

forest ecology

Quantifying Uncertainty in Forest Nutrient Budgets

Ruth D. Yanai, Carrie R. Levine, Mark B. Green, and John L. Campbell

Nutrient budgets for forested ecosystems have rarely included error analysis, in spite of the importance of uncertainty to interpretation and extrapolation of the results. Uncertainty derives from natural spatial and temporal variation and also from knowledge uncertainty in measurement and models. For example, when estimating forest biomass, researchers commonly report sampling uncertainty but rarely propagate the uncertainty in the allometric equations used to estimate tree biomass, much less the uncertainty in the selection of which allometric equations to use. Change over time may have less uncertainty than a single measurement, if the measures are consistently biased, as by the use of inaccurate allometric equations or soil sampling techniques. Quantifying uncertainty is not as difficult as is sometimes believed. Here, we describe recent progress in quantifying uncertainty in biomass, soils, and hydrologic inputs and outputs, using examples from the Hubbard Brook Experimental Forest, New Hampshire, USA.

Keywords: allometry, soil, input-output, Hubbard Brook Experimental Forest

Ecosystem nutrient cycling is a relatively new field of scientific inquiry, compared to botany, soil science, or silviculture. In the 1960s, Ovington (1962) proposed the woodland ecosystem concept, and the International Biosphere Project (1964–1974) initiated the development of allometric equations to describe forest biomass and nutrient content (Aber and Melillo 1991). At the Hubbard Brook Experimental Forest in New Hampshire, where the USDA Forest Service was monitoring precipitation and stream discharge in small headwater catchments, Herb Bormann had the idea of measuring the nutrient concentrations of

precipitation and stream water, and thereby constructing a budget for ecosystem inputs and outputs of nutrients (Bormann and Likens 1967).

Forests pose special problems when it comes to constructing ecosystem budgets. In ecosystems of smaller physical stature, such as grasslands, plots can be harvested and the biomass weighed and sampled for nutrient analysis. For a forest ecosystem, it is possible, but not usually desirable, to estimate the biomass and nutrient content by harvesting (Arthur et al. 2001). More commonly, forest biomass is estimated through the use of allometric equations relating biomass to nonde-

structive measurements such as height and diameter (Jenkins et al. 2004). Estimating the nutrient content of forest biomass requires allometric estimates by tissue type because the nutrient concentrations of wood, leaves, and bark vary widely. Species differ in their allometry and also in nutrient concentrations, such that mixed-species stands require dozens of parameters to describe the biomass and nutrient concentrations of the tissue types of each of the most prevalent species (e.g., Whittaker et al. 1979).

Do Forest Nutrient Budgets Have No Error?

In the 1960s, when biomass equations were being developed and used for the first generation of ecosystem budgets, there was no attempt made to provide confidence limits with the estimates. The publication describing the biomass equations developed at Hubbard Brook in 1965 was no exception. The authors wrote, “The problem of confidence limits for treatment of forest samples by logarithmic regression is unsolved” (Whittaker et al. 1974, p. 241). It was not true that the uncertainty associated with regression was unknown to statisticians

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Affiliations: Ruth D. Yanai (rdyanai@syr.edu), Department of Forest and Natural Resources Management, SUNY College of Environmental Science and Forestry, 106 Marshall Hall, 1 Forestry Drive, Syracuse, NY, 13210. Carrie R. Levine (crlevine@berkeley.edu), Department of Environmental Science, Policy and Management, University of California at Berkeley, 137 Mulford Hall, Berkeley, CA 94720. Mark B. Green (mgreen@plymouth.edu), Center for the Environment, MSC 63, Plymouth State University, 17 High Street, Plymouth, NH 03264 and Northern Research Station, USDA Forest Service, 271 Mast Road, Durham, NH 03824. John L. Campbell (jlcampbell@fs.fed.us), Northern Research Station, USDA Forest Service, 271 Mast Road, Durham, NH 03824.

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Measurement Uncertainty



DBH measurement: 0.02%

Sampling Uncertainty

Spatial and Temporal Variability



5 plots: 13%

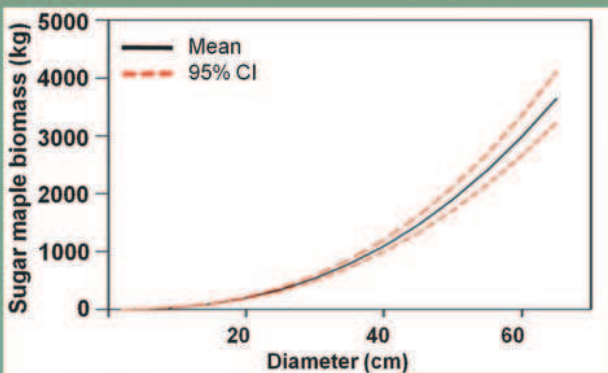
15 plots: 6%

30 plots: 3%

N concentration:
3%

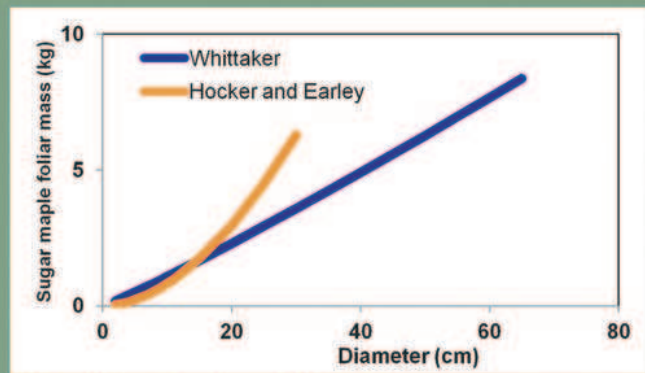
Model Uncertainty

Error within models



Allometric equations: 5%

Error between models



Model selection: 20-40%

Figure 1. Sources of uncertainty in nutrient content of forest biomass. The estimates of measurement uncertainty, sampling uncertainty, and error within models are from Hubbard Brook (Yanai et al. 2010). Uncertainty in the N concentration of tissues is due to analytical uncertainty, which is a type of measurement error, as well as to variation among the trees sampled, which is due to natural variation. Magnitudes of uncertainty are shown as the coefficient of variation.

