} \times (1 - R_a) \quad (1a)$$

$$R_a = 7.825 + 1.145T \quad (1b)$$

$$\text{GPP} = [S \times C \times \text{fPAR} \times \varepsilon \times p(T) \times \text{CO}_2 \text{ fert}] \quad (1c)$$

where S is global solar radiation (MJ·m⁻²·d⁻¹); C is climate efficiency (McCree 1972); fPAR is fraction of absorbed photosynthetically active radiation derived from NDVI; ε is photosynthetic efficiency (g C/MJ absorbed PAR; Wofsy et al. 1993); $p(T)$ is normalized temperature dependency factor; CO₂ fert is normalized CO₂ fertilization factor (Veroustraete et al. 2002); R_a is percentage of gross photosynthesis consumed as respiration, modeled with Eq. 1b (Goward and Dye 1987:167); and T is temperature (°C).

Annual MODIS vegetation indices.—Since 2000, the MODIS instrument onboard NASA's Terra platform has collected data in seven spectral bands that were explicitly designed for land surface monitoring (Justice

et al. 1997, Justice and Townsend 2002). We acquired both the normalized difference vegetation index (NDVI) and the enhanced vegetation index (EVI) from the MODIS earth observation system (EOS) data gateway. The EVI is less sensitive to soil and atmospheric effects, through the inclusion of blue spectral wavelengths, and remains sensitive to increases in canopy density somewhat beyond where NDVI becomes saturated (Huete et al. 2002). Averaged annual maximum (2000–2004) NDVI and EVI were derived for this study. EVI is calculated as

$$\text{EVI} = G \frac{\text{NIR} - R}{\text{NIR} + C_1R - C_2B + L} \quad (2)$$

where NIR, R , and B are reflectances in the near infrared, red, and blue bands, respectively. C_1 and C_2 are aerosol resistance coefficients ($C_1 = 6$; $C_2 = 7.5$); G is the gain factor ($G = 2.5$); and L is the canopy background adjustment that addresses nonlinear, differential NIR and radiant transfer through a canopy ($L = 1$).

MODIS GPP annual.—MODIS standard vegetation index products are provided as 16-d composite images at 1-km resolution. A full description of the model is provided elsewhere (Running et al. 2004). For the United States, five years (January 2000–December 2004) of MOD-17 collection 4.5, 8-d GPP data were acquired from the Numerical Terradynamics Simulation Group at the University of Montana (data *available online*).⁶ Annual GPP values were derived by summing values for 8-d periods each year and then averaging over the 5-yr period. This model calculates respiration as an exponential function of air temperature and assumes that a fixed proportion of NPP is allocated to roots.

3-PGS annual GPP.—3-PGS was developed by Coops et al. (1998) as a simplified version of the original 3-PG model (Landsberg and Waring 1997). It is driven primarily by photosynthetically active radiation (PAR), fPAR provided as a MODIS product, a photosynthetic efficiency term related to soil nitrogen content, and monthly climatic data that include averaged daily radiation, vapor pressure deficits, temperature extremes, and the number of days of frost, which together constrain photosynthesis (and transpiration) below their potentials. In contrast to other models, NPP is derived as a fixed ratio of GPP, and the fraction allocated to roots decreases as GPP increases. A more detailed description of the model as well as the data sets and methods used to calculate forest GPP across the United States are presented elsewhere (Nightingale et al. 2007).

Growing season GPP.—Previous studies have emphasized that competition for resources is most intense during the growing season (e.g., Waring et al. 2002). Because many forests contain a mixture of evergreen and deciduous tree species, we compare GPP estimates for the growing season as well as for the entire year. To

⁶ (<http://www.ntsug.umt.edu/>)

define the growing season, we used the seasonal-midpoint technique (White et al. 1997, Schwartz et al. 2002) with MODIS EVI data. The approach involves finding the midpoint between the minimum and maximum 5-yr averaged EVI for each forested pixel within the United States. We determined the growing season for each GPP data set based on each model's minimum time step (i.e., 8-d for MODIS, 10-d for SPOT, and monthly for 3-PGS). During the period for which EVI rose above the midpoint value, GPP was summed to provide a growing season value.

