

Michael D. Jennings · John W. Williams
Mark R. Stromberg

Diversity and productivity of plant communities across the Inland Northwest, USA

Received: 17 May 2004 / Accepted: 20 December 2004 / Published online: 10 March 2005
© Springer-Verlag 2005

Abstract No definitive explanation for the form of the relationship between species diversity and ecosystem productivity exists nor is there agreement on the mechanisms linking diversity and productivity across scales. Here, we examine changes in the form of the diversity–productivity relationship within and across the plant communities at three observational scales: plots, alliances, and physiognomic vegetation types (PVTs). Vascular plant richness data are from 4,760 20 m² vegetation field plots. Productivity estimates in grams carbon per square meter are from annual net primary productivity (ANPP) models. Analyses with generalized linear models confirm scale dependence in the species diversity–productivity relationship. At the plot focus, the observed diversity–productivity relationship was weak. When plot data were aggregated to a focus of

vegetation alliances, a hump-shaped relationship was observed. Species turnover among plots cannot explain the observed hump-shaped relationship at the alliance focus because we used mean plot richness across plots as our index of species richness for alliances and PVTs. The sorting of alliances along the productivity gradient appears to follow regional patterns of moisture availability, with alliances that occupy dry environments occurring within the increasing phase of the hump-shaped pattern, alliances that occupy mesic to hydric environments occurring near the top or in the decreasing phase of the curve, and alliances that occupy the wettest environments having the fewest species and the highest ANPP. This pattern is consistent with the intermediate productivity theory but appears to be inconsistent with the predictions of water–energy theory.

Communicated by Jim Ehleringer

M. D. Jennings
National Center for Ecological Analysis and Synthesis/Donald
Bren School of Environmental Science and Management,
University of California, Santa Barbara, CA, USA

J. W. Williams
National Center for Ecological Analysis and Synthesis,
University of California, Berkeley, CA, USA

M. R. Stromberg
Hastings Natural History Reservation,
Museum of Vertebrate Zoology, University of California,
38601 E. Carmel Valley Road, Carmel Valley,
Berkeley, CA, USA
E-mail: stromberg@berkeley.edu

Present address: M. D. Jennings (✉)
The Nature Conservancy, Global Priorities Group,
University of Idaho, Department of Geography,
Moscow, ID, 83844 USA
E-mail: jennings@uidaho.edu
Tel.: +1-208-8823882
Fax: +1-208-8823020

Present address: J. W. Williams
Department of Geography, University of Wisconsin,
Madison, WI, USA
E-mail: jwwilliams1@wisc.edu

Keywords Biodiversity · Primary productivity ·
Community ecology · GLM

Introduction

Central to the policy aspects of the present-day rapid alterations in biodiversity, land use, and climate change is the question of the relationship between species diversity and ecosystem function, in particular ecosystem productivity (Chapin et al. 2000; Tilman 2000; Naeem 2002; Schulze and Mooney 1993). There are, however, two different ways by which this relationship has been examined and discussed. On the one hand is the question of whether species diversity per se affects the amount of biomass produced at a given site, perhaps due to niche complementarity, sampling effects (e.g., Hector and Schmid 1999; Tilman et al. 1997; Huston 1997), or mechanisms not yet described. On the other hand is the question of whether the amount of biomass produced at a site affects the number of species found at that site (e.g., Grace 1999; Grime 1973a). The former question is framed in terms of biomass productivity (referred to

here as annual net primary productivity, or ANPP) being in some way dependent on species diversity (S ; we symbolize this relationship as $ANPP \sim S$). The latter question is framed in terms of species diversity being in some way dependent on productivity (symbolized as $S \sim ANPP$).

The difference between the two questions is an important one because the first question assumes the ongoing problem of biodiversity loss and asks how such losses could affect ecosystem services, for example by losing functional redundancies and material process steps. The second question assumes the changes in productivity and asks how such changes could affect species diversity, for example, how might climate change affect biodiversity either directly or indirectly through changes in ecosystem dynamics? Although the two are coupled, researchers have yet to explain exactly how in a spatially extensible way. In this study we focus on the latter question: the dependence of species diversity on biomass productivity ($S \sim ANPP$).

Connell and Orias (1964) dealt conceptually with the issue of ecosystem regulation of species diversity, proposing that the diversity of a given community is a function of the amount of energy flowing through its food web. They hypothesize that the energy flow is a product of limiting physical factors, environmental stability, and biological interaction. Whittaker and Niering (1975) show a hump-shaped form in the relation between species diversity and both moisture and elevation gradients. They conclude that relationships between diversity and productivity in their study area are a function of the plant community's growth form components (tree, shrub, herb), and that those relationships are complex. Rosenzweig (1995) reviews ten hypotheses for the often observed hump-shaped diversity–productivity relationship. He accepts the Wright et al. (1993) application of Preston's (1962) lognormal species-area theory to explain the ascending portion of the hump-shaped form of the relationship. However, he finds no convincing theory that can explain the declining portion of the hump-shaped form, and notes that most mechanisms are likely to apply to only a limited set of scales.

A recent focus has been on the role of spatial scale, and both theory and observations indicate that the diversity–productivity relationship is scale dependent. Gross et al. (2000) show scale dependence in terms of focus (the spatial scale to which the data are aggregated) and extent (the universe of analysis) for herbaceous plant communities (see Scheiner et al. 2000, for an explanation of the components of spatial scale). Mittelbach et al. (2001) show that for vascular plants, hump-shaped relationships tend to be more common at local to regional extents and positive linear relationships more common at continental to global extents. Chase and Leibold (2002) provide evidence of scale dependence in the relationship between species diversity and biomass productivity in ponds. In one of the broadest reviews of the relationship between species diversity and primary productivity, Waide et al. (1999) assembled 200 statis-

tical diversity–productivity relationships from 154 published sources. Although they found strong evidence of scale dependence, they found no clear pattern in the form of the diversity–productivity relationship. Guo and Berry (1998) show that the form of different local relationships between species diversity and biomass can accumulate sequentially along the productivity gradient into a hump-shaped form when the extent is broadened to include a greater range of productivity and environments. Scheiner et al. (2000) term this the “pattern accumulation hypothesis.” Under this hypothesis, when the local forms of diversity–productivity relationships accumulate to a more general pattern, local-scale processes may be responsible for regional patterns of the relationship.

Scheiner and Jones (2002) examined issues of scale with respect to the form (e.g., hump-shaped, u-shaped) of the diversity–productivity relationship using Curtis' (1959) field plots for species counts, and estimates of productivity from a Biome-BGC model (Running and Hunt 1993) having a 0.5° latitude \times 0.5° longitude ground resolution (about 52 km^2). They found no simple pattern, and found that the form of the relationship depended on geographic scale as well as the ecological hierarchy of analysis (communities and formations). Scheiner and Jones (2002) provide two hypotheses for the scale dependency in the different forms (humped-shaped, u-shaped) of diversity–productivity relationships that they observed. First, as grain size increases species numbers are added because of environmental heterogeneity, yet productivity values are averaged. Second, species diversity is greatest at intermediate levels of productivity because those habitats are more common.

