Ecography

Supplementary material

Appendix 1: Historical climate data

We used historical climate data from a local weather station (Wausau, WI; latitude 45.949° N) to compare temperature and precipitation in the meteorological winter of 2016 (December 1, 2015 to February 29, 2016) to historical averages for December to February (1981 to 2010). The 30-year average winter air temperature does not vary substantially across our study area (range: -9.7°C to -10.2°C), but average annual snowfall varies by more than a factor of two (range: 130 cm to 282 cm, Wisconsin Climatology Office). However, the winter of 2016 was the third-warmest winter on record (NCEI 2015). Winter 2016 daily maximum temperatures (mean: -0.8°C) were 2.6°C warmer than average, and winter 2016 daily minimum temperatures (mean: -8.2°C) were 4.5°C warmer than average, leading to 15 fewer days where daily maximum temperatures were < 0°C in winter 2016. In 2016, this weather station reported 61.2 cm of snowfall, compared to a historical average of 93.9 cm. Meanwhile, north-central Wisconsin observed 16.2 cm rain in winter 2016, almost twice as much as the historical average (8.4 cm).

Appendix 2: Small-mammal live-trapping analysis

To quantify variation in small mammal communities across our study area, we conducted two live-trapping sessions at each site: one four-night session in June and one three-night session in July 2016. Paired live-traps (H.B. Sherman Live Traps, Inc., Tallahassee FL) were placed on a 4 x 4 grid, with trap-pairs placed 10 m apart (n = 32 traps/site). Traps were pre-baited with oat seeds for one night. We checked traps in the morning in all sessions, but due to cold overnight temperatures in the June session, we also checked traps in the evening to release diurnal small mammals (i.e., *Tamias striatus*). All captured individuals were identified to species, and given an ear tag with a unique ID number (National Tag Co., Lexington KY). Due to the distance between sites, sampling was conducted over two sessions, with sites stratified within each group to yield equal effort across latitude. To account for small differences in trapping effort due to disturbed traps, we considered traps that were closed and empty to represent 0.5 trap-nights, and divided the number of captures for each species at each site by the total trapping effort at that site (Nelson and Clark 1973).

Myodes gapperi was present at five out of ten sites, and *M. gapperi* live-captures per 100 trap-nights ranged from 0 to 5 (a total of 11.2 captures per 100 trap-nights, 4.3% of total captures). Importantly, a linear regression model showed that the number of *M. gapperi* captures at site was not significantly associated with our snowfall recorded at a site ($F_{1,8} = 0.02$, $R^2 = 0.02$, $P = 0.88$). However, *M. gapperi* was not the dominant small mammal species at any site, as *Peromyscus leucopus* (185.3 captures per 100 trap-nights, 71.2% of total captures), *P. maniculatus* (31.0 captures per 100 trap-nights, 11.9% of total captures), and *Tamias striatus* (28.5 captures per 100 trap-nights, 10.9% of total captures) were more abundant. *Glaucomys*

volans (4.2 captures per 100 trap-nights, 1.6% of total captures) was also present throughout the

study area.

Appendix 3: Soil temperature data analysis

Growing degree-days (GDD) are widely used to model the effects of climate change (e.g., Marino et al. 2011, Augspurger 2013), because the timing of important phenological events, such as leaf-out date or flowering date can often be predicted by cumulative GDD (e.g., Raulier and Bernier 2000). Growing degree-days are most often calculated using the following formula:

$$GDD = T_{observed} - T_{base}$$

where negative values are replaced with zeros, and daily GDD values are summed over time. Most GDD calculations average daily maximum and daily minimum temperatures because these data are commonly reported by weather stations, but this technique can lead to bias when daily maxima exceed the base temperature and daily minima do not (Allen 1976). Here, we use hourly temperature data collected by iButton Thermochrons (Appendix 4) to avoid this bias. Temperature data were collected from 6 iButtons at each site (one in each of the plots used in this study, as well as two adjacent plots which received identical snow removal, herbivore exclosure, and seedling transplant proceedures). For sake of interpretation, these calculations, more appropriately called cumulative growing degree-hours, were divided by 24 to express values as GDD. However, some iButtons failed prematurely, leading to unbalanced periods of data collection among plots (range: 13 to 42 days, mean ± standard error: 33.1 ± 2.1 days). Importantly, iButton failure did not differ between snow removal treatments (linear mixed-effects model with a random intercept term for site, $F_{1,8.6} = 0.20$, $P = 0.66$). We accounted for unequal data collection by dividing the cumulative GDD recorded in each plot by the number of observations made, and multiplied this value by the length of our snow-removal treatment (n = 42 days).

