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Seasonal and inter-annual variability in litter decomposition and nitrogen availability in a mid-Appalachian watershed

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Abstract. The role that microclimates play on soil decomposition is poorly understood. Though litter decomposition is controlled by climate and substrate quality at coarse spatial scales, at the watershed scale, microclimates mediated by forest structure and landscape position can influence decomposition rates and in turn affect nitrogen cycling. To evaluate the effects of landscape position and vegetation heterogeneity on decomposition, we employed a two-year litterbag study (2011–2013) using yellow birch leaf litter across the Weimer Run watershed, a cool, humid watershed located near Davis, West Virginia. From our results, we created a spatially explicit empirical model that we tested against both a single-pool and three-pool decomposition model, each based on climate and derived from the Long-Term Intersite Decomposition Experiment Team. Initial litter decomposition varied by elevation, with greater rates of decomposition at locations lower in the watershed. Decomposition rates differed by elevation, except during the first winter of the study. No differences in decomposition rates were seen among elevation levels when snowfall was below average for the first winter (2011–2012). During the second winter (2012–2013), elevation levels showed separation in decomposition rates, with higher elevations exhibiting lower decomposition rate. This suggests important controls on decomposition exerted by the presence or absence of snow, inter-annual climate variability, and the interaction of both with topography. Our empirical model showed greater rates of decomposition during early stages of decomposition (<12 months), but converged with the three-pool decomposition model after 20 months. Plant available nitrogen differed by vegetation cover, largely driven by greater availability of nitrate (NO_3^-) beneath areas of canopy closure in the forest. Controls on decomposition and nitrogen cycling within the Weimer Run watershed vary spatially by elevation and vegetation cover and are subject to complex interactions and differ from standard models of decomposition. The effect of the inter-annual variance of snow depth on litter decomposition is of note and an important consideration moving forward. Climate-based models of decomposition greatly underestimate initial rates of decomposition, potentially leading to under-accounting and compounded uncertainty.

Key words: complex topography; inter-annual climate variability; litter decomposition; nitrogen cycling; snow.

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INTRODUCTION

Decomposition is a key aspect of global nutrient and element cycling (Olson 1963, Raich and Schlesinger 1992, Vitousek 2004, Bonan et al. 2013) that integrates the chemical, physical, and biological processes involved in the breakdown of organic matter into labile, inorganic component forms (Berg and McClaugherty 2008) and more recalcitrant, complex organics (Chapin et al. 2002). At regional and global scales, decomposition is controlled by climate and substrate

quality (Meentemeyer 1978, Aerts 1997, Silver and Miya 2001, Zhou et al. 2008) with broad-scale estimates of decomposition rates established from globally distributed, long-term decomposition studies (e.g., Long-term Intersite Decomposition Experiment Team [LIDET]; Gholz et al. 2000, Bonan et al. 2013). At these large scales, derived variables such as the climate decomposition index (CDI) have been shown to be strong predictors of decomposition rates (Adair et al. 2008). Climate decomposition index is calculated from air temperature, precipitation, and potential evapotranspiration (PET) and has been incorporated in ecosystem models (e.g., CENTURY). However, this broad-scale approach likely obscures the influence of intra-site ecosystem heterogeneities and climate variability, which may lead to unquantified uncertainty. These uncertainties are potentially quite high in ecosystems with strong seasonality or that are physically and biologically complex, such as mountainous watersheds.

At finer scales, decomposition is influenced by soil fauna composition and abundance (Singh and Gupta 1977) and interactions among varying leaf litter species (Hättenschwiler and Gasser 2005). However, the physical–biological structure and complexity of a system—from topographic heterogeneity to vegetation distribution—can profoundly influence decomposition by affecting the ground surface and altering microclimates. Litterfall amounts may decrease with increasing elevation over significant elevation gradients, but forest floor litter mass may increase due to slower turnover rates (Zhou et al. 2014). This effect can be compounded as elevation gradients often result in coniferous tree supplantation of deciduous trees at higher elevations (Reiners and Lang 1987). Across the mid-Appalachians, red spruce and balsam fir line the ridgetops. The additive effects of the more recalcitrant nature of this coniferous litter combined with decreased temperatures (Zhou et al. 2014) at altitude may account for increased forest floor mass as a function of lowered decomposition rates. Shanks and Olson (1961) showed differences in first-year decomposition rates of leaf litter from five different species of deciduous trees along an elevation gradient in the southern Appalachians. Decomposition rates were faster at lower elevations and faster underneath deciduous trees. Elevation effects can be seen across less extreme elevation gradients as well. Dwyer and Merriam (1981) showed that fine-scale forest floor topography (e.g., hummocks and hollows) was correlated with soil temperature along hillslopes in subalpine forests and affected leaf litter decomposition. Downslope winds may also result in the redistribution of fallen litter from higher to lower elevations, or increased heterogeneity in forest litter distribution due to aggregation around fallen logs, branches, or in depressions (Orndorff and Lang 1981).

Microclimates are determined by ecosystem structure—including forest heterogeneity and fragmentation (Hastwell and Morris 2013). The physical structure of plant communities can affect moisture and temperature regimes (Hastwell and Morris 2013, Atkins et al. 2015) through canopy-gap controls on wind, solar radiation, and rainfall interception and redirection (Belsky and Canham 1994, Breshears 2006). The effects of forest structure on litter decomposition rates can be significant (Hastwell and Morris 2013). There is a need to better constrain the high uncertainties in the spatial and temporal variation of decomposition rates, particularly in eastern North American forests such as those of the mid-Appalachians that may experience severe impacts from global climate change (Walter et al. 2017). Decreasing uncertainty can lead to improved understanding of the interactions among decomposition dynamics, nutrient cycling, and environmental heterogeneities.