One of the major limiting factors to understanding $S \sim ANPP$ across scales is the number of field samples available to study $S \sim ANPP$ at broad spatial and ecological scales. While a number of studies using original field measurements (where the field samples were collected for that study) have been carried out with a plot-level focus at localized extents (i.e. Grace 1999; Guo and Berry 1998), fewer have been carried out at small regional extents (i.e. Chase and Leibold 2002, though the focus was a pond), and, to our knowledge, no studies using original field measurements have been carried out with a plot-sized focus across a large regional extent (i.e. $> 500,000 \text{ km}^2$). Studies that cover intermediate to large areas have had to rely on combining datasets often developed for other purposes (e.g., Gross et al. 2000) as well as using proxy measures of productivity such as rainfall or actual evapotranspiration (i.e. Mittelbach et al. 2001). The way in which species richness and productivity are estimated varies with scale, confounding analyses of scale dependence (Mittelbach et al. 2001).

In this study, we explored $S \sim NPP$ across a large geographic region using S values observed in 4,760 vegetation field plots and modeled values of ANPP. We examined the patterns of S and NPP within and across vegetation community units (“alliances”; Jennings et al.

2004) that are defined as a part of a larger effort to describe the vegetation communities of North America (Grossman et al. 1998; Barbour et al. 2000). Such a classification of the landscape into vegetation community units is necessary for comparing natural communities. We restricted our analysis to a subset of field plots that meet the criteria of defined vegetation alliance (nevertheless using over 4,500 sampling points). In particular, we examined $S \sim ANPP$ with respect to (a) vegetation alliances, (b) more general physiognomic vegetation types (PVTs) (i.e. conifer forest, shrub-steppe, wetland grassland), and (c) plant species life forms (herb, shrub, tree).

Study area

The study area is the Inland Northwest (INW) of the United States, which is located between 107°W and 123°W longitude and 39°N to 49°N latitude and is about 941,000 km² in size (Fig. 1). We used this area for the study because of the combined opportunity presented by the field plot data and the detailed ANPP estimations. No other large region of the world has such an extensive collection of field plots co-occurring with estimated ANPP values across large environmental gradients. We delineated the study area based on ecological sections of Bailey et al. (1994) that form a contiguous region containing the field plots (Fig. 1). About 41% of the study area is covered by tree-dominated vegetation, 33% by shrub-dominated vegetation, and 10% by herbaceous-dominated vegetation. Almost 16% is covered by other classes such as agriculture, water, or lands barren of vegetation. The broad patterns of vegetation are strongly influenced by the region's climate and landform (Daubenmire 1956).



Fig. 1 Location of the study area in North America

Methods

Field data

A set of field plot records was developed from an initial collection of 39,131 records from 11 different sources collected between 1972 and 2001; 80% were collected since 1986. Univariate outliers were identified for logical consistency of latitude, longitude, year collected, elevation, slope, aspect, and percent species cover values. All plot records containing outliers of these variables were removed. Records having other than a 20 m² plot size were removed. All taxa were standardized to a single species level synonym based on the PLANTS database (USDA NRCS 2000).

To examine $S \sim ANPP$ relationship at various ecological levels of organization, the remaining plot records were classified to existing alliance concepts formally defined and described in the International Classification of Ecological Communities (NatureServe 2002). Alliances are named according to their dominant plant species (Table 1; Jennings et al. 2004). Criteria for assigning sets of plots to alliances included the identity of the dominant species, their percent cover, the identity of the subdominant species and their percent cover, as well as geographic range, elevation range, and ground slope gradient and aspect. Descriptive parameters of each alliance were developed as a set of structured query language statements that were applied to the database. Summary statistics were tabulated in both sample space and species space for each set of records extracted. Examples of the summary statistics include mean and standard deviation of species cover values, the skew in species cover value distributions, species diversity, and the evenness of plot compositions. Altogether, we assigned the plots to 39 alliances out of approximately 100 alliances known from the region.

Each set of field plot records attributed to an alliance was subjected to a multivariate outlier analysis for species cover values using a frequency distribution of Sorensen distance measures (McCune and Mefford 1999). Field plots more than two standard deviations from the mean distance were removed. The sets of field plots for each alliance were then tested against a null hypothesis of having no more structure than a randomly selected set using a Mantel test (Sokal 1979; McCune and Mefford 1999). Given the phytosociological nature of these data a P value of 0.1 was used as a threshold of significance. Sets of field plot records assigned to an alliance having a Mantel $P > 0.1$ were not used. We then used a nonmetric multidimensional scaling procedure (Kruskal 1964) to reduce dimensionality, measure, and confirm the floristic distinctness of each alliance data set from all other field plots, as can be seen in Fig. 2 for the *Artemisia arbuscula* alliance.

Alliances were further classified to one of five PVTs that represent structural properties of the vegetation

Table 1 Vegetation alliances and number of plots analyzed per alliance

Alliance name	Number of plots	Code
<i>Abies amabilis</i>	37	abam
<i>Abies grandis</i>	316	abgr
<i>Abies lasiocarpa</i>	569	abla
<i>Abies lasiocarpa</i> – <i>Acer glabrum</i>	129	ablaacgl
<i>Abies lasiocarpa</i> – <i>Pinus albicaulis</i>	173	ablapial
<i>Acer glabrum</i>	9	acgl
<i>Alnus sinuata</i>	44	alsi
<i>Amelanchier alnifolia</i>	33	amal
<i>Artemisia arbuscula</i>	74	arar
<i>Artemisia tridentata</i>	485	artr
<i>Betula nana</i>	10	bena
<i>Calamagrostis canadensis</i>	32	caca
<i>Carex nigricans</i>	28	cani
<i>Carex spectabilis</i>	19	casp
<i>Cornus sericea</i>	30	cose
<i>Festuca idahoensis</i>	31	feid
<i>Festuca idahoensis</i> Alpine	465	feidalp
<i>Juniperus scopulorum</i>	25	jusc
<i>Leymus cinereus</i>	70	leci
<i>Pentaphylloides floribunda</i>	93	pefl
<i>Phyllodoce empetriformis</i>	19	phem
<i>Pinus albicaulis</i>	120	pial
<i>Pinus contorta</i>	444	pico
<i>Pinus contorta</i> – <i>Populus tremuloides</i>	16	picopotr
<i>Pinus ponderosa</i> – <i>Pseudotsuga menziesii</i>	468	pipopsme
<i>Poa secunda</i>	24	pose
<i>Populus tremuloides</i>	260	potr
<i>Prunus virginiana</i>	26	prvi
<i>Pseudoroegneria spicata</i>	289	pssp
<i>Pseudotsuga menziesii</i> – <i>Quercus garryana</i>	13	psmequga
<i>Pseudotsuga menziesii</i> woodland	347	psmewood
<i>Rosa Woodsii</i>	19	rowo
<i>Rubus parviflorus</i>	15	rupa
<i>Salix geeyeriana</i>	32	sage
<i>Salix monica</i>	12	samo
<i>Salix pseudomyrsinites</i>	22	saps
<i>Thuja plicata</i>	50	thpl
<i>Tsuga heterophylla</i>	35	tshe
<i>Tsuga mertensiana</i> – <i>Abies amabilis</i>	79	tsmeabam
Total	4,760	

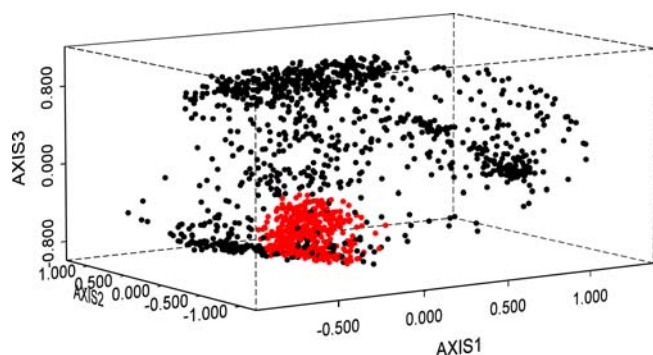


Fig. 2 Results from a NMDS ordination of field plots dominated by shrubs. The positions of those plots classified as members of the *Artemisia arbuscula* alliance are shown in red and emphasized by their size, the positions of all other shrubland plots are shown in black

(Table 2). For example, the *Alnus sinuata* alliance was assigned to the Mesic Shrubland physiognomic group. Several alliances were unassigned to PVTs.

