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Sampling effort and uncertainty in leaf litterfall mass and nutrient flux in northern hardwood forests

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Abstract.   Designs for litterfall sampling can be improved by understanding the sources of uncertainty in litterfall mass and nutrient concentration. We compared the coefficient of variation of leaf litterfall mass and nutrient concentrations (nitrogen, phosphorus, calcium, magnesium, and potassium) at different spatial scales and across years for six northern hardwood species from 23 stands in the White Mountains of New Hampshire, USA. Stands with steeper slopes ($P = 0.01$), higher elevations ($P = 0.05$), and more westerly aspect ($P = 0.002$) had higher interannual variation in litter mass, probably due to a litter trap design that allowed litter to blow into traps in windy years. The spatial variation of nutrient concentrations varied more across stands than within stands for all elements ($P < 0.001$). Phosphorus was the most spatially variable of all nutrients across stands ($P < 0.001$). Litter nutrient concentrations varied less from year to year than litter mass, but the magnitude of difference depended on the element and tree species. We compared the relative importance of variation in mass vs. concentration to estimates of nutrient flux by simulating different sampling intensities of one while holding the other constant. In this dataset, interannual variability of leaf litter mass contributed more to uncertainty in litterfall flux calculations than interannual variation in nutrient concentrations. Optimal sampling schemes will depend on the elements of interest and local factors affecting spatial and temporal variability.

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INTRODUCTION

Leaf litterfall is probably the most commonly measured flux in forested ecosystems. It represents a major carbon and nutrient flux, it can indicate productivity and nutrient status, and it is relatively easy to measure. Some uncertainty in litterfall estimates is due to imperfect measurement, such as errors in collection, sample processing, and sample analysis. In addition, litterfall mass and nutrient concentration vary spatially and interannually, which contribute to uncertainty in characterizing average values over space and time. Unlike measurement errors, natural variation cannot be reduced but can be better characterized by improved sampling schemes. Quantifying how these sources of variation contribute to uncertainty in nutrient flux estimates could help guide the design of litterfall sampling systems.

Previous studies of sampling efficiency have focused more on characterizing leaf litter mass than chemistry. Studies of spatial variation in litterfall mass have examined the effect of collector size (McShane et al. 1983, Morrison 1991, Búrquez et al. 1999), design (Búrquez et al. 1999), position (Welbourn et al. 1981, Boerner and Kooser 1989), and number (McShane et al. 1983, Morrison 1991, Búrquez et al. 1999, Finotti et al. 2003, Dellenbaugh et al. 2007). Studies of temporal variation in litterfall mass have addressed seasonal and interannual variability (Gresham 1982, Stocker et al. 1995).

Litterfall nutrient concentrations vary across species (Côté and Fyles 1994, Lovett et al. 2004). Within species, nutrient concentrations can vary with soil chemistry, as reported within a hemlock–hardwood forest stand (Ferrari 1999) and across landscapes in northern hardwoods (Lucash et al. 2012). In an analysis of 13 northern hardwood stands in the White Mountains of New Hampshire, litterfall concentrations of most elements, with the notable exception of nitrogen, varied more across stands than years (Yanai et al. 2012). That study described spatial variability of leaf litter nutrient concentrations across stands but not within them (Yanai et al. 2012). Here, we extend that analysis by adding a second dataset that includes within-stand variation in litterfall nutrients.

We characterized the spatial and interannual variability of litterfall mass and nutrient concentrations in 10 stands from a study of multiple element limitation in northern hardwood ecosystems (MELNHE) and from 13 stands in a chronosequence (CHRONOS) study previously analyzed by Yanai et al. (2012). In addition to characterizing variability in leaf litter mass and nutrient concentrations across space and time, we explored stand-level characteristics that could explain variability in leaf litter mass, such as age, slope, aspect, and elevation. Finally, we simulated various mass and nutrient sampling schemes to describe the relationship between sampling effort and uncertainty, which can guide the design of future studies of litter mass and nutrient fluxes.

METHODS

Site description

We used litterfall data from two studies involving a total of 23 hardwood stands in the White Mountains of central New Hampshire. Litterfall measurements in 13 of these stands began in 1993 in a chronosequence study (CHRONOS) in sites used for earlier ecosystem studies (Federer 1984). Litter measurements in the other 10 stands began in 2004 and 2008 and are part of MELNHE (Fisk et al. 2013). Soils across the study sites are primarily well-drained Spodosols developed in glacial drift (Vadeboncoeur et al. 2014). The climate is humid continental, with temperature averaging 5°C and annual precipitation averaging 1400 mm (Bailey et al. 2003).

Stands differ in age, slope, aspect, elevation (Table 1), and species composition (Table 2). Aspect and slope in the CHRONOS stands were characterized using digital elevation models based on Global Positioning System coordinates (USGS Earth Explorer 2016). In the MELNHE stands, at each litterfall trap aspect was measured using a compass and slope was measured using a hypsometer, and stand-level estimates were calculated as the mean of all measurements. Stand ages were estimated using timber sale records or dendrochronology with the exception of the oldest stands (HBO and JBO), which were likely cut between 1890 and 1910 when much of the region was logged (Thompson et al. 2013).

Litter collection

Litter was collected in traps consisting of plastic laundry baskets. The traps were staked to position them slightly above the forest floor to allow water to drain through holes drilled in the bottoms of the baskets. Trap size in the CHRONOS stands differed between 1993 and 1997 (collecting area of 0.15 m^2, height of 0.35 m, and holes of 4 × 4 cm on the sides) and 2003–2013 (collecting area of 0.23 m^2, height of 0.25 m, and holes of 2 × 5 cm on the sides); traps in the MELNHE stands were identical to those used in CHRONOS in the 2000s. The difference in spatial variability between the two periods with different trap sizes in the CHRONOS stands was small (11% lower in the 2000s than the 1990s) and insignificant, based on a paired t test ($P = 0.68$). For temporal variability, the difference was 9% in the same direction with $P = 0.20$. Thus, as might be expected, variability was smaller with a larger trap, but because this effect was not statistically significant, we did not include it in our models.

Litter traps were systematically arranged in each stand, and sample locations were consistent

Table 1. Characteristics of the 23 northern hardwood stands used in this study listed from youngest to oldest.

Stand	Year cut	Latitude	Longitude	Elevation (m a.s.l.)	Aspect	Slope (%)	Area (m^2)	Mean annual litterfall mass (g/m^2)
MELNHE								
C1	1990	44°02′ N	71°19′ W	570	SE	5–20	3600	296
C2	1988	44°04′ N	71°16′ W	340	NE	15–30	3600	299
C4	1979	44°03′ N	71°16′ W	410	NE	20–25	3600	306
C6	1975	44°02′ N	71°16′ W	460	NNW	13–20	3600	339
JBM	1974	44°03′ N	71°88′ W	730	WNW	25–35	1600	296
HBM	1966	43°93′ N	71°73′ W	500	S	10–25	1600	390
JBO	1924	44°03′ N	71°88′ W	730	WNW	30–40	3600	314
HBO	1913	43°93′ N	71°73′ W	500	S	25–35	3600	363
C9	1890	44°03′ N	71°17′ W	440	NE	10–35	3600	351
C8	1883	44°03′ N	71°18′ W	330	NE	5–35	3600	317
CHRONOS								
H6	1984	44°03′ N	71°17′ W	330	NNE	13	3000	251
M6	1979–1980	44°00′ N	71°25′ W	540	WNW	18	3000	234
M5	1976–1977	44°13′ N	71°14′ W	630	SSW	26	3000	286
HB101	1971	43°94′ N	71°74′ W	520	S	19	3000	260
H5	1967	44°03′ N	71°17′ W	360	NNE	16	2000	291
T20	1958	44°04′ N	71°25′ W	540	ESE	13	3000	272
M4	1949–1950	44°09′ N	71°14′ W	460	NNE	9	3000	288
T30	1948	44°09 N	71°14′ W	550	NNE	10	3000	297
H1	1939	44°03′ N	71°17′ W	320	Flat	3	990	299
H4	1933–1935	44°03′ N	71°17′ W	350	NNE	16	2500	303
M3	1910	44°13′ N	71°15′ W	580	SSW	25	3000	280
H2	1875	44°03′ N	71°17′ W	320	Flat	4	3000	273
H3	1875	44°03′ N	71°17′ W	320	Flat	2	3000	281