In cold environments where there is frequent snowfall, carbon and nutrient cycling processes during the winter are driven by the physical properties and duration of the snowpack which acts as an insulative layer on the landscape (Saccone et al. 2013). A deep, well-formed snowpack limits the depth of soil freezing and can keep the soil surface at or above freezing temperatures during the winter. Climate-driven loss of snowpack may result in increased frequency of freeze–thaw cycles and harsher conditions during the winter for sub-nivean environments (Bokhorst et al. 2010, Saccone et al. 2013) affecting decomposition and nutrient cycling.

Nitrogen cycling is an intrinsic component of litter decomposition, the spatial variance of which is influenced by vegetation cover heterogeneity and forest structure (Reich et al. 2001).

Closed canopy areas of mature, conifer forests in the Upper Peninsula of Michigan have been shown to exhibit greater nitrogen mineralization rates than open, forest gaps (Schliemann and Bockheim 2014). And, while N mineralization rates increase with elevation in the mountains of the southern Appalachians (Garten and Van Miegroet 1994), at elevations above 700 m, there is increased variance among areas of differing vegetation, with significantly higher N mineralization rates occurring in areas where evergreen shrubs are absent—an indication that vegetation can differentially affect N mineralization in these ecosystems (Knoepp and Swank 1998).

N mineralization rates can also vary inter-annually; as an example, the watersheds at Coweeta Hydrologic Laboratory, located in the southern Appalachians, show evidence that inter-annual variance in N mineralization can be attributed to differences in rainfall rather than temperature, with increases in N mineralization rates during years of higher rainfall (Knoepp and Swank 1998). The temporal nature of N cycling can be affected by vegetation as well. The evergreen shrub layer of the southern and mid-Appalachians is dominated by mountain laurel (*Kalmia latifolia*) and rhododendron (*Rhododendron* spp.), species with highly recalcitrant litter that slows N cycling and increases N retention in the system—with N retention estimated to peak at 30 yr after shrub-stand establishment (Chastain et al. 2006).

Differences in N mineralization along elevation and vegetation gradients can be a function of the variance of soil temperature, soil moisture, and substrate quality (Powers 1990). While the forests and watersheds of the southern Appalachians share many similarities with the mid-Appalachians, there are important, ecologically relevant differences. Mid-Appalachian forests are often far less botanically diverse than their southern neighbors. Due to their more northerly latitude, mid-Appalachian forests are subject to colder winter temperatures, shorter growing seasons, increased snowfall, and more persistent snow coverage. These ecosystem factors would be expected to impact litter decomposition and nitrogen cycling.

Our understanding of the influence of the interactions between forest vegetation heterogeneity and elevation gradients on litter decomposition within cool, humid temperate watersheds is lacking. By discretizing the landscape within a watershed into both elevation and vegetation cover classes, we can attempt to parse out the controls exerted on decomposition and N availability by environmental heterogeneities. By employing a combined approach using litterbags in a factorial design across elevation and vegetation gradients coupled with measures of nitrogen availability, we ask the following questions:

1. What are the effects of vegetation cover on litter decomposition and N dynamics across an elevation gradient within a cool, humid watershed in West Virginia?
2. How does N availability during the growing season vary among vegetation cover classes across an elevation gradient within a cool, humid watershed in West Virginia?
3. How do decomposition dynamics respond to inter-annual variations in snow cover and snowpack depth?

Methods

Site description

The study was conducted in the Weimer Run watershed (374 ha), located in the Little Canaan Wildlife Management Area near Davis, West Virginia (39.1175–79.4430). The watershed has an elevation gradient of 940–1175 m with mixed northern hardwood–coniferous forest cover (Fortney 1975, Atkins et al. 2015). A prominent under-story vegetation layer exists in the watershed, populated by *Rhododendron maximum, Kalmia latifolia, Osmundastrum cinnamomeum*, and *Osmunda claytoniana* (Fortney, 1975). Mean annual precipitation is 1450 mm/yr (PRISM Climate Group). The mean daily maximum July temperature is 18.8°C, and the mean daily maximum January temperature is −3.9°C (National Climatic Data Center [NCDC], Davis, West Virginia, USA).

Elevation and vegetation cover classes

Three elevation classes were established along the northeastern aspect of the watershed to form an elevation gradient: LOW (975 m), MID (1050 m), and HIGH (1100 m). At each elevation level, three 2 × 2 m plots of three different vegetation cover classes were established—for a total of 27 plots across the entire watershed. The

vegetation cover classes were defined as follows: CANOPY, closed canopy, forest interior with no shrub layer (canopy species included *Acer rubrum* and *Betula alleghaniensis*); SHRUB, closed canopy, forest interior, with dense shrub layer, dominated by *R. maximum*; and OPEN, forest gap with no canopy closure, within the forest interior (Atkins et al. 2015).