These data have various origins and are not regularly distributed across the study area (Fig. 1). Our processes of data selection, standardization, and analysis, however, were designed to minimize these limitations and produce a high-quality set of field plot data. Although the plot distributions are not random, there is no reason to expect any systematic bias in the data that would affect our findings. The data set provides a uniquely large number of samples occurring over a broad geographic region.

Productivity data

Annual net primary productivity in grams carbon per square meter for each of the field plot sites was estimated from a Biome-BGC simulation (public communication: Numerical Terradynamic Simulation Group, University of Montana, URL: <http://www.forestry.umt.edu/ntsg/>; Running and Hunt 1993) of the study area (Inter-

Table 2 Physiognomic vegetation types (PVTs), number of plots per PVT, and their constituent alliances

PVT name	Number of plots	Constituent alliances
Conifer Forest	2449	abam, abgr, abla, ablaacgl, ablapi, pial, pico, picopotr, pipopsme, psmequga, thpl, tshe, tsmeabam
Warm Shrubland	559	arar, artr
Mesic Shrubland	364	acgl, als, amal, bena, cose, pefl, phem, prvi, rowo, rupa, sage, samo, saps
Upland Grass	677	feid, feidalp, leci, pose, pssp
Wetland Grass	47	cani, casp
Unassigned	664	caca, jusc, potr, psmewood
TOTAL	4760	

mountain Fire Science Lab 1996) for 1988 at a 2 km² ground resolution. The accuracy and sensitivity of Biome-BGC has been extensively documented and tested (White et al. 2000), particularly for the intermountain west where it was first developed and tested. Evaluations include nine sensitivity test sites of forest, shrubland, and grassland vegetation within our study area (White et al. 2000, Appendix C) as well as field-data-to-model comparisons at seven sites ($r^2=0.82$) within and adjacent to the INW (Running 1994). In the INW, simulated ANPP values range from 0 to >1,000 g C m².

Data integration and preparation

ANPP values were spatially associated with each field plot by intersecting the Biome-BGC grid with the field plot coordinates using geographic information system software. A significant limitation of this approach in associating the ANPP data with the field plots is that the ANPP grid cells are of a larger spatial grain than the plot data. However, the spatial resolution of the ANPP data we used is high compared to other terrestrial ecosystem models, which typically operate at 0.5°×0.5° grid cells or larger (e.g., VEMAP Members 1995; Cramer et al. 1999). Variations in field plot species diversity at any of these spatially more coarse scales are not inconsequential. Field plot species diversity values for plots that are within 2 km of each other have a standard deviation of approximately four species, compared to a mean of approximately 20 species. This scale mismatch is an important source of uncertainty when our focus is the plot, but is minor when the focus is broadened to alliances and PVTs (Scheiner and Jones 2002).

Table 3 Combinations of foci (statistical units) and extents (universe of analysis)

	EXTENT		
	Alliance	PVT	Ecoregion
FOCUS			
Plot	X	X	X
Alliance			X
PVT			X

Analyses

We examined $S \sim ANPP$ across a range of ecological foci and extents (sensu Scheiner et al. 2000), where the grain size is the original unit of observation, the focus is the unit at which data are analyzed, and the extent is the universe in which the foci occur. The foci considered were: a field plot, an alliance, and a PVT. The extents at which these foci were examined were: alliance, PVT, and the entire INW ecoregion. The combinations of extent and foci that we considered were: (1) focus = field plot, extent = INW; (2) focus = field plot, extent = alliance for all 39 alliances; (3) focus = field plot, extent = PVT for all five vegetation types; (4) focus = alliance, extent = INW; and (5) focus = PVT, extent = INW (Table 3).

For all analyses, a generalized linear model (GLM; McCullagh and Nelder 1989) with a linear and quadratic term was used to check for linear and unimodal (hump-shaped or u-shaped) relationships between species diversity and ANPP. We used a Poisson error distribution, standard practice when the dependent variable represents count data (Crawley 1993), but we did not log-transform the dependent variable (S). A log transformation is generally recommended for count data to avoid negative predicted values (Nicholls 1989; Crawley 1993) and has been used in previous analyses of diversity–productivity relationships (Mittelbach et al. 2001), but was avoided here because the log transformation could change the apparent form of the modeled relationship. No negative species diversity values were predicted within the range of the ANPP data. All relationships with a significant quadratic term were tested for unimodality with the Mitchell-Olds and Shaw test (MOS; Mitchell-Olds and Shaw 1987; Leibold 1999; Mittelbach et al. 2001), and deemed to be significantly unimodal within the given range of ANPP values if $P \leq 0.05$. All GLM analyses were carried out in Matlab (Matlab r13, The Mathworks, Natick, MA, USA) using the procedure “glmfit.” Goodness of fit for the GLM analyses was assessed by calculating the cumulative distribution function for the χ^2 statistic (Vincent and Haworth 1983).

Conventional tests of association between two variables assume that observations are independent, an assumption that fails when both variables are spatially autocorrelated. In such cases, variables may appear to be significantly correlated when in fact the apparent association is due to similar responses by the variables to

the underlying spatial characteristics of the system (Haining 1997, p 321). However, if only one variable is spatially autocorrelated, the conventional GLM test can be used safely (Cliff and Ord 1981, p 189). In our data both species diversity and ANPP were positively autocorrelated when evaluated with Moran's statistic (Kaluzny et al. 1998), and initial analyses showed that significant spatial structure persisted in the residuals of approximately half of the regressions at the plot focus. To minimize the potential effects of spatial dependence at the plot focus, the spatial structure was removed from the independent variable (ANPP; Cliff and Ord 1981) prior to the GLM analyses by implementing a spatial

multivariate linear regression of ANPP against latitude and longitude (ANPP~LAT+LON) using a moving-average autoregressive model from S-PLUS 2000 (Insightful Corporation; Venables and Ripley 2002). The spatially detrended residuals were then added to the mean ANPP value of all field plots to create a dataset of spatially detrended ANPP values for the GLM analyses. However, there is an analytical cost to spatially detrending ANPP in that spatial pattern not due only to autocorrelation may also be removed (Hawkins and Porter 2003).

As the alliances and PVTs are ecological entities, analyses at these foci did not include spatial detrending.