Note: Annual litterfall mass was based on 2005 and 2009–2012 in the MELNHE stands and 1993–1996 and 2003–2005 in the CHRONOS stands.

across sampling years. In the CHRONOS study, each stand contained five lines 50 m in length, except in one small stand where lines were 33 m. All stands had three litter traps evenly spaced in each line (Yanai et al. 2012). Each of the MELNHE stands contained three replicate plots in 2005, and a fourth plot was added to each stand in 2009. All MELNHE plots were 900 m^2, except for two young stands in which plots were 400 m^2. In all MELNHE plots, five litter traps were placed in each plot, one in each of the four corners and one in the center. The CHRONOS stands have 15–20 traps, while the MELNHE stands have 20 traps.

Litter was collected from 1993–1997 to 2003–2006 in the CHRONOS stands and from 2005–2006 to 2009–2013 in the MELNHE stands. Litter traps were emptied three times per year: in autumn after leaf fall, in the spring after snowmelt, and again in August prior to the start of the next litterfall season. We report annual litter production from August to August, rather than using the calendar year, so that leaves retained

over the winter (mostly beech) are part of the cohort with which they were produced. The August trap collection yields very little (typically zero) leaf mass, but is very important for ensuring that baskets are ready for the peak collection in the fall. In the spring of 2006, litter traps were emptied but the material was not collected. We corrected for this omission based on the mean annual contribution of spring litter to total annual mass for each stand.

Beginning in the summer of 2011, nutrients were added to plots in the MELNHE stands at the rate of 10 kg·ha^{-1}·yr^{-1} of P as NaPO$_4$ and 30 kg·ha^{-1}·yr^{-1} N as NH$_4$NO$_3$ (Fisk et al. 2013). These are modest rates of nutrient addition, and no treatment effect on litterfall mass was detected in this dataset (ending August 2013) based on a one-way ANOVA for each year ($P \geq 0.13$). We did not consider the effects of nutrient treatment in our analyses of the data.

Litter samples were collected for chemical analysis during rain-free periods in the fall, on

Table 2. Basal area (m^2/ha) of the 23 northern hardwood stands used in this study listed from youngest to oldest.

Stand	American beech	Pin cherry	Sugar maple	Red maple	White birch	Yellow birch	Other species	Total
MELNHE								
C1	0.7	5.1	0.4	0.01	1.6	1.8	0.9	10.5
C2	1.2	8.1	1.5	0.3	1.2	6.7	3.2	22.2
C4	2.6	4.6	6.1	0.0	4.1	1.1	4.3	22.8
C6	0.8	14.9	0.9	0.01	0.2	7.0	1.6	25.4
JBM	3.9	6.3	3.4	0.07	5.8	2.2	4.1	25.8
HBM	8.7	0.8	4.5	2.9	0.4	6.7	5.6	29.6
JBO	5.9	*0.05*	2.5	1.6	8.8	4.5	9.7	33.0
HBO	6.8	0.0	7.1	0.1	4.2	4.1	8.3	30.6
C9	2.3	0.0	10.3	10.9	4.9	0.0	5.3	33.7
C8	2.7	0.0	3.9	1.1	21.4	0.9	8.2	38.2
CHRONOS								
H6	12.3	0.0	3.0	5.9	2.7	5.5	2.5	31.9
M6	5.0	0.0	11.5	4.2	0.0	1.7	11.0	33.4
M5	7.9	0.0	0.7	16.3	1.8	6.6	0.7	34.0
HB101	4.7	9.7	0.3	1.2	7.5	1.0	0.8	25.2
H5	7.8	4.7	0.0	4.9	2.9	1.6	1.5	23.4
T20	5.5	2.3	*0.2*	2.9	10.2	3.6	8.2	32.9
M4	5.9	1.8	1.3	7.4	6.3	6.6	0.8	30.1
T30	*1.2*	1.9	2.4	0.0	2.5	8.9	11	27.9
H1	*1.5*	*0.9*	2.2	1.1	2.1	7.6	14.0	29.4
H4	*2.0*	0.0	28.2	0.0	0.0	7.0	1.6	35.6
M3	9.9	0.0	3.1	0.0	0.0	19.7	1.2	33.9
H2	10.2	0.0	17.1	0.0	0.0	6.1	0.7	32.7
H3	16.4	0.0	12.8	1.7	0.0	3.3	1.0	35.2

Notes: Basal area by species is reported for 2011 for the MELNHE stands and 1994 for the CHRONOS stands. Values in italics indicate the species were not sampled for measuring litter nutrient concentration.

tarps or in baskets in the 1990s and in netting suspended above the ground in the 2000s. Species analyzed for chemistry were American beech (*Fagus grandifolia* Ehrh.), pin cherry (*Prunus pensylvanica* L.f.), white birch (*Betula papyrifera* Marsh.), yellow birch (*Betula alleghaniensis* Britton), red maple (*Acer rubrum* L.), and sugar maple (*Acer saccharum* Marsh.). These species account for 82–99% of the litter mass, depending on the stand (averaged across years).

Litter processing

Litter was sorted to species in all years in the CHRONOS stands except 2005, and in 2009 and 2010 in the MELNHE stands. Litter was oven-dried at 60°C before weighing. Samples were ground with a Wiley Mill to pass a 20-mesh screen, and ~0.25 g was ashed at 470°C and dissolved in 5 mL of 6 mol/L HNO_3 on a hot plate, except for samples from 2004. These samples were ground to a fine powder in SPX CertiPrep 8000 Mixer/Mill (Metuchen, New Jersey, USA)

and digested in 9 mL of 6 mol/L HNO_3 using high-pressure microwave digestion in reinforced XP-1500 Teflon vessels (MARS 5; CEM Corporation, Matthews, North Carolina, USA). Concentrations of P, Ca, Mg, and K for the CHRONOS samples from the 1990s were analyzed by Atomic Absorption Spectrophotometer 4000 (Perkin-Elmer, Wellesley, Massachusetts, USA). The CHRONOS samples from the 2000s and all the MELNHE samples were analyzed using inductively coupled plasma optical emission spectroscopy (ICP-OES; PE-3300DV; PerkinElmer, Shelton, Connecticut, and Norwalk, Connecticut, USA). Nitrogen in CHRONOS samples from 1996 to 2004 was analyzed using a LECO 2000 CN analyzer (LECO Corporation, St. Joseph, Michigan, USA, Brown University). For MELNHE samples, N was analyzed using a CN analyzer (Flash EA 1112 series; CE Elantech, Lakewood, New Jersey, USA, Cornell University). In all cases, quality control was ensured by including standard reference materials (orchard leaves) from

the National Institute of Standards and Technology (NIST).