Estimates of tree species richness

A total of 174 207 field plots of tree composition were acquired from the USDA Forest Service's Forest Inventory and Analysis (FIA) database. FIA surveys were originally conducted using variable radius plots, where sampling area varies as a function of prism angle size and distance of trees from a central sampling point. Although the sampled area can be estimated from mean tree diameter, large variations around the mean result in questionable estimates of tree species richness per unit area. Over the last five years, FIA surveys have adopted a standard fixed-radius plot layout, covering a total area of 0.067 ha or 17 fixed-area plots/ha (USDA 2004). Fixed-radius plots, however, are only available for a limited number of states and the sampling density is sparse compared to variable-radius plots. To use the more extensive variable-radius plot data, we derived a conversion where two independent estimates of species richness for both types of samples were available within the same 1000-km² cell:

$$y = 5.096 + 0.837x \quad (3)$$

where x is the number of species recorded on 17 variable-area plots, and y is the number of species recorded on 17 (equivalent to 1 ha) fixed-area plots ($r^2 = 0.74$).

To protect proprietary information on private land, the FIA program has established a policy of offsetting some plots locations by up to 1.6 km. To maintain ecological integrity, plot locations are not transferred to areas representing different types of forests. For most forest attributes, research has shown that the effects of these spatial redistributions are negligible for areas the size that we use in this study (McRoberts et al. 2005).

To obtain a satisfactory species-area curve that approached an asymptote, at least 15 FIA plots were required within a 1000-km² cell. With a sample of 15 or more, a logarithmic relation between the accumulated number of species and increasing plot area produced an $r^2 > 0.95$ for 96% of the 2693 forested cells sampled. Because the surveys may start or stop in areas with high or low species diversity, we smoothed the curves by averaging the results attained from four sequential analyses; first by listing plots for each set of cells by number of species recorded in ascending order, then in descending order, before randomly reordering the sequence twice. As the number of plots sampled within

a 1000-km² unit often far exceeded the minimum of 15, we standardized estimates for 17 fixed-radius plots, equivalent to one hectare, based on cell-specific slope and intercept values derived from a log-function of each species-area curve. Fig. 1a shows the 1000-km² sampling grid across the United States and the estimated tree species richness per hectare in each qualified cell. The species lists, presented with both common and scientific names, for the designated ecoregions and each qualified 1000-km² cell are available online.⁷ The source of these lists should be appropriately acknowledged.

Regional classification and analysis of tree richness-productivity relationships

Ecoregions and forest classification.—Forested areas across the United States were defined using the MODIS-derived UMD (University of Maryland) land cover classification scheme. We further stratified the analysis into nine broad ecoregions (Fig. 1b) using the level I classification of North America from the U.S. Environmental Protection Agency (EPA) (available online).⁸ Ecoregions are recognized as areas with some commonality in physiography, vegetation, and climate (CEC 1997).

Comparison of GPP and tree richness data.—We extracted an estimate of 5-yr averaged GPP from each data set for all forested pixels located within each qualified 1000-km² grid cell. Simple ordinary least squares regression analyses were applied to evaluate the best statistical relationship between estimates of GPP and tree species richness across the entire country and within each of the nine recognized ecoregions.

RESULTS

Estimates of GPP

Across the country, all modeled estimates of GPP for forested areas averaged between 10 and 15 Mg C·ha⁻¹·yr⁻¹. Although productivity estimates were highly correlated among models (Table 2), 3-PGS predicted the widest range in values. In Fig. 2, the maximum 5-yr averages of NDVI and EVI values are plotted in reference to annual GPP values derived with 3-PGS. Both vegetation indices saturate at levels of productivity below 15 Mg C·ha⁻¹·yr⁻¹, leaving potentially 25% of the forested area assigned higher values of GPP indiscernible.

Productivity comparisons with species richness

Graphs showing the statistical best fit between predicted productivity and tree richness data are presented for the various models in Fig. 3. Only the 3-PGS model fit a polynomial (unimodal) relation as a result of being able to discriminate differences in soil

