

Divergence in Forest-Type Response to Climate and Weather: Evidence for Regional Links Between Forest-Type Evenness and Net Primary Productivity

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ABSTRACT

Climate change is altering long-term climatic conditions and increasing the magnitude of weather fluctuations. Assessing the consequences of these changes for terrestrial ecosystems requires understanding how different vegetation types respond to climate and weather. This study examined 20 years of regional-scale remotely sensed net primary productivity (NPP) in forests of the northern Lake States to identify how the relationship between NPP and climate or weather differ among forest types, and if NPP patterns are influenced by landscape-scale evenness of forest-type abundance. These results underscore the positive relationship between temperature and NPP. Importantly, these results indicate significant differences among broadly defined forest types in response to both climate and weather. Essentially all weather variables that were strongly related to annual NPP displayed significant differences among forest

types, suggesting complementarity in response to environmental fluctuations. In addition, this study found that forest-type evenness (within $8 \times 8 \text{ km}^2$ areas) is positively related to long-term NPP mean and negatively related to NPP variability, suggesting that NPP in pixels with greater forest-type evenness is both higher and more stable through time. This is landscape- to subcontinental-scale evidence of a relationship between primary productivity and one measure of biological diversity. These results imply that anthropogenic or natural processes that influence the proportional abundance of forest types within landscapes may influence long-term productivity patterns.

Key words: net primary productivity; climate change; biodiversity; ecosystem function; regional analysis; remote sensing; land management.

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INTRODUCTION

Net primary productivity (NPP) is commonly used as an integrative measure of ecosystem function and the capacity to produce and sustain ecosystem goods and services (Symstad and others 2003; Hooper and others 2005; Srivastava and Vellend

2005). The influence of both climatic conditions and weather fluctuations on spatial and temporal patterns of NPP in terrestrial ecosystems has long been recognized (Rosenzweig 1968; Lieth and others 1975; Potter and others 1999). Less clear, however, is how the impact of climate and/or weather on NPP varies among vegetation types, and by association, how the composition and abundance of vegetation types influence ecosystem-level NPP response to fluctuating environmental conditions (Cottingham and others 2001; Symstad and others 2003). Climate change is anticipated to alter both long-term climatic conditions and increase the magnitude of weather fluctuations (IPCC 2007; Karl and others 2008). Assessing the consequences of these changes for productivity at landscape or larger areas require insight into the differences and similarities among the plant communities that comprise the landscape. In particular, understanding how different communities respond to climate or weather is necessary to recognize how and when the composition and abundance of communities will impact NPP in a changing and increasingly variable environment.

The relationship between the ecosystem composition, often characterized as a component of biological diversity, and ecosystem function, including NPP, is an ongoing debate that, despite a long history in the ecological literature, has received substantial attention in recent years (Chapin and others 2000; McCann 2000; Loreau and others 2001; Hooper and others 2005). Ecological theory suggests that variation in life-history traits among species or functional groups may capitalize on complementarity in resource utilization or acquisition that results in enhanced overall ecosystem function (for example, productivity) and/or stability (for example, variation in productivity through time) in systems with higher species or functional group richness (McNaughton 1977; Ives and others 1999; Naeem 2002; Hooper and others 2005; Loreau 2010). Although several studies have identified relationships between biological diversity and either the magnitude of ecosystem function (Hooper and Vitousek 1997; Tilman and others 1997a; Hector and others 1999) or the variability in ecosystem function over time (Tilman and Downing 1994; Naeem and Li 1997; Yachi and Loreau 1999; Bai and others 2004), those results continue to be questioned for several reasons including experimental design and interpretation (Pimm 1984; Givnish 1994; Naeem 2002; Pfisterer and Schmid 2002; Naeem and Wright 2003). Biological diversity may be progressively more important for sustaining ecosystem function in the context of increased

environmental fluctuations and intensified disturbance regimes that are anticipated over the next several decades.

Furthermore, these global change processes may be resulting in widespread alterations to some aspects of biological diversity (Sala and others 2000; Novacek and Cleland 2001), moving the diversity-ecosystem function debate beyond theoretical ecology into land management relevance (Chapin and others 2000; Hooper and others 2005; Srivastava and Vellend 2005; Diaz and others 2007). Because changing climate and disturbance regimes may reduce diversity, understanding the relationship between broadly defined measures of biological diversity and ecosystem function over larger areas is increasingly relevant to land managers and policy makers (Chapin and others 2000; Elmqvist and others 2003; Hooper and others 2005; Srivastava and Vellend 2005; Diaz and others 2007). However, most previous studies typically fall short of assessing the consequences of anticipated reductions in aspects of biodiversity at spatial scales relevant to land management. For example, evidence for a positive relationship between species richness and either overall ecosystem function or stability in ecosystem function is derived primarily from studies of extremely small-scale manipulative experiments (Tilman and Downing 1994; Hooper and Vitousek 1997; Loreau and Hector 2001) or theoretical models (Tilman and others 1997b; Yachi and Loreau 1999; Lehman and Tilman 2000). As a consequence, conclusions from these experiments are difficult to separate from experimental design and challenging to relate to un-manipulated systems (Huston 1997; Naeem 2002; Naeem and Wright 2003). Consequently, recent reviews have identified the need for studies over larger spatial areas (McCann 2000; Cottingham and others 2001; Loreau and others 2001; Symstad and others 2003; Srivastava and Vellend 2005) and with more direct application to land management practices (Chapin and others 2000; Elmqvist and others 2003; Srivastava and Vellend 2005).

This study provides one perspective on some of these challenges by examining how forest type (an integrated representation of the plant community that is directly relatable to land management practices) influences the response of NPP to climate or weather at regional scales. The overall goal of this study is to identify how forest type, climatic conditions, and weather fluctuations combine to influence observed patterns of net primary productivity in forests of the northern Lake States, USA. This study provides insight into both the challenge of spatial scale and the practical application by

addressing three questions about controls over net primary productivity. First, how is long-term NPP mean and variability, as characterized by satellite remote sensing, related to climatic conditions, and do those relationships differ among forest types? Second, how are annual variations in NPP related to fluctuations in weather conditions, and do those relationships differ among forest types? Third, does the composition of forest types within a landscape impact long-term patterns of NPP mean and variability?