(Snedecor 1956), but to make use of this information was beyond the computing capabilities available to most scientists at that time.

Without confidence in these estimates, or rather, without a quantitative evaluation of uncertainty in the estimates, how is it possible to compare one measurement to another? In the first nitrogen budget published for Hubbard Brook (Bormann et al. 1977), sources of N ($6.5 \text{ kg ha}^{-1} \text{ yr}^{-1}$ in precipitation) were compared to sinks for N ($9.0 \text{ kg ha}^{-1} \text{ yr}^{-1}$ in forest growth, 7.7 in forest floor accumulation, and 4.0 in streamwater outputs), and the difference, a shortfall of $14.2 \text{ kg ha}^{-1} \text{ yr}^{-1}$, was attributed to N fixation. But each of these sources and sinks has uncertainty, and the assumption that the mineral soil was neither a source nor a sink also has uncertainty.

It has been 35 years since the publication of that budget, and we don't yet have an answer as to the uncertainty in the budget closure, which requires estimating the uncertainty in all the sources and sinks for N, including biomass, soils, and gaseous and dissolved inputs and outputs of nutrients.

To our knowledge, there has yet to be a complete uncertainty analysis published for any forest nutrient budget. Gradually, researchers are developing approaches to quantifying uncertainty in ecosystem studies.

In this paper, we illustrate current approaches to uncertainty analysis, using the

Management and Policy Implications

The pools and fluxes of nutrients and other elements in forested ecosystems can be difficult to measure and have commonly been reported without any indication of uncertainty in the results. Now forest ecosystem scientists are developing methods for describing the uncertainty in ecosystem budgets. Confidence intervals are important to determining the significance of findings, for example when reporting change over time or differences following treatments. Identifying the most important sources of uncertainty allows research and measurements to be focused where the need for information is greatest. Environmental monitoring plans should be designed to best collect the information necessary to meet management and policy goals.

example of the N budget for the Hubbard Brook Experimental Forest in New Hampshire, USA. These examples have been developed through the efforts of a research network called QUEST (Quantifying Uncertainty in Ecosystem Studies). The aim of QUEST is to promote the use of uncertainty analysis, provide guidance to researchers interested in uncertainty analysis, and support both developers and users of uncertainty analyses. QUEST has a website (www.quantifyinguncertainty.org) with news feed, relevant papers, and examples of code in SAS, R, STATA, and Excel.

Sources of Uncertainty

In general, it is helpful to distinguish categories of sources of uncertainty, some of which arise from imperfect knowledge (measurement uncertainty, model selection) and some from inherent variability in the system studied (sampling uncertainty in space and time) (Harmon et al. 2007). In the case of the nutrient content of forest biomass, for example (Figure 1), measurement uncertainty would include the uncertainty in tree inventory (McRoberts et al. 1994) and in the laboratory analysis of nutrient concentrations (e.g., Buso et al. 2000). The allometric models used to predict biomass as a function of tree diameter have uncertainty in the regression (Yanai et al. 2010), and choosing which set of allometric equations to use introduces even greater uncertainty (Melson et al. 2011). Model uncertainty could be tested by harvesting (Arthur et al. 2001) and reduced by sampling greater numbers of trees. In contrast, natural variability in space cannot be reduced by more intensive sampling, although more sampling allows this variation to be better described.

Uncertainty in Biomass Estimates—Our First Success

Estimating uncertainty in the nutrient contents of forest biomass is daunting because of the complexity of the calculations. In the case of the Hubbard Brook budget for Watershed 6 (W6) in 1965, there were 3987 trees in the inventory, biomass equations for five tree species and five tissue types (Whittaker et al. 1974) and tissue chemistry for six tree species and seven tissue types (Likens and Bormann 1970). Fortunately, because both the biomass equations and the tissue chemistry are based on multiple trees, there is a clear basis for describing the uncertainty in all the equations and parameters in the