⁷ <http://loki.stockton.edu/~fanw/>

⁸ <http://www.epa.gov/wed/pages/ecoregions.htm>

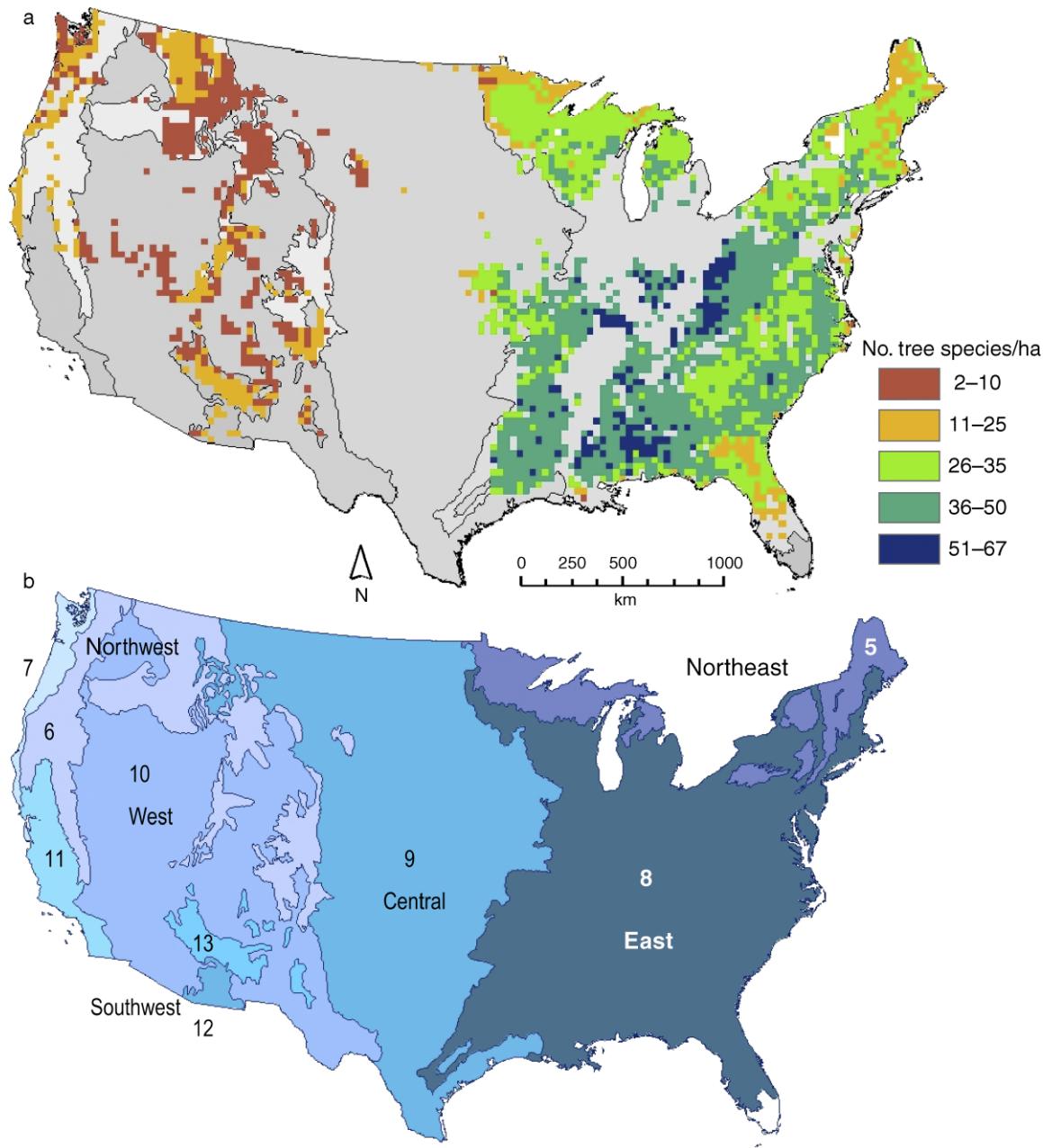


FIG. 1. (a) Map showing the distribution of tree species richness recorded in 2693 sampled 1000-km² cells across the United States, derived from the USDA Forest Service's Forest Inventory and Analysis (FIA) database. (b) Delineation of level I EPA ecoregions (with their original assigned numbers) are color-coded from light blue in the west to darker blue in the east, reflecting the general pattern of increasing tree richness from west to east across the country.

properties associated with highly productive forests that contain only a few tree species. The other models fit exponential or power functions that predicted a continued steep rise in tree richness with increases in GPP (Fig. 3). The SPOT growing-season model accounted for the highest variation in tree richness (77%), whereas the 3-PGS model accounted for the least variation (52–53%). The least data-demanding models using maximum vegetation indices, NDVI or EVI,

accounted for more variation (55% and 68%, respectively) than the most data-demanding 3-PGS model.

