Biol Fertil Soils (2012) 48:413–424
DOI 10.1007/s00374-011-0636-3

ORIGINAL PAPER

Impact of a reduced winter snowpack on litter arthropod abundance and diversity in a northern hardwood forest ecosystem

Pamela H. Templer · Andrew F. Schiller · Nathan W. Fuller · Anne M. Socci · John L. Campbell · John E. Drake · Thomas H. Kunz

Received: 20 July 2011 / Revised: 15 October 2011 / Accepted: 19 October 2011 / Published online: 23 November 2011

Abstract Projected changes in climate for the northeastern USA over the next 100 years include a reduction in the depth and duration of the winter snowpack, which could affect soil temperatures and frost regimes. We conducted a snow-removal experiment in a northern hardwood forest at the Hubbard Brook Experimental Forest in central New Hampshire over 2 years to induce soil freezing and evaluate its effect on the abundance, richness, and diversity of soil arthropods during the growing season. Snow removal at the beginning of winter increased the depth and duration of soil frost, decreased soil temperatures, and led to a reduced abundance of some arthropod taxa, including Araneae (reduced by 57%; $P=0.0001$), Pseudoscorpionida (75%; $P<0.0001$), Hymenoptera (57%; $P=0.0033$), Collembola (24%; $P=0.0019$), adult Coleoptera (23%; $P=0.0057$), and larval Diptera (33%; $P<0.0001$) and an increase in other taxa, including Hemiptera (increased by 7%; $P=0.032$). Taxa that did not respond significantly to snow removal included Chilopoda ($P=0.55$), Acari ($P=0.66$), Diplopoda ($P=0.66$), adult Diptera ($P=0.54$), and larval Coleoptera ($P=0.39$). A delayed snowpack over two winters also resulted in decreased arthropod richness by 30% ($P<0.0001$) and Simpson's index of diversity by 22% ($P=0.0002$) during the two subsequent growing seasons. Results of this study demonstrate that predicted changes in the winter snowpack and depth and duration of soil frost may reduce the abundance and alter the community composition of arthropods living in the forest floor of northern hardwood forests, which could have implications for the structure and function of northern forest ecosystems.

Keywords Climate change · Hardwood forest · Hubbard Brook experimental forest · Northern forest · Litter arthropods · Soil fauna

Introduction

Climate models for the northeastern USA over the next century predict an increase in air temperature between 2.8°C and 4.3°C and a decrease in the average number of days per year when a snowpack will cover the forest floor (Hayhoe et al. 2007, 2008; Campbell et al. 2010). Warmer temperatures may benefit some litter arthropods by allowing them to expand their ranges and to increase their rates of reproduction (Rodenhouse et al. 2009; Ladanyi and Horvath 2010). However, a reduction in snowpack depth and duration could offset these changes and lead to increased arthropod mortality because the snowpack plays an important role in insulating soil arthropods from freezing temperatures (Bale 1991). When a sufficiently deep snowpack accumulates, soils are buffered and soil temperatures tend to become decoupled from air temperatures (Edwards and Cresser 1992). A deep, insulating snowpack also maintains subnivean water availability by preventing freezing, thereby allowing arthropods to avoid mortality caused by freezing and/or desiccation during the winter.

P. H. Templer (✉) · A. F. Schiller · N. W. Fuller · A. M. Socci · J. E. Drake · T. H. Kunz
Center for Ecology and Conservation Biology,
Department of Biology, Boston University,
5 Cummington Street,
Boston, MA 02215, USA
e-mail: ptempler@bu.edu

J. L. Campbell
USDA Forest Service, Northern Research Station,
271 Mast Road,
Durham, NH 03824, USA

A study in a managed pine (*Pinus sylvestris*) plantation in Finland (Sulkava and Huhta 2003) showed that prolonged exposure to soil frost in winter leads to decreased abundance of some taxa of soil arthropods. In their study, Sulkava and Huhta (2003) used roofs to prevent snow from accumulating on the forest floor throughout winter. We are not aware of any studies that have examined the influence of a delayed winter snowpack, that more closely mimics projected changes in winter climate, on the abundance, richness, and diversity of litter arthropod communities in unmanaged temperate forest ecosystems. While it has been postulated that colder soil temperatures in winter could lead to changes in arthropod abundance, few studies have experimentally tested this hypothesis (Bale and Hayward 2010).

Factors that alter arthropod abundance, richness, and diversity could lead to changes in rates of carbon and nutrient cycling in temperate forest soils because these organisms play an important role in the decomposition of organic matter. For example, arthropods enhance rates of decomposition (Seastedt and Crossley 1983; Hättenschwiler and Gasser 2005; Wall et al. 2008; Rouifed et al. 2010), mineralization (Verhoef and Brussaard 1990), and microbial respiration (Hanlon and Anderson 1979; Kaneda and Kaneko 2008). Additionally, they can alter fungal biomass through selective feeding (e.g., preferring to feed on saprotrophs vs. ectomychorrizae; Schneider et al. 2005), exerting an indirect influence on soil processes. Soil arthropods can also lead to increases in nutrient uptake and growth of plants because their effects on soil can contribute to greater nutrient availability for roots (Setälä and Huhta 1991). Thus, increased mortality of arthropods has the potential to slow litter decomposition and reduce plant N availability in temperate forests.

Soil heterotrophs, including arthropods, are strongly influenced by soil temperatures (von Lützow and Kögel-Knabner 2009) because they are poikilothermic (i.e., their internal body temperature varies with the temperature of the environment; Salt 1961) and because their large surface area to volume ratio makes them highly susceptible to evaporative water loss (Ring and Danks 1994). Common causes of temperature-related injury and mortality among arthropods include intracellular ice formation, excessive dehydration (Duman 2001), membrane phase transitions of lipids, or denaturation of proteins (Renault et al. 2004). Many soil arthropods in temperate ecosystems have evolved mechanisms for cold tolerance and freeze resistance such as increasing polyol concentration, increasing body fat (Bale 2002), reconstructing lipid membranes (Tomcala et al. 2006), removal of ice nucleators, and use of anti-freeze proteins (Lee 1989; Duman 2001). Although soil arthropods can often tolerate temperatures below those that commonly occur in temperate soils insulated by snow in winter (Bale 2002), delayed accumulation of a winter snowpack and concomitant prolonged exposure to frozen soils could expose arthropods to temperatures sufficiently low to increase rates of mortality.

In this study, we tested the hypothesis that a decrease in the accumulation of a winter snowpack, and the resulting decrease in soil temperature and increase in soil frost, alters arthropod population abundance, richness, and diversity in the forest floor of a mixed northern hardwood forest during the following growing season.