Data analysis

Calculating and comparing litterfall variation.— This paper addresses spatial and interannual variation in litter mass and nutrient concentration by making use of two datasets collected differently across space and time. For some sources of variation, it was appropriate to combine the datasets; others required that they be treated separately.

We used the coefficient of variation (CV) to characterize variability in litterfall mass and concentration. The CV is the standard deviation divided by the mean. Because it is unitless, it can be compared for variables that differ in magnitude, such as concentrations of different elements or masses of different species.

To characterize stand-level spatial variability in litterfall mass, we calculated the CV across litter traps for each stand (15 traps per stand for CHRONOS and 15–20 for MELNHE) using the mean of all years for each trap. Similarly, we characterized interannual variability as the CV across years of the mean mass of all litter traps in each stand (7 years in CHRONOS and five in MELNHE stands). We compared our estimates of spatial and interannual variation using one-way ANOVA on the spatial and temporal CV with stands as replicates. Two stands in the CHRONOS study had extremely high interannual variability. To test whether the differences we report depend on these outliers, we also performed this analysis while excluding these two stands.

Our analysis of spatial variation of litterfall chemistry was restricted to the MELNHE dataset, as samples were composited within stand before analysis for the CHRONOS study. To characterize spatial variability in the nutrient concentrations of leaf litter, we calculated the CV of concentration for each nutrient and each species in the MELNHE stands at three different spatial scales: variation among the five litter traps within a plot, variation among the four plots within a stand, and variation among the 10 stands. This approach has the advantage of allowing us to use three-way ANOVA to test the variability in litter nutrient concentrations as a function of scale (three levels: within plots, within stands, and across stands), species (six levels), nutrient element (five levels), and their two-way interactions, with the CV of

nutrient concentrations as the dependent variable (Table 3). We also used two-way ANOVA to test the variability only within stands as a function of species and nutrient element.

In contrast, the spatially intensive MELNHE data were collected for only two years prior to nutrient additions, so we relied on the CHRONOS data for our analysis of interannual variation in chemistry. Yanai et al. (2012) reported interannual variation in litterfall nutrients in the CHRONOS study separately for each element and species. Our ANOVA on interannual variation of litterfall chemistry used that dataset but included element and species as predictor variables. Interannual variation of nutrient concentration was calculated as the CV across annual collections in each of the CHRONOS stands (5 years for each species). We performed a two-way ANOVA to test the effects of element and species on interannual variation.

We also compared spatial variation in nutrient concentrations in MELNHE to the interannual variation in nutrient concentrations in the CHRONOS qualitatively, because the two datasets were from different studies.

The CV was log-transformed in all of the analyses to meet the assumption of normality of the residuals.

For this and all other ANOVA models, Tukey's honestly significant difference was used to compare means.

Table 3. ANOVA table for three-way ANOVA model testing the effects of scale (three levels), species (six levels), and elements (five levels) on the log-transformed coefficient of variation of nutrient concentrations of leaf litterfall, using dataset from MELNHE stands.

Source	df	SS	MS	*F*	*P*
Model	49	3.16	0.06	3.00	<0.0001
Error	40	0.80	0.02		
Corrected total	89	3.96			
Scale	2	1.44	0.72	36.04	<0.0001
Species	5	0.20	0.04	1.99	0.10
Element	4	0.48	0.12	5.83	0.001
Scale × element	8	0.24	0.03	1.54	0.17
Scale × species	10	0.40	0.04	2.08	0.05
Element × species	20	0.40	0.02	1.21	0.30

Notes: df, degrees of freedom; SS, sum of squares; MS, mean sum of squares. The sample size for this analysis was 90.

Modeling the effects of stand characteristics.—We chose to combine the CHRONOS and MELNHE datasets in our analysis of the effect of stand characteristics on the spatial variation in litter mass. Because the spatial configuration and total number of litter traps differed between the two studies, we included a class variable in our analyses to distinguish the CHRONOS and MELNHE studies.

Characteristics tested as predictors of variation in litterfall mass were stand age, slope, elevation, and aspect. Aspect was represented by sine (north–south) and cosine (east–west) of the azimuth. To identify which stand characteristics best predict the variation of litterfall mass within stands, we used regression models. For spatial variation, the dependent variable was the CV across litter traps for each stand averaged across years, with study (CHRONOS vs. MELNHE) included as a class variable in the model. For temporal variation, the dependent variable was the interannual CV within stands, based on the average across traps. This analysis was run separately for the CHRONOS and MELNHE datasets because they were observed in different years.

To generate candidate models, we used stepwise regression with forward selection and backward elimination with $\alpha = 0.10$ for both directions. The best models were the ones with the lowest Akaike's information criterion (AIC). If two models had similar AICs (differing by <2), we chose the one with fewer variables (Burnham and Anderson 2002). To avoid multicollinearity, variance inflation factors (VIFs) were calculated for variables in each candidate regression model (Table 4). Variables with a VIF > 5 were not included when proposing candidate regression models (Freund and Littell 2000).

We compared individual relationships between dependent variables and predictors using Pearson correlations. Two stands had extremely high interannual variability, so we ran our models with and without these observations to characterize their influence on our results.

Characterizing the effect of sampling effort using bootstrapping.—Litter traps in both studies were organized spatially, within plots in the MELNHE stands and along transects in the CHRONOS stands. For each stand, we used one-way ANOVA to test the similarity of litterfall mass collected in different traps within plots or transects. Because plots and transects were not significant predictors of litterfall mass within stands ($P \geq 0.38$), we treated each litter trap as independent, using up to 20 traps to characterize a stand for the analysis of sampling effort. Measurements of litterfall from trees isolated from conspecifics in a mixed hardwood–conifer forest in Michigan showed that litter falls up to 10 m from a tree (Ferrari and Sugita 1996); our baskets are at least 14 m separated from one another.

We used bootstrapping to describe how different sampling schemes would impact uncertainty

Table 4. The best five candidate regression models for predicting spatial and interannual variation (coefficient of variation [%]) of litter mass within stand.

Variable	Explaining spatial variability (CHRONOS and MELNHE combined)					Explaining interannual variability									
						MELNHE					CHRONOS				
Model	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Elevation (m)			0.0004	−0.002		0.02	0.03	0.03	0.03				0.02	0.02	
Slope (%)		0.03			−0.01	0.3				0.8	0.7	1.1	0.8		1.1
Stand age (yr)									0.01	−0.04					0.04
Cos	−0.58			−0.76	−0.64			1.1			−5.0			−7.5	
Sin															
Study	0.27	0.38	0.13	0.2	0.16	25	25	27	27	29	52	52	53	54	54
AIC	44	45	45	46	46	0.74	0.67	0.69	0.68	0.62	0.70	0.63	0.66	0.61	0.65
R^2	0.037	0.007	0.001	0.05	0.04	2	1	2	2	2	2	1	2	2	2
k†	2	2	2	3	3	1	2	3	4	5	1	2	3	4	5

Notes: Variance inflation factors for all the variables in each model were ≤2.4. Coefficients for variables included in the models are shown. The models are numbered by corrected Akaike's information criterion (AIC) from lowest (best) to highest. A difference in model AIC (Δi) > 2 indicates a difference between models.

