

Snow depth and woody debris drive variation in small-mammal winter seed removal

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Abstract

Aims: In temperate forests, small increases in winter temperature can lead to substantial decreases in snow accumulation, which may alter plant–consumer interactions such as seed predation. However, seed predation by small mammals may also be affected by local habitat structure (e.g., downed woody debris). We tested whether the effect of snow depth on seed predation by small mammals depends on habitat structure (woody debris) that may influence small-mammal foraging behavior.

Location: Northern temperate forests in Wisconsin, USA.

Methods: We performed a factorial manipulation of snow depth and woody debris presence at 10 sites that differed in site-level ambient woody debris. At these sites, we monitored seed removal of four temperate tree species (*Abies balsamea*, *Acer rubrum*, *Acer saccharum*, *Pinus resinosa*).

Results: Mean rates of winter seed removal varied among species, as did the effects of snow depth and woody debris. The presence of woody debris decreased *Abies balsamea* seed removal in plots with snow removed. Regardless of woody debris, snow removal increased *Acer saccharum* seed removal. *Acer rubrum* seed removal was lowest at sites with high site-level woody debris volume, especially in plots with snow removed.

Conclusions: Warming winter temperatures may amplify seed removal for some tree species, but local-scale heterogeneity in woody debris may modify these effects. Because the effects of woody debris and snow removal were much stronger for some tree species than others, changes in seed removal associated with reduced future snow cover or changes in forest management may accelerate regional changes in forest composition.

KEYWORDS

Abies balsamea, *Acer rubrum*, *Acer saccharum*, *Myodes gapperi*, northern temperate forest, *Peromyscus leucopus*, seed predation, winter climate change

1 | INTRODUCTION

Climate change has the potential to alter the strength of biotic interactions, which may lead to unexpected decreases in species

persistence (Brown & Vellend, 2014), ecosystem function (Grimm et al. 2013), and disease transmission (Garrett et al. 2006). Although rarely studied, species interactions may be most profoundly affected by climate change during winter (Kreyling, 2010; Williams et al. 2014;

Penczykowski et al. 2017). Even small increases in winter temperatures can decrease snowfall and snow accumulation in temperate forests (Kreyling, 2010; Pauli et al. 2013), eliminating refuge habitat at the snow–soil interface (i.e., the subnivium; Pauli et al. 2013; Zuckerberg & Pauli, 2018). The loss of the subnivium can alter the strength of many important species interactions, including predation (Sonerud, 1986; Kausrud et al. 2008) and herbivory (Fisichelli et al. 2012; Martin & Maron, 2012; Sanders-DeMott et al. 2018). However, given the complex effect of subnivium in reducing both metabolic costs and predation risk (Pauli et al. 2013), the direction and strength of these effects often depends strongly on local context (Maron et al. 2014; Guiden et al. 2019). Experiments that manipulate the availability of subnivium across gradients in climate or predation risk will therefore improve our ability to predict the effect of winter climate change on species interactions, and corresponding climate-mediated shifts in abundance and distribution (Brown & Vellend, 2014; Guiden et al. 2019).

Temperate forests are experiencing disproportionately large and fast decreases in snowfall due to rising winter temperatures (Kreyling, 2010; Drescher & Thomas, 2013; Zhu et al. 2017). However, little is known about how decreased snowfall will alter interactions between plants and consumers, such as small mammals (Guiden et al. 2019). Many small-mammal species remain active over winter (Wolff & Durr, 1986; Guiden & Orrock, 2020), and their winter foraging can have a strong effect on plant survival and diversity in the growing season (Howe & Brown, 2000; Korslund & Steen, 2006; Guiden et al. 2019). Seeds represent an important food source for many temperate forest small mammals (Lobo, 2014), particularly in winter when other resources are scarce (Banks & Dickman, 2000; Howe & Brown, 2000). However, small mammals can exhibit preferences for some seeds based on physical and chemical seed traits (Schmidt, 2000; Schnurr et al. 2002, 2004; Lobo et al. 2009), suggesting that winter climate change might increase seed predation on some, but not all plant species.