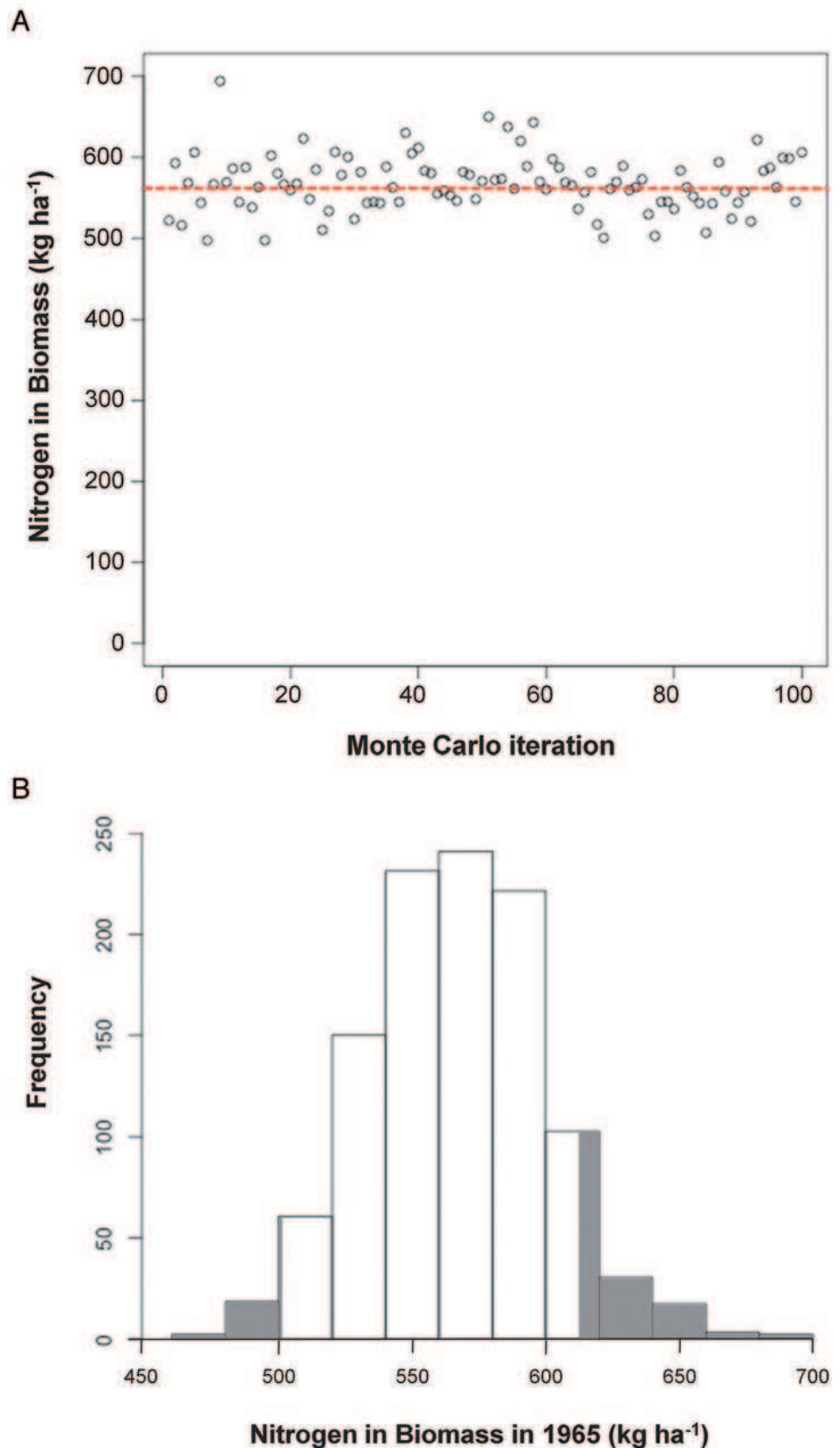


Figure 2. Uncertainty in the N contents of biomass at the Hubbard Brook Experimental Forest, reflecting both uncertainty in allometric equations and in tissue N concentrations. **A.** Monte Carlo results of N in biomass in 1965 for 100 iterations. **B.** Frequency distribution of 1000 iterations of N in biomass in 1965, showing the 95% confidence interval in white (from 562 to 671 kg N/ha).

calculation. This uncertainty can be propagated through thousands of calculations without challenging the capacity of modern desktop computers.

We used a Monte Carlo approach, in which the entire calculation of biomass was repeated many times, using random sampling of the biomass and nutrient concentrations of tissue types, by species, using the statistical distribution of the sampled trees. Figure 2A shows the results of 100 such calculations applied to stand inventory from W6 in 1965. The distribution of 1000 such results was analyzed to describe the uncertainty in the calculations: the mean was 566 kg N ha⁻¹, close to that reported by Bormann et al. (1977) (their value was 532 kg N ha⁻¹, which did not include standing dead biomass), and the uncertainty, which has never before been estimated, showed a 95% confidence interval ranging from 502 to 636 kg N ha⁻¹ (Figure 2B).

One reason that this type of result is rarely reported is that although the uncertainty in regression is well defined, the statistics needed to calculate it have not traditionally been reported with regression results. The standard error of the estimate (based on the sum of squared deviations of the dependent variable) is commonly reported, but not the mean of the independent variables (tree diameter, in this case) or the sum of squared deviations of the independent variable from the mean. These latter two statistics are important because the uncertainty of the prediction increases for observations farther from the mean of the sampled population. In the case of forest biomass, this means that uncertainty in very large trees (larger than those on which the allometric equations were derived) can be large (Figure 3), which is important if they represent a large fraction of the total biomass.

Thus, although estimating uncertainty in forest biomass should be straightforward, it is often not possible to implement from the information available. Some researchers (Chave et al. 2004, Fahey et al. 2005, Harmon et al. 2007) have used the standard error of the estimate (Equation 4 in Yanai et al. 2010). However, this approach gives an uncertainty about double that of the uncertainty in the regression prediction (Equation 5 in Yanai et al. 2010), for the trees in our survey.