Maps comparing estimates of GPP from MODIS, SPOT, and 3-PGS show general agreement in spatial patterns (Fig. 4). Areas with low productivity (<10 Mg C·ha⁻¹·yr⁻¹) are located in the central west (not to be confused with the coastal west) and southwest United States, and support few tree species (Fig. 1a). Forests with moderate levels of productivity (10–20 Mg

TABLE 2. Correlation matrix for models used to predict forest productivity.

GPP measure	3-PGS	MODIS	SPOT	3-PGS GS	MODIS GS	SPOT GS	Av max NDVI	Av max EVI
3-PGS	1	0.77	0.69	0.96	0.77	0.63	0.68	0.69
MODIS		1	0.91	0.48	0.85	0.69	0.66	0.59
SPOT			1	0.43	0.78	0.80	0.62	0.61
3-PGS GS				1	0.71	0.66	0.74	0.78
MODIS GS					1	0.90	0.85	0.84
SPOT GS						1	0.80	0.86
Av max NDVI							1	0.89

Notes: See the *Materials and methods* section for definitions of abbreviations used on this table. "GS" = growing season; "Av max" = averaged annual maximum.

$\text{C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) are located mainly in the east and northeast United States and support a moderate to high complement of tree species (Fig. 1a). The highest range in GPP values ($20\text{--}30 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) occurs predominately in the northwestern part of the country within the maritime influence of the Pacific Ocean. This area is clearly distinguished with the 3-PGS model, but is less well delineated by the other process-based models (Fig. 4) or by the vegetation indices (Waring et al. 2006: Fig. 2). Elsewhere, the biggest discrepancies among model predictions were in the southeast where 3-PGS predicted GPP values between 10 and 15 $\text{Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ while the MODIS and SPOT models were generally higher, between 15 and 20 $\text{Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (Fig. 4).

No significant associations between tree richness and GPP were apparent for the majority of individual level 1

ecoregions. The central ecoregion (Number 9 in Fig. 1b) was the only one to encompass a sufficiently full range in forest productivity derived with the 3-PGS model to generate a power or polynomial relationship that accounted for $>30\%$ of the observed variation in tree richness.

DISCUSSION

Productivity estimates

In regard to using vegetation indices or modeled estimates of GPP as surrogates for potential productivity, we might conclude for this study that the simpler the formulation, the better. The correlation matrix presented in Table 2 indicates that predictions of productivity were closely associated with one another. This would not be the case if we had compared NPP values. The

