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Modelled photosynthesis predicts woody plant richness at three geographic scales across the north-western United States

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ABSTRACT

Aim We analyse regional patterns of woody plant species richness collected from field data in relation to modelled gross photosynthesis, P_g , compare the performance of P_g in relation to other productivity surrogates, and examine the effect of increasing scale on the productivity–richness relationship.

Location The forested areas in the north-western states of Oregon, Washington, Idaho, and Montana, USA.

Methods Data on shrub and tree species richness were assembled from federal vegetation surveys and compared with modelled growing season gross photosynthesis, P_g (the sum of above- and below-ground production plus autotrophic respiration) and two measures of spatial heterogeneity. We analysed the productivity–richness relationship at different scales by changing the focus size through spatial aggregation of field plots using 100 and 1000 km² windows covering the study area. Regression residuals were plotted spatially. Using the best available tree data set (Continuous Vegetation Survey: CVS), we compared different productivity indices, such as actual evapotranspiration and average temperature, in their ability to predict patterns of tree species richness.

Results The highest species richness (species/unit area) occurred at intermediate levels of productivity. After accounting for variable sampling intensity, the richness–productivity relationship improved as more field plots were aggregated. At coarser levels of aggregation, modelled productivity accounted for 57–71% of the variation in richness patterns for shrubs and trees (CVS data set). Measures of spatial heterogeneity accounted for more variation in richness patterns aggregated by 100 km² windows than aggregation by 1000 km² windows. P_g was a better predictor of tree richness in Oregon and Washington (CVS data set) than any surrogate productivity index.

Main conclusions P_g was observed to be a strong unimodal predictor of both tree (CVS) and shrub (FIA) richness when field data were aggregated. For the tree data set examined, seasonally integrated estimates of photosynthesis (P_g) predicted tree richness patterns better than climatic indices did.

Keywords

Species richness, woody plants, photosynthesis, productivity, temperate forest, multiple scales, AIC.

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INTRODUCTION

As regional and global patterns in species distribution have been observed and these data made more widely available, the priority for research has shifted from documentation to prediction of distributional patterns and interpretation of their causes. This

focus is both challenging and important in the face of current rates of habitat loss and the need to address the effects of climate change over the coming decades. To date, there has been considerable progress in predicting how species richness varies spatially as a function of climate, environmental heterogeneity, and the scale of analysis (Wright *et al.*, 1993; Waide *et al.*, 1999; Mittelbach

et al., 2001; Hawkins *et al.*, 2003). The creation of a conceptually simple regional model that integrates more functionally how climate, soils, and topography affect species richness would enable prediction of biodiversity in areas without extensive field sampling and therefore be essential for many conservation and management applications.

Many current models of species richness use estimates of latent heat exchange (e.g. actual evapotranspiration) or other combinations of variables to represent energy or productivity (reviews by Wright *et al.*, 1993; Waide *et al.*, 1999; Mittelbach *et al.*, 2001; Hawkins *et al.*, 2003); recent models often include measures of landscape heterogeneity or topography (Hawkins *et al.*, 2003). Of the 37 vascular plant richness–productivity data sets reviewed by Mittelbach *et al.* (2001; but see comment by Whittaker & Heegaard, 2003), approximately 70% of regional scale studies used precipitation as a productivity surrogate. At continental to global studies, 70% of the papers reviewed used annual actual evapotranspiration (AET) as a surrogate for net primary production (P_n). Just 14 of the 85 broad-scale studies of different taxa reviewed by Hawkins *et al.* (2003) included a direct measure of productivity.

The predictive power of climatically-driven models has been improved notably by incorporating more sound physics in the estimation of evapotranspiration and by refining the analysis from annual to monthly time steps (e.g. Venevsky & Veneskaia, 2003). Further improvement in the predictive power of species-richness models might also result, we hypothesize, if estimates of biological productivity were improved, as suggested from analysis in the temperate forests of Europe, eastern North America, and East Asia (Adams & Woodward, 1989). Field estimates of above-ground forest productivity in the Pacific North-west, USA also support the contention that a more direct measure of productivity should provide better predictions of plant species richness (Waring *et al.*, 2002). In the latter case, woody plant richness increased and then decreased across a productivity gradient that varied more than 10-fold. While many regional studies of temperate plant richness have shown a similar trend, elsewhere and at other scales, the correlation with productivity has been found to be positive, negative, nonexistent, or U-shaped (Mittelbach *et al.*, 2001).

Despite past evidence of the strength of the productivity–richness relationship, there are myriad other variables recognized to influence community composition, some more difficult to measure and quantify than others. Habitat heterogeneity has been recognized to have an influence on biodiversity (e.g. Kerr & Packer, 1997; Burnett *et al.*, 1998; Nichols *et al.*, 1998). Topographic heterogeneity is easier to quantify than many other variables (such as historical conditions) because of the prevalence of digital elevation models, but how best to express topographic heterogeneity in a manner that reflects its effect on plants, for example, is still unresolved.

The extent that relationships between productivity and species richness reflect sampling at various scales or underlying differences in biogeography is also not clear. Grime (1973, 1979) proposed that a decrease in plant richness at higher levels of productivity should be expected, as a few fast-growing species can create a

dense canopy that limits light for the establishment and growth of other taxa. Where productivity is low, harsh environmental restrictions limit plant growth and species richness. Sampling a narrow range in regional productivity could result in a positive, a negative, or no correlation with species richness (Rosenzweig & Abramsky, 1993). In addition to problems associated with spatial analysis of species-richness, the measurement of productivity itself is a challenge. With perennial vegetation, growth rates vary with age and disturbance history, as well as with site conditions. Foresters address these problems in part by standardizing site comparisons to maximum mean annual increment of wood growth of fully stocked stands achieved over a growth cycle. Empirically-based yield tables report the maximum current and mean annual growth rates for different aged forests that occupy environments with different growth potential, characterized by the site index: the tree height attained at 50 or 100 years. If tree ages vary, or the composition of a forest is mixed, estimates of maximum mean annual increment are assumed to correspond to those measured shortly after canopy closure.

Not only are field measurements of above-ground current growth difficult to compare without reference to age, they ignore the variable fraction (30–60%) of net primary production allocated below ground (Landsberg & Gower, 1997; Waring & Running, 1998). Net primary production (P_n) has been estimated at a few widely dispersed sites where carbon balances have been calculated by monitoring respiration as well as growth. For temperate forests, total P_n appears to be a nearly constant fraction (c. 50%) of gross photosynthesis, P_g (Waring *et al.*, 1998; Gifford, 2003). If the ratio of P_n/P_g is relatively constant, we then have the opportunity to model the general and well-understood process of photosynthesis across landscapes, and to assume that total P_n , regardless of the species composition, will be directly related (although the allocation of growth may differ substantially among species).

Regional and continental studies often depend on species range maps to estimate species richness (e.g. Currie & Paquin, 1987; Currie, 1991), yet at finer spatial scales these generalized maps can prove problematic, because species' ranges are disjunctive. The window sizes utilized in such studies (c. 50,000–96,000 km²) encompass many different ecosystems, making interpretations difficult. Amid the different approaches of fine-scale species-richness measurements based on field data (e.g. grain size of 1–100 m²) and coarse-scale estimates using range maps, we have chosen an intermediate scale of analysis (grain sizes 690 m²–18 ha). By aggregating field data to achieve a coarser scale estimate of species richness we hope to follow Latham & Ricklefs's (1993a) recommendation to preserve information on local community assemblages. At the same time, we recognize that gathering species richness data from field studies for regional level analyses is challenging because of varying plot sizes and different sampling schemes (Gentry & Dodson, 1987; Latham & Ricklefs, 1993a).