Small mammals extensively use subnivium as habitat (Korslund & Steen, 2006; Kausrud et al. 2008; Guiden & Orrock, 2020), but it is unclear how loss of the subnivium, as expected under winter climate change (Pauli et al. 2013; Zuckerberg & Pauli, 2018), will alter small-mammal winter foraging patterns. Deep snow can obscure food resources, making foraging more difficult (Anderson, 1986; Shimano & Masuzawa, 1998; Guiden et al. 2019), but also provide safety from predators or extreme cold, thus increasing small-mammal activity (Sonerud, 1986; Korslund & Steen, 2006; Kausrud et al. 2008). These context-dependent results reflect the trade-offs between benefits and costs of foraging that govern small-mammal foraging decisions (Brown & Kotler, 2004). Predicting how winter climate change will alter small-mammal foraging behavior will therefore require understanding how the local environment can shift the costs and benefits of foraging. For example, as snow accumulation is reduced, small mammals will lose a historically important predation refuge (Pauli et al. 2013), but small food resources such as seeds or seedlings may become more apparent (Guiden et al. 2019). Whether reduced snow accumulation leads to a net increase or decrease in small-mammal

foraging may therefore depend on the availability of alternative winter predation refugia, such as woody debris (Loeb, 1999; McCay, 2000; Sullivan et al. 2012; Malo et al. 2013; Guiden & Orrock, 2017).

In this study, we examined variation in small-mammal winter seed removal of five tree species commonly found in northern temperate forests. We hypothesized that changes in winter habitat structure would alter the magnitude of seed removal by small mammals during winter. We predicted that snow removal would increase the apparentness of seeds (Guiden et al. 2019), increasing seed removal by small mammals. Because woody debris might replace the predation refuge provided by the subnivium (Pauli et al. 2013; Guiden & Orrock, 2017), we also predicted that where snow is removed, seed removal would be greatest in habitats with woody debris.

2 | METHODS

2.1 | Study area

This study was conducted at 10 sites in northern Wisconsin, USA spanning a 45-km latitudinal gradient (45.80° N to 46.13° N, Appendix S1). Sites were selected to represent closed-canopy mixed-deciduous forests with similar overstorey species and snow conditions. In June 2017, we randomly selected a GPS point within each site and centered a 30 m × 30 m grid on this point. We recorded the diameter at breast height of all trees >2 m tall in this grid. The most common tree species at these sites were, in order of decreasing basal area, *Acer saccharum* (Sapindaceae), *Quercus rubra* (Fagaceae), *Populus grandidentata* (Salicaceae), *Acer rubrum* (Sapindaceae), *Pinus resinosa* (Pinaceae), and *Abies balsamea* (Pinaceae). Live-trapping data indicate that common small mammal species in this area include *Peromyscus leucopus* (white-footed mouse) and *Myodes gapperi* (southern red-backed vole, Guiden & Orrock, 2020). *Peromyscus maniculatus* (deer mouse) was rarely captured at one site (Guiden & Orrock, 2020).

2.2 | Field methods

In order to understand the potential interactive effects of reduced snow and woody debris, we performed a factorial manipulation of snow depth and woody debris presence. In August 2017, we established eight 2 m × 2 m plots within each site; plots were evenly spaced 3 m apart. We removed all woody debris within the plots, as well as all woody debris within a 0.5-m radius around the plot. Half of the plots ($n = 4$ plots per site, $n = 40$ plots total) were randomly selected to have woody debris added, and half of the plots were left with no woody debris as a control. In October 2017, woody-debris addition plots received a standardized piece of untreated pine lumber (10 cm × 10 cm × 100 cm); this volume corresponded to the median volume of woody debris removed from plots (mean ± SE: 9.71 ± 0.10 cm, interquartile range: 6–16). We used standardized pieces of woody debris to manipulate only the structural effects of woody debris on small-mammal behavior. Using



woody debris collected at the site could have biased our results by introducing site-specific differences in the size and decay class of ambient woody debris (e.g., arthropods use older woody debris as habitat, providing small mammals with a food supplement in addition to a predation refuge, McCay, 2000). To account for site-specific differences in woody debris at larger spatial scales (i.e., the spatial scale of a small-mammal home range), we estimated the volume of woody debris at each site. We established four equally spaced 30-m transects within each site and used point-intercept surveys to estimate woody-debris volume along these transects (Forbes, 1961). Starting in December 2017, we measured snow depth in each plot approximately every three weeks. Within each woody-debris treatment, half of the plots were selected to have snow removed starting February 2018, and half were left unmanipulated as a control (Guiden et al. 2019).

