Winter Ecology: Insights from Biology and History
2017 Northeastern Naturalist 24(Special Issue 7):B209–B234

Winter Climate Change Influences on Soil Faunal Distribution and Abundance: Implications for Decomposition in the Northern Forest

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Abstract - Winter is typically considered a dormant period in northern forests, but important ecological processes continue during this season in these ecosystems. At the Hubbard Brook Experimental Forest, located in the White Mountains of New Hampshire, we used an elevational climate gradient to investigate how changes in winter climate affect the litter and soil invertebrate community and related decomposition rates of *Acer saccharum* (Sugar Maple) litter over a 2-year period. The overall abundance and richness of litter invertebrates declined with increasing elevation, while the diversity and abundance of soil invertebrates was similar across the gradient. Snow depth and soil temperature were correlated to the abundance and distribution of the litter invertebrate community, whereas soil organic matter, soil moisture, and soil frost were correlated with the distribution and abundance of the soil invertebrate community. Decomposition rates were initially faster at lower-elevation sites following 1 year of decomposition, then stabilized at the end of 2 years with no difference between higher- and lower-elevation sites. This pattern may be explained by the distribution and abundance of the litter and soil invertebrates. Higher abundances of litter invertebrates, especially Collembola, at lower-elevation sites contribute to faster initial breakdown of litter, while greater abundances of Acari in soils at higher elevation contribute to the later stages of decay. The interaction between decomposition and the associated invertebrate community responded to changes in climatic conditions, with both soil temperature and soil moisture being important determinants.

Introduction

Climate change is altering both patterns and processes in the world's ecosystems, and the forests of northeastern North America are no exception (Beier et al.

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Manuscript Editor: Ivan Fernandez

2008, Campbell et al. 2009, Durán et al. 2014, Mohan et al. 2009). Species composition, hydrologic patterns, and soil processes are changing in response to climate change, as are key ecosystem processes such as decomposition and biogeochemical cycling (Beier et al. 2008; Christenson et al. 2010; Durán et al. 2014, 2016; Pendall et al. 2008). Decomposition of plant litter is a fundamental ecological process, integral to energy flow in food-webs, nutrient cycling, and soil formation (Swift et al. 1979). As such, these processes are critical to maintaining services and the resilience of ecosystems to both anthropogenic and natural changes (Groffman et al. 2004). Both decomposition and element-cycling regulate nutrient availability, net primary productivity, and ecosystem carbon storage (Hobbie 1992). But how does climate change both directly and indirectly influence these important processes? Our work at the Hubbard Brook Experimental Forest (HBEF), located in the White Mountains of central New Hampshire, helps to address this key question through investigation of the influence of winter climate change on the structure and function of northern temperate forests (Durán et al. 2014; Groffman et al. 2009, 2012; Templer 2012). We have found strong impacts of snow depth, which influences soil freezing, decomposition, nutrient availability, and carbon storage (Christenson et al. 2010; Durán et al. 2014, 2016; Reinmann and Templer 2016; Steinweg et al. 2008; Templer et al. 2012a). What is less well understood is the biotic response to changes in snow depth. More specifically, how are litter and soil invertebrates influenced by soil freezing and in turn, how do these organisms impact decomposition?

Winter climate change in the northeastern US over the last several decades has been characterized by an overall reduction in snow pack depth and duration (Campbell et al. 2009, Groffman et al. 2012, Kreyling 2010). Snow insulates the soil system, and loss of snowpack creates colder soils with greater frequency and intensity of soil freeze/thaw cycles (Campbell et al. 2010, Durán et al. 2014). These changes alter microbial activity and community composition (Schadt et al. 2003, Schimel and Clein 1996, Schmidt and Lipson 2004, Sorensen et al. 2016a), increase N losses through greater export of nitrate (NO_3^-) in soil solution (Brooks et al. 1998, Fitzhugh et al. 2001, Mitchell et al. 1996), and increase gaseous fluxes from the forest floor to the atmosphere (Groffman et al. 2006). Soil freezing-induced losses of N are driven by increases in fine-root mortality, decreases in root vitality, and reductions in N uptake by trees (Campbell et al. 2009, Cleavitt et al. 2008, Tierney et al. 2001). Warmer temperatures and wetter conditions increase decomposition rates (Berg 2014, Harmon et al. 2009, Robinson et al. 1995); however, we have a limited understanding of how changes in winter climate can affect decomposition (Henry 2007).

Research at the HBEF has shed light on the impact that frozen soil from a lack of snow cover can have on decomposition. Experimental snow removal conducted during the months of December and January increased soil freezing and reduced litter decomposition rates (Christenson et al. 2010), but the mechanisms driving this response are unclear, as soil frost has not been found to affect soil enzyme activity or microbial biomass or activity (Groffman et al. 2001, Sorensen et al. 2016a). Christenson et al. (2010) speculated that soil freezing could impact the soil fauna,

potentially decreasing decomposition. Efforts by Templer et al. (2012) support this idea, as experimental snow removal resulted in an overall reduction in abundance and diversity of soil invertebrates.

Soil- and litter-dwelling invertebrates, along with soil microbes, are responsible for the primary decomposition process of fragmenting and moving litter within the forest floor and upper mineral soil horizons (Chamberlain et al. 2006, Swift et al. 1979, Wall 2012). The fragmentation of litter and the products generated through invertebrate activity (i.e., excrement, invertebrate detritus) accelerate subsequent microbial processing and cycling (Edwards 2000). Even though many of the same soil and litter invertebrates are found across ecosystem types, including arctic and Antarctic biomes, these organisms appear sensitive to soil-freezing conditions, with reported reductions in both total abundance and diversity following soil-freezing events (Coulson et al. 1996, Sulkava and Huta 2003, Templer et al. 2012). Sulkava and Huta (2003) found that exceptionally low soil temperatures (-16 °C) strongly suppressed abundance of soil fauna in a laboratory microcosm study, while snow-free conditions at their field site in central Finland resulted in both decreased density and richness of soil fauna. In a snow-removal experiment at the HBEF by Templer et al. (2012), litter invertebrate abundance and diversity were also reduced by soil-freezing conditions. While these short-term experiments point to the sensitivity of arthropods to soil freezing, it remains unclear how local invertebrate communities respond to more chronic stresses in the environment that might be associated with long-term warming winters and the reduction of snowpack.

Within colder biomes, enchytraeids, nematodes, and microarthropods, including Acari and Collembola, are the most dominant soil fauna (Aerts 2006). All of these organisms have evolved specific mechanisms to tolerate freezing conditions, including increased body fat (Bale et al. 2002) and the production of anti-freeze proteins (Lee 1989). These terrestrial litter and soil invertebrates can be grouped by relative size (i.e., micro: <0.1 mm, meso: 0.1–2.0 mm, and macro: >2.0 mm) and primary functional role (i.e., what they eat), and are important regulators of both physical and chemical decomposition (Wall 2012). Soil nematodes are small roundworms (<0.1 mm) that feed on bacteria, fungi, and live and dead plant material (Wall 2012). Given their feeding habits, nematodes have the ability to affect decomposition both directly through ingestion and egestion of dead plants, and indirectly through ingestion of bacteria and fungi that are the major organisms involved in the N cycle. Larger invertebrates (0.2–10.0 mm), including Acari and Collembola, are typically dominant in temperate forest soils (Wall 2012). Within Acari, oribatid mites feed on fungi and detritus, whereas Collembola are grazers of fungi. Both groups are important detritivores, shredding larger dead material into smaller fragments that are more easily accessed by microbes, as well as contributing highly labile N and C to the soil environment through excretion (Edwards 2000).

Our 2 major study objectives address the need to better understand how climate change influences the distribution and abundance of soil and litter fauna, and in turn, how these changes regulate important ecological processes. First, we aimed to determine whether the community structure and abundance of soil and litter

fauna change along a natural elevational gradient within northern hardwood forests at the HBEF. Second, we intended to determine whether the variation in composition or abundance of the invertebrate community at low- and high-elevation sites contributes to variation in decomposition rate. We used both observational and experimental approaches to understand and document the role of soil invertebrates in controlling this ecosystem process.