With the recent availability of spatially extrapolated climatic data and simplifications in ecological process models, we have chosen to model productivity spatially as gross photosynthesis during the growing season P_g , and to compare this measure to woody plant species richness derived from field surveys. We

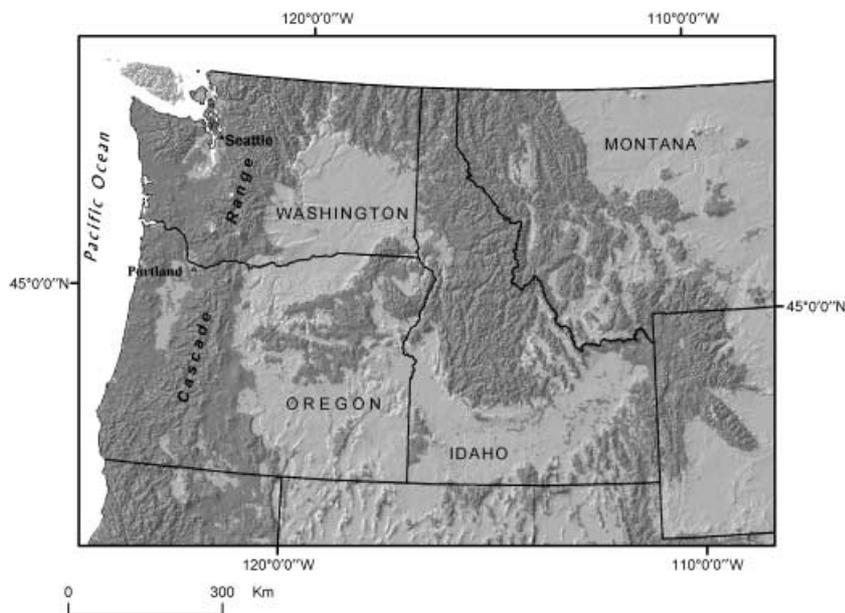


Figure 1 Map of study area (Oregon, Washington, Idaho and western Montana) showing forested areas in dark grey.

extracted fine-scale species richness data from regional field surveys (*c.* 200 m² and 1 ha plots) and aggregated this information using increasingly larger spatial windows to investigate the effect of scale on the productivity vs. species richness relationship. For one field data set, we evaluated the performance of P_g in predicting tree species richness compared to other commonly used productivity surrogates such as AET, potential evapotranspiration (PET), vapour pressure deficit (VPD), annual precipitation (PRECIP) and mean annual temperature (TEMP).

METHODS

Study area

The study area encompasses *c.* 630,000 km² (roughly the size of Spain and Portugal combined), which includes all forested portions of the Pacific and inland Northwest (Fig. 1) between 45° and 49° N latitude and 109°–123° W longitude, and encompasses elevations from sea level to 4400 m. The dominant coniferous forests alone have been classified into more than 200 recognized plant communities (Franklin & Dyrness, 1988) but this region contains far fewer tree species than other temperate forests in the Northern Hemisphere (e.g. Latham & Ricklefs, 1993b; Table 26.1). The study area includes a wide span of plant productivity, with P_n values ranging from 3 to 35 Mg ha⁻¹ year⁻¹, equal to that found throughout the entire nation (Jarvis & Leverenz, 1983).

Data processing

The finest geographical resolution of the independent variables used in this analysis was 1 km², matching the highest resolution regional climatic data available (DAYMET, Thornton *et al.*, 1997). Information on species richness was gathered from much smaller-sized field plots. Species presence–absence matrices were created

for three distinct data sets: shrubs, and two different tree data sets. Using a geographical information system and manipulation of these matrices [ARC/INFO 8 Desktop and Workstation packages from Environmental Systems Research Institute (2001) and Microsoft Access] unique species found in field plots within 100 and 1000 km² raster cells or ‘windows’ were summed and compared to the P_g raster layer across the forested areas of the study region.

Species richness data

We chose to collect species richness information from field data because it is the best representative data source of species distributions in the north-western United States. Our goal was to obtain a current and comprehensive list of species presence that could not be satisfied with existing but overly general tree species range maps (Little, 1971); species range maps for shrubs have not yet been developed for this area. We used two generally different data sets both collected by the US Forest Service (USFS). The Forest Inventory and Analysis (FIA) data set covers the entire United States and surveys both trees and shrubs, but field methods vary among sampling periods, by geographical region, and across different ownerships. The Current Vegetation Survey (CVS) is a uniform data set of tree species collected only for the states of Oregon and Washington (Max *et al.*, 1996). The CVS survey was conducted on public lands using 1 ha circular plots that included four subplots of nested concentric rings to provide adequate sampling of smaller as well as larger diameter trees. In total, 10,317 plots surveyed within the last decade were available for analysis. CVS data plots are dispersed in a regular grid pattern across the landscape approximately 3 km apart. Both the CVS and FIA data sets included information on tree seedlings and saplings acquired from measurements on subplots.

The USFS FIA surveys used in this study consist of variable radius plots for trees and small fixed radius plots for shrubs

Table 1 Forest Inventory and Analysis shrub data base; final plot size and original plot and subplot sizes

Region	Size of plot area for this study, m ²	Percentage of original subplots considered to be one plot*	Size of subplot, m ²	Total size of original plot, m ²
Eastern Oregon	138	100%	27.5	138
Western Oregon	157	40%	78.5	393
Eastern Washington	157	40%	78.5	393
Western Washington	171	100%	34.2	171
Rocky Mountain Region (Montana and Idaho)	202	20%	202.0	1012

*All plots selected for use in this study originally had five subplots each.

(Woudenberg & Farrenkopf, 1995). Variable radius plots sampled using a prism are well suited for estimating basal area but produce a biased tree species-richness count towards those trees with larger diameters. In addition, prism sampling does not provide direct knowledge of plot area, although recent efforts have been made to establish correlations where fixed and variable area plot data are available (Weihong Fan, Richard Stockton College of New Jersey, pers. comm.). FIA survey plots follow a regular grid pattern with 5 km spacing between plots. Geographical coordinates of plot location were offset by as much as 3 km by the USFS to maintain confidentiality. The survey information was available from the Pacific Northwest (PNW) regional office website in Portland, Oregon, and from the Rocky Mountain (RM) regional office in Ogden, Utah (Sharon Woudenberg, pers. comm.). The FIA surveys differ across the study area in relation to administrative region. Surveys cover private lands in Oregon and Washington and both public and private lands in Idaho and Montana. For the variable radius tree surveys, the number of subplots that comprises a plot varied in the RM region and therefore we obtained a subset of plots having exactly five subplots to coincide with the five subplots recorded in PNW surveys (the current countrywide FIA plot design has four subplots). Codes for species identification and distinction between tree and shrub life forms both vary between the PNW and RM regions. In some cases the regions use different synonyms to code the same species. By calculating species richness for both regions independently, we avoided increasing the species numbers artificially (because of different synonyms) that would have resulted by joining both regional data sets. Because of project time limitations we were unable to reclassify life-form categories species by species consistently across the region.

Procedures for FIA shrub surveys varied by region in the size of field plots and by tally method. Both the PNW and the RM surveyed shrubs covering at least 5% of each subplot and RM limited this to the four most common species per subplot. Although we were unable to compensate fully for different approaches in tallying species, we combined a number of subplots and reduced the range of area sampled to reasonable values between 137.5 and 202 m² per shrub plot (Table 1). Because of the variable field sampling methods, we limited our use of these data sets to species presence-absence only rather than incorporate information on abundance.

In spite of inconsistencies in sampling, we considered it appropriate to explore the use of the FIA data set at the regional scale; it is the only regional data set in the United States that includes both trees and shrubs. We selected 5484 FIA plots with data acquired over a period of 20 years, where trees were present on all subplots (and therefore were of the same 'condition class' or earth cover). These plots sampled areas that differed in natural disturbance history (e.g. fire) and management (e.g. length of the timber harvest cycle), which in this region can influence plant species richness (Halpern & Spies, 1995). The CVS data set, which was exclusively restricted to federal land, might be expected to reflect relatively less disturbed conditions compared to the FIA surveys on both public and private lands.

Increasing grain size

To make the field data more suitable for regional analysis, we 'scaled-up' species richness information by aggregating neighbouring plots, thereby increasing the grain size of analysis. We used 100 km² (10 × 10 km) and 1000 km² (31.6 × 31.6 km) windows that were distributed regularly across the four-state region to maintain constant 'focus'. Because the term 'focus' (Scheiner *et al.*, 2000) can refer to the calculation of a mean value when aggregating multiple plots rather than the tally of unique species, we will refer to these units as windows of aggregation or levels of analysis. These window sizes were selected because they incorporated an adequate number of field plots to examine the effects of plot aggregation. For each geographically located window, all unique species were tallied from all field plots encountered using the species presence-absence matrices. An important distinction in this study is between the window area or region of field plot aggregation (100 and 1000 km² windows) and the actual surveyed area on the ground made up of aggregated plots (e.g. 10 1-ha field plots), which would be considered the 'grain' size of analysis. The spatial patterns of the field plots varied in concentration and pattern across the area for a variety of reasons, primarily because of different patterns in land ownership. We chose not to use a nearest-neighbour plot selection (e.g. Scheiner & Jones, 2002) because of the variable and often large distances between field plots. We used the same scaling-up process for all data sets. To examine for possible scaling artefacts, we randomized (or 'shuffled' the columns of) the original CVS tree

Table 2 Data sets used in analysis: details of standardization and data ranges of plots per window

Data set	Scale of analysis	No. of field plots to which data sets were standardised	Grain size (area surveyed on the ground)	Range of field plots per window*	Number of observations
Shrubs FIA	Plot	—	138–202 m ²	—	5483
	100 km ²	5	690–1010 m ²	4–11	751
	1000 km ²	15	2070–3030 m ²	10–40	269
Trees FIA	Plot	—	No area measure	—	5484
	100 km ²	5	No area measure	4–11	446
	1000 km ²	15	No area measure	10–41	211
Trees CVS	Plot	—	1 ha	—	10,317
	100 km ²	10	10 ha	9–15	586
	1000 km ²	18	18 ha	10–120	193

*Dependent upon spatial density of original field surveys.

presence–absence matrix and summed unique (randomized) species at 100 and 1000 km². Randomized species richness values were compared with P_g averaged over the same window sizes.