MATERIALS AND METHODS

Study Region

The U.S. northern Lake States region includes the northern parts of Minnesota, Wisconsin, and Michigan (Figure 1). Climate is characterized by short, mild summers and long, cold winters with a

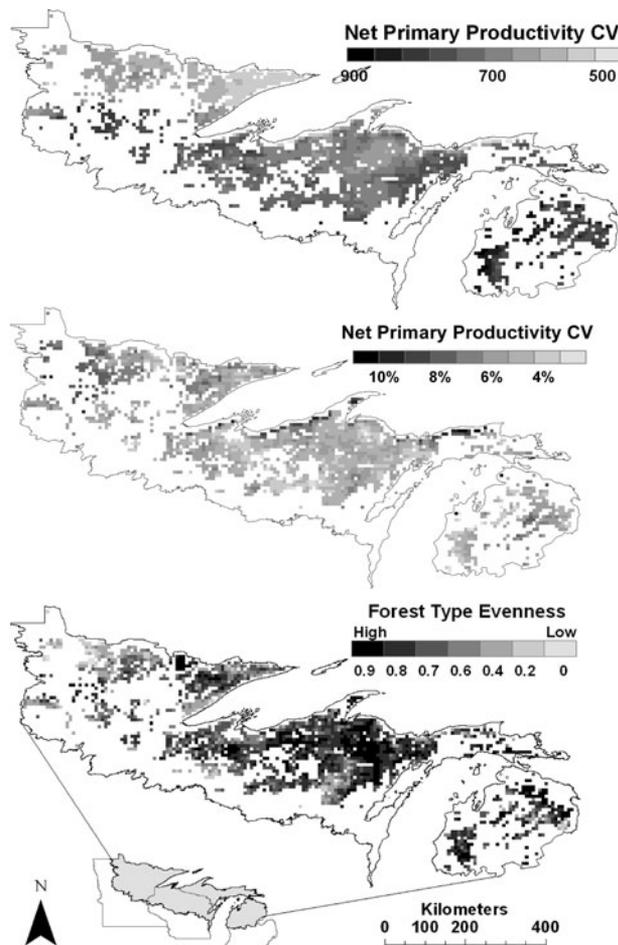


Figure 1. NPP mean, NPP CV, and evenness in abundance of the four major forest types for all $8 \times 8 \text{ km}^2$ AVHRR pixels with greater than 70% forest cover (2069 pixels out of 5150 in the U.S. Northern Lake States).

north-south gradient in mean annual temperature that ranges from around 2°C in northern Minnesota to 8°C in central Michigan and an east-west gradient in annual precipitation that ranges from 500 mm in central Minnesota to 800 mm in parts of Wisconsin and Michigan (<http://prism.oregon-state.edu>). Soils include a large component of nutrient-poor sands derived from glacial outwash, as well as silt loams from moraines and, occasionally, clays in former lake beds (USDA 1989). Forests in the northern Lake States include four major forest types: aspen-birch, upland conifer, northern hardwoods and lowlands and primarily conifers (Cleland and others 2007). Aspen-birch forests consist primarily of quaking and big-toothed aspen (*Populus tremuloides* and *P. grandidentata*) and paper birch (*Betula papyrifera*), whereas upland conifer forests are dominated by red pine (*Pinus resinosa*), white pine (*P. strobus*), or jack pine (*P. banksiana*) and contain some white spruce (*Picea glauca*). Northern hardwoods are dominated by sugar maple (*Acer saccharum*), northern red oak (*Quercus rubra*), yellow birch (*Betula alleghaniensis*), basswood (*Tilia americana*), and American beech (*Fagus grandifolia*) to the east. Lowland forests are dominated by black spruce (*Picea mariana*), tamarack (*Larix laricina*), and northern white cedar (*Thuja occidentalis*). Other prevalent species found in this region include balsam fir (*Abies balsamea*), bur oak (*Quercus macrocarpa*), and eastern hemlock (*Tsuga canadensis*) (Delcourt and Delcourt 2000).

Forests of the northern Lake States represent a particularly appealing region to examine the influence of plant composition on the relationship between NPP and environmental conditions because the region contains a diverse set of forest types whose distribution and abundance has been substantially altered since European settlement. Extensive logging in the late 1800s through early 1900s has impacted the vast bulk of forest area in the region (Frelich 1995). Region-wide logging, followed by slash-fueled fires resulted in large decreases in pine abundance and large increases in aspen abundance throughout the region (for example, Friedman and Reich 2005). The current landscape includes a mix of managed production forests and reserves and it is becoming increasingly more patchy at landscape scales (Mladenoff and others 1993) yet more regionally homogeneous (Schulte and others 2007).

Net Primary Productivity data

A 20-year (1981–2000) record of annual NPP based on the global production efficiency model

(GLO-PEM) was accessed from the Global Land Cover Facility (www.landcover.org/data/glopem with methodological details at www.landcover.org/library/guide/GLOPEM_documentation_18Aug03.pdf) and was derived from Advanced Very High Resolution Radiometer (AVHRR) images (Prince 1991; Prince and Goward 1995). GLO-PEM estimates aboveground and belowground productivity and results from GLO-PEM compare favorably against field-measured NPP observations through time (Goetz and others 2000) and space (Goetz and others 1999a, b). NPP estimates from GLO-PEM have been found to be consistent to other regional and global ecosystem models in both overall NPP magnitude as well as temporal and spatial variability (Kicklighter and others 1999; Ruimy and others 1999). In addition, GLO-PEM NPP means and standard deviations are similar to NPP means and standard deviations from field measurements in several biomes across the globe (Zheng and others 2003). The 20-year dataset used in this study has been used to assess the global patterns in NPP variability and long-term NPP trends (Franklin 2010; Cao and others 2002, 2003). The work presented here focuses on the influence of vegetation composition on NPP patterns within a single forested region.

Forest Type data

Forest types were defined based on vegetation cover data provided by the GAP analysis programs for Minnesota, Michigan, and Wisconsin (<http://lc.gapanalysisprogram.com/landcoverviewer/Downloads.aspx>) derived from LANDSAT classifications, and were reclassified into six broad categories: aspen-birch, upland conifer, mixed hardwood, lowland conifer, non-forested land, and water. These forest-type definitions are based on the dominant trees species at a given site, and do not provide any insight about tree age structure, successional stage, underlying soil conditions, or understory composition.