Another issue that causes confusion in uncertainty analysis of forest biomass is

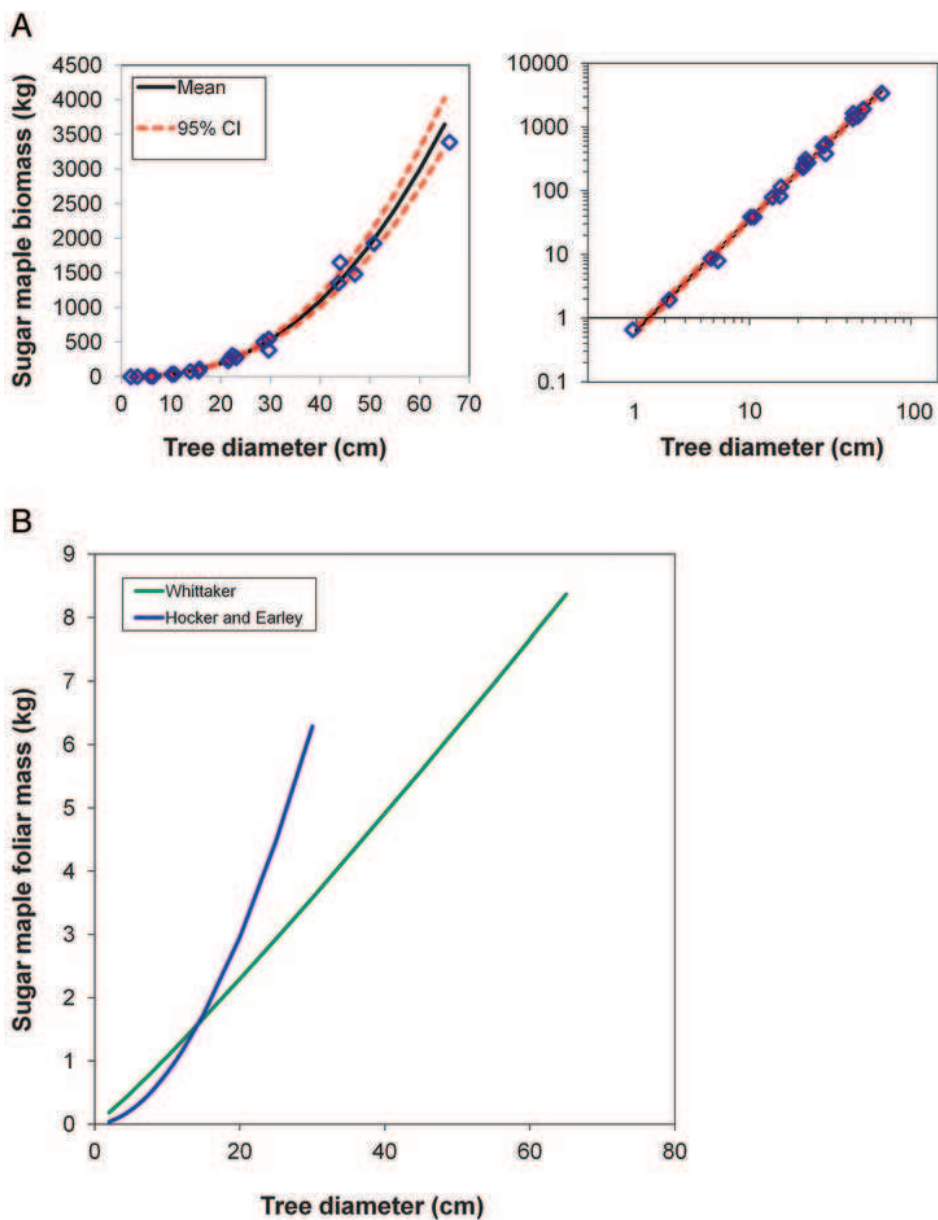


Figure 3. Uncertainty in biomass equations. A. Uncertainty in the equation describing sugar maple biomass as a function of tree diameter (Whittaker et al. 1974). The first graph shows the observations in the original units; the second graph shows the log-transformed data to which the equation was fit. B. Comparison of two different models describing foliar biomass of sugar maple from tree diameter (Whittaker et al. 1974, Hocker and Early 1983).

whether to use the uncertainty in individual estimates (described by the SD in the case of an univariate distribution such as N concentration) or the uncertainty in the population mean (the standard error, for N concentration). When describing the population of trees in an ecosystem, or calculating mass per unit area, the standard error, or the analogous measure of uncertainty in regression, is the appropriate distribution to sample in a Monte Carlo simulation. The uncertainty in the mean represents the possibility of bias in the estimate. It is important that each random sample of the biomass estimates and N

concentrations be applied to all the trees in the inventory. The random sampling should not apply individually to each tree in the inventory, as these errors would cancel out, half being positive and half being negative. With an infinite number of trees, applying the uncertainty to each tree would result in zero error. Clearly this is incorrect: our allometric equations were based on 14–15 trees of each species, and they do not become more perfect estimates of the population mean when they are applied to greater numbers of trees.

For errors that pertain independently

to individuals, it is appropriate to apply a random sample of the error to each tree. This is the case with the measurement error in diameter. We included measurement error in tree diameter in an earlier Monte Carlo analysis and found it to amount to only 0.0002 of the biomass or N content estimate (0.02%, Yanai et al. 2010). To identify the sources of uncertainty and how they contribute to an estimate, it is helpful to step through the methods used and consider whether a measurement or model error applies to an individual measurement or to the entire population (Harmon et al. 2007).

There are also other sources of uncertainty not captured by propagating the errors in the biomass equations and nutrient concentrations. In the Hubbard Brook example, there are species that were not described by Whittaker, which are estimated using equations for other species or from other sites. This is an example of model selection error, which can be very large. For five tree species in northwestern Oregon, models differed by 20–40% in estimates of forest biomass (Melson et al. 2011). In New Hampshire northern hardwoods, two sets of allometric models differed by up to 72% for a particular species, but these differences cancelled out at the stand level (Fatemi et al. 2011). Applying multiple models can indicate the possible magnitude of model selection uncertainty.

Sampling error is important in most estimates of uncertainty in forest inventory. In the case of Hubbard Brook W6 tree inventories (every 5 years since 1977), all trees >10 cm diameter at breast height (dbh) are measured, and sampling is not a source of uncertainty. We simulated sampling uncertainty by selecting plots (25 m × 25 m) at random (stratified by elevation) from the 208 plots in the 2002 survey, without including uncertainty in the allometric equations (Figure 4). To estimate the mean within 10% with 95% confidence would require ten plots, on average; 32 plots would give an estimate within 5% of the mean (Figure 5). However, increasing the number of plots cannot make the estimate more accurate than the uncertainty in the allometric estimates of N content, which was 566 ± 67 kg ha⁻¹, or ± 12% of the mean (Figure 2).

