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## ANALYSIS

# Biodiversity and ecosystem services: A multi-scale empirical study of the relationship between species richness and net primary production

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## ABSTRACT

Biodiversity (BD) and Net Primary Productivity (NPP) are intricately linked in complex ecosystems such that a change in the state of one of these variables can be expected to have an impact on the other. Using multiple regression analysis at the site and ecoregion scales in North America, we estimated relationships between BD (using plant species richness as a proxy) and NPP (as a proxy for ecosystem services). At the site scale, we found that 57% of the variation in NPP was correlated with variation in BD after effects of temperature and precipitation were accounted for. At the ecoregion scale, 3 temperature ranges were found to be important. At low temperatures ( $-2.1$  °C average) BD was negatively correlated with NPP. At mid-temperatures ( $5.3$  °C average) there was no correlation. At high temperatures ( $13$  °C average) BD was positively correlated with NPP, accounting for approximately 26% of the variation in NPP after effects of temperature and precipitation were accounted for. The general conclusion of positive links between BD and ecosystem functioning from earlier experimental results in micro and mesocosms was qualified by our results, and strengthened at high temperature ranges. Our results can also be linked to estimates of the total value of ecosystem services to derive an estimate of the value of the biodiversity contribution to these services. We tentatively conclude from this that a 1% change in BD in the high temperature range (which includes most of the world's BD) corresponds to approximately a 1/2% change in the value of ecosystem services.

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## 1. Introduction

Biodiversity is the variability among living organisms from all sources. This includes diversity within species, between species and of ecosystems (Heywood, 1995). In the past 100 years biodiversity loss has been so dramatic that it has been recognized as a global change in its own right (Walker

and Steffen, 1996). This has raised numerous concerns, including the possibility that the functioning of earth's ecosystems might be threatened by biodiversity loss (Ehrlich and Ehrlich, 1981; Schulze and H.A., 1993).

Ecosystem functions refer variously to the habitat, biological or system properties, or processes of ecosystems. Ecosystem goods (such as food) and services (such as waste

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assimilation) represent the benefits human populations derive, directly or indirectly, from ecosystem functions (Costanza et al., 1997). If biodiversity has an influence on ecosystem functioning (in addition to any other roles it may play) then it will affect ecosystem goods and services and human welfare. Research on the relationship between biodiversity and ecosystem functioning (BDEF) is therefore of direct relevance to public policy, and this relationship has been the subject of considerable interest and controversy over the past decade (Cameron, 2002).

The relationship between biodiversity and ecosystem functioning has historically been a central concern of ecologists. But the direction and underlying mechanisms of this relationship has been a topic of ongoing controversy, which has been complicated by the many different types (e.g. species, genetic, community, functional) and measures (e.g. richness, evenness, Shannon–Weaver) of diversity. The discussion has also been complicated because in the public policy arena, the term biodiversity is often erroneously equated with the totality of life, rather than its variability.

In 1972 Robert May, using linear stability analysis on models based on randomly constructed communities with randomly assigned interaction strengths, found that in general diversity tends to destabilize community dynamics (May, 1972). This result was at odds with the earlier hypotheses (Odum, 1953; MacArthur, 1955; Elton, 1958) that diversity leads to increased productivity and stability in ecological communities.

Recent studies have attempted to understand the effects of diversity on ecosystem functioning using experimental ecosystems, including microcosms (Naeem et al., 1994, 1996) and grassland mesocosms (Naeem et al., 1994, 1996; Tilman and Downing, 1994; Tilman et al., 1996, 1997). These studies seem to provide experimental evidence for a positive relationship between biodiversity and ecosystem functioning in general, and between biodiversity and NPP in particular (Naeem et al., 1995; Tilman et al., 1996, 1997; Lawton, 1998). However, some have argued that the micro and mesocosm experiments showed no “real” effect of biodiversity because the results of these experiments were only due to “sampling effect” artifacts of the way the experiments were conducted (Aarssen, 1997; Grime, 1997; Huston, 1997; Wardle et al., 1997).

The debate continues. Recent experimental studies have claimed various relationships such as increases in biodiversity positively affecting productivity but decreasing stability (Pfisterer and Schmid, 2002); increases in biodiversity increasing productivity but only due to one or two highly productive species (Paine, 2002); and Willms et al. (2002) suggests that there is no general relationship between these two factors due to species specific effects and unique trophic links. Further, Wardle and Zackrisson’s (2005) studies on island ecosystems found that effect of biotic losses on ecosystem functions depends greatly on individual biotic and abiotic characteristics of the system.

Obviously, the links between biodiversity and ecosystem functioning are complex, and it should come as no surprise that simple answers have not emerged. It is also the case that small scale, short duration micro and mesocosm experiments (while attractive because they are the only controlled experiments that can reasonably be done on these questions) cannot

necessarily be directly extrapolated to the real world. These short-term, small-scale experiments rely on communities that are synthesized from relatively small species pools and in which conditions are highly controlled. Practical limitations simply preclude controlled experiments that can span the large spatial scales, the long temporal scales, and the representative diversity and environmental gradients that are properly the concern of work in this area. This limits our ability to directly extrapolate the results of small-scale experiments to longer time scales and larger spatial scales (Symstad et al., 2003). Additional information on larger scales is thus essential in informing the debate about the interpretation of experiments designed to examine the relationship between biodiversity and ecosystem functioning and services, and the applicability of those experiments to the “real world” (Kinzig et al., 2002).

Part of the fuel for the ongoing debate on the subject, is the fact that biodiversity is both a cause of ecosystem functioning and a response to changing conditions (Hooper et al., 2005). The components of complex ecological systems, like those investigated in the BDEF relationship, also operate at different but overlapping spatial and temporal scales (Limburg et al., 2002). The assumption that causal chains operate on one temporal and spatial scale at a time is inconsistent with what we know about ecological systems (Allen and Starr, 1982). Rather than a linear additive process, complex systems are defined by feedback loops, blurring the distinction between cause and effect. This blurring of cause and effect contributes to the BDEF debate.