Materials and methods

Site description

The Hubbard Brook Experimental Forest is located in the White Mountain National Forest in central New Hampshire and is a National Science Foundation Long-Term Ecological Research site. Canopy vegetation is predominantly northern hardwoods with coniferous species more prevalent at higher elevations (800–900 m) and on steeper slopes. Hardwood tree species include sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*); conifer species include red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*). Soils consist of base-poor spodosols that developed on glacial till and bedrock is generally shallow (~1 m; Johnson et al. 2000). The climate is cool, humid, and continental. The winter snowpack is usually continuous and lasts from mid-December to mid-April. Soil frost is present approximately two out of every 3 years, with an average annual maximum depth of 6 cm (Campbell et al. 2010).

Sampling

We collected litter from four paired plots that each contained a reference and treatment plot (each plot 13× 13 m^2) at the Hubbard Brook Experimental Forest. Each plot contained at least three mature sugar maple trees and included American beech saplings in the understory. Snow was removed via shoveling from the treatment plots within 48 h of snowfall for the first 5 weeks of winter in 2008/2009 and 2009/2010 to mimic a later onset and accumulation of the winter snowpack. During the snow-removal period, a 3-cm base of snow was maintained on the treatment plots to avoid disturbing the soil and litter during snow removal and to maintain the albedo of a snow-covered forest floor. Researchers wore snowshoes while shoveling in winter to reduce the degree of compaction caused by walking in the plots. We believe that the combination of the relatively large surface area of snowshoes (inducing a smaller degree of compaction compared to wearing boots) and the remaining 3-cm base of snow minimized disturbance to the forest floor beneath the snowpack. However, to account for any change in litter mass caused by shoveling, we measured the mass of litter collected per unit area on each sampling date. Reduction in litter mass could lead to less foraging space for arthropods. We randomly collected Oi and Oe horizons together (hereafter referred to as "litter"; $n=3$ per plot) from each plot during six dates each in the 2009 (20×20 cm^2 for each sub-sample) and 2010 (10×10 cm^2 each sub-sample) growing seasons (May through August), with more intensive sampling conducted at the beginning of the growing season when we expected to observe larger effects of soil frost from the previous winter. Our sampling area was smaller in 2010 than 2009 to minimize disturbance to the plots, which are part of an ongoing, long-term experiment. We accounted for this change in sample size by presenting all abundance data per unit area (m^{-2}). Litter samples were transported in individual paper bags from the field to the laboratory for processing. Each paper bag was sealed with staples to contain the arthropods, while allowing for gas exchange. Litter samples were stored at 4°C until arthropod extraction, which was initiated within 24 h of field sampling.

Each sub-sample of litter was placed in an individual Tullgren funnel from which arthropods were extracted. Funnels were 20 cm in diameter at the top and 2.5 cm in diameter at the bottom. Metal hardware cloth (0.5-cm mesh size) was placed inside each funnel at the bottom to prevent litter from falling through the funnel, while permitting arthropod passage. To reduce the possibility of arthropod escape, cheesecloth was placed over the top of each funnel and secured with a rubber band. A 60 W light bulb was positioned directly above each funnel and operated for a minimum of 48 h. Heat and litter desiccation induced by the light bulbs triggered arthropod movement from the litter into a collection jar containing 40–60 ml of 70% ethanol at the bottom of each funnel. Specimens were preserved in a minimum of 20 ml of 70% ethanol until sorted. Dry litter mass was obtained after arthropod extraction and desiccation in a convection oven at 55–60°C for at least 48 h. Percent moisture of litter was determined from the following equation:

$$\text{Percent Moisture} = 100^{*}(\text{field moist litter mass} - \text{dry litter mass})^{*}\text{dry litter mass}^{-1} \quad (1)$$

Arthropods were identified and counted using a dissecting microscope. Arthropods were sorted into the following categories: Acari (mites), Pseudoscorpionida (pseudoscorpions), Araneae (spiders), Diplopoda (millipedes), Collembola (springtails), Chilopoda (centipedes), Hemiptera (true bugs), Hymenoptera (ants, bees, and wasps), both adult and larval Coleoptera (beetles), and both adult and larval Diptera (flies). We did not classify arthropods into functional groups because soil arthropods are known to exhibit several different feeding strategies in different soil conditions (Wolters 2000) and are thought to be primarily generalist feeders (Maraun et al. 2003; Halaj et al. 2005). Moreover, the diversity of soil arthropods and an incomplete knowledge of their dietary habits make identifying their functional roles difficult (Setälä 2002; Setälä and Aarnio 2002).

We calculated taxon richness by counting the number of arthropod orders present in each plot during each sampling date; these included Araneae, Coleoptera *(*adults), Diptera (adults), Hemiptera, Hymenoptera, and Pseudoscorpionida. We did not include the other taxa (i.e., Acari, Pseudoscorpionida, Diplopoda, Collembola, and Chilopoda) in measures of richness or diversity because they were not at the same taxonomic level. We calculated Simpson's index among orders using the following equation (Simpson 1949):

$$D = \sum (n/N)^2, \quad (2)$$

where n is the number of individuals of a particular order and N is the total abundance of all orders per plot per sampling date. Using this equation, D ranges from zero (infinite diversity) to 1 (no diversity). We present 1-D, Simpson's index of diversity, in Fig. 5.

Soil temperature was measured within each plot with copper-constantan thermocouples inserted at three depths (1, 3, and 7 cm). Temperature measurements were made at 10-s intervals and hourly averages were logged. Soil temperature for each arthropod sampling date was calculated as the 24-h average for the day the sample was collected. We measured snow depth weekly throughout each winter using a Mt. Rose snow corer at four locations within each plot. Depth of soil frost was measured using four frost tubes per plot (Ricard et al. 1976). Frost tubes were constructed from flexible PVC tubing (1.3 cm in diameter) filled with methylene blue dye. The flexible tube was inserted into a rigid PVC pipe to a soil depth of 50 cm.

To determine frost depth, we removed the dye-filled tubes from the rigid pipe and measured the length of ice in the tube beneath the soil surface (the dye is excluded from the ice upon freezing).

Statistical analyses

We used a repeated measures generalized linear model with a Poisson distribution that corrected for overdispersion (Bolker et al. 2008) for arthropod abundance, order richness and diversity using the GENMOD procedure of the SAS system (Version 9.1) as described by Pedan (2001). We used a repeated measures analysis of variance to evaluate the effects of snow removal on response variables including depth and duration of snow and soil frost, litter moisture and temperature using SAS JMP software (Version 8.0.2, 2009).

Results

Depth and duration of snow and soil frost

The reference plots had a continuous snowpack between 25 November 2008 and 14 April 2009 (maximum snow depth= 98.6 cm) and between 11 December 2009 and 25 March 2010 (maximum snow depth=48.7 cm). Snow was present on the treatment plots between 4 February and 9 April 2009 (maximum snow depth=53.9 cm) and between 11 February and 25 March 2010 (maximum snow depth=19.8 cm).