Litterbag experiment

To assess relative decomposition rates, five litterbags containing a common, senescent litter (*B. alleghaniensis*) were placed within each plot. The litterbags were constructed using a fine mesh nylon with openings of 0.92 mm^2 (0.96 × 0.96 mm; thickness of nylon = 0.1 mm). The edges of each bag were sealed using a ULINE H-163 Poly bag impulse heat sealer (U-Line; Pleasant Prairie, Wisconsin, USA). The impulse sealer allows for a non-reactive, weatherproof seal. The finished size of each bag was approximately 15 × 15 cm.

A common litter was used to control for species effects. Litter for each elevation level was collected at that level (e.g., litter used in litterbags at the LOW elevation level came from trees located near those plots). Litter was collected during September 2011, in litter traps. All senescent litter used was <7 d old, as traps were placed during the second week of September 2011, and all litter was collected the following week. Senescent litter was taken to the laboratory and sorted to ensure that only intact *B. alleghaniensis* leaves were used. Leaves were oven-dried for 72 h at 60°C. Each litterbag was filled with 2 ± 0.05 g of oven-dried litter, then individually weighed and tagged with a 1″ × 3–1/2″ (2.54 × 8.89 cm) all-weather, aluminum PermaTag (Forestry Suppliers; Jackson, Mississippi, USA). Each tag was marked with a unique identifying number corresponding to plot replicate, elevation level, and vegetation cover class.

Litterbags were attached to an aluminum wire via openings in the PermaTags on each bag. The aluminum wire was then staked to the ground using landscape pins (Forestry Suppliers). Litterbags were arranged in a circle to make sure that no bag was touching another and were placed on the soil surface, fully inside the assigned plot. Five litterbags were placed at each plot on 1 October 2011. The retrieval schedule was as follows: (1) November 2011 (1 month); (2) June 2012 (8 months); (3) October 2012 (12 months); (4) June 2013 (20 months); and (5) October 2013 (24 months).

Total leaf carbon and nitrogen were assessed for initial litter and for each litter collection as outlined above using a NA 2500 Elemental Analyzer (CE Instruments, Wigan, UK). Initial leaf litter C and N values were based on analysis of leaf litter of recently senesced leaves at each elevation level (e.g., initial values of C and N for leaves at the LOW elevation were based on C and N values derived from analysis of leaves collected at that level—as outlined previously).

Nitrogen availability

Supply rates of plant available nitrogen in the soil were estimated in the field using plant root simulator probes (PRS probes; Western Ag. Innovations, Saskatoon, Saskatchewan, Canada) which have been shown to be an effective and efficient tool at measuring available nitrogen (Johnson et al. 2004). Probes were incubated in the soils from 0 to 10 cm depth for three deployments in 2010: (1) between 14 June and 14 July (30 d); (2) 1 August–1 September (30 d); and (3) 1 September–6 October (36 d). Following incubations, they were collected, refrigerated, rinsed with deionized water, and shipped to Western Ag Innovations for analyses of NH_4^+ and NO_3^-.

Soils and the organic layer

Organic layer depth for each plot was determined at three points within the plot and then averaged for a plot mean organic layer depth during the fall of 2013. Organic layer soil samples were oven-dried at 105°C and sieved to 2 mm, with roots and gravel removed, and then analyzed for total soil carbon and nitrogen using a NA 2500 Elemental Analyzer.

Data analysis and model comparisons

Relative decomposition rates of leaf litter were calculated using a single-pool negative exponential model:

$$M_t = M_0 \exp(-kt) \quad (1)$$

where M_t is the mass of litter at time t, M_0 is the initial mass of litter, e is the base of the natural logarithm, and k is the decomposition constant.

Decomposition rates were not normally distributed and were analyzed using a Kruskal–Wallis test to compare differences by both elevation and vegetation classes.

Soil nutrient availability was compared across elevation, vegetation cover class, and elevation by vegetation cover class within each time period using analysis of variance (ANOVA). Differences among time periods were not reasonably comparable based on the method used to calculate NH_4^+ and NO_3^- by Western Ag.

Differences in organic layer depth (cm), organic layer C (%), organic layer N (%), and organic layer C:N were evaluated using ANOVA. Additionally, organic layer C, organic layer N, and organic layer C:N were further evaluated using analysis of covariance (ANCOVA) with organic layer depth as a covariate. All data analyses were conducted in R 3.4 (R Core Team 2017).

Empirically derived estimates of litter decomposition were compared to modeled estimates of expected decomposition based on CDI modeling approaches as outlined in Adair et al. (2008):

$$\mathrm{CDI}_i = F_t(T_i) \times F_w(\mathrm{PPT}_i, \mathrm{PET}_i) \tag{2}$$

$$F_t(T_i) = 0.5766 \times \exp\left[308.56 \times \left(\frac{1}{56.02} - \frac{1}{(273 + T_i) - 227.13}\right)\right] \tag{3}$$

$$F_w(\mathrm{PPT}_i, \mathrm{PET}_i) = \frac{1}{1 + 30 \times \exp\left(-8.5 \times \frac{\mathrm{PPT}_i}{\mathrm{PET}_i}\right)} \tag{4}$$

where T_i is mean monthly temperature (°C), PPT_i is monthly precipitation (mm), PET_i is monthly PET (mm), and CDI_i is the monthly CDI. A singular CDI value is derived for the site based on the average of monthly CDIs (CDI_i). Data from the NCDC (Station ID: GHCND:USC00462211) from 2010 to 2012 were used to calculate monthly means of temperature, precipitation, and PET. Potential evapotranspiration was calculated as a function of mean daily air temperature (T), saturation vapor pressure ($E_s(T)$ in kPa), and day length (D) (Hamon 1963):

$$\mathrm{PET} = 29.8 \times D \times \frac{e_s(T)}{T + 273.2} \times 1.2 \tag{5}$$

