AGU PUBLICATIONS

JGR

Journal of Geophysical Research: Biogeosciences

RESEARCH ARTICLE

10.1002/2013JG002392

Special Section:
Experiment-Model Integration in Terrestrial Ecosystem Study: Current Practices and Future Challenges

Key Points:

- Drivers of model uncertainty are shared across biomes and functional types
- Growth respiration, mortality, and stomatal regulation drive uncertainty
- Accessible informatics tools facilitate model-data synthesis

Correspondence to:
M. C. Dietze,
dietze@bu.edu

Citation:
Dietze, M. C., et al. (2014), A quantitative assessment of a terrestrial biosphere model's data needs across North American biomes, *J. Geophys. Res. Biogeosci.*, *119*, 286–300, doi:10.1002/2013JG002392.

Received 6 JUN 2013
Accepted 18 JAN 2014
Accepted article online 5 FEB 2014
Published online 19 MAR 2014

A quantitative assessment of a terrestrial biosphere model's data needs across North American biomes

Michael C. Dietze[1], Shawn P. Serbin[2], Carl Davidson[3], Ankur R. Desai[4], Xiaohui Feng[3], Ryan Kelly[3], Rob Kooper[5], David LeBauer[6], Joshua Mantooth[1], Kenton McHenry[5], and Dan Wang[7]

[1]Department of Earth and Environment, Boston University, Boston, Massachusetts, USA, [2]Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, Wisconsin, USA, [3]Department of Plant Biology, University of Illinois Urbana-Champaign, Urbana, Illinois, USA, [4]Department of Atmospheric and Oceanic Sciences, University of Wisconsin-Madison, Madison, Wisconsin, USA, [5]National Center for Supercomputing Applications, Urbana, Illinois, USA, [6]Energy Biosciences Institute, University of Illinois Urbana-Champaign, Urbana, Illinois, USA, [7]International Center for Ecology, Meteorology, and Environment, School of Applied Meteorology, Nanjing University of Information Science and Technology, Nanjing, China

Abstract Terrestrial biosphere models are designed to synthesize our current understanding of how ecosystems function, test competing hypotheses of ecosystem function against observations, and predict responses to novel conditions such as those expected under climate change. Reducing uncertainties in such models can improve both basic scientific understanding and our predictive capacity, but rarely are ecosystem models employed in the design of field campaigns. We provide a synthesis of carbon cycle uncertainty analyses conducted using the Predictive Ecosystem Analyzer ecoinformatics workflow with the Ecosystem Demography model v2. This work is a synthesis of multiple projects, using Bayesian data assimilation techniques to incorporate field data and trait databases across temperate forests, grasslands, agriculture, short rotation forestry, boreal forests, and tundra. We report on a number of data needs that span a wide array of diverse biomes, such as the need for better constraint on growth respiration, mortality, stomatal conductance, and water uptake. We also identify data needs that are biome specific, such as photosynthetic quantum efficiency at high latitudes. We recommend that future data collection efforts balance the bias of past measurements toward aboveground processes in temperate biomes with the sensitivities of different processes as represented by ecosystem models.

1. Introduction

Many of the most pressing questions in environmental research are motivated by uncertainty about what the future will hold during a period of rapid global change and thus cannot be fully addressed by direct observation or experimentation. Ecosystem models represent a formalized distillation of our current understanding of how ecosystems work and are one of the most common tools for projecting ecosystem dynamics over time and space. Models can also be viewed as a scaffold for the synthesis of observational data and partitioning of uncertainty, providing a framework for reconciling differences among data sets operating at different spatial and temporal scales [*Dietze et al*., 2013].

Given our reliance on models, it is important to ask, *what factors drive model uncertainty?* Since models encapsulate our understanding of a system, this is not only a pragmatic question for the purpose of ecological forecasting but also a conceptual question about what we do and do not understand about how ecosystems function. Improving the precision of model projections is a major motivation of ecological research. Previously, we advocated the use of model uncertainty analysis as a key component of improving feedbacks between models and data [*Dietze et al*., 2013; *LeBauer et al*., 2013]. Uncertainty analysis can be used to identify the key factors driving predictive uncertainty and to prioritize both synthesis efforts and the collection of new field data. The goal of this paper is to demonstrate and extend this approach to a wide range of biomes and plant functional types (PFTs) across North America in order to provide a quantitative, model-driven assessment of uncertainties and research priorities for improved prediction of the carbon cycle and vegetation dynamics. Specifically, herein we focus on uncertainty associated with model parameter choice and aim to identify the key sources of uncertainty in a sophisticated terrestrial biosphere model, the Ecosystem Demography model (ED) [*Moorcroft et al*., 2001; *Medvigy et al*., 2009].

The role of sensitivity analysis is well appreciated and frequently employed in ecology generally and in ecosystem modeling specifically. As such, a variety of methods are available depending on model complexity and the number of parameters involved [*Zaehle et al.*, 2005; *Cariboni et al.*, 2007; *Saltelli et al.*, 2008]. The general goal of sensitivity analysis is to elucidate how model output changes in response to changes in the inputs. Numerically, this is often achieved by perturbing the parameters of a model, individually or in groups, by some specified fixed amount (e.g., ± 10%) or drawing them randomly from a specified range (e.g., uniform ±25%). However, sensitivity by itself can be misleading, as a highly sensitive parameter that is well constrained by observations may actually exert less influence on model output than a less sensitive but poorly constrained parameter. Reliance on sensitivity alone could thus lead one to focus efforts on a parameter that is already well characterized by observations and likely subject to diminishing returns for further effort. By contrast, reliance on estimates of parameter uncertainty alone could also be misleading if this focuses efforts on parameters that are poorly constrained but insensitive and thus make a negligible contribution to model uncertainty. Uncertainty analysis aims to combine these pieces of information in order to estimate the contribution of different parameters to this predictive uncertainty in model outputs. While uncertainty analysis has had some application in ecosystem ecology, it has generally been limited to single-site analyses using simple models [*Xu et al.*, 2006; *Keenan et al.*, 2012]. Expanding the use of uncertainty analysis would enable ecologists to leverage models to better investigate underlying patterns of uncertainty and make general recommendations of where limited resources might be deployed most efficiently.

If our goal is to understand and reduce uncertainty about how ecosystems function, an important question is whether there are common patterns in parameter uncertainty across a range of vegetation types. Sources of uncertainty may be shared across all vegetation types, or there may be consistent patterns that vary by growth form (e.g., herbaceous versus woody), phenology (evergreen versus deciduous), life history differences (e.g., shade tolerance), or across climatic or edaphic gradients. These patterns may be due to differences in model sensitivity or may reflect the legacy of biased sampling toward specific ecosystems and processes. Therefore, it is also important to know whether the uncertainty attributed to a parameter is driven by data limitation or the inherent sensitivity of the model to those parameters. Processes that influence model predictions due to high uncertainty can often be constrained efficiently through targeted field campaigns or organized synthesis efforts [*Kattge et al.*, 2011; *Davidson*, 2012]. These parameters frequently benefit from an efficient return on investment, as parameter uncertainty can decrease quickly with a moderate sample size. By contrast, processes that are already constrained by data but remain highly sensitive are often more challenging to constrain further as sampling is already in a region of diminishing returns. However, even in this case a careful partitioning of uncertainty may reveal opportunities for improvement. For example, if most of the variability in a parameter occurs when moving from site to site, but most of the past sampling has been done intensively at a small number of sites, then increasing sampling in space or investigating the causes of spatial variability may efficiently reduce uncertainty [*LeBauer et al.*, 2013].

A primary limitation to uncertainty analysis in ecosystem modeling is that traditional approaches to modeling and model calibration treat parameters as unknown but fixed constants to be estimated by maximizing a likelihood or minimizing a cost function such as a sum of squares [*Hilborn and Mangel*, 1997]. Fortunately, in recent years there has been a growing interest in Bayesian model-data fusion approaches that treat model parameters as probability distributions [*Dietze et al.*, 2013]. We employ one such approach here by using a hierarchical Bayesian meta-analysis to combine plant trait data from across numerous studies. By treating parameters as distributions, and by estimating these parameters from a synthesis of available data, we shift from asking questions about model sensitivity to asking where additional measurements should be prioritized given what is already known about a system.

Another limitation to the regular application of uncertainty analyses when working with sophisticated models is the complexity of managing the analysis. To address this issue, we employ the Predictive Ecosystem Analyzer (PEcAn) to automate the process of analyzing model predictive uncertainty across a wide range of PFTs. PEcAn is a suite of ecosystem modeling tools used to manage information, analysis, and data-model fusion [*LeBauer et al.*, 2013]. PEcAn is not a model itself but a collection of modules in a workflow that wrap around an ecosystem model to make the process of modeling more accessible to a larger community and to facilitate data-model feedbacks [*Dietze et al.*, 2013]. PEcAn has previously been applied to switchgrass [*LeBauer et al.*, 2013], poplar [*Wang et al.*, 2013], and low tundra [*Davidson*, 2012] to quantify sources of uncertainty and aid data-model fusion.