Within a subset of plots at each site, we added a motion-activated camera in the center of one plot for each treatment combination ($n = 40$ plots total), allowing us to identify foraging small-mammal species. Cameras (Essential E3, Bushnell Corporation, Overland Park KS, USA) were programmed to take photographs, attached to a translucent plastic box (58 cm length \times 41 cm width \times 31 cm height; for a diagram of the camera set-up, see Guiden & Orrock, 2020), and pointed at the ground in the plot center. Boxes were made of a translucent plastic material that did not intercept light, and therefore was unlikely to provide an artificial predation refuge for small mammals that might bias activity patterns. However, we added boxes to all 80 plots (including plots without cameras) to control for any potential small-mammal behavioral changes due to the presence of the box, allowing us to pool seed removal data from plots with and without cameras. Due to malfunctions (the motion-activation sensor triggering continuously after snow removal), cameras only reliably collected data through mid-February 2018 (Guiden & Orrock, 2020). While these data only provide an indication of early-winter small-mammal activity, early-winter activity was substantially greater than late-winter activity in these plots (Guiden & Orrock, 2020).

In each experimental plot, we monitored seed removal of five common northern temperate forest tree species that are commonly consumed by small mammals (*Abies balsamea*, *Acer rubrum*, *Acer saccharum*, *Pinus resinosa*, *Quercus rubra*). All seeds were obtained from a commercial supplier (Sheffield's Seeds, Locke, NY, USA). On December 7 2017, we added 10 seeds from each species and spread them evenly throughout the camera box. In order to account for potential differences in background seed availability (i.e., seeds present in the litter that we did not add) driven by variation in canopy composition and masting dynamics (Schnurr et al. 2002), we also established two 2 m \times 2 m "seed rain plots" at each site. Snow depth and woody debris were never manipulated in seed rain plots.

All remaining seeds were collected between 5 May 2018 and 12 May 2018. At each experimental and seed rain plot, we collected all visible seeds from the top of the leaf litter, and carefully collected leaf litter and the first 1 cm of soil. Leaf litter and soil samples were sieved to recover buried seeds, which were classified as damaged or intact.

2.3 | Data analysis

For each woody species in our study, we constructed a generalized linear mixed model with a binomial distribution, using the *lme4* package in R (Bates et al. 2015). The proportion of seeds removed was modeled as a function of snow removal treatment, woody-debris addition, site-level woody-debris volume, and all possible interactions. We also included the number of conspecific seeds found in seed rain plots as a covariate. Each model included a random intercept term for site. In the rare cases where we recovered more than 10 seeds in a plot ($n = 12$, <4% of observations), we set the proportion of intact seeds to 1; analyses conducted without those observations reached identical conclusions to those presented here (Appendix S2). Seed removal could represent either seed predation (Guiden & Orrock, 2017) or seed dispersal (Vander Wall, 2010). While our experimental design did not track seed fate, there was consistent evidence of in situ seed predation in experimental plots (see *Results*). The number of intact seeds remaining in our plots therefore provided a conservative estimate of seed survival (Bartowitz & Orrock, 2016). Because *Quercus rubra* seeds were much more common in seed rain plots (mean = 6.7, range: 0–26) compared to experimental plots (mean = 1.6, range: 0–21), we considered our estimates of *Quercus rubra* survival to be unreliable and excluded this species from further analysis. All analyses were performed using R version 3.6.1 (R Core Team, 2019), and results are presented as estimated marginal means \pm one standard error (Lenth, 2019) unless otherwise specified.

3 | RESULTS

The number of intact seeds recovered differed among the woody species used in this study (Appendix S2). *Abies balsamea* had the highest mean number of seeds found intact (2.49 ± 0.24), followed by *Acer saccharum* (1.41 ± 0.29) and *Pinus resinosa* (1.35 ± 0.32 seeds). *Acer rubrum* seeds were least likely to be recovered intact (0.63 ± 0.17).

The effect of snow removal and woody-debris addition on seed removal differed among seed species (Table 1, Figure 1), but in some cases, the effect of the snow removal treatment depended on ambient woody-debris volume (Table 1, Figure 2). Snow removal decreased the proportion of intact *Abies balsamea* seeds recovered, but only in plots with woody debris added (snow removal \times woody debris addition: $\chi^2 = 4.83$, $p = 0.02$; Figure 1a). More intact *Acer rubrum* seeds were recovered at sites with more ambient woody debris (ambient woody debris: $\chi^2 = 5.30$, $p = 0.02$; Figure 2b), but this pattern was driven by plots with snow removed (snow removal \times ambient woody debris: $\chi^2 = 6.88$, $p = 0.008$). We recovered 6% more intact *Acer saccharum* seeds in plots with ambient snow (0.171 ± 0.035) compared to plots with snow removed (0.116 ± 0.027 , $\chi^2 = 3.98$, $p = 0.04$; Figure 1c). The proportion of intact *Pinus resinosa* seeds recovered showed little response to snow removal, woody-debris addition, or their interaction (Table 1). In all species, finding more seeds in seed rain plots was associated with greater seed recovery in our experimental plots (Table 1).