A correction coefficient of 1.2 is used to adjust Hamon's method (Sun et al. 2002). $e_s(T)$ is the saturation vapor pressure (kPa) from Campbell (1998):

$$e_s(T) = 0.611 \exp\left(\frac{17.502 \times T}{T + 240.97}\right) \tag{6}$$

Adair et al. (2008) suggest that a three-pool model that includes lignin and cellulose concentrations as secondary and tertiary pools in the model (the first pool being the remaining fraction) is the best model to predict decomposition. A standard single-pool CDI model was also tested for comparison:

Single-pool model.—

$$M_t = M_0 \exp(-k \times \mathrm{CDI} \times t) \tag{7}$$

Adair et al. (2008) derive a k value of 0.5278 for this model that is adjusted by the CDI. The CDI value for the Weimer Run watershed is 0.59.

Three-pool model.—

$$M_t = M_1 \exp(-1.0669 \times \mathrm{CDI} \times t) + M_2 \exp(-0.7676 \times \mathrm{CDI} \times t) + M_3 \exp(0 \times \mathrm{CDI} \times t) \tag{8}$$

where M_1 is defined as $100 - M_2 - M_3$, M_2 is the initial cellulose concentration (36.79%) and M_3 is the initial lignin concentration (20.94%). Initial lignin and cellulose concentrations were calculated as the mean of all *B. alleghaniensis* foliar chemistry data from the Northeastern Ecosystem Research Cooperative Foliar Chemistry Database (NERC 2017).

Both the single-pool CDI model and three-pool CDI model were then compared to a spatially explicit, empirically derived watershed model that considers landscape position:

$$M_t = M_{\mathrm{LOW}} \exp(-k_1 \times t) + M_{\mathrm{MID}} \exp(-k_3 \times t) + M_{\mathrm{HIGH}} \exp(-k_3 \times t) \tag{9}$$

Results

Litterbag experiment

Litter decomposition rates were consistent with expectations with greater amounts of mass remaining at landscape positions lower in the watershed after two years (LOW 41.1%, MID 44.4%, and HIGH 47.8%). Results from beneath

vegetation cover classes after two years were also as expected, with OPEN sites having the lowest values of total leaf litter mass remaining (41.7%), followed by CANOPY sites (44.2%) and SHRUB sites (47.7%; Figs. 1, 2).

Relative decomposition rates (k) and total mass remaining (%) among elevation classes were influenced strongly by season (Appendix S1: Table S1), with significant differences after 1 month (November, 2011; $P = 0.02$) and 12 months (October 2012; $P = 0.02$). Both mass loss and k show nearly significant differences at 20 months (June 2013; $P = 0.05$) and 24 months (October 2013; $P = 0.05$). At 8 months (June 2012), the greatest homogeneity in decomposition rates with regard to elevation was present. This is of note because the winter of 2011–2012 had below-average snowfall, with much of the watershed free of snow for the entire winter and soil temperatures well below average. In comparison, the winter of 2012–2013, which corresponds with collection after 20 and 24 months, was a year of average to above-average snowfall (Fig. 3). No statistically significant differences in decomposition or mass loss are seen by vegetation cover for the entire length of the experiment (Appendix S1: Table S2).

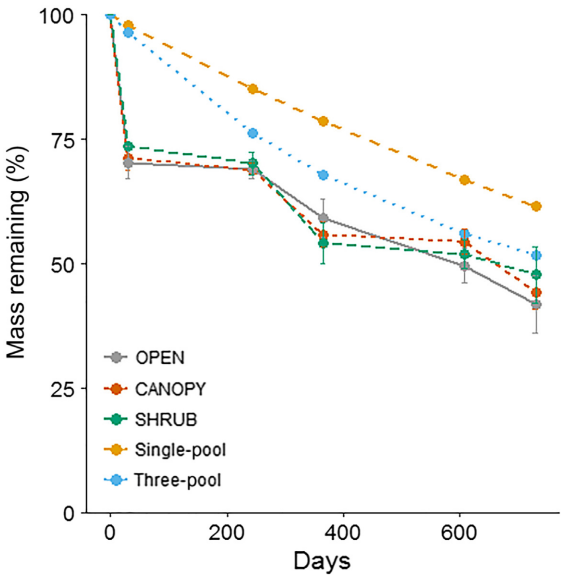

Fig. 1. Litterfall mass remaining (%) by vegetation cover class (OPEN, CANOPY, and SHRUB) with modeled decomposition estimates from both the single-pool (Eq. 7) and three-pool decay model (Eq. 8).