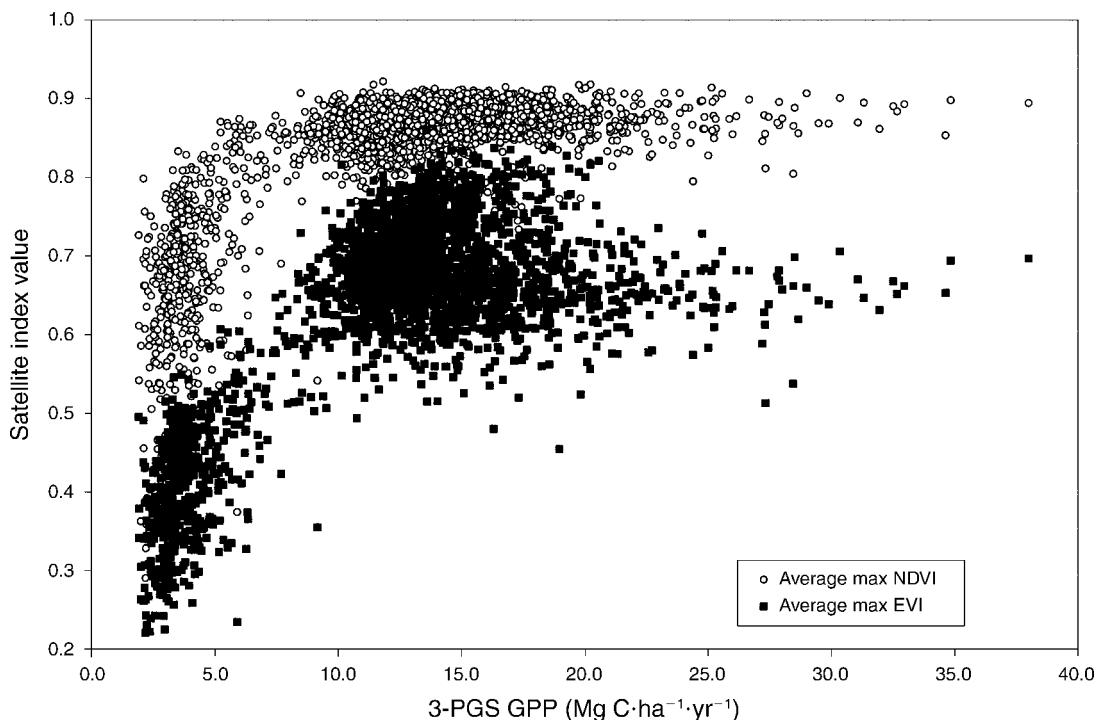


FIG. 2. In reference to 3-PGS estimates of GPP, averaged maximum annual values of normalized difference vegetation and the enhanced vegetation indices (NDVI and EVI) saturate at $<15 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. No units are associated with the satellite index: values are dimensionless, scaled between 0 and 1.