Table 1. Parameters Varied in the ED Model

Name	Controls
Growth Resp	Costs of biosynthesis
Water Cond	Soil water uptake
Stomatal Slope	Stomatal conductance
Quantum Eff.	Light-limited photosynthesis
Mortality	Mortality from carbon limitation
Leaf Resp	Leaf maintenance respiration
Vcmax	Maximum rate of carboxylation
Leaf:Root	Leaf-to-fine root biomass ratio
Root Turnover	Root litter
Root Resp	Root maintenance respiration
SLA	Specific leaf area
Reproduction	Allocation between reproduction and stem growth

Here we extend this approach to assess the predictive uncertainty in net primary productivity (NPP) for a wide range of biomes and plant functional types in order to look for generalities and patterns in model parameter uncertainty. We focus on NPP because it is a major component of the terrestrial carbon cycle that has been widely estimated [*Scurlock et al.*, 1999; *Luyssaert et al.*, 2007; *Cleveland et al.*, 2011]. Limiting this initial analysis to NPP allows us to focus on a subset of processes related to ecophysiology and demography, rather than also including land-surface biophysics and biogeochemistry. We specifically assess the contributions of 12 parameters controlling photosynthesis, respiration, allocation, water use, and plant demography at time scales ranging from 1 to 10 years. Previous research has suggested that ecosystem models display high sensitivity to photosynthetic parameters, specific leaf area, and stomatal conductance [*White et al.*, 2000]. Our a priori hypothesis is that parameters related to ecophysiology will be most important at short time scales, while those related to demography will increase in importance over longer time scales. We further hypothesize that the primary drivers of uncertainty will be shared across biomes but that the importance of temperature-limited parameters (e.g., maximum rate of carboxylation) will increase with latitude and the opposite trend will prevail among parameters related to moisture limitation (e.g., stomatal conductance).

2. Methods

2.1. Ecosystem Demography Model

The Ecosystem Demography (ED v2.2) model is a size- and age-structured terrestrial biosphere model designed to efficiently simulate plant-, patch-, and landscape-level dynamics on a regional scale [*Moorcroft et al.*, 2001; *Medvigy et al.*, 2009]. ED contains a standard ecophysiological approach to plant-level carbon and water fluxes combined with a simplified CENTURY soil biogeochemistry submodel [*Bolker et al.*, 1998] and dynamic land surface biophysics based on the Land Ecosystem—Atmosphere Feedback model (LEAF) [*Walko et al.*, 2000]. Unlike most regional-scale biosphere models, ED also captures the community processes found in forest gap models, such as size-structured competition among multiple functional groups, and an explicit representation of growth, mortality, recruitment, and disturbance [*Pacala et al.*, 1996]. For this analysis, we focus on NPP and selected a dozen parameters related to plant ecophysiology and demography for further study (Table 1). These parameters were chosen based on prior experience and previous PEcAn analyses [*Davidson*, 2012; *Wang et al.*, 2013; *LeBauer et al.*, 2013], as well as the need to work with a common set of parameters across evergreen trees, deciduous trees, and nonwoody vegetation. For the latter reason, we dropped leaf turnover rate (not used for deciduous) and stem biomass allometries (not used for nonwoody vegetation) despite the fact that they are known to be important for some PFTs. We also did not consider parameters related to biogeochemistry, radiative transfer, and biophysics, despite the fact that they may have indirect impacts on NPP. Below we briefly describe the PFT-specific demographic and physiological processes and parameters in the model that are included in this analysis.

At the leaf level, ED takes an enzyme kinetic approach to photosynthesis, using the Farquhar model [*Farquhar et al.*, 1980] for C3 and the intercellular transport model [*Collatz et al.*, 1992] for C4. Within these models $V_{c,max}$ controls the maximum rate of carboxylation and *quantum efficiency* determines the amount of carbon fixed per photon of absorbed radiation [*Bernacchi et al.*, 2013]. In both the model and in the estimation of $V_{c,max}$ from A-Ci data we have not included mesophyll conductance, which is internally consistent but potentially differs from newer estimates that include this additional term. Stomatal conductance is modeled using the [*Leuning*, 1995] variant of the Ball-Berry model, which is primarily controlled by the *stomatal slope* parameter. Stomatal slope (m) relates stomatal conductance

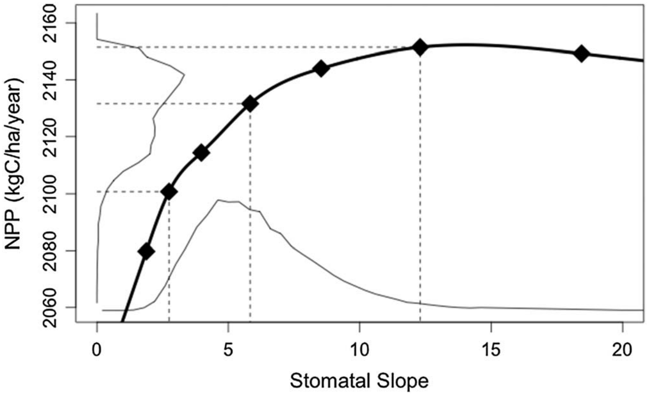

Figure 1. Example uncertainty analysis for the 10 year mean NPP response of temperate midsuccessional hardwoods to the stomatal slope parameter. The probability density on the *x* axis captures the uncertainty in the stomatal slope parameter as estimated by the Bayesian meta-analysis. The solid diamonds represent the sensitivity analysis, depicting the NPP projections of the ED model for different values of stomatal slope, and the solid line is the spline fit to these points. The predictive uncertainty in NPP due to stomatal slope is represented by the probability density on the *y* axis, which is generated by transforming the parameter distribution through the spline sensitivity function. The partial variance is the variance of this predictive distribution divided by the sum of the variances across all parameters.

(g_s) to a composite term involving photosynthetic rate (A), CO_2 concentration (c_s), and vapor pressure deficit (D_s)

$$g_s = g_0 + mA/\left[(c_s - \Gamma)\left(1 + \frac{D_s}{D_0}\right)\right]$$

where g_0 is a small, PFT-specific conductance when stomata are closed, Γ is the CO_2 compensation point, and D_0 is set to 1.0 kPa for all PFTs. Additional stomatal control is provided by the soil moisture supply term, which is proportional to available soil moisture, fine root biomass, and a *water conductance* parameter. If the water supply is less than the demand predicted by the coupled photosynthesis/conductance model, then photosynthesis, transpiration, and stomatal conductance are all linearly reduced until supply meets demand. Leaf-level fluxes are scaled to crown-level fluxes based on *specific leaf area* (SLA). Leaf biomass is determined based on empirical power-law allometric relationships with diameter at breast height, while fine root biomass is set based on a *leaf:root ratio*. *Leaf and fine root respiration* are both proportional to biomass and have an Arrhenius temperature response. *Growth respiration* is assumed a constant fraction of net assimilation associated with biosynthesis. The turnover of leaves and fine roots to litter are based on *turnover coefficients*, though for deciduous PFTs, leaf turnover is dominated by phenology. The allocation of stored nonstructural carbon between stem growth and reproduction (*r_fract*) is controlled by a fixed parameter. Mortality rate declines exponentially as a function of carbon balance (CB) multiplied by a rate parameter (*mort2*)

$$\exp(-mort2 \times \mathrm{CB}/\mathrm{CB}_{\mathrm{max}})$$

where $\mathrm{CB}_{\mathrm{max}}$ is the carbon balance of an individual that is not limited by light, moisture, or nutrients.

2.2. PEcAn Uncertainty Analysis

The uncertainty analysis workflow in PEcAn consists of three automated steps: (1) a meta-analysis to summarize observational trait data and constrain ecosystem model parameters; (2) a parameter sensitivity analysis; and (3) a variance decomposition analysis that uses the outputs from the first two steps to partition predictive uncertainty into the contributions from different model parameters. The details of each of these steps are described elsewhere [*LeBauer et al*., 2013] and are only briefly summarized here and in Figure 1. Prior to the meta-analysis, trait data were collected from a combination of literature synthesis and direct measurements. The literature search was conducted using Web of Science and Google Scholar with keyword combinations corresponding to each trait and the species that comprise each PFT, with relevant information extracted from the text, tables, and figures. This synthesis was conducted by individual members of this research team working on different PFTs in different biomes and collectively represents many person-years of

Table 2. Study Sites[a]

Name	Lat/Lon	Met
Toolik LTER, AK	68.6 N, 149.6 W	NARR
BOREAS, SK (CA-OBs)	54.0 N, 105.1 W	Tower
Sylvania (US-Syv)	46.2 N, 89.3 W	Tower
WLEF, WI (US-PFa)	45.9 N, 90.3 W	Tower
Rhinelander, WI	45.6 N, 89.4 W	NARR
Tully, NY	42.8 N, 76.1 W	NARR
EBI Farm, IL	40.1 N, 88.2 W	NARR
Plymouth, NC (US-NC2)	35.8 N, 76.7 W	Tower

[a] Fluxnet tower designations are given parenthetically. NARR, North American Regional Reanalysis.

effort. This information is stored in PEcAn's companion trait database, BETYdb (http://betydb.org), as the sample mean, error statistics, and sample size, along with metadata including treatment, site, and species within each individual study. As of May 2013, BETYdb contained 29,600 records spanning 2700 species and 252 traits (LeBauer et al. manuscript in preparation). The database also stores the list of species and parameters that define a PFT for each model in PEcAn, and user-specified prior probability distributions on each parameter. A simple Web interface makes it straightforward for users to add new trait data and define new PFTs at whatever taxonomic resolution is required. PEcAn then maps model parameters to available trait data.