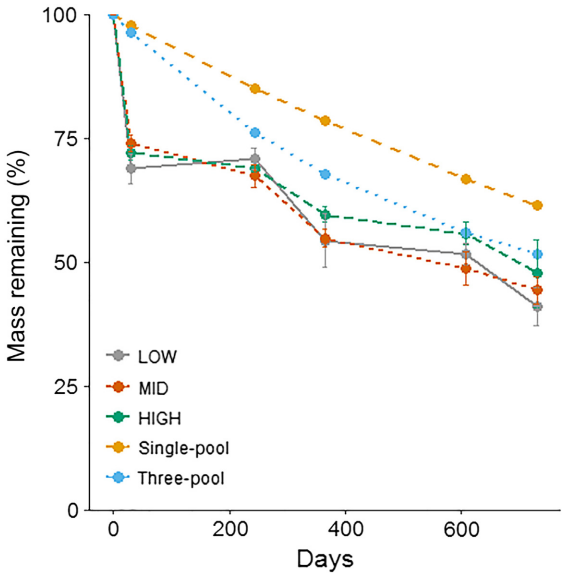

Fig. 2. Litterfall mass remaining (%) by elevation class (LOW, MID, and HIGH) with modeled decomposition estimates from both the single-pool (Eq. 7) and three-pool decay model (Eq. 8).

Initial values of litter C and N differed slightly by elevation class (carbon: LOW = 51.1 ± 0.3; MID = 52.7 ± 0.4; and HIGH = 53.3 ± 0.5; nitrogen: LOW = 2.2 ± 0.1; MID = 2.47 ± 0.0; and HIGH = 2.51 ± 0.1 with ± indicating standard deviation). Litter C:N ratio diverged underneath shrub plots from the other vegetation cover classes after 20 months (Fig. 4) driven by a decrease in N (Fig. 4). This collection period followed the second winter where both snowfall and snow depth were above the long-term mean (Fig. 3). Mean leaf litter C:N ratio for litterbag litter collected beneath shrubs was 24.32 during this collection and was much higher than at any other point. Elevated C:N ratios beneath shrubs were present across the elevation gradient. Overall decomposition rates were negatively correlated with final leaf N content ($r = -0.37$).

Nitrogen availability

Plant available soil nitrogen in the summer of 2010, measured with resin probes as NO_3^- and NH_4^+, was greater in plots beneath the forest canopy than other cover types (Table 1), an effect more pronounced at positions lower in the watershed. Plant available soil nitrogen was generally lower in August than in either June/July or

Fig. 3. Snow depth from nearby weather station CAAW2 (Canaan Valley Station 2, 39.05361, −79.44833). 2011–2012 total snowfall = 2984 mm; 2012–2013 total snowfall = 5684 mm.

September. While some plots show greater N in September, accurate comparisons between September and other months cannot be made due to the discrepancy in incubation time. However, by comparing plots within months, inferences can be made. Two-way ANOVA results comparing total inorganic N, NO_3^-, and NH_4^+ with respect to elevation, vegetation, and elevation × vegetation for June show differences in total inorganic N by vegetation cover ($F = 3.62$ $P = 0.04$), a pattern likely driven by statistically significant differences in NO_3^-, with greater NO_3^- availability in plots beneath the forest canopy ($F = 4.29$; $P = 0.03$; Appendix S1: Fig. S2) than other plots. No other significant relationships or differences were found in any other month (Table 1; Appendix S1: Table S2).

Organic layer

Two-way ANOVA results of organic layer depth show no differences among elevation and vegetation cover classes, though organic layer depth increases with elevation (Table 2; Appendix S1: Fig. S4). Organic layer C (%) does differ by vegetation ($F = 3.88$; $P = 0.04$), with shrub plots having significantly greater organic soil C (%). This in turn drives up the C:N ratios in shrub plot soils ($F = 7.03$; $P < 0.01$).

Model comparisons

The three-pool CDI decomposition model begins to converge with empirical measurements of decomposition at 20 months, but greatly underestimates the initial slope of decomposition

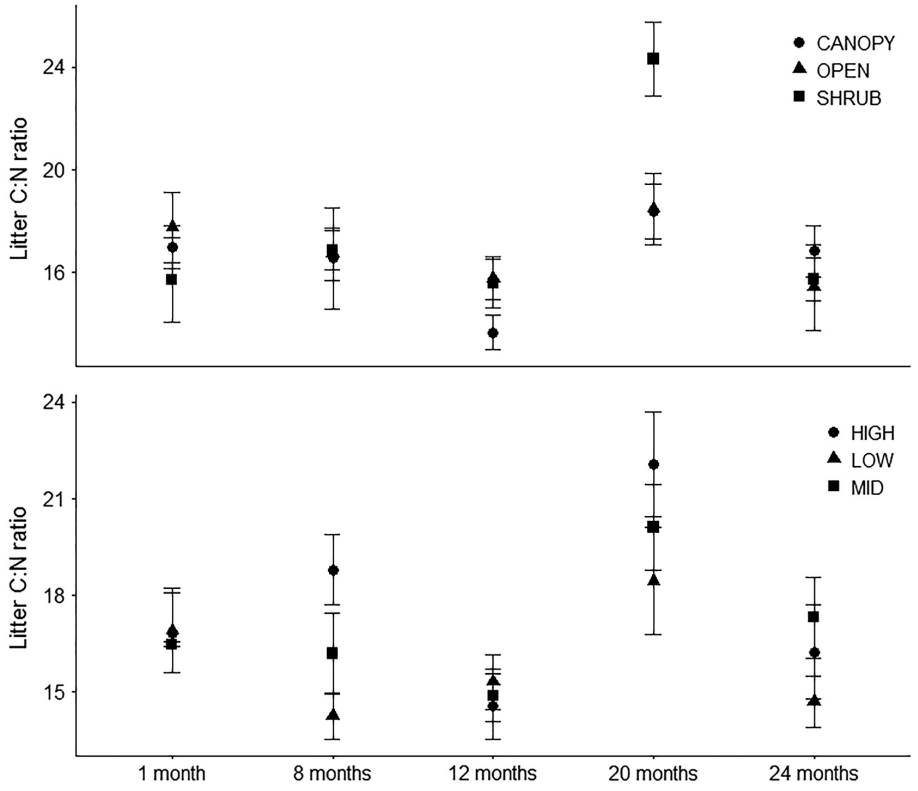

Fig. 4. Leaf litter C:N ratios following collection. Error bars indicate standard error. At top, by elevation class; at bottom, by vegetation.