Table 4 Results from GLM models where the focus was the field plot and extents varied from the entire study area to the general PVTs and to the alliances

Focus	Extent	Linear <i>P</i> value	Quadratic <i>P</i> value	Linear term	Quadratic term	Dev.	df	χ^2
Plots	Entire INW	0.082	< 0.001	-6.972E-04	9.264E-06	21228.7	4757	> 0.999
PVTs								
Plots	Conifer forest	< 0.001	< 0.001	-2.085E-03	-9.858E-06	10982.1	2771	> 0.999
	Warm shrubland	0.143	< 0.001	-2.213E-03	-2.751E-05	1645.9	361	> 0.999
	Mesic shrubland	0.365	< 0.001	1.431E-03	7.079E-05	2474.2	566	> 0.999
	Upland grassland	0.010	0.161	3.788E-03	-1.162E-05	3400.3	674	> 0.999
	Wetland grassland	0.063	0.013	3.459E-03	1.612E-05	232.6	71	> 0.999
Individual alliances								
Plots	<i>Abies amabilis</i>	0.199	0.006	5.303E-03	-5.124E-05	107.7	34	> 0.999
	<i>Abies grandis</i>	0.513	< 0.001	1.745E-03	-9.422E-05	738.0	313	> 0.999
	<i>Abies lasiocarpa</i>	0.772	< 0.001	-3.783E-04	2.994E-05	2028.7	566	> 0.999
	<i>Abies lasiocarpa</i> - <i>Acer glabrum</i>	0.539	0.969	-2.382E-03	-9.769E-07	241.9	126	> 0.999
	<i>Abies lasiocarpa</i> - <i>Pinus albicaulis</i>	0.943	0.170	-0.000140	-1.443E-05	442.3	170	> 0.999
	<i>Acer glabrum</i>	0.017	0.003	-4.361E-02	-3.988E-04	10.9	6	0.908
	<i>Alnus sinuata</i>	0.352	0.982	6.278E-03	-8.874E-07	92.8	41	> 0.999
	<i>Amelanchier alnifolia</i>	0.155	0.636	7.457E-03	1.522E-05	120.9	30	> 0.999
	<i>Artemisia arbuscula</i>	0.010	0.215	-1.019E-02	-3.157E-05	115.3	71	0.999
	<i>Artemisia tridentata</i>	0.314	< 0.001	1.731E-03	6.984E-05	2134.6	482	> 0.999
	<i>Betula nana</i>	0.407	0.803	2.948E-02	-9.477E-05	33.1	7	> 0.999
	<i>Calamagrostis canadensis</i>	0.830	< 0.001	7.767E-04	-6.665E-05	120.8	29	> 0.999
	<i>Carex nigricans</i>	0.015	0.341	-8.673E-03	7.644E-06	65.8	25	> 0.999
	<i>Carex spectabilis</i>	0.881	0.735	-1.008E-03	8.942E-06	24.0	16	0.910
	<i>Cornus sericea</i>	0.259	0.003	4.801E-03	5.362E-05	111.8	27	> 0.999
	<i>Festuca idahoensis</i> alpine	0.340	0.190	1.824E-03	1.358E-05	1979.0	462	> 0.999
	<i>Festuca idahoensis</i>	0.666	0.731	-2.657E-03	9.647E-06	129.5	28	> 0.999
	<i>Juniperus scopulorum</i>	0.070	< 0.001	-1.725E-02	-3.839E-04	179.0	22	> 0.999
	<i>Leymus cinereus</i>	< 0.001	< 0.001	-1.563E-02	9.258E-05	274.1	67	> 0.999
	<i>Pentaphylloides floribunda</i>	0.675	0.009	1.596E-03	-6.365E-05	373.5	90	> 0.999
	<i>Phyllodoce empetriformis</i>	0.101	0.064	-1.376E-02	-3.751E-05	6.6	16	0.019
	<i>Pinus albicaulis</i>	0.197	0.933	2.989E-03	-1.015E-06	444.0	117	> 0.999
	<i>Pinus contorta</i>	0.009	0.050	-4.009E-03	1.665E-05	1573.4	441	> 0.999
	<i>Pinus contorta</i> - <i>Populus tremuloides</i>	0.386	0.278	5.763E-03	-3.117E-05	46.5	13	> 0.999
	<i>Pinus ponderosa</i> - <i>Pseudotsuga menziesii</i>	0.929	0.001	1.283E-04	2.194E-05	1391.6	465	> 0.999
	<i>Poa secunda</i>	0.026	< 0.001	-1.925E-02	-2.535E-04	52.7	21	> 0.999
	<i>Populus tremuloides</i>	0.175	0.477	-3.254E-03	7.893E-06	46.5	257	> 0.999
	<i>Prunus virginiana</i>	0.053	0.009	1.194E-02	-1.343E-04	40.4	23	0.986
	<i>Pseudotsuga menziesii</i> - <i>Quercus garryana</i>	0.235	0.904	1.164E-02	6.624E-06	21.0	10	0.979
	<i>Pseudotsuga menziesii</i> woodland	0.112	< 0.001	3.633E-03	5.841E-05	112.8	344	> 0.999
	<i>Pseudoroegneria spicata</i>	0.375	0.993	-2.899E-03	-1.326E-07	457.1	84	> 0.999
	<i>Rosa woodsii</i>	0.031	0.163	3.193E-02	1.179E-04	106.4	16	> 0.999
	<i>Rubus parviflorus</i>	0.662	0.377	6.510E-03	-1.233E-04	39.2	12	> 0.999
	<i>Salix geyeriana</i>	0.016	0.377	-1.00589	3.711E-05	145.8	29	> 0.999
	<i>Salix monica</i>	0.178	0.730	1.00132	-3.330E-05	32.7	9	> 0.999
	<i>Salix pseudomyrsinites</i>	0.058	0.071	1.00642E	1.370E-04	89.2	19	> 0.999
	<i>Thuja plicata</i>	0.003	0.869	-2.00019	8.391E-06	194.2	47	> 0.999
	<i>Tsuga heterophylla</i>	0.063	0.824	-8.700E-03	-6.044E-06	58.5	32	0.997
	<i>Tsuga mertensiana</i> - <i>Abies amabilis</i>	< 0.001	0.093	-9.562E-03	-2.001E-05	143.9	76	> 0.999
Alliance	Entire INW	0.131	< 0.001	-0.00623	-0.113E-03	32.59	36	0.369
PVT	Entire INW	0.146	0.0573	-0.0236	-0.297E-03	0.14	2	0.069

Instead, we recentered the ANPP values prior to regression to avoid co-dependence between the linear and quadratic coefficients (Neter et al. 1996). Recentering involved subtracting the mean NPP from all NPP values prior to GLM analysis and did not alter the form of the relationship. Mean NPP among alliances was 490.5 and 483 g C m² among PVTs.

Results

Diversity–productivity relationships across scales

At the plot focus at any extent (alliance, PVT, and INW) there were at best only weak relationships between S and ANPP (Table 4). For example, at the plot focus and