Within the PEcAn framework, a hierarchical Bayes meta-analytic model is fit for each trait within each PFT. The primary output of interest from the meta-analysis is the posterior probability distribution for the mean of an ecosystem model parameter (Table 4). The meta-analysis further partitions the variability in trait observations into the within-site versus across-sites components. It also accounts for a fixed effect for greenhouse studies and a random effect for any experimental treatments within a study. The Bayesian approach allows us to update our prior probabilities based on the observed trait data, and the hierarchical meta-analysis accounts for the fact that our best estimate of a parameter must come from a synthesis across studies, not from arbitrarily choosing any one published estimate and then setting the parameter to a fixed value [*Koricheva et al.*, 2013].

The PEcAn sensitivity analysis consists of univariate perturbations to the model parameters to evaluate how a specific model output (in this case NPP) changes as the parameter changes. A univariate approach was taken to focus on the main effects and to reduce the dimensionality of the analysis. Previous work found that the multivariate interactions only accounted for ~20% of the total variation in ED, and ~80% of this difference was attributable to truncation errors, not parameter covariance [*LeBauer et al.*, 2013]. In PEcAn, the model perturbations are based on the quantiles of the parameter's posterior distribution, such that each parameter is moved in proportion to its uncertainty (Figure 1). Specifically, we varied the parameters to the quantile equivalents of ±1, 2, and 3 standard deviations. The response function (i.e., model output as a function of a parameter value) for each parameter within each PFT is then approximated using a spline.

The PEcAn variance decomposition analysis estimates the uncertainty in model predictions (outputs) associated with each model parameter (inputs). This is done using a Monte Carlo generalization of the Delta method, by transforming the posterior parameter distribution through the spline sensitivity function (Figure 1). Because the *predictive uncertainty* is directly a product of *parameter uncertainty* and *model sensitivity*, we also report these quantities. To facilitate comparisons among parameters, parameter variance and model sensitivity are normalized as the posterior coefficient of variation and elasticity (sensitivity normed by both the parameter and output means), respectively, which are unitless quantities. Furthermore, the predictive uncertainties associated with each model parameter are expressed as the proportion that each variable contributes to the overall predictive variance. Finally, we want to reiterate that this analysis is specifically focused on partitioning the uncertainty associated with parameter error and does not address the partitioning of model residual error. By analogy to regression models, we are focusing on the model's confidence interval rather than its predictive interval. The correct treatment of model residual error is beyond the scope of the current analysis as it involves the partitioning of residual error into observation error versus process error and the partitioning of process error into spatial and temporally autocorrelated components, other persistent random effects (e.g., species), and model structural errors [*McMahon et al.*, 2009]. While a full accounting of model errors is the ultimate goal [*Medlyn et al.*, 2005], parameter error is responsible for most of the observed differences among ecosystem models [*Schwalm et al.*, 2010; *Dietze et al.*, 2011].

2.3. Multisite Protocol

As noted in the previous section, the goal of this analysis is to assess the contributions of different model parameters to uncertainty in predicted NPP for biomes across North America. All model runs were conducted in PEcAn version 1.2.6 using ED version 2.2 following a standard protocol. Sensitivity analysis model runs for each PFT were a minimum of 10 years in length, with uncertainties averaged over three time periods: 1 year,

Table 3. Plant Functional Types

Biome	PFT	Site
Tundra	Graminoid	Toolik
	Evergreen Shrub	Toolik
	Deciduous Shrub	Toolik
Boreal	Spruce	BOREAS
Temperate forest	Early Successional Hardwood	WLEF
	Poplar	Rhinelander
	Willow	Tully
	Midsuccessional Hardwood	WLEF
	Late Successional Hardwood	WLEF
	Northern Pine	WLEF
	Southern Pine	US-NC2
Temperate grassland	Forb	EBI Farm
	Legume	EBI Farm
	C3 Grass	EBI Farm
	C4 Grass	EBI Farm
	Switchgrass	EBI Farm
	Miscanthus	EBI Farm

5 years, and 10 years. Analyses were conducted for 17 PFTs at eight sites throughout North America representing a range of biomes including Arctic tundra, boreal forest, temperate deciduous and coniferous forests, grasslands, and agriculture (Tables 2 and 3). Sites were selected to provide meteorological data and site-specific initial conditions for the model and include long-term ecological research stations, flux towers, and other existing experimental plots. When available, meteorological driver data were derived from local eddy covariance (EC) micrometeorological tower observations [*Baldocchi*, 2003]. In cases where either sites did not contain an EC tower or the observational record was considerably shorter in duration than the 10 year period, we utilized downscaled climate drivers from the North American Regional Reanalysis [*Messinger et al.*, 2006]. For native forest sites, initial conditions were derived from available forest plot data at each site. For short-rotation forestry sites, the focal region for analysis was stands aged 5–15 years, which are the peak years for productivity. For grassland sites, vegetation was run from near bare ground to steady state. Since the total variance was very different for different PFTs, comparisons were made based on the proportion of the predictive variance in NPP that was attributable to each variable within each PFT. For a given variable, patterns in partial variance were compared to patterns in elasticity and coefficient of variance in order to attribute predictive uncertainty to parameter uncertainty versus model sensitivity. Analysis of variance was also used to determine the importance of parameter, PFT, and simulation time period in explaining patterns in partial variance.

3. Results and Discussion

3.1. Drivers of Model Uncertainty

The interpretation of the results focuses on *predictive uncertainty* as the primary response variable, which is expressed as the proportion of the predictive variance attributed to each parameter within each PFT. The primary explanatory variables are the *model sensitivity*, expressed in terms of elasticity, and the *parameter uncertainty*, expressed in terms of the coefficient of variation of the parameter's probability distribution. Overall, there was a strong effect of parameter ($df = 11$, $F = 401.1$, $p < 0.001$) and a parameter by PFT interaction ($df = 171$, $F = 21.5$, $p < 0.0001$) on predictive uncertainty. However, we did not observe a significant effect of simulation time period (1, 5, or 10 years) on patterns of uncertainty; therefore, the results below are presented as an average over the three periods considered. The lack of an effect of simulation time was somewhat surprising, because we hypothesized that different parameters would be important over different time scales, with parameters controlling slow processes such as mortality and recruitment increasing in importance as the analysis period was lengthened. The insensitivity to simulation time may be a result of the rather short periods considered (in terms of ecological phenomena), and analyses evaluating the sensitivity of the ED model on a centennial time scale are currently in progress (Raczka, manuscript in preparation). Classifying our PFTs into three higher-level "life form" groups—evergreen woody, deciduous woody, nonwoody—and averaging over all years, we found that there was a significant life form by variable interaction ($df = 22$, $F = 2.8541$, $p < 0.0001$). While the overall pattern of uncertainty is consistent across life forms (Figure 2), in much of the discussion below we highlight variability within and across life forms as we find that these differences explain many of the observed patterns.

Looking across all PFTs and all years (Figure 3), growth respiration was responsible for the highest fraction of predictive uncertainty in modeled NPP (mean 37%) (Figure 2). On average the deciduous hardwoods had a higher fraction of uncertainty associated with growth respiration, while evergreen conifers and nonwoody PFTs were similar. The classic growth-maintenance respiration paradigm lumps together any respiratory

Table 4. Model Parameter Posterior Distributions, Median, and 2 Sigma credible interval (CI) (95.45%)