Uncertainty in Biomass Accumulation—Inaccuracies Cancel Out

The analysis above describes uncertainty in the amount of N in forest biomass. For many purposes, the change in a nutrient

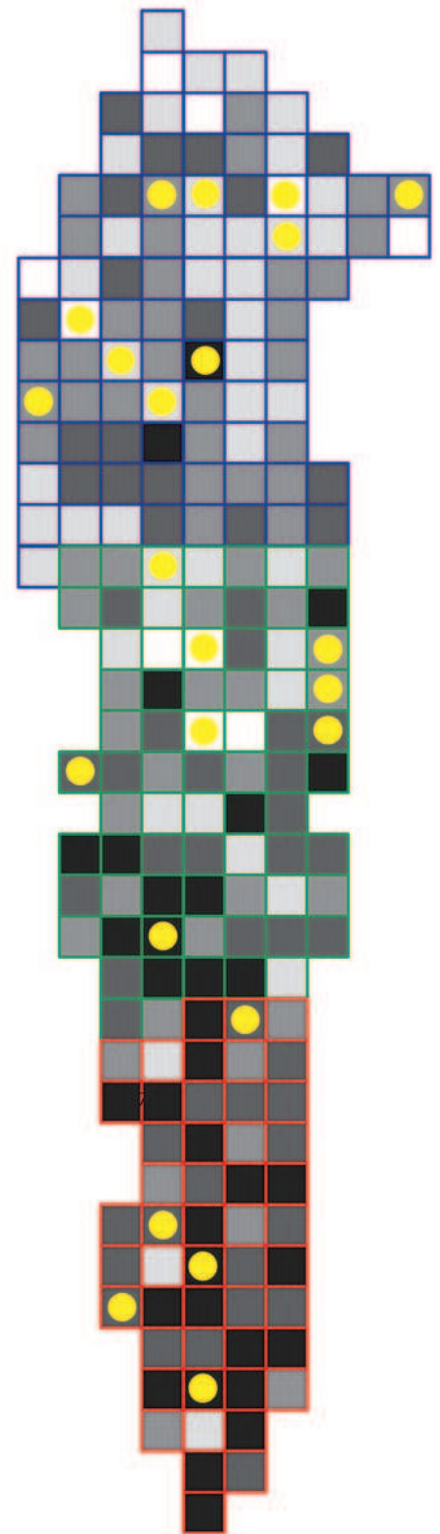
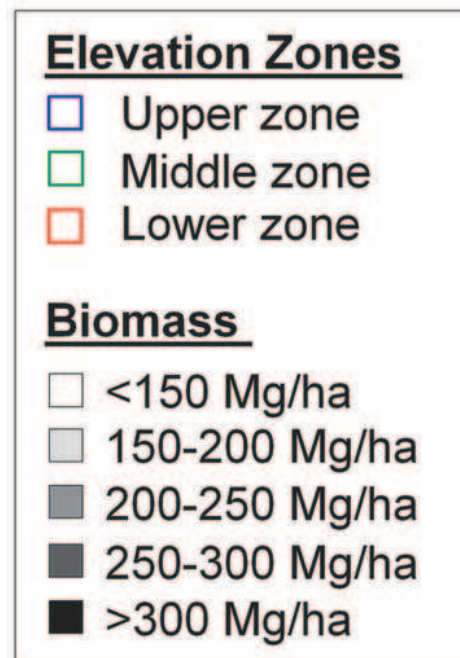


Figure 4. Map of Hubbard Brook Watershed 6 divided into 208 plots; biomass for each plot is from 2002. Yellow circles indicate a random sample of 20% of the plots, stratified by elevation zone.

pool is more important than the size of the pool. This is the case for balancing an ecosystem budget, in which sinks and sources of a nutrient are compared. Similarly, for global carbon budgets, it is more important to know the sink or source

strength of the biomass than to know the size of carbon pools that are not changing.

At Hubbard Brook, the reference W6 has been measured every 5 years since 1977 (Siccama et al. 2007). Figure 6A shows the results of 100 Monte Carlo estimates for the