Field Site Description

Study sites were located at the HBEF (43°56'N, 71°45'W), located in central New Hampshire, USA, which is dominated by mature northern hardwood forest with a greater abundance of *Picea rubra* Sarg. (Red Spruce) and *Abies balsamea* (L.) Mill. (Balsam Fir) at the highest elevations (Schwarz et al. 2003). The major overstory tree species include: *Acer saccharum* Marsh. (Sugar Maple), *Betula alleghaniensis* Britt. (Yellow Birch), *Pinus resinosa* Sol. Ex Aiton (Red Pine), *Fagus grandifolia* Ehrh. (American Beech), *Fraxinus americana* L. (White Ash), and *Acer rubrum* L. (Red Maple). Soils at the HBEF are generally spodosols developed from unsorted basal till materials that can vary in depth from 75 to 100 cm and have a low pH (4.0) (Likens and Bormann 1995). In the area of our study plots, Bohlen et al. (2001) described a thick organic horizon (6.5 cm deep) overlaying deeper mineral soils. The snow pack is generally present from mid-November to mid-April (165 days, 30-year average) with average January air temperatures of -9 °C and average winter (December–March) temperatures of -4.7 °C (Hamburg et al. 2013, Hardy et al. 2001). Soils tend to freeze 2 out of every 3 years, and the long-term average annual maximum frost depth is 6 cm (Campbell et al. 2010, Cleavitt et al. 2008, Hardy et al. 2001). Once the ground freezes, it typically remains frozen underneath the snowpack for the entire winter. Average summer air temperature is 19 ºC in July, and average annual precipitation is 1400 mm (Bailey et al. 2003, Hamburg et al. 2013).

In 2010, as part of a larger climate-change project at the HBEF (Durán et al. 2016, Sorensen et al. 2016b), 20 circular plots (diameter = 10 m) were established across an elevation gradient from 375 to 770 m above and located on both south- and north-facing slopes. All 20 plots are dominated by Sugar Maple trees, with American Beech in the understory, and have similar topography. We measured abundance and diversity of litter and soil arthropods in 18 of the 20 plots in June 2011. Additionally, we selected 6 of the 20 plots to examine decomposition in concert with litter and soil invertebrates over 2 years. Three of these plots were located at higher elevation (539 m, 555 m, and 595 m) with north-facing slopes (identified as the intensive high sites), and 3 plots were at lower elevation (375 m, 411 m, and 511 m) with south-facing slopes (identified as intensive low sites). Continuous measures of soil temperature were taken from November 2010 to December 2012 at a depth of 5 cm, and soil frost and snow depth were measured weekly from December 2010 through snowmelt in April 2011. We calculated means of soil temperature over the 2-year period by season (winter = December–February, spring = March–May, summer = June–August, and fall = September–November). In general, the high-elevation sites are cooler and have deeper snow

during winter compared to the low-elevation sites, which are warmer with less snow (Durán et al. 2014).

Methods

Invertebrate field collection and laboratory processing

In each of the 18 elevation-gradient plots, we assessed the invertebrate community composition and abundance separately for the surface litter (not part of the Oi) and for soil depths of 0–5 cm and 5–10 cm; the soil samples included varying amounts of forest-floor horizons (Oi, Oe, Oa) depending upon their variable thickness. This approach was taken in order to relate soil invertebrates to soil frost depth measured from the soil surface. We collected 3 replicate surface litter samples at random within each plot over a 2-day period on 11–12 June 2011 (18 sites * 3 replicates = 54 total litter samples) to assess litter invertebrates. Each sample, which included woody debris, was collected within a 25 cm x 25 cm area. After removing surface litter, we collected 2 replicate 4-cm diameter x 10-cm depth intact soil core samples at random in each plot (18 sites * 2 replicates = 36 soil cores total). We divided each soil core into 2 sections: 0–5 cm and 5–10 cm depths (72 total soil samples). All samples were stored in Ziploc® freezer bags and placed in coolers with insulated ice packs to keep the samples at ~5 ºC during the transport to the laboratory, where they were stored at 4 ºC. We extracted invertebrates (see below) from litter samples within 48 hours of collection and from soil samples within 72 hours of collection. No precipitation occurred during sampling.

Leaf litter invertebrate extraction

We recorded the total fresh mass of each litter sample before sample processing. A 50-g (fresh weight) subsample of leaf litter from each sample was transferred to a Berlese funnel, covered with a fine-mesh screen (2 mm) to inhibit escape by invertebrates, and heated from above with a 60-W incandescent light source for 48 hours (Ruess 1995). Leaf-litter invertebrates were collected from below the funnel and stored in glass vials containing 70% ethyl alcohol. After invertebrate extraction, we dried leaf litter for 48 hours at 60 °C to determine moisture content. We used the dry mass of the sample extracted to express abundance and richness of invertebrates on a per gram dry weight basis. We used a dissecting microscope (Olympus SZH10 Research Stereo, Olympus Corp., Tokyo, Japan) to identifiy all invertebrates to order when possible.

Soil invertebrate extraction

We quantified soil invertebrates using the Berlese method (Ruess 1995) separately for the 0–5 cm and 5–10 cm depths of 1 intact, replicate soil core from each plot. The core was weighed fresh, broken apart, wrapped in a double layer of cheesecloth and placed in a funnel on a wire support frame underneath a 60-W incandescent light source for 24 hours. By gently breaking apart the small core, a shorter duration exposure to the light/heat source was required than if the cores had been left whole. After 24 h, the cores were dry and crumbly to the touch indicating

that mobile organisms would have moved away from the light/heat source. Invertebrates were collected from beneath the funnel and stored in glass vials containing 70% ethyl alcohol. After extraction, the soil from the core was dried for 48 hours at 60 °C. We measured dry mass and calculated moisture content of the soil sample. We used a muffle furnace at 550 ºC to determine percent organic matter by loss-on-ignition (Carter 1993).

Soil invertebrates were identified, counted, and weighed as described for the litter samples. For both litter and soil invertebrates, we categorized individuals as predators if they were known to be obligate predators; as non-predators if they were identified as generalists, herbivores, or detritivores; or as "both" predator and non-predator if species within the group could be either (following Wall 2012).

Litterboxes

At each of the 6 intensive sites, we established four 1 m x 2 m litterbox plots by installing mesh-screen walls (30 cm height above the forest floor) and subdivided each plot with mesh screen to create eight 50 x 50 cm subplots. Each of these subplots had ~85 g of Sugar Maple leaf litter applied in October 2011 with mesh covering the litter to separate the experimental litter addition from natural leaf fall (this set up accommodated a related ^{15}N ^{13}C-labelled litter study; see Sorensen et al. 2016). We selected Sugar Maple litter for the experimental litter addition as it is the dominant canopy tree in these plots. Our goal was to determine if the decomposition rate of Sugar Maple litter differs between the intensive high- and low-elevation sites. The subplots were sampled over a 2-year period, with litter collected from 1 subplot of each 1 m x 2 m plot over 7 collections (December 2011; March, May, July, and October 2012; and May and October 2013). We quantified mass loss at 2 time periods (October 2012 and 2013) for each subplot. During the first year of decomposition (October 2011–October 2012) , we followed the methods described above to extract the invertebrates from the litter that we collected from each subplot over the 5 sampling dates. We also collected soil invertebrates in the soils directly beneath the removed litter using a soil core and extracted them as previously described.

Data analyses

We calculated the number (abundance) of invertebrates and taxa richness (i.e., the number of orders identified) per g of litter or soil dry weight extracted and determined community diversity using the Shannon Diversity Index (H'). To evaluate elevation zone differences and the influence of aspect on our measures, we also grouped the elevation gradient plots into 3 categories—low (375–401 m), medium (511–632 m), and high (670–770 m) elevation—and identified the aspect of these plot groupings (north or south).

We tested data for normality of distribution using the Shapiro-Wilk test (PROC UNIVARIATE, SAS 9.3; Cary, NC) and log-transformed non-normally distributed dependent variables before analysis. Least-squares regression was used to determine strength of linear relationships across the elevation gradient for abundance and richness. We tested correlations between abiotic factors and invertebrate abundance

and richness across the elevation gradient with the Pearson correlation coefficient (PROC CORR, SAS 9.3), and employed a 2-way ANOVA and a Student–Newman–Keuls post hoc test (PROC GLM, SAS 9.3) to determine significant differences in abiotic conditions measured across the elevation zones with elevation group (low, medium, high) and aspect (south, north) as main effects. To determine differences in mass loss of maple litter in the litterboxes, we utilized a 2-way ANOVA and a Student–Newman–Keuls post hoc test with time (1st year, 2nd year) and elevation (low, high) as the main effects. This approach was also used to determine significant differences for invertebrate abundance measured in the litterboxes with sampling date (December 2011; March, May, July, and October 2012) and elevation (low, high) as the main effects.

Results

Environmental gradient conditions

There were differences in snow and frost depth measured across the gradient over 2 years, as well as differences in soil temperature recorded over multiple seasons (Table 1). Snow depth was significantly deeper at high-elevation sites for both south- ($P < 0.0001$) and north- ($P = 0.0005$) facing slopes (Table 1). For south-facing slopes, frost depth was significantly deeper at low- and medium-elevation plots ($P = 0.006$), whereas there was no difference in the plots with north-facing slopes (Table 1). Soil moisture and organic matter content did not differ across the gradient in June 2011 (Table 1). Mean soil temperature did vary across the gradient by season (Table 1). Spring soil temperatures were highest among the south-facing slope sites at the low-elevation plots ($P = 0.002$) and among the north-facing slope sites at the medium-elevation plots ($P = 0.001$) (Table 1). Summer and fall soil temperatures were also highest at the low- and medium-elevation plots for south- and north-facing slope sites, respectively ($P < 0.0001$, $P < 0.0001$, $P = 0.002$, $P < 0.0001$; Table 1). Winter soil temperatures were not different across the elevation gradient.