	Growth Resp	Leaf Resp	Mortality	Quantum Eff.	Root Resp	Root Turnover	Reproduction	SLA	Stomatal Slope	Vcmax	Water Cond	Root:Leaf
Tundra Gram.	0.35 (0.12, 0.65)	0.93 (0.51, 1.4)	20 (1.6, 82)	0.071 (0.025, 0.12)	7.4 (3.7, 11)	0.19 (0.018, 2.1)	0.31 (0.05, 0.72)	10 (9.4, 11)	5.8 (2.7, 12)	109 (35,336)	0.0044 (1.1e−05, 1.7)	1.6 (1.5, 1.7)
Tundra EG	0.35 (0.12, 0.65)	3.3 (2.7, 3.9)	20 (1.6, 80)	0.071 (0.026, 0.12)	7.9 (3.6, 18)	0.19 (0.018, 2.1)	0.31 (0.049, 0.72)	7.3 (6.8, 7.7)	5.8 (2.7, 12)	48 (37, 123)	0.0045 (0.002, 0.01)	0.86 (0.78, 0.95)
Tundra Decid	0.35 (0.12, 0.65)	2.5 (2.4, 2.6)	20 (1.6, 82)	0.072 (0.026, 0.12)	8.3 (1.5, 19)	0.19 (0.017, 2.2)	0.31 (0.049, 0.73)	13 (13, 14)	5.8 (2.7, 12)	109 (35, 338)	0.0045 (0.002, 0.01)	4.1 (3.8, 4.4)
Boreal Spruce	0.35 (0.12, 0.65)	0.86 (0.29, 1.8)	20 (1.6, 83)	0.051 (0.039, 0.064)	3.7 (1.9, 5.4)	0.68 (0.073, 2)	0.32 (0.051, 0.73)	8.6 (8.2, 8.9)	5.8 (2.7, 12)	19 (12, 27)	0.0046 (1.1e−05, 1.9)	0.77 (0.11, 5.7)
N. Pine	0.35 (0.12, 0.65)	1.1 (0.93, 1.3)	20 (1.6, 81)	0.057 (0.042, 0.073)	12 (11, 12)	0.68 (0.074, 2)	0.31 (0.051, 0.72)	9 (8.5, 9.6)	5.8 (2.7, 12)	70 (60, 80)	0.0044 (1.1e−05, 1.9)	0.78 (0.11, 5.7)
Early HW	0.35 (0.12, 0.65)	1.7 (1.7, 1.8)	20 (1.7, 82)	0.057 (0.055, 0.06)	2.8 (1.7, 4)	1.3 (1.1, 1.5)	0.31 (0.049, 0.72)	20 (20, 20)	6.1 (5.3, 7)	56 (54, 58)	0.0045 (1.2e−05, 1.8)	0.64 (0.61, 0.66)
Willow	0.35 (0.12, 0.65)	2.8 (1.8, 3.8)	20 (1.7, 83)	0.043 (0.037, 0.048)	6.1 (2, 13)	0.68 (0.078, 2)	0.31 (0.049, 0.72)	16 (16, 16)	6 (3.7, 7.6)	58 (46, 70)	0.0045 (0.002, 0.01)	4.2 (3.7, 4.6)
Poplar	0.35 (0.12, 0.65)	1.6 (1.3, 1.9)	20 (1.7, 82)	0.068 (0.066, 0.07)	1.3 (1.1, 1.5)	0.68 (0.071, 2)	0.24 (0.23, 0.24)	18 (18, 19)	5.9 (5.1, 6.7)	70 (64, 75)	0.0045 (0.002, 0.01)	1.2 (0.37, 4.1)
Mid HW	0.35 (0.12, 0.65)	0.69 (0.61, 0.78)	20 (1.6, 82)	0.038 (0.036, 0.04)	5.3 (4.5, 6)	0.68 (0.074, 2)	0.31 (0.052, 0.73)	21 (21, 22)	5.8 (2.7, 13)	50 (46, 54)	0.0042 (1.1e−05, 1.7)	1 (0.94, 1.1)
Late HW	0.35 (0.12, 0.66)	2.4 (2.4, 2.4)	20 (1.6, 81)	0.045 (0.042, 0.047)	5.4 (4.9, 6)	0.68 (0.077, 2)	0.31 (0.051, 0.72)	17 (17, 17)	5.8 (2.7, 12)	81 (78, 84)	0.0046 (1.1e−05, 1.8)	1 (0.9, 1.1)
Forb	0.27 (0.06, 0.6)	1.3 (0.84, 1.8)	20 (1.6, 83)	0.064 (0.06, 0.067)	6.1 (2, 14)	0.53 (0.072, 1.5)	0.13 (0.11, 0.14)	14 (12, 17)	14 (14, 15)	83 (79, 88)	0.0045 (1.2e−05, 1.8)	1.5 (1.2, 1.7)
Legume	0.27 (0.06, 0.6)	1.3 (0.56, 2.2)	20 (1.5, 82)	0.069 (0.063, 0.076)	5.5 (1.5, 10)	0.53 (0.065, 1.5)	0.3 (0.23, 0.36)	14 (8.5, 20)	13 (7.9, 23)	118 (106, 129)	0.0046 (1.1e−05, 1.9)	2.2 (0.42, 12)
C3 Grass	0.27 (0.06, 0.6)	1 (0.79, 1.3)	20 (1.6, 81)	0.057 (0.042, 0.071)	5.4 (1.5, 10)	0.53 (0.067, 1.5)	0.32 (0.052, 0.72)	15 (15, 16)	13 (7.9, 22)	58 (44, 71)	0.0045 (1.1e−05, 1.7)	2.2 (0.42, 12)
C4 Grass	0.27 (0.058, 0.6)	1.9 (0.52, 7.0)	20 (1.5, 82)	0.052 (0.048, 0.056)	5.1 (3.7, 6.7)	0.67 (0.2, 1.1)	0.31 (0.051, 0.72)	23 (22, 23)	12 (12, 12)	21 (19, 24)	0.0045 (1.1e−05, 1.8)	1.9 (1.7, 2.1)
Switchgrass	0.27 (0.058, 0.61)	1.9 (0.52, 7.0)	20 (1.6, 82)	0.055 (0.047, 0.066)	5.1 (3.7, 6.7)	0.67 (0.2, 1.1)	0.31 (0.05, 0.72)	17 (16, 18)	4.1 (3.8, 4.3)	25 (18, 31)	0.0047 (1.2e−05, 1.8)	1.3 (0.87, 1.8)
Miscanthus	0.27 (0.058, 0.61)	1.9 (0.52, 7.0)	20 (1.5, 81)	0.061 (0.056, 0.067)	1.8 (1.7, 2)	0.53 (0.07, 1.5)	0.31 (0.048, 0.72)	15 (15, 16)	3.4 (1.3, 5.5)	29 (24, 34)	0.0045 (1.1e−05, 1.8)	2.2 (0.4, 12)
S. Pine	0.45 (0.16, 0.78)	1.5 (1.4, 1.5)	20 (1.7, 82)	0.033 (0.024, 0.042)	12 (12, 13)	1.1 (0.96, 1.2)	0.31 (0.051, 0.72)	8.3 (7.9, 8.7)	5.8 (2.7, 12)	65 (63, 67)	0.0045 (0.002, 0.01)	1.8 (1.6, 1.9)

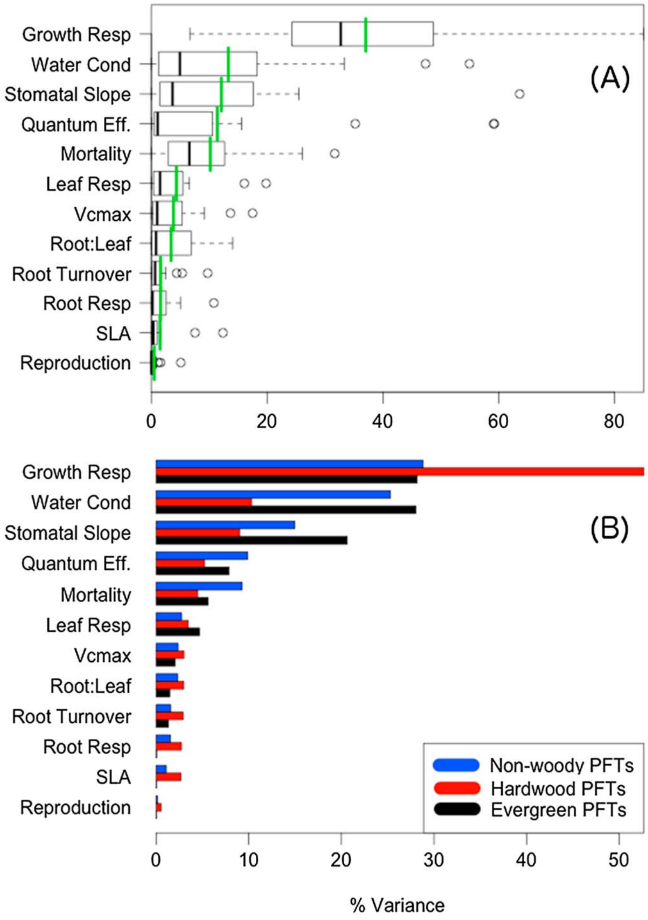

Figure 2. Overall pattern of partial variance by variable. (a) Boxplot of partial variances by variable across PFTs with the mean indicated by the vertical green bar. (b) Barplot of mean partial variances across evergreen, deciduous hardwood, and nonwoody life forms. Variability is dominated by growth respiration, but stomatal slope, water conductance, mortality, and quantum efficiency are also consistently important across life forms.

processes that are proportional to gross primary productivity into "growth" respiration and any process proportional to pool biomass into "maintenance" [*Amthor*, 2000; *Cannell*, 2000; *Thornley*, 2000]. Because of this, growth respiration is challenging to directly measure, so there were no direct estimates in our database and the priors were relatively broad. Therefore, the observed differences among PFTs in predictive uncertainty are primarily a reflection of differences in sensitivity since in all cases the variability in parameter uncertainty is just a reflection of the prior. Reducing parameter uncertainty in growth respiration is clearly a priority, but doing so is nontrivial because it reflects a latent, unobserved process. Because we can make direct observations on most other pools, processes, and parameters, growth respiration in essence absorbs much of the residual variability and helps close the carbon budget. Data assimilation offers a promising means to improve growth respiration estimates [*Dietze et al*., 2013], and we have employed this approach in the past [*Davidson*, 2012; *Wang et al*., 2013]. However, given that this parameter dominates predictive uncertainty across such a large scale, it is critical to ask whether there are additional direct constraints or different model formulations that can help ensure biological realism and explain variability in the process.