In this paper we try to address the BDEF relationship while leaving the ‘prime mover’ discussion aside. Our investigation specifically looks at the relationship between NPP and vascular plant diversity (hereon biodiversity or BD). This relationship is likely characterized by the following simultaneous causal links:

- NPP responding to temperature, precipitation, soil characteristics and other abiotic factors
- BD responding to temperature, precipitation, soil characteristics and other abiotic factors
- NPP responding to BD
- BD responding to NPP

The very nature of ecological systems forces us to consider these multiple relationships between NPP and BD. Assuming temperature and precipitation (as well as other determinants of system productivity) are positive antecedents of both BD and NPP, the relationship between BD and NPP can be characterized as one of the following (Fig. 1):

In Case 1, the positive relationship between BD and NPP is amplified by the antecedent influence of temperature and precipitation. If this were the case, we would predict that the bivariate coefficient of variation between NPP and BD should be greater (in absolute value) than the partial correlation coefficient, controlling for temperature and precipitation. In Case 2, the negative relationship between BD and NPP is suppressed by the abiotic influences. In this case, the partial correlation coefficient would be more (in absolute value) than the bivariate coefficient between NPP and BD. Note that nothing in this analysis assumes

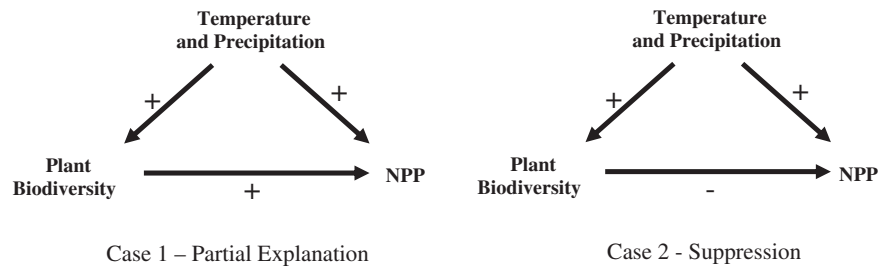


Fig. 1 – Possible causal chains between BD, NPP and abiotic factors.

causality. The arrow between BD and NPP could also go in the other direction.

In order to address this relationship we synthesized empirical data at the site and eco-region scales. Recent advances in the availability of biodiversity and NPP data have made this synthesis possible.

## 2. Methods

Biodiversity takes many forms (e.g. genetic, functional, and landscape diversity) in addition to simple species richness (Tilman and Lehman, 2002). However, measurements of these other aspects are in general not available at large scales, and the number of species has been the focus of most of the recent research on the BDEF relationship. We therefore used species richness as a (admittedly imperfect) proxy for biodiversity. Within this, we focused on vascular plant species richness because it was both available at both of our scales of interest and most directly relevant to NPP.

There is a long list (Costanza et al., 1997; de Groot et al., 2002) of ecosystem services, but there is limited data on most of them. However, aboveground net primary production (NPP) data are available at multiple scales and NPP has been shown to correlate with the total value of ecosystem services (Costanza et al., 1998). NPP measurements are also widely employed in BDEF research at the micro- and mesocosm scales. In addition, NPP is commonly used as an index to reflect ecosystem response to climate change (McCarthy and Intergovernmental Panel on Climate Change Working Group II, 2001). In general, aboveground NPP is much more readily available than total (above and below ground) NPP, so we used aboveground NPP for this study.

For the “site” scale of analysis (Scale 1) we performed an extensive literature search using the ISI Web of Knowledge and other tools (i.e. library-based bibliographic search engines) and were able to obtain approximately 200 observations on NPP from a total of 52 spatial locations globally. However, we found no observational studies that directly measured both NPP and total plant diversity simultaneously at specific locations. For the most part, the studies we encountered were species-specific, linking limited groups of species to NPP. Therefore, we were forced to search for data on biodiversity, environmental variables, and NPP separately, with spatial location as the key link among these data. Long-Term Ecological Research (LTER) and Forest Service research sites in North America were the only sites for which the required data were available (Knapp and Smith, 2001).

Although limited in number, these sites span a wide range geographically and biophysically from temperate forests, to tundra to high mountain meadows. For NPP data in our Scale 2 (ecoregion) analysis we used recent global NPP satellite derived estimates, as explained below.

Biodiversity data were the main variable of interest for the study and also the most difficult to standardize across sites. Our search revealed numerous gaps in the literature for biodiversity counts in spite of the increasing effort within the field to develop more accurate biodiversity figures. For our Scale 1 analysis, a few sites had biodiversity counts for the site, but not necessarily from the exact plots where the NPP data was derived. While this is a limitation, it is a bias that applies to all sites equally. The sites for which some information for both NPP and biodiversity was available was limited to 11 usable sites. Obtaining better biodiversity data for additional sites for which NPP measurements are ongoing could greatly expand the number of usable data points. For Scale 2, we used the work on North American Ecoregions of Ricketts et al. (1999) on biodiversity by ecoregion.

In addition to biodiversity, several physical environmental factors are important in explaining variations in ecosystem functions and services across sites. Temperature, precipitation, and soil organic matter content are three such factors we were able to include in this analysis. Temperature and precipitation have long been known to explain much of the basic global pattern of NPP (Lieth, 1978). Precipitation and temperature data were obtained from the Global Climate Database (Leemans and Cramer, 1991). Station data were extrapolated to create a full-coverage map for the entire United States in order to estimate the values for each of our sites.

We determined the soil type at each site using the FAO Digital Soil Map of the World (1995) and the latitudes and longitudes of the study sites. The FAO map yielded two useful figures for organic carbon content; the percent organic carbon of the topsoil and the percent organic content of the subsoil. The first thirty centimeters of soil was considered topsoil, while 30 to 100 cm was considered to be subsoil. Weighted averages were calculated when different horizons were present.

## 3. Scale 1: site level analysis

Table 1 is a list of all the data used in the regression analysis of NPP with biodiversity and physical characteristics at the site scale. Step-wise regression was used to determine the most

**Table 1 – Data used in Scale 1 (Site) NPP regression model**

Site location	NPP (g/m <sup>2</sup> /yr)	Vascular plants (number)	Growing season precipitation (mm)	Organic carbon upper soil (%)	Organic carbon lower soil (%)	Growing season temperature (°C)
	NPP	BD	P <sub>g</sub>	O <sub>u</sub>	O <sub>L</sub>	T
Arctic LTER	140.75833	395	53	0.31	0.2	6.3
Bonanza Creek LTER	299.8475	214	136	2.59	0.55	11.3
Cedar Creek LTER	277.26588	796	315	0.29	0.23	20.2
Harvard Forest	744.5	225	493	3	1	20
Hubbard Brook LTER	704.5	256	482	0.44	0.28	18
Jornada LTER	229.07333	354	128	0.4	0.25	21.4
Kellogg Biological Station	430.997	436	435	0.57	0.28	19
Konza Prairie LTER	442.6	576	565	1.53	0.695	22.8
Niwot Ridge LTER	198.74267	716	108	3.2	0.94	19.4
Sevilleta LTER	184.5	822	91	0.4	0.25	20.5
Shortgrass Steppe LTER	116.5	333	217	1.83	0.87	16.4
Superior National Forest	507.65	1460	295	0.44	0.28	17.2

significant determinants of NPP over the entire data set. BD was incorporated untransformed and log-transformed. Step-wise regression yielded the following as the best model:

$$NPP = \alpha + \beta_1 * P + \beta_2 * BD + \beta_3 * \ln(BD)$$

NPP Aboveground Net Primary Production  
 BD vascular plant species number  
 P growing season precipitation

Temperature, and organic carbon content proved not to be significant explanatory variables at this scale.