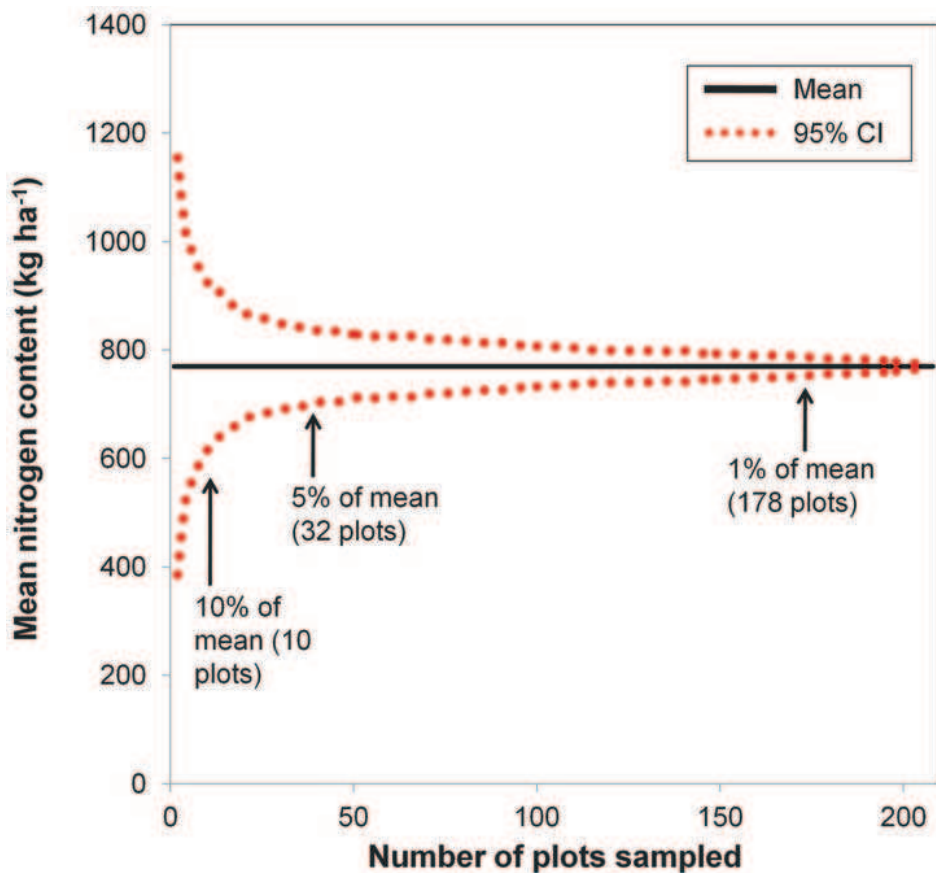


Figure 5. Uncertainty in estimates of N content for Hubbard Brook W6 in 2002 as a function of the number of plots sampled. Estimates are based on 500 random samples of the number of plots indicated, stratified by elevation as shown in Figure 4.

1982 and 1987 inventory of W6, with the uncertainty in allometry and N concentrations sampled simultaneously for the two sampling dates at each iteration. Note that although the distributions of the two samples overlap, the 1987 value is without exception higher than the corresponding 1982 value from the same iteration of the Monte Carlo. The uncertainty in the difference over the 5-yr time interval is ± 13 kg N ha⁻¹, Figure 6B. For budgeting N fluxes in the ecosystem, the rate of N accumulation in biomass has an uncertainty of $\pm 0.6 - 4.7$ kg N ha⁻¹ yr⁻¹ (for all combinations of time intervals, data not shown).

This is another important point in Monte Carlo sampling for uncertainty analysis. Because an error in the allometry or N concentrations represents a bias in the calculation, the uncertainty in the difference over time (± 13 kg N ha⁻¹, Figure 6B) is much less than the uncertainty in the mean at one point in time (± 67 kg N ha⁻¹, Figure 2B). The same is true for biomass or carbon accumulation: uncertainty in the pool size due

to bias in the estimate can be large compared to the uncertainty in change over time.

Change over time in the N concentration of tissues is another possible source of error in ecosystem budgets. In leaves of the major species, which have been sampled annually since 1992 near W6 (Fahey 2004), N concentrations differ by up to 12% from the concentrations reported from 1965 (Likens and Bormann 1970), depending on the species. Leaves make up 9% of the total N budget. Tissues comprising greater portions of the N budget, namely roots (36%), branches (28%), and wood (17%), are more difficult to sample than leaves, and they are not routinely monitored. However, this source of uncertainty is not likely to be large compared to the other fluxes in the ecosystem. To account for a missing source of 14.2 kg ha⁻¹ yr⁻¹, the concentrations of N in the biomass would have had to decline by 28%, weighted across all tissue types, from 1965–1977, the period for which the missing source was estimated, which seems unlikely. There are greater uncertainties in

other parts of the budget, such as the change in soil N content.

Uncertainty in Soils

Forest soils are notoriously heterogeneous, with both horizontal and vertical spatial variation contributing uncertainty to most sampling approaches. The most accurate method for estimating nutrient pools in soils is probably the quantitative soil pit (Vadeboncoeur et al. 2012), but estimates at the stand level are not very precise if the number of pits is small, each pit being time-consuming to excavate. More precise estimates can be made for the same investment in effort by taking a greater number of soil cores, but coring is inaccurate in rocky soils (Levine et al. 2012).

Soil N storage has been evaluated at Hubbard Brook in W5, beginning in 1983, prior to the whole-tree clearcut of the watershed. The excavation of 59 quantitative soil pits in W5, a monumental effort, allowed the quantification of soil mass, rock volume, and nutrient content across the 23-ha watershed; the N content of the mineral soil was estimated at 5900 ± 370 kg ha⁻¹ (Huntington et al. 1988). Thus a change over time of 730 kg ha⁻¹ (1.96 times the s.e.) would be detectable at 95% confidence, which means that a budget error of 14.2 kg ha⁻¹ yr⁻¹ would be measurable as a change in the mineral soil only after about 50 years of observation. In rereasuring soils in W5, pits were excavated at points that were selected in advance to be as similar as possible and located ~ 6 m apart. From 1983 to 1991, 8 years postharvest, there was a nonsignificant decline of 500 kg N ha⁻¹ ($P = 0.33$) (Johnson 1995). Assuming zero change in the absence of harvesting may be justified, but a zero with a large uncertainty.

Again, we are more often interested in changes in soil storage of C and nutrients than in the total stores. A large fraction of soil stores is not very dynamic, and those portions that do not respond to management, disturbance, climate change, etc., are not relevant to change over time. If it were possible to repeatedly sample soils at the same point, nondestructively, then the spatial variability in forest soils would not be such a handicap to detecting change over time (Wielopolski et al. 2010).