Growth respiration integrates a number of respiratory processes thought to be more closely tied to the amount of new assimilation than the size of existing biomass pools. There is some disagreement among researchers regarding which processes to include; nevertheless, all growth respiration calculations include the direct costs of biosynthesis (a.k.a. local growth) and many also include the energy required for nitrate reduction, N_2 fixation, the uptake of N and other ions, and phloem loading [*Amthor*, 2000; *Cannell*, 2000; *Thornley*, 2000]. One approach that has been suggested is to model each of these terms individually, while

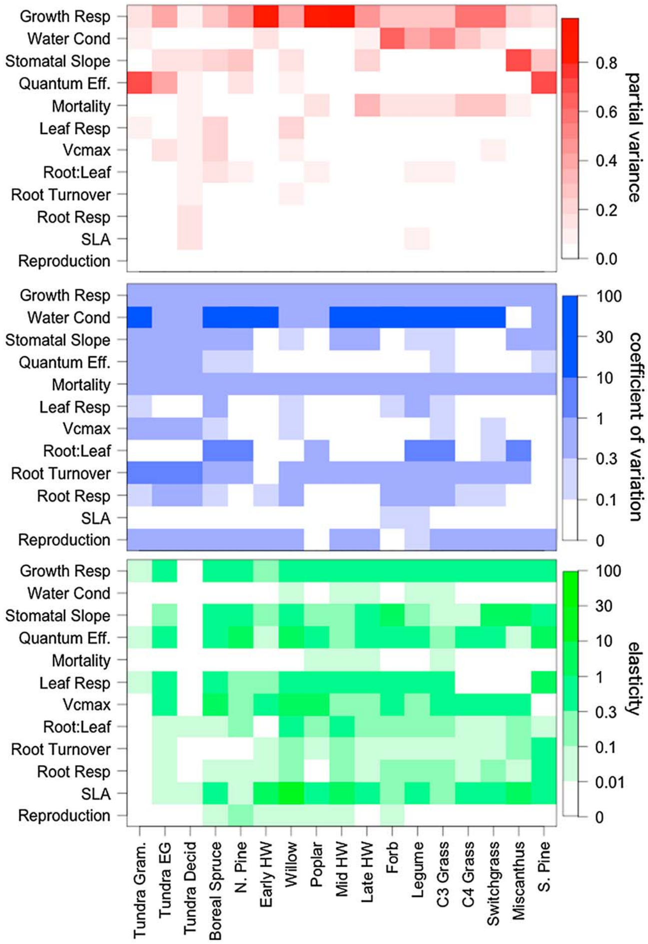

Figure 3. Matrix plots of (a) partial variance, (b) coefficient of variance, and (c) elasticity by variable and PFT ordered from top to bottom by the across-species mean. Both coefficient of variance and elasticity are on a log scale. Partial variance expresses the proportion of the predictive uncertainty in NPP that can be attributed to each parameter. This quantity is controlled by the sensitivity of NPP to each parameter and the uncertainty in the parameter estimate. Model sensitivity and parameter uncertainty are expressed here in terms of their unitless equivalents—elasticity and coefficient of variation, respectively.

also including a residual respiration term to represent factors not considered explicitly [*Cannell*, 2000]. The costs of biosynthesis can be estimated using the classic "pathway analysis" approach [*Penning de Vries et al.*, 1974] of summing the carbon costs of synthesizing different macromolecules weighted by their fractional contribution to different tissue types. In this approach different constituents are typically grouped into larger classes, such as protein, carbohydrates, lipids, lignin, and organic acids. Even with such broad classes, and assuming a simple division of biomass into just leaves, stems, and roots, this approach proposes to reduce uncertainty by replacing a poorly constrained one-parameter model with an 18-parameter model: five growth efficiencies; a three-by-five matrix of composition (with one column being constrained to one minus the sum across each row), and a residual respiration term. For growth efficiency, there would still be variability associated with aggregating the construction costs of different compounds within each bin, as well as potential interspecific variability in biosynthesis, while for the composition, there would be interspecific and intraspecific variability within PFTs. However, except for the residual, each of these parameters would be observable, and the hope is that the overall variance would be lower. There are also positive side effects of this approach, such as improving allocation models by acknowledging that different pools have different costs to the plant. The challenge comes from the need to estimate the molecular composition, as these data are in short supply and current plant trait databases [*Kattge et al.*, 2011] only cover a subset of compounds. The most common compositional data comprise total C and N content, with some data available on lignin, chlorophyll, and nonstructural carbohydrates. There is a need to enhance these databases on a global scale by pulling together existing compositional data for a broader suite of compounds and filling in databases with new measurements. In addition, remote sensing approaches can provide information on the spatial patterns of relevant foliar chemistry and morphological traits (e.g., C, N, SLA, lignin, chlorophyll, and foliar isotopic composition) that could be used to inform ecosystem models [*Martin and Aber*, 1997; *Townsend et al.*, 2003; *Kleinebecker et al.*, 2009; *Ustin et al.*, 2009; *Asner et al.*, 2011; *Serbin et al.*, 2012]. One hope is that existing traits (C:N, SLA, wood density, etc.) will correlate with composition so that this partial but more abundant information, while insufficient to uniquely identify compositional “fingerprints”, will provide an additional constraint to reduce uncertainties.

After growth respiration, there is a collection of four parameters (water conductance, stomatal slope, mortality rate coefficient, and quantum efficiency) that each contribute around 10% to model predictive uncertainty, with the exact rank depending upon life form and summary statistic (e.g., mean versus median). Based on medians, the mortality rate coefficient was the second most important parameter and was generally more highly ranked among nonwoody PFTs. The latter pattern is not surprising given the more rapid reproduction, high stem density, and higher stem turnover characteristic of grasslands. Across all PFTs, the differences in the importance of mortality are largely driven by variation in sensitivity. For long-lived woody vegetation, we expect the sensitivity to mortality to continue to increase over time, and preliminary results are consistent with this pattern (B. Raczka, unpublished data, 2014). This high sensitivity to mortality reflects the inclusion of demographic processes in the ED model. These processes are absent from many ecosystem models, which frequently represent mortality as an invariant flux to coarse woody debris [*King et al.*, 1997; *Thornton et al.*, 2002]. However, long-lived organisms are known to be particularly sensitive to mortality rate [*Franco and Silvertown*, 1996; *Caswell*, 2001] and there is a growing body of literature demonstrating large-scale variability in patterns of background mortality rate in response to climate, pollution, and competitive interactions [*van Mantgem et al.*, 2009; *Lines et al.*, 2010; *Dietze and Moorcroft*, 2011; *Luo and Chen*, 2011]. More dramatically, drought, insects, and pathogens can cause widespread plant mortality but are absent from most ecosystem models, where the most common forms of disturbance are fire and land use [*Allen et al.*, 2010; *Hicke et al.*, 2012]. Within the ED model, mortality is tied to carbon balance [*Moorcroft et al.*, 2001; *Fisher et al.*, 2010]. While there is debate about the relative importance of carbon versus hydraulic limitation in driving drought mortality, especially in more open and arid western temperate forests [*McDowell and Sevanto*, 2010; *Sala et al.*, 2010; *McDowell*, 2011], the conceptual argument for the role of carbon limitation in competitive successional dynamics is strong [*Dietze and Moorcroft*, 2011]. However, mortality models are limited by both data and the need for a more detailed understanding of the mortality process. Constraining the link between carbon and background mortality rates is very challenging given the low mortality rates in long-lived plants, which limits the availability of observational data. More productive approaches are likely to include using data assimilation to link large-scale forest inventory data to survey data on nonstructural carbon reserves, as well as fine-scale ecophysiological experiments to better elucidate the underlying processes.