Climate and Weather Data

Monthly weather data from 1981 to 2000 were provided in 800-m resolution gridded format by the PRISM Climate Group (www.prism.oregon-state.edu). AVHRR data from this period are 8×8 km² pixels, so vegetation cover and weather data were re-sampled to match the spatial resolution and pixel locations of the NPP data. Annual and seasonal climate for each AVHRR pixel were calculated as 20-year mean temperature or precipitation observation, whereas annual and seasonal

weather were expressed as deviations from those means in each year. Within each AVHRR pixel, vegetation cover was summarized as the proportion of the four forest types, non-forest land and water. Because this analysis focused on the role of different forest types, analysis was restricted to AVHRR pixels consisting of greater than 70% forest cover (Figure 1: 2069 pixels).

Analysis

To address question 1, NPP mean and CV, and mean annual and seasonal temperature and precipitation were calculated for each pixel over the 20-year period. NPP mean and CV were related to each climate variable via linear regression in which each pixel is a datapoint. Separate regressions were conducted using pixels for each forest type and significant differences in NPP-climate slopes among forest types were determined from *t* statistics with $n - 4$ degrees of freedom as

$$t = \frac{b_i - b_j}{\sqrt{s_{b_i}^2 + s_{b_j}^2}}$$

where *i* and *j* are forest types being compared, b_i and b_j are NPP-climate slopes from forest types *i* and *j*, and s_{b_i} and s_{b_j} are standard errors of b_i and b_j , respectively (Ott 1993).

To address question 2, annual NPP, and annual and seasonal temperature and precipitation observations were subtracted from the 20-year means of each variable for each pixel. For each pixel, NPP deviations were related to annual and seasonal temperatures or precipitation deviations using linear regressions ($n = 20$). NPP deviations were compared to weather deviations from the current year, as well as the previous 2 years. Results were expressed as the proportion of all pixels in each forest type that display a significant relationship between NPP and a particular weather variable, which provides insight into the pervasiveness of a relationship throughout the region, and the mean of all statistically significant slopes, which provides insight into the potential magnitude of the impact of a weather fluctuation on NPP. Analysis of variance was used to determine statistically significant differences in mean NPP-weather slopes among forest types. The overall strength of the relationship between annual NPP fluctuations and weather was assessed as the r^2 from a stepwise linear regression of NPP fluctuations as a function of the first eight principal weather components. Principal components analysis on weather data and regression of NPP on principal weather components were

conducted separately for each pixel and results are summarized as mean r^2 in pixels of each forest type.

To address question 3, evenness in the relative abundance of each forest type within each $8 \times 8 \text{ km}^2$ pixel was calculated as $(\sum_1^4 p_i \ln(p_i)) / \ln(4)$, where i is forest type 1 through 4 above and p_i is the proportion of the pixel occupied by forest type i . Evenness values (range 0–1) were arc-sin-square-root transformed to achieve normality. To remove the effects of regional climate patterns on NPP mean and CV, a principal components analysis was performed on the annual and seasonal climatic conditions and the first eight principal components (accounting for >95% of the variability in climate) were included as independent variables in stepwise regression analysis predicting NPP mean and CV. Residuals from the best regression models were used as climate-controlled, dependent variables for assessing how forest type evenness relates to NPP mean and CV.

All statistical analyses were conducted in SAS version 9.2 (SAS Institute, Cary, NC, USA.)

RESULTS

Forest Type and NPP

NPP mean was highest in pixels with greater than 50% upland conifers (731 g m^{-2}), intermediate in pixels with mixed forests or pixels with greater than 50% northern hardwoods (715 and 719 g m^{-2} , respectively), lower in pixels with greater than 50% lowland conifers (705 g m^{-2}) and lowest in pixels with greater than 50% aspen-birch forests (688 g m^{-2}). However, no differences among forest types in NPP mean remained significant after controlling for long-term climatic influences on NPP mean. Mean temporal NPP coefficient of variation was slightly higher in lowland conifers (58%) than the other forest types (53–56%). After controlling for climatic influences, NPP CV was highest in aspen-birch, lowland conifer, and northern hardwood forests, lower in upland conifers; mixed forests were not different from any other forest type.

Climate and NPP

Comparison of long-term climatic conditions with NPP mean indicates that annual and seasonal temperatures were positively related to NPP mean for all forest types except summer temperature for lowland conifers (Figure 2A). The magnitude of the temperature-NPP slope varied somewhat among

forest types (Table A1.1 in Supplementary material). NPP mean was most strongly related to temperature in aspen-birch and upland conifer forests and generally less related to temperature in other forest types. Long-term precipitation conditions were less consistently related to NPP mean, with the exception of spring precipitation; NPP mean is higher for all forest types in areas with high spring precipitation (Figure 2B). Forest NPP mean in aspen-birch forests was lower in areas with high winter and fall precipitation, whereas NPP of other forest types are either higher or not related. NPP mean was negatively related to summer precipitation in upland and lowland conifers and mixed forests. Annual precipitation was positively related to NPP mean in lowland conifers and mixed forests, but negatively related to NPP mean in aspen-birch forests.

The relationship between NPP CV and long-term temperature varied with season and forest type (Figure 2C; Table A1.2 in Supplementary material). In aspen-birch forests, NPP-CV was positively related to spring and summer temperature, whereas in northern hardwoods, NPP CV was negatively related to spring and summer temperature, but positively related to winter and fall temperature. NPP CV in lowland conifers was negatively related to winter, fall, and annual temperatures, but strongly positively related to summer temperature. NPP CV in upland conifers was unrelated to temperature. NPP CV was negatively related to precipitation in most forest types and most seasons (Figure 2D), notably winter precipitation and NPP CV in northern hardwoods and summer precipitation and NPP CV in lowland conifers, which were positively related.

In general, climatic conditions accounted for more of the variation in NPP mean than NPP CV and temperature displayed much more explanatory power with respect to NPP mean than precipitation (Figure 2). The notable exception to this was lowland conifers, where winter, spring, fall, or annual precipitation accounted for greater than 40% of the variability in either NPP mean or NPP CV. Across the entire region, overall climatic conditions (represented by the first eight principal components) accounted for 54% of the variability in NPP mean and 21% of the variability in NPP CV (Tables A3.2, A3.3 in Supplementary material).