TABLE 1 Results of binomial generalized linear mixed models describing the proportion of seeds recovered intact for four temperate tree species (*Abies balsamea*, *Acer rubrum*, *Acer saccharum*, *Pinus resinosa*) as a function of snow removal (SNOW), woody debris addition (WD), site-level ambient woody debris (SITE WD), and all possible interactions

Predictor	<i>Abies balsamea</i> ($R^2 = 0.24$)	<i>Acer rubrum</i> ($R^2 = 0.25$)	<i>Acer saccharum</i> ($R^2 = 0.16$)	<i>Pinus resinosa</i> ($R^2 = 0.17$)
SEED RAIN	$\beta = 0.089 \pm 0.026$ $\chi^2 = 11.67$ $p < 0.001$	$\beta = 1.36 \pm 0.62$ $\chi^2 = 4.80$ $p = 0.02$	$\beta = 0.097 \pm 0.035$ $\chi^2 = 7.72$ $p = 0.005$	$\beta = 0.303 \pm 0.138$ $\chi^2 = 4.85$ $p = 0.02$
SNOW	$\beta = 0.510 \pm 0.207$ $\chi^2 = 1.58$ $p = 0.21$	$\beta = 0.354 \pm 0.418$ $\chi^2 = 0.22$ $p = 0.63$	$\beta = 0.509 \pm 0.262$ $\chi^2 = 3.98$ $p = 0.04$	$\beta = 0.031 \pm 0.242$ $\chi^2 = 0.30$ $p = 0.58$
WD	$\beta = 0.133 \pm 0.191$ $\chi^2 = 1.20$ $p = 0.27$	$\beta = -0.270 \pm 0.342$ $\chi^2 = 2.82$ $p = 0.09$	$\beta = 0.052 \pm 0.232$ $\chi^2 = 0.03$ $p = 0.84$	$\beta = 0.071 \pm 0.249$ $\chi^2 = 0.15$ $p = 0.69$
AMB.WD	$\beta = 0.001 \pm 0.148$ $\chi^2 = 0.08$ $p = 0.77$	$\beta = -0.234 \pm 0.385$ $\chi^2 = 5.30$ $p = 0.02$	$\beta = 0.096 \pm 0.253$ $\chi^2 = 0.01$ $p = 0.91$	$\beta = -0.002 \pm 0.286$ $\chi^2 = 0.44$ $p = 0.50$
SNOW \times WD	$\beta = -0.629 \pm 0.283$ $\chi^2 = 4.83$ $p = 0.02$	$\beta = -0.198 \pm 0.548$ $\chi^2 = 0.04$ $p = 0.83$	$\beta = -0.134 \pm 0.371$ $\chi^2 = 0.15$ $p = 0.69$	$\beta = 0.073 \pm 0.352$ $\chi^2 = 0.09$ $p = 0.76$
SNOW \times AMB.WD	$\beta = 0.046 \pm 0.221$ $\chi^2 = 0.32$ $p = 0.57$	$\beta = -0.882 \pm 0.437$ $\chi^2 = 6.88$ $p = 0.008$	$\beta = 0.238 \pm 0.237$ $\chi^2 = 2.05$ $p = 0.15$	$\beta = 0.014 \pm 0.294$ $\chi^2 = 0.83$ $p = 0.36$
WD \times AMB.WD	$\beta = 0.035 \pm 0.201$ $\chi^2 = 0.23$ $p = 0.62$	$\beta = -0.204 \pm 0.395$ $\chi^2 = 0.13$ $p = 0.72$	$\beta = 0.072 \pm 0.215$ $\chi^2 = 0.21$ $p = 0.64$	$\beta = -0.473 \pm 0.287$ $\chi^2 = 2.11$ $p = 0.14$
SNOW \times WD \times AMB.WD	$\beta = -0.237 \pm 0.297$ $\chi^2 = 0.63$ $p = 0.43$	$\beta = 0.207 \pm 0.557$ $\chi^2 = 0.14$ $p = 0.71$	$\beta = 0.008 \pm 0.335$ $\chi^2 = 0.01$ $p = 0.98$	$\beta = 0.356 \pm 0.418$ $\chi^2 = 0.72$ $p = 0.39$

Higher proportions of seeds recovered (positive slopes) indicate less seed removal. We also included ambient seed rain (SEED RAIN) as a covariate. We did not model *Quercus rubra* seed removal given the low number of intact seeds in experimental plots and high number of seeds in seed rain plots. Significant ($p \leq 0.05$) p -values are bolded. Each model included eight estimated parameters, and was fit using observations from $n = 80$ observations (eight observations at 10 sites).