The snow-removal treatment resulted in significantly greater depth and duration of soil frost compared with the reference plots in both years ($P<0.05$). For example, the maximum depth of soil frost in 2008/2009 was 6.5±0.7 vs. 37.2±1.9 cm for the reference and treatment plots, respectively, and 5.4±0.5 vs. 37.5±3.2 cm in 2009/2010. Soil frost was present in the reference plots for 99 and 133 days with an average depth of 2.2±0.5 and 1.5±0.4 cm in the winters of 2008/2009 and 2009/2010, respectively. In contrast, soil frost was present in the treatment plots for 147 and 169 days with an average depth of 25.1±3.0 and 21.4±2.8 cm in the winters of 2008/2009 and 2009/2010, respectively.

The snow-removal treatment resulted in significantly colder soils during both winters (1 January–30 April 2009 and 2010; $P=0.0085$ at 3-cm depth; Fig. 1). The mean soil temperature (at 3-cm depth) during this 4-month period was 1.22±0.15°C and 2.03±0.18°C in the reference plots in 2009 and 2010, respectively. The mean soil temperature during this 4-month period was −0.63±0.16°C and −0.09±0.20°C in the snow-removal plots in 2009 and 2010, respectively. The moisture content of litter collected during the growing season was not significantly different between the reference and treatment plots in 2009 or 2010 ($P=0.10$ in 2009 and $P=0.36$ in 2010; Table 1).

Litter mass per unit area did not differ significantly between the reference and snow-removal plots in 2009 ($P=0.31$) or 2010 ($P=0.67$), indicating that the shoveling treatment did not alter the mass of litter per unit area.

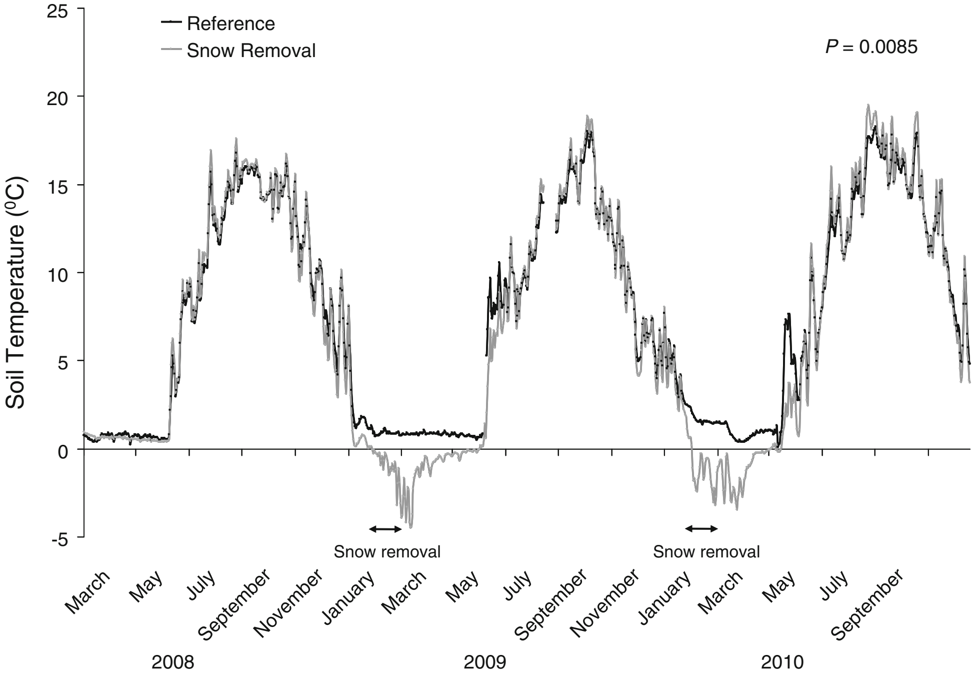


Fig. 1 Soil temperature at 3-cm depth in reference and snow-removal plots between 16 January 2008 and 2 November 2010. Snow was removed following snowfall events in 17 December 2008 to 19 January 2009 and 11 December 2009 to 20 January 2010, as indicated in the figure. *P* value shown for effect of snow removal on soil temperature from 1 January to 30 April in 2009 and 2010

Table 1 Air temperature, soil temperature (at three depths) and percent moisture among reference and treatment plots on each sampling date

Date	Plot	Air temperature (°C)	1-cm soil depth	3-cm soil depth	7-cm soil depth	% moisture
2009						
1 Jan–30 April	Reference	−3.97 (0.73)	0.97 (0.19)	1.22 (0.15)	1.23 (0.15)	
	Snow removal		−0.64 (0.19)	−0.63 (0.16)	−0.49 (0.11)	
1 May	Reference	12.72	8.81 (0.18)	7.95 (0.20)	7.83 (0.05)	178.93 (22.72)
	Snow removal		7.20 (1.13)	6.32 (1.18)	5.02 (1.38)	171.58 (14.30)
8 May	Reference	13.35	10.91 (1.12)	9.78 (1.16)	9.63 (0.98)	158.62 (7.38)
	Snow removal		8.42 (1.12)	7.61 (1.28)	6.32 (1.26)	188.46 (10.88)
12 May	Reference	7.58	8.14 (0.48)	8.02 (0.32)	7.94 (0.33)	96.47 (9.28)
	Snow removal		6.74 (0.50)	6.57 (0.59)	6.25 (0.65)	93.04 (5.13)
29 May	Reference	8.96	7.77 (0.14)	7.55 (0.10)	7.5 (0.08)	247.43 (11.65)
	Snow removal		7.62 (0.18)	7.42 (0.19)	7.24 (0.21)	242.45 (21.59)
28 June	Reference	16.66	14.6 (0.04)	13.94 (0.04)	13.82 (0.09)	189.20 (4.02)
	Snow removal		14.97 (0.33)	14.57 (0.33)	13.89 (0.37)	180.65 (10.57)
7 August	Reference	14.64	14.61 (0.07)	14.76 (0.01)	14.74 (0.01)	128.35 (1.28)
	Snow removal		14.73 (0.16)	14.77 (0.13)	14.78 (0.08)	122.54 (17.70)
2010						
1 Jan–30 April	Reference	−0.82 (0.65)	1.83 (0.22)	2.03 (0.18)	2.10 (0.18)	
	Snow removal		−0.09 (0.22)	−0.09 (0.20)	−0.03 (0.16)	
30 April	Reference	10.65	5.49 (0.40)	4.70 (0.36)	4.60 (0.28)	166.64 (12.86)
	Snow removal		4.78 (0.80)	4.33 (0.79)	3.92 (0.84)	165.57 (9.64)
10 May	Reference	2.34	4.60 (0.71)	4.98 (0.53)	4.94 (0.67)	114.92 (21.53)
	Snow removal		4.28 (0.27)	4.47 (0.31)	4.77 (0.42)	124.36 (11.14)
20 May	Reference	15.93	10.95 (0.13)	9.73 (0.24)	9.60 (0.02)	103.79 (11.56)
	Snow removal		10.88 (0.52)	10.31 (0.54)	9.51 (0.65)	95.23 (8.83)
29 May	Reference	16.38	13.31 (0.07)	12.60 (0.02)	12.54 (0.16)	30.37 (4.04)
	Snow removal		13.58 (0.46)	13.22 (0.43)	12.61 (0.56)	31.99 (8.13)
29 June	Reference	18.86	16.44 (0.34)	15.69 (0.52)	15.61 (0.32)	184.9 (14.44)
	Snow removal		16.89 (0.35)	16.51 (0.51)	15.77 (0.62)	151.20 (7.58)
10 August	Reference	19.91	17.42 (0.00)	16.78 (0.19)	16.73 (0.02)	124.27 (22.67)
	Snow removal		17.93 (0.29)	17.62 (0.37)	16.97 (0.50)	104.90 (13.92)