For stomatal slope [*Leuning*, 1995], among the evergreen PFTs, there is a clear trend in increasing partial variance from north to south that is driven by an increase in sensitivity, while for the deciduous PFTs, this gradient is less clear and variation is driven mostly by differences in parameter uncertainty. For most nonwoody PFTs, the partial variances attributed to stomatal slope were low. The exception to this pattern was the C4 perennial grass Miscanthus, which has the highest uncertainty among this group. Both patterns are consistent with our experience with switchgrass [*LeBauer et al.*, 2013], where we found that stomatal slope was an important parameter but one that was well-constrained by a relatively small number of direct measurements. Thus, for conifers, where no measurements were available, we see the expected increase in sensitivity as both average photosynthetic rate and vapor pressure deficit increase from north to south. However, this pattern is overshadowed by patterns of data availability for all PFTs. Stomatal slope can be estimated from leaf-level gas exchange through stomatal response curves, but these curves are much more time consuming than standard A-Ci curves as stomata equilibrate at slower time scales than leaf biochemistry [*Leakey et al.*, 2006]. Survey-style photosynthesis data can also be used to estimate stomatal slope, though with considerably higher noise, while traditional response curve data (e.g., A-Ci and A-Q) are liable to produce biased estimates [*Leakey et al.*, 2006]. Unlike the other parameters we identify, there is a targeted synthesis project for stomatal slope (Stomatal Behaviour Synthesis Project, http://bio.mq.edu.au/stomata/), though it is still in its nascent phases and there remains a clear demand for new measurements on previously unmeasured species. There has also been a suite of targeted measurements on a dozen temperate deciduous species initiated based on an earlier version of this analysis (Wolz and Leakey, manuscript in preparation).

For water conductance, the proportion of variance is largest for temperate nonwoody vegetation, moderate for temperate woody, and lowest in the north regardless of growth form. Due to a lack of direct measurements, parameter uncertainty was generally high across PFTs. Sensitivity tended to be low but was higher for nonwoody vegetation, and differences in sensitivity explained the variability among nonwoody PFTs. Overall, the dominant role of parameter uncertainty over sensitivity in driving the importance of water conductance suggests that adding even a small amount of data constraint is likely to be effective in reducing predictive uncertainty.

Unlike the many other parameters, the formulation of how soil moisture limits transpiration and photosynthesis is more idiosyncratic across ecosystem models [*De Kauwe et al*., 2013]. Within ED, the water conductance term is not a directly measurable trait but rather is a rate parameter setting an upper bound on transpiration as a function of soil moisture and root biomass. This parameter can be estimated through the assimilation of eddy covariance carbon and water flux data, though the constraint is often weak [*Medvigy et al*., 2009]. A more direct approach would be to use sap-flux data [*Oren et al*., 1999; *Ewers*, 2002] to measure transpiration directly, though care must be taken in this approach due to stem storage and azimuthal inhomogeneities in sap flux. This approach to identifying water limitation would require a well-constrained estimate of the stomatal slope parameter in order to estimate transpiration in the absence of soil limitation, as well as direct measurements of soil moisture and any relevant covariates (e.g., fine root biomass). Finally, as with growth respiration, it is possible to develop a more mechanistic approach to the problem by modeling hydraulic conductivity and embolism risk explicitly based on water potential and a series of empirically measureable conductances along the path from the root to the leaf [*Jackson et al*., 2000; *Bohrer et al*., 2005; *Sperry*, 2011]. However, this approach substitutes the difficulty in parameterizing the soil moisture versus stomatal conductance relationship with the challenge of estimating the relationship between leaf water potential and stomatal closure, which is also not fully understood, and involves additional factors related to hormone signaling that are not captured by a hydraulic approach [*Schroeder et al*., 2001]. Still, taken together, the high partial variances associated with stomatal slope and water conductance suggest that our uncertainties surrounding water relations are more important for understanding and predicting carbon fluxes than the uncertainties surrounding most of the carbon fluxes themselves. This conclusion is consistent with a recent model-data synthesis at the Free Air CO_2 Enrichment (FACE) experiments that found considerable variation among models in the representation of stomatal conductance and soil moisture constraints on transpiration, which translated to substantial variability in predicted NPP and water use efficiency at high CO_2 [*De Kauwe et al*., 2013]. Similarly, climate change projections of a large-scale Amazonian dieback [*Cox et al*., 2004; *Huntingford et al*., 2008] have been attributed to stomatal and soil-moisture controls on transpiration [*Harper et al*., 2010].

Quantum efficiency, which is the primary driver of photosynthetic rates at low light levels, was found to have relatively high partial variance at high latitudes regardless of life form. Somewhat counterintuitively, the primary driver of this pattern was not reduced light availability and shorter growing season at high latitudes but rather the consistently higher parameter uncertainty due to limited data. Fortunately, data constraint is straightforward based on leaf-level gas exchange measurements of light response curves [*Bernacchi et al*., 2013], so future data-collection efforts could easily reduce uncertainty in modeled high-latitude NPP.

Counter to our hypotheses, other parameters associated with photosynthesis and maintenance respiration, such as $V_{c,\max}$ and SLA, were not identified among the most important contributors to model uncertainty. However, this result remains compatible with prior research suggesting these processes are the primary controls on NPP [*White et al*., 2000]. These parameters did show high sensitivity, but with few exceptions, had comparatively low uncertainty due to the availability of trait data. Leaf respiration and $V_{c,\max}$ tended to be more important at high latitude, while the pattern of importance for root:leaf ratio was driven by parameter uncertainty. Finally, uncertainty for the tundra deciduous PFT was more evenly distributed among parameter than for most other PFTs. This PFT also displayed the lowest productivity across all PFTs considered in this study, with many parameter combinations leading to local extinction.

3.2. Model-Data Feedbacks

These analyses were facilitated by the use of the open-source PEcAn framework, which enabled a group of researchers to collectively produce a synthetic analysis that integrated projects focused on subsets of PFTs within a more limited geographic range. Working within a common and accessible software system made it easier to perform analyses that were reproducible and directly comparable. While this analysis focused on the Ecosystem Demography model, there are other ecosystem models coupled to the PEcAn framework, and adding new models is relatively straightforward given the modular design of the system. This design opens the door to employing systems like PEcAn in multimodel syntheses and model-data comparison activities [*Schwalm et al*., 2010; *Dietze et al*., 2011], which have traditionally suffered from difficulties in partitioning model uncertainties. For example, within most model intercomparisons, it is challenging to separate parameter uncertainties from model structural uncertainties, though the stated goals of such projects are often to assess just the latter. Extending our analysis to a multimodel context would be very informative, as it would clarify which data needs are common across models and which are unique to specific model structures. Through the PEcAn framework, we can more easily involve a larger community effort to address these issues.

Likewise, while we succeeded in assessing uncertainty across a broad geographic scale, including a wide range of biomes and PFTs, there were also biomes that were absent from our analyses. Ongoing research by our team does not currently include work in tropical, arid, or semi-arid systems. Because of this, there are insufficient data in our trait database for these regions, as the underlying literature synthesis required to construct parameter distributions represents many years of research effort. However, as noted in section 1, it is these distributions that are necessary to move from a sensitivity analysis to a more informative uncertainty analysis. Conducting uncertainty analyses without the literature synthesis could easily suggest that research effort be mistakenly prioritized toward variables that are actually well known. Had we relied on sensitivity alone in the above analysis, we would have mistakenly focused on SLA, the variable with the highest mean elasticity, and concluded that quantum efficiency, with the second highest elasticity, should be prioritize at all sites, not just the northern ones. We also would have ignored water conductance and mortality, which have low elasticities but high uncertainties.

The preceding analysis focused specifically on the NPP response to ecophysiological and demographic parameters, but similar analyses could be easily extended to parameters controlling biogeochemistry, radiative transfer, and land surface biophysics, and to additional response variables related to community structure and composition and the overall fluxes of carbon, water, and energy. These analyses would likely identify additional parameters that are important to specific model outputs as well as parameters that are important across multiple outputs. For example, in applying PEcAn to the tundra, we found that similar, but not identical, sets of parameters were important for simulating diameter growth, aboveground biomass, and net ecosystem exchange [*Davidson*, 2012]. Similarly, it would be useful to extend these analyses to consider uncertainties associated with initial conditions and model drivers. The advantage of the PEcAn framework is that for a given output, these uncertainty analyses could all be done coherently so as to allow the direct comparison of the uncertainties between different processes, such as simultaneously comparing the importance of initial conditions, drivers, and parameters across different submodels.

4. Conclusions

Our goal was to quantitatively assess the uncertainties in a sophisticated terrestrial biosphere model for a wide range of biomes and plant functional types (PFTs) across North America, in order to identify parameters and processes most in need of further data constraint. We used PEcAn to assess the uncertainty in NPP predictions by the ED model for a dozen variables in 17 PFTs across four major biomes and found that the overall uncertainty was dominated by five parameters. Growth respiration was consistently the largest source of uncertainty. To address this issue, we advocate the extension of plant trait databases to include more detailed information on tissue chemistry in order to better facilitate the application of the classic “pathway analysis” approach [*Penning de Vries et al*., 1974] across biomes. The relationship between mortality and carbon balance was consistently important across both temperate trees and nonwoody vegetation. The dynamics of nonstructural carbon in general, and its causal connection to mortality in particular, are actively debated in the literature [*Dietze et al*., 2014], and thus, the importance of this relationship highlights the need for both mechanistic physiological experiments and large-scale observational studies in this area.