Weather and NPP

Relationships between annual NPP and weather fluctuations during the year of observation and previous years indicate significant differences

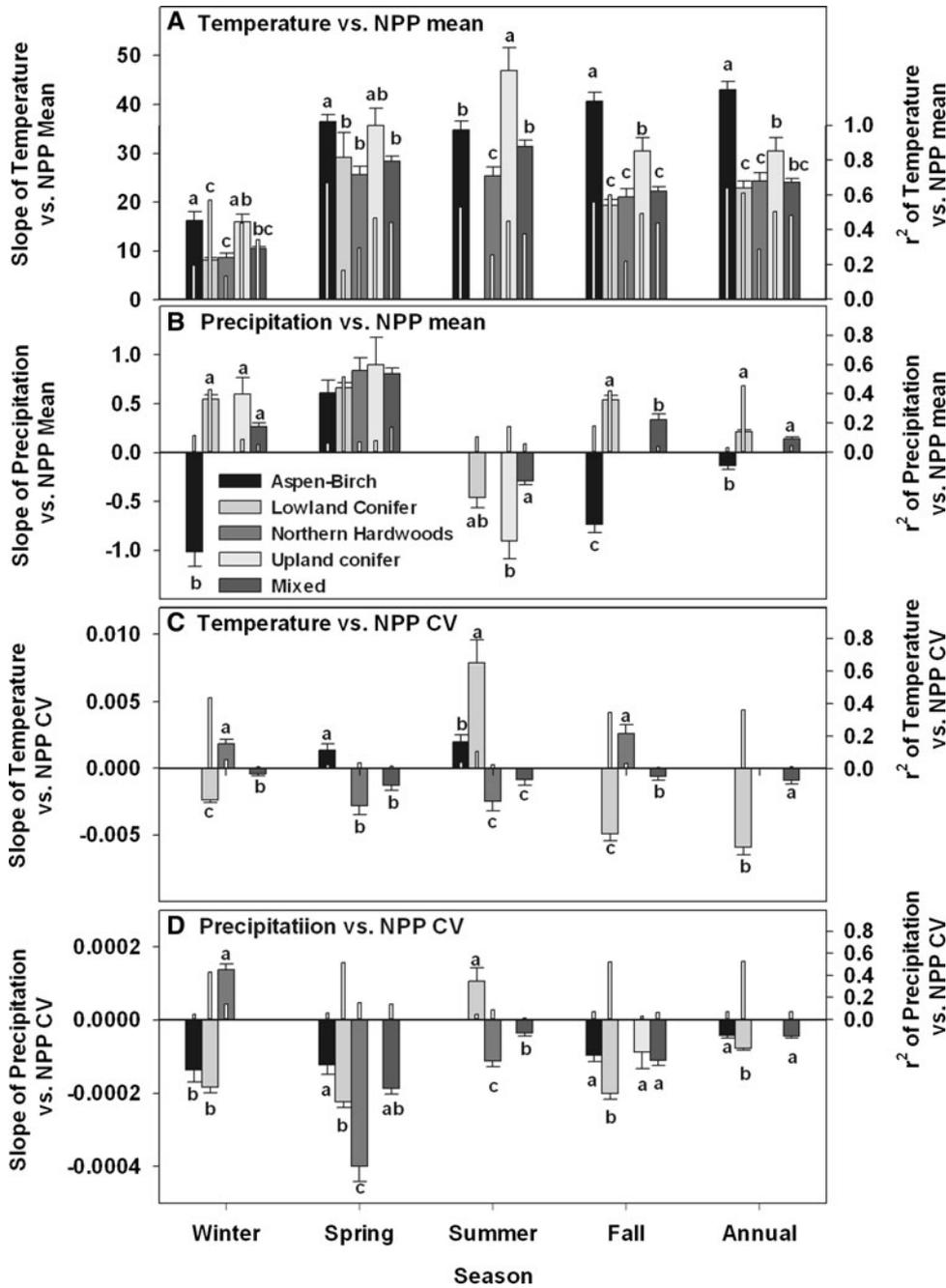


Figure 2. Relationship between net primary productivity (mean and coefficient of variation) and climatic conditions for forested pixels in the U.S. northern Lake States. Gray-scale bars correspond to left y-axis and indicate the slopes of significant relationships between NPP mean (A, B) or NPP CV (C, D) and annual and seasonal temperatures (A, C) or precipitation (B, D). Letters indicate significant differences in slopes among forest types. Narrow white bars with black border correspond to the right axis and indicate the proportion of variation in NPP mean or CV that can be explained by each climate variable (only positive values). Bars are grouped by season with each group containing, from left to right, aspen-birch, lowland conifer, northern hardwoods, upland conifer, and mixed forests. Additional details available in Appendix 1 of Supplementary material.

among forest types in the relationship between NPP and weather (Figure 3; Tables A2.1, A2.2 in Supplementary material). Temperature of the current year, notably spring and fall temperatures, was strongly related to NPP in 11–78% of all pixels from forest types, although the slope of the NPP–temperature relation displayed differences among forest types. Precipitation in the current year was more weakly related to NPP and the direction of the relationship varied across season and forest type. Annual and fall precipitations during the previous

year were negatively related to NPP in 10–30% of pixels across all forest types. However, winter precipitation in the previous year was positively related to NPP, especially in northern hardwoods and upland conifers. Across all forest types, NPP in 47–72% of pixels was positively related to winter precipitation 2 years prior to the growing season and NPP in 34–61% of pixels were negatively related to spring temperature 2 years prior to the growing season. For both of these 2-year lagged weather conditions, the slope of the NPP–weather