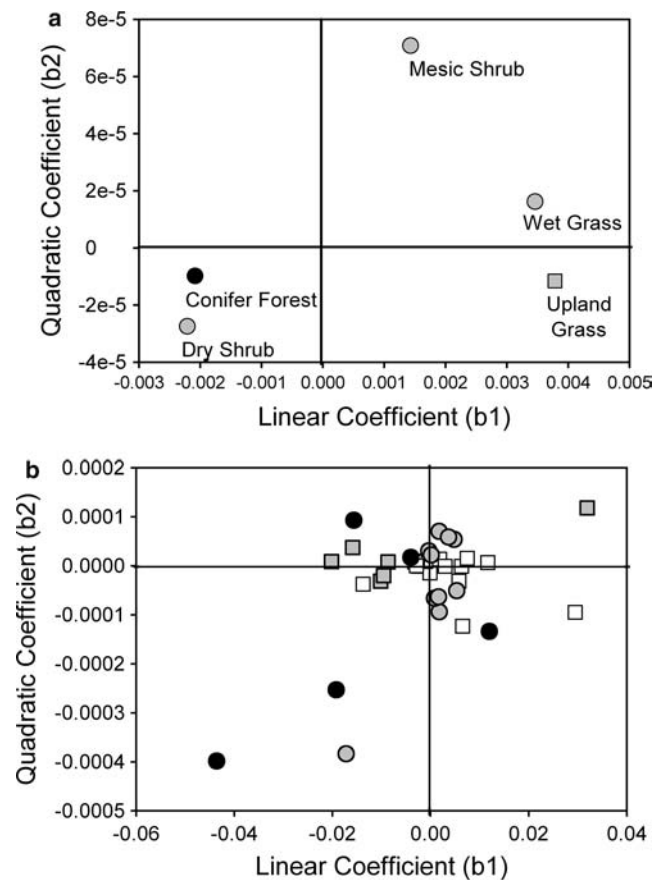


Fig. 3 Plots of the linear and quadratic coefficient terms for the $S \sim \text{ANPP}$ GLM regressions at the plot focus, for (a) 5 PVTs and (b) the 39 alliances. Symbols indicate whether neither relationship was significant (empty squares), only the linear term was significant (gray squares), only the quadratic term was significant (gray circles), or both terms were significant (black circles). Significant positive quadratic coefficients correspond to u-shaped relationships; significant negative quadratic coefficients correspond to hump shaped relationships. The low values of the coefficients are mainly due to the different units and ranges of the independent and dependent variables (grams carbon per square meter versus species counts). More telling is the fact that the cluster of coefficients is approximately symmetric around the origin, indicating that at the plot focus, no single form of $S \sim \text{ANPP}$ predominates

INW ecoregion extent there was a significant ($P \leq 0.05$) linear relationship between S and ANPP with a very poor fit ($\chi^2 > 0.999$) to the data (Table 4).

At the plot focus and the PVT extent (when plot data were analyzed by the more general PVTs, such as mesic shrubland), only one vegetation type (upland grassland) had a significant linear term; however, four out of five had significant quadratic terms. Of those having a significant quadratic term, two were positive and two were negative. All of these passed the MOS test, indicating that their maxima or minima occurred within the observed range of ANPP values. These GLM models showed a low goodness of fit ($\chi^2 > 0.999$). When the linear and quadratic coefficients for the GLM analyses at plot focus and PVT extent were plotted against each other they showed a dispersed but indefinite pattern (Table 4, Fig. 3a), suggesting that no single form of the relationship predominated.

At the plot focus and alliance extent (when the plot data were analyzed by alliance), 12 (32%) alliances had significant linear terms and 15 (40%) had significant quadratic terms ($P \leq 0.05$). Of the 15 alliances with significant quadratic terms, seven had positive correlations (a u-shaped form) and eight had negative correlations (a hump-shaped form; Fig. 3b). Each of the GLM models for these 15 alliances passed the MOS test. Goodness of fit is low (Table 4). When linear and quadratic coefficients were plotted against each other they clustered around the 0,0 coordinate showing no obvious asymmetry (Fig. 3b), indicating that no single form of $S \sim \text{ANPP}$ dominated (i.e. hump-shaped, u-shaped, linear).

At the alliance focus and ecoregional (INW) extent (where alliance plot data were aggregated to mean values and analyzed across the study region) a clear pattern emerged (Fig. 4, Table 4). The linear term P value was

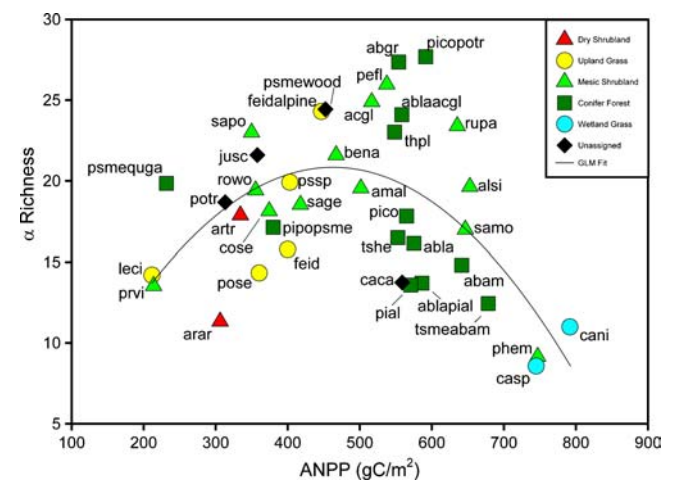


Fig. 4 $S \sim \text{ANPP}$ for the INW when the focus is the alliances and the extent is the INW. ANPP is represented by the mean for each alliance, and diversity is represented by the mean alpha-diversity within each alliance. The symbol for each alliance indicates its physiognomic vegetation type (Table 2)

not significant at $P \leq 0.05$, however the quadratic P value was significant. The quadratic coefficient of correlation was negative (hump-shaped) and passed the MOS test. The goodness of fit at this focus ($\chi^2 = 0.369$) improved substantially over those at a plot focus (Table 4).

At a PVT focus and ecoregional extent, the pattern is similar to the alliance focus of the same extent (Fig. 5). The quadratic coefficient was more strongly negative than the alliance focus, and it also passed the MOS test. Deviance from the model is quite low, even considering the low degrees of freedom, indicating a good fit to the data ($\chi^2 = 0.069$) (Table 4).

Variations in communities and plant life forms across the productivity gradient

The arrangement of alliances across the ANPP gradient (Fig. 4) appears to be sorted by variations in moisture availability. Alliances that occupy dry environments (i.e. *Artemisia arbuscula* alliance, *Poa secunda* alliance, and *Pseudotsuga menziesii*—*Quercus garryana* alliance) all occur within the increasing phase of the hump-shaped pattern, having ANPP values less than 450 g C m². Although some mesic shrubland types also occur in the increasing phase (13%), all other vegetation types that occupy mesic to hydric environments (i.e. *Abies grandis* alliance, *Rubus parviflorus* alliance, and *Carex nigricans* alliance) occur either near the apex or in the decreasing phase of the hump-shaped pattern. Those that occupy the wettest environments have the least number of species and the highest ANPP. Most conifer forest alliances (85%) occur along a relatively narrow productivity gradient in the middle range of ANPP values and show both the highest S values and largest range in S values. The mesic shrubland types occur along the broadest

productivity gradient. Although the range of S values for mesic shrublands may seem similar to that for conifer forest alliances, it is almost doubled by just two alliances (the *Phyllodoce empetriformis* and *Prunus virginiana* alliances), that occur at either end of the productivity gradient and both of which have low S values. Upland grasses occur at the lower end of the productivity gradient and have relatively low S values. The *Carex* alliance types show the greatest productivity levels yet the lowest S values (Fig. 4).

Partitioning S by plant life form at the alliance focus (Fig. 6) reveals that the observed hump-shaped form of $S \sim \text{ANPP}$ seen in Fig. 4 derives primarily from the distribution of forb species along the ANPP gradient. Although most of the species richness is made up by forbs and they show a stronger response to the ANPP gradient, significant hump-shaped relationships also occur with shrubs and trees. There is a negative linear trend in graminoid richness along the ANPP gradient.