† Number of model parameters.

in litterfall estimates. We calculated the standard error (SE) associated with estimates of litterfall mass, incrementally increasing the number of sampling units (litter traps for spatial variability and years for interannual variability), from two traps and two years up to the total number of sampling units present in each dataset (20 traps and 5 years in MELNHE stands, 15 traps and 7 years in CHRONOS stands). For each sampling scheme, the SE was calculated for every possible combination of observations. For example, for a sampling scheme of two litter traps and two years per stand, the SE was calculated for all possible pairs of litter traps and all possible pairs of years for that stand, and the mean of those SEs was reported. Because the number of litter traps and the years sampled differed between the CHRONOS and MELNHE stands, these analyses were conducted separately on the two datasets. We also conducted similar analyses using random sampling with replacement for 10,000 iterations, which is a useful method for larger datasets (Levine et al. 2014), and obtained similar results.

To compare the relative effects of sampling effort for mass versus chemistry on uncertainty in litterfall nutrient flux estimates, we used the approach described above, using the CHRONOS dataset, which had a longer record of sampling than MELNHE. In calculating leaf litterfall nutrient flux, we omitted species for which we did not have concentration data. We varied the number of sampling years for litterfall chemistry (using all possible combinations) while multiplying each species by a constant mass (the mean for that species across years) and then conducted a similar analysis by varying the number of years sampled for mass while multiplying by constant nutrient concentrations.

SAS 9.4 (SAS Institute 2013, Raleigh, North Carolina, USA) was used for statistical analysis.

RESULTS

Variability in litterfall mass and concentrations

Interannual variation in litterfall mass, described by the CV across years, was greater than spatial variation in 22 of our 26 stands ($P < 0.001$; Fig. 1). Notable outliers were two CHRONOS stands, M3 and M5, which were very steep and had the highest interannual variation. When these two stands were excluded from the analysis, interannual variation (CV = 17.6% ± 1.0%) was still significantly higher
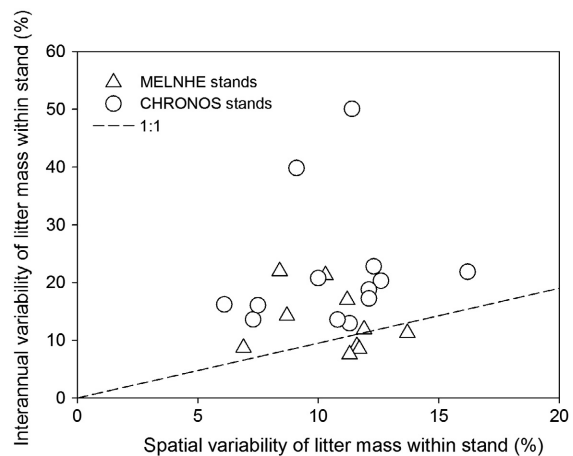

Fig. 1. Spatial variability (*x*-axis) and interannual variability (*y*-axis) of total litterfall mass, represented by the coefficient of variation (CV). Each point represents one stand (23 stands total). Spatial CVs were calculated using 20 (MELNHE) or 15 (CHRONOS) litter traps per stand. Temporal CVs were calculated using 5 (MELNHE) or 7 (CHRONOS) years of annual means per stand.

than spatial variation (10.7% ± 0.5%) in a general linear model that included study (CHRONOS vs. MELNHE) as a covariate ($P < 0.001$).

In our analysis of spatial variation in litterfall chemistry in the MELNHE stands, concentrations varied the most across stands (mean CV of 24%) and least within plots (CV = 10%, $P < 0.0001$; Fig. 2, Table 3). The average within-stand variation across elements was 14%, but the magnitude of spatial variation depended on the element ($P = 0.001$). Phosphorus concentrations varied most (CV = 21%, averaged across species), and Ca concentrations varied least (12%). The main effect of species on spatial variability was not significant in our three-way ANOVA ($P = 0.10$), but there was a marginally significant ($P = 0.05$) interaction of species and scale. This interaction was due to red maple, which was the least variable of all species within plot (4%), and the most variable across stands (29%) based on the test of Tukey's honestly significant differences (Fig. 2). Within stands, we found marginally significant differences in the spatial variability of concentration among elements ($P = 0.08$). Phosphorus was the most variable (CV = 18%), followed by K (16%), Mg (15%), N (12%), and Ca (11%). The variability
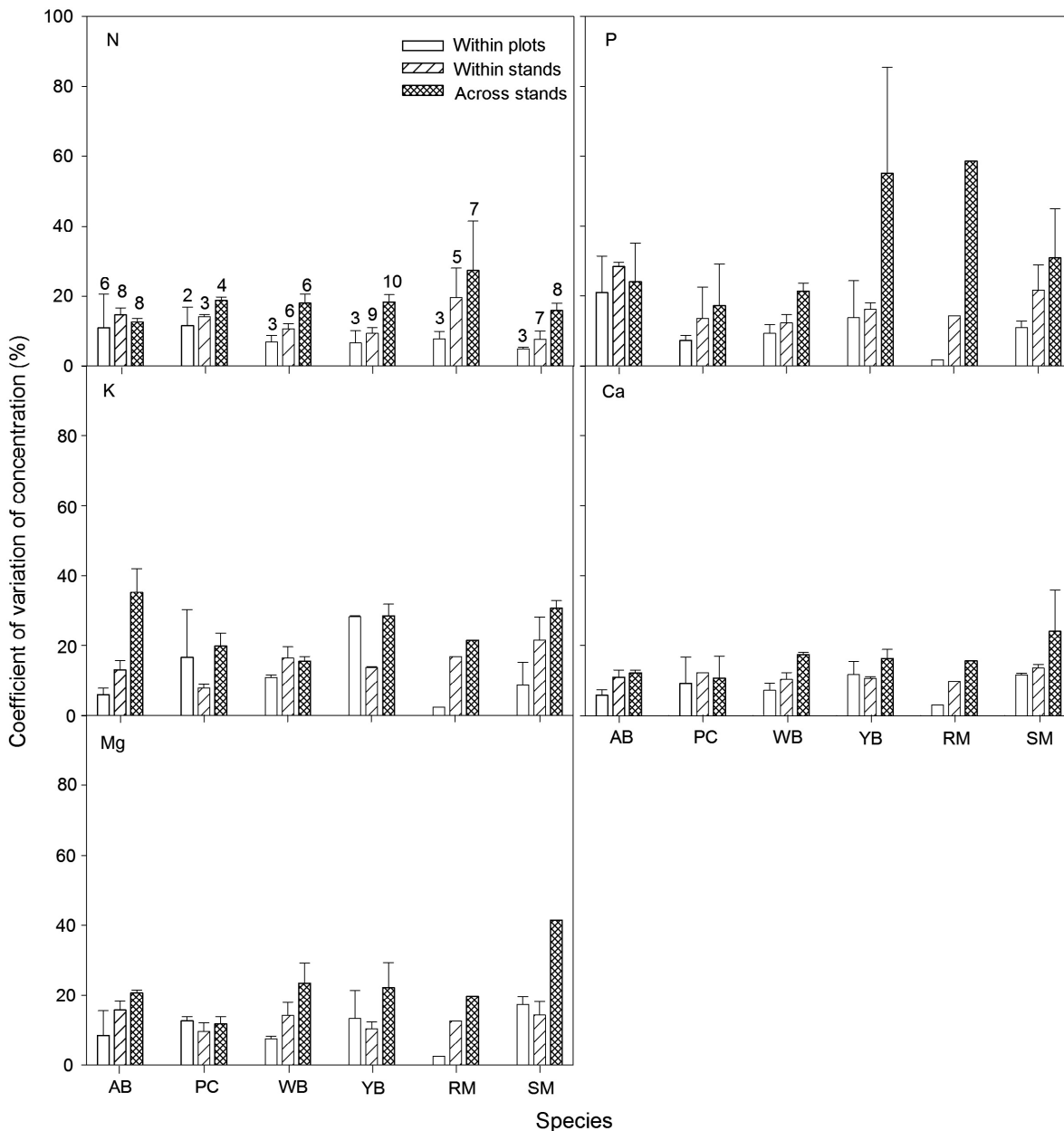
Fig. 2. Spatial variability (coefficient of variation, CV) of litterfall nutrient concentrations by species in MELNHE stands at three different spatial scales (within plots, within stands, and across stands). Sample sizes are shown in the first panel. Error bars represent the standard error of two years (except for red maple, which was analyzed in only one year for most elements). Species codes are AB, American beech; PC, pin cherry; WB, white birch; YB, yellow birch; RM, red maple; and SM, sugar maple.