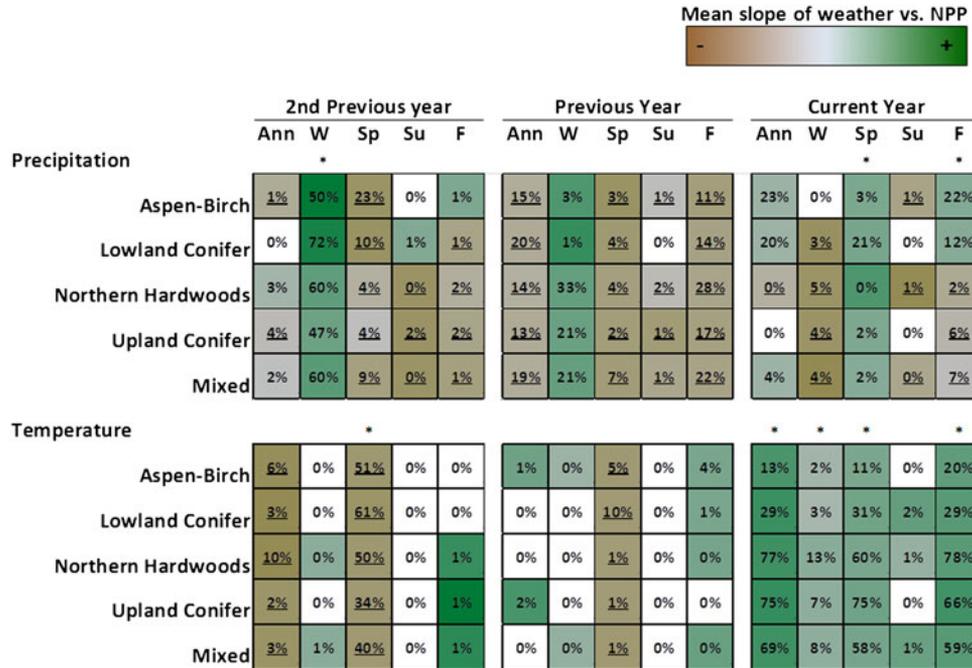


Figure 3. Relationship between weather conditions and annual NPP fluctuations for forests of the Northern Lake States. Weather is shown as annual (Ann) and seasonal (W = winter; Sp = spring; Su = summer; F = fall) values for the current and previous 2 years. Shading and underlining indicates mean slope between weather and NPP (with brown and underlined indicating negative slopes and green indicating positive slopes) for pixels with statistically significant relationships and values indicate the percentage of pixels with significant slopes in each forest type. *Statistically significant differences among forest types, even after accounting for the impact of long-term climatic conditions on NPP response to weather. Additional details available in Appendix 2 of Supplementary material. (Color figure online).

relationship varied significantly among forest types. Across all pixels, overall weather conditions (represented by the first eight principal components) accounted for 54% of interannual NPP variation. In pixels comprised primarily by an individual forest type, weather conditions accounted for 43, 49, 54, and 60% of NPP fluctuations in lowland conifers, aspen-birch, upland conifers, and northern hardwoods, respectively.

Evenness and NPP

After controlling for relationships between regional climate patterns and both NPP mean and CV, evenness in the abundance of forest types was positively related to NPP mean and negatively related to NPP CV (Figure 4). This indicates that, even after accounting for the influence of climate, NPP in pixels with greater forest type evenness is both higher and more stable through time.

DISCUSSION

These GLO-PEM NPP estimates are generally consistent with field measurements of NPP for the

northern Lake States. Gower and others (2001) compiled field observations of NPP from boreal ecosystems across the globe and generated a range of 100–600 g m⁻² y⁻¹. By comparison, the mean GLO-PEM NPP values from the northwest part of the region, which is on the southern edge of the boreal forest, were approximately 500 g m⁻² y⁻¹ (Figure 1), essentially identical to the estimates for southern Ontario developed by Liu and others (2002). The higher GLO-PEM NPP estimates of 600–800 g m⁻² y⁻¹ in the warmer and wetter conditions of the central and eastern side of the region are similar to field measurements for deciduous forests in that area (Curtis and others 2002). Although differences in NPP among forest types have been observed in previous studies (for example, Gower and others 1997), the large pixels examined in this study always encompassed multiple forest types, effectively minimizing the perceived differences among forest types, which were defined here as pixels with greater than 50% of a single forest type.

This examination of NPP response to both long-term climatic conditions and short-term weather fluctuations suggests some insights that are easily

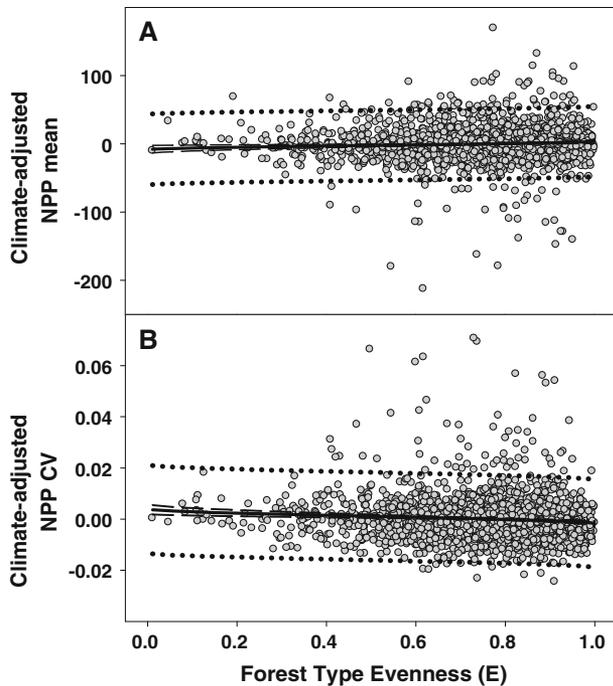


Figure 4. Relationship between forest type evenness (E) and both climate-adjusted NPP mean (A : NPP mean vs. $\sin^{-1} \sqrt{E}$; slope = 8.06 ± 2.84 , $P = 0.0045$) and climate-adjusted NPP CV (B : NPP CV vs. $\sin^{-1} \sqrt{E}$; slope = -0.0038 ± 0.0009 , $P < 0.0001$) within forested $8 \times 8 \text{ km}^2$ pixels of the northern Lake States. *Gray points* are individual pixels; *dashed* and *dotted lines* are 95% confidence and prediction intervals, respectively; non-linearity arises from back-transforming $\sin^{-1} \sqrt{E}$.

anticipated and others that are less intuitive. Encouragingly, many of the results about the relationship between either climate or weather and NPP apparent in these satellite-derived datasets are supported by field investigations with more direct measurements of NPP. For example, consistent with previous studies, these results underscore the overall positive relationship between temperature and productivity in northern forests (Potter and others 1999; Cao and others 2002; Boisvenue and Running 2006; Gough and others 2008; Chuixiang and others 2010). In particular, the importance of spring temperature in northern forests is supported by micrometeorological studies which demonstrated a positive relationship between net ecosystem productivity and spring temperatures, suggesting that warm spring conditions lead to longer growing seasons and overall positive productivity response (White and others 1999; Barr and others 2004; Baldocchi and others 2005; Gough and others 2008; Richardson and others

2009). Also consistent with previous work, these results suggest that, even within a relatively small region, climate exerts substantial influence over spatial patterns of primary productivity (Bradford and others 2006). Further, the lack of significant differences in NPP mean among forest types after controlling for climate indicates that, at the regional scale, observed differences in productivity among forest types can be explained entirely by climatic conditions. Widespread forest management may have contributed to minimizing apparent productivity differences among forest types, possibly by adding amendments to enhance soil fertility in low productivity soils. In addition, although climatic conditions exert clear influence over the magnitude of primary productivity, the variability of NPP is generally less related to climate (Figure 2).