One important consideration when using GDD in ecological analysis is selecting an appropriate threshold temperature. Often, 10°C is used as the base temperature (Marino et al. 2011, Augspurger 2013), which provides a good approximation for *Acer saccharum* leaf-out date (Raulier and Bernier 2000). However, in order to justify this temperature threshold, we analyzed GDD using several thresholds (5°C, 7.5°C, 10°C) to see if threshold choice affected our interpretation of these data (Table S1).

In order to understand the response of GDD to our snow removal experiment, we modeled GDD at each threshold as a function of snow removal using linear mixed models with a random intercept term for site. Because conifer species may have cooler winter soil temperatures (Petty et al. 2015), we included the presence of conifer species (*Abies balsamea*, *Picea glauca*, *Pinus resinosa*, and *Tsuga canadensis*) and a snow removal × conifer interaction in all models. A linear regression model showed that conifer presence at a site was not significantly associated with average snow depth at a site ($F_{1,8} = 0.64$, $R^2 = 0.07$, $P = 0.45$). In all models, snow removal increased GDD ($P < 0.001$) and sites with conifers in the canopy had lower GDD ($P < 0.05$). Strong snow removal × conifer interactions ($P < 0.001$) suggested that snow removal increased GDD the most at sites with without conifers in the canopy (Figure A1A). Because our results did not differ based on the GDD threshold used (Table A1), we used the 10°C GDD calculations in our analyses in the main text, as this value has been demonstrated to capture leaf-out phenology of at least one of our focal species, *A. saccharum* (Raulier and Bernier 2000), and is also the most conservative threshold for GDD calculation.

Increased soil temperature variability is also an ecologically important outcome of reduced snow that might physically damage root tissue by heaving and cracking soil (Tierney et al. 2001, Drescher and Thomas 2013). We defined a freeze-thaw event as any instance at which

soil temperature crossed 0°C, and summed the number of freeze-thaw events per plot after the start of our snow removal treatment (February 19-21, 2016). Similar to our approach to GDD, we standardized the number of freeze-thaw events observed based on the number of observations each iButton made.

Table A1: Regression results for linear mixed models describing log-transformed cumulative growing-degree days as a function of snow removal treatment, presence of conifers in the canopy, and a snow removal × conifer interaction. Models also included a random intercept term for site. Asterisks indicate significant F values: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

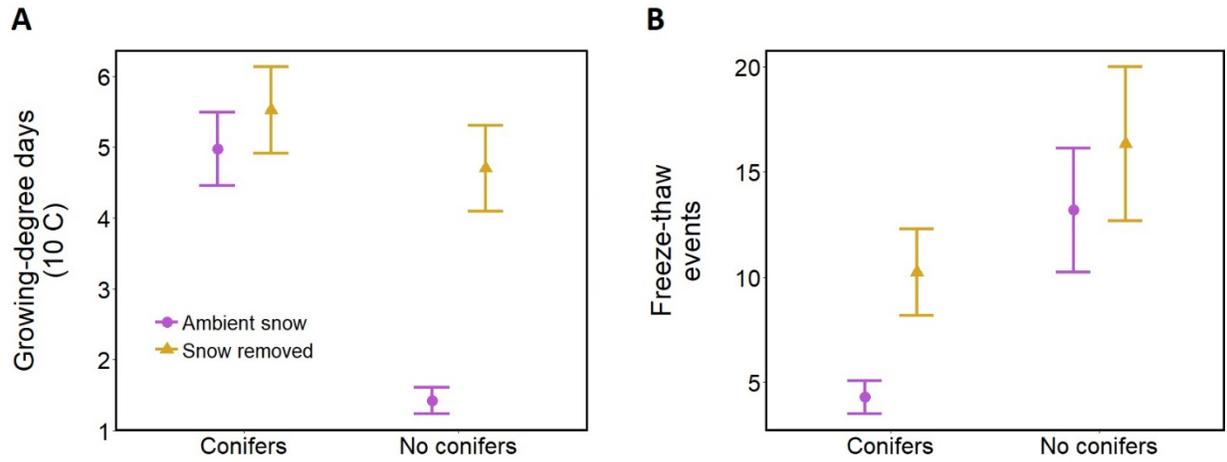| Soil temperature threshold	Snow removal	Conifer	Snow removal × Conifer
10°C	$F_{1,26.7} = 69.94$***	$F_{1,7.9} = 23.93$***	$F_{1,26.6} = 59.92$***
7.5°C	$F_{1,26.3} = 52.38$***	$F_{1,7.9} = 14.81$**	$F_{1,26.3} = 48.63$***
5°C	$F_{1,26.2} = 18.97$***	$F_{1,8.0} = 13.20$*	$F_{1,26.2} = 18.74$***

Figure A1: Response of A) cumulative growing degree-days and B) freeze-thaw frequency to snow removal, presence of conifers in the canopy, and a snow removal × conifer interaction.