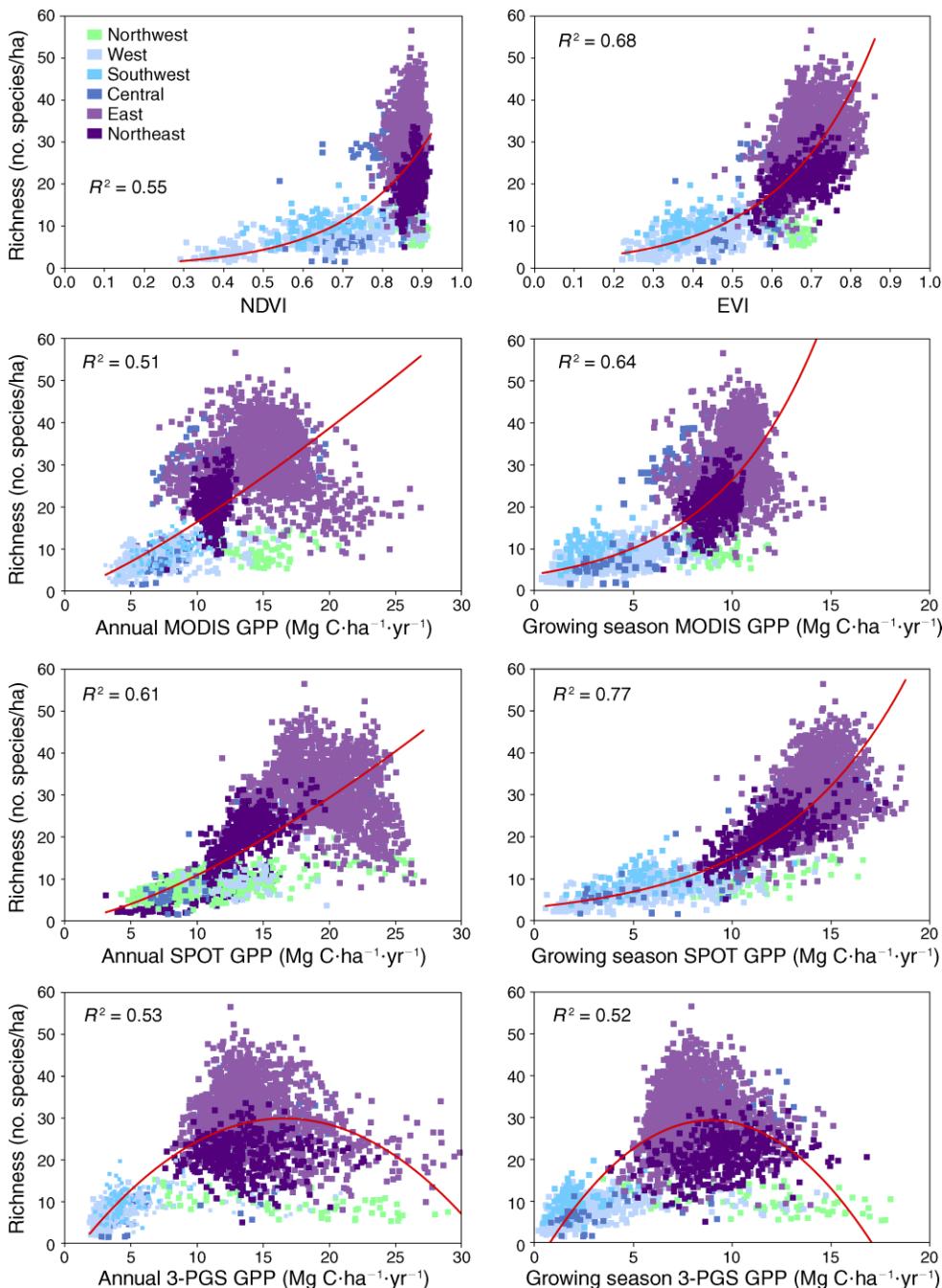


FIG. 3. Association between modeled estimates of 5-yr averaged annual and growing season GPP, or maximum values of NDVI and EVI, and tree species richness per hectare within 2693 1000-km² cells distributed across the United States.

maximum EVI has an average correlation coefficient of 0.75 with the other seven formulations, including annual and growing season estimates of GPP.

Differences among model predictions are apparent, however, as shown in Fig. 4. Because all three process-based models use fPAR and solar radiation in computing GPP at 1 km resolution, those variables are not involved in explaining spatial variation in predicted

GPP. Nor is the degree of disturbance within 1000 km² likely to be a factor, because only units recognized as forested were analyzed. The major difference among the three models is that 3-PGS requires soil information. With such data (and precipitation), 3-PGS computes site-specific water balances and assigns values to soil fertility that define the maximum photosynthetic efficiency (ϵ). These differences in model requirements for