One potentially surprising result is the lack of relationship between summer weather or climate conditions, either temperature or precipitation, and NPP (Figures 2, 3). This is likely a consequence of the strongly continental climate in the northern Lake States, which includes dramatic seasonal temperature fluctuations that make spring and fall conditions very influential over growing season length and annual productivity. Also somewhat surprising was the strength and consistency of relationships between NPP and weather conditions that occurred 2 years prior to the growing season (Figure 3). The strong positive relationship between NPP and winter precipitation 2 years before the growing season and the strong negative relationship between NPP and spring temperature 2 years before the growing season both appear to suggest that the length and/or severity of that winter can influence current productivity. Because it is unlikely that water availability in the current year is strongly impacted by these distantly lagged winter–spring conditions, these consistent relationships may be a consequence of delayed positive physiological responses to high snowpack in previous years. This delayed growth response may be a consequence of trees storing and subsequently mobilizing carbohydrate reserves, thus delaying the apparent utilization of photosynthetic products. Such lagged growth response to weather has been identified in previous work and is commonly explored through dendrochronological methods (Fritts 1971, 1976). For example, Chhin and others (2008) found that growth of lodgepole pine, although only weakly related to conditions in the current growing season, was negatively related to previous growing season temperature and precipitation in the preceding winter/spring and positively

related to previous growing season precipitation and temperature in the preceding winter/spring.

Essentially all the weather variables that appear most influential over NPP also displayed significantly different relationships with NPP among forest types. Overall response to weather fluctuations was lowest in lowland conifers and aspen-birch, although this may be a consequence of those systems existing in higher proportions in the western, colder, and drier part of the region. Although the impact of drought on growth and mortality may be partially moderated by increasing atmospheric CO₂ concentrations (Soule and Knapp 2006; Wyckoff and Bowers 2010), increasing variability in weather conditions is still likely to have a substantial impact on primary productivity. Previous study has identified consistent patterns among forest types in NPP response to weather fluctuations and, in some cases, demonstrated that weather response can depend on overall climate (Carrer and others 2007; Chhin and others 2008; Lo and others 2010). Examining sites from southern Wisconsin to northern Michigan, Graumlich (1993) found that growth of pines was positively related to warm spring conditions and cool summer conditions and only weakly related to growing season precipitation. By contrast, growth of hardwoods appears positively related to growing season precipitation, but response to temperature fluctuation depended on climate: growth of hardwoods in xeric sites was negatively related to summer temperature, whereas growth of hardwoods in mesic sites was negatively related to April temperature and positively related to May temperature (Graumlich 1993; Wyckoff and Bowers 2010). In boreal aspen forests, productivity is positively related to growing season length (influenced largely by spring temperature), except under severe drought conditions (Hogg and others 2002, 2005; Barr and others 2007).

These differences among broad forest types in response of NPP to weather conditions appear dramatic enough to facilitate higher productivity in areas comprised of more even mixtures of forest types. Although such complementarity among plant species or functional groups has been demonstrated in plot-level field studies (Hector and others 1999; Loreau and Hector 2001; Bai and others 2004; Cardinale and others 2007), evidence for complementarity over large areas and in broad functional groups has remained elusive. Top-down, regional examinations, especially those utilizing large pixels like this study, are fraught with uncontrollable sources of variation, notably natural disturbances, land-use practices, and variability in

soil conditions. These multiple sources of variability likely contribute to the relatively modest magnitude of change in NPP or NPP CV that can be attributed to forest type evenness. After accounting for climatic conditions, predicted NPP mean and NPP CV across the range of forest type evenness examined changed only approximately 15 g m⁻² y⁻¹ and 0.6%, respectively (Figure 4). Nevertheless, the significant relationships between forest type evenness and both NPP and NPP CV suggest that the landscape-scale distribution and abundance of broadly defined forest types may impact ecosystem function over large areas.

The positive relationship between evenness and NPP mean and the negative relationship between evenness and NPP CV are consistent with previous plot-level manipulative studies which found that experimental treatments with higher diversity tend to have high productivity (Hooper and Vitousek 1997; Tilman and others 1997a; Hector and others 1999) and generally higher stability in productivity over time (Tilman and Downing 1994; Naeem and Li 1997; Bai and others 2004). However, the interpretation of a mechanism linking higher mean NPP and forest type evenness may be more challenging than the plot-scale results, because the forest types are, by definition, separated in space. Thus, greater forest-type evenness within the landscape cannot directly lead to greater resource utilization (assuming that resources cannot be shared across space). Although divergent responses to weather or climate may allow some forest types to compensate for others during environmental fluctuations (Tilman and Downing 1994; Naeem and Li 1997; Yachi and Loreau 1999; Bai and others 2004), potentially leading to greater NPP stability in more even landscapes, this mechanism cannot account for higher mean NPP in more even landscapes. One potential explanation for the relationship between NPP mean and forest-type evenness is that pixels with greater forest-type evenness may have more diversity within individual forest types (that is, greater alpha diversity). Such links between measures of biological diversity across spatial scales remain a research priority (Loreau and others 2001; Symstad and others 2003).

Regardless of mechanism, the significant relationships between forest-type evenness and NPP presented here complement previous studies in three important ways. First, the sampling units of this study for both forest type and NPP are 8 × 8 km² pixels, dramatically different from the small experimental plots examined in most studies. This is perhaps the first direct evidence that biological diversity impacts ecosystem processes over

such large areas and suggests that processes, anthropogenic or natural that modify the proportional abundance of forest types within landscapes may influence long-term productivity patterns. Second, the composition of forest types within the pixels have not been intentionally manipulated to include highly divergent states of diversity, suggesting that even relatively modest variation in the abundance of forest types may impact the magnitude and stability of NPP. Finally, the relationship between forest-type evenness and NPP was significant in spite of the fact that the categories of plant diversity were broad forest types, as opposed to the species or functional group level categories commonly used in other studies. The definition of forest types as implemented in this study is extremely broad—lumping all forests in the region into four general types. Nevertheless, the relationship between evenness and NPP was significant despite the substantial intra-type variation created by these broad forest types. By necessity, land management often focuses on broad vegetation categories rather than individual species. These results suggest that variations in even those broad categories may influence ecosystem functioning.

This study represents a top-down approach to assessing how NPP is influenced by climate, weather, and forest types and compliments studies examining these patterns over smaller spatial areas. The result that forest types respond differently to variations in both climate and weather can be further explored via repeated plot measurements or dendrochronology. Likewise, further examinations of NPP and evenness at site to landscape scales are needed to determine how this relationship depends on spatial scale.