All predictors were tested for suitably normal distributions using Q-normal plots. Tolerances were calculated for each of the predictor variables to test for collinearity. Tolerance for the biodiversity terms was only 0.09 suggesting a high level of collinearity. However, neither term was significant alone implying a nonlinear relationship. We recalculated the coefficients using a generalized linear model that showed the coefficient estimates to not be biased.

Table 2 shows the Ordinary Least Squares (OLS) regression coefficients for this model.

R<sup>2</sup> for the model was 0.85 with p=0.0011. The squared partial correlation for the two BD terms controlling for temperature and precipitation reveals that 57% of the variation in NPP was correlated with variation in BD, though with such a small number of data points this figure has a low statistical power. Using the regression model, we can calculate the partial derivative of NPP with respect to BD:

$$\partial NPP / \partial BD = 0.857 - \frac{542.9}{BD}$$

For 8 out of 12 sites, this yields a negative correlation between marginal NPP and marginal BD, with influence becoming increasingly negative with lower diversity. This equation implies that the marginal rate of change of NPP with BD increases with increasing BD.

#### 4. Scale 2: North American eco-region analysis

Ecoregions are defined as a physical area having similar environmental/geophysical conditions as well as a similar assemblage of natural communities and ecosystem dynamics. North America has been divided into 116 eco-regions for which data has been assembled for several types of biological diversity (including vascular plant, tree species, snails, butterflies, birds, and mammals), geophysical characteristics, and habitat threats (Ricketts et al., 1999).

The Numerical Terradynamic Simulation Group (NTSG), at the University of Montana used MODIS 1 km<sup>2</sup> resolution satellite imagery from 2001 coupled with parameters derived from the Biome-BGC, a globalized version of the Forest-BGC model (Running and Coughlan, 1988; Turner et al., 2003), to estimate NPP as a function of Leaf Area Index (LAI), Fractional Photosynthetically Active Radiation (FPAR), temperature, precipitation and soil properties. Eight-day estimates of NPP are averaged over an entire year (2001, in this case), correcting for seasonal variation. Explicit details concerning the algorithms used to derive NPP estimates can be found at the NTSG website at: <http://www.ntsug.umt.edu>.

Due to the size of this dataset, we resampled the 1 km<sup>2</sup> MODIS/NTSG data to 10 km<sup>2</sup> resolution using a nearest neighbor interpolation method. Global land cover data was obtained from the United Nations Environment Network website at: <http://www.unep.net/>. This data was derived from AVHRR satellite data

**Table 2 – Plot scale regression coefficients**

Parameter	Coefficient	Std. error	p-value
Constant	2977.3	896.3	0.0105
Ln(BD)	-542.9	168.1	0.012
BD	0.857	0.276	0.0146
P	0.876	0.163	0.0007

**Table 3 – Regression coefficients for model covering entire ecoregion temperature range**

Parameter	Coefficient	Std. error	p-value
Constant	-43.3	147.4	0.77
Ln(BD)	-103.7	46.5	0.0281
BD	0.159	0.047	0.0011
T	13.6	2	<0.0001
ln(P)	195.3	45.6	<0.0001

(1 km resolution) and was classified into 19 land cover categories. NPP values that were labeled *crop*, *urban*, *barren*, *ice* or *water*, were removed from the analysis. NPP values for agricultural areas were removed from the analysis because it was expected that high fertilizer and irrigation inputs to these lands would boost NPP estimates but have a negative effect on biodiversity, thus reducing the relationship between NPP and biodiversity for intensively managed or altered lands. Therefore the aggregate area included in the analysis is loosely defined as ‘natural area.’ The remaining NPP values were then aggregated by eco-region to produce estimates of the average annual aboveground NPP for North American eco-regions for the year 2001. From this combination of sources we obtained data for 102 ecoregions for the following parameters: Number of Vascular Plants per 10,000 km<sup>2</sup> (hereafter BD for biodiversity), Net Primary Production (NPP), Mean Annual Precipitation (P), and Mean Annual Temperature (T). These data are listed in Appendix Table A1.

While it would have been preferable to use direct measurements of NPP rather than modeled data based on remote sensing images, this was not an option. Further, since temperature and precipitation are drivers of both NPP and plant diversity, it is critical that they be incorporated in our model despite the fact that these parameters were also used to derive the NPP estimates.

Step-wise regression was used to determine the most significant determinants of NPP over the entire data set. Precipitation was log-transformed and BD was incorporated untransformed and log-transformed. Step-wise regression yielded the following as the best model:

$$NPP = \alpha + \beta_1 * T + \beta_2 * \ln(P) + \beta_3 * BD + \beta_4 * \ln(BD)$$

All predictors were tested for suitably normal distributions using Q-normal plots. Tolerances were calculated for each of

the predictor variables to test for collinearity. All tolerances were high except for BD, which had a tolerance of 0.28. Since the threshold of inappropriately high collinearity is generally set between 0.20 and 0.25, we retained the parameter. By including both BD and ln(BD), we are able to model a more non-linear relationship between BD and NPP, a strategy that is supported by the site-scale results above. Table 3 shows the Ordinary Least Squares (OLS) regression coefficients for this model.

R<sup>2</sup> for the model was 0.58 with p<0.0001. The squared partial correlation for the two BD terms controlling for temperature and precipitation was calculated to be 0.10 implying that BD accounted for 10% of the variation in NPP, assuming this causal direction. Using the regression model, we can calculate the partial derivative of NPP with respect to BD:

$$\partial NPP / \partial BD = 0.159 - \frac{103.7}{BD}$$

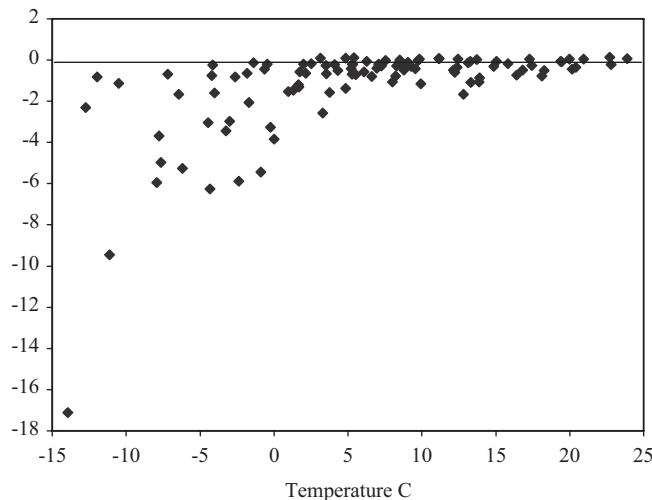
For the vast majority of ecoregions, this yields a negative correlation between marginal NPP and marginal BD, with influence becoming increasingly negative with lower temperature (Fig. 2).