Invertebrate abundance, richness, diversity and distribution across the gradient

We identified a total of 21 invertebrate taxanomi groups (orders, phyla, and a class) representing both predatory and non-predatory invertebrates (Table 2). The most abundant (i.e., highest density) invertebrates in the litter were Acari and Collembola, followed by Diptera and Coleoptera, whereas Acari, Collembola, and Nematoda were the most abundant in soils (Table 2).

Litter invertebrates

Overall, we found a strong negative linear correlation between elevation and the mean abundances ($R^2 = 0.496$, $P = 0.001$) and total richness ($R^2 = 0.240$ $P = 0.03$) of leaf-litter invertebrates (Fig. 1, Table 3). Abundance was significantly different at each elevation grouping ($P = 0.0001$; Fig. 2A), with the greatest abundance at the low-elevation sites. Richness was significantly higher ($P = 0.03$) at the low-elevation sites compared to the middle- and high-elevation sites (Fig. 2B).

Table 1. Means (± standard error) of snow and frost depth (winter 2010/2011) soil moisture and organic matter content (June 2011) and soil temperature (determined seasonally from November 2010 to December 2012) at sites grouped by elevation (low: 375–401 m, medium: 511–632 m, high: 670–770 m) and aspect. Values with different letters are significantly different ($P < 0.05$) across elevation; upper case letters denote differences for south-aspect elevation comparisons and lower case letters for north-aspect comparisons.

Aspect	Elev.	Soil depth (cm)	Moisture (%)	SOM (%)	Snow depth (cm)	Frost depth (cm)	Mean soil temperature (°C)			
							Winter	Spring	Summer	Fall
South	Low				17.92 (± 1.49)C	4.14 (± 0.69)A	1.05 (± 0.10)	6.52 (± 0.34)A	16.15 (± 0.02 A	12.43 (± 0.21)A
		0–5	72.5 (± 13.3)	63.1 (± 25.2)						
		5–10	51.4 (± 15.7)	26.2 (± 13.3)						
	Medium				27.02 (± 2.48)B	4.35 (± 2.03)A	0.83 (± 0.36)	5.47 (± 0.53)B	15.09 (± 0.37B	10.06 (± 1.09)B
		0–5	68.8 (± 14.2)	65.7 (± 29.9)						
		5–10	56.5 (± 21.7)	48.2 (± 35.6)						
	High				31.80 (± 1.87)A	1.56 (± 0.18)B	1.01 (± 0.23)	5.61 (± 0.19)B	14.49 (± 0.29)C	9.24 (± 0.45)B
		0–5	62.3 (± 15.4)	49.6 (± 28.0)						
		5–10	52.8 (± 18.3)	33.7 (± 28.9)						
North	Medium				29.01 (± 1.62)b	3.08 (± 2.19)	0.79 (± 0.51)	4.63 (± 0.36)a	14.89 (± 0.20)a	10.49 (± 1.31)a
		0–5	68.8 (± 12.5)	55.9 (± 26.9)						
		5–10	48.9 (± 16.6)	27.9 (± 27.2)						
	High				35.73 (± 4.33)a	4.36 (± 2.26)	0.42 (± 0.06)	3.84 (± 0.36)b	14.08 (± 0.20)b	8.50 (± 0.17)b
		0–5	65.5 (± 14.1)	60.3 (± 29.2)						
		5–10	56.1 (± 16.4)	40.9 (± 30.1)						

Table 2. Litter and soil fauna mean abundance across the elevation gradient for each order/group identified and the classification of size (Micro: <0.2 mm, Meso: 0.2–10 mm, Macro: >10 mm) and trophic designation. Abundance values are mean number of individuals/g dry wt substrate extracted with standard deviation. $n = 54$ for litter abundance and $n = 36$ for soil abundance. Size class and Major food supply based on Wall et al. (2012:30) and Arnett (2000:189, 241, 287, 531, 615). Taxonomic Group are designated predator or non-predator based on primary feeding strategy. NF = not found.

Taxonomic group	Faunal size class	Litter abundance	Soil abundance 0–5 cm	Soil abundance 5–10 cm	Major food supply	Trophic designation
Acari	Meso	30.155 (± 11.665)	2.170 (± 2.300)	0.263 (± 0.384)	Plants, bacteria, fungi, soil fauna	Both
Collembola	Meso	4.590 (± 2.967)	0.823 (± 0.984)	0.158 (± 0.438)	Fungi, roots, algae	Non-predator
Diptera	Macro	0.356 (± 0.536)	0.087 (± 0.177)	0.015 (± 0.032)	Detritus, bacteria, fungi, soil fauna	Non-predator
Coleoptera	Macro	0.215 (± 0.183)	0.026 (± 0.042)	0.004 (± 0.017)	Soil fauna, roots, detritus	Both
Araneae	Macro	0.127 (± 0.214)	0.011 (± 0.026)	0.002 (± 0.010)	Soil fauna	Predator
Psocoptera	Meso	0.139 (± 0.261)	NF	NF	Detritus	Non-predator
Diplopoda	Macro	0.141 (± 0.189)	0.013 (± 0.043)	0.000 (± 0.000)	Detritus	Non-predator
Thysanoptera	Meso	0.036 (± 0.217)	0.011 (± 0.024)	0.007 (± 0.025)	Plants, fungi	Non-predator
Chilopoda	Macro	0.012 (± 0.025)	0.002 (± 0.010)	0.000 (± 0.000)	Soil fauna	Predator
Pseudoscorpion	Meso	0.023(± 0.046)	0.003 (± 0.011)	0.0008 (± 0.005)	Soil fauna	Predator
Lepidoptera	Macro	0.004 (± 0.018)	NF	NF	Plants	Non-predator
Trichoptera	Meso + macro	0.007 (± 0.044)	NF	NF	Plants, detritus	Non-predator
Isopoda	Macro	0.003 (± 0.014)	NF	NF	Detritus	Non-predator
Pauropoda	Meso	0.003 (± 0.013)	NF	NF	Fungi, detritus	Non-predator
Gastropoda	Macro	0.008 (± 0.025)	NF	NF	Detritus, plants	Non-predator
Nematoda	Micro	0.043 (± 0.078)	0.363 (± 0.385)	0.074 (± 0.110)	Roots, bacteria, fungi, soil fauna	Both
Annelida	Macro	0.034 (± 0.083)	0.032 (± 0.072)	0.012 (± 0.025)	Detritus	Non-predator
Hymenoptera	Meso + macro	0.015 (± 0.055)	0.0008 (± 0.005)	0.003 (± 0.014)	Plants, fauna	Both
Mantodea	Macro	0.001 (± 0.008)	NF	NF	Animals	Predator
Homoptera	Meso + macro	0.001 (± 0.009)	NF	NF	Plants	Non-predator
Hemiptera	Meso + macro	NF	0.002 (± 0.013)	0.0 (± 0.0)	Plants, fauna	Both

Aspect was also related to abundance and diversity of litter invertebrates. We found significant negative linear correlations between litter invertebrate abundance (R^2 = 0.584, P = 0.01) and richness (R^2 = 0.477, P = 0.027) and elevation in the south-facing sites but not on the north-facing sites (Figs. 3, 4). Leaf-litter invertebrates were significantly more abundant in the south-facing sites compared