Table 1. Analysis of variance results of nitrogen availability from Western Ag plant root simulator probes.

	June (30 d)		August (30 d)		September (36 d)
Species	*F*	*P*	*F*	*P*	*F*
Total N					
ELEV	1.357	0.286	0.193	0.827	0.789
VEG	3.618	**0.047**	1.447	0.271	1.609
ELEV:VEG	0.953	0.953	0.938	0.472	1.195
NO_3^-					
ELEV	0.271	0.765	2.006	0.174	0.467
VEG	4.293	**0.029**	2.586	0.113	1.444
ELEV:VEG	0.742	0.576	1.643	0.223	1.401
NH_4^+					
ELEV	2.467	0.113	0.208	0.815	0.818
VEG	2.008	0.163	0.869	0.442	1.729
ELEV:VEG	0.109	0.978	0.962	0.461	1.449

Notes: Collected during the summer of 2010. Statistically significant results shown in bold.

that occurs <8 months after litterfall (Figs. 1, 2). The single-pool CDI model fails to converge with empirical data during the two-year timeframe of this study.

Discussion

We find that spatial variance in initial decomposition of yellow birch leaf litter is primarily influenced by elevation, and secondarily by vegetation cover, with the greatest rates of decomposition found in open areas at lower elevations in the watershed. Elevation levels diverge in decomposition rates during the summer months, with greater decomposition at points lower in the watershed. Open forest gaps, lower in the watershed, tend to have greater light exposure, higher soil temperatures (OPEN = 15.6°C; SHRUB = 14.9°C; and CANOPY = 15.1°C), and greater

Table 2. Analysis of covariance (ANCOVA) results of organic layer C, N, and C:N.

Layer	ANCOVA results	
	F	*P*
Organic layer C		
Organic layer depth	0.49	0.491
ELEV	0.56	0.584
VEG	4.57	**0.029**
ELEV:VEG	0.30	0.869
Organic layer N		
Organic layer depth	2.16	0.162
ELEV	0.56	0.581
VEG	3.36	0.064
ELEV:VEG	0.74	0.579
Organic layer C:N		
Organic layer depth	0.04	0.841
ELEV	0.93	0.415
VEG	6.87	**0.008**
ELEV:VEG	0.86	0.507

Notes: Organic layer depth (cm) was used as the covariate. Statistically significant results shown in bold.

soil moisture (OPEN = 0.43 m^3/m^3; SHRUB = 0.32 m^3/m^3; and CANOPY = 0.41 m^3/m^3 measured as water-filled pore space; from Atkins et al. 2015). Given these environmental conditions, these results are expected. After one year of decomposition, similar significant results are seen (Appendix S1: Table S2). However, there are discrepancies during the winter months.

Seasonality and snowfall

Decomposition dynamics during and following the winter of 2011–2012 are an interesting anomaly in the findings. All other sampling times show significant or nearly significant differences in decomposition by elevation, yet the differences were less clear during this period (November 2011–June 2012). Snowfall during this winter totaled 2984 mm compared to the following winter (2012–2013) when snowfall totaled 5684 mm (Fig. 3). During the winter of 2011–2012, 65.9% of the time between 1 October and 31 May, snow depth was recorded at 0, whereas only 43.2% of the time during the winter of 2012–2013 was snow depth recorded at 0 (based on daily measurements of snow depth from the NCDC). Relatively low snowfall results in a spotty, underdeveloped snowpack that can lead to more prevalent and deeper soil freezing (Reinmann and Templer 2016), whereas soils beneath a well-developed snowpack remain at or above freezing during the course of the winter. Our results show support for decreased snowfall and the resultant absent or undeveloped snowpack leading to decreased decomposition and the minimization of expected altitudinal effects in this watershed. Altered snow regimes resulting in changing patterns in snow depth and inter-annual climatic variability affect water cycling which also controls carbon and nutrient cycling (e.g., nitrogen) with potential ecosystem cascades.