of concentrations within stands did not differ significantly among species ($P = 0.3$).

The magnitude of interannual variability depended on the element ($P < 0.001$), following the same general pattern as spatial variability, with P (CV = 29%) and K (24%) displaying significantly higher variation than Mg (17%), which was higher than Ca (13%) and N (12%). Interannual variability did not differ significantly among species ($P = 0.36$).

This temporal variation in nutrient concentrations in the CHRONOS dataset can be compared to the spatial variation in nutrient concentrations in MELNHE. For P, K, and Mg, interannual variability was greater than spatial variability for all species (Fig. 3). For Ca and N, the differences between spatial and interannual variability were not consistent across species.
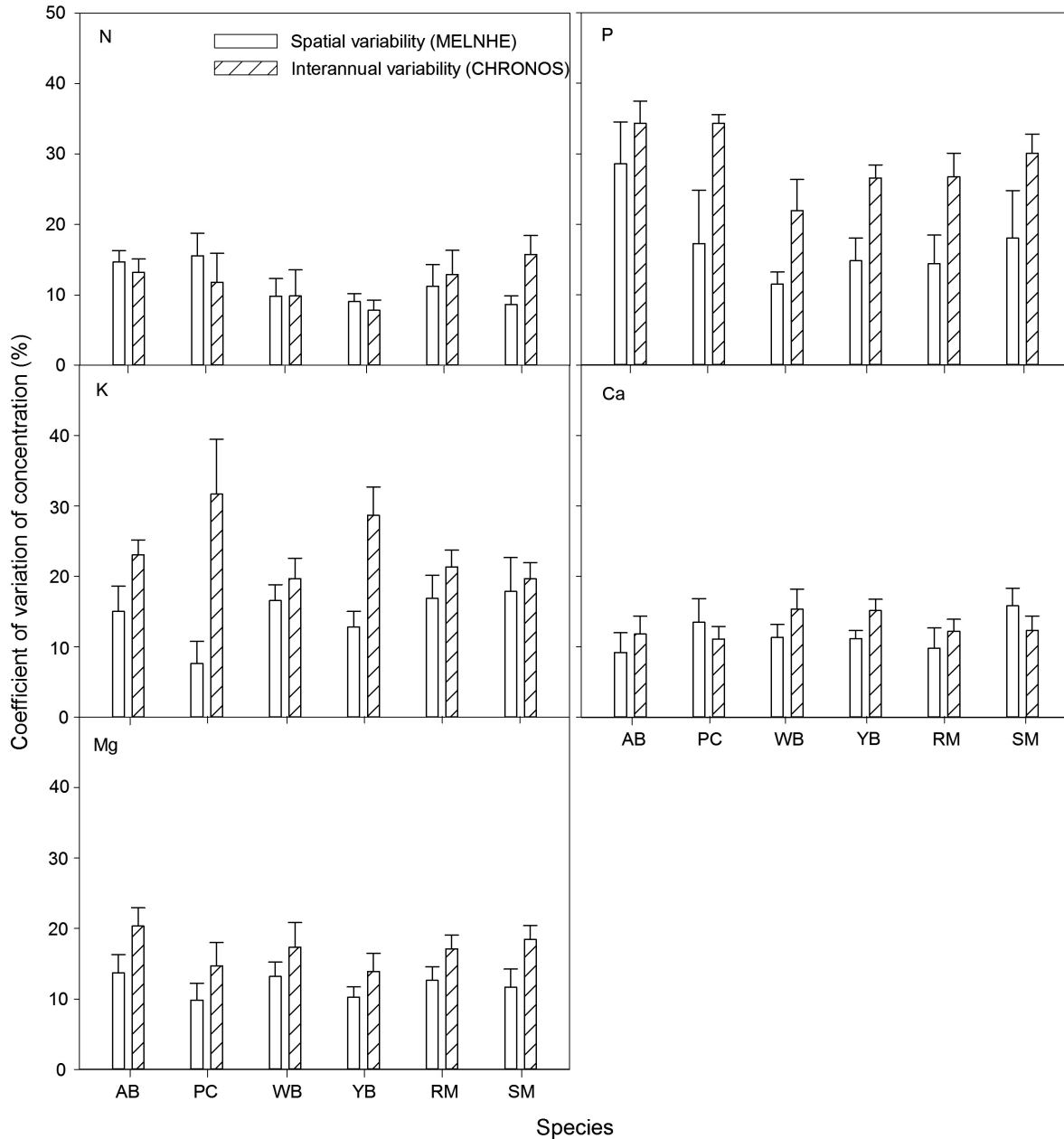

Fig. 3. Comparison of spatial variability (MELNHE) and interannual variability (CHRONOS). Spatial variability of litterfall chemistry was calculated as the coefficient of variation (CV) of multiple plots in the MELNHE sites (four plots for each species). Interannual variability of litterfall chemistry was calculated as the CV of multiple years in the CHRONOS sites (five years for each species). Error bars represent the standard error of variation among stands.

Stand characteristics as predictors of litterfall mass variability

None of the stand characteristics we measured predicted spatial variability of litterfall mass ($P \geq 0.39$), based on a Pearson correlation analysis. We also evaluated a number of regression models describing the effects of different stand characteristics on spatial variation of litterfall mass (Table 4), all of which included a variable for study (MELNHE vs. CHRONOS). None of the stand characteristics (slope, aspect, elevation, or age) predicted the spatial variability of litterfall mass (Table 4).

Interannual variability in litterfall mass was better explained than spatial variability by stand characteristics. In both the CHRONOS ($P = 0.001$) and MELNHE ($P = 0.02$) datasets, stands with steeper slopes had greater interannual variability (Fig. 4). Interannual variability in litterfall mass increased with elevation in both datasets ($P = 0.01$ in CHRONOS, $P < 0.01$ in MELNHE; Fig. 4). Aspect was a significant predictor of interannual variation in CHRONOS ($P < 0.01$) but not MELNHE ($P = 0.92$; Fig. 4). Excluding the two CHRONOS stands with extreme interannual variability, slope and aspect were still correlated with interannual variability ($P < 0.01$) but elevation was not ($P = 0.11$). Stand age had no effect on interannual variability of litterfall mass within stand in either the MELNHE ($P = 0.92$) or CHRONOS datasets ($P = 0.43$).