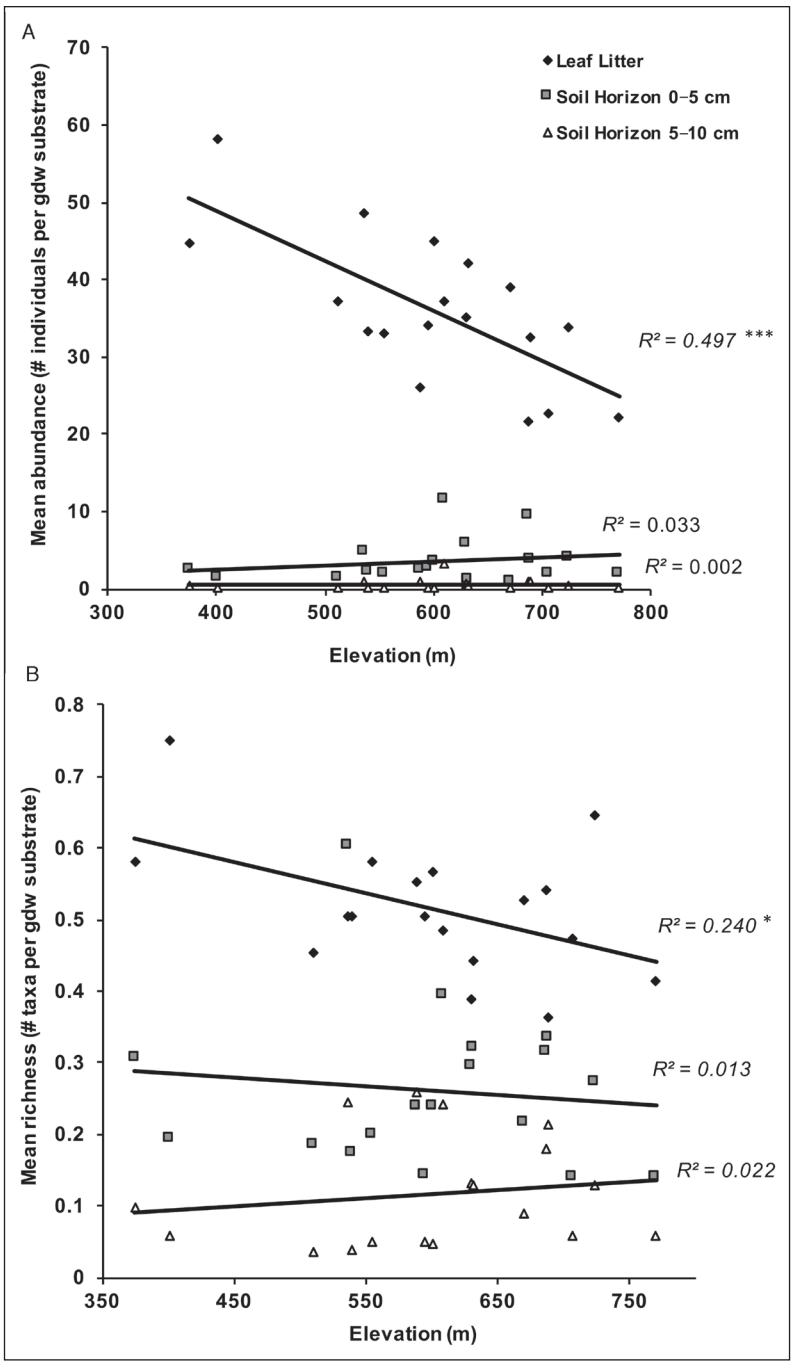

Figure 1. (A) mean abundance and (B) richness of litter and soil invertebrates collected along the 20 elevation gradient plots in June 2011. * signifies $P < 0.05$, *** signifies $P < 0.001$.

Table 3. Pearson correlation coefficients (*R*) for relationships between invertebrate abundance and richness with abiotic factors from the gradient survey, June 2011. Litter *n* = 54, soil *n* = 36.

	Litter		Soil 0–5 cm		Soil 5–10 cm	
Abitotic factors	Abundance	Richness	Abundance	Richness	Abundance	Richness
Elevation	-0.534***	-0.298*	0.151	-0.093	0.048	0.125
Moisture (%)	-0.052	0.014	0.362*	0.711***	0.594***	0.790***
Soil organic matter (%)	0.095	0.138	0.491***	0.755***	0.676***	0.818***
Snow depth (cm)	-0.535**	-0.219*	0.124	-0.131	0.035	0.152
Frost depth (cm)	0.21	0.124	0.266	0.514***	0.158	0.379*
Winter soil temperature (°C)	0.19	-0.067	-0.091	-0.142	-0.012	-0.299
Spring soil temperature (°C)	0.483***	0.145	-0.184	-0.057	-0.066	-0.233
Summer soil temperature (°C)	0.562***	0.277*	-0.176	0.053	-0.08	-0.15
Fall soil temperature (°C)	0.403**	0.205	-0.239	-0.136	-0.188	-0.366*

*Significance at 0.05 probability level
**Significance at 0.01 probability level
***Significance at 0.001 probability level

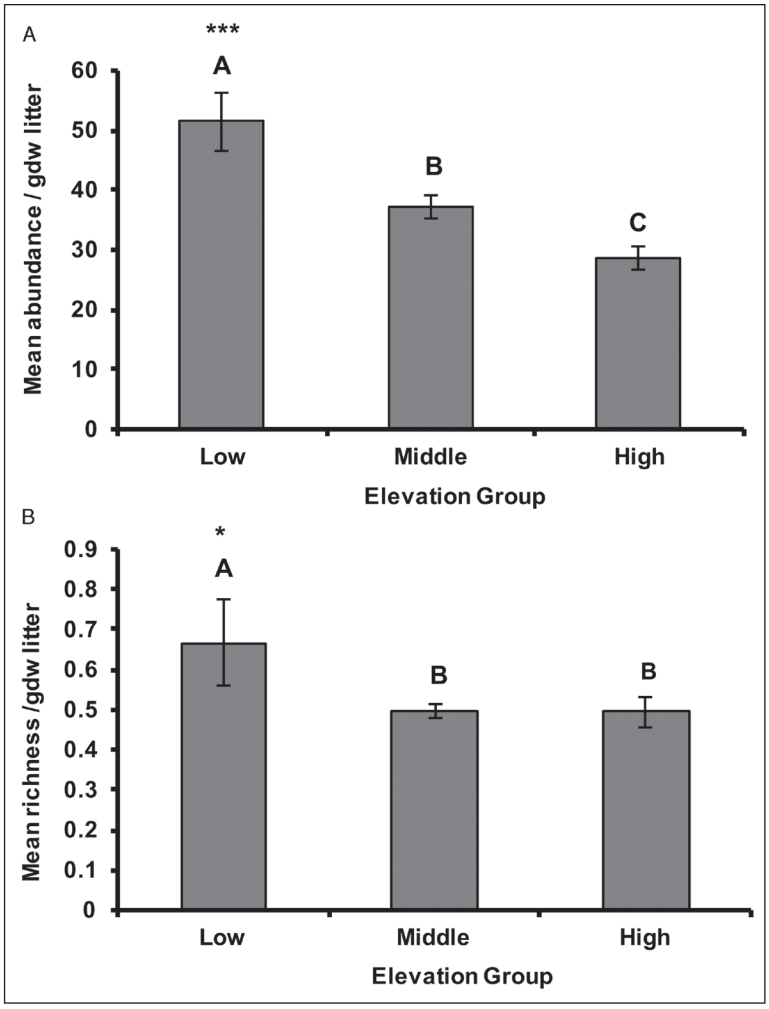

Figure 2. (A) mean abundance and (B) richness of litter invertebrates found at each of 3 distinct elevation groups (low = 375–401 m, middle = 511–632 m, high = 670–770 m). Different letters denote statistically significant differences between the groups. * signifies $P < 0.05$, *** signifies $P < 0.001$. Values are means with standard error. $n = 6$ (low), $n = 30$ (middle), $n = 18$ (high).

to the north-facing sites ($P = 0.005$; Fig. 5A). North-facing sites had significantly higher leaf-litter invertebrate diversity compared to south-facing sites ($P = 0.026$; Fig. 5B).

Litter invertebrate abundances were negatively correlated with snow depth and positively correlated with spring, summer, and fall soil temperatures (Table 3).