However, further exploration using stepwise regression revealed a significant interaction between ln(BD) and temperature. This led us to hypothesize a variation in the relationship between NPP and BD over a temperature gradient.

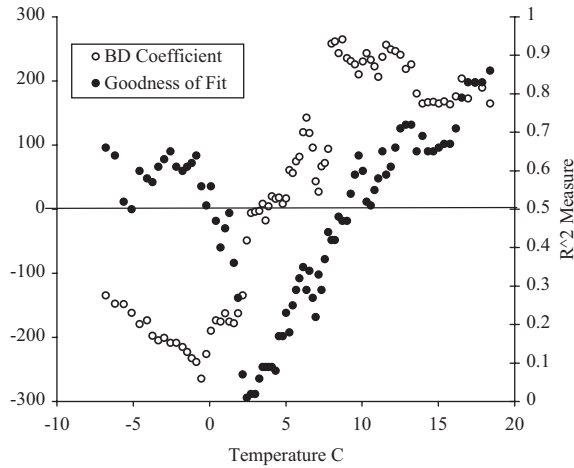
To assess this, we performed the following analysis. First, we ordered the ecoregions by mean annual temperature. Then using the model:

$$NPP = \alpha + \beta_1 * T + \beta_2 * \ln(P) + \beta_3 * \ln(BD),$$

We performed OLS regression using a moving window of 20 data points. We began with the 20 coldest ecoregions, and after each regression moved the window one data point in the direction of higher temperature. This yielded 83 individual regression outputs from which we took the R<sup>2</sup> measure of goodness of fit and the estimated coefficient for ln(BD). We also calculated the average of temperature for all twenty data points in each subset. Finally, we plotted the goodness of fit and the coefficient for ln(BD) as a function of average temperature (Fig. 3).



**Fig. 2 – Marginal change in NPP with biodiversity over all temperatures.**



**Fig. 3 – Scale 2 regression results over moving window regression.**

Two patterns are apparent. First is the strong dependence of the coefficient of ln(BD) on temperature. Here there are three modes of behavior: consistently negative at low temperatures, consistently positive at high temperatures, and a strong linear trend from low to high at mid-range temperatures. Further, there appear to be two abrupt transition points that demarcate the boundaries between these modes, one at about 2 °C and the other around 8 °C. Goodness of fit on the other hand follows a V-shaped trend. Fit is fairly high at low and high temperatures, but low at mid-range temperatures, approaching zero at an average temperature of 2.5 °C. It is logical that the model should express the weakest fit in the same range at which ln(BD) has the most indeterminate relationship to NPP.

Based on the output in Fig. 3 we divided the data set into three subsets with an overlap of 10 data points to account for the scale of the moving window regression. Thus the three subsets are data points 1–45 (low temperature range), 35–61 (mid-temperature range) and 51–102 (high temperature range). The subsets had an average mean annual temperature of –2.1, 5.3, and 13.0 °Celsius respectively. Stepwise regression was used to determine the best model in all three ranges with the following results.

### 5. Low temperature

At low temperatures, the mean summer temperature (ST) explains the vast majority of variation in NPP at the ecoregional scale ( $R^2 \sim 0.53$ ). Further, neither BD nor ln(BD) were significant alone, but together they greatly improved the model. All other variables, including surprisingly precipitation, were not significant. This yielded the model:

$$NPP = \alpha + \beta_1 * ST + \beta_2 * BD + \beta_3 * \ln(BD).$$

Ordinary Least Squares (OLS) regression coefficients for this model are shown in Table 4.

$R^2$  for the model was 0.65 with  $p < 0.0001$ . The squared partial correlation for the BD terms controlling for summer

temperature was 0.25. Therefore in this analysis 25% of the variation in NPP corresponded to variation in biodiversity. Using the regression model, we can calculate the partial derivative of NPP with respect to BD:

$$\partial NPP / \partial BD = 0.286 - \frac{115.3}{BD}.$$

As with the regression over the entire data set, this is largely negative (Fig. 4). Note that the  $R^2$  measure for NPP as a function of BD and ln(BD) alone is only 0.07, significantly less than the squared partial correlation. This is consistent with BD having a suppression effect on NPP where summer temperature has a positive effect on both BD and NPP (Fig. 2).

### 6. Mid-temperature

Stepwise regression over data points 35–61 yielded no variables significant at the 0.10 level. Log-transformed annual precipitation was a mediocre predictor of NPP ( $R^2 \sim 0.09$ ).

### 7. High temperature

In the high temperature range, we could not use Summer Temperature (ST) because the tolerance was only 0.10 indicating an unacceptable level of collinearity in the predictor variables. Stepwise regression using all variables but ST yielded the following model:

$$NPP = \alpha + \beta_1 * T + \beta_2 * \ln(P) + \beta_3 * \ln(BD).$$

Ordinary Least Squares (OLS) regression coefficients for this model are shown in Table 5.

$R^2$  for the model was 0.65 with  $p < 0.0001$ . The squared partial correlation for ln(BD) was 0.26 suggesting that BD accounted for approximately 26% of the variation in NPP (Fig. 5). This is nearly equal to the bivariate correlation for ln(BD) suggesting a minimal influence of temperature upon BD at this range. Indeed, the bivariate correlation between temperature and ln(BD) is only 0.07.

There were three significant outliers in this data set—Queen Charlotte Islands, Northern California Coastal Forests, and the Sonoran Desert. Queen Charlotte Islands had the highest precipitation of all ecoregions in the data set by almost 20%, while the Sonoran Desert had one of lowest. The Northern California Coastal Forests has the second highest rate of NPP. These outliers suggest marginal effects missed by the linearity of the model. When they are removed, goodness of fit

**Table 4 – Regression coefficients for low temperature ecoregions**

Parameter	Coefficient	Std. error	p-value
Constant	78.5	81.3	0.34
ln(BD)	–115.3	43.5	0.011
BD	0.286	0.078	0.0007
ST	33.1	4.05	<0.0001

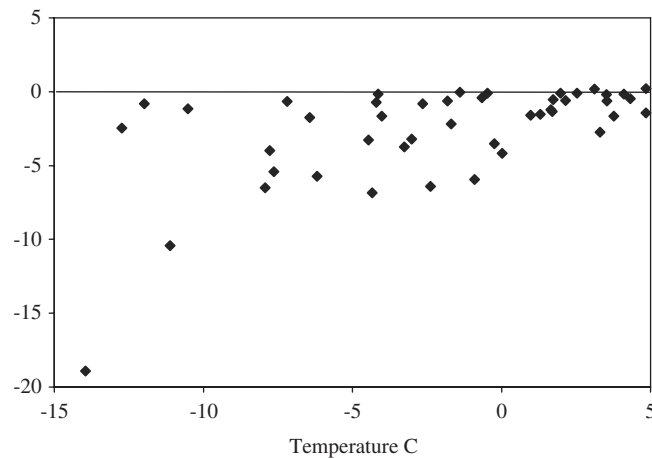


Fig. 4—Marginal change in NPP with biodiversity in the low temperature model.

increases significantly ( $R^2=0.72$ ), but regression coefficients are not much affected.