Standardizing for area sampled

We chose to tally unique species for multiple field plots within 100 km² and 1000 km² focal windows and therefore windows contained a variable number of field plots. We limited our analysis to amply populated windows and standardized the variable sampling per window using a simple multiplier based on a species–area curve to attain appropriate estimates of species richness.

We first plotted the relationship between the average number of species per 100 km² and 1000 km² window against plot area sampled for each data set. After selecting an approximate asymptote for each data set, we solved the logarithmic species–area curve for species richness for all possible number of plots, divided these numbers by the equation result of the asymptote, and used the inverse of this number to multiply the original species richness numbers that resulted from the aggregation of a variable number of plots (Table 2; examples of this process are shown for the 100 km² CVS data set in Fig. 2a,b). Differences between original data and standardized 100 km² CVS data are shown in Fig. 2b. The standardized grain sizes (although composed of dispersed field plots) of the scaled-up 100 and 1000 km² data sets were 10 and 18 ha for CVS trees, and 690–1010 m² and 2070–3030 m² for FIA shrubs, respectively (FIA tree grain sizes cannot be determined because of field sampling methods).

We investigated species–area relationships for different sub-regions such as ecoregions for the data sets. In most cases, no unique species–area relationships were found (that had sufficient numbers of samples) that differed markedly from the average relationship for the entire study area. Often a ‘true’ and distinct asymptote was not clearly definable (as can be seen in Fig. 2a), yet we did not extrapolate beyond the number of field plots sampled with the species–area relationships. We restricted our analysis to aggregation windows that had ample numbers of field plots: at least four FIA plots and nine CVS plots for 100 km² windows and at least 10 field plots per 1000 km² window for all data sets. These methods, that we have developed to address

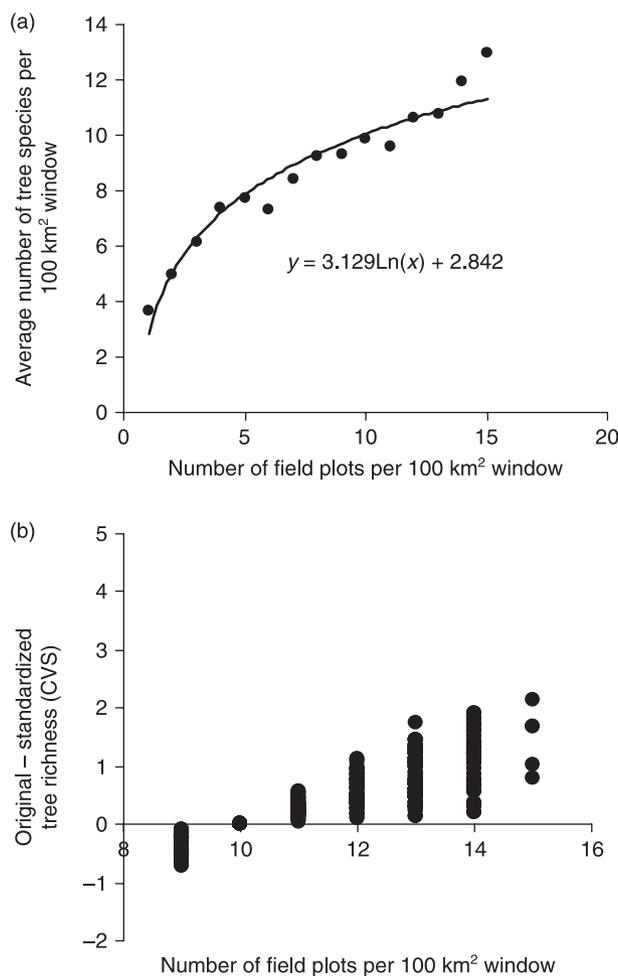


Figure 2 Details from the standardization procedure for the 100 km² CVS data set. (a) Species–area relationship. (b) Difference in values between original and standardized values by number of field observations per window.

variable field survey sizes, are not intended for use at a fine or local scale or for the calculation of exact species numbers. We judge them appropriate for the goals and scale of our study, and their application allows us to take full advantage of the field data

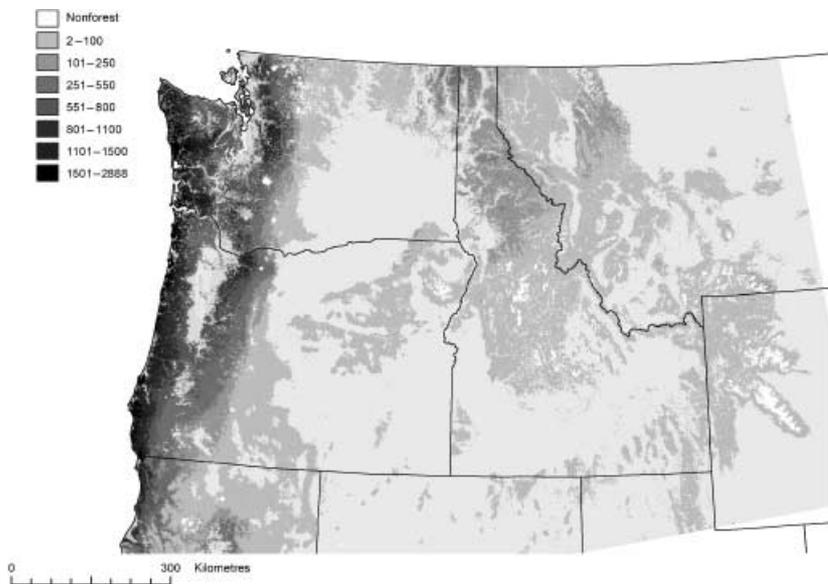


Figure 3 Annual gross primary production for forests, $\text{g C m}^{-2} \text{ year}^{-1}$, derived from 3-PG model.

available. We confirmed the validity of our standardization approach by comparing richness–productivity relationships of windows with identical numbers of survey plots derived from subsets of the original richness data (not standardized).

Modelled photosynthesis

We chose to calculate productivity with a physiologically-based process model to represent, as accurately as currently possible, how water and energy affect and limit plant growth across a region. Gross primary production (P_g), as defined in this study, represents gross photosynthesis during the growing season by a young, fully stocked forest stand, given constraints imposed by climate and soils. P_g represents photosynthate that goes to both above- and below-ground forest growth (*c.* 50%) as well as to autotrophic respiration (*c.* 50%). We previously modelled gross photosynthesis at a monthly time step for an entire year (Swenson & Waring, 2005; Fig. 3), but recognize that spring and summer represent the major period of activity for all vegetation (see Waring *et al.*, 2002; Fig. 1). Therefore, values for the months of May to August were summed to represent the amount of carbon taken up by all species, deciduous and evergreen, during what we consider the representative growing season for the region (P_g). At higher elevations where spring frosts are prevalent or where drought limits the effective growing season, the model reduces estimates of P_g to near zero. We refer to this calculation of P_g as representative of ‘modelled productivity’ throughout the paper. The physiological process model 3-PG (Physiological Principles for Predicting Growth) was used in ‘spatial’ mode (Tickle *et al.*, 2001).

In such process models, the relative importance of environmental factors to plants (e.g. light, soil water, humidity deficits, CO_2 levels, temperature, and soil fertility) changes throughout the year, even when the value of one factor is the same at different time periods (see reviews by Shugart, 1984; Waring & Running,

1998). For example, low evaporative demand during wet winters or droughty summers exert different constraints on photosynthesis based on differences in stomatal conductance and light absorbed by the canopy.

3-PG relies on a number of established biophysical relationships and several simplifying assumptions documented elsewhere (Landsberg & Waring, 1997). For the simulations, the model was driven with DAYMET monthly geographical climate data: minimum and maximum temperature, daytime vapour pressure deficit, precipitation, and radiation. The DAYMET climate information consists of averaged monthly summaries (1980–98) extrapolated spatially over the terrain from over 6000 weather stations (Thornton *et al.*, 1997). To estimate soil fertility for the model we chose nitrogen (N) as a fertility index because it is the most limiting factor for tree growth in the Pacific Northwest (Blake *et al.*, 1990; White, 2000). Klinka & Carter (1990) reported that variation in site indices for Douglas fir across three climatic zones in British Columbia was highly correlated with mineralizable nitrogen, the form most available for root uptake. Spatial estimates of soil nitrogen content were derived by Weihong Fan (Richard Stockton College, pers. comm.) from STASGO soil maps (USDA, 1991) and land use information (Anderson, 1967; Vogelmann *et al.*, 2001). Using the same set of environmental data, 3-PG generates a series of products including monthly and annual estimates of gross photosynthesis and wood production.