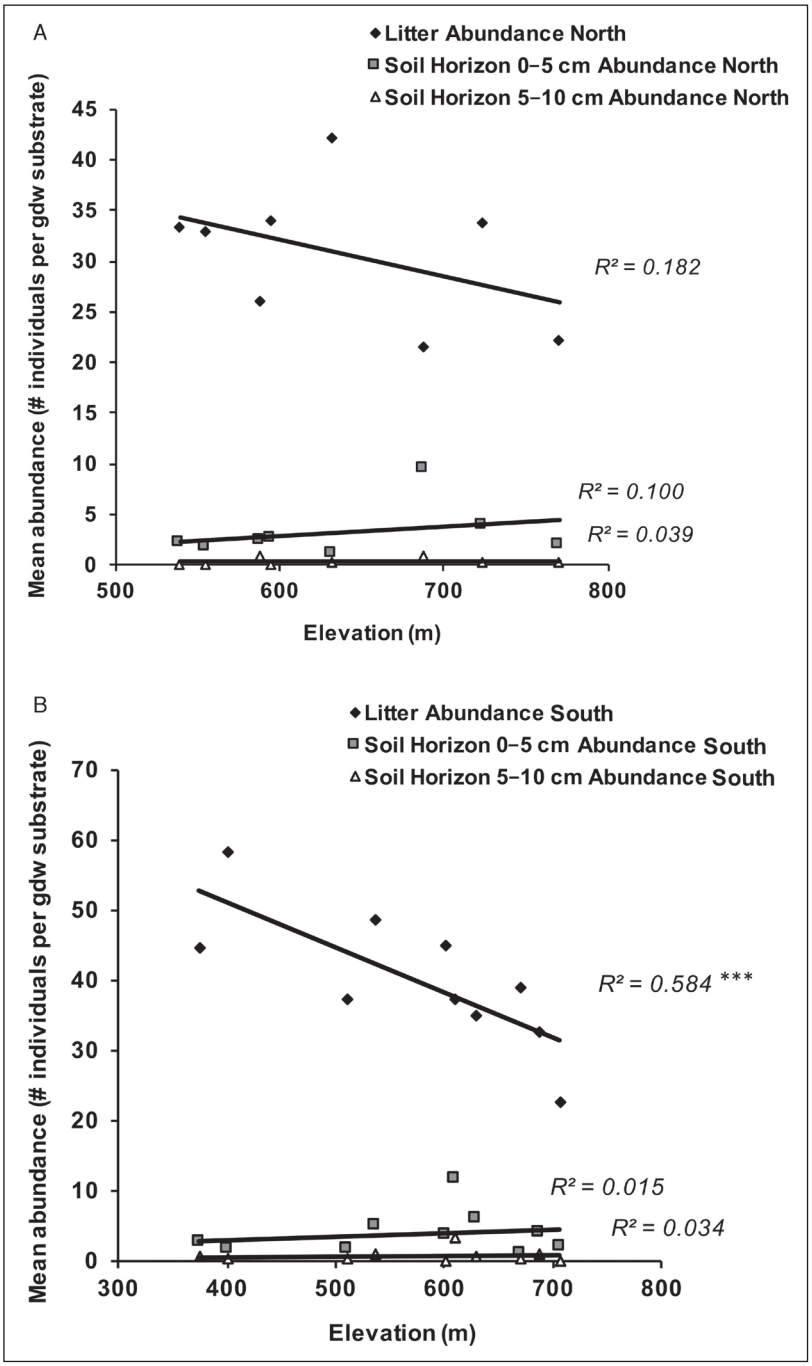

Figure 3. Mean abundance of leaf litter and soil invertebrates comparing (A) north- to (B) south-facing slopes across the elevation gradient. * signifies $P < 0.05$, *** signifies $P < 0.001$.

Litter invertebrate richness was also negatively correlated with snow depth and positively correlated with summer soil temperature (Table 3).

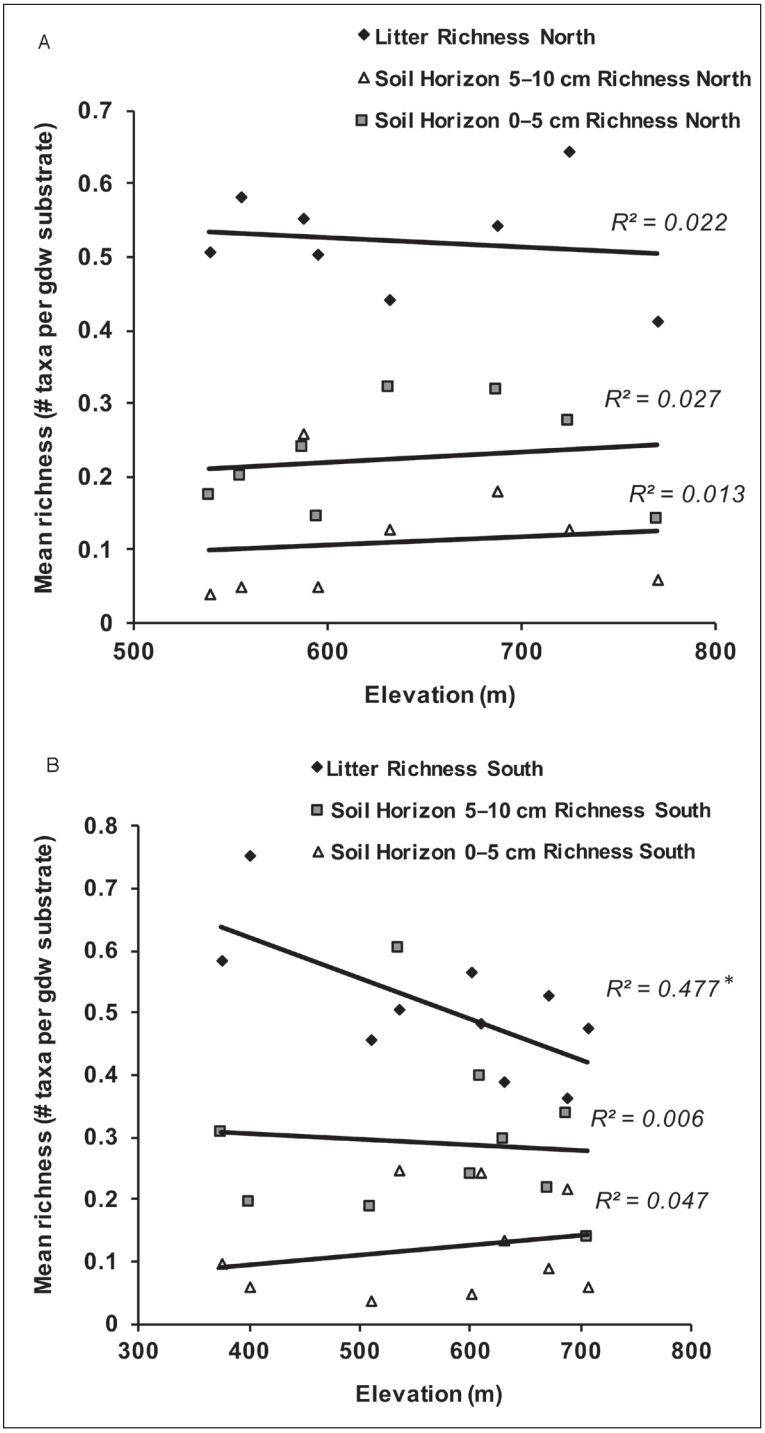

Figure 4. Richness of leaf litter and soil invertebrates comparing (A) north- to (B) south-facing slopes across the elevation gradient. * signifies $P < 0.05$, *** signifies $P < 0.001$.

Soil invertebrates

Soil fauna did not vary with elevation; we found no significant differences for either richness or abundance across the elevation gradient (Fig. 1, Table 3). Similarly, soil invertebrate abundance and richness were not related to slope aspect (Figs. 3, 4).