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REFERENCES

- Bai YF, Han XG, Wu JG, Chen ZZ, Li LH. 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature* 431:181–4.
- Baldocchi DD, Black TA, Curtis PS, Falge E, Fuentes JD, Granier A, Gu L, Knohl A, Pilegaard K, Schmid HP, Valentini R, Wilson K, Wofsy S, Xu L, Yamamoto S. 2005. Predicting the onset of net carbon uptake by deciduous forests with soil temperature and climate data: a synthesis of FLUXNET data. *Int J Biometeorol* 49:377–87.
- Barr AG, Black TA, Hogg EH, Kljun N, Morgenstern K, Nesic Z. 2004. Inter-annual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem production. *Agric For Meteorol* 126:237–55.
- Barr AG, Black TA, Hogg EH, Griffis TJ, Morgenstern K, Kljun N, Theede A, Nesic Z. 2007. Climatic controls on the carbon and water balances of a boreal aspen forest, 1994–2003. *Glob Change Biol* 13:561–76.
- Boisvenue C, Running SW. 2006. Impacts of climate change on natural forest productivity—evidence since the middle of the 20th century. *Glob Change Biol* 12:862–82.
- Bradford JB, Lauenroth WK, Burke IC, Paruelo JM. 2006. The influence of climate, soils, weather, and land use on primary production and biomass seasonality in the US Great Plains. *Ecosystems* 9:934–50.
- Cao MK, Prince SD, Shugart HH. 2002. Increasing terrestrial carbon uptake from the 1980s to the 1990s with changes in climate and atmospheric CO₂. *Glob Biogeochem Cycles* 16.
- Cao MK, Prince SD, Li KR, Tao B, Small J, Shao XM. 2003. Response of terrestrial carbon uptake to climate interannual variability in China. *Glob Change Biol* 9:536–46.
- Cardinale BJ, Wright JP, Cadotte MW, Carroll IT, Hector A, Srivastava DS, Loreau M, Weis JJ. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proc Natl Acad Sci USA* 104:18123–8.
- Carrer M, Nola P, Eduard JL, Motta R, Urbinati C. 2007. Regional variability of climate-growth relationships in *Pinus cembra* high elevation forests in the Alps. *J Ecol* 95:1072–83.
- 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* 405:234–42.
- Chhin S, Hogg EH, Lieffers VJ, Huang S. 2008. Influences of climate on the radial growth of lodgepole pine in Alberta. *Botany* 86:167–78.
- Chuixiang Y et al. 2010. Climate control of terrestrial carbon exchange across biomes and continents. *Environ Res Lett* 5:034007.
- Cleland DT, Freeouf JA, Keys JE, Nowacki GJ, Carpenter CA, McNab WH. 2007. Ecological subregions: sections and subsections for the conterminous United States. Gen. Tech. Report WO-76D [Map on CD-ROM] (A.M. Sloan, cartographer). Washington, DC: U.S. Department of Agriculture, Forest Service, presentation scale 1:3,500,000; colored.
- Cottingham KL, Brown BL, Lennon JT. 2001. Biodiversity may regulate the temporal variability of ecological systems. *Ecol Lett* 4:72–85.
- Curtis PS, Hanson PJ, Bolstad P, Barford C, Randolph JC, Schmid HP, Wilson KB. 2002. Biometric and Eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. *Agric For Meteorol* 113:3–19.
- Delcourt HR, Delcourt PA. 2000. Eastern deciduous forests. In: Barbour MG, Billings WD, Eds. *North American terrestrial vegetation*. Cambridge: Cambridge University Press. p 357–95.
- Diaz S, Lavorel S, de Bello F, Quetier F, Grigulis K, Robson M. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proc Natl Acad Sci USA* 104:20684–9.
- Elmqvist T, Folke C, Nystrom M, Peterson G, Bengtsson J, Walker B, Norberg J. 2003. Response diversity, ecosystem change, and resilience. *Front Ecol Environ* 1:488–94.
- Franklin J. 2010. Moving beyond static species distribution models in support of conservation biogeography. *Divers Distrib* 16:321–30.
- Frelch LE. 1995. Old forest in the Lake States today and before European settlement. *Nat Areas J* 15:157–67.