## 8. Discussion: the empirical link between BD and NPP

The results generate a number of discussion points. This investigation implies that the marginal rate of change of NPP with BD increases with increasing BD. While the data at Scale 1 is sparse and difficult to validate, it is worth noting a very similar model was found as at the ecoregion scale with comparable coefficient estimates. It suggests that if additional observations become available, it would be worth looking for a similar pattern of temperature dependency as was discovered at the ecoregion scale.

The number of observations available for Scale 2 provided latitude for a more rigorous statistical investigation. By including both BD and  $\ln(\text{BD})$ , we were able to model a more non-linear relationship between BD and NPP. Obviously the feedback effects between BD and NPP (Hooper et al., 2005) force nonlinearities, but these effects are poorly understood.

The moving window regression, with 83 model runs, suggested that it was inappropriate to fit the same model over the entire temperature gradient. Ecosystem function studies have long recognized the varying effects of temperature as a ‘modulator’ of ecosystem processes with various effects (Hooper et al., 2005). With regard to the relationship between NPP and BD, temperature plays a dual role. In all cases, it is an antecedent of both NPP and BD that must be accounted for in determining the strength of the relationship between those two. However, it also appears to modulate both

the strength and sign of the relationship between NPP and BD as well. At high temperatures, the strength of the relationship between BD and NPP is not as strong as the bivariate correlation coefficient indicates because of the antecedent effects of temperature. At low temperatures, the bivariate coefficient is an understatement of the strength of the relationship because temperature acts as a suppressing factor.

Further, at the low temperature end the data suggests that high biodiversity has a negative effect on NPP. For the mid-temperature range we found no strong relationship in our investigations. If data were available for other abiotic factors (soil water content, soil carbon) perhaps a relationship would surface. It is also possible that at middle range temperatures the relationship between the predictor variables and NPP is not monotonic and therefore exhibits a canceling effect.

In our high temperature range, we found NPP and diversity to be strongly linked. Assuming BD as independent, high biodiversity had a strong positive effect on NPP accounting for up to 26% of the variation. There were a number of factors we were unable to include in the model, like soil water and soil nitrogen content. These characteristics in natural systems can have large impacts on NPP and BD (Huston and McBride, 2002). Since these factors are likely to interact in complex ways with the biotic and abiotic factors already included in the model it is possible that their exclusion resulted in biased estimates of model coefficients.

In this investigation we could not address causality as it is traditionally handled. The BDEF debate is particularly heated on the causality issue. On the one side the argument purports that high biodiversity drives high productivity due to more efficient resource utilization. The other side emphasizes the control of biodiversity by system productivity by mechanisms such as competition relaxation. At the same time it has been widely agreed that the relationship is bi-directional (Hooper et al., 2005). More likely both productivity and biodiversity co-vary in a complex relationship with other factors, such as has been shown for human management of ecosystems (Cameron, 2002). While the ‘primary’ direction of causality may be important for ecological studies, it may also be impossible to discover. In addition, from a systems point of view it is not particularly relevant to talk about a ‘primary’

Table 5—Regression coefficients for high temperature ecoregions

Parameter	Coefficient	Std. error	p-value
Constant	-1011.8	172.5	<0.0001
$\ln(\text{BD})$	184.3	44.4	0.0001
$\ln(\text{P})$	333.3	54	<000.1
T	9.62	3.44	0.0075

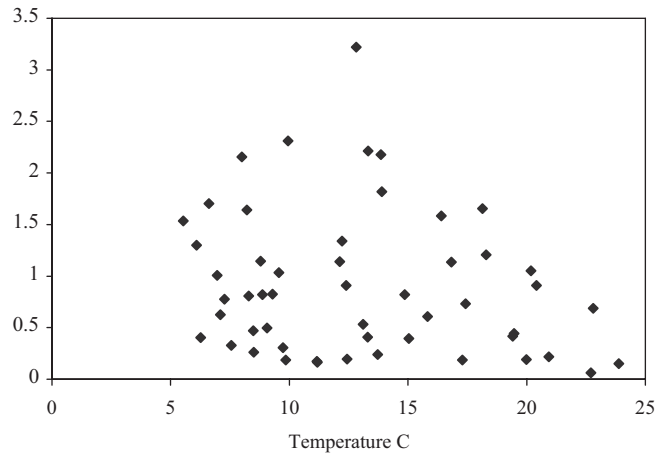


Fig. 5 – Marginal change in NPP with biodiversity in the high temperature model.

direction of causality. In spite of this, the relationship between productivity and diversity has large implications for economic, ecological and policy decisions.

### 9. Ecosystem service value and biodiversity

We hope that this analysis aids in understanding the complex relationships between biodiversity and ecosystem functioning. Ecosystem functioning supports ecosystem services, which are those functions of ecosystems that support human welfare, either directly or indirectly. Ecosystem services have been estimated to contribute roughly \$33 trillion/yr<sup>1</sup> globally to human welfare (Costanza et al., 1997). While NPP does not pick up all ecosystem services, it is a key indicator of ecosystem functioning and has been shown to correlate with the overall value of ecosystem services (Costanza et al., 1998; Fig. 6). This is to be expected, since NPP is a measure of the solar energy captured by the system and available to drive the functioning of the system.

In our analysis we find a strong positive relationship between biodiversity and NPP in certain temperature regimes, such that a change in biodiversity correlates with a change in NPP.