Observation and model comparison

The three-pool CDI model of decomposition, derived from the LIDET experiment, begins to converge with our empirical data at or near 20 months, while the single-pool model fails to converge over the two years of the study period (Figs. 1, 2). This is potentially an important implication for the use of these models. For longer-term studies, a three-pool CDI model would be appropriate. However, the initial underestimation of decomposition rates greatly affects carbon accounting. For example, litterfall mass at the Fernow Experimental Forest, located ~25 km to the east–southeast of the Weimer Run watershed, has an established range of 1.92–5.57 Mg $ha^{-1}{\cdot}yr^{-1}$ (Adams 2008), values in line with those of other central hardwood forests (Jenkins 2002). Fernow is similar to Weimer Run, but with a longer growing season. If we assume a conservative estimate of 2 Mg $ha^{-1}{\cdot}yr^{-1}$ of litterfall (~1 Mg $ha^{-1}{\cdot}yr^{-1}$ of C) for Weimer Run, we can compare the amount of C released from decomposition between an elevational composite, empirically based model (empirical model) of decomposition and the three-pool CDI model. Discretization of the Weimer Run watershed by elevation class shows that 31.7% of the watershed is in the LOW elevation, 41.3% in the MID elevation, and 26.9% classified as HIGH elevation (J. W. Atkins, H. E. Epstein, and D. L. Welsch, *unpublished manuscript*). After one month, the empirical model estimates 103.9 Mg C released, while the three-pool CDI model estimates only 7.4 Mg C. While estimates converge at 20 months as outlined previously (empirical model = 178.8 Mg C; three-pool CDI model = 173.9 Mg C), at sub-annual time scales C budgeting is substantially underestimated at the watershed scale by the CDI model.

Vegetation cover and C:N ratio

Differences in decomposition rates by vegetation cover classes may not be evident for several reasons. There may be fine-scale, localized differences in the microbial communities to which the lack of differences in decomposition could be attributed. These localized differences could be in part driven by microtopography. There is perhaps also variation in microbial composition and biomass associated with different vegetation-derived organic matter. Inferred increases in N mineralization seen beneath shrubs during periods of heavy snow indicate this as a possibility.

The relatively high N content of recently senesced yellow birch litter (overall mean initial senescent yellow birch litter: N% = 2.4; C% = 52.1; C:N = 21.7, n = 12), though within the range of past work (Schulz et al. 1982), may act as a top-down control on decomposition, whereby yellow birch litter decomposes readily despite bottom-up controls from differences in the microbial and fungal communities, along with different microclimates driven by the varying vegetation structure in this system. The absence of significant differences in decomposition rates by vegetation cover class is an unexpected result that necessitates future inquiry.

Elevated C:N ratios in leaf litter collected beneath shrub plots following the second winter in our study, where snowfall and snow depth were above long-term means, suggest that N mineralization rates increased beneath shrubs during the winter as this change in C:N is driven by decreased N (Fig. 5). A persistent, developed snowpack moderates soil temperature and moisture, creating conditions conducive to microbial activity, thus increasing decomposition and N mineralization. Conversely, the absence of snow could lead to decreased N mineralization in the system. Loss of snow driven by changes in climate and inter-annual variability could lead to colder soil temperatures and decreased plant available N within the system, which in turn could affect C sequestration, through limitations of plant growth from lack of N.

Elevated N may be observed in leaf litter over the course of decomposition, if this is a primarily bacterially dominated system, as soil bacteria typically have lower C:N ratios (5–10) than soil fungi (8–15) which leads to greater immobilization of N over the course of decomposition (Strickland and Rousk 2010). The C:N ratio of our litter remains rather low, below the estimated threshold for immobilization versus mineralization (~25:1; Chapin et al. 2002). The ratio of fungal to bacterial dominance is expected to decrease in areas of high N deposition or across increasing depositional gradients, as increased N deposition decreases fungal abundance (Lilleskov et al. 2002, Strickland and Rousk 2010). The Weimer Run watershed is

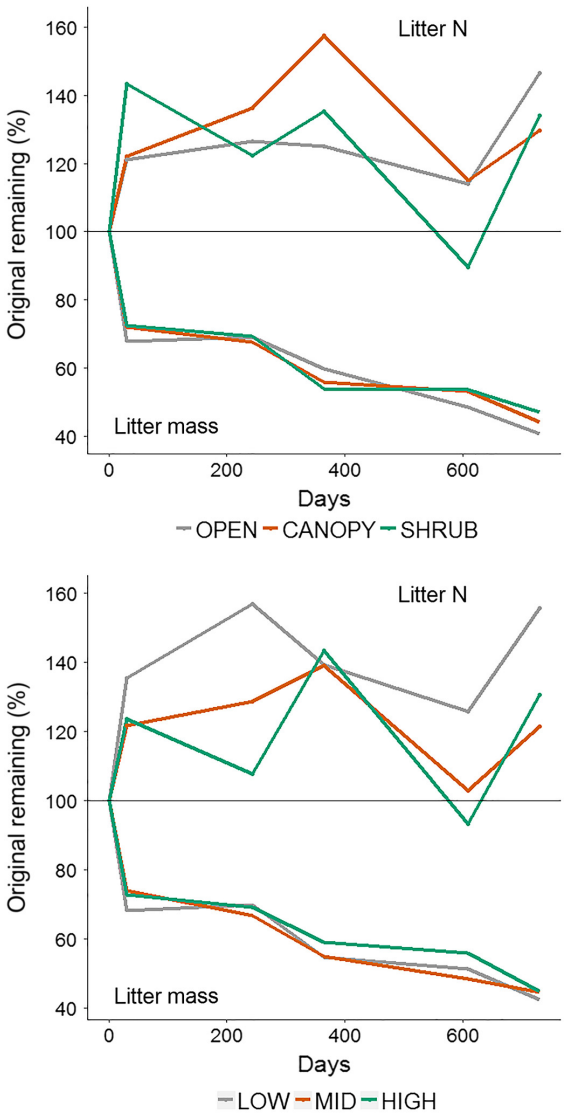

Fig. 5. Mass of litter remaining and percent nitrogen based on initial values (at top, by elevation class; at bottom, by vegetation class).

located in an area of West Virginia that receives high rates of both nitrate (12.09 kg/ha 2010–2012 mean) and ammonium deposition (3.11 kg/ha 2010–2012 mean; National Atmospheric Deposition Program [NADP]; Station WV18, Parsons, West Virginia, USA). However, the soils within the Weimer Run watershed are very acidic (below pH 4.3) and very wet (Atkins et al. 2015), conditions that do favor fungal over bacterial abundance (Rousk et al. 2009).