To evaluate the general reliability of the modelling approach we converted maximum mean annual increment wood growth estimates to the height growth expected for Douglas fir at 100 years using McArdle’s (1961) forestry yield tables (Swenson & Waring, 2005). Modelled estimates of predicted tree heights at 100 years were in reasonable agreement with field estimates for this regional study ($R^2 = 0.53$; SE of estimate: 7.6 m; $P < 0.0001$; $n = 5263$). We had evidence that no systematic bias existed in estimating soil fertility (which affects photosynthetic capacity),

Table 3 List of productivity measures compared to tree species richness (CVS) in the states of Oregon and Washington

Explanatory variables	Symbol	Units	Range of values
<i>Productivity estimates and surrogates</i>			
Annual gross primary production (3-PG, with DAYMET climate data)	P_a	$\text{g C m}^{-2} \text{yr}^{-1}$	92–2960
Growing season gross primary production; May–August (3-PG, with DAYMET climate data)	P_g	$\text{g C m}^{-2} \text{time}^{-1}$	50–1750
Average annual actual evapotranspiration (3-PG, DAYMET climate data)	AET	mm	28–126
Mean annual potential evapotranspiration (Thornthwaite method with DAYMET climate data)	PET	mm	230–539
Average annual daytime vapour pressure deficit (DAYMET climate data)	VPD	millibars	3.2–10.1
Average monthly daytime vapour pressure deficit during May–August (DAYMET climate data)	VPD_g	millibars	5–17
Total annual precipitation (DAYMET climate data)	PRECIP	cm	33–490
Mean annual temperature (DAYMET climate data)	TEMP	$^{\circ}\text{C}$	0.82–11.5

from the evenness in distribution of regression residuals of site index predictions plotted against soil nitrogen content and plotted geographically across state of Oregon, with respect to mapped soil fertility (Swenson & Waring, 2005). We have more confidence in the predictions of gross photosynthesis than for above-ground growth estimates because accurately modelling allocation below- and above-ground continues to be a challenge for ecologists.

Comparison of productivity indices

We compared various climatic indices that have served as productivity surrogates with modelled productivity to establish the strongest predictor of tree richness patterns in the Pacific Northwest. We conducted this analysis with the CVS data set (at 100 and 1000 km² levels of aggregation) because it represents the most recently collected and consistently sampled field data with the largest size field plots. Based on past studies of woody plant and tree species richness, we chose to compare AET, PET, VPD, PRECIP, and TEMP. The ranges of these climate variables shown in Table 3 are representative of the forested areas in the Pacific north western United States. AET is often highly correlated with above-ground terrestrial primary productivity particularly when compared to densely planted crops (Rosenzweig, 1968; Leith, 1975), yet very different precipitation and radiation patterns may produce similar annual AET values, resulting in limited predictive power (Whittaker & Field, 2000). PET is an estimate of potential evaporative water loss based on the incoming heat energy (specifically, incident solar radiation). Mean monthly daytime VPD has also been considered as a surrogate to AET and photosynthesis because of its large effect on leaf stomatal conductance and importance in creating evaporative demand. PRECIP has been used in many studies of richness in the past, yet plant growth responds in conjunction with other factors, to the water immediately available in the soil (e.g. percolation, ground water) rather than directly to the amount of precipitation.

We created and ranked statistical models of each productivity index. Single variable models were created to represent linear productivity–richness relationships as well as quadratic models for each variable to approximate a unimodal relationship. All climate information used to calculate predictor variables was

from DAYMET digital geographical climate data (Thornton *et al.*, 1997). AET was generated by the 3-PG model using the Penman–Monteith equation, while PET was calculated using the Thornthwaite method (Thornthwaite & Mather, 1957; no latitudinal scaling). Daytime vapour pressure deficit (VPD) was calculated with DAYMET information following the methods of Waring & McDowell (2002). Mean annual temperature and annual precipitation (PRECIP) were taken directly from the DAYMET climate data; the natural log of PRECIP was also considered.

Spatial heterogeneity

Topographic pattern varies considerably across the study area. To examine the strength of its role in accounting for species richness patterns in our data sets, we calculated the standard deviation and range of elevation values (based on a 90-m resolution digital elevation model) within 1 km² (for analysis with plot level data), and 100 and 1000 km² windows. We use linear and non-linear regression to compare heterogeneity to richness and P_g .

Statistical analysis

Each of the three species richness data set was compared to P_g through regression analysis at the scale of plot, and field plots aggregated by 100 km² and 1000 km² windows. The nine data sets were examined for both linear (increasing or decreasing) and unimodal relationships (by including the squared term of P_g in the models). No outliers were excluded from any data set. To compare the modelled productivity layer with surrogates of productivity, we used an information-theoretical approach (Burnham & Anderson, 2002) to rank competing models in their ability to predict patterns of tree richness (CVS). Candidate models were ranked using Akaike's information criterion (AIC) and AIC difference values were calculated between the highest ranked model and the remaining models. The difference values were used to calculate Akaike's weights, which estimate the relative likelihood of a model being most appropriate for the data set. We included in the analyses the null model, containing only the intercept, to test if added variables improved upon this. All statistical analysis was performed using SAS and SPLUS software (SAS, Inc. version 8, 1999 and S-PLUS, version 6.1, 2001).

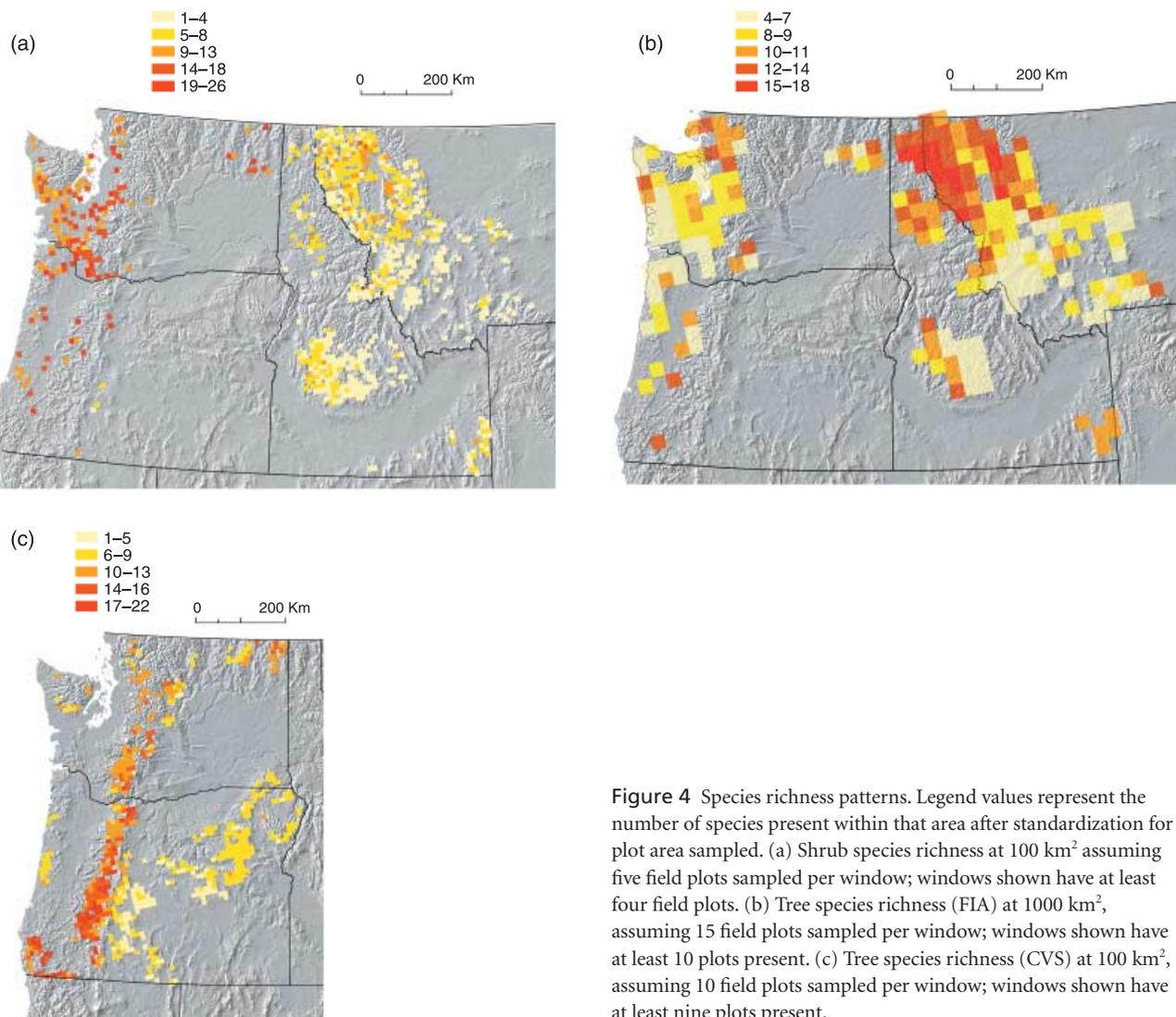


Figure 4 Species richness patterns. Legend values represent the number of species present within that area after standardization for plot area sampled. (a) Shrub species richness at 100 km² assuming five field plots sampled per window; windows shown have at least four field plots. (b) Tree species richness (FIA) at 1000 km², assuming 15 field plots sampled per window; windows shown have at least 10 plots present. (c) Tree species richness (CVS) at 100 km², assuming 10 field plots sampled per window; windows shown have at least nine plots present.