The forest floor is easier than the mineral soil to sample repeatedly (Yanai et al. 2003). At Hubbard Brook, forest floors have been sampled consistently at a 5-yr interval since 1977, allowing the rate of change over

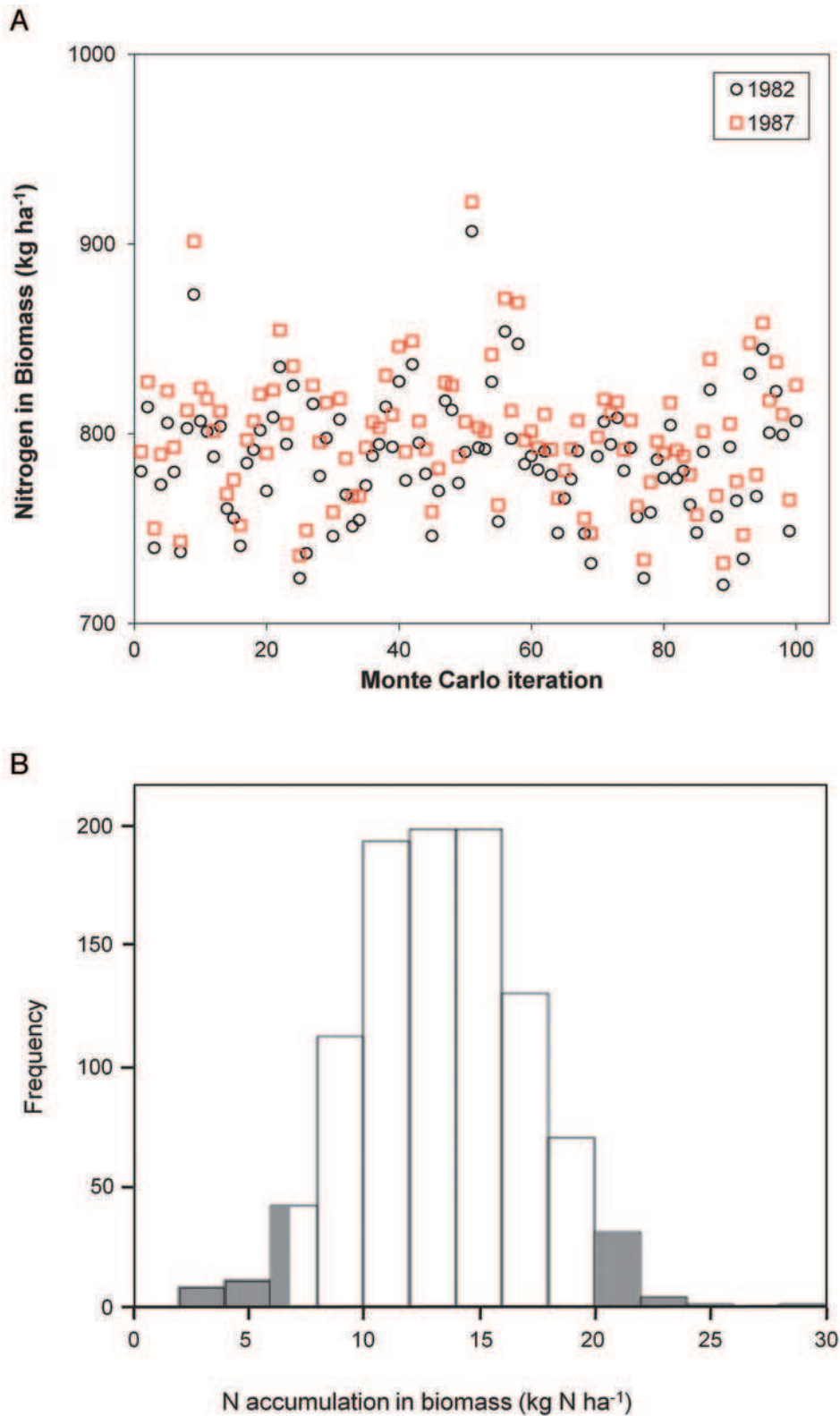


Figure 6. Uncertainty in the change in N contents of biomass at the Hubbard Brook Experimental Forest over a 5-year period. **A.** Monte Carlo results of N in biomass in 1997 and 2002, 100 iterations. **B.** Frequency distribution of 1000 iterations of the difference between 1997 and 2002, showing the 95% confidence interval in white (from 14 to 24 $\text{kg ha}^{-1} \text{yr}^{-1}$).

time to be described by linear regression, with associated uncertainty. Unfortunately, even with 59–87 samples at each collection

date, the variation is so high that the 95% confidence interval on the slope for the change in forest floor mass from 1976 to

1997 was $1.66 \text{ Mg ha}^{-1} \text{yr}^{-1}$, with a nonsignificant decline of $0.8 \text{ Mg ha}^{-1} \text{yr}^{-1}$ ($P = 0.61$; data from Yanai et al. 1999). Assuming an N concentration of 1.5% (Johnson 1995), this represents a change in N content of $-11 \pm 21 \text{ kg N ha}^{-1} \text{yr}^{-1}$. Although the estimated rate of change is not statistically significant, the uncertainty is important to our confidence in ecosystem budgets, and contributes to the difficulty of quantifying a budget closure error.

Closing the Budget

The most difficult and as yet unattained goal of uncertainty analysis in ecosystem studies is to determine the uncertainty in budget closure, such as the $14.2 \text{ kg ha}^{-1} \text{yr}^{-1}$ of missing N in the 1965 budget for Hubbard Brook. This requires estimating uncertainty not only in changes in the pools of N internal to the ecosystem, such as the living biomass, forest floor, and mineral soil, but also the inputs of N to the system in precipitation, the outputs in stream water, and gaseous exchange with the atmosphere.

Stream water export of nutrients is difficult to characterize because of high variability over time in both discharge and concentration. Although stream discharge is measured continuously, and has been since the advent of chart recorders, stream nutrient concentrations have conventionally been sampled at frequencies of weekly or less (Likens et al. 2002). Recently, advances in sensor design have enabled more frequent measurement of nutrient concentration (e.g., Pellerin et al. 2009). High-frequency concentration data can be subsampled to generate lower frequency data to identify the relationship of uncertainty to sampling effort (Stelzer and Likens 2006, Birgand et al. 2010).

Traditional methods for calculating solute fluxes include assuming constant concentrations between measurements, interpolating linearly between measurements, and using correlations with variables such as discharge to predict chemical concentrations. The model selected is known to affect flux estimates (Johnes 2007, Birgand et al. 2010, Wang et al. 2011), and is thus a source of uncertainty. We are currently conducting a comparison of models applied to multiple solutes at multiple sites, including a more advanced composite approach to interpolation of solute concentration (Aulenbach and Hooper 2006; Figure 7).