Values shown are means with standard error in parentheses

Arthropod abundance

For most arthropod taxa, snow removal led to a significant decrease in their overall abundance (Figs. 2, 3, and 4); these included Araneae (reduced by 57%; $P=0.0001$), Pseudoscorpionida (reduced by 75%; $P<0.0001$), Hymenoptera (reduced by 57%; $P=0.0033$), Collembola (reduced by 24%; $P=0.0019$), adult Coleoptera (reduced by 23%; $P=0.0057$), and larval Diptera (reduced by 33%; $P<0.0001$). Acari and Collembola were the most abundant taxa of arthropods found in all plots and dates sampled, accounting for more than 44-fold of all other arthropods groups combined (Figs. 2, 3, and 4). Diplopoda was least abundant taxa (Fig. 4). Taxa that did not respond significantly to snow removal included Chilopoda ($P=0.55$), Acari ($P=0.66$), Diplopoda ($P=0.66$), adult Diptera ($P=0.54$), and larval Coleoptera ($P=0.39$). While abundance of arthropods varied by date, we found no significant interactions between date sampled and treatment, nor did we observe a clear pattern of emergence (i.e., increase in arthropod abundance) throughout the growing season.

Richness of orders and Simpson's index of diversity were both significantly higher in reference plots compared with snow-removal treatment plots throughout both years ($P<0.0001$ for order richness and $P=0.0002$ for Simpson's index of diversity; Fig. 5).

Discussion

Projections for climate change in the northeastern USA over the next 100 years indicate warmer temperatures,

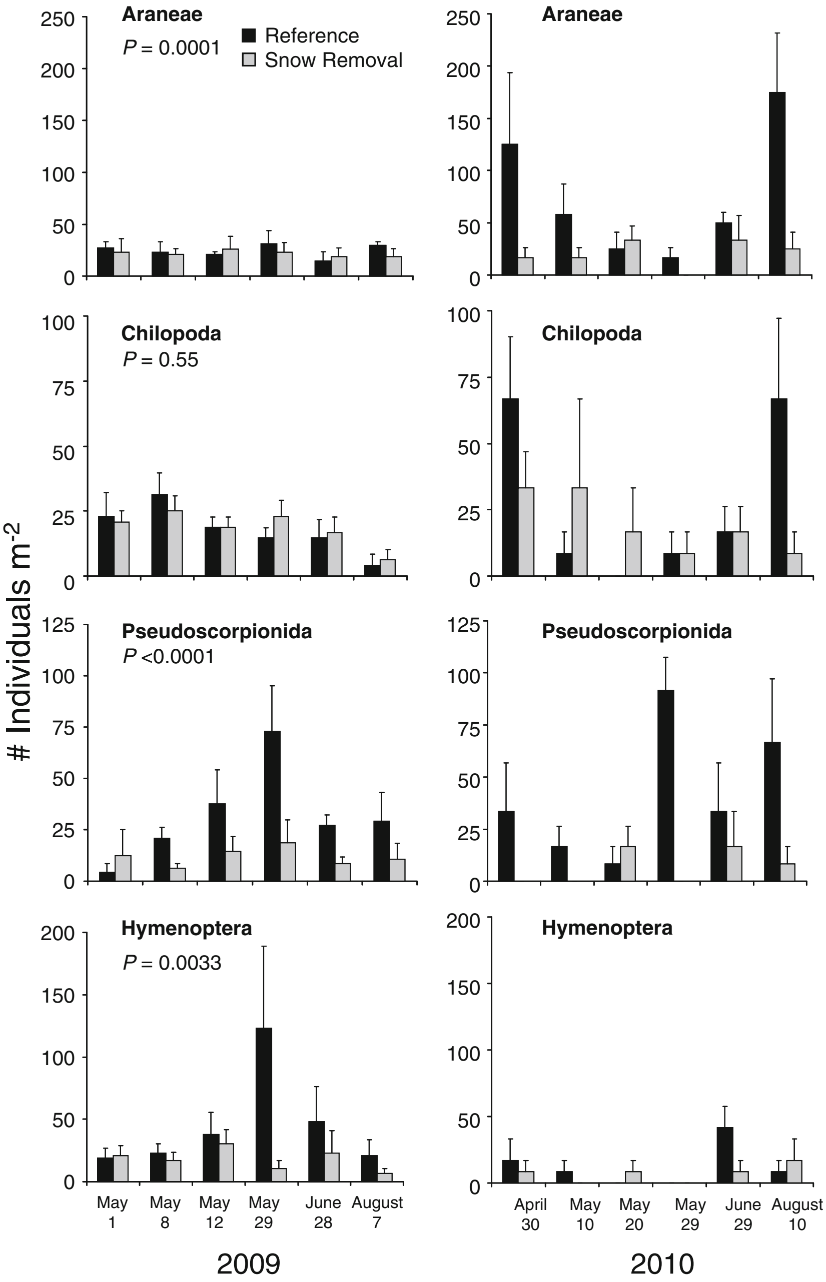


Fig. 2 Abundance of Araneae, Chilopoda, Pseudoscorpionida, and Hymenoptera during the growing seasons of 2009 and 2010. *P* values shown for effect of snow removal on arthropod abundance across both years. Values are mean and standard error. Note that arthropods were sampled more frequently at the beginning of the growing season compared to later in the growing season

longer growing seasons and a shorter duration and depth of the winter snowpack (Hayhoe et al. 2007). While warmer temperatures could lead to greater abundance, expanded distribution and increased reproductive rates of some soil arthropods (Rodenhouse et al. 2009), a shallower winter snowpack could offset these effects of climate change and lead to increased mortality of arthropods if they are not able to withstand sudden shifts in temperatures during the coldest months of the year. Results of this study show that an experimentally delayed and reduced accumulation of the winter snowpack in a northern hardwood forest, and the subsequent decrease in soil temperature and increase in soil frost, leads to a decreased abundance of some arthropod taxa, as well as decreased richness and diversity of arthropods in the following growing season. Variation among taxa in the three variables noted above could be explained by differences in tolerance to low temperatures or soil frost, varying responses to moisture, or trophic interactions among biota. It is possible that compaction caused by foot traffic during shoveling impacted arthropod abundance. However, we made considerable effort to minimize disturbance to the forest floor and therefore do not think this could explain the observed results of this experiment. In fact, bulk density of soils (Oe+Oa