Our cameras primarily detected two small-mammal species foraging in our experimental plots: *Peromyscus leucopus* (detected in 30% of plots, mean number of photographs per plot = 9.97 ± 1.71 , range = 0–409) and *Myodes gapperi* (detected in 22% of plots, mean = 6.95 ± 1.51 , range = 0–77). Our snow removal and woody-debris addition treatments, as well as site-level woody debris, did not affect the number of photographs of either species (Appendix S2).

4 | DISCUSSION

Snow depth can dictate the strength of plant–herbivore interactions during winter (Fisichelli et al. 2012; Guiden et al. 2019), but relatively little is known about winter seed predation and how it may be modified by winter climate change or local habitat structure. Using an experimental approach, we reveal the existence of species-specific effects of snow depth and woody debris on seed removal. These results have

two important implications that we discuss below. First, because snow removal increased seed removal by small mammals in some cases, winter climate change may amplify winter seed predation of some tree species, but not others, in temperate forests. Second, the effect of site-level woody-debris volume on seed removal suggests that land managers may be able to increase overwinter seed survival for some species by manipulating woody debris. By explicitly considering how snow depth alters species interactions during winter, ecologists may be able to better anticipate changes in temperate forest diversity associated with winter climate change (Fisichelli et al., 2014a, 2014b).

4.1 | Winter climate change may amplify seed removal by small mammals

Snow depth has a complex effect on small-mammal winter foraging behavior. Deep snow is typically thought to benefit small

FIGURE 1 Effect of snow removal and woody debris addition (red circles: woody debris added, blue triangles: no woody debris added) treatments on seed removal of (a) *Abies balsamea*, (b) *Acer rubrum*, (c) *Acer saccharum*, and (d) *Pinus resinosa*. Higher values on the Y-axis indicate less seed removal. Points represent estimated marginal means \pm one standard error. Within a panel, points sharing a letter have statistically similar mean proportions of seeds intact

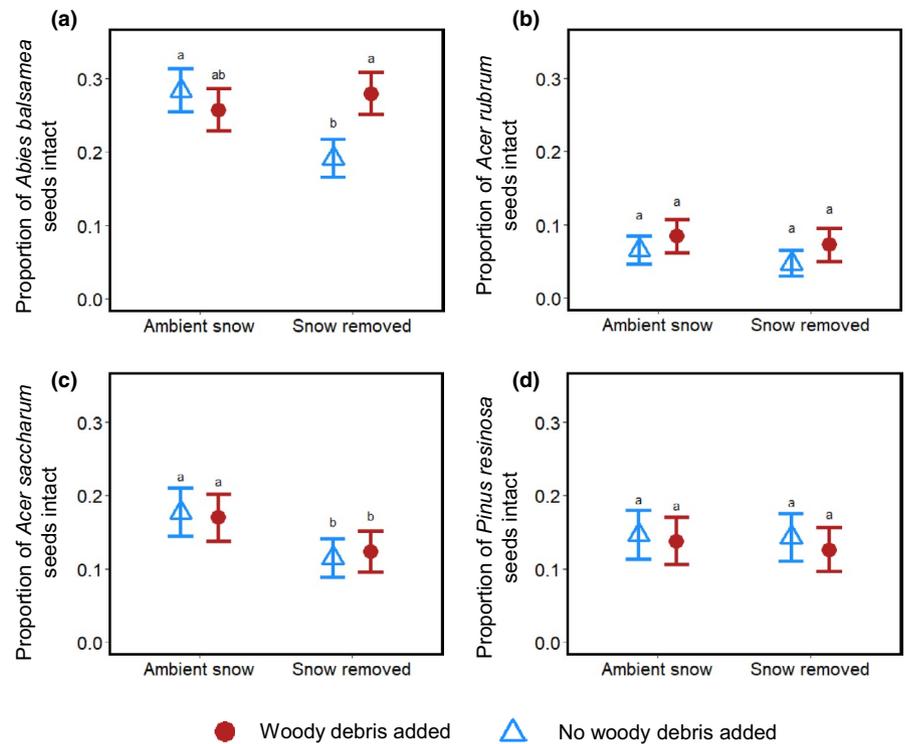