Appendix 4: Herbivore exclosure design

Exclosures were constructed of a 1 m x 0.5 m length of 1 cm^2 mesh hardware cloth; wrapped into a 0.33 m diameter cylinder (Figure A1). We prevented small mammals from climbing into the exclosures by fastening a 15 cm band of aluminum flashing around the top of the cylinder. Four pinewood stakes, in which the bottom edge was cut at a 45-degree angle, were stapled to the hardware cloth cage in order to provide structural support, and allowed the exclosures to be driven into the ground with a rubber mallet. Two zip-ties kept the cylindrical shape of the exclosure. Importantly, the open-top design meant that randomly selected sampling points immediately outside the exclosures had similar leaf litter depth (t = 0.78, P = 0.47) and snow depth (t = 0.31, P = 0.78) compared to the inside of exclosures. Once assembled, exclosures were buried 5-10 cm under soil surface to prevent small mammals from tunneling in, resulting in a cage that stood approximately 0.4 m above ground. Thus, from July to November 2015, all transplanted seedlings were protected from small-mammal herbivory. It is possible that larger herbivores (e.g., white-tailed deer) could have consumed seedlings, but this is unlikely due to the height and small diameter of the exclosures. We controlled for any artifacts in herbivore behavior or soil disturbance introduced when cutting cages by cutting similar holes in the other two treatments, and then immediately re-sealing holes with an 8 x 8 cm piece of hardware cloth fastened to the cage using cage clips (Miller Manufacturing, Glencoe MN).

Figure A1: Photograph of small mammal exclosures deployed over winter. The open-top design ensured that snow depth and leaf litter deposition inside the exclosures matched ambient snow depth and leaf litter deposition outside the exclosures.

Appendix 5: Supplemental snow removal methods

While there are many methods of snow removal that each have a unique suite of benefits and drawbacks, we chose shoveling because this minimizes soil disturbance and realistically causes soil temperature to track air temperatures (Kreyling 2010, Tessier 2017). Snow shoveling is sometimes criticized for its potential to disturb the vegetation being monitored, but because we transplanted seedlings into small exclosures, we avoided this potential pitfall by carefully removing snow from the inside of cages with small shovels (diameter of shovel blade = 7.5 cm). In order to understand the effect of snow removal on soil temperature (Pauli et al. 2013, Petty et al. 2015), we programmed iButton Thermochrons (Maxim Integrated, San Jose CA) to record hourly temperature data, sealed the iButtons in paraffin, and buried one per plot approximately 2 cm below the soil surface (Lundquist and Lott 2010). In cases where snow was < 5 cm deep, we lightly raked snow with shovels to mimic potential snow compaction that occurred from snow shoveling or walking around plots. Our rectangular plot design made it possible to remove snow without walking into the plot boundary, minimizing unintended snow compaction. Because snow shoveling compacted snow around the plot perimeter, we also walked around control plots 3-4 times to mimic this snow compaction in the control treatment. All snow was deposited a minimum of 4 m away from plots in small piles to avoid introducing artifacts in herbivore behavior resulting from a large pile of compacted snow.

Appendix 6: Supplementary information for multiple regression models

All models included a three-way interaction describing the potential for small-mammal herbivory to change as a function of snow removal, (herbivory treatment × snow removal × presence of *Myodes gapperi*). In order to describe the potential for snow removal to alter soil temperatures, we also included a snow removal × conifer presence interaction. In addition, we included a × snow depth (after shoveling) interaction to capture how the strength of small-mammal herbivory changed across our snow depth gradient. However, because *T. canadensis* survival was low (see Results, main text), models with three-way interactions did not converge, so we only report significant two-way interactions. For generalized linear mixed models, we report chi-squared values with one degree of freedom (Bates et al. 2014). For linear mixed models, we report the denominator degrees of freedom, which were obtained from the "car" package in R (Fox and Wiesberg 2011) in order to be sure our split-split-plot design was properly accounted for in the model error structures. We also checked denominator degrees of freedom for the generalized linear mixed models by re-analyzing these models as linearized mixed-models with a Gaussian distribution, solely to ensure that our experimental design was properly accounted for in our analyses (Guiden, unpublished data). To ensure that assumptions for multiple regression were met, we assessed variance inflation factors (VIFs) for each model term, and considered VIF < 10 to indicate acceptable levels of multicollinearity (Dorman et al. 2013).