We find this relationship to be dynamic at various levels of temperature (scale 2). The most compelling finding, in relation to the global loss of species, is the strong positive relationship between biodiversity and NPP at the ecoregion scale at higher temperatures. In order to assess the impact of changing diversity on the production of ecosystem services, we performed a new regression in this high temperature range using the log of NPP as the dependent variable in order to measure elasticity of NPP with respect to biodiversity. The regression equation for this was:

$$\ln(\text{NPP}) = \alpha + \beta_1 * T + \beta_2 * \ln(P) + \beta_3 * \ln(\text{BD}).$$

The regression coefficient for ln(BD) was 0.173 (R<sup>2</sup>=0.61, p<0.0001). We then combined this with earlier results for the

relationship between NPP and the value of ecosystem services<sup>2</sup> by biome (Costanza et al., 1998). The equation for terrestrial biomes was:

$$\ln(V) = -12.057 + 2.599\ln(\text{NPP}) \quad R^2 = .96, F = 98.1, \text{Prob} > F = .002$$

where V is the annual value of ecosystem services in \$US/ha/yr (note, however that this relationship is based on only 5 data points — Fig. 6). Combining these two equations, one first sees that a one percent change in BD corresponds to a 0.173% change in NPP which in turn corresponds to a 0.45% change in ecosystems services. In other words, given the current complex relationship between biodiversity, net primary production and ecosystem services, we estimate (admittedly with fairly low precision) that a one percent loss in biodiversity in “warm” ecoregions could result in about a half a percent reduction in the value of ecosystems services provided by those regions. Another way of saying this is that the elasticity of supply of ecosystem services with respect to biodiversity is approximately 0.45.

On a related topic, the correlation between NPP and latitude is well known (Lieth, 1978). It has been estimated that approximately 70% of the global NPP occurs in Africa and South America (Imhoff et al., 2004). These entire continents fall within the high temperature range of our model (average temperature 13 °C). Therefore, where the world’s NPP is the highest (low latitudes), biodiversity is likely to be a crucial and positive factor. Additionally, it has been estimated that human appropriation of NPP is greater than 30% of the yearly global NPP (Vitousek et al., 1986; Rojstaczer et al., 2001). With most of global NPP occurring in low latitudes, the positive relationship between biodiversity and NPP at lower latitudes means that humanity is highly dependent on biodiversity for a large portion of its raw food, materials and other ecosystem services.

<sup>2</sup> This value was estimated from the aggregation of 17 services for 16 different biomes. Thus, a change in “value” can mean different things in different places (e.g. waste recycling verses recreational or cultural benefits). Also, while the value was estimated in dollars, it includes the full spectrum of benefits of (mainly non-marketed) ecosystem services, ranging from raw food to cultural aesthetic, and scientific benefits.

<sup>1</sup> This number was in 1994 \$US. Converting to 2004 \$US using the US Consumer Price Index yields a value of \$42 Trillion. This only adjusts for inflation, not the increasing scarcity of ecosystem services.



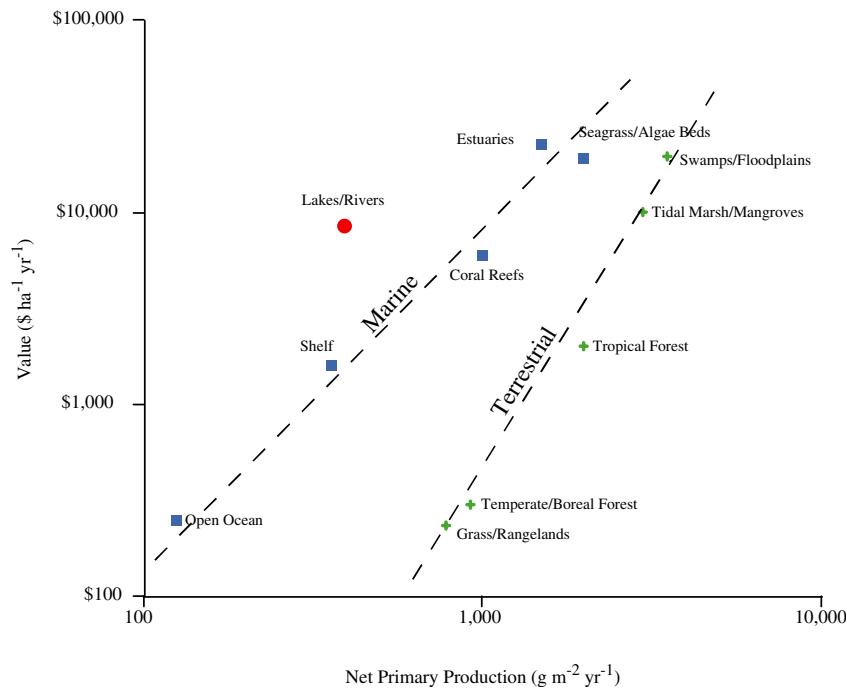


Fig. 6 – Relationship between Net Primary Production and the value of ecosystem services by biome (from Costanza et al., 1998).

Obviously, these estimates are still fairly crude, due to biodiversity data limitations and limits on our knowledge of the links between NPP and the value of ecosystem services. As new, higher resolution data on global patterns of biodiversity, NPP, and ecosystem services become available, we will no doubt be able to significantly improve the analysis. At the same time our empirical results at two spatial scales add further texture to earlier experimental results in micro and mesocosms, and may help us to better understand the nature of the BDEF relationship across scales. We know that at larger spatial and temporal scales more biodiversity is needed to supply a steady flow of ecosystem goods and services, hence biodiversity is a key economic, social and ecological management goal (Hooper et al., 2005). In addition to all the other reasons that biodiversity is important, it is fundamentally essential to sustain welfare of humans on the planet.

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### Appendix A

Table A1 – Data used in the ecoregion (scale 2) analysis

	Ecoregion	NPP (g/m <sup>2</sup> /yr)	ln (NPP)	Vascular plant richness	Natural area (ha)	BD (per 10,000 km <sup>2</sup> natural area)	ln (BD)	Summer temperature (C)	Precipitation (mm/yr)	Average annual temperature (C)
1	Alaska Peninsula Montane Taiga	170.69	2.23	510	3,613,116	141.15	2.15	10.54	1019	1.74
2	Alaska/St. Elias Range Tundra	98.33	1.99	747	13,147,339	56.82	1.75	8.41	838	-6.44
3	Alberta Mountain Forests	309.63	2.49	660	3,889,440	169.69	2.23	10.55	369	-0.65

Table A1 (continued)