We examined the potential for pattern accumulation by overlaying the curves from the 15 alliances that had a significant quadratic GLM coefficient (Fig. 7). While an unambiguous pattern accumulating from the plot focus

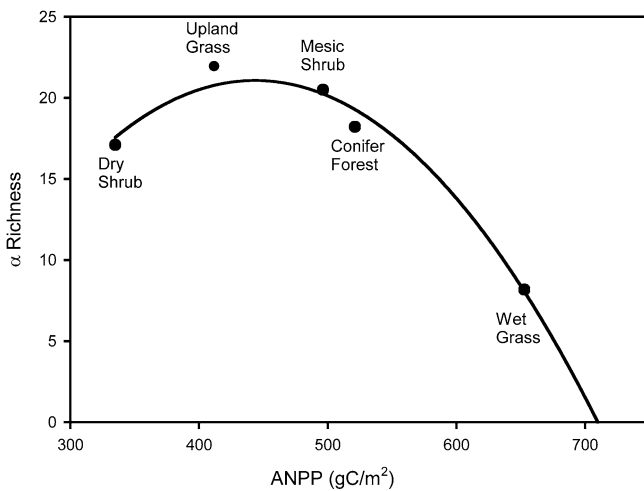


Fig. 5 $S \sim \text{ANPP}$ for the INW when the focus is expanded to physiognomic vegetation types. As in Fig. 4 where the focus is the alliance, ANPP and alpha-diversity are the mean field plot values for each PVT

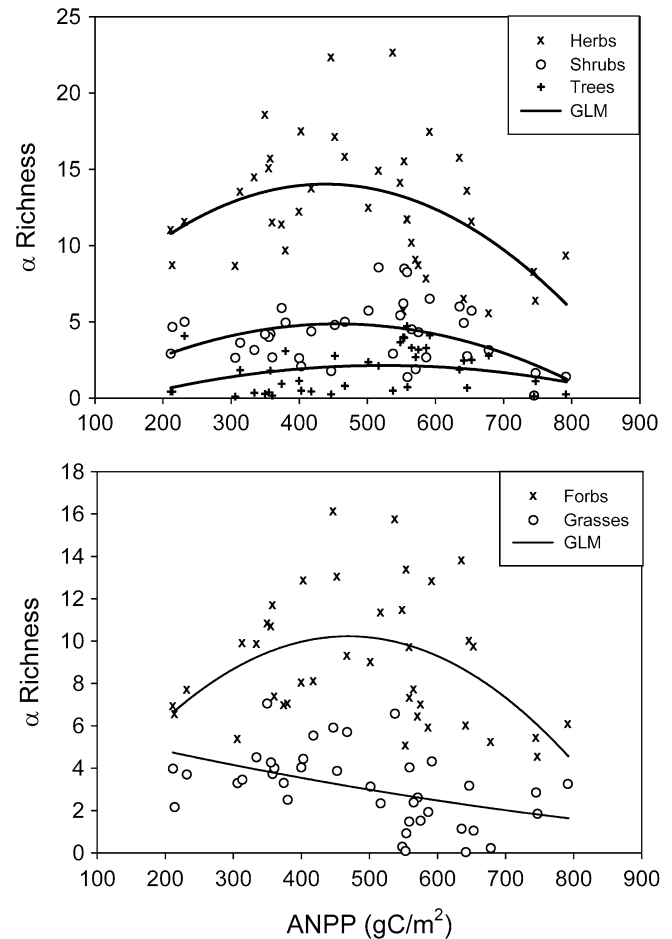


Fig. 6 $S \sim \text{ANPP}$ at the alliance focus and INW extent (as in Fig. 4). **a** Plant species diversity here is parsed by major life forms. **b** Herb types are further parsed into forbs and grasses

(Fig. 7) to the alliance focus (Fig. 4) is not obvious, most of the curves at the lower half of the NPP gradient in Fig. 7 are ascending, and most at the upper half are descending.

Discussion

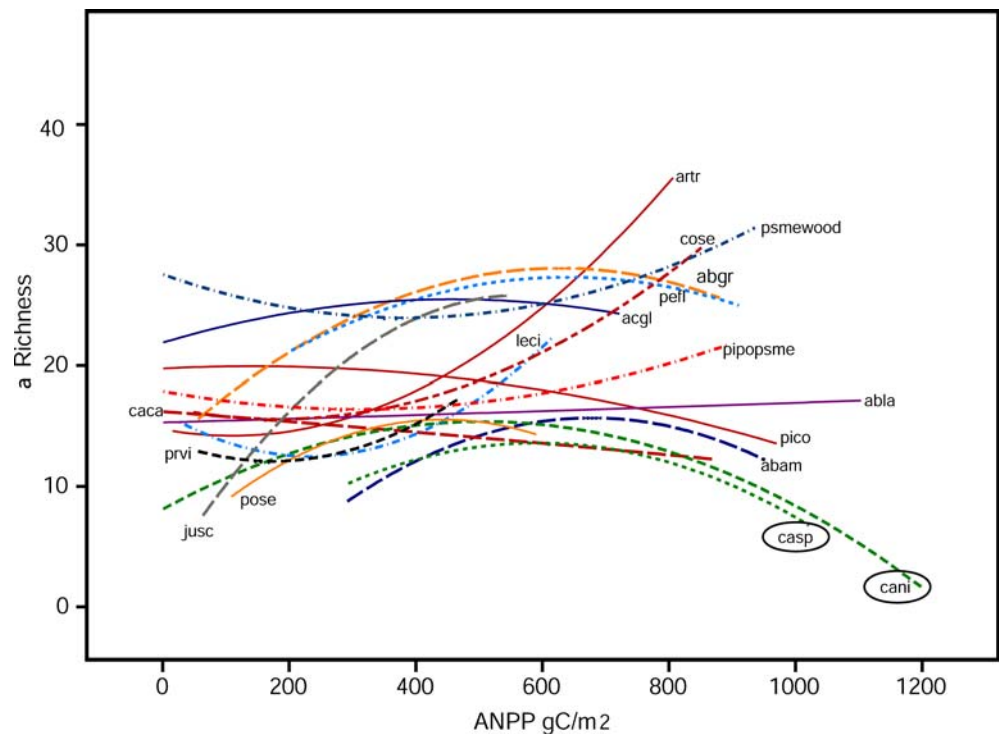
In this study, $S \sim ANPP$ clearly depends on the scale of observation. At the focus of the plot, regardless of extent, there is little discernable pattern. When the focus is broadened to the alliance or PVT, a hump-shaped pattern emerges. The forms of $S \sim ANPP$ found at the alliance and PVT foci within the INW were similar. This scale-dependence of $S \sim ANPP$ is consistent with previous reviews of $S \sim ANPP$ (e.g., Scheiner and Jones 2002; Mittelbach et al. 2001).

The evidence for pattern accumulation is ambiguous. When the $S \sim ANPP$ curves for the plot focus and alliance extent are overlaid (Fig. 7), most of the curves at the lower half of the productivity gradient are positive (increasing in diversity and productivity). At the higher half of the productivity gradient most of the curves are negative. The collective set of plot focus curves in Fig. 7 does not obviously accumulate to a pattern similar to the alliance focus curve in Fig. 4. Without formal methods for measuring pattern accumulation, though, we are unable to quantify the extent to which pattern accumulation may occur among the alliance-level $S \sim ANPP$ relationships examined in this study. Development of such a method would be a logical next step, but is beyond the scope of this paper.