For the CHRONOS dataset, the model with the lowest AIC and fewest variables had only slope as a predictor variable, while for MELNHE, the best model had only elevation (Table 4).

Simulated effects of sampling effort on uncertainty in mass, concentration, and nutrient flux

Our bootstrap analysis shows how uncertainty in litterfall mass decreases with sampling effort (Fig. 5). The SE in litterfall mass decreased with both increased spatial and temporal sampling effort. The steepness of the lines decreases as the number of traps increases, meaning that a greater improvement would be achieved by adding more sampling years as the number of traps increases. The uncertainty in litterfall mass as a function of sampling effort was similar between the CHRONOS and the MELNHE studies, with MELNHE having slightly less variability in both space and time.
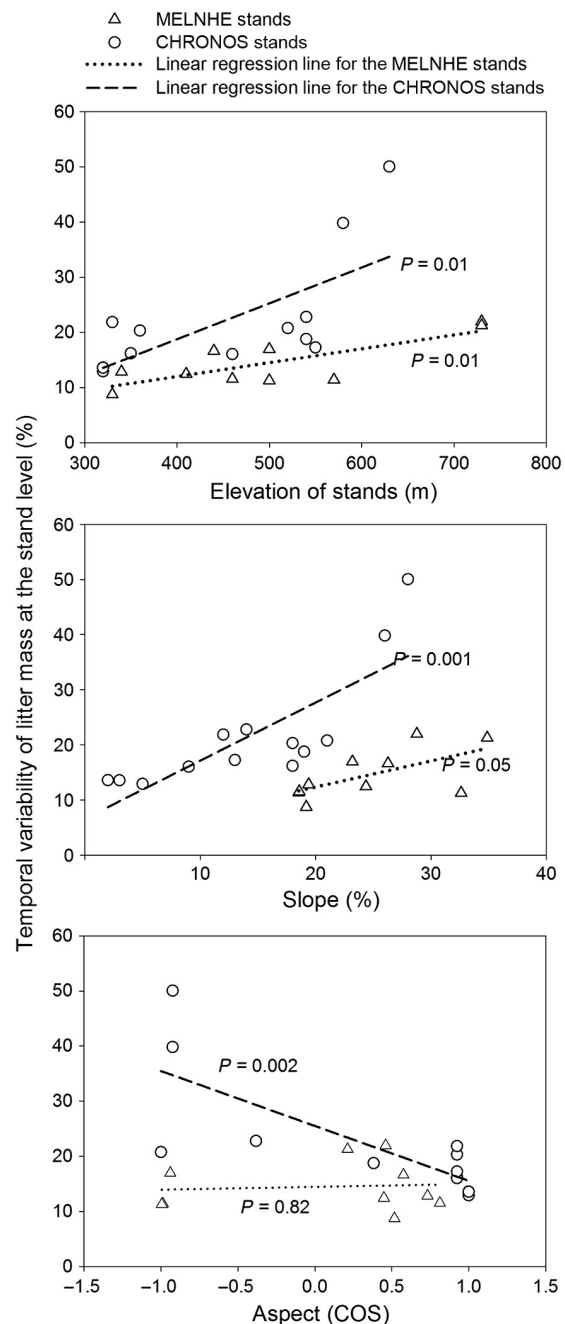

Fig. 4. Interannual variation of litterfall mass (coefficient of variation) predicted by elevation, slope, and aspect. Lines and fit statistics reflect the results of simple linear regressions for each study.

Temporal uncertainty in litter nutrient concentrations decreased with more years of sampling (Fig. 6). The uncertainty in nutrient concentration
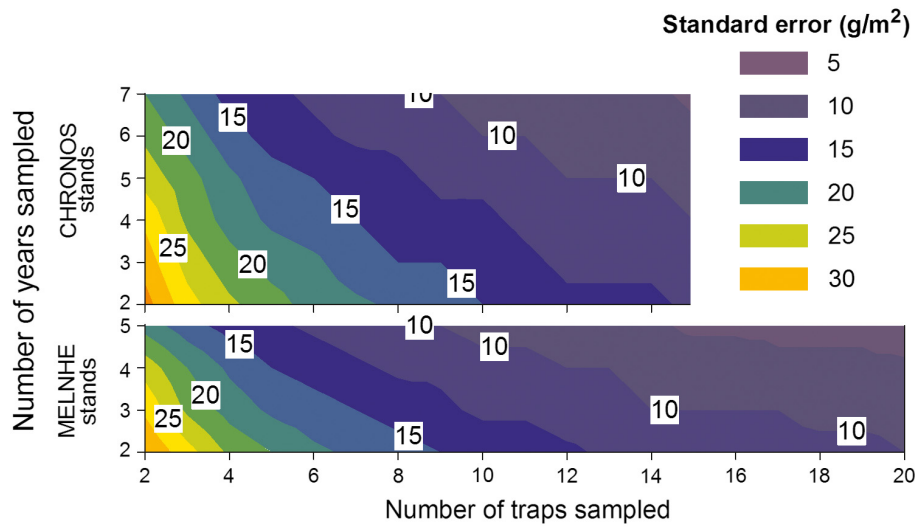
Fig. 5. Sampling intensity (numbers of traps and sampling years) affects uncertainty in litterfall mass in MELNHE and CHRONOS stands.
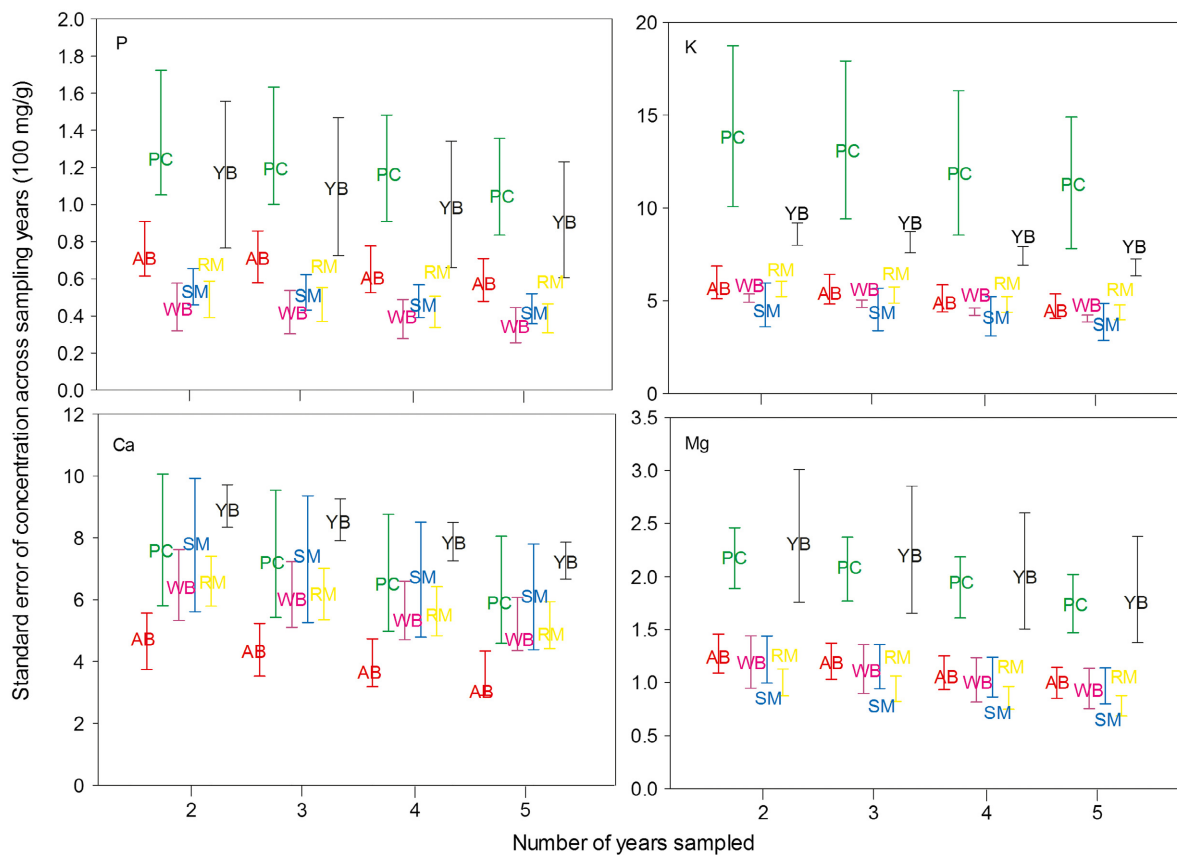