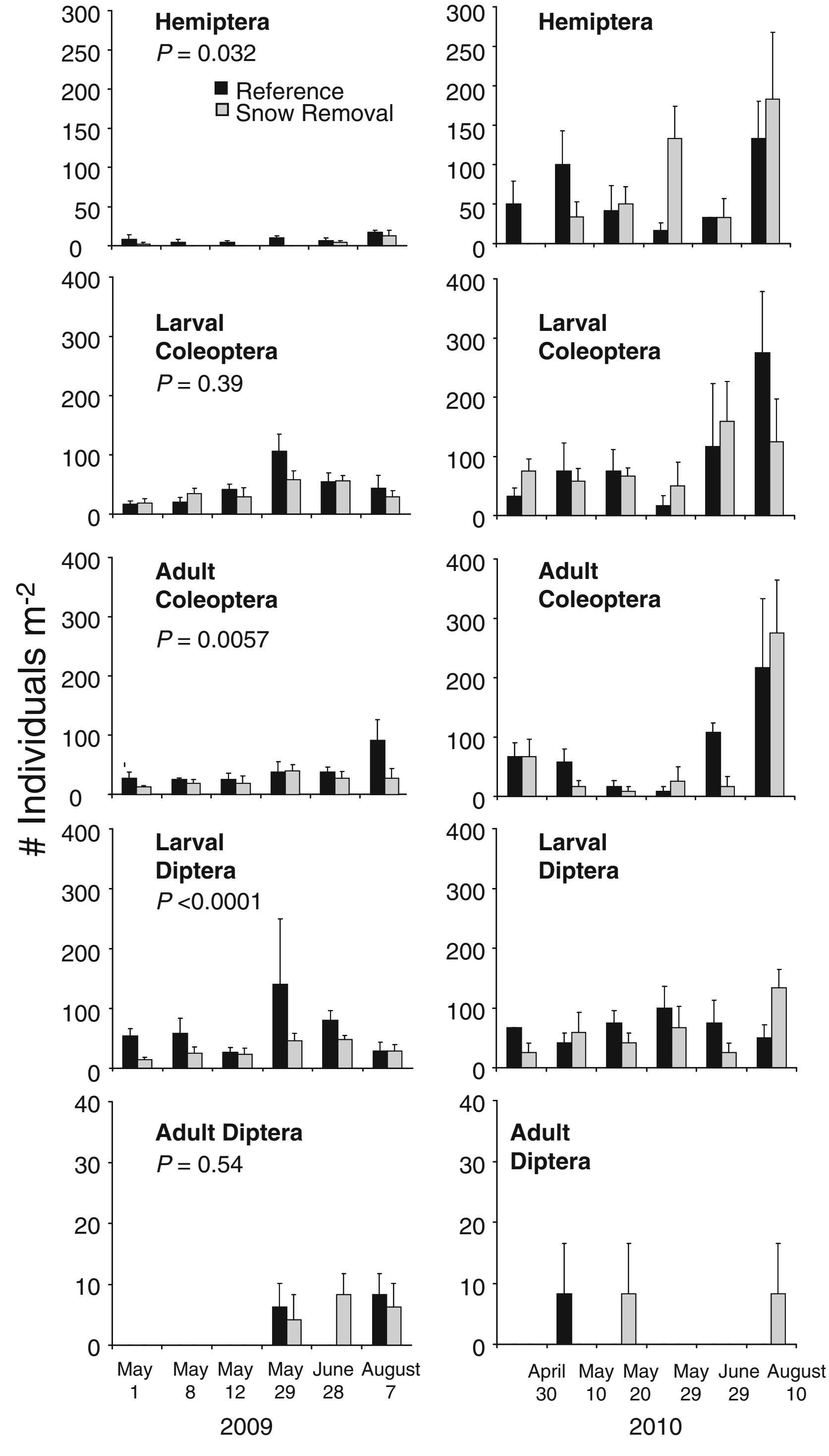
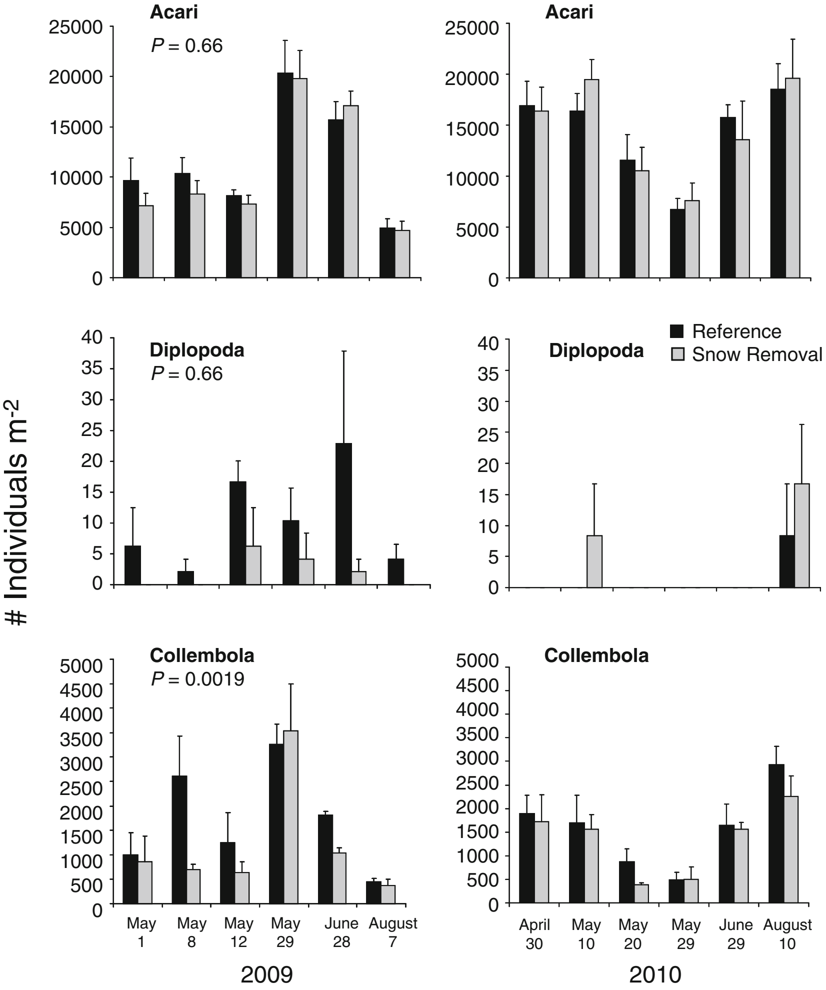


Fig. 3 Abundance of Hemiptera, larval and adult Coleoptera and larval and adult Diptera during the growing seasons of 2009 and 2010. *P* values shown for effect of snow removal on arthropod abundance across both years. Values are mean and standard error. Note that arthropods were sampled more frequently at the beginning of the growing season compared to later in the growing season

horizon) was not significantly different among the reference and treatment plots ($P=0.18$).