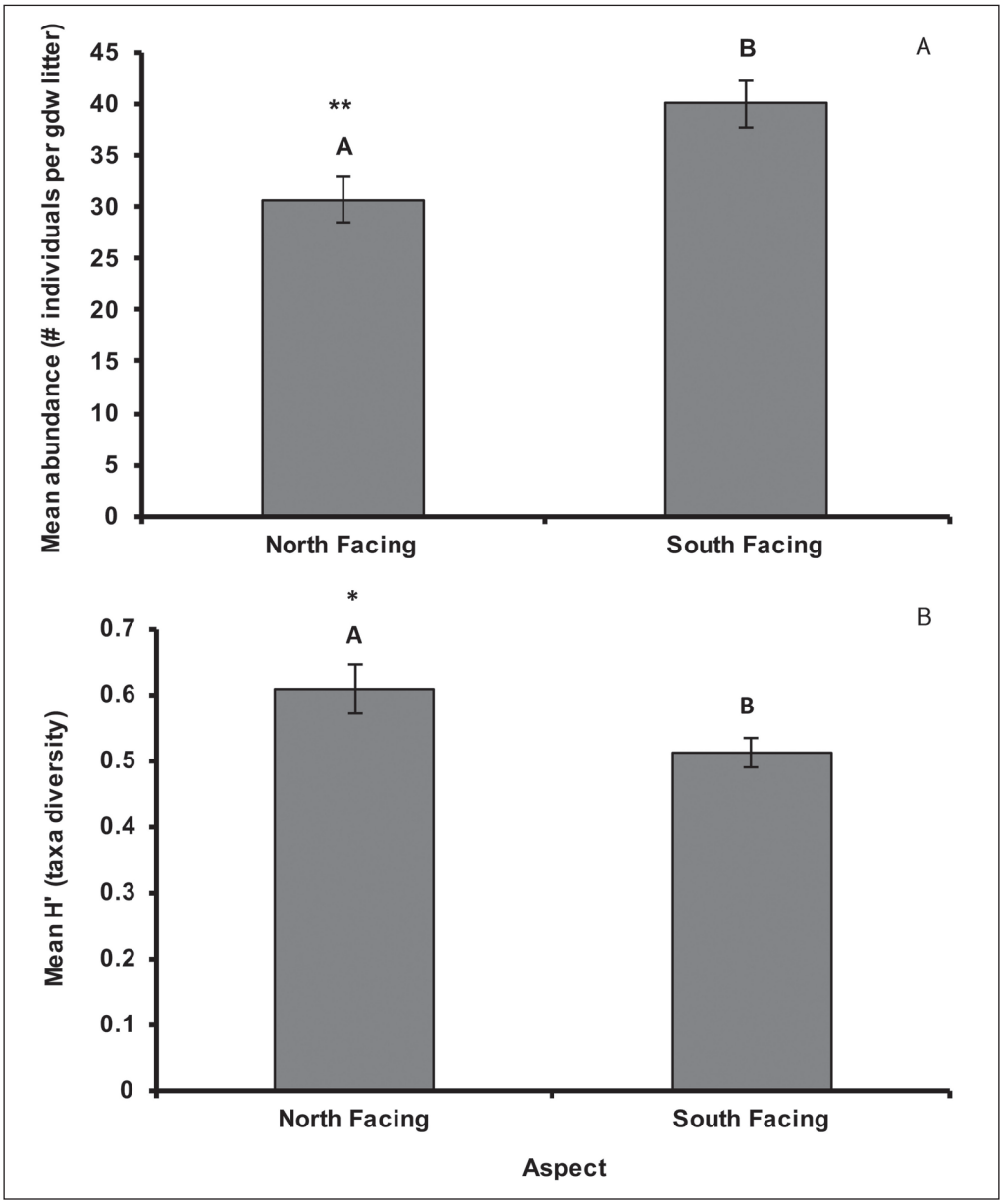

Figure 5. (A) abundance and (B) diversity of leaf litter invertebrates by aspect. Diversity is represented by H' (calculated Shannon index). Values are means with standard error. Different letters denote statistically significant difference. * signifies $P < 0.05$, ** signifies $P < 0.01$. $n = 24$ (north), $n = 30$ (south).

Moisture and soil organic matter content were positively correlated with the abundance and richness of soil invertebrates at both soil depths (Table 3). Frost depth was positively correlated to soil faunal richness in both the surface (0–5 cm) and deeper (5–10 cm) soils (Table 3). Mean fall soil temperature was negatively correlated with soil invertebrate richness in soil depths of 5–10 cm (Table 3).

Decomposition and invertebrate abundances in litterboxes

The first year of decomposition was significantly slower (i.e. more mass remaining) at the high-elevation intensive sites compared to the low-elevation intensive sites ($P = 0.004$; Fig. 6). After 2 years, mass loss was similar across the 2 elevations (Fig. 6). Litter invertebrates extracted from this decomposing litter and soil invertebrates extracted from the soil below the decomposing litter varied in abundances during the first year of decomposition (Figs. 7, 8).

Litter invertebrates

Total abundance of litter invertebrates extracted from the decomposing Sugar Maple litter differed across time and elevation (Table 4; Figs. 7, 8). This pattern

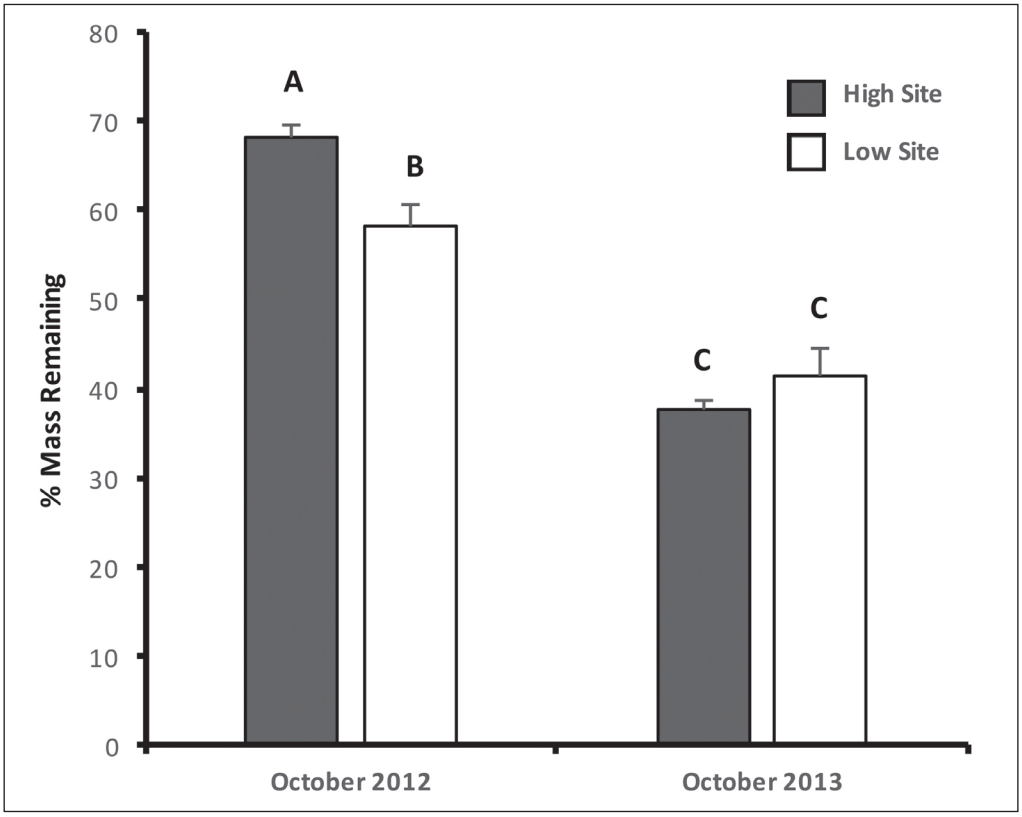

Figure 6. Percent mass of litter remaining on the intensive high versus intensive low elevation litterboxes at the end of 1 year of decomposition (October 2012) and at the end of 2 years of decomposition (October 2013). Values are means with standard error. Different letters denote statistically significant ($P < 0.01$) difference. $n = 12$.

Table 4. Two-way ANOVA results for abundances of invertebrates (total, Acari, or Collembola) in each of the substrates extracted (litter, soils 0–5 cm depth, soils 5–10 cm depth) expressed as abundance/gdw substrate extracted, collected in the litterboxes over 5 time periods during the first year of decomposition.

Substrate/abundance	Source	*F*-ratio	df	*P*-value
Litter				
Total	Time	58.80	4, 108	<0.0001
	Elevation	4.50	1, 108	0.0360
	Elev x Time	4.94	4, 108	0.0011
Acari	Time	63.47	4, 106	<0.0001
	Elevation	6.58	1, 106	0.0120
	Elev x Time	7.03	4, 106	<0.0001
Collembola	Time	16.24	3, 83	<0.0001
	Elevation	-	0	-
	Elev x Time	5.39	3, 83	0.0005
Soil 0–5 cm				
Total	Time	24.15	4, 110	<0.0001
	Elevation	1.48	1, 110	0.2250
	Elev x Time	4.01	4, 110	0.0045
Acari	Time	29.12	4, 110	<0.0001
	Elevation	0.74	1, 110	0.3910
	Elev x Time	4.32	4, 110	0.0030
Collembola	Time	4.22	4, 100	0.0030
	Elevation	4.18	1, 100	0.0440
	Elev x Time	1.88	4, 100	0.1190
Soil 5–10 cm				
Total	Time	7.97	4, 101	<0.0001
	Elevation	2.22	1, 101	0.1390
	Elev x Time	0.51	4, 101	0.7310
Acari	Time	7.99	4, 98	<0.0001
	Elevation	1.15	1, 98	0.2860
	Elev x Time	0.51	4, 98	0.7260
Collembola	Time	0.96	4, 55	0.4390
	Elevation	1.03	1, 55	0.3160
	Elev x Time	0.35	4, 55	0.8400

Figures 7 and 8 (following 2 pages). Abundance of invertebrates found in litterbox litter, shallow soils and deeper soils at the intensive low-elevation (Fig. 7) and high-elevation (Fig. 8) sites sampled during the first year of decomposition. The total abundances include all invertebrates extracted from a substrate. Values are means with standard error. Different letters denote statistically significant ($P < 0.05$) differences across dates for each abundance compared at either low or high elevation (upper case letters are used for total invertebrates, while lower case letters are used for Acari or Collembola). Note that Acari and Collembola represent almost all of the total invertebrates found in the extracted substrates. $n = 12$.