Table A1: ANOVA table for a generalized linear mixed model describing *Acer saccharum* survival as a function of herbivory treatment (Herb), snow removal treatment (Snow), the presence of *Myodes gapperi* (*Myodes*), and all possible interactions. We also modeled *A.*

saccharum responses to soil temperatures by including an interaction between snow removal treatment and conifer presence (Conifer). In order to capture changes in the strength of small-mammal herbivory across our snow depth gradient we included an interaction between herbivory treatment and snow depth after removal (Snow depth). A random intercept was included for site, as well as plot nested within site.

Predictor variable	χ^2	D.f.	P	VIF
Snow	1.55	1	0.21	5.79
Herb	0.12	1	0.73	6.83
Myodes	1.37	1	0.24	3.70
Conifer	0.18	1	0.67	1.90
Snow depth	0.06	1	0.81	3.67
Snow × Herb	0.58	1	0.45	6.14
Snow × Myodes	1.12	1	0.29	4.32
Herb × *Myodes*	**5.18**	**1**	**0.02**	**4.84**
Snow × Conifer	**3.87**	**1**	**0.05**	**2.89**
Herb × Snow depth	0.71	1	0.40	5.31
Snow × Herb × *Myodes*	0.51	1	0.47	3.59

Table A2: ANOVA table for a generalized linear mixed model describing *Tsuga canadensis* survival as a function of herbivory treatment (Herb), snow removal treatment (Snow), the presence of *Myodes gapperi* (*Myodes*), and conifer presence (Conifer). In order to capture changes in the strength of small-mammal herbivory across our snow depth gradient we included

an interaction between herbivory treatment and snow depth after removal (Snow depth). A
random intercept was included for site, as well as plot nested within site.

Predictor variable	χ^2	D.f.	P	VIF
Snow	0.01	1	0.92	8.12
Herb	1.64	1	0.06	4.81
Myodes	0.17	1	0.68	2.01
Conifer	2.68	1	0.11	4.16
Snow depth	0.13	1	0.72	2.99
Herb × Snow depth	**5.23**	**1**	**0.02**	**6.17**

Table A3: ANOVA table for a generalized linear mixed model describing *Acer saccharum* leaf-out as a function of herbivory treatment (Herb), snow removal treatment (Snow), the presence of *Myodes gapperi* (*Myodes*), and all possible interactions. We also modeled *A. saccharum* responses to soil temperatures by including an interaction between snow removal treatment and conifer presence (Conifer). In order to capture changes in the strength of small-mammal herbivory across our snow depth gradient we included an interaction between herbivory treatment and snow depth after removal (Snow depth). We also included a term for sampling date, which was expressed as an ordinal variable (Session). A random intercept was included for site, as well as plot nested within site.

Predictor variable	χ^2	D.f.	*P*	VIF
Session	**58.00**	**1**	**< 0.0001**	**1.68**
Snow	0.32	1	0.57	6.55
Herb	**5.18**	**1**	**0.02**	**9.19**
Conifer	**10.84**	**1**	**0.0009**	**4.81**
Myodes	0.75	1	0.39	3.83
Snow depth	0.65	1	0.42	5.10
Snow × Herb	0.80	1	0.37	9.42
Snow × Conifer	**3.65**	**1**	**0.05**	**6.35**
Herb × Conifer	0.07	1	0.79	7.11
Snow × *Myodes*	0.15	1	0.70	5.20
Herb × *Myodes*	1.11	1	0.29	5.27
Herb × Snow depth	**4.56**	**1**	**0.03**	**6.93**
Snow × Herb × Conifer	0.01	1	0.92	6.70

Snow × Herb × *Myodes*	0.86	1	0.35	6.08

Table A4: ANOVA table for a linear mixed model describing *Acer saccharum* relative stem growth rate as a function of herbivory treatment (Herb), snow removal treatment (Snow), the presence of *Myodes gapperi* (*Myodes*), and all possible interactions. We also modeled *A. saccharum* responses to soil temperatures by including an interaction between snow removal treatment and conifer presence (Conifer). In order to capture changes in the strength of small-mammal herbivory across our snow depth gradient we included an interaction between herbivory treatment and snow depth after removal (Snow depth). A random intercept was included for site, as well as plot nested within site.