Other sources of uncertainty in stream export of nutrients include analytical uncer-

Measurement Uncertainty



Water chemistry:
0-3%

Stage height:
1%

Gap filling:
1%

Sampling Uncertainty

Spatial and Temporal Variability

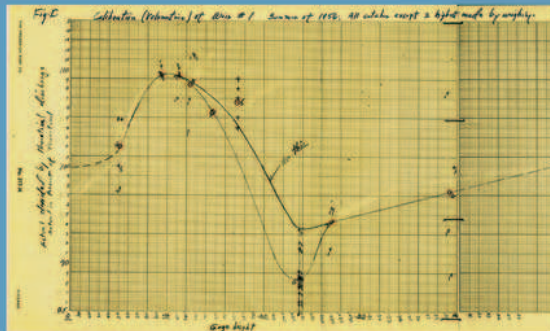


Across streams:
3-9%

Across years:
23%

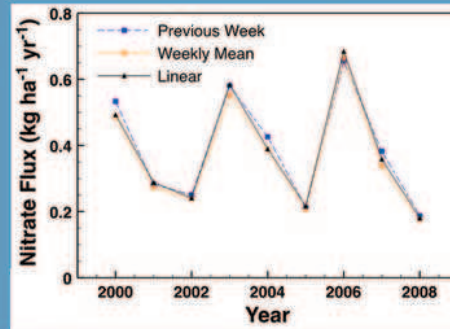
Model Uncertainty

Error within models



Height-discharge calibration: 0.1-2%

Error between models



Model selection: 1-2%

Figure 7. Sources of uncertainty in stream export of nutrients, illustrated with values for streams at the Hubbard Brook Experimental Forest, except for uncertainty due to gaps of 1–2 weeks in stream discharge at Gomadanzan, Japan (Tokuchi, Fukushima, and Matsuzaki, per comm.). Uncertainty in stage height is the effect on annual flux of the uncertainty in weekly readings. Sampling uncertainty describes the range in runoff variability for 2000–2009. The height-discharge relationship is calibrated only at low flow; uncertainty at high flows may be very large. Model selection error is for the long-term average export of calcium and nitrate.

tainty in the laboratory, discharge uncertainty, and uncertainty in delineating the watershed boundary (Figure 7). The most important source may be the uncertainty in discharge at high flows; discharge is often more variable than streamwater concentration (e.g., Godsey et al. 2009).

In contrast to stream export, which has uncertainty due to temporal variation, uncertainty in atmospheric deposition is primarily due to spatial variation (Weathers et al. 2006). Precipitation amounts are measured at short intervals (15 minute steps or shorter) or are cumulative, giving good estimates of rainfall amounts at a point. The chemistry of precipitation is also commonly measured on an accumulated sample and is thus representative of the entire time inter-

val (Martin et al. 2000). The uncertainty in a point estimate of elemental deposition may thus be quite low, reflecting the instrumental and analytical uncertainty rather than sampling uncertainty.

Spatial variability in precipitation, however, introduces uncertainty in interpolation between precipitation stations. Various methods of interpolation are used in precipitation and atmospheric deposition studies (Weathers et al. 2006, Garcia et al. 2008), such that model selection is a source of uncertainty. We compared several interpolation methods (Thiessen polygon, spline, inverse distance weighting, kriging, and regression modeling) and found differences of less than 1% across the methods for annual precipitation of the nine watersheds at Hub-

bard Brook (data not shown). Additional challenges to be addressed in estimates of atmospheric inputs are associated with the difficulty of monitoring dry deposition and cloud deposition and their interaction with vegetation structure.

Finally, for nitrogen, gaseous fluxes could be important in balancing the ecosystem nutrient budget. The imbalance in the 1965 N budget sparked interest in quantifying N fixation (Roskoski 1980); currently, the N budget closure suggests a missing sink, not a missing source, and researchers are measuring denitrification. These gaseous fluxes are difficult to estimate, both because of measurement challenges and because of high spatial and temporal variability (Groffman et al. 2009).

The pursuit of closure in nutrient budgets can provide insight about ecosystem processes and also suggest where more research is needed.

Value of Uncertainty Analysis to Improve Scientific Knowledge

Uncertainty analysis can identify opportunities for reducing uncertainty by better allocation of sampling resources. For example, in the case of the N content of forest biomass, uncertainty analysis shows which of the allometric equations are most important to improve, based on their contribution to the overall uncertainty. Individual equations, such as that for bark biomass, may be highly uncertain but not contribute as much to overall uncertainty as an equation with lower uncertainty that describes a more massive ecosystem component, such as wood biomass (Yanai et al. 2010). In the Hubbard Brook allometric equations, the tissues that contribute the greatest uncertainty to the N content of biomass are the branches, because they have both high uncertainty in the biomass equation and high N content (Yanai et al. 2010). An optimized sampling design for describing tree allometry might therefore involve greater numbers of trees to describe branch biomass and fewer to describe bark biomass. Simulating sampling designs of varying sampling intensity (e.g., Figure 5) is another approach to evaluating the efficiency of forest measurements.

There are many sampling designs in place that do not optimally allocate resources, and the framework of uncertainty analysis can provide a basis for rational discussion of alternative designs. For example, we can evaluate whether monitoring programs would benefit more by improving characterization of spatial versus temporal variation, as in the case of seasonal sampling of lakes and streams. For forest soils, detecting change over time is limited by extreme spatial variability, making it attractive to allocate resources to methods development. Uncertainty analysis has the potential to improve the efficiency of information gained given the resources expended, for all kinds of sampling designs.

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