The importance of both stomatal slope and water conductance highlights the close connection between the carbon and water cycles and the need for a better understanding of plant water regulation even across non-arid vegetation types. The importance of stomatal slope generally increased when moving from north to south, but the overall pattern was most responsive to differences in the availability of data. The importance of quantum efficiency at high latitudes was found to be driven primarily by parameter uncertainty, which highlights the need for basic leaf-level gas exchange research in these understudied systems. $V_{c,\mathrm{max}}$ and SLA, despite being highly sensitive in this and other models, were notably absent due to strong data constraints. Further work is required to extend these analyses to tropical and arid biomes, additional models, processes, and response variables, and to assess uncertainties in initial conditions and model drivers in the same framework as parameter uncertainty. Finally, uncertainty analysis is only one component of model assessment, and parameter error is only one source of model error, and additional work is needed to assess structural errors and partition process variability. Nonetheless, this study identifies key areas of uncertainty in our understanding of plant ecology and physiology and finds consistent patterns to these uncertainties that reflect latitudinal gradients in both model sensitivity and data availability.

Acknowledgments

This work was supported by the Energy Biosciences Institute, NSF grants ARC 1023477 and ABI 1062547 to the University of Illinois Urbana-Champaign and ABI 1062204 to the University of Wisconsin Madison.

References

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, and E. H. (Ted) Hogg (2010), A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests, *For. Ecol. Manage.*, *259*(4), 660–684, doi:10.1016/j.foreco.2009.09.001.

Amthor, J. (2000), The McCree–de Wit–Penning de Vries–Thornley respiration paradigms: 30 years later, *Ann. Bot.*, *86*(1), 1–20, doi:10.1006/anbo.2000.1175.

Asner, G. P., R. E. Martin, D. E. Knapp, R. Tupayachi, C. Anderson, L. Carranza, P. Martinez, M. Houcheime, F. Sinca, and P. Weiss (2011), Spectroscopy of canopy chemicals in humid tropical forests, *Remote Sens. Environ.*, *115*(12), 3587–3598, doi:10.1016/j.rse.2011.08.020.

Baldocchi, D. D. (2003), Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: Past, present and future, *Global Change Biol.*, *9*, 479–492.

Bernacchi, C. J., J. E. Bagley, S. P. Serbin, U. M. Ruiz-Vera, D. M. Rosenthal, and A. Vanloocke (2013), Modelling C3 photosynthesis from the chloroplast to the ecosystem., *Plant. Cell Environ.*, *36*(9), 1641–1657, doi:10.1111/pce.12118.

Bohrer, G., H. Mourad, T. a. Laursen, D. Drewry, R. Avissar, D. Poggi, R. Oren, and G. G. Katul (2005), Finite element tree crown hydrodynamics model (FETCH) using porous media flow within branching elements: A new representation of tree hydrodynamics, *Water Resour. Res.*, *41*(11), 1–17, doi:10.1029/2005WR004181.

Bolker, B., S. Pacala, and W. P. Jr (1998), Linear Analysis of soil decomposition: Insights from the CENTURY model, *Ecol. Appl.*, *8*(2), 425–439, doi:10.1890/1051-0761(1998)008[0425:LAOSDI]2.0.CO;2.

Cannell, M. (2000), Modelling the components of plant respiration: Some guiding principles, *Ann. Bot.*, *85*(1), 45–54, doi:10.1006/anbo.1999.0996.

Cariboni, J., D. Gatelli, R. Liska, and a. Saltelli (2007), The role of sensitivity analysis in ecological modelling, *Ecol. Modell.*, *203*(1-2), 167–182, doi:10.1016/j.ecolmodel.2005.10.045.

Caswell, H. (2001), *Matrix Population Models*, 2nd ed., Sinauer Associates, Sunderland, MA.

Cleveland, C. C., et al. (2011), Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis., *Ecol. Lett.*, *14*(9), 939–947, doi:10.1111/j.1461-0248.2011.01658.x.

Collatz, G., M. Ribas-Carbo, and J. A. Berry (1992), Coupled photosynthesis-stomatal conductance model for leaves of C4 plants, *Aust. J. Plant Physiol.*, *19*(5), 519, doi:10.1071/PP9920519.

Cox, P. M., R. a. Betts, M. Collins, P. P. Harris, C. Huntingford, and C. D. Jones (2004), Amazonian forest dieback under climate-carbon cycle projections for the 21st century, *Theor. Appl. Climatol.*, *78*(1-3), 137–156, doi:10.1007/s00704-004-0049-4.

Davidson, C. D. (2012), *The Modeled Effects of Fire on Carbon Balance and Vegetation Abundance in Alaskan Tundra*, 163 pp., University of Illinois, Urbana-Champaign.

De Kauwe, M. G., et al. (2013), Forest water use and water use efficiency at elevated CO_2: A model-data intercomparison at two contrasting temperate forest FACE sites, *Global Change Biol.*, *19*, 1759–1779, doi:10.1111/gcb.12164.

Dietze, M. C., and P. R. Moorcroft (2011), Tree mortality in the eastern and central United States: Patterns and drivers, *Glob. Chang. Biol.*, *17*(11), 3312–3326, doi:10.1111/j.1365-2486.2011.02477.x.

Dietze, M. C., A. Sala, M. S. Carbone, C. I. Czimczik, J. A. Mantooth, A. D. Richardson, and R. Vargas (2014), Nonstructural carbon in woody plants., *Annu. Rev. Plant Biol.*, *65*, 1–21, doi:10.1146/annurev-arplant-050213-040054.

Dietze, M. C., D. S. LeBauer, and R. Kooper (2013), On improving the communication between models and data, *Plant Cell Environ.*, *36*(9), 1575–1585, doi:10.1111/pce.12043.

Dietze, M., et al. (2011), Characterizing the performance of ecosystem models across time scales: A spectral analysis of the North American Carbon Program site-level synthesis, *J. Geophys. Res.*, *116*, G04029, doi:10.1029/2011JG001661.

Ewers, B. E. (2002), Tree species effects on stand transpiration in northern Wisconsin, *Water Resour. Res.*, *38*(7), 1103, doi:10.1029/2001WR000830.

Farquhar, G., S. Caemmerer, and J. A. Berry (1980), A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species, *Planta*, *149*(1), 78–90.

Fisher, R., N. McDowell, D. Purves, P. Moorcroft, S. Sitch, P. Cox, C. Huntingford, P. Meir, and F. Ian Woodward (2010), Assessing uncertainties in a second-generation dynamic vegetation model caused by ecological scale limitations., *New Phytol.*, 666–681, doi:10.1111/j.1469-8137.2010.03340.x.

Franco, M., and J. Silvertown (1996), Life history variation in plants: An exploration of the fast-slow continuum hypothesis, *Philos. Trans. R. Soc. B Biol. Sci.*, *351*(1345), 1341–1348, doi:10.1098/rstb.1996.0117.

Harper, A. B., A. S. Denning, I. T. Baker, M. D. Branson, L. Prihodko, and D. a. Randall (2010), Role of deep soil moisture in modulating climate in the Amazon rainforest, *Geophys. Res. Lett.*, *37*, L05802, doi:10.1029/2009GL042302.

Hicke, J. A., et al. (2012), Effects of biotic disturbances on forest carbon cycling in the United States and Canada, *Glob. Chang. Biol.*, *18*, 7–34, doi:10.1111/j.1365-2486.2011.02543.x.

Hilborn, R., and M. Mangel (1997), *The Ecological Detective: Confronting Models With Data*, 1st ed., Princeton University Press, Princeton, NJ.

Huntingford, C., et al. (2008), Towards quantifying uncertainty in predictions of Amazon "dieback"., *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*, *363*(1498), 1857–1864, doi:10.1098/rstb.2007.0028.

Jackson, R. B., J. S. Sperry, and T. E. Dawson (2000), Root water uptake and transport: using physiological processes in global predictions, *Trends Plant Sci.*, *5*(11), 482–488.

Kattge, J., et al. (2011), TRY—A global database of plant traits, *Glob. Chang. Biol.*, *17*(9), 2905–2935, doi:10.1111/j.1365-2486.2011.02451.x.

Keenan, T. F., E. Davidson, A. Moffat, W. Munger, and A. D. Richardson (2012), Using model-data fusion to interpret past trends, and quantify uncertainties in future projections, of terrestrial ecosystem carbon cycling, *Glob. Chang. Biol.*, *18*, 2555–2569, doi:10.1111/j.1365-2486.2012.02684.x.

King, A. W., W. M. Post, and S. D. Wullschleger (1997), The potential response of terrestrial carbon storage to changes in climate and atmospheric CO_2, *Clim. Change*, *35*, 199–227.

Kleinebecker, T., S. R. Schmidt, C. Fritz, A. J. P. Smolders, and N. Hölzel (2009), Prediction of delta(13)C and delta(15)N in plant tissues with near-infrared reflectance spectroscopy., *New Phytol.*, *184*(3), 732–739, doi:10.1111/j.1469-8137.2009.02995.x.