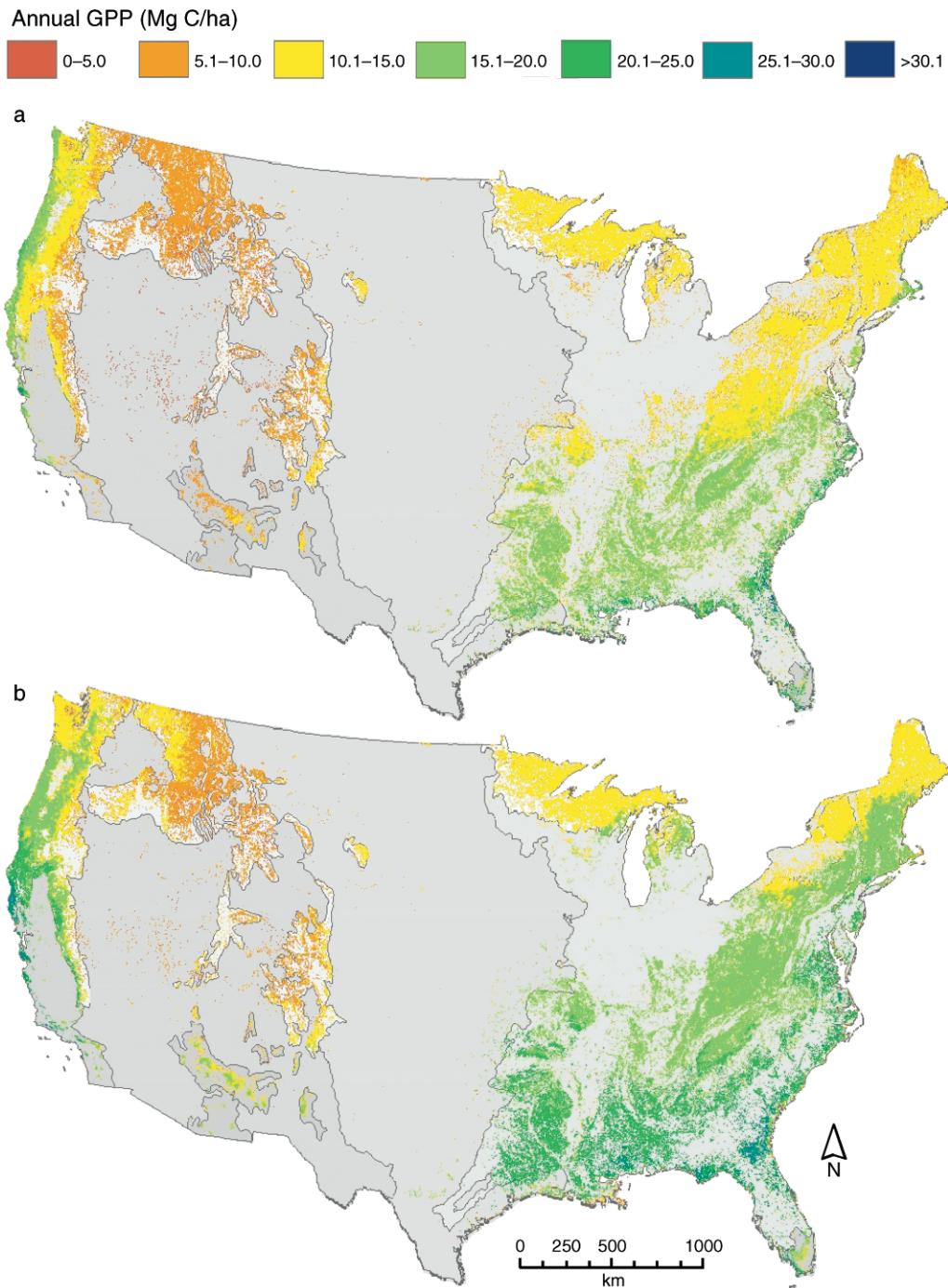


FIG. 4. Spatial distributions of mean annual GPP across forested areas in the United States predicted by the three process-based models: (a) MODIS, (b) SPOT, and (c) 3-PGS.

soil data explain why GPP values generated by 3-PGS are lower than MODIS or SPOT model projections in drought-prone regions of the central west, and in presumably nutrient-deficient areas in the southeast (Fig. 4). Nightingale et al. (2007) present a detailed comparison of MODIS and 3-PGS with sensitivity analyses. The difficulties of attaining reliable soil data

on water holding capacity and nutrient content are challenging enough at point sources. Extrapolation of soil information to regions and continents, while admittedly inaccurate, allows identification of areas where refinement in measurements would be most valuable (e.g., in Fig. 4, the central west and southeast regions).

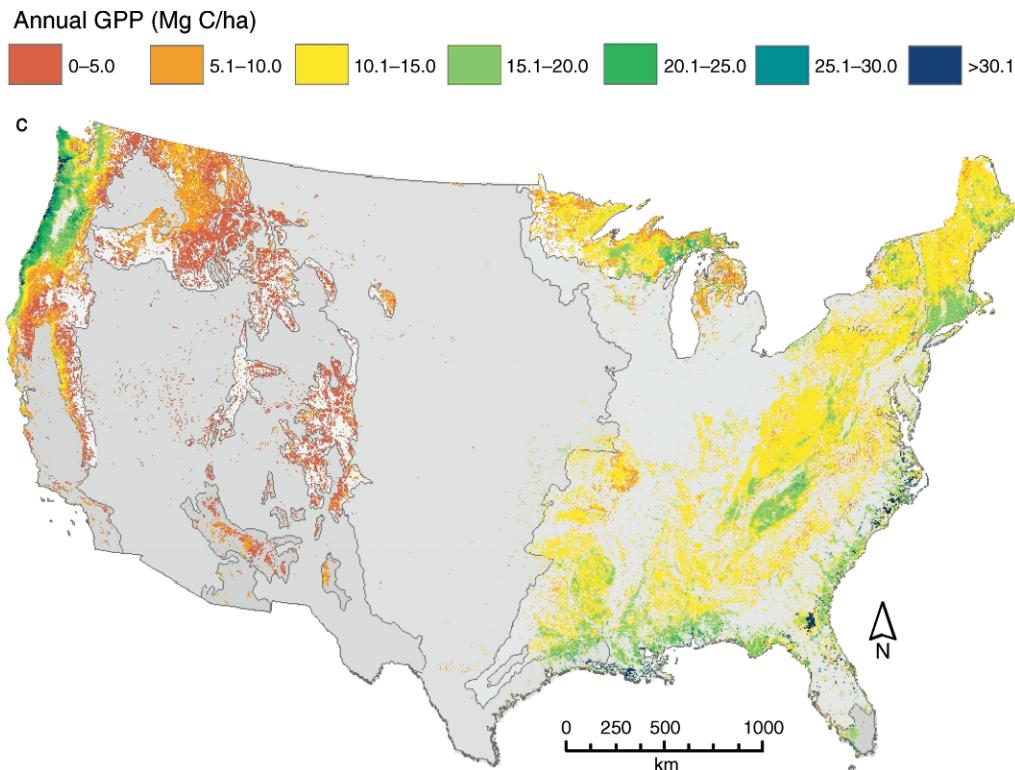


FIG. 4. Continued.