The apparent, albeit weak, accumulation of pattern from small focal scales to large suggests that the mechanisms influencing $S \sim ANPP$ at the local scale may differ from those operating at regional or landscape scales. However, our finding of little pattern of accumulation contrasts with the findings of Guo and Berry (1998), perhaps due to the differences in scale between studies. Guo and Berry (1998) examined microhabitat (0.25 m²) in five types of habitats (shrub, half-shrub, open, k-rat mound, and ant mound) of unknown floristic composition over a 20 ha extent. It may be that the pattern accumulation hypothesis itself only explains variations in the form of $S \sim ANPP$ across a limited range of spatial and ecological scales. This problem can only be solved with better methods for quantifying the accumulation of pattern and broader networks of NPP measurements collected in the field in association with species censuses.

Scheiner and Jones (2002) also found that $S \sim ANPP$ varied with changes in spatial and ecological focus, and that the strength of the relationship was relatively weak at smaller foci. However, they reported the emergence of a u-shaped relationship when the focus was broadened to community types. A key difference between this study and that of Scheiner and Jones (2002) is the range of ANPP considered (INW: 200–800 g C m²; Wisconsin: 500–850 g C m²). Over the range of values reported in Scheiner and Jones (2002) we would only capture the right half of the hump-shaped relationship, the alliances that occur in mesic to hydric environments (Fig. 4). Guo and Berry (1998) found that the size of the range of the

Fig. 7 $S \sim ANPP$ at the plot focus and the alliance extent. CASP and CANI, circled at lower right of graph, have nonsignificant P values and are included to provide perspective of the alliances at the far end of the gradient. All other curves are of the 15 alliances having significant quadratic terms



productivity gradient was a key factor in the hump-shaped form of the relationship.

Several authors have suggested that hump-shaped $S \sim \text{ANPP}$ relationships may be more common at local scales, and positive linear or monotonic relationships more common at regional to global scales (Chase and Leibold 2002; Mittelbach et al 2001; Bond and Chase 2002). Chase and Leibold (2002) propose that species turnover among localities may generate this scale-dependence. In comparison, we found a strong hump-shaped $S \sim \text{ANPP}$ relationship at broad ecological foci and ecoregional extent. Our use of mean plot richness, instead of total richness for each alliance or PVT, excludes species turnover among plots as a mechanism for generating the regionally hump-shaped $S \sim \text{ANPP}$. It is noteworthy that when we examined $S \sim \text{ANPP}$ by plant life forms we found in all communities that herbaceous species contribute most of the diversity (Fig. 6a), and that of these most are forbs (Fig. 6b). We are conducting further analyses of patterns of species turnover within and across alliances to assess the combined effects of local richness and beta diversity. Additionally, mechanisms reported by some authors are from studies limited to plant communities of a similar type (e.g. Grime 1973a; Grace 2001; Guo and Berry 1998), whereas the hump-shaped relationship observed here spans a wide range of plant communities and vegetation physiognomies, as well as a broad productivity gradient.

The response pattern of species diversity cannot be easily explained by null models that predict species diversity as a function of the number of individuals in each plot (Oksanen 1996). Although we do not have information on the number of individuals in each plot, and so cannot test this hypothesis numerically, in our data the most species-rich plots are also the ones that have the largest individuals, such as the *Abies grandis* alliance (Fig. 4). If the number of species in a plot is in part an inverse function of the size of individuals, one would expect that plots from alliances dominated by grasses, forbs, and sedges would also have the most species. However, in this study those alliances occupy the extremes of the productivity gradient and are the most species-poor (Fig. 4).

We found that the communities that occupy similar environments (i.e. dry shrub-steppe, prairie, montane forest, wetlands) also occupy similar positions along the diversity and ANPP gradients. A moisture gradient is clearly coincident with the ANPP gradient (Fig. 4). The increasing phase of $S \sim \text{ANPP}$ at both the alliance and the PVT foci is likely a stress gradient of xeric to mesic conditions. This is consistent with the theory that areas of low productivity will support relatively lower species populations, making some species more prone to rarity and extirpation, resulting in lower levels of species diversity (Rosenzweig 1995; Wright et al. 1993). It is also consistent with and similar to the intermediate productivity theory (Grime 1973b), that in stressful environments the number of species is

limited because the pool of species adapted to the stress condition is small. Species numbers increase along a gradient of decreasing stress (in this study, along a gradient of increasing moisture reflected by the increasing ANPP) until the most competitive species limit species numbers by their dominance over available resources, and species richness then declines. Under this scenario, places of intermediate productivity support more species.

The decrease in species richness at higher ANPP and at apparently higher levels of moisture availability is, however, inconsistent with the water–energy theory (Hawkins 2003; O'Brien 1993; O'Brien 1998), which predict a monotonic or saturating increase in richness with increasing energy and water availability. In this case the exact mechanisms underlying the decrease in richness along the upper half of the ANPP gradient are not clear. We suggest three possible and perhaps overlapping explanations. First, the decrease in richness may be due to increased intensity of competition under high levels of resource availability (Grime 1973b). Second, physical stressors, such as low oxygen levels in saturated soils, may limit species richness in the alliances that occur in such environments. Third, the high-productivity alliances in this study may have relatively small aerial extents and thus fewer species. Interestingly, the *Carex* alliances, which are the least rich, consist of those few species adapted to an environment stressful to most others of the species pool, an environment where the subsidy of water and nutrients have great potential for productivity but the physical condition requires significantly different physiologies to use them. Distinguishing among these theories would require revisiting the original plots and collecting additional measurements of environmental properties, such as oxygen and nutrient levels, as well as measuring indices of competition intensity. The competition hypothesis could also be tested by indexing the plant species of the region for their competitive strength, another area for future research.

Acknowledgements We gratefully acknowledge Mike Austin, Sandy Andelman, Robert Waide and Frank Davis for their reviews and comments, and John Harris for geostatistical advice. This research was supported by the Knowledge Network for Biocomplexity project funded by the National Science Foundation's Knowledge and Distributed Intelligence Program (NSF; Grant# DEB 99-80154), the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant#DEB-0072909), the University of California, and the Santa Barbara campus. Support was also provided by the U.S. Geological Survey.

References

- Abrams PA (1995) Monotonic or unimodal diversity–productivity gradient: what does competition theory predict? *Ecology* 76:2019–2027
- Bailey RG, Avers PE, King T, McNab WH (1994) Ecoregions and subregions of the United States (map). USDA Forest Service; 1:7,500,000 with supplementary table of map unit descriptions. Washington DC