- Friedman SK, Reich PB. 2005. Regional legacies of logging: departure from presettlement forest conditions in northern Minnesota. *Ecol Appl* 15:726–44.
- Fritts HC. 1971. Dendroclimatology and dendroecology. *Quat Res* 1:419–49.
- Fritts HC. 1976. Tree rings and climate. London: Academic Press.
- Givnish TJ. 1994. Does diversity beget stability. *Nature* 371:113–14.
- Goetz SJ, Prince SD, Goward SN, Thawley MM, Small J. 1999a. Satellite remote sensing of primary production: an improved production efficiency modeling approach. *Ecol Model* 122:239–55.
- Goetz SJ, Prince SD, Goward SN, Thawley MM, Small J, Johnston A. 1999b. Mapping net primary production and related biophysical variables with remote sensing: application to the BOREAS region. *J Geophys Res Atmos* 104:27719–34.
- Goetz SJ, Prince SD, Small J, Gleason ACR. 2000. Interannual variability of global terrestrial primary production: results of a model driven with satellite observations. *J Geophys Res Atmos* 105:20077–91.
- Gough CM, Vogel CS, Schmid HP, Curtis PS. 2008. Controls on annual forest carbon storage: lessons from the past and predictions for the future. *Bioscience* 58:609–22.
- Gower ST, Vogel JG, Norman JM, Kucharik CJ, Steele SJ, Stow TK. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. *J Geophys Res Atmos* 102:29029–41.
- Gower ST, Krankina O, Olson RJ, Apps M, Linder S, Wang C. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. *Ecol Appl* 11:1395–411.
- Graumlich LJ. 1993. Response of tree growth to climatic variation in the mixed conifer and deciduous forests of the upper Great-Lakes region. *Can J For Res* 23:133–43.
- Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J, Harris R, Hogberg P, Huss-Danell K, Joshi J, Jumpponen A, Körner C, Leadley PW, Loreau M, Minns A, Mulder CPH, O'Donovan G, Otway SJ, Pereira JS, Prinz A, Read DJ, Scherer-Lorenzen M, Schulze ED, Siamantziouras ASD, Spehn EM, Terry AC, Troumbis AY, Woodward FI, Yachi S, Lawton JH. 1999. Plant diversity and productivity experiments in European grasslands. *Science* 286:1123–7.
- Hogg EH, Brandt JP, Kochtubajda B. 2002. Growth and dieback of Aspen forests in northwestern Alberta, Canada, in relation to climate and insects. *Can J For Res* 32:823–32.
- Hogg EH, Brandt JP, Kochtubajda B. 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951–2000. *Can J For Res* 35:610–22.
- Hooper DU, Vitousek PM. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* 277:1302–5.
- Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75:3–35.
- Huston MA. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110:449–60.
- IPCC. 2007. Summary for policymakers. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL, Eds. *Climate change 2007: The physical science basis*. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press.
- Ives AR, Gross K, Klug JL. 1999. Stability and variability in competitive communities. *Science* 286:542–4.
- Karl TR, Meehl GA, Peterson TC, Kunkel KE, W.J. Gutowski J, Easterling DR. 2008. Executive summary. In: Karl TR, Meehl GA, Miller CD, Hassol SJ, Waple AM, Murray WL, Eds., *Weather and Climate Extremes in a Changing Climate. Regions of Focus: North America, Hawaii, Caribbean, and U.S. Pacific Islands. A Report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research*, Washington, DC.
- Kicklighter DW, Bondeau A, Schloss AL, Kaduk J, McGuire AD. 1999. Comparing global models of terrestrial net primary productivity (NPP): global pattern and differentiation by major biomes. *Glob Change Biol* 5:16–24.
- Lehman CL, Tilman D. 2000. Biodiversity, stability, and productivity in competitive communities. *Am Nat* 156:534–52.
- Lieth H, Lieth H, Whittaker RH. 1975. *Modeling the primary productivity of the world*. New York (NY): Springer. pp 237–63.
- Liu J, Chen JM, Cihlar J, Chen W. 2002. Net primary productivity mapped for Canada at 1-km resolution. *Glob Ecol Biogeogr* 11:115–29.
- Lo YH, Blanco JA, Seely B, Welham C, Kimmins JP. 2010. Relationships between climate and tree radial growth in interior British Columbia, Canada. *For Ecol Manag* 259:932–42.
- Loreau M. 2010. Linking biodiversity and ecosystems: towards a unifying ecological theory. *Philos Trans Roy Soc B* 365:49–60.
- Loreau M, Hector A. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–6.
- Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:804–8.
- McCann KS. 2000. The diversity-stability debate. *Nature* 405:228–33.
- McNaughton SJ. 1977. Diversity and stability of ecological communities—comment on the role of empiricism in ecology. *Am Nat* 111:515–25.
- Mladenoff DJ, White MA, Pastor J, Crow TR. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. *Ecol Appl* 3:294–306.
- Naeem S. 2002. Ecosystem consequences of biodiversity loss: the evolution of a paradigm. *Ecology* 83:1537–52.
- Naeem S, Li SB. 1997. Biodiversity enhances ecosystem reliability. *Nature* 390:507–9.
- Naeem S, Wright JP. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecol Lett* 6:567–79.
- Novacek MJ, Cleland EE. 2001. The current biodiversity extinction event: scenarios for mitigation and recovery. *Proc Natl Acad Sci USA* 98:5466–70.
- Ott RL. 1993. *An introduction to statistical methods and data analysis*. Belmont (CA): Wadsworth Publishing Company.
- Pfisterer AB, Schmid B. 2002. Diversity-dependent production can decrease the stability of ecosystem functioning. *Nature* 416:84–6.
- Pimm SL. 1984. The complexity and stability of ecosystems. *Nature* 307:321–6.

- Potter CS, Klooster S, Brooks V. 1999. Interannual variability in terrestrial net primary production: exploration of trends and controls on regional to global scales. *Ecosystems* 2:36–48.
- Prince SD. 1991. A model of regional primary production for use with coarse resolution satellite data. *Int J Remote Sens* 12:1313–30.
- Prince SD, Goward SN. 1995. Global primary production: a remote sensing approach. *J Biogeogr* 22:815–35.
- Richardson AD, Hollinger DY, Dail DB, Lee JT, Munger JW, O'Keefe J. 2009. Influence of spring phenology on seasonal and annual carbon balance in two contrasting New England forests. *Tree Physiol* 29:321–31.
- Rosenzweig ML. 1968. Net primary production of terrestrial communities: prediction from climatological data. *Am Nat* 102:67–74.
- Ruimy A, Kergoat L, Bondeau A. 1999. Comparing global models of terrestrial net primary productivity (NPP): analysis of differences in light absorption and light-use efficiency. *Glob Change Biol* 5:56–64.
- Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH. 2000. Biodiversity—global biodiversity scenarios for the year 2100. *Science* 287:1770–4.
- Schulte LA, Mladenoff DJ, Crow TR, Merrick LC, Cleland DT. 2007. Homogenization of northern U.S. Great Lakes forests due to land use. *Landscape Ecol* 22:1089–103.
- Soule PT, Knapp PA. 2006. Radial growth rate increases in naturally occurring ponderosa pine trees: a late-20th century CO₂ fertilization effect? *New Phytol* 171:379–90.
- Srivastava DS, Vellend M. 2005. Biodiversity-ecosystem function research: is it relevant to conservation? *Annu Rev Ecol Evol Syst* 36:267–94.
- Symstad AJ, Chapin FS, Wall DH, Gross KL, Huenneke LF, Mittelbach GG, Peters DPC, Tilman D. 2003. Long-term and large-scale perspectives on the relationship between biodiversity and ecosystem functioning. *Bioscience* 53:89–98.
- Tilman D, Downing JA. 1994. Biodiversity and stability in grasslands. *Nature* 367:363–5.
- Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E. 1997a. The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300–2.
- Tilman D, Lehman CL, Thomson KT. 1997b. Plant diversity and ecosystem productivity: theoretical considerations. *Proc Natl Acad Sci USA* 94:1857–61.
- USDA SCS. 1989. STATSGO Soil Maps. National Cartographic Center, Fort Worth, TX, USA.
- White MA, Running SW, Thornton PE. 1999. The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest. *Int J Biometeorol* 42:139–45.
- Wyckoff PH, Bowers R. 2010. Response of the prairie-forest border to climate change: impacts of increasing drought may be mitigated by increasing CO₂. *J Ecol* 98:197–208.
- Yachi S, Loreau M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc Natl Acad Sci USA* 96:1463–8.
- Zheng D, Prince S, Wright R. 2003. Terrestrial net primary production estimates for 0.5° grid cells from field observations—a contribution to global biogeochemical modeling. *Glob Change Biol* 9:46–64.