Predictor variable	F	Numerator D.f.	Denominator D.f.	*P*	VIF
Snow	0.79	1	25.7	0.38	9.0
Herb	0.25	1	20.7	0.62	10.4
Conifer	0.01	1	5.6	0.93	2.1
Myodes	0.10	1	5.4	0.77	2.5
Snow depth	0.41	1	31.0	0.53	13.7
Snow × Herb	.20	1	27.6	0.65	9.9
Snow × Conifer	0.27	1	16.0	0.61	4.3
Herb × Conifer	1.56	1	20.4	0.23	4.5
Snow × *Myodes*	0.01	1	16.7	0.92	4.8
Herb × *Myodes*	2.03	1	22.0	0.17	4.9
Herb × Snow depth	0.16	1	38.8	0.69	14.6
Snow × Herb × Conifer	0.62	1	20.9	0.44	4.9

Snow × Herb × *Myodes*	1.48	1	20.8	0.24	6.1

Appendix 7: *Myodes gapperi* activity explains patterns of seedling damage

Despite an understanding that small mammal herbivores play an important role in plant recruitment in old fields (Ostfeld et al. 1997), heath (Korslund and Steen 2006), and boreal forests (Hansson 1986, Sullivan and Sullivan 2008), few studies have investigated the consequences of small mammal seedling herbivory in temperate forests (Cleavitt et al. 2014), particularly in the context of winter climate change. From March 2016 to May 2016, we surveyed seedlings for stem damage in order to understand where seedling stems showed signs of herbivore damage. Seedlings were assigned to one of four categories: undamaged, stem missing, damage near apical meristem, or severe stem damage below apical meristem. Small-mammal herbivores characteristically attack seedlings along the lower portion of the stem, either clipping the stem or removing bark (Hansson 1986, Ostfeld et al. 1997, Vehvila and Koricheva 2006), whereas ungulates are more likely to attack buds higher up on the stem (Palmer and Truscott 2003, Vehvila and Koricheva 2006).

To investigate whether *M. gapperi* was primarily responsible for attacking seedlings, we subset our data to include only seedlings with severe stem damage below the apical meristem in herbivore access or herbivore exclosure plots. We pooled stem damage by herbivore treatment and site, and modeled the incidence of stem damage in these seedlings as a function of adult *M. gapperi* captured in summer 2016, herbivore treatment (herbivore exclosure, herbivore access), and a *M. gapperi* x herbivore treatment interaction. This generalized linear mixed model used a negative binomial error distribution to account for over-dispersion in the incidence of seedling damage and a random intercept term for site. We then modeled a) seedling survival in September 2016 as a function of stem damage, using a generalized linear mixed model with a binomial distribution, as well as b) leaf-out date of surviving seedlings as a function of stem damage,

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using a linear mixed model. These models incorporated a random intercept term for herbivory treatment, nested within snow removal treatment, nested within site.

Stem damage was found on 25% of *A. saccharum* seedlings (n = 20 damaged seedlings). Stem damage occurred most often in the herbivore access treatment when *M. gapperi* was abundant (*M. gapperi* × herbivore treatment interaction: $\chi^2 = 8.34$, d.f. = 1, $P < 0.004$, Figure S1A), although we found no main effect of *M. gapperi* ($\chi^2 = 0.09$, d.f. = 1, $P = 0.76$) or herbivore treatment ($\chi^2 = 0.68$, d.f. = 1, $P = 0.41$). Survival of damaged seedlings (0.258 ± 0.123) was less than one-third of survival of undamaged seedlings (0.877± 0.072, $\chi^2 = 8.42$, d.f. = 1, $P < 0.004$, Figure S1B). On average, damaged seedlings that survived until the end of the study leafed out 7 days later than undamaged seedlings ($F_{1,66.4} = 4.51$, $P = 0.04$, Figure S1C). These data, along with the strong relationship between *A. saccharum* survival in the herbivore access treatment and *M. gapperi* abundance (see Results in main text), support our hypothesis that *M. gapperi* was primarily responsible for the observed small mammal seedling herbivory in this study.

Figure A1: A) *Acer saccharum* seedling stem damage occurring below the apical meristem, which is characteristic of small-mammal seedling herbivory, as a function of *Myodes gapperi* live-captures per 100 trap nights in summer 2016. Seedling damage was aggregated for each herbivore treatment (orange triangles: herbivore exclosure; green circles: herbivore access) at each of 10 sites. Curves represent predictions from a fitted generalized linear mixed model with a negative binomial error structure. B) Least-square means of *A. saccharum* survival for damaged and undamaged seedlings. Error bars represent one standard error. C) Least-square means of *A. saccharum* leaf-out date (day of year) for damaged and undamaged seedlings. Error bars represent one standard error.

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