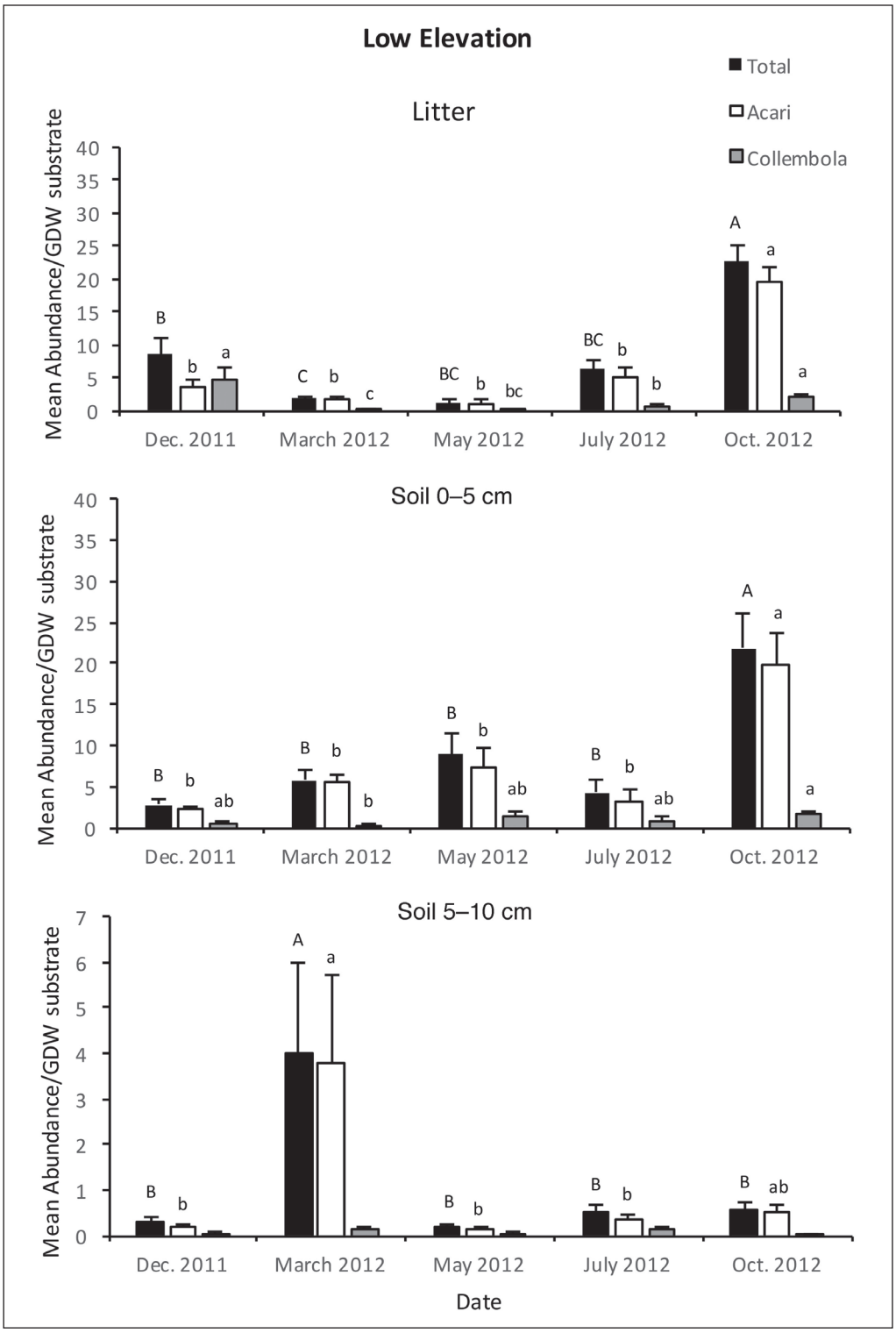

Figure. 7. [See preceding page for caption.]

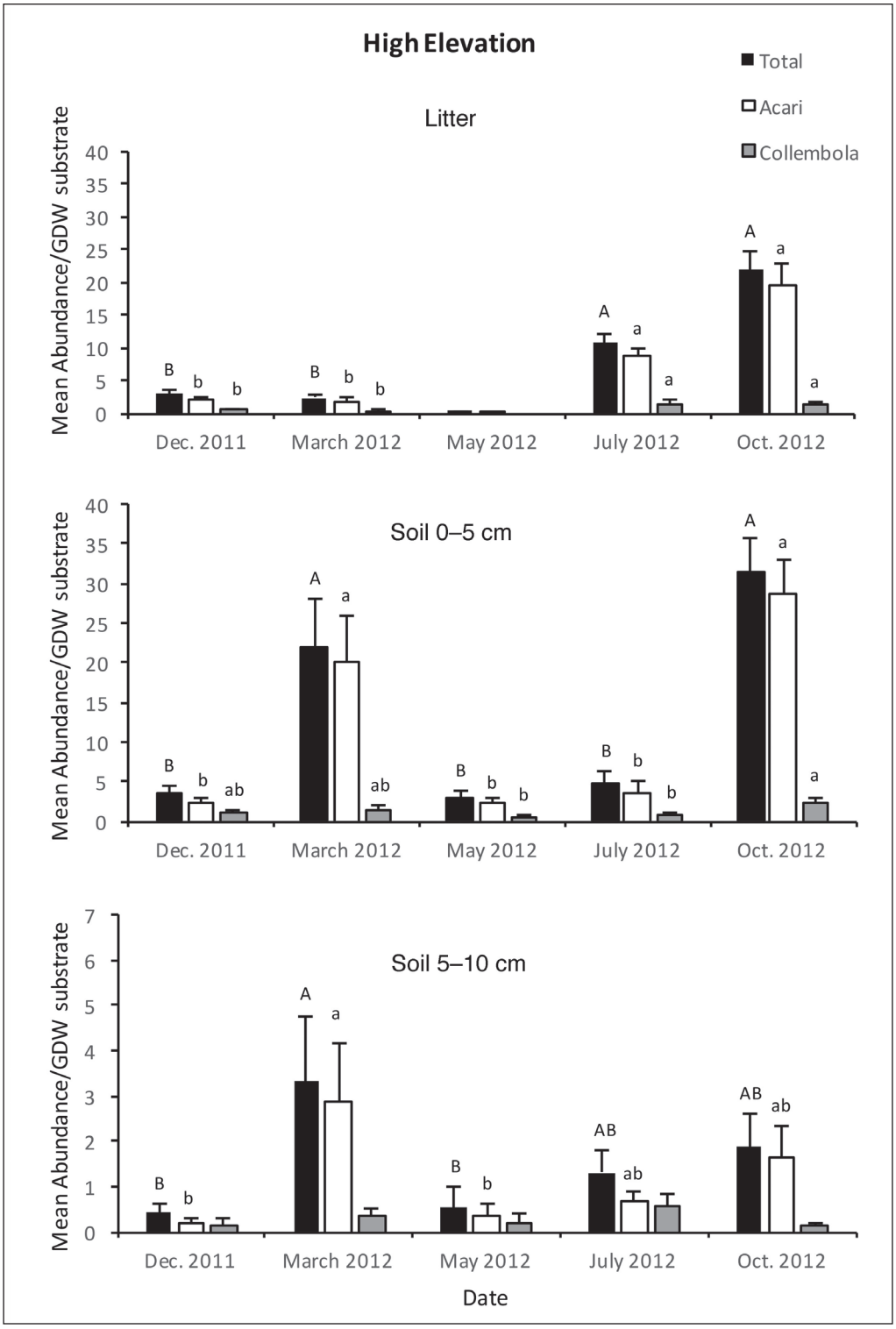

Figure. 8. [See page 16 for caption.]

was also observed in the 2 most dominant invertebrates extracted from the litter that make up this total abundance, Acari and Collembola (Table 4; Figs. 7, 8). Abundance of total litter invertebrates was highest in October 2012 for both elevations, with Acari being the dominant contributor to this pattern (Figs. 7, 8). Abundance was also higher in the low-elevation litterboxes sampled on December 2011, one month after leaf-litter application, with Collembola as a significant contributor to the total abundance (Figs. 7, 8).

Soil invertebrates

Invertebrates extracted from the soils below the litter also differed across time but were not different between the 2 elevations (Table 4; Figs. 7, 8). In the 0–5 cm soil depths, total abundances were higher in October 2012 across the 2 elevations (Figs. 7, 8). There was also a high abundance observed in March 2012 at high elevation, with Acari the dominant contributor to this total abundance (Figs. 7, 8). There were significantly fewer individuals observed in the 5–10 cm soil depths, and these invertebrates also differed across time but not elevation (Table 4; Figs. 7, 8).

Discussion

There are challenges in understanding how climate change will impact decomposition and invertebrate communities in northern forests through changes in winter snow and soil frost conditions. We expected to see differences in both decomposition and the invertebrate community composition across the elevation gradient at the HBEF, with slower loss of litter mass at sites with less snow and greater soil freezing depth and a correspondingly lower abundance and diversity of invertebrates. Contrary to our expectation, we observed the opposite pattern, with greater loss of litter mass in the first year of decomposition at the lower intensive sites compared to the higher intensive sites and an overall higher abundance and richness of litter invertebrates at lower elevation. By the end of the second year, however, we found no difference in total loss of leaf-litter mass across the sites.