Fig. 6. Interannual variability in litter chemistry as a function of sampling effort. Species codes are AB, American beech; PC, pin cherry; WB, white birch; YB, yellow birch; RM, red maple; and SM, sugar maple. Error bars represent the standard error across the 13 CHRONOS stands.

as a function of temporal sampling effort was similar for all species and elements, with the SE decreasing by 5–7% for each added sampling year. Pin cherry and yellow birch exhibited greater variation in nutrient concentrations across years than other species for P ($P = 0.09$) and Mg ($P = 0.08$) but not for Ca ($P = 0.28$) with five years sampled. The temporal variation of K concentrations had a greater variation across stands in pin cherry than other species ($P = 0.004$). The temporal uncertainty among different species was more similar for Ca than other nutrient elements (Fig. 6). Unfortunately, we did not have enough years of data to include N concentrations in the bootstrapping exercise.

Overall, litter mass exhibited higher SE across years than nutrient concentrations, making litterfall mass the greater source of temporal uncertainty in nutrient flux (Fig. 7). However, the relative contribution of litter mass and nutrient concentrations to uncertainty in flux varied by element. For Ca, interannual variation in concentration was relatively low and uncertainty in mass had the greatest effect on the uncertainty in Ca flux. At the other extreme, for P concentrations, uncertainty in concentration contributed as much uncertainty as mass to the final flux calculation (Fig. 7).

DISCUSSION

Litterfall mass

Our average interannual variability of litterfall mass (CV = 18% ± 2%) was similar to the interannual variability of hard beech (*Nothofagus truncate*) litterfall mass in New Zealand (20%; Alley et al. 2010) and deciduous litterfall mass in West Virginia (14%; Adams 2008). The interannual
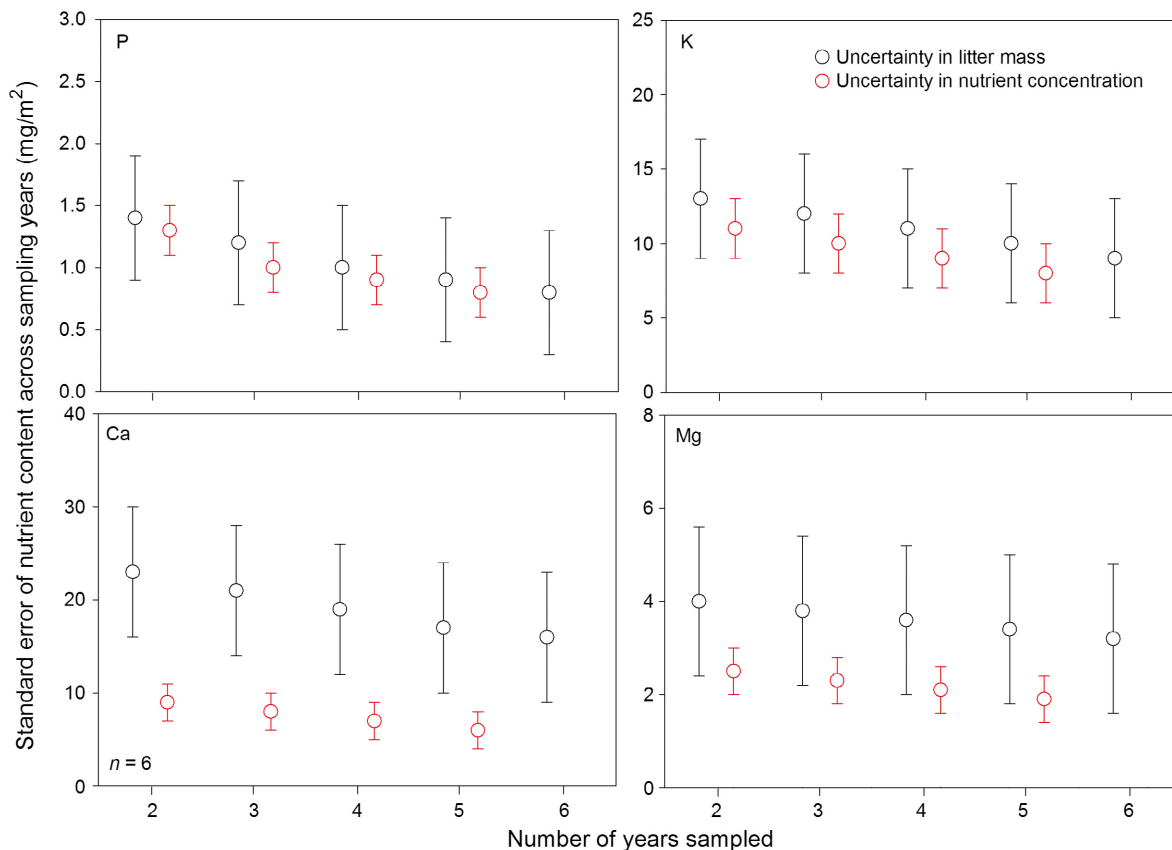

Fig. 7. Interannual variability in nutrient flux as a function of sampling effort. Uncertainty in litterfall mass or in nutrient concentration explains the uncertainty source of calculated nutrient flux by fixing nutrient concentration or mass constant across years. Error bars represent the standard error across the 13 CHRONOS stands.

variability in a mixed hardwood stand New York was only 3% (Welbourn et al. 1981), based on just two years of observation. Our average spatial variability of litterfall mass (CV = 10.6% ± 0.5%) was similar to that in deciduous forests in southern New Hampshire (9.7%; Dellenbaugh et al. 2007).

Our finding that stands on steeper slopes had higher interannual variability could be explained by the effect of wind. Earlier studies have suggested that wind is a major factor in the redistribution of leaf litter (Gloyne 1964, Staelens et al. 2003) especially on steep slopes (Welbourn et al. 1981). A previous analysis of the CHRONOS data reported higher litterfall masses in windy years, which was attributed to litter from the ground blowing into the traps (Yanai et al. 2012). We found that among the CHRONOS stands, the steeper ones had higher interannual variability in litterfall mass (Fig. 1), even when very windy years (Yanai et al. 2012) were excluded. It was surprising that we did not find an effect of slope on spatial variability, only on interannual variability (Table 4).