Based on our study design, we cannot determine whether it is the difference in soil temperature or moisture caused by snow removal that affected the abundance, richness, and diversity of arthropods. While snow removal did not result in any differences in moisture availability or soil temperature during the growing season, it is possible that water availability during the winter was reduced in the treatment plots due to freezing, which could contribute to changes in arthropod abundance. Our experimental snow-removal treatment resulted in a prolonged period of below-freezing soil temperatures and deep soil frost. Sulkava and Huhta (2003) showed that prolonged expo-

Fig. 4 Abundance of Acari, Diplopoda, and Collembola during the growing seasons of 2009 and 2010. *P* values shown for effect of snow removal on arthropod abundance across both years. Values are mean and standard error. Note that arthropods were sampled more frequently at the beginning of the growing season compared to later in the growing season



sure to frost in soils from a pine plantation had a stronger effect on arthropod abundance than an increase in freeze-thaw cycles. Our results in a temperate hardwood forest support this observation and show that prolonged exposure to soil frost can reduce the abundance and diversity of arthropod assemblages in forest ecosystems. Our results support the hypothesis that a delayed and reduced winter snowpack could significantly alter the abundance, richness, and diversity of arthropods in temperate hardwood forests.

Arthropods that responded to a reduced snowpack

The significant reduction in abundance recorded for some groups of arthropods in the treatment plots compared with the reference plots suggests that exposure to low temperatures and/or increased desiccation in winter was sufficient to induce mortality. For example, a significant reduction in abundance of Collembola occurred in treatment plots despite the fact that soil temperatures recorded in our study were above previously documented lethal levels for this group. Past studies have shown that Collembola can survive exposure to temperatures as low as −24°C to −38°C (Zettel 2000), but air and soil temperatures remained above these thresholds in both reference and treatment plots in 2009 and 2010. Past studies have shown that prolonged exposure (e.g., 1–3 months) of arthropods to relatively cold temperatures, even ones above their lower thresholds for survival, can induce mortality (Bale 1991). The relatively long period of exposure to below-freezing temperatures (approximately 5 months in both 2009 and 2010) in our snow-removal plots may have decreased the abundance of Collembola (Nedved et al. 1998). Alternatively, desiccation caused by a reduction in water availability in winter may have contributed to their reduced abundance in the treatment plots. Whatever the cause, our results show that a smaller winter snowpack in temperate hardwood forests could lead to a decline in the abundance of Collembola in these ecosystems.

Collembola are most commonly identified as secondary decomposers due to their direct top-down influence on microbial activity through grazing (Hanlon and Anderson 1979; Filser 2002), but they are also considered to be

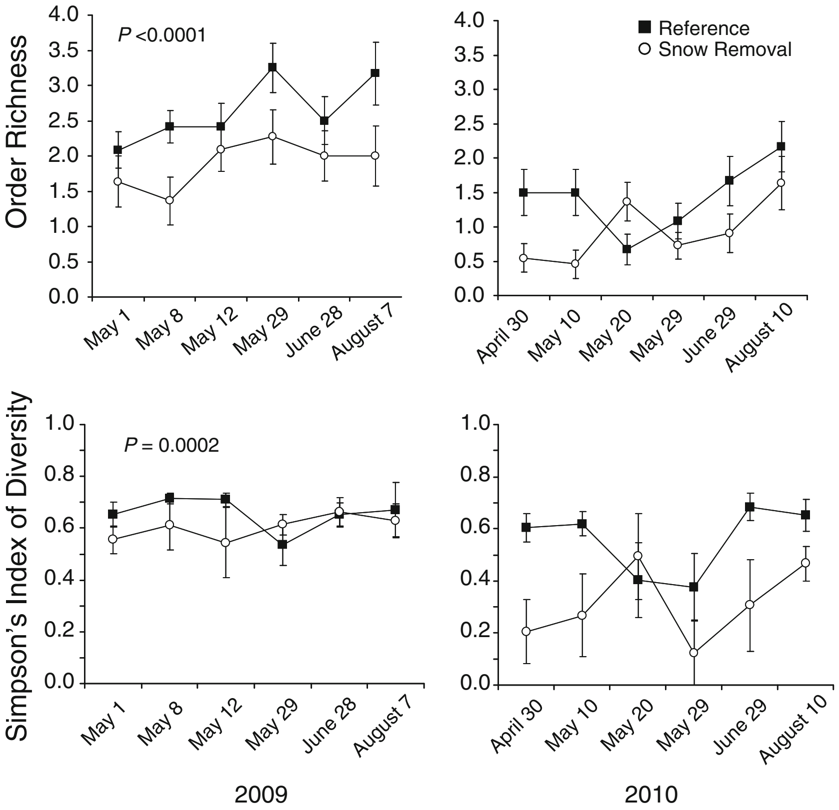


Fig. 5 Ordinal richness and Simpson's index of diversity of arthropod orders in litter during the growing seasons of 2009 and 2010. *P* values shown for effect of snow removal on order richness and Simpson's index of diversity (1-D) across both years. A value of zero indicates homogeneity and a value of one indicates infinite diversity. Values are mean and standard error. Note that order richness and diversity were measured more frequently at the beginning of the growing season compared to later in the growing season

omnivorous (Maraun et al. 2003). Because of the positive relationship between the abundance of Collembola and rates of C and N mineralization, and soil respiration (Kaneda and Kaneko 2008), significant reductions in their abundance following winters with a shallower snowpack and deep soil frost could contribute to decreased rates of C and N cycling during the subsequent growing season.

Soil arthropod predators such as Araneae (2010 only) and Pseudoscorpionida (2009 and 2010) also responded negatively to increased soil frost and decreased temperatures. Predators of arthropods in soil are known to negatively affect the biomass of prey populations (Setälä 2002; Wise 2004), which may reduce prey abundance, total soil arthropod richness and overall arthropod diversity. Soil predators can drive top–down interactions in the soil ecosystem by influencing the breakdown of leaf litter through their consumption of herbivores and detritivores (Kajak 1995). Quite often, the result of experimental reductions of predator abundance is a slowing of decomposition rates, although recent experiments suggest that the impact of predators on decomposition rates depends on environmental factors (Lensing and Wise 2006). The abundance of predators, namely spiders, can be mediated by bottom-up processes, which are usually related to the available surface area in a patticular habitat (Bultman and Uetz 1984; Wagner et al. 2003). Thus, while we observed changes in predator abundance, whether this trend is due to a response to soil frost or to a decline in prey abundance (e.g., Collembola) remains to be tested. In the case of a top–down mediated ecosystem, decreases in predator population abundance could have a positive effect on both their prey's biomass and function in forest soils, an interaction that may be affected by global climate change (Lensing and Wise 2006).