Using the results of the richness- P_g statistical analysis we plotted regression model residuals geographically by linking a data base of residual values to the geographical information system.

RESULTS

Maps of species richness

Maps of shrub and tree richness aggregated by 100 km² and 1000 km² windows and standardized for the number of field plots (area) showed varied patterns (Fig. 4a–c). These maps do not represent total species found within each window, but the number that would be found given a specified or standard number of field plots. Shrub richness aggregated by 100 km² windows (Fig. 4a; standardized grain of five aggregated field plots), appeared highest in Oregon and Washington with a lesser peak in northwest Montana. High FIA tree richness aggregated by 1000 km² windows (Fig. 4b; standardized grain of 15 aggre-

gated field plots) was concentrated in northwest Montana and in the Idaho panhandle. Tree richness derived from the CVS surveys aggregated by 100 km² windows (Fig. 4c; standardized grain of 10-ha field plots) indicated relatively high tree richness in the central Cascade Range in Washington, the central and southern Cascades in Oregon, and the Siskiyou mountains in southwestern Oregon.

Productivity–richness relationship

Across the region, tree and shrub richness, predicted as a function of P_g , exhibited a unimodal form that was enhanced at coarser scales (by increasing the focal window) for all cases except one (Fig. 5a–i; Table 4). The FIA shrub and tree models yielded their strongest relationship for the 1000 km² level of analysis (Fig. 5c and f, respectively); whereas the CVS tree data set produced the strongest relationship at the 100 km² level of analysis (Fig. 5h). Comparing all data sets at all scales, the two most successful models evaluated in terms of the R^2 values, resulted from the

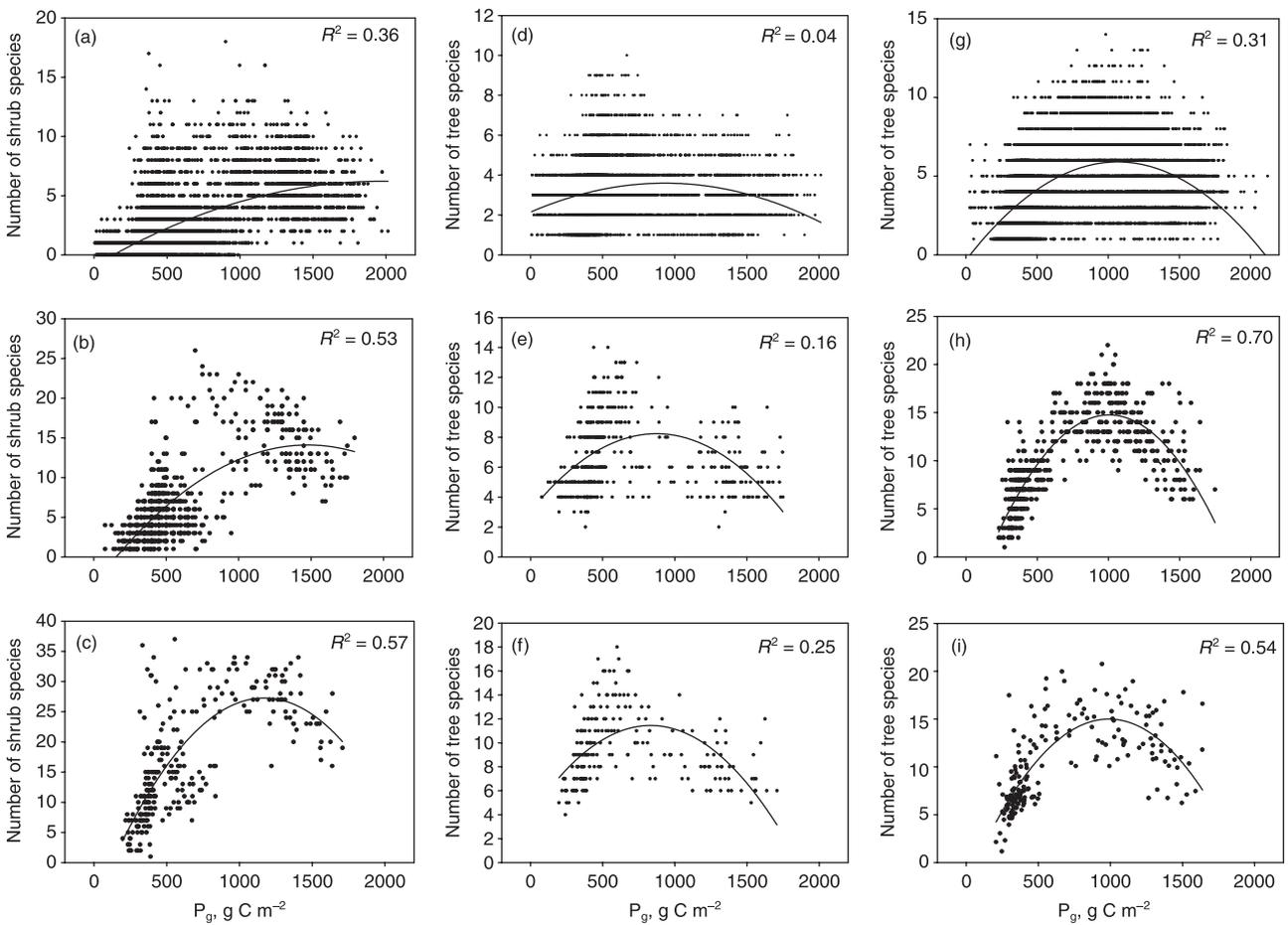


Figure 5 Relationship between modelled P_g (gross photosynthesis) and woody plant richness for three data sets. Shrubs at (a) plot (b) 100 km², and (c) 1000 km² levels of aggregation, FIA trees at (d) plot (e) 100 km², and (f) 1000 km² levels, and CVS trees at (g) plot, (h) 100 km², and (i) 1000 km² levels of aggregation.

Table 4 Regression results with P_g and P_g^2 as independent variables. All 2nd-order polynomial statistical models and parameter estimates have P -value < 0.0001; Linear models have P -value < 0.0001 unless otherwise shown

Data set	Scale of analysis	Linear relationship R^2 (P -value)	2nd-Order polynomial (unimodal) R^2	2nd-Order polynomial model (standard errors)
Shrubs, FIA	Plot	0.30	0.36	$Y = -0.931 + 0.0073(P_g) - 1.9 \times 10^{-6}(P_g^2)$ (0.115) (0.0003) (0.2 × 10 ⁻⁶)
	100 km ²	0.05	0.53	$Y = -3.562 + 0.0239(P_g) - 8.0 \times 10^{-6}(P_g^2)$ (0.591) (0.0017) (1.0 × 10 ⁻⁶)
	1000 km ²	0.44	0.57	$Y = -6.682 + 0.0575(P_g) - 24.4 \times 10^{-6}(P_g^2)$ (1.685) (0.0049) (2.8 × 10 ⁻⁶)
Trees, FIA	Plot	0.00002 $P = 0.72$	0.04	$Y = 2.143 + 0.0031(P_g) - 1.7 \times 10^{-6}(P_g^2)$ (0.076) (0.0002) (0.2 × 10 ⁻⁶)
	100 km ²	0.006 $P = 0.10$	0.16	$Y = 3.047 + 0.0118(P_g) - 6.7 \times 10^{-6}(P_g^2)$ (0.475) (0.0014) (0.7 × 10 ⁻⁶)
	1000 km ²	0.01 $P = 0.14$	0.25	$Y = 4.000 + 0.0178(P_g) - 10.7 \times 10^{-6}(P_g^2)$ (0.799) (0.0023) (1.3 × 10 ⁻⁶)
Trees, CVS	Plot	0.165	0.31	$Y = -0.311 + 0.0116(P_g) - 10.0 \times 10^{-6}(P_g^2)$ (0.076) (0.0002) (0.1 × 10 ⁻⁶)
	100 km ²	0.37	0.70	$Y = -5.416 + 0.0398(P_g) - 19.7 \times 10^{-6}(P_g^2)$ (0.459) (0.0013) (0.8 × 10 ⁻⁶)
	1000 km ²	0.27	0.54	$Y = -2.203 + 0.0350(P_g) - 0.01 \times 10^{-5}(P_g^2)$ (0.927) (0.0028) (0.0000)

100 km² CVS tree and 1000 km² FIA shrub data sets. The FIA tree data set produced weaker relationships at all scales.