Our other two significant predictors of interannual variation, elevation and aspect (Fig. 4), may also act through their effects on wind exposure. Wind speeds in this region tend to increase with elevation (Reiners and Lang 1979), as does slope in our stands ($R^2 = 0.44$, $P < 0.001$ data not shown). Thus, slope and elevation may be surrogates for wind, which we did not measure. Similarly, the effect of aspect may reflect the predominantly westerly winds in our region; the cosine of azimuth (east–west) was significant (Fig. 4) but not the sine (north–south). Similarly, in the Allegheny Plateau, litter redistribution due to wind was significantly greater on east-facing slopes than west-facing slopes and greater in upper-slope than lower-slope positions (Boerner and Kooser 1989). Increased drying of litter on southwest-facing slopes (Cantlon 1953) may also contribute to litterfall variation, as lighter, drier litter may be more susceptible to redistribution. The sites that have the highest interannual variation, M3 and M5, face southwest (Table 1) and had exceptionally high litterfall mass in 2004, which had a very dry and windy autumn (Yanai et al. 2012).

Litterfall nutrient concentrations

Differences in the variability of leaf litter concentrations among elements may reflect differences in their biogeochemical cycling. Many elements are resorbed from leaves before senescence. In our study sites, P resorption generally exceeds N resorption and is much more variable (See et al. 2015). Magnesium and K are resorbed, although to a lesser degree than P and N (Duchesne et al. 2001, Hagen-Thorn et al. 2006). Potassium is not covalently bonded and is the most susceptible to leaching. Thus, the higher interannual variation than spatial variation within stands in P and K (Fig. 3) may reflect differences in weather conditions influencing resorption and leaching in the autumn. High spatial variation in P and K might also reflect variation in parent materials or soil conditions across our stands, with differences in N availability contributing to the demand for P conservation (See et al. 2015). Spatial variability in leaf litter Ca concentrations was low relative to the other elements (Fig. 2). Foliar Ca is relatively immobile and not subject to resorption, as it serves a structural role in cell walls. Thus, the range seen in leaf litter Ca concentrations reflects mainly variation in uptake, while the other elements are affected by variation in uptake, resorption, and leaching. Spatial variability in N concentrations was low within stands, consistent with its low variability in foliage (Yang et al. 2015).

Species differences in interannual variation may be partially explained by differences in the phenology of senescence. We attempted to sample litter during peak leaf fall for chemical analysis, but the timing of peak leaf fall differs by species. For many species, litterfall nutrient concentrations decrease throughout the autumn (Gosz et al. 1972, Grizzard et al. 1976, Yang et al. 2005) due to ongoing resorption and leaching. The high variability seen in pin cherry concentrations (Fig. 6) may reflect its early senescence relative to the other species in these plots (M. A. Morley, G. E. Walsh, R. D. Yanai et al., *unpublished data*). In some years, the pin cherry leaves we collected for chemical analysis may have been among the last leaves of the season to fall for this species. This may explain why P, as a highly resorbed element, and K, as a readily leached element, had the highest interannual variation in pin cherry. Sampling multiple species at the same time, which is a considerable convenience, may introduce a bias in concentration estimates, with concentrations of early senescing species being underestimated and late senescing species being overestimated.

Recommendations for litterfall measurements

For researchers monitoring leaf litter production, understanding the magnitude of spatial and interannual variability can help guide decisions to improve allocation of sampling effort. In this study, interannual variability of litter mass was larger than spatial variability within a stand (Fig. 1), suggesting that sampling for additional years would be of greater value than adding more litter traps when the variation in space and variation in time are of equal concern. When studying the effects of a singular event, such as a disturbance, understanding the variation in space is the only concern.

If interannual variability is partly due to overestimating litterfall mass in windy years on steep slopes, then improvements to litter trap design could help to reduce measurement error associated with estimates of mass flux. Litter traps in our stands were placed close above the forest floor, which led to an over-estimation of litterfall mass in windy years due to leaves blowing in from the ground nearby (Yanai et al. 2012). This issue may be remedied by raising litterfall traps off the ground, which we have done on the steep slopes where we observed elevated litter mass. Ironically, raised litterfall traps can lead to the opposite problem. When elevated, litterfall traps with porous bottoms (which allow for water drainage) enable wind gusts from underneath to blow leaves out of the trap, leading to an under-estimation of litter flux in windy years. This has been observed in other northern hardwood plots and can be prevented by placing shields underneath elevated traps such that wind is dampened but water can still drain out (J. Love, Coweeta Hydrological Laboratory, *personal communication*). Alternatively, taller walls on litter traps placed on the ground would help prevent litter from blowing in and out of traps. The efficacy of these improvements for decreasing measurement error will depend on the importance of wind in the system.

Measurement error contributes to the uncertainty we observed, as is always the case. In addition to errors in the collection of litter in traps, there are measurement errors in obtaining dry weights, sorting leaves by species, and analyzing samples for nutrient concentrations. When there is a bias, such as overcatch by traps on the ground or undercatch by elevated traps, this contributes error not reflected in spatial or temporal variability, but variability due to measurement error explains some of the sampling error we report. The magnitude of this contribution is likely to be small. For uncertainty in chemical analysis, CVs of 1–8% are common for leaf tissues (Yang et al. 2015). We found some errors in litter mass due to loss of litter sorted by species in the MELNHE study (45 of 1000 litter traps), but dropping these values improved CVs by only 0.2%. Thus, the greatest potential for improving confidence in litter estimates is in reducing sampling error in space and time.

Reducing uncertainty in litter nutrient concentrations is complicated by the fact that sources of variability differ by element and species. Specifically, P and K vary more spatially and temporally than Ca or N, with Mg being intermediate. This means that greater numbers of traps, stands, and years would be needed to characterize litter concentrations of P and K than other elements. However, the incremental cost of analyzing for Ca and Mg in addition to P and K is negligible. Even for N concentrations, which require a separate laboratory analysis, the analytical cost pales in comparison with the cost of collecting samples in the field. Optimal sampling design will depend on which elements are most important to the research objectives.

Species differ in their nutrient variability, possibly reflecting phenological differences at the time of sampling, as discussed above. Study designs that involve frequent litter collection are protected from this source of error. The cost of analyzing multiple samples can be reduced by compositing sequential samples. It is also common to composite samples from multiple traps before chemical analysis (Knoepp et al. 2008, Lucash et al. 2012). Compositing allows greater sampling intensity for the same cost, giving a better estimate of the mean, but at the expense of characterizing the variability. If understanding variation in space or time is important to the goals of the study, then compositing may have drawbacks.

The calculation of litterfall nutrient flux requires the estimation of both litterfall mass and nutrient concentrations. Species composition is also an important variable. It may be sufficient to sort only a subsample of the traps used to collect litter mass to estimate species composition (Dellenbaugh et al. 2007). Another option is to use basal area or biomass to estimate species composition (Yanai et al. 2012). Whether sampling efforts

should be allocated more toward mass or nutrient concentration varies with the target element. For Ca, Mg, and K, interannual variation in litterfall mass contributed more uncertainty to litterfall nutrient flux estimates than interannual variation in concentration. This is good news for researchers, as collecting mass alone is cheaper without the subsequent chemical analysis of samples. For monitoring P flux, greater effort might be needed to characterize litter chemistry than for the other elements, including N.

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