Koricheva, J., J. Gurevitch, and K. Mengersen (2013), *Handbook of Meta-analysis in Ecology and Evolution*, Princeton Univ. Press, Princeton, NJ.

Leakey, A. D. B., C. J. Bernacchi, D. R. Ort, and S. P. Long (2006), Long-term growth of soybean at elevated [CO2] does not cause acclimation of stomatal conductance under fully open-air conditions., *Plant. Cell Environ.*, *29*(9), 1794–1800, doi:10.1111/j.1365-3040.2006.01556.x.

LeBauer, D. S., D. Wang, K. T. Richter, C. C. Davidson, and M. C. Dietze (2013), Facilitating feedbacks between field measurements and ecosystem models, *Ecol. Monogr.*, *83*(2), 133–154.

Leuning, R. (1995), A critical appraisal of a combined stomatal-photosynthesis model for C3 plants, *Plant, Cell Environ.*, *18*(4), 339–355, doi:10.1111/j.1365-3040.1995.tb00370.x.

Lines, E. R., D. a Coomes, and D. W. Purves (2010), Influences of forest structure, climate and species composition on tree mortality across the eastern US., *PLoS One*, *5*(10), e13212, doi:10.1371/journal.pone.0013212.

Luo, Y., and H. Y. H. Chen (2011), Competition, species interaction and ageing control tree mortality in boreal forests, *J. Ecol.*, *99*(6), 1470–1480, doi:10.1111/j.1365-2745.2011.01882.x.

Luyssaert, S., et al. (2007), CO_2 balance of boreal, temperate, and tropical forests derived from a global database, *Glob. Chang. Biol.*, *13*(12), 2509–2537, doi:10.1111/j.1365-2486.2007.01439.x.

Martin, M., and J. Aber (1997), High spectral resolution remote sensing of forest canopy lignin, nitrogen, and ecosystem processes, *Ecol. Appl.*, *7*(2), 431–443, doi:10.1890/1051-0761(1997)007%5B0431:HSRRSO%5D2.0.CO.

McDowell, N. G. (2011), Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality., *Plant Physiol.*, *155*(3), 1051–1059, doi:10.1104/pp.110.170704.

McDowell, N. G., and S. Sevanto (2010), The mechanisms of carbon starvation: how, when, or does it even occur at all?, *New Phytol.*, *186*(2), 264–266, doi:10.1111/j.1469-8137.2010.03232.x.

McMahon, S. M., M. C. Dietze, M. H. Hersh, E. V. Moran, and J. S. Clark (2009), A predictive framework to understand forest responses to global change, *Year Ecol. Conserv. Biol.*, *1162*, 221–236, doi:10.1111/j.1749-6632.2009.04495.x.

Medlyn, B., A. Robinson, R. Clement, and R. E. McMurtie (2005), On the validation of models of forest CO_2 exchange using eddy covariance data: some perils and pitfalls, *Tree Physiol.*, *25*, 839–857. [online] Available from: http://treephys.oxfordjournals.org/content/25/7/839.short (Accessed 22 August 2013).

Medvigy, D. M., S. C. Wofsy, J. W. Munger, D. Y. Hollinger, and P. R. Moorcroft (2009), Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2, *J. Geophys. Res.*, *114*, G01002, doi:10.1029/2008JG000812.

Messinger, F., G. Dimego, E. Kalnay, K. Mitchell, and P. C. Shafran. (2006), North American Regional Reanalysis, *Bull. Am. Meteorol. Soc.*, *87*, 343.

Moorcroft, P. R., G. C. Hurtt, and S. W. Pacala (2001), A method for scaling vegetation dynamics: The Ecosystem Demography model (ED), *Ecol. Monogr.*, *71*(4), 557–586, doi:10.1890/0012-9615(2001)071[0557:AMFSVD]2.0.CO;2.

Oren, R., J. S. Sperry, G. G. Katul, D. E. Pataki, B. E. Ewers, N. Phillips, and K. V. R. Schäfer (1999), Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit, *Plant Cell Environ.*, *22*, 1515–1526.

Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander Jr, R. K. Kobe, and E. Ribbens (1996), Forest models defined by field measurements: Estimation, error analysis and dynamics, *Ecol. Monogr.*, *66*(1), 1–43.

Penning de Vries, F., A. Brunsting, and H. Van Laar (1974), Products, requirements and efficiency of biosynthesis: A quantitative approach, *J. Theor. Biol.*, *45*, 339–377.

Sala, A., F. Piper, and G. Hoch (2010), Physiological mechanisms of drought-induced tree mortality are far from being resolved., *New Phytol.*, *186*(2), 274–81, doi:10.1111/j.1469-8137.2009.03167.x.

Saltelli, A., M. Ratto, T. Andres, F. Campolongo, J. Cariboni, D. Gatelli, M. Saisana, and S. Tarantola (2008), *Global Sensitivity Analysis. The Primer*, 1st ed., John Wiley ,West Sussex, England.

Schroeder, J., J. Kwak, and G. Allen (2001), Guard cell abscisic acid signalling and engineering drought hardiness in plants, *Nature*, *410*, 327–330. [online] Available from: http://www.nature.com/nature/journal/v410/n6826/abs/410327a0.html (Accessed 21 May 2013).

Schwalm, C. R., et al. (2010), A model-data intercomparison of CO_2 exchange across North America: Results from the North American Carbon Program site synthesis, *J. Geophys. Res.*, *115*, doi:10.1029/2009JG001229.

Scurlock, J., W. Cramer, R. Olson, W. J. Parton, and S. Prince (1999), Terrestrial NPP: Toward a consistent data set for global model evaluation, *Ecol. Appl.*, *9*(3), 913–919, doi:10.1890/1051-0761(1999)009%5B0913:TNTACD%5D2.0.CO.

Serbin, S. P., D. N. Dillaway, E. L. Kruger, and P. a Townsend (2012), Leaf optical properties reflect variation in photosynthetic metabolism and its sensitivity to temperature., *J. Exp. Bot.*, *63*(1), 489–502, doi:10.1093/jxb/err294.

Sperry, J. (2011), Hydraulics of vascular water transport, in *Mechanical Integration of Plant Cells and Plants*, pp. 303–327, Springer Berlin Heidelberg, doi:10.1007/978-3-642-19091-9_12.

Thornley, J. (2000), Modelling the components of plant respiration: Representation and realism, *Ann. Bot.*, *85*(1), 55–67, doi:10.1006/anbo.1999.0997.

Thornton, P. E., et al. (2002), Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests, *Agric. For. Meteorol.*, *113*(1-4), 185–222. [online] Available from: http://linkinghub.elsevier.com/retrieve/pii/S0168192302001089.

Townsend, P., J. R. Foster, R. A. C. Jr, and W. S. Currie (2003), Application of imaging spectroscopy to mapping canopy nitrogen in the forests of the central Appalachian Mountains using Hyperion and AVIRIS, *IEEE Trans. Geosci. Remote Sens. Remote Sens.*, *41*(6), 1347–1354.

Ustin, S. L., a. a. Gitelson, S. Jacquemoud, M. Schaepman, G. P. Asner, J. a. Gamon, and P. Zarco-Tejada (2009), Retrieval of foliar information about plant pigment systems from high resolution spectroscopy, *Remote Sens. Environ.*, *113*, S67–S77, doi:10.1016/j.rse.2008.10.019.

Van Mantgem, P. J., et al. (2009), Widespread increase of tree mortality rates in the western United States., *Science,323*(5913), 521–524, doi:10.1126/science.1165000.

Walko, R. L., et al. (2000), Coupled atmosphere–biophysics–hydrology models for environmental modeling, *J. Appl. Meteorol.*, *39*(6), 931–944, doi:10.1175/1520-0450(2000)039<0931:CABHMF>2.0.CO;2.

Wang, D., D. S. Lebauer, and M. C. Dietze (2013), Predicted yields of short-rotation hybrid poplar (*Populus* spp.) for the contiguous US., *Ecol. Appl.*, *23*, 944–958.

White, M. a., P. E. Thornton, S. W. Running, and R. R. Nemani (2000), Parameterization and sensitivity analysis of the BIOME–BGC terrestrial ecosystem model: Net primary production controls, *Earth Interact.*, *4*(3), 1–85, doi:10.1175/1087-3562(2000)004<0003:PASAOT>2.0.CO;2.

Xu, T., L. White, D. Hui, and Y. Luo (2006), Probabilistic inversion of a terrestrial ecosystem model: Analysis of uncertainty in parameter estimation and model prediction, *Global Biogeochem. Cycles*, *20*, GB2007, doi:10.1029/2005GB002468.

Zaehle, S., S. Sitch, B. Smith, and F. Hatterman (2005), Effects of parameter uncertainties on the modeling of terrestrial biosphere dynamics, *Global Biogeochem. Cycles*, *19*, GB3020, doi:10.1029/2004GB002395.