We found that local variation in topographic heterogeneity has more effect at the smaller sized aggregation windows (100 km²) than at the larger ones (1000 km²). Calculations of topographic variation (based on the range and standard deviation of 90-m digital elevation values within a given window) generally accounted for < 0.25 of the observed variation in predicted shrub richness at the 100 km² level of analysis and < 0.15 at the 1000 km² level (with either a linear or curvilinear relationship). For the FIA tree data set, topographic heterogeneity accounted for < 0.11 of the variation in richness for both window sizes. With the more comprehensive CVS tree data set, topographic variation accounted for approximately 40% of the observed variation in richness at the 100 km² level and about 20% at the 1000 km² level of analysis. At 100 km², the shape of this relationship was distinctly hump-shaped and resembled the tree (CVS) richness– P_g curve; R^2 between P_g and heterogeneity was 0.27 for this data set. In most cases spatial heterogeneity measures were correlated with P_g to a similar extent that heterogeneity and richness were correlated. Because of this correlation, adding the variable of spatial heterogeneity to the P_g –richness models did little to improve model performance as shown by the R^2 .

To validate our method of area standardization, we compared the P_g –richness relationship of 100 km² standardized data sets to subsets that sampled exactly the same field area (subsets of windows that had the same number of field plots); 1000 km² level data sets did not contain enough windows that had the same number of field plots for analysis. The resulting relationships between richness and productivity were very similar in distribution to those obtained with the standardized data sets (Fig. 6a,b,c vs. Fig. 5b,e,h, respectively; subsets with the maximum number of samples are shown). The CVS tree fixed-area subset at 100 km² exhibited a consistent unimodal relationship (Fig. 6c); the overall average of the R^2 values from all possible CVS subsets (Table 5, third column) was 0.70, the same value attained for the data set at 100 km² when standardized to 10 plots. Fixed-area subsets (same number of field plots) of shrub and FIA tree data sets produced similar results (Table 5, Fig. 6b and c), yet the comparison could not be made with all possible subsets because of inadequate sample numbers. When we examined the CVS data set for possible scaling artefacts by randomizing the species presence–absence matrix for both 100 and 1000 km² data sets, we found no relationship between species richness and P_g ($R^2 < 0.02$).

Comparison of productivity indices

We compared modelled P_g to surrogates commonly used to predict patterns of species richness with the CVS data set for Oregon and Washington at the 100 km² level of analysis. The ‘unimodal’ (quadratic) model of P_g was selected as the best among competing models in accounting for patterns of tree richness (Table 6). No other model followed closely behind, given that models with $\Delta AIC > 4$ should not be considered as viable alternatives (Burnham & Anderson, 2002). The quadratic P_g model attained

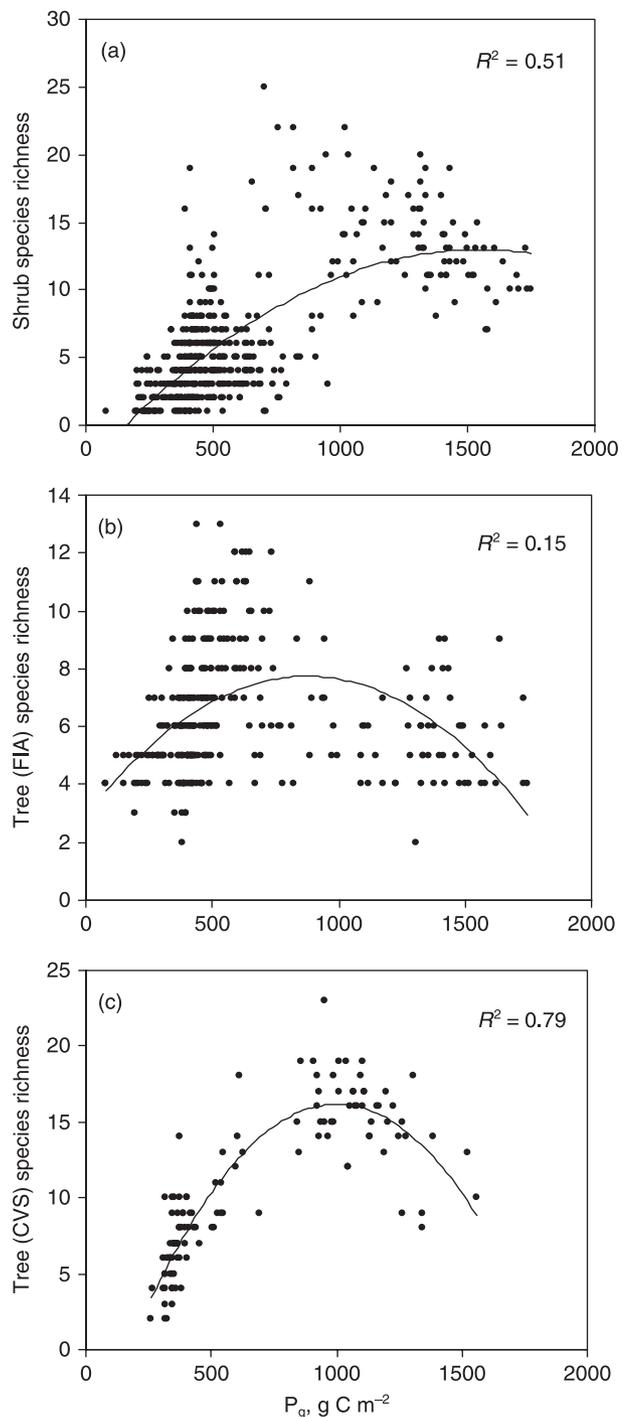


Figure 6 Richness–productivity relationships of 100 km² exact-area subsets: (a) shrub species richness with exactly four field plots per window ($n = 489$) (b) tree species richness (FIA) with exactly four field plots per window ($n = 303$), and (c) tree species richness (CVS) with exactly 13 field plots per window ($n = 118$).

an Akaike weight of 1.0, indicating a 100% likelihood of being the best model for the data set. At the field plot level, P_g was the strongest predictor of tree richness (Table 4, $R^2 = 0.31$), and was followed by growing season AET ($R^2 = 0.23$). For the 1000 km² window analysis, P_g was also the strongest predictor (Table 4,

Table 5 Justification for standardizing sample area technique: regression results from subsamples of data set with exactly the same area sampled per 100 km² window*

Data set	Exact no. of plots per 100 km ² window	N	Productivity-relationship, R ²	Productivity-relationship for standardized data set, R ²
Shrubs (FIA)	4	489	0.51	0.53
	5	127	0.59	0.53
	6	79	0.74	0.53
Tree (FIA)	4	303	0.15	0.16
	5	85	0.16	0.16
Tree (CVS)	9	102	0.67	0.70
	10	101	0.75	0.70
	11	102	0.61	0.70
	12	117	0.72	0.70
	13	118	0.79	0.70
	14	41	0.70	0.70

*Only subsets with adequate sampling shown; > 40.

Table 6 Results of model selection among productivity surrogates for the CVS tree data set; top eight of 20 models

AIC	Variables	Akaike weight	Delta AIC
2022	P _g , P _g ²	1.0	—
2106	P _a , P _a ²	0	83
2178	PRECIP, PRECIP ²	0	156
2221	AET, AET ²	0	199
2293	Ln(PRECIP)	0	271
2323	AET	0	301
2369	P _g	0	346
2397	PRECIP	0	375

Best model equation:

$$\text{Tree species richness} = -5.69 + 2.04(P_g) - 0.05(P_g^2).$$

R² = 0.55) and was followed by growing season precipitation (R² = 0.52).

Mapping of residuals

Model residuals were plotted geographically for three data sets to illustrate the extent of agreement with model predictions (Fig. 7a,b, and c; same data sets as shown in Fig. 4b,f, and h, respectively). The 100 km² shrub model (Fig. 7a) indicates clumps of positive deviations, where actual shrub richness was higher than model predictions, south of Seattle, Washington to the Oregon border, in north-eastern Washington, and in north-western Montana. Shrub richness was lower than model predictions in northern Idaho, along the Idaho/Montana border, and in the north-eastern corner of the study area in Montana. The CVS tree species mapped regression residuals (Fig. 7c) indicate isolated areas that deviate from model predictions in Oregon and Washington. The regression model under-predicted tree richness in southwest Oregon, along the southern Cascade Range, and in the northern Cascades of Washington.