In concert with any future field surveys, it would be desirable to provide site-specific measures of potential aboveground NPP, attained through age and height measurements on dominant and codominant trees unconstrained by competition throughout their life. Such data are not available from the FIA databases due to compositing of information from trees of different species and ages.

Tree diversity

Tree diversity data were critical to our analysis of the status of vegetation under current climatic conditions (2000–2004). Range maps have served as alternative sources for analyses similar to those presented here (Currie and Paquin 1987), but lack the dynamics provided by sequentially acquired (decadal) field surveys. The broad geographic patterns in tree diversity presented in Fig. 1a, although similar to those one might generate from historical range maps, provide a standard for future maps that might be expected to differ as a result of climate change and land conversion from indigenous forests.

The scale of analyses at a resolution of 1000 km² in our study was as refined as the FIA database would allow. Estimation of tree diversity per hectare, derived through conversion of variable-radius to fixed-area plots, is a major step forward in providing a benchmark for future comparisons. It would be desirable to have the precise location of all survey plots and to increase plot

sizes to a hectare. Provided with such field surveys, the extrapolation of climatic and vegetation data would be more comparable. Alternatively, exact locations of plots might not be required if 10 ha of fixed-area plots were available within a 10 × 10 km cell. With such a database, Swenson and Waring (2006) were able to account for 70% of the observed variation in tree richness predicted with modeled GPP across the states of Oregon and Washington compared with 16% of the variation accounted for with only an accumulated area of 1 ha (FIA) sample per 100-km² cell.

Productivity–tree diversity relationships

Across the United States, modeled estimates of annual or growing season GPP, or maximum values of NDVI and EVI, served as reasonably good predictors of tree diversity. We expected GPP to be a good integrator of climatic (and soil) constraints on productivity, and one for which sensitivity analyses permits identification of the most restrictive environmental factor (e.g., Nemani et al. 2003). In regards to future comparisons, if climatic variation was the major cause in modifying tree richness patterns, we would expect a close correlation between maximum NDVI or EVI and MODIS and SPOT predictions of GPP, because the latter models are constrained primarily by climate, whereas the vegetation indices are sensitive to disturbance as well. Thus if fire, air pollution, hurricanes, or other disturbances result in forest conversion, or significantly reduced canopies, the

vegetation indices would not be expected to remain in close correlation with estimates of GPP. The MODIS satellite quantifies annually at 1-km resolution the degree of disturbance by combining information from EVI with that acquired with thermal bands to confirm changes in land cover over time (Mildrexler et al. 2007).

We were surprised that better correlations between GPP and tree diversity were not found within more than one (Number 9) of the nine broadly defined ecoregions. In part, this may reflect too narrow a range in environments (and GPP), as demonstrated by the clustering of data points in Fig. 3, color-coded to match ecoregions delineated in Fig. 1b. Swenson and Waring (2006) confirmed that pooling data across just two broad ecoregions in the Pacific Northwest (Numbers 6 and 7) provided a full of range in productivity as measured across the continent, and produced good correlation between modeled GPP and tree diversity. In addition, FIA plot sizes are extremely small, requiring 1000-km² grid cells to gain an adequate sample for estimating species richness per unit area. A 10-fold increase in plot size would permit a similar reduction in the size of grid cells, with corresponding reduction in local environmental variation (Swenson and Waring 2006).

Whether the hypothesized reason for reduced tree diversity at high levels of productivity (competition for light) is true remains in doubt until finer resolution analyses can be made. Only in the Pacific Northwest did we find high levels of productivity associated with low levels of tree diversity. The Pacific Northwest is a region recognized to have lost a much richer flora during the late Pliocene; thus evolutionary history may play a role in the relationship reported between 3-PGS estimates of GPP and country-wide patterns in tree diversity (Waring et al. 2006).

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