Arthropods that did not respond to a reduced snowpack

The lack of response by Chilopoda, larval Coleoptera, adult Diptera, Acari, and Diplopoda to a reduced snowpack may be due to species-specific life history traits and behavioral strategies to avoid cold-induced mortality. Many groups of arthropods have behavioral and physiological strategies that mitigate or prevent cold-induced mortality. Because specific strategies are unique to certain groups, it is difficult to generalize about entire arthropod taxa, especially the hyperdiverse orders Coleoptera and Hymenoptera. However, our data show that, because larval Coleoptera, Hymenoptera, and Chilopoda did not respond to a delayed snowpack, they are somehow able to compensate for extreme cold by employing behavioral or physiological strategies that are more effective than those used by the other arthropod groups found in this study. Further research is needed to determine the species composition of soil arthropods in northern hardwood forests, their life history traits, and the survival strategies employed by each group to prevent large scale population declines. However, given the wide range of feeding habits within Coleoptera and Hymenoptera, there could be long-term effects of soil frost on these groups due its effects on root growth and survival. For example, some Coleoptera feed on roots as larvae (Stevens et al. 2002). Soil frost negatively affects roots, leading to increased mortality (Tierney et al. 2001) and decreased vitality of surviving roots (Cleavitt et al. 2008). It is possible that repeated seasonal damage to fine root systems could lead to a legacy effect of reduced abundance of Coleoptera in subsequent years.

Because soil arthropods were able to travel freely to and from our plots, we cannot rule out the possibility that our observations are due to arthropod movement. Certain members of our targeted taxa are capable of moving greater distances than others (e.g., winged insects vs. Collembola). While we attempted to compensate for this by sampling often during the early growing season, highly mobile arthropods that emerge during early spring may have biased our observations. Future studies of this kind would benefit greatly from the incorporation of barriers to arthropod movements.

Changes in richness and diversity and implications for forest ecosystems

Reductions in ordinal richness and diversity in the snow-removal plots reflect the change in abundance of some groups of arthropods. With a reduction in snowpack depth, only arthropod taxa that have an especially high tolerance to a prolonged period (in this study approximately 5 months) of freezing and desiccation could survive the winter, effectively selecting for a subset of orders and reducing overall diversity. The significant decrease in ordinal diversity and richness during both years could have significant implications for ecosystem function of northern hardwood forests. For example, greater soil arthropod diversity has been associated with greater rates of above-ground net primary productivity (Naeem et al. 1994; Laakso and Setälä 1999). Thus, a significant reduction in diversity caused by the shallower winter snowpack in this study could lead to changes in plant dynamics by altering the rates of nutrient release from litter decomposition. Shifts in microbial community composition and function with changing temperatures have been recognized as a potential regulator of soil C stocks (von Lützow and Kögel-Knabner 2009); our study suggests that understanding of future soil C dynamics also requires consideration of temperature effects on soil fauna, such as arthropods, and their function. Future studies should help to elucidate the mechanism behind decreases in diversity observed in this study by determining changes in trophic interactions among soil arthropods as a result of a reduced snowpack.

A significant reduction in abundance of arthropods could result in reduced food availability for vertebrate insectivores and have negative consequences for reproduction, winter survival, or migration of these higher trophic levels. For example, reduction in migratory bird populations in Europe has been postulated to be a consequence of climate change (Saino et al. 2011). Because these birds time migration based on internal mechanisms and not environmental cues, their spring arrival no longer coincides optimally with insect emergence, which is timed by local environmental cues. Thus, arthropod availability during the breeding season is low and adult birds are unable to sufficiently feed their chicks (Both and Visser 2001; Both et al. 2006). Insectivorous bats may also experience similar effects, but it is unclear how they will be influenced by climate change (Jones et al. 2009; Adams 2010; Frick et al. 2010; Nebel et al. 2010). Thus, changes in assemblage structure, including shifts in ordinal richness or diversity of arthropods, could have cascading effects on the abundance of predators and hence forest function. Because arthropods represent food for higher trophic levels and influence nutrient cycling in forest ecosystems, it is important for the mechanisms behind the patterns we observed to be better understood to make explicit predictions about the effects of winter climate change on predator abundance and forest structure and function.

Acknowledgments Funding for this project was provided by the Andrew W. Mellon Foundation, the Boston University Undergraduate Research Opportunities Program (UROP), and the Northeastern States Research Cooperative (NSRC) – a joint program of the University of Vermont, the University of New Hampshire, the University of Maine, SUNY-ESF, and the Northern Research Station, USDA Forest Service. We thank Duncan Adams, Justin Brigham, Christopher Freeman, Meghan Gagne, Glenn Harrington, Stephanie Juice, Michael Mangiante, Matt Ross, Bethel Steele, Phil Thompson, Alexandra Webster, and Tammy Wooster for field assistance. Ian Halm from the USDA Forest Service provided logistical support at the Hubbard Brook Experimental Forest. We are grateful for helpful comments and suggestions on an earlier draft of this manuscript from Stephanie Juice, Nick Rodenhouse, Kimberly Wallin and Alexandra Webster. This manuscript is a contribution of the Hubbard Brook Ecosystem Study. Hubbard Brook is part of the Long-Term Ecological Research (LTER) network, which is supported by the National Science Foundation. The Hubbard Brook Experimental Forest is operated and maintained by the USDA Forest Service, Northern Research Station, Newtown Square, PA.

References

Adams RA (2010) Bat reproduction declines when conditions mimic climate change projections for western North America. Ecol 91:2437–2445

Bale JS (1991) Insects at low temperatures: a predictable relationship? Funct Ecol 5:291–298

Bale JS (2002) Insects at low temperatures: from molecular biology to distributions and abundance. Philos Trans R Soc Lond B Biol Sci 357:849–862

Bale JS, Hayward SAL (2010) Insect overwintering in a changing climate. J Exp Biol 213:980–994

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JS (2008) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135

Both C, Visser ME (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nat 411:296–298

Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. Nat 441:81–83

Bultman TL, Uetz GW (1984) Effect of structure and nutritional quality of litter on abundances of litter-dwelling arthropods. Am Midl Nat 111:165–172

Campbell JL, Ollinger SV, Flerchinger GN, Wicklein H, Hayhoe K, Bailey AS (2010) Past and projected future changes in snowpack and soil frost at the Hubbard Brook Experimental Forest, New Hampshire, USA. Hydrol Process 24:2465–2480

Cleavitt NL, Fahey TJ, Groffman PM, Hardy JP, Henry KS, Driscoll CT (2008) Effects of soil freezing on fine roots in a northern hardwood forest. Can J For Res 38:82–91

Duman JG (2001) Antifreeze and ice nucleator proteins in terrestrial arthropods. Annu Rev Physiol 63:327–357

Edwards AC, Cresser MS (1992) Freezing and its effect on chemical and biological properties of soil. Adv Soil Sci 18:61–79

Filser J (2002) The role of Collembola in carbon and nitrogen cycling in soil. Pedobiol 46:234–245

Frick WF, Reynolds DS, Kunz TH (2010) Influence of climate and reproductive timing on demography of little brown myotis (Myotis lucifugus). J Anim Ecol 79:128–136

Halaj J, Peck RW, Niwa CG (2005) Trophic structure of a macroarthropod litter food web in managed coniferous forest stands: a stable isotope analysis with ∂^{15}N and ∂^{13}C. Pedobiol 49:109–118

Hanlon RDG, Anderson JM (1979) The effects of collembolan grazing on microbial activity in decomposing leaf litter. Oecologia 38:93–99

Hättenschwiler S, Gasser P (2005) Soil animals alter plant litter diversity effects on decomposition. Proc Natl Acad Sci 5:1519–1524

Hayhoe K, Wake CP, Huntington TG et al (2007) Past and future changes in climate and hydrological indicators in the US Northeast. Clim Dyn 28:381–407

Hayhoe K, Wake C, Anderson B et al (2008) Regional climate projections for the Northeast USA. Mitig Adapt Strategies Glob Change 13:425–426

Johnson CE, Driscoll CT, Siccama TG, Likens GE (2000) Element fluxes and landscape position in a northern hardwood forest watershed ecosystem. Ecosyst 3:159–184

Jones G, Jacobs DS, Kunz TH, Willig MR, Racey PA (2009) Carpe noctem: the importance of bats as bioindicators. Endanger Species Res 8:93–115

Kajak A (1995) The role of soil predators in decomposition processes. Eur J Entomol 92:573–580

Kaneda S, Kaneko N (2008) Collembolans feeding on soil affect carbon and nitrogen mineralization by their influence on microbial and nematode activities. Biol Fertil Soils 44:435–442

Laakso J, Setälä H (1999) Sensitivity of primary production to changes in the architecture of belowground food webs. Oikos 87:57–64

Ladanyi M, Horvath L (2010) A review of the potential climate change impact on insect populations—general and agricultural aspects. Appl Ecol Environ Res 8:143–152

Lee RE (1989) Insect cold-hardiness: to freeze or not to freeze. Bioscience 39:308–313

Lensing JR, Wise DH (2006) Predicted climate change alters the indirect effect of predators on an ecosystem process. P Natl Acad Sci USA 103:15502–15505

Maraun M, Martens H, Migge S, Theenhaus A, Scheu S (2003) Adding to 'the enigma of soil animal diversity': fungal feeders and saprophagous soil invertebrates prefer similar food substrates. Eur J Soil Biol 39:85–95

Naeem S, Thompson LJ, Lawler SP, Woodfin L, Woodfin RM (1994) Declining biodiversity can alter the performance of ecosystems. Nat 368:734–737

Nebel S, Mills A, McCracken DD, Taylor PD (2010) Declines of aerial insectivores in North America follow a geographic gradient. Avian Conserv Ecol 5:1

Nedved O, Lavy D, Verhoef A (1998) Modeling the time-temperature relationship in cold injury and effect of high-temperature interruptions on survival in a chill sensitive collembolan. Funct Ecol 12:816–824

Pedan A (2001) Analysis of count data using SAS. Paper presented at the 26th International SAS Conference, Long Beach, CA.

Renault D, Nedved O, Hervant F, Vernon P (2004) The importance of fluctuating thermal regimes for repairing chill injuries in the tropical beetle *Alphitobius diaperinus* (Coleoptera: Tenebrionidae) during exposure to low temperature. Physiol Entomol 29:139–145

Ricard JA, Tobiasson W, Greatorex A (1976) The field-assembled frost gage. Technical note. Cold Regions Research Engineering Laboratory, US Army Corps Engineering, Hanover, NH. 7 pp

Ring RA, Danks HV (1994) Desiccation and cryoprotection: overlapping adaptations. Cryo-Lett 15:181–190

Rodenhouse NL, Christenson LM, Parry D, Green LE (2009) Climate change effects on native fauna of northeastern forests. Can J For Res 39:249–263

Rouifed S, Handa IT, David JF, Hättenschwiler S (2010) The importance of biotic factors in predicting global change effects on decomposition of temperate forest leaf litter. Oecologia 163:247–256

Saino N, Ambrosini R, Rubolini D et al (2011) Climate warming, ecological mismatch at arrival and population decline in migratory birds. Proc R Soc 278:835–842

Salt RW (1961) Principles of insect cold-hardiness. Annu Rev Entomol 6:55–74

Schneider K, Renker C, Maraun M (2005) Oribatid mite (Acari, Oribatida) feeding on ectomychorrhizal fungi. Mycorrhiza 16:67–72

Seastedt TR, Crossley DA (1983) Nutrients in forest litter treated with naphthalene and simulated throughfall: a field microcosm study. Soil Biol Biochem 15:159–165

Setälä H (2002) Sensitivity of ecosystem functioning to changes in trophic, structure, functional group composition and species diversity in belowground food webs. Ecol Res 17:207–215

Setälä H, Aarnio T (2002) Vertical stratification and trophic interactions among organisms of a soil decomposer food web—a field experiment using ^{15}N as a tool. Eur J Soil Biol 38:29–34

Setälä H, Huhta V (1991) Soil fauna increase *Betula pendula* growth: laboratory experiments with coniferous forest floor. Ecol 72:665–671

Simpson EH (1949) Measurement of diversity. Nature 163:688

Stevens GN, Jones RH, Mitchell RJ (2002) Rapid fine root disappearance in a pine woodland: a substantial carbon flux. Can J For Res 32:2225–2230

Sulkava P, Huhta V (2003) Effects of hard frost and freeze–thaw cycles on decomposer communities and N mineralization in boreal forest soil. Appl Soil Ecol 22:225–239

Tierney GL, Fahey TJ, Groffman PM, Hardy JP, Fitzhugh RD, Driscoll CT (2001) Soil freezing alters fine root dynamics in a northern hardwood forest. Biogeochem 56:175–190

Tomcala A, Tollarova M, Overgaard J, Simek P, Kostal V (2006) Seasonal acquisition of chill tolerance and restructuring of membrane glycerophospholipids in an overwintering insect: triggering by low temperature, desiccation and diapause progression. J Exp Biol 209:4102–4114

Verhoef HA, Brussaard L (1990) Decomposition and nitrogen mineralization in natural and agro-ecosystems: the contribution of soil animals. Biogeochem 11:175–211

von Lützow M, Kögel-Knabner I (2009) Temperature sensitivity of soil organic matter decomposition—what do we know? Biol Fertil Soils 46:1–15

Wagner JD, Toft S, Wise DH (2003) Spatial stratification in litter depth by forest-floor spiders. J Arachnol 31:28–39

Wall DH, Bradford MA, St. John MG et al (2008) Global decomposition experiment shows soil animal impacts on decomposition are climate-dependant. Glob Change Biol 14:2661–2677

Wise DH (2004) Wandering spiders limit densities of a major microbi-detritivore in the forest-floor food web. Pedobiologia 48:181–188

Wolters V (2000) Invertebrate control of organic matter stability. Biol Fertil Soils 31:1–19

Zettel J (2000) Alpine Collembola—adaptations and strategies for survival in harsh environments. Zool 102:73–89