DISCUSSION

A relatively strong unimodal P_g-richness relationship was revealed for most data sets that generally improved at larger grain sizes. We attribute this strengthening of the relationship at coarser scales of analysis to the exclusion of under-sampled areas (e.g. < 5 field plots per window), a more thorough sampling of the species present (by aggregating multiple plots) and a decreased influence of field plot location as compared to the plot level analysis. The relationship varied among data sets, where the weakest was recorded for the FIA tree data which has the most variable and undefined field plot sizes, and locational offset of plot location. The CVS tree surveys in Oregon and Washington yielded the best predictive relationship between P_g and tree richness at all scales (Table 4). Larger plots, more consistent sampling procedures, and knowledge of their true location appeared to help account for the relatively higher predictive power of the model with CVS data as compared to the FIA data sets. Additionally, because the CVS plots were concentrated within two states on federally-owned land (with less frequent timber harvest), disturbance may play a lesser role than would be the case on private lands. Species richness maps from the CVS survey (Fig. 4c) show an overall smoother richness gradient than other data sets. We believe that this pattern is based on the markedly larger CVS field plot size relative to the FIA data set (the CVS 1-ha plots are 50 times larger than the FIA shrub plots used in this study). Larger field plots translate to a more complete tally of species present. As the window size increased to 1000 km², it appears that the increased averaging of the variation in P_g degraded the relationship, while relatively fewer new species were added to the pool across the windows. This may indicate that there is an appropriate scale to analyse this relationship for this particular data set, and although we have not defined this exactly, it is closer to 10-ha field plots aggregated at 100 km² windows rather than 18 ha at 1000 km². The FIA tree field data (with small, variable radius plots) appear to be inadequate for regional analysis using our methods. The newest FIA surveys using fixed-area plots

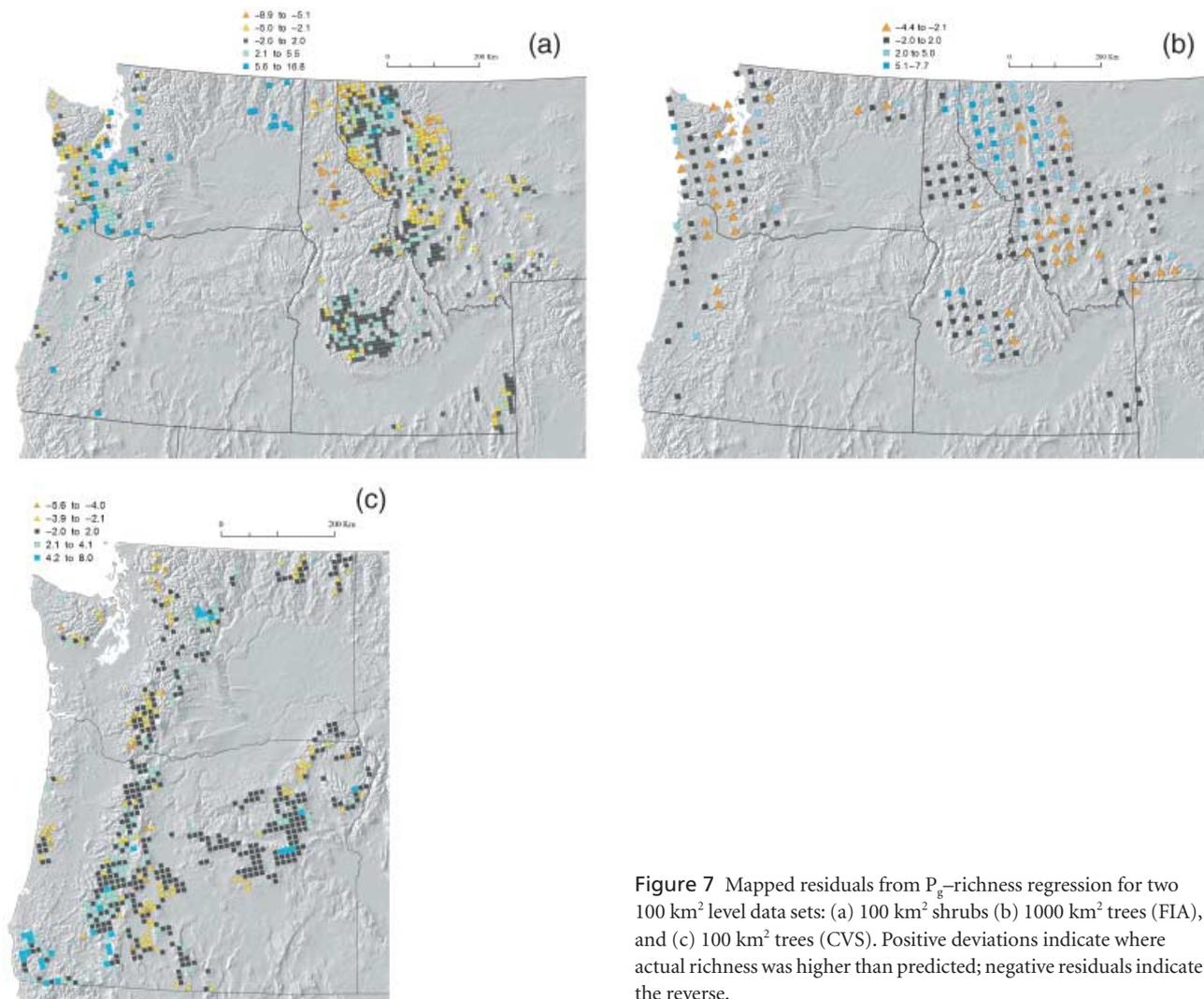


Figure 7 Mapped residuals from P_g -richness regression for two 100 km² level data sets: (a) 100 km² shrubs (b) 1000 km² trees (FIA), and (c) 100 km² trees (CVS). Positive deviations indicate where actual richness was higher than predicted; negative residuals indicate the reverse.

(USDA, 2002) should be valuable in providing fixed-area estimates of richness.

Although there is general consensus that harsh conditions limit species richness at low productivity levels, there are various theories as to why species richness decreases at higher levels of productivity. The sites with the highest productivity in our study area (western Oregon and Washington, Fig. 3) are dominated by a few superior competitors that exclude other species primarily by shading. Typical shade-intolerant and fast-growing tree species include Douglas fir (*Pseudotsuga menziesii*) and alder (*Alnus* sp.) in the upper canopy, which become established following disturbance and quickly achieve a closed canopy. In competition with these fast-growing, upper-canopy species are slower-growing shade-tolerant species such as western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), Pacific silver fir (*Abies amabilis*), and Pacific yew (*Taxus brevifolia*). With a maximum combined leaf area index of 10, few species of shrubs or other understorey plants are found commonly.

We examined the presence of some of these key tree competitors (CVS data set) at the 100 km² data set across the productivity

gradient in Oregon and Washington. Douglas fir was present in 100% of the windows with an average productivity of over 1000 g C m⁻² (Fig. 8a), while red alder, although distributed less widely (Fig. 8b), was present on 92% of the highly productive sites (> 1200 g C m⁻² during the growing season). Slower-growing shade-tolerant species, such as western hemlock and western red cedar, were present on c. 90% or more of 100 km² windows producing on average > 1000 g C m⁻² (Fig. 8c and d, respectively). We believe that where these highly competitive species are present, competitive exclusion for light reduces species richness. Research of forest canopies in our study area has shown that forests with dense canopies allow little light penetration and therefore have low vascular plant species richness (Waring & Major, 1964; Waring, 1969; Franklin & Dyrness, 1988; Runyon *et al.*, 1994). Although competitive exclusion might be expected to operate only between individuals and species in a stand, it appears as a strong influence in our study because we have based our analysis on field data. Competitive exclusion is reflected across the region because these superior competitors' ranges extend across broad areas.