	Ecoregion	NPP (g/m <sup>2</sup> /yr)	ln (NPP)	Vascular plant richness	Natural area (ha)	BD (per 10,000 km <sup>2</sup> natural area)	ln (BD)	Summer temperature (C)	Precipitation (mm/yr)	Average annual temperature (C)
4	Alberta/British Columbia Foothills Forest	529.06	2.72	740	12,026,477	61.53	1.79	14.05	420	0.98
5	Aleutian Islands Tundra	278.22	2.44	388	286,764	1353.03	3.13	8.20	925	3.13
6	Allegheny Highlands Forests	382.80	2.58	1883	8,241,231	228.49	2.36	19.93	1034	8.29
7	Appalachia/Blue Ridge Forests	572.76	2.76	2398	14,828,035	161.72	2.21	22.18	1156	12.12
8	Appalachian Mixed Mesophytic Forests	534.26	2.73	2487	18,050,094	137.78	2.14	22.43	1167	12.22
9	Arctic Coastal Tundra	90.73	1.96	539	5,107,118	105.54	2.02	5.89	111	-11.97
10	Arctic Foothills Tundra	96.93	1.99	580	7,195,035	80.61	1.91	5.94	112	-10.51
11	Arizona Mountains Forests	392.06	2.59	2204	10,854,545	203.05	2.31	22.56	151	12.39
12	Atlantic Coastal Pine Barrens	649.83	2.81	632	672,167	940.24	2.97	22.90	1058	12.43
13	Beringia Lowland Tundra	140.60	2.15	553	11,800,737	46.86	1.67	10.62	598	-1.69
14	Beringia Upland Tundra	107.61	2.03	538	9,080,866	59.25	1.77	9.65	442	-4.01
15	Blue Mountain Forests	374.65	2.57	1134	6,189,344	183.22	2.26	16.97	305	6.96
16	Brooks/British Range Tundra	95.48	1.98	593	14,158,680	41.88	1.62	5.27	150	-12.74
17	California Central Valley Grasslands	534.61	2.73	1682	3,597,998	467.48	2.67	22.03	364	15.03
18	California Coastal Sage and Chaparral	471.86	2.67	1491	1,952,235	763.74	2.88	18.10	203	13.72
19	California Interior Chaparral and Woodland	689.42	2.84	2105	6,093,221	345.47	2.54	18.53	410	13.11
20	California Montane Chaparral and Woodland	528.68	2.72	2075	1,957,412	1060.07	3.03	16.43	255	11.15
21	Canadian Aspen Forest and Parklands	380.05	2.58	1464	22,932,526	63.84	1.81	15.91	417	1.30
22	Cascade Mountains Leeward Forests	382.98	2.58	1328	4,543,093	292.31	2.47	11.10	617	1.98
23	Central and Southern Cascades Forests	615.36	2.79	1296	4,384,978	295.55	2.47	14.71	654	7.08
24	Central and Southern Mixed Grasslands	472.33	2.67	2081	20,517,248	101.43	2.01	26.00	642	13.89
25	Central Canadian Shield Forests	481.21	2.68	1246	41,134,273	30.29	1.48	14.86	751	-0.24
26	Central Forest/Grassland Transitional Zone	529.50	2.72	2124	25,513,367	83.25	1.92	24.98	916	13.32

(continued on next page)

Table A1 (continued)

	Ecoregion	NPP (g/m <sup>2</sup> /yr)	ln (NPP)	Vascular plant richness	Natural area (ha)	BD (per 10,000 km <sup>2</sup> natural area)	ln (BD)	Summer temperature (C)	Precipitation (mm/yr)	Average annual temperature (C)
27	Central Pacific Coastal Forests	682.04	2.83	1109	6,878,342	161.23	2.21	13.85	1512	8.79
28	Central Tall Grasslands	356.66	2.55	1779	2,546,902	698.50	2.84	22.19	739	8.51
29	Central US Hardwood Forests	458.00	2.66	2332	27,562,726	84.61	1.93	24.52	1187	13.87
30	Chihuahuan Desert	289.92	2.46	2263	20,294,885	111.51	2.05	26.23	275	18.13
31	Colorado Plateau Shrublands	245.22	2.39	2556	32,050,685	79.75	1.90	21.22	218	9.94
32	Colorado Rockies Forests	476.41	2.68	1626	13,141,409	123.73	2.09	16.40	245	5.28
33	Cook Inlet Taiga	171.68	2.23	738	2,467,411	299.10	2.48	12.07	438	-0.47
34	Copper Plateau Taiga	161.59	2.21	407	1,549,253	262.71	2.42	9.36	973	-4.13
35	East Central Texas Forests	615.06	2.79	1553	1,593,082	974.84	2.99	28.56	940	19.99
36	Eastern Canadian Forests	404.46	2.61	1140	43,933,120	25.95	1.41	12.78	1010	0.02
37	Eastern Canadian Shield Taiga	239.35	2.38	925	57,244,775	16.16	1.21	9.95	589	-4.33
38	Eastern Cascades Forests	468.22	2.67	1224	5,169,011	236.80	2.37	16.33	393	7.27
39	Eastern Forest/ Boreal Transition	431.85	2.64	1228	32,265,635	38.06	1.58	16.97	952	3.30
40	Eastern Great Lakes Lowland Forests	311.03	2.49	1381	9,750,002	141.64	2.15	18.89	966	6.09
41	Edwards Plateau Savannas	627.34	2.80	2361	5,698,855	414.29	2.62	28.19	655	19.46
42	Everglades	942.56	2.97	1362	1,100,109	1238.06	3.09	27.73	1433	23.88
43	Flint Hills Grasslands	544.17	2.74	1174	2,607,547	450.23	2.65	25.68	842	13.29
44	Florida Sand Pine Scrub	872.04	2.94	951	311,631	3051.68	3.48	27.30	1359	22.70
45	Fraser Plateau and Basin Complex	383.67	2.58	1012	13,163,580	76.88	1.89	12.09	647	1.66
46	Great Basin Montane Forests	240.90	2.38	1043	569,664	1830.90	3.26	15.45	149	5.40
47	Great Basin Shrub Steppe	208.99	2.32	2519	29,462,050	85.50	1.93	18.58	211	8.00
48	Gulf of St. Lawrence Lowland Forests	326.09	2.51	1033	3,507,432	294.52	2.47	16.80	1300	5.32
49	Interior Alaska/ Tukon Lowland Taiga	196.05	2.29	810	42,301,085	19.15	1.28	10.67	370	-6.19
50	Interior Yukon/ Alaska Alpine Tundra	212.78	2.33	617	22,834,531	27.02	1.43	9.64	703	-7.78
51	Klamath- Siskiyou Forests	610.00	2.79	1859	4,739,896	392.20	2.59	14.71	554	8.48
52	Low Arctic Tundra	132.21	2.12	497	46,077,817	10.79	1.03	7.28	239	-11.12
53	Madrean Sky Islands Montane Forests	355.40	2.55	1139	1,140,862	998.37	3.00	26.73	156	17.29
54	Middle Arctic Tundra	56.47	1.75	371	61,755,681	6.01	0.78	4.09	181	-13.95