Given these caveats, it is possible that much of the effects of soil pH and nutrient addition examined in studies writ large are masked by methodologies that cannot accurately and conclusively determine fungal abundance (Strickland and Rousk 2010). There could also be substantial mosaicking of fungal and bacterial communities within the watershed. Our work points toward the need for further study, both broadly and within this watershed, to examine soil fungal and bacterial groups explicitly in order to tease out differences in composition and abundance along with their controls on decomposition across complex terrain.

Nitrogen availability

Plant available nitrogen, as assessed by Western Ag PRS probes, varies with vegetation, with more plant available N in areas beneath the forest canopy, early in the growing season (June). This pattern is driven by greater availability of NO_3^- which implies either greater rates of nitrification in those areas, low NO_3^- losses, or low NO_3^- uptake by vegetation—or some combination of all three processes. A comparison of the NH_4^+ to NO_3^- ratio by vegetation shows that more NO_3^- beneath shrubs and forest canopy areas is available relative to NH_4^+, implying greater rates of nitrification (Appendix S1: Fig. S4). However, the caveat should be made that direct rates of nitrification were not measured during this study. The environments beneath shrubs and canopy areas could be more conducive to nitrification, due to lower soil bulk density and higher soil porosity than open areas of the forest, despite being cooler and wetter than open areas.

Organic layer

Organic layer depth was notably deeper beneath shrubs and at higher elevations. Deeper organic soils at elevation imply lower rates of decomposition, which is in line with our findings. Higher organic layer C:N ratios beneath *Rhododendron* spp. shrubs, given their ericoid mycorrhizal associations, could lend credence to the idea of greater fungal dominance within the watershed. Conversely, nitrogen availability data coupled with implied spatial dynamics of nitrification driven by soil moisture heterogeneity (both spatial and temporal) might contradict these assertions. However, this is a very wet watershed, and lateral transfers and flows that distribute inorganic N and other nutrients more evenly are likely to be important, yet were not specifically assessed.

Threshold effects of elevation gradients

Litter decomposition has been shown to vary with elevation in the Coopers Rock State Forest in West Virginia, with higher decomposition rates along ridges and valleys and lower decomposition rates at mid-slope positions (Orndorff and Lang 1981). However, despite sharing similar climatology with Weimer Run, the elevation range tested in Coopers Rock State Forest (262–792 m) is much lower than the entire Weimer Run watershed (940–1175 m). The differences seen in decomposition along slopes at lower elevations than those tested in this study highlight the point that elevation in isolation is not a clear index of controls on decomposition in the Weimer Run watershed. This points toward a threshold effect of elevation on decomposition and element cycling that is not well understood. This possible explanation may be why differences in decomposition past one year along the elevation gradient are modulated by snowfall and the presence or absence of snowpack, and converge with broad-scale model estimates of decomposition rates.

There is a seasonal component to decomposition dynamics present in this mid-Appalachian watershed that is not evident in currently employed models of decomposition. This omission could lead to underestimating C fluxes at sub-annual time scales and lead to the propagation of uncertainty. The examination of the spatial distribution of fungal and bacterial functional groups in relation to landscape position and vegetation could further elucidate the controls on decomposition, organic layer dynamics,

and nutrient cycling in this watershed. Landscape position should be considered not only as elevation, but also along determined flow paths within the watershed that could be defined via geospatial techniques (Seibert and McGlynn 2007).

Conclusions

By employing a litterbag study using a common leaf litter (yellow birch), this study showed that initial decomposition of leaf litter varies with elevation, with greater rates of decomposition at locations lower in the watershed. Initial rates of decomposition differ significantly from standard models of decomposition by greater that 20%. Elevational effects on decomposition are only apparent within the study period during the winter with greater snowfall and longer snowpack duration. However, there are no observed differences in decomposition rates by vegetation cover class either within or among elevation classes considered in this study. Organic layer depth also increases with increasing elevation, which agrees with observed lower rates of decomposition at higher elevations. Organic layer C:N ratios are higher in plots beneath shrubs at higher elevations in the watershed. Nitrogen availability, as measured using Western Ag PRS probes, differs seasonally and by vegetation cover. Both landscape position and vegetation cover influence decomposition, nutrient availability, and organic layer development within this watershed; however, there is a complex relationship with inter-annual climate variability that exerts strong controls on these ecosystem properties. Our results, viewed within the context of climate change, indicate that inter-annual climate variability, in this case snowpack dynamics, can alter the magnitude of carbon cycling processes. The terrestrial biosphere is a significant sink for anthropogenic carbon emissions (Müller et al. 2016), and understanding these complex relationships and how they may change in both the near and distant future is crucial.

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Data Availability

All data and code for this work are available on GitHub: https://github.com/atkinsjeff/cvi_decomp2017

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1908/full