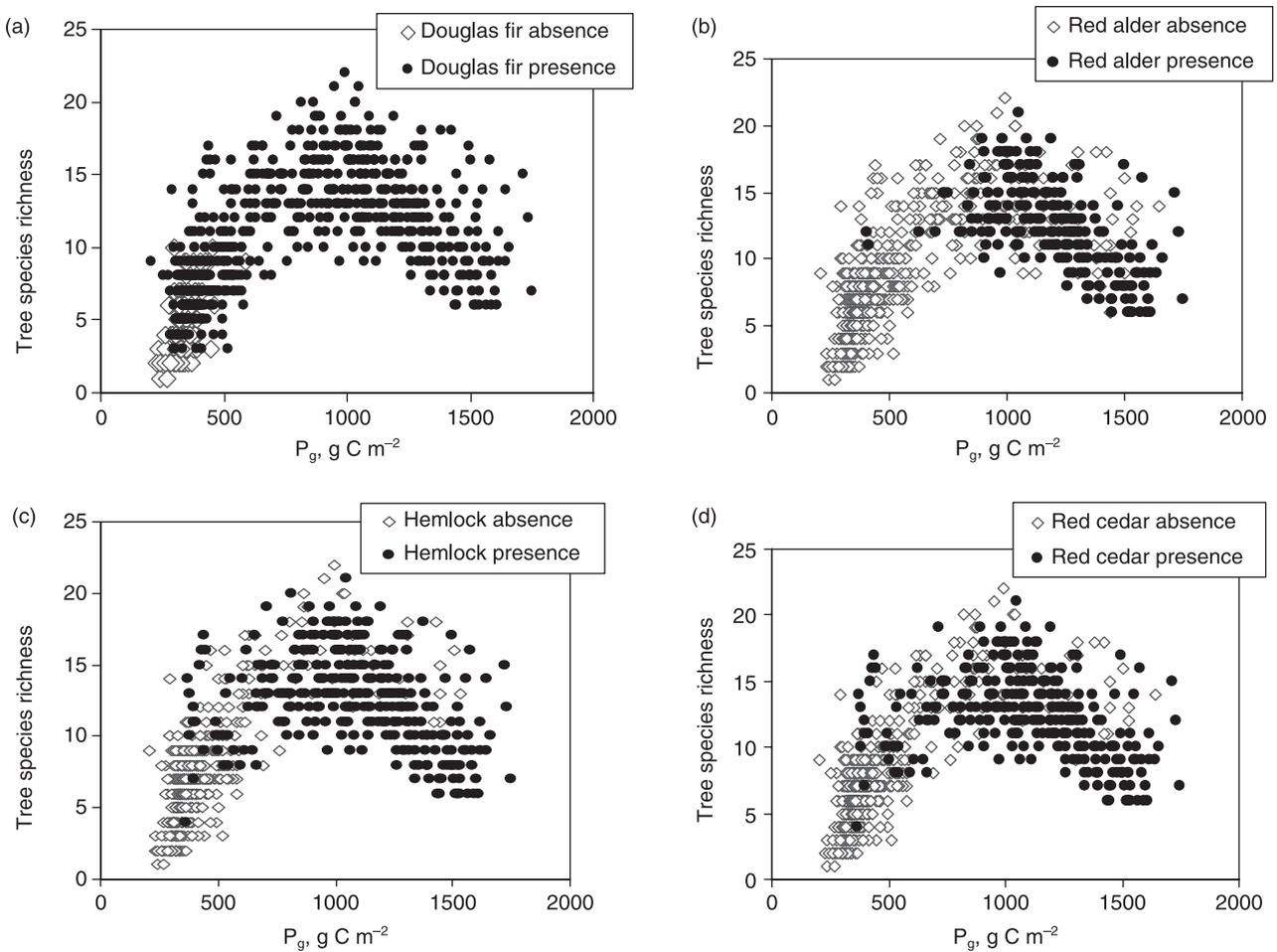


Figure 8 Presence–absence along the productivity gradient for 100 km² level of aggregation for CVS tree species: (a) Douglas fir (*Pseudotsuga menziesii*), (b) red alder (*Alnus rubra*), (c) western hemlock (*Tsuga heterophylla*) and (d) western red cedar (*Thuja plicata*).

Our maps of the residuals from the richness- P_g statistical model show that the smaller errors (Fig. 7a,b,c, black squares) were well distributed across the region. The areas where model estimates were in substantial error are clustered geographically and may indicate the influence of more localized variables such as historical circumstances, or perhaps where environmental heterogeneity differs from our methods of characterization. These residuals are based upon the P_g -richness statistical quadratic model in the form of: $y = a + bx + cx^2$. Although the CVS data set follows this statistical model assumption closely, it is evident that the statistical model could be further refined for the FIA trees and shrub data sets to quantify the distribution more accurately.

It has been suggested that a unimodal shape may result as a scaling artefact, reflecting more geographical variation in terms of species richness at increasing grain size and a result of spatially averaging productivity values (Tilman, 1982, 1988; Huston & DeAngelis, 1994). In the case of our study, however, the unimodal pattern was expressed consistently at all scales and data sets including the plot level (Fig. 5), where no averaging took place. Additionally, when we selected a subset of windows with the same number of field plots, the same distinct curve was present

(Fig. 6a,b,c). Therefore, while it is possible that a scaling artefact may be present (a form of this can be seen in Fig. 5 as the range in productivity values narrows with increasing window size), we believe that the strengthening of the relationship with scale is most attributable to the exclusion of under-sampled plots and a more comprehensive tally of the species present. The strengthening of the P_g -richness relationship with scale has also been found in other temperate forest systems by aggregating field data, although often with much smaller plots (e.g. Schuster & Diekmann, 2005; plot size of 1–100 m²).

Our experience in this study reinforces the importance and brings to light the difficulty of attaining similarly sized field plots by uniting data sets across a region and by aggregating these plots by coarser spatial units. For our data sets, distinct local species–area relationships were not expressed, thus one relationship was used for the entire study area. Further examination of the spatial variability of species–area relationships would be merited; a more precise adjustment for plot area sampled would produce more accurate estimates of species richness. We found that the P_g -richness relationship for subsets with a fixed area showed a similar relationship to standardized data sets (Fig. 6a,b,c vs.

Fig. 5b,e,h). Compared to the data sets standardized for area (Table 5, last column), some increase in predictive power was attained in a 100 km² CVS tree subset of windows having exactly 13 sample plots (Table 5, $R^2 = 0.79$) and with a shrub subset having exactly six plots per window (Table 5, $R^2 = 0.74$). We developed this method of scaling-up field data to maintain comparable grain size so as to minimize distance between field plots at coarser scales and to maximize our number of samples.

In our study area, reliable maps do not exist and if created would probably be based upon the same field data used in our study. Whether our method using field data provides a more accurate portrayal of geographical species distributions than the use of modelled range maps remains to be tested at this mid-scale. Range maps, in the best of cases, are extrapolations based upon species field plots, ecological understanding, and ancillary data (e.g. elevation, precipitation); their resulting accuracy depends heavily on the variability of these input factors as well as the type of model used in creating them (Loiselle *et al.*, 2003). Because we had a relatively comprehensive data base available for this study, we chose to preserve the original information present in the field data as much as possible.

Long-term variability in climate could influence current species composition and therefore richness. There are limits to using averaged climate conditions over a period of 18 years to run the process model in a region where trees may persist for centuries. At finer scales than we considered, variation in soil properties as well as topographic diversity could become increasingly important. Unfortunately, accurate forest soil information is difficult to quantify at a resolution of 1 km², and nearly impossible to attain at finer resolutions over broad areas. Another improvement that could be made to our methods is a more precise definition of the growing season that would take into account local scale climate and elevation.

By scaling-up fine-scale field plot data across a region, this study addresses a unique scale of analysis that has rarely been studied. We have provided a regional extent example using fine-scale data of a productivity–richness trend that has been found across the globe in temperate zones. Our research supports the existence of a unimodal relationship between richness and productivity (measured by gross photosynthesis, assuming a constant ratio of autotrophic respiration with P_g , also with total P_n) for woody plants across the Pacific and inland Northwest at a range of different grain sizes. Because of historical extinctions during the Pleistocene, our study area has relatively lower species richness than other temperate forest regions of the world (Waring & Franklin, 1979), as well as the addition of strong competitors. The degree to which our findings depend upon the scale of analysis (using field data), the presence of strong competitors, or the generally low regional species richness, remains to be tested in other temperate forest regions.

No other alternative climatic or productivity index did better than P_g for predicting species richness of trees (CVS), and the same variable was suitable for predicting shrub richness. The generally strong predictive power of P_g may result from choosing a variable that is coupled directly to growth and expresses light limitations in the understorey as it increases to its highest values.

Also contributing to the success of the productivity–richness models was the use of field data across a region rather than relying on existing but overly general range maps for trees (Little, 1971). As far as we know, this is the first effort of its kind to join Forest Inventory Analysis data sets from these separate USFS regions (Pacific Northwest and Rocky Mountain) for regional species-richness analysis. We believe our methods can be exported to other regions where adequate species richness information has been gathered and suitable climatic data exist.

ACKNOWLEDGEMENTS

We would like to thank the National Council for Air and Stream Improvement for funding the dissertation work of Jennifer Swenson. For assistance in this research we would like to thank Andrew Hansen and Linda Phillips, Montana State University, Larry Irwin, Craig Loehle, and other NCASI collaborators, Nicholas Coops, University of British Columbia, Weihong Fan, Richard Stockton College, Ramakrishna Nemani, NASA AIMES, Janet Ohmann, USFS–PNW, Andrew Gray and Susana Melson of USFS–FIA–PNW, Frank Spirek, PNW Siuslaw, Sharon W. Woudenberg, John T. Nelson and Michael J. Wilson of USFS–FIA–RMR, Peter Thornton (DAYMET) of NCAR, Anders Siggins, CSIRO, Daniel Sarr of the National Park Service, and Manuela Huso and Steve Van Tuyl, Oregon State University. Financial support from NASA grant NNG04GK26G was attained for the reproduction of colour imagery and salary to R.H. Waring to complete this work. This study provided the basis for funding the NASA grant to expand the approach to the contiguous United States. We are indebted to Eileen O'Brien, Richard Field and an anonymous reviewer for their insightful and thorough review of this manuscript.

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Editor: Tim Blackburn