We found different responses in the invertebrate community across the elevational climatic gradient to varying abiotic conditions. Litter invertebrates responded negatively to snow depth but positively to soil temperature, while soil invertebrates were positively correlated to soil moisture and organic matter content (Table 3). Both the litter and soil invertebrate communities across our study sites were dominated by Acari (mites) and Collembola. Templer et al. (2012) reported high abundances of both of these taxonomic groups in the litter layer at the HBEF, finding that Collembola responded negatively (less abundant) to soil freezing conditions induced by removal of winter snow, while Acari abundances were unaffected. They attributed this response in Collembola to decreased soil temperature. Our data support a similar response of the litter invertebrates, but a different response of the soil invertebrate community. Whereas soil temperature appears to be key in regulating abundance of leaf-litter invertebrates, soil moisture and organic matter content were more strongly correlated to soil invertebrate abundances in our study. A similar observation was made by Mitchell (1978) in *Populus* (aspen) woodland soils in

Alberta, Canada, where oribatid mites were positively correlated with soil moisture and depth of organic horizons. Coulson et al. (2000) found different responses in mites and Collembola to changes in temperature in the high arctic, where freezing soil temperatures killed Collembola but generally did not have the same effect on mites. Both temperature and other soil properties (i.e., moisture, organic matter) affect the invertebrate community at the HBEF, and the latter may offset the impact of temperature change on invertebrate response.

Litter invertebrates responded most significantly to soil temperature, especially in 3 of the 4 seasons measured (spring, summer, and fall) (Table 3). Exothermic organisms, such as soil and litter invertebrates, are influenced by temperature, with warmer temperatures being associated with greater species abundance and richness (Bale et al. 2002, Thomsen et al. 2016). Mean annual air temperatures along the HBEF elevation gradient varied by ~2 °C (Durán et al. 2014), with low-elevation sites and southerly facing slopes experiencing warmer conditions. We found the greatest abundance and richness in the litter invertebrate community in these south-facing, low-elevation locations (Figs. 1, 3, 4). Interestingly, litter invertebrates were negatively correlated with snow depth (Table 3). We originally hypothesized that snow depth would be beneficial to the invertebrate community, but this does not appear to be true for the litter invertebrates. Snow depth was more shallow on the lowest-elevation sites with a south aspect (Table 1) and deeper at the higher sites. We could be observing the effects of an earlier soil warming at the lower south-aspect sites with melting of the shallower snow pack earlier in the spring allowing for increases in soil temperature for the litter invertebrate community. Earlier loss of snow pack could lead to less moisture available later in the summer, but we did not find any difference in soil moisture conditions at the time of our study. Moreover, the litter invertebrates were not correlated to soil moisture (Table 3). Mitchell (1978) made a similar observation, where the oribatid mites he observed were not correlated to moisture in the litter layer.

Decomposition is strongly controlled by moisture, temperature, climate, organic matter quality, and soil organisms (the microbi-detritivores) (Aerts 2006, Couteaux et al. 1995). We found an interesting pattern in our decomposition study, in which the decomposition rate after 1 year was slower at the higher-elevation plots compared to the lower-elevation plots (Fig. 6). After 2 years, this pattern reversed, where litter decomposition was slightly slower in lower-elevation sites that experienced less snow and deeper soil frost (Fig. 6). This observation is similar to the finding of Christenson et al. (2010) of slower 2-year decomposition in plots at Hubbard Brook that had snow experimentally removed to induce soil freezing. Durán et al. (2016) reported no significant difference in soil moisture across these gradient sites, but did find that soils at the high-elevation sites experienced significantly lower temperature compared to the low-elevation sites from Fall 2011 to Fall 2012. Durán et al. (2016) measured the largest difference in soil temperature between the low- and high-elevation sites in spring 2012. The difference in litter decomposition is indirectly related to the difference in soil temperature, where colder temperatures decrease microbial and invertebrate activity and hence slow decomposition.

Microbial activity regulates rates of decomposition (Aerts 2006, Berg 2014), and Sorensen et al. (2016b) found significantly higher rates of net N mineralization and nitrification in the intensive high sites compared to the intensive low sites, attributing these differences to reduced enzyme activity functioning under colder temperatures. Durán et al. (2014) also reported lower rates of microbial N production at the low-elevation sites. They attributed lower microbial activity to less snow and greater soil temperature variability associated with soil freeze–thaw events, but soil organic matter content, quality, and soil moisture could also influence overall activity. Since microbial activity is lower at the low-elevation sites, we expected decomposition to be slower; surprisingly, we found greater decomposition at the low-elevation sites in year 1 (Figs. 7, 8). Moreover, given the higher N mineralization rates reported by Sorensen et al. (2016b) at the higher-elevation sites, we expected to observe faster decomposition at these sites, but we found the opposite pattern.

Litter invertebrate abundances were higher at lower and mid-elevations (Figs. 1, 2), and these invertebrates may be an important regulator of decomposition in the first year, with warmer temperatures indirectly mediating decomposition through increased abundance of the litter invertebrate community. Gonzales and Seastedt (2001) found mixed evidence for additive effects of climate and the presence of soil animals on decomposition patterns. In wet tropical zones, the presence of invertebrates increased loss of detrital organic matter mass, but they did not see this pattern in dry tropical areas. This finding would indicate that moisture plays a key role in regulating decomposition along with the invertebrate organisms. We did not find differences in moisture conditions across our gradient during sampling; therefore, we have no evidence that moisture is limiting the litter invertebrate community, with decomposition being most influenced by a greater abundance of invertebrates. Additionally, in the alpine area studied, Gonzales and Seastedt (2001) found that the presence of soil organisms increased the loss of total litter mass regardless of location on north- or south-facing slopes, indicating that the soil organisms were active regardless of slope aspect. We did find a higher abundance of litter invertebrates on the south-facing sites (Fig. 5), and this higher abundance may be the key regulator of the decomposition patterns that we observed.

If temperature is the most important factor controlling the abundance of litter invertebrates in our study, do seasonal soil temperature changes influence the overall pattern of decomposition? In a temperate mire ecosystem, Standen (1978) found that season, along with litter species and the number of active soil animals all influenced decomposition. We measured the invertebrate community over 4 seasons during the first year of decomposition and found differences in abundances for both Acri and Collembola (Figs. 7, 8). We know that litter fauna are important decomposers in the first year, fragmenting litter and excreting highly labile N and C (Aerts 2006, Wall 2012), which could accelerate the rate of mass loss. Collembola, which were more abundant in the litter substrate at the intensive low-elevation sites compared to the intensive high-elevation sites after the first month of decomposition (December 2011 sample date), may be the important early regulator of

decomposition in the first months following leaf drop (Figs. 7, 8). Warmer surface soil temperature that is conducive to higher Collembola abundance could explain why decomposition is faster at the low-elevation sites. But what could explain the pattern observed at the end of 2 years of decomposition? By the second year, much of the litter remaining is more resistant to breakdown and accumulates in the forest floor (Bardgett and Chan 1999). It is perhaps at this stage that litter becomes more exposed to soil invertebrates compared to the invertebrates found only in the litter. It appears that the shallow soils (0–5 cm depth) provide suitable conditions for a greater Acari abundance at the high-elevation sites during the end of the winter, and this finding may help to explain why decomposition "catches up" at the end of 2 years when comparing the low- to high-elevation sites. It is interesting to note that the deeper, 5–10 cm soils have significantly less abundance of invertebrates compared to the litter or shallow soil substrates; however, these soils may be important sources or refugia for invertebrates, with significantly greater abundances detected in these soils at the high-elevation sites. This pattern is most likely associated with snow and frost depth, where the deepest frost measured over the 2 years was ~5 cm, with less snow and deeper frost at the low-elevation sites.

Decomposition and nutrient cycling are important processes that regulate overall forest productivity and stability. The response of decomposition and carbon loss to changing climate can be affected by some of the smallest members of forest ecosystems: the invertebrates. Litter and soil invertebrate communities are important regulators of both decomposition and N cycling. Our study indicates a complex and possibly variable response by the litter or soil invertebrate communities. The litter invertebrate community appears to be more responsive and perhaps susceptible to variation in temperature, with Collembola being especially sensitive. The soil invertebrate community may also be affected by temperature and soil freezing, but may be more directly controlled by changes in water availability and soil organic matter content. Following the abundance and activity of these 2 groups of organisms in the future may provide an understanding of how nutrient cycling and forest productivity could be altered through changes in invertebrate-modified decomposition rates. Changes in winter climate via changes in snow depth and duration may be leading to increased soil-freezing events and these changes have the ability to alter faunal abundances and diversity. The link between soil-freezing, higher aboveground temperatures, and water availability needs to be further explored to determine which condition will have the largest impact on invertebrate community members and their control on ecosystem processes.

Acknowledgments

We would like to thank Jill Josimivitch, Jacob Damsky, and Samantha McClenahan for extensive assistance in both the field and laboratory. This project was funded by the National Science Foundation (NSF) through Grant DEB 0949300 (Ecosystem Studies). This research was conducted at the HBEF, which is owned and operated by the Northeastern Research Station, USDA Forest Service. This paper is a contribution to the Hubbard Brook Ecosystem Study.

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