- Barbour MG, Glenn-Lewin D, Loucks O (2000) Progress towards North American vegetation classification at physiognomic and floristic levels. In: White PS, Micina L, Lepš J (eds) *Vegetation science in retrospect and perspective*, Proceedings of the 41st IAVS symposium. Opulus, Grangårde, pp 111–114
- Bond M, Chase JM (2002) Biodiversity and ecosystem functioning at local and regional spatial scales. *Ecol Lett* 5:467–470
- Chapin FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Diaz S (2000) Consequences of changing biodiversity. *Nature* 405:234–242
- Chase JM, Leibold MA (2002) Spatial scale dictates the productivity–biodiversity relationship. *Nature* 416:427–430
- Cliff AD, Ord JK, (1981) *Spatial processes models and applications*. Pion Limited, London
- Connell JH, Orias L (1964) The ecological regulation of species diversity. *Am Nat* 98:399–414
- Cramer W, Kicklighter DW, Bondeau A, Moore A III, Churkina G, Nemry B, Ruimy A, Schloss AL (1999) Comparing global models of terrestrial net primary productivity (NPP): overview and key results. *Global Change Biol* 5:1–15
- Crawley MJ (1993) *GLIM for ecologists*. Blackwell, Oxford
- Curtis JT (1959) *The vegetation of Wisconsin*. University of Wisconsin Press, Madison
- Daubenmire RF (1956) Climate as a determinant of vegetation in eastern Washington. *Ecol Monogr* 26:131–154
- Grace JB (1999) The factors controlling species density in herbaceous plant communities: an assessment. *Perspect Plant Ecol Evol Syst* 2:1–28
- Grace JB (2001) The roles of community biomass and species pools in the regulation of plant diversity. *Oikos* 92:193–207
- Grime JP (1973a) Competitive exclusion in herbaceous vegetation. *Nature* 242:344–347
- Grime JP (1973b) Control of species density in herbaceous vegetation. *J Environ Manage* 1:151–167
- Gross KL, Willig MR, Gough L, Inouye R, Cox SB (2000) Patterns of species density and productivity at different spatial scales in herbaceous plant communities. *Oikos* 89:417–427
- Grossman DH, Faber-Langendoen D, Weakley AS, Anderson M, Bourgeron P, Crawford R, Goodin K, Landaal S, Metzler K, Patterson K, Pyne M, Reid M, Sneddon L (1998) *International classification of ecological communities: terrestrial vegetation of the United States, vol I, The National Vegetation Classification System: development, status, and applications*. The Nature Conservancy, Arlington, Virginia, USA
- Guo Q, Berry WL (1998) Species richness and biomass: dissection of the hump-shaped relationships. *Ecology* 79:2555–2559
- Haining R (1990) *Spatial data analysis in the social and environmental sciences*. Cambridge University Press, Cambridge
- Hawkins BA, Porter EE (2003) Does herbivore density depend on plant diversity? The case of California butterflies. *Am Nat* 161:40–49
- Hawkins BA, Field R, Cornell HV, Currie DJ, Guégan J-F, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84:3105–3117
- Hector A, Schmid B (1999) Plant diversity and productivity experiments in European grasslands. *Science* 286:1123–1127
- Huston MA (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110:449–460
- Intermountain Fire Science Lab (1996) Net primary productivity. Missoula, Montana, USA (web resource URL: <http://www.icbemp.gov/spatial/crbsum/>)
- Jennings M, Faber-Langendoen D, Peet R, Loucks O, Glenn-Lewin D, Damman A, Barbour M, Pfister R, Grossman D, Roberts D, Tart D, Walker M, Talbot S, Walker J, Hartshorn G, Waggoner G, Abrams M, Hill A, Rejmanek M (2004) Guidelines for establishing and revising associations and alliances of the U.S. National Vegetation Classification: Version 4.0. Vegetation Classification Panel of the Ecological Society of America, Washington, (web resource URL: http://esa.org/veg-web/docFiles/NVC_Guidelines-v40.pdf)
- Kaluzny SP, Vega SC, Cardoso TP, Shelly AA (1998) *S+ spatial stats*. Springer, Berlin Heidelberg New York
- Kruskal JB (1964) Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29:115–129
- Leibold MA (1999) Biodiversity and nutrient enrichment in pond plankton communities. *Evol Ecol Res* 1:73–95
- McCullagh P, Nelder JA (1989) *Generalized linear models*. Chapman and Hall, New York
- McCune B, Mefford MJ (1999) *Multivariate analysis of ecological data, version 4.17*. MjM Software, Gleneden Beach
- Mitchell-Olds T, Shaw RG (1987) Regression analysis of natural selection: statistical influence and biological interpretation. *Evolution* 41:1149–1161
- Mittelbach GG, Steiner CF, Scheiner S, Gross K, Reynolds HL, Waide R, Willig M, Dodson SI, and Gough L (2001) What is the observed relationship between species richness and productivity? *Ecology* 82(9):2381–2396
- Naem S (2002) Ecosystem consequences of biodiversity loss: the evolution of a paradigm. *Ecology* 83:1537–1552
- NatureServe (2002) *NatureServe Explorer: an online encyclopedia of life, Version 1.6*. NatureServe, Arlington, Virginia, USA (web resource URL: <http://www.natureserve.org/explorer>)
- Neter J, Kutner MH, Nachtsheim CJ, Wasserman W (1996) *Applied linear statistical models, 4th edn*. R.D. Irwin, Chicago
- Nicholls AO (1989) How to make biological surveys go further with generalized linear models. *Biol Conserv* 50:51–75
- O'Brien EM (1993) Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. *J Biog* 20:181–198
- O'Brien EM (1998) Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. *J Biog* 25:379–398
- Oksanen J (1996) Is the humped relationship between species richness and biomass an artifact due to plot size? *J Ecol* 84:293–295
- Preston FW (1962) Canonical distribution of commonness and rarity: part 1. *Ecology* 43:185–215
- Rosenzweig ML (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge
- Running SW (1994) Testing forest-BCG ecosystem process simulations across a climate gradient in Oregon. *Ecol Appl* 4:238–274
- Running SW, Hunt ER Jr (1993) Generalization of a forest ecosystem process model for other biomes, Biome-BGC, and an application for global-scale models. In: Ehleringer JR, Field C (eds) *Scaling processes between leaf and landscape levels*. Academic, London, pp 141–158
- Scheiner SM, Jones S (2002) Diversity, productivity and scale in Wisconsin vegetation. *Evol Ecol Res* 4:1097–1117
- Scheiner SM, Cox SB, Willig M, Mittelbach GG, Osenberg C, and Kaspari M (2000) Species richness-area curves and Simpson's paradox. *Evol Ecol Res* 2:791–802
- Schulze ED, Mooney HA (1993) *Biodiversity and ecosystem function*. Springer, Berlin Heidelberg New York
- Sokal RR (1979) Testing statistical significance of geographic variation patterns. *Syst Zool* 28:627–632
- Tilman D (2000) Causes, consequences and ethics of biodiversity. *Nature* 405:208–211
- Tilman D, Lehman CL, Thomson KT (1997) Plant diversity and ecosystem productivity: theoretical considerations. *Proc Natl Acad Sci USA* 94:1857–1861
- USDA NRCS (2000) *The PLANTS database*. National Plant Data Center, Baton Rouge, Louisiana, USA (web resource URL: <http://plants.usda.gov>)
- VEMAP Members (1995) *Vegetation/ecosystem modeling and analysis project (VEMAP): Comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO₂ doubling*. *Global Biogeochem Cycles* 9:407–438

- Venables WN, Ripley BB (2002) *Modern applied statistics with S*. Springer, Berlin Heidelberg New York
- Vincent PJ, Haworth JM (1983) Poisson regression models of species abundance. *J Biogeogr* 10:153–160
- Waide B, Willing MR, Steiner CF, Mittelbach G, Gough L, Dodson SI, Juday GP, Parmenter R (1999) The relationship between productivity and species richness. *Annu Rev Ecol Syst* 30:257–300
- White MA, Thornton PE, Running SW, Nemani RR (2000) Parameterization and sensitivity analysis of the BIOME–BGC terrestrial ecosystem model: net primary production controls. *Earth Interact* 4(3):1–85
- Whittaker RH, Niering WA (1975) Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production, and diversity along the elevation gradient. *Ecology* 56:771–790
- Wright DH, Currie DJ, Maurer BA (1993) Energy supply and patterns of species richness on local and regional scales. In: Ricklefs RE, Schulter D (eds) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago