ECOGRAPHY

Research

Seedling responses to decreased snow depend on canopy composition and small-mammal herbivore presence

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Ecography
42: 1–11, 2018
doi: 10.1111/ecog.03948

Subject Editor: Eric Post
Editor-in-Chief:
Jens-Christian Svenning
Accepted 11 September 2018

Winter is becoming warmer and shorter across the northern hemisphere, and reductions in snow depth can decrease tree seedling survival by exposing seedlings to harmful microclimates. Similarly, herbivory by small mammals can also limit the survival and distribution of woody plants, but it is unclear whether winter climate change will alter small-mammal herbivory. Although small-scale experiments show that snow removal can either increase or decrease both soil temperatures and herbivory, we currently lack snow-removal experiments replicated across large spatial scales that are needed to understand the effect of reduced snow. To examine how winter herbivory and snow conditions influence seedling dynamics, we transplanted *Acer saccharum* and *Tsuga canadensis* seedlings across a 180 km latitudinal gradient in northern Wisconsin, where snow depth varied seven-fold among sites. Seedlings were transplanted into one of two herbivory treatments (small-mammal exclosure, small-mammal access) and one of two late-winter snow removal treatments (snow removed, snow unmanipulated). Snow removal increased soil freeze-thaw frequency and cumulative growing degree-days (GDD), but the magnitude of these effects depended on forest canopy composition. *Acer saccharum* survival decreased where snow was removed, but only at sites without conifers. Excluding small mammals increased *A. saccharum* survival at sites where the small-mammal herbivore *Myodes gapperi* was present. Excluding small mammals also increased *T. canadensis* survival in plots with < 5 cm snow. Because variation in canopy composition and *M. gapperi* presence were important predictors of seedling survival across the snow-depth gradient, these results reveal complexity in the ability to accurately predict patterns of winter seedling survival over large spatial scales. Global change scenarios that project future patterns of seedling recruitment may benefit from explicitly considering interactions between snow conditions and small-mammal winter herbivory.

Keywords: winter climate change, *Myodes gapperi*, northern temperate

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Introduction

Climate change is projected to alter patterns of forest biodiversity by shifting the ranges of many species poleward (Parmesan et al. 1999, Iverson et al. 2008), but observational evidence suggests the ranges of many temperate tree species are contracting or not shifting (Zhu et al. 2012). Discrepancies between model projections and observational data may arise because abiotic conditions (e.g. freezing events) and biotic interactions (e.g. herbivory) can limit tree seedling survival and performance, either alone or in concert (Tylianakis et al. 2008, Brown and Vellend 2014, Urban et al. 2016). For example, hot and dry conditions may directly increase tree mortality (Chmura et al. 2011), but may also increase herbivory, resulting in landscape-wide changes in plant survival (Raffa et al. 2008). Despite the possibility that climate and herbivory can interact to generate non-intuitive shifts in consumer pressure (Brown and Vellend 2014), few studies examine potential changes in herbivory along gradients of important climate variables, such as snow depth, which represents a key knowledge gap in efforts to predict changes in community dynamics under future climate scenarios.

Climate and climate-mediated changes in herbivory may both have particularly strong effects in temperate ecosystems, where snow cover directly influences overwinter plant survival (Tessier 2017) and also moderates herbivory (Swihart and Bryant 2001, Roy et al. 2004, Martin and Maron 2012, Christenson et al. 2014). These effects are important to understand because warming winter temperatures are decreasing snow depth and snow cover across the northern hemisphere (Dye 2002, Henry 2008, Brown and Robinson 2011), possibly exposing plants to damaging freeze-thaw events that increase mortality or delay phenology (Tierney et al. 2001, Inouye 2008, Kreyling et al. 2010). Predicting the effect of winter climate change on plant–herbivore interactions is difficult because snow cover can have multiple effects on herbivores, and the relative magnitude of these effects is poorly understood. Small mammals, such as the southern red-backed vole *Myodes gapperi*, can be important consumers of seeds or seedlings in temperate ecosystems during winter (Haken and Batzli 1996, Ostfeld et al. 1997, Howe and Brown 2000, Manson et al. 2001, Korslund and Steen 2006, Sullivan and Sullivan 2008), and snow cover may facilitate herbivory by small mammals by providing a refuge from predation or extreme temperatures (Kausrud et al. 2008, Pauli et al. 2013, Sultaire et al. 2016, Sanders-DeMott et al. 2018). Alternatively, small mammals may find seeds and seedlings more readily in areas with less snow (i.e. reduced snow increases food apparency; Anderson 1986, Shimano and Masuzawa 1998). Because of the potential for interactions among regional-scale abiotic gradients in winter conditions and the strength of small-mammal herbivory, experiments that manipulate snow depth and small-mammal access should be replicated across large spatial scales in order to understand the unique and interactive contributions of winter climate and herbivores to large-scale patterns in tree seedling survival and performance (Maron et al. 2014, Penczykowski et al. 2017).

In this study, we examined the response of seedlings to experimental manipulations of snow depth and small-mammal herbivory along a natural gradient in snow accumulation (Notaro et al. 2011). Using exclosures that manipulated small-mammal access, we monitored the effects of small-mammal herbivory and experimental snow removal on seedling survival, phenology, and growth of two regionally important foundation species, sugar maple *Acer saccharum* and eastern hemlock *Tsuga canadensis*. We hypothesized that snow removal would increase late-winter soil temperature variability, reducing seedling survival and delaying leaf-out of deciduous seedlings. We also expected snow depth to influence winter herbivory by small mammals, leading us to evaluate two competing hypotheses: a) snow removal would reduce small-mammal herbivory by eliminating important winter habitat and restricting herbivore movement (Korslund and Steen 2006), or b) snow removal would increase small-mammal herbivory by increasing seedling apparency (Anderson 1986).

Material and methods

Study area and focal species

This work was conducted at ten sites representing closed-canopy oak/maple forests spanning a 180 km latitudinal gradient in northern Wisconsin, USA (44.55 to 46.14°N, Fig. 1A). Sites were selected to span a gradient in snowfall, and snowfall generally increased with latitude ($r^2 = 0.45$, $F_{1,8} = 7.11$, $p = 0.03$) as sites approached the Lake Superior snowbelt (Supplementary material Appendix 1). Common tree species in these forests included (in descending order of basal area) *Acer saccharum* (Sapindaceae), *Quercus rubra* (Fagaceae), *Abies balsamea* (Pinaceae), *Acer rubrum* (Sapindaceae), and *Tsuga canadensis* (Pinaceae). Because snow accumulation and winter soil temperatures can differ considerably between coniferous and deciduous forests (Petty et al. 2015), we classified sites according to the presence of conifers. Conifers (*Abies balsamea*, *Pinus resinosa*, *P. strobus*, and *Tsuga canadensis*) were present at four sites, where they comprised ≥ 0.328 basal area fraction. Because the abundance of small mammals can strongly influence tree seedling survival (Gill 1992), we quantified variation in the small mammal community of each site using live-trapping (Stephens and Anderson 2014, Supplementary material Appendix 2). *Myodes gapperi* was present at half of the sites (n = 5), but *M. gapperi* presence was not correlated with snow depth (Supplementary material Appendix 2).

We investigated the response of *A. saccharum* and *T. canadensis* seedlings to winter herbivory and decreased snow depth. These species are projected to decline in importance throughout northern temperate forests in the next

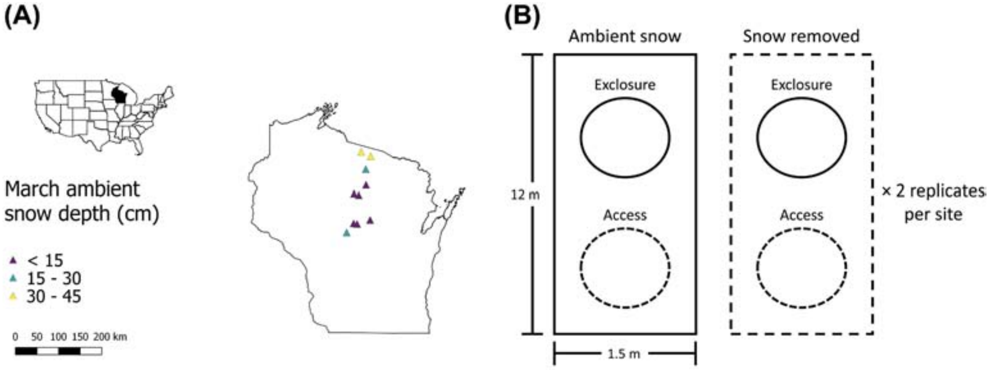

Figure 1. (A) Map of study area. Triangles represent the 10 sites used in this study and are color-coded to show variation in ambient snow depth. (B) Experimental design used at each site to manipulate snow depth and winter herbivory.

century as mean temperatures warm (Iverson et al. 2008), and anecdotal evidence suggests that these seedlings may be vulnerable to winter herbivory by voles (Cleavitt et al. 2014). *Acer saccharum* and *T. canadensis* seeds were obtained from the Wisconsin Dept of Natural Resources Griffith State Nursery (Wisconsin Rapids, WI). All seeds were cold-stratified at 1°C for eight weeks, after which they were placed in a growth chamber (model E-41L2, Percival Scientific, Perry IA) programmed to a 12-h 25°/15°C, light/dark cycle to induce germination (Burns and Honkala 1990). Emerging seedlings were transferred to containers with potting medium (Metromix 366, Sun Gro Horticulture, Agawam, MA) in a greenhouse, where they received supplemental light and daily watering. Seedlings also received fertilizer (Peters Professional 20-10-20, Everris NA, Dublin, OH) 3–4 times per week at 380 ppm nitrogen. Although fertilizing seedlings makes our results more relevant for applied practices (since seedlings are often fertilized prior to transplanting in restoration and regeneration, Jacobs et al 2005), fertilizer may also make seedlings more palatable to small mammals (Ball et al. 2000). While we did not find evidence that our transplanted seedlings had greater browse damage compared to naturally recruiting seedlings in our study sites (Guiden unpubl.), and seedlings received the same fertilizer in each treatment, our estimates of herbivory may represent higher levels than would have been experienced by non-fertilized seedlings. Because we continuously transferred seedlings to the greenhouse, seedling age at the time of transplant ranged from approximately four to six weeks, but seedling age was stratified by treatment and site.

Experimental design

Each 18 × 12 m site was subdivided into four 12 × 1.5 m plots. Within each plot, we installed two open-top cylindrical small-mammal exclosures (height = 0.40 m^2, diameter = 0.33 m^2) in June 2015, for a total of 8 exclosures at each site (Fig. 1B; for details about exclosure design, see Supplementary material Appendix 4). Once exclosures were installed, we transplanted 80 *A. saccharum* and 58 *T. canadensis* seedlings into the exclosures on 20–21 July 2015 (maximum of 1 seedling per species per exclosure), and did not give seedlings any supplemental water or fertilizer. The lower number of *T. canadensis* seedlings was a result of low germination success. Immediately before transplanting, we measured the aboveground stem height of each seedling. We placed a small wooden popsicle stick approximately 5 cm away from seedlings to help relocate seedlings (Schnurr et al. 2004). We recorded seedling survival and damage in September 2015, June 2016, and September 2016. Seedlings were considered alive if stem and leaf tissue were both present. Seedlings were also observed in March, April, and May 2016. Because we could not distinguish dead seedlings from those that had not yet leafed out, we did not model seedling survival in March through May, but these data were used to quantify the effect of snow removal and winter herbivory on seedling phenology.

On 6–7 November, 2015, prior to the onset of snow, we conducted an herbivory experiment to investigate the importance of small mammal herbivory during winter in northern temperate forests (Fig. 1B). One of two exclosures per plot was designated as a control treatment, in which seedlings experienced no herbivory. A second exclosure was used to manipulate small-mammal herbivore access throughout winter, which had two 7 × 7 cm holes to allow small mammals to freely enter the exclosures and consume seedlings. By placing seedlings in an 'open' exclosure, we created a pseudo-exclosure treatment that controlled for potential differences in microclimate elicited by our exclosure design (Radtke and Wilson 2015).

We monitored snow depth and soil temperatures throughout winter. In order to track differences in snow accumulation among sites, two snow-depth measurements were made in each plot with a graded polyvinyl chloride (PVC) pole every two weeks from December 2015 to March 2016. Before the onset of snow, we buried one iButton Thermochron (Maxim Integrated, San Jose, CA) in each plot to record soil temperature every hour (Supplementary material Appendix 5). Soil temperature data were used to calculate cumulative growing degree-days and freeze-thaw events (Supplementary material Appendix 3).

Starting in February 2016, we experimentally removed snow to evaluate the role of snow cover in affecting seedling survival and small-mammal herbivory. Adjacent plots were paired (n = 3 plot pairs per site), and within each pair one plot was randomly designated to have snow removed (Fig. 1B). We removed snow by shoveling until snow was 5 cm deep (Hardy et al. 2001, Drescher and Thomas 2013, Christenson et al. 2014); see Supplementary material Appendix 5 for additional information. The second plot was designated as a control with ambient (i.e. unmanipulated) snow depth. Our experiment therefore had a split-split-plot design, where herbivore treatment was nested within snow removal treatment, which was nested within site. Immediately after shoveling, we recorded three additional snow depth measurements in each plot in order to quantify the effect size of snow removal, which were averaged to determine snow depth after shoveling. Although many snow-removal treatments remove snow throughout the entire winter (Groffman et al. 2001, Drescher and Thomas 2013), we restricted our shoveling treatment to three sessions in the late winter and early spring of 2016 to mimic the most likely winter climate change scenarios in this region (i.e. shallower snow depth in late winter; Brown and Robinson 2011, Notaro et al. 2011): mid-February (19–21 February), early March (4–5 March), and mid-March (18 March). While we reduced snow depth in order to manipulate the availability of subnivium habitat, changing soil temperatures and herbivore behavior (Pauli et al. 2013, Penczykowski et al. 2017), it is important to note that snow removal also potentially reduces soil water and nutrient availability (Hardy et al. 2001).

Statistical analysis

We quantified the effect of snow removal on snow accumulation and soil temperatures across the ten sites in this study area using linear regression. For each snow removal session (mid-February, early March, mid-March), we modeled the mean snow depth in each plot after removal as a function of snow removal treatment and shoveling session, using a linear mixed model with a random intercept term for site. To understand how our snow-removal treatment altered soil temperature, we modelled the effect of snow removal on cumulative growing-degree days (GDD), using a growing threshold of 10°C (Raulier and Bernier 2000), and the frequency of freeze-thaw events using MANOVA. Subsequently, we modeled the response of soil temperature variables to snow removal with univariate ANOVA. Because conifers can have a strong influence on winter soil temperatures (Petty et al. 2015), we included the presence or absence of conifers in the canopy as a covariate in univariate models (Supplementary material Appendix 3).

We used Kaplan–Meier survival analysis ('survival' package in R; Therneau and Grambsch 2000) to evaluate the time course of survival across the four periods when seedlings were checked in the field. This provided a seasonal estimate of survival, but we were unable to detect differences in the time course of survival between herbivory and snow-removal treatments due to the relatively low number of sampling points. In order to understand the interactive effects of reduced snow cover and small-mammal herbivory on seedling survival, we constructed a generalized linear mixed model with a binomial error structure ('lme4' package in R; Bates et al. 2015). Seedling survival at the end of the study (September 2016) was used as the response variable. We tested the effect of small-mammal winter herbivory by modeling *Acer saccharum* seedling survival as a function of snow removal treatment (ambient snow, snow removed), herbivory treatment (small-mammal access, small-mammal exclosure), *M. gapperi* presence or absence, and all possible interactions. Our model also accounted for seedling responses to changes in microclimate caused by snow removal by including the presence or absence of conifers at each site (which had a strong effect on soil temperatures, see Results and Supplementary material Appendix 2), as well as a snow removal × conifer interaction. Finally, we included snow depth after shoveling (measured in early March, to capture peak differences in snow depth among sites), and a snow depth × herbivory treatment interaction. This interaction described possible changes in small-mammal herbivory across the snow depth gradient. A continuous measure of snow depth was necessary to capture the effect of snow on small-mammal herbivory because the effect size of our snow removal treatment varied across the snow depth gradient: early snow retreat at sites with shallow snow resulted in a smaller snow-removal effect size at sites with relatively little snow. *Tsuga canadensis* survival was modeled similarly, but due to the low number of surviving *T. canadensis* seedlings (see Results), models with three-way interactions did not converge, so we report only main effects and significant two-way interactions.

In addition to *Acer saccharum* seedling survival, we modeled the response of leaf phenology to winter herbivory and snow conditions in surviving seedlings. We did not model *Tsuga canadensis* phenology due to low numbers of surviving individuals. We recorded seedling leaf phenology in March 2016, April 2016, mid-May 2016, and late May 2016 by classifying each *A. saccharum* seedling into one of three categories based on the most advanced stage present: dormant, buds opening, or new leaf tissue visible (Wesołowski and Rowiński 2006). For analysis, we used the most conservative approach possible and only considered seedlings with new, unfolded leaf tissue visible as having initiated leaf-out. Seedling leaf-out was modeled as a binomial variable at each of the four sampling dates. This model was structured similarly to the model of survival described above, but included sampling date as an ordinal predictor variable and a random intercept for each unique seedling.

We also measured stem height of all species (measured as the distance between the apical meristem and the ground) in June 2016, as *A. saccharum* stem growth is typically completed for the season at this time (Burns and Honkala 1990). To understand how snow removal and herbivory affected seedling growth, we calculated relative stem growth rate for each seedling. Relative stem growth rate, calculated as the difference of log-transformed stem height in 2016 from log-transformed stem height in 2015, divided by the time interval between measurements ($t = 0.96$ yr), accounts for differences in growth rate due to differences in initial size or study duration (Gibson 2002). Seedling growth was modeled as a linear mixed-effects model in the 'lme4' package in R, using similar model structures as described for models of survival. In all survival and performance models, a random intercept term was included for plot nested within site to account for our split-plot design (Schielzeth and Nakagawa 2013). All analyses were conducted in R (R Core Team), and post-hoc pairwise comparisons were conducted using the 'lsmeans' package in R (Lenth 2016). Detailed results for all mixed-effects models are provided in Supplementary material Appendix 6.

Data deposition

Data available from Figshare Digital Repository: <http://dx.doi.org/10.6084/m9.figshare.7201493> (Guiden et al. 2018).

Results

The winter of 2015–2016 was abnormally warm and had below-average snowfall (Supplementary material Appendix 1). Across the snow depth gradient encompassed by our sites, we observed the greatest variation in ambient snow depth in early March (range: 6.3 to 42.2 cm; Fig. 2A). In addition to this natural snow depth gradient, our shoveling treatment reduced snow depth by an average of 15.7 ± 3.4 cm in snow-removal plots in mid-February and 15.2 ± 3.8 cm in early March (Fig. 2A). Differences in snow depth between snow-removal and ambient-snow plots largely disappeared by mid-March with the onset of spring, when shoveling only reduced snow depth by 1.1 ± 0.5 cm (Fig. 2A). During the 42 d between the initiation of our snow-removal treatment and final snow retreat, snow removal increased both freeze-thaw frequency and growing degree-days (MANOVA: $F_{2,35} = 17.59$, $p < 0.001$). Univariate tests showed that snow-removal plots experienced 72% more freeze-thaw events (12.93 ± 1.94 freeze-thaw events) compared to plots with ambient snow depth (7.53 ± 1.08 freeze-thaw events, $F_{1,24.6} = 22.30$, $p < 0.001$), but snow removal increased freeze-thaw frequency the most at sites with conifers (snow removal × conifer interaction: $F_{1,24.6} = 7.69$, $p = 0.01$, Supplementary material Appendix 3). Additionally, snow-removal plots accumulated 92% more growing degree-days (5.09 ± 0.43) compared to plots with ambient snow depth (2.66 ± 0.22, $F_{1,26.7} = 69.94$, $p < 0.001$), which was driven by an increase in GDD at sites with no conifers (snow removal × conifer interaction: $F_{1,26.6} = 59.92$, $p < 0.001$, Supplementary material Appendix 3). Whereas unmanipulated control plots were characterized by either high GDD or high freeze-thaw frequency depending on the presence of conifers, snow-removal plots experienced a combination of both high GDD and high freeze-thaw frequency that was rarely seen in plots with ambient snow depth (Fig. 2B).

Patterns of seedling survival differed considerably between *A. saccharum* and *T. canadensis*. At the conclusion of the experiment (September 2016), *A. saccharum* seedling survival was relatively high (0.561 ± 0.045, Kaplan–Meier estimator ± standard error), whereas *T. canadensis* seedling survival was almost an order of magnitude lower (0.067 ± 0.026). The time interval encompassing winter and spring represented the greatest period of seedling mortality for both species. *Acer saccharum* survival decreased from 0.994 ± 0.006 in September 2015 to 0.676 ± 0.035 in June 2016 ($n = 15$ deaths, $\chi^2 = 4.18$, $df = 1$, $p = 0.04$) and *T. canadensis* survival decreased from 0.860 ± 0.035 in September 2015 to 0.130 ± 0.034 in June 2016 ($n = 25$ deaths, $\chi^2 = 136.5$, $df = 1$, $p < 0.001$).

Winter microclimate and small-mammal herbivory were important predictors of *A. saccharum* seedling survival, as demonstrated by a significant interaction between *M. gapperi* presence and herbivory treatment ($\chi^2 = 5.18$, $df = 1$, $p = 0.02$, Fig. 3A). This interaction arose because seedling survival in the herbivore-access treatment was lower at sites where *M. gapperi* were captured compared to sites

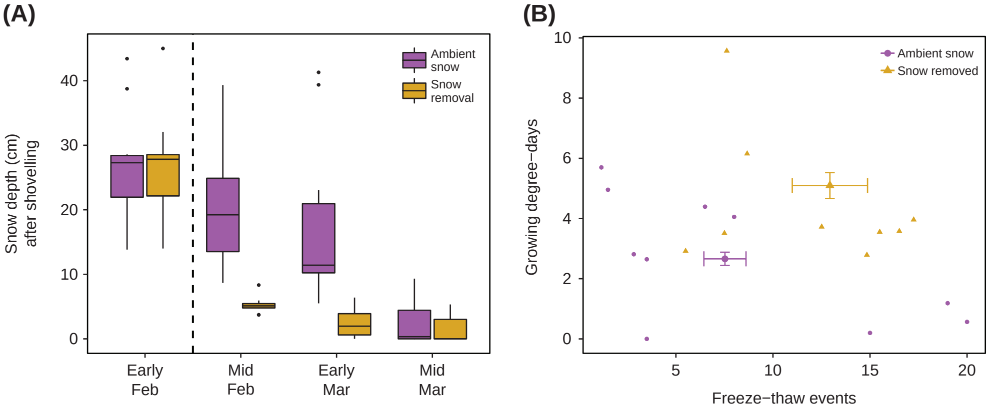

Figure 2. (A) Changes in snow depth over time in snow-removal plots (gold) and unmanipulated control plots (purple). Snow removal began 17 February 2016 (dashed line). (B) Biplot of cumulative soil growing degree-days (10°C threshold) and freeze-thaw frequency in snow-removal plots (gold triangles) and unmanipulated control plots (purple circles). Large points with error bars represent least-squares means ± one standard error for each snow removal treatment.

where *M. gapperi* were not captured (pairwise comparison: $z=2.64$, $p=0.04$). Seedling survival in herbivore exclosures did not differ between sites with and without *M. gapperi* (pairwise comparison: $z=1.41$, $p=0.50$). There was no main effect of small-mammal exclosures ($\chi^2=0.12$, $df=1$, $p=0.73$) or *M. gapperi* presence ($\chi^2=1.37$, $df=1$, $p=0.24$) on seedling survival. Seedling survival was reduced in plots with snow removed, but only at sites without conifers (snow removal × conifer: $\chi^2=3.87$, $df=1$, $p=0.05$, Fig. 4A). There was no significant main effect of snow removal ($\chi^2=1.55$, $df=1$, $p=0.21$) or conifers ($\chi^2=0.18$, $df=1$, $p=0.67$). *Acer saccharum* survival was not affected by snow depth after shoveling ($\chi^2=0.06$, $df=1$, $p=0.81$), or a snow depth × herbivory treatment interaction ($\chi^2=0.71$, $df=1$, $p=0.40$).

While *T. canadensis* survival was low throughout the study area, winter herbivory and snow conditions may explain some variation in *T. canadensis* seedling survival. *Tsuga canadensis* survival increased in plots with low snow depth, but only where small-mammal herbivores were excluded ($\chi^2=5.23$, $df=1$, $p=0.02$, Fig. 3B). There was a marginally significant main effect of herbivory treatment ($\chi^2=1.64$, $df=1$, $p=0.06$), suggesting that survival was approximately three times greater in small-mammal exclosures (0.178 ± 0.073) compared to the small-mammal access treatment (0.067 ± 0.046). There was no significant main effect of snow depth on *T. canadensis* seedling survival ($\chi^2=0.13$, $df=1$, $p=0.72$). *Tsuga canadensis* survival was not affected by snow removal ($\chi^2=0.01$, $df=1$, $p=0.92$), conifers ($\chi^2=2.68$, $df=1$, $p=0.11$), or *M. gapperi* presence ($\chi^2=0.17$, $df=1$, $p=0.68$).

The probability of *Acer saccharum* leaf out increased at later sampling dates ($\chi^2=58.00$, $df=1$, $p < 0.0001$), but snow conditions and herbivory had a strong effect on the timing of seedling leaf-out. A significant snow depth × herbivory interaction suggested that small-mammal herbivory delayed leaf-out, but only in plots with shallow snow ($\chi^2=4.56$, $df=1$, $p=0.03$, Fig. 3C). Seedlings in small-mammal exclosures leafed out earlier on average than seedlings in the small-mammal access treatment ($\chi^2=5.18$, $df=1$, $p=0.02$), but there was no significant main effect of snow depth after shoveling on seedling leaf-out date ($\chi^2=0.65$, $df=1$, $p=0.42$). Delayed leaf-out in the herbivore access treatment was driven by seedlings with obvious signs of stem damage (Supplementary material Appendix 7). Additionally, a significant snow removal × conifer interaction ($\chi^2=3.65$, $df=1$, $p=0.05$) and main effect of conifers ($\chi^2=10.84$, $df=1$, $p=0.001$) suggested that seedlings leafed out later in sites with conifers, particularly in plots

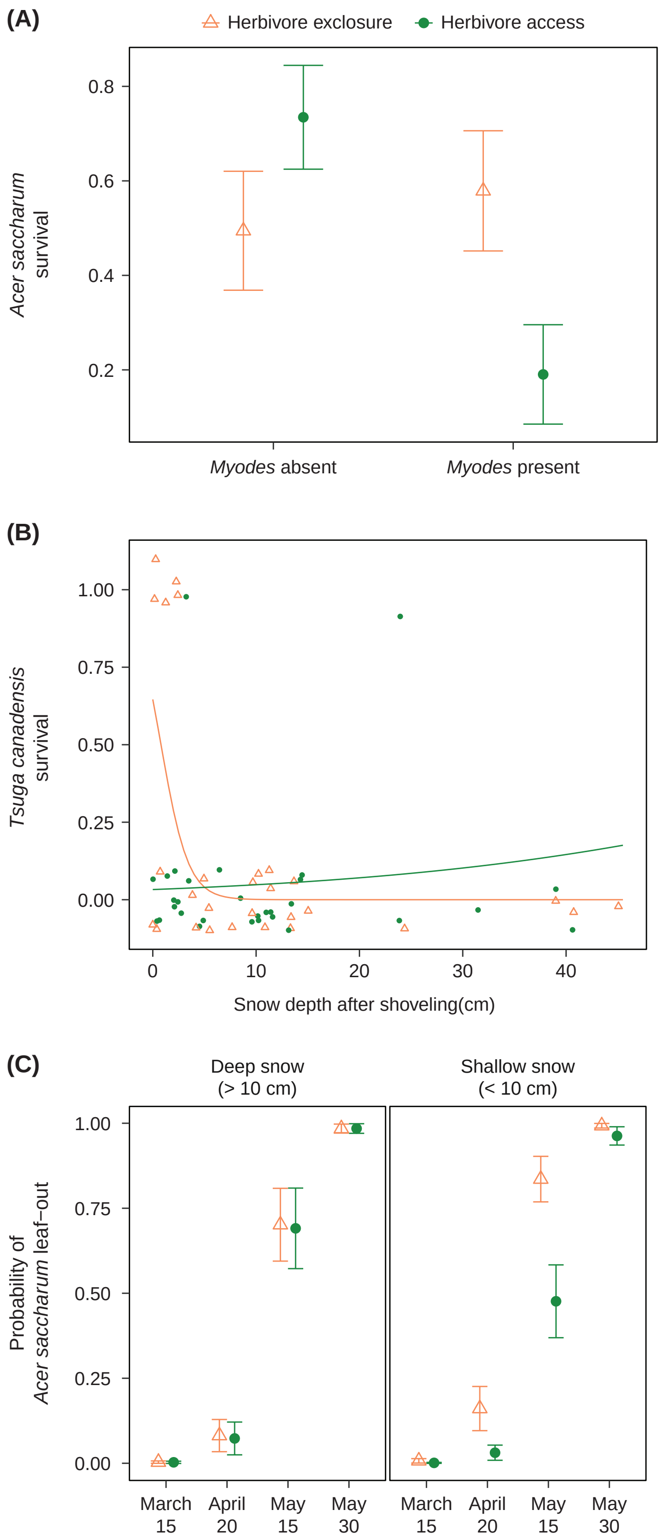

Figure 3. Winter herbivory by small mammals influenced seedling survival and phenology. (A) *Acer saccharum* seedling survival decreased at sites with *Myodes gapperi* (southern red-backed vole), but only in plots that allowed herbivore access (green circles). Points represent least-square means ± one standard error. (B) *Tsuga canadensis* seedling survival increased in plots with shallow snow,

Figure 3. Continued

but only in small-mammal herbivore exclosures (orange triangles). Curves represent estimated response variable values for herbivore access (green lines) and herbivore exclosures (orange lines). Points represent raw data spread out to reduce point overlap. (C) *Acer saccharum* leaf-out occurred earlier in shallow snow, but only where herbivores were excluded. Points represent least-square means ± one standard error.

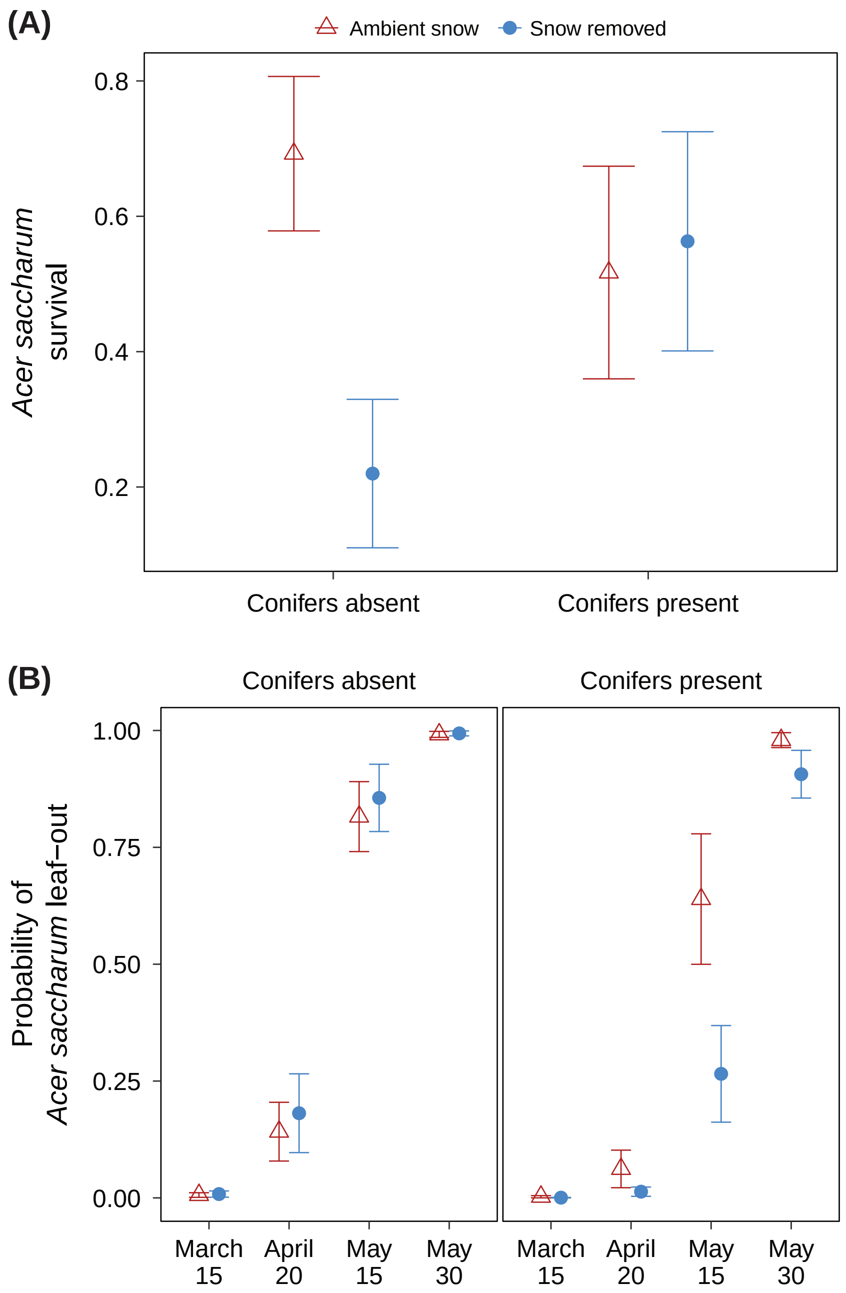

Figure 4. Winter microclimate had strong effects on *Acer saccharum* survival and phenology. (A) Seedling survival decreased in plots with snow removed, but only at sites where conifers were absent. Points represent least-square means ± one standard error. (B) Seedling leaf-out occurred later in plots with snow removed, but only at sites with conifers.

with snow removed (Fig. 4B). However, leaf-out date was unaffected by the main effect of snow removal ($\chi^2 = 0.75$, df = 1, p = 0.39), snow depth after shoveling ($\chi^2 = 0.65$, df = 1, p = 0.42), or *M. gapperi* presence ($\chi^2 = 0.75$, df = 1, p = 0.39), and there was no significant snow removal × herbivory interaction ($\chi^2 = 0.80$, df = 1, p = 0.37), snow removal × *M. gapperi* presence interaction ($\chi^2 = 0.15$, df = 1, p = 0.70), herbivory × conifer interaction ($\chi^2 = 0.07$, df = 1, p = 0.79) or herbivory × *M. gapperi* presence interaction ($\chi^2 = 1.11$, p = 0.29). We found no effect of snow removal or herbivore exclosure on seedling growth (Supplementary material Appendix 6).

Discussion

Projected shifts in winter climate may alter snow cover and snow depth in northern temperate ecosystems (Notaro et al. 2011), potentially changing the survival and distribution of tree seedlings by modifying plant–herbivore interactions.

Using an experiment that manipulated snow cover and winter herbivory across sites that varied substantially in snowfall, we found evidence that winter herbivory by small mammals reduced *A. saccharum* and *T. canadensis* survival and delayed *A. saccharum* leaf-out, and that these negative effects were often strongest in areas characterized by shallow snow (Fig. 3). We also found that snow removal decreased seedling survival at sites without conifers, but delayed leaf-out at sites with conifers (Fig. 4). Three implications of these results are discussed below. First, reduced snow depth might change foraging behavior of small-mammal herbivores in temperate forests by increasing seedling apparency. Second, by altering seedling phenology, winter herbivory and winter climate change might indirectly shape subsequent plant–herbivore interactions in spring and summer. Third, predicting the ecological effects of reduced snow cover will require an understanding of factors influencing local soil temperatures. These findings suggest that winter herbivory and snow conditions can have important effects on seedling dynamics observed in summer, but that the effects of winter climate change can vary substantially across landscapes.

Snow depth drives variation in small-mammal winter herbivory

In boreal systems, deep snow generally increases small-mammal herbivory by decreasing predation risk or providing a stable subnivium habitat where small mammals can locate seedlings (Korslund and Steen 2006, Kausrud et al. 2008, Penczykowski et al. 2017). However, in the temperate forests we studied, the negative effects of small-mammal herbivory were strongest in shallow snow. Herbivore exclosures in shallow snow marginally increased *T. canadensis* survival (Fig. 3B) and prevented *A. saccharum* seedling damage that was associated with delayed leaf-out (Fig. 3C, Supplementary material Appendix 7). We suggest that these patterns were observed because in a historically warm winter (Supplementary material Appendix 1) where subnivium formation was rare, snow removal primarily altered the apparency of seedlings to small mammal herbivores (i.e. seedlings were more likely to be discovered by small-mammal herbivores where snow was shallow). Snow can reduce seedling apparency to large ungulate herbivores (Christenson et al. 2014), and anecdotal evidence from temperate systems suggest that snow cover may also obscure seeds from small mammals (Anderson 1986, Shimano and Masuzawa 1998). However, the small spatial extent of our snow manipulation (12 × 1.5 m plots) may not alter small-mammal behavior in the same way that projected regional declines in snowfall could alter behavior in the future. Coupling snow-removal experiments with long-term observational studies of winter habitat (Kausrud et al. 2008) could therefore improve our understanding of how regional changes in snow depth alter small-mammal foraging decisions.

While large ungulate herbivores can limit *A. saccharum* and *T. canadensis* seedling survival (Salk et al. 2011), our experiment demonstrates that voles can also be important seedling herbivores in temperate forests (Fig. 3A, Supplementary material Appendix 7). This finding could help land managers predict patterns of seedling mortality or damage in northern temperate forests, as our results suggest that seedlings face the highest risk of small-mammal herbivory in stands with *M. gapperi* in years with shallow snow cover. The weak effect of *M. gapperi* on *T. canadensis* survival suggests that low *T. canadensis* seedling survival, likely driven by unfavorable climatic conditions, reduced the number of *T. canadensis* seedlings available for *M. gapperi* to encounter. However, even after escaping herbivory as seedlings, trees may face *M. gapperi* herbivory as saplings that could delay phenology or decrease survival (Sanders-DeMott et al. 2018). While we found important negative effects of *M. gapperi* herbivory, warming temperatures in this region have been associated with declines in *M. gapperi* relative abundance (Myers et al. 2009). Therefore, it will be important to consider how winter climate change will alter seedling herbivory by both voles and other herbivore guilds that typically benefit from reduced snow, such as large ungulates (Murray et al. 2014).

Winter climate and herbivory may affect plant–herbivore dynamics in the growing season

Understanding links between winter conditions and summer seedling performance could improve our ability to predict conditions that cause herbivores to limit plant establishment (Patankar et al. 2013), helping to resolve the considerable variation often observed in plant–herbivore interactions (Agrawal 2011). While shallow snow and winter herbivory can be important causes of plant mortality (Howe and Brown 2000, Schaberg et al. 2008, Martin and Maron 2012, Drescher and Thomas 2013, Drescher 2014), the potential for variation in winter climates to influence herbivory of surviving individuals is less understood (Connolly et al. 2017). Here, we show that winter herbivory and variable winter soil temperatures may delay *A. saccharum* seedling leaf-out, and suggest that seedlings that survive harsh winter conditions could alter herbivory in the growing season.

We found evidence that leaf-out in deciduous tree seedlings can be delayed by both winter herbivory (Fig. 3B, Supplementary material Appendix 7; Herder et al. 2009), and variable winter temperatures (Fig. 4B; Bokhorst et al. 2011). While damage from either winter herbivory or winter climate may have lethal effects on seedlings (Fig. 3A, Fig. 4A, Supplementary material Appendix 7), damaged seedlings that survive winter may suffer subtler sublethal effects. For example, leaf phenology can play a key role in plant–herbivore interactions in spring and summer by either increasing or decreasing the temporal overlap of invertebrate herbivores and expanding seedling leaves (Boege and Marquis 2005). Understanding phenological shifts by both seedlings (Fig. 4B) and invertebrate herbivores (Pureswaran et al. 2014) to changing winter temperatures could provide important insights about how winter climate change modifies herbivory in the growing season. Additionally, winter injuries can alter the morphology and chemistry of leaves produced in spring. Injured seedlings may produce poorly defended leaves that are more susceptible to invertebrate herbivory (Herder et al. 2009, Patankar et al. 2013), or low-quality leaves that are avoided by herbivores (St. Clair et al. 2009). Future studies that focus on the effect of winter injuries on plant phenology, and in particular how phenology may shape seedling defense (Bryant 2003), could identify patterns in what we currently interpret as idiosyncratic responses of spring and summer herbivory to variation in winter climate (Roy et al. 2004).

Spatial variation in the effects of snow removal

The effects of climate change may vary across relatively short spatial scales (Ordonez and Williams 2013), making it difficult to predict the ecological consequences of climate change for plant communities. For example, warmer winters with reduced snow can either increase the duration of soil freezing and the frequency of damaging freeze-thaw events (Tierney et al. 2001), or increase the length of the growing season (Sherwood et al. 2017). The large spatial extent of our study helps resolve previously observed discrepancies in snow removal experiments by showing that the effects of snow removal can vary along canopy composition gradients (Supplementary material Appendix 2): removing snow at sites without conifers increased cumulative GDD, but removing snow at sites with conifers increased freeze-thaw frequency (Fig. 2B). Even seemingly small increases in winter temperatures, such as those observed at sites without conifers, can decrease cold tolerance in seedlings (Zhu et al. 2002), causing increased seedling mortality following freeze-thaw events (Fig. 4A, Kreyling 2010). Alternatively, in habitats with conifers, reduced snow depth may be more likely to delay the initiation of growth, rather than kill seedlings outright (Fig. 4B, Blume-Werry et al. 2016). While our results demonstrate that the role of snow varies across space in warmer-than-average winters, future studies will be needed to describe potential spatial variation in the effect of snow removal during winters with average temperatures (Pauli et al. 2013).

Adaptation to winter temperature variability may increase the survival of southern tree species relative to northern tree species in sites where seedlings experience an early growing season together with increased freeze-thaw frequency. Our study area represents the northern end of the *A. saccharum* distribution, but marks the southern end of the *T. canadensis* distribution (Burns and Honkala 1990, Fisichelli et al. 2014). Frequent freeze-thaw events may contribute to recruitment failure in relict *T. canadensis* populations (Friesner and Potzger 1944), but freeze-thaw events are relatively common throughout most of the current *A. saccharum* distribution (Hershfield 1974, Burns and Honkala 1990). Land managers may be able insulate soil near frost-sensitive seedlings where winter temperatures preclude the formation of a subnivium, either by increasing the cover of moss or lichen seedbeds (Wheeler et al. 2011) or covering soil with bags of perlite before winter (Schaberg et al. 2008).

Conclusions

Snow depth can be a key predictor of northern temperate forest composition (Henne et al. 2007) and might also affect the strength of winter herbivory by changing herbivore behavior (Fisichelli et al. 2012, Martin and Maron 2012). Despite calls to integrate species interactions into models of future plant species distributions (Urban et al. 2016), the potential for reduced snow cover to limit seedling establishment is not often explicitly considered in efforts to map projected range shifts. Our data show that the effects of winter climate change on soil temperatures, and consequently seedling dynamics, will likely vary across regional landscapes, and that snow depth may play an underappreciated role in shaping winter herbivory by small mammals. This work suggests several new directions for future research. We show that snow cover and small-mammal herbivory can interact to decrease seedling survival in a relatively small sample of seedlings, but small-mammal foraging may change as a function of seedling density (Manson et al. 1998). Snow-removal studies that also manipulate seedling density could help us understand the importance of snow for small-mammal herbivory and seedling survival following high-mast versus low-mast years. Additionally, variation in canopy composition may provide land managers with a means of predicting the effects of reduced snow on winter soil temperatures, and consequently seedling survival, across large spatial scales (Zuckerberg and Pauli 2018). While ecologists grapple with the challenge of predicting species distributions and abundances in a rapidly changing world, understanding the intricate links between winter and summer processes could provide an important perspective in predicting the future composition of northern temperate forests.

Acknowledgements – This work was made possible by outstanding logistical support from Trout Lake Field Station. We thank J. Casper, L. Maillefer, and M. Rowe for field assistance. S. Bartel, B. Bron, J. Chandler, R. Eddy, and H. Howe provided valuable feedback on the manuscript.

Funding – This work was funded by an AFRI-NIFA Fellowship (grant # 2014-02074) awarded to JLO and BMC, as well as a Vilas Associates Fellowship awarded to JLO. PWG was supported by a National Science Foundation IGERT award (grant # DGE-1144752) while writing this manuscript as well as Doctoral Dissertation Improvement Grant funding from NSF (grant # DEB-1701506).

Author contributions – PWG, BMC, and JLO contributed to experimental design; PWG and BMC collected data; PWG performed all analyses and led preparation of the manuscript; BMC and JLO helped revise the manuscript.

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Supplementary material (Appendix ECOG-3948 at <www.ecography.org/appendix/ecog-03948>). Appendix 1–7.