**Table A1 (continued)**

	Ecoregion	NPP (g/m <sup>2</sup> /yr)	ln (NPP)	Vascular plant richness	Natural area (ha)	BD (per 10,000 km <sup>2</sup> natural area)	ln (BD)	Summer temperature (C)	Precipitation (mm/yr)	Average annual temperature (C)
55	Middle Atlantic Coastal Forests	697.72	2.84	1488	9,165,263	162.35	2.21	25.84	1184	16.82
56	Midwestern Canadian Shield Forests	509.51	2.71	797	46,352,489	17.19	1.24	14.50	451	-2.38
57	Mississippi Lowland Forests	526.90	2.72	1468	5,846,978	251.07	2.40	26.77	1357	17.43
58	Mojave Desert	135.21	2.13	2490	11,081,656	224.70	2.35	24.58	164	14.86
59	Montana Valley and Foothill Grasslands	268.73	2.43	1197	6,742,422	177.53	2.25	16.81	325	5.22
60	Muskwa/Slave Lake Forests	507.62	2.71	722	25,100,768	28.76	1.46	13.98	342	-3.26
61	Nebraska Sandhills Mixed Grasslands	342.07	2.53	1185	5,271,180	224.81	2.35	22.30	459	8.87
62	New England/Acadian Forests	339.61	2.53	1496	22,270,268	67.17	1.83	16.55	1270	4.84
63	Newfoundland Highland Forests	410.64	2.61	473	1,542,584	306.63	2.49	12.54	1352	2.53
64	North Central Rockies Forests	358.93	2.56	1695	23,805,001	71.20	1.85	12.33	368	1.70
65	Northeastern Coastal Forests	411.69	2.61	1695	7,584,866	223.47	2.35	20.50	1114	9.29
66	Northern British Columbia Mountain Forest	292.56	2.47	909	7,056,476	128.82	2.11	10.18	519	-1.81
67	Northern California Coastal Forests	874.84	2.94	1212	1,214,663	997.81	3.00	13.25	709	9.85
68	Northern Cordillera Forests	214.61	2.33	823	25,383,183	32.42	1.51	9.97	410	-4.46
69	Northern Mixed Grasslands	270.46	2.43	1595	10,328,619	154.43	2.19	18.75	429	4.32
70	Northern Pacific Central Forests	173.64	2.24	615	4,682,783	131.33	2.12	9.95	1535	2.16
71	Northern Tall Grasslands	289.20	2.46	1055	4,236,236	249.04	2.40	19.03	497	3.53
72	Northern Transitional Alpine Forests	141.14	2.15	876	2,499,187	350.51	2.54	9.16	1018	-1.39
73	Northwest Territories Taiga	262.95	2.42	576	28,534,671	20.19	1.31	11.83	233	-7.64
74	Okanogan Forests	451.18	2.65	1355	5,074,620	267.02	2.43	14.09	419	4.11
75	Ozark Mountain Forests	673.96	2.83	1743	5,738,142	303.76	2.48	26.06	1207	15.83
76	Pacific Coastal Mountain Icefields and Tu	76.11	1.88	792	7,447,346	106.35	2.03	8.03	1273	-2.64
77	Palouse Grasslands	271.31	2.43	1290	3,465,190	372.27	2.57	19.06	422	9.06
78	Piney Woods Forests	699.00	2.84	1729	11,304,749	152.94	2.18	27.24	1274	18.29
79	Puget Sound Lowland Forests	599.69	2.78	1100	1,837,128	598.76	2.78	15.85	1025	9.73
80	Queen Charlotte Islands	383.72	2.58	459	819,493	560.10	2.75	12.20	1812	7.55
81	Sierra Nevada Forests	346.83	2.54	2373	5,200,739	456.28	2.66	13.83	233	6.26
82	Snake/Columbia Shrub Steppe	220.20	2.34	2169	19,308,886	112.33	2.05	18.61	305	8.21

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Table A1 (continued)

	Ecoregion	NPP (g/m <sup>2</sup> /yr)	ln (NPP)	Vascular plant richness	Natural area (ha)	BD (per 10,000 km <sup>2</sup> natural area)	ln (BD)	Summer temperature (C)	Precipitation (mm/yr)	Average annual temperature (C)
83	Sonoran Desert	150.59	2.18	2068	10,219,109	202.37	2.31	28.34	188	20.40
84	South Avalon- Burin Oceanic Barrens	660.97	2.82	258	176,648	1460.53	3.16	13.05	1518	4.85
85	South Central Rockies Forests	336.65	2.53	1933	15,233,309	126.89	2.10	15.08	224	3.53
86	Southeastern Conifer Forests	787.78	2.90	3095	17,675,006	175.11	2.24	27.12	1396	20.17
87	Southeastern Mixed Forests	587.54	2.77	3363	28,871,384	116.48	2.07	25.70	1249	16.40
88	Southern Great Lakes Forests	353.89	2.55	2243	12,586,073	178.21	2.25	21.31	898	9.55
89	Southern Hudson Bay Taiga	464.57	2.67	1178	35,656,983	33.04	1.52	12.90	634	-3.01
90	Tamaulipan Mezquital	536.64	2.73	1487	5,559,790	267.46	2.43	29.69	599	22.81
91	Texas Blackland Prairies	588.33	2.77	1531	3,460,244	442.45	2.65	28.60	913	19.40
92	Tornгат Mountain Tundra	92.38	1.97	286	2,323,213	123.11	2.09	4.79	480	-7.18
93	Upper Midwest Forest/ Savanna Transition	324.75	2.51	1420	13,131,875	108.13	2.03	20.25	762	6.61
94	Wasatch and Uinta Montane Forests	275.34	2.44	1109	3,953,948	280.48	2.45	16.84	222	5.30
95	Western Canadian Forests	562.97	2.75	613	33,046,364	18.55	1.27	14.96	397	-0.90
96	Western Canadian Shield Taiga	275.28	2.44	720	42,459,611	16.96	1.23	10.87	284	-7.93
97	Western Great Lakes Forests	521.06	2.72	1459	24,320,875	59.99	1.78	17.73	705	3.76
98	Western Gulf Coastal Grasslands	683.00	2.83	2165	2,560,269	845.61	2.93	28.26	1137	20.94
99	Western Short Grasslands	354.65	2.55	2359	41,245,593	57.19	1.76	24.17	444	12.82
100	Willamette Valley Forests	703.35	2.85	1067	937,610	1138.00	3.06	17.92	970	11.18
101	Wyoming Basin Shrub Steppe	183.18	2.26	1557	12,979,396	119.96	2.08	17.76	273	5.53
102	Yukon Interior Dry Forests	268.63	2.43	692	6,075,359	113.90	2.06	10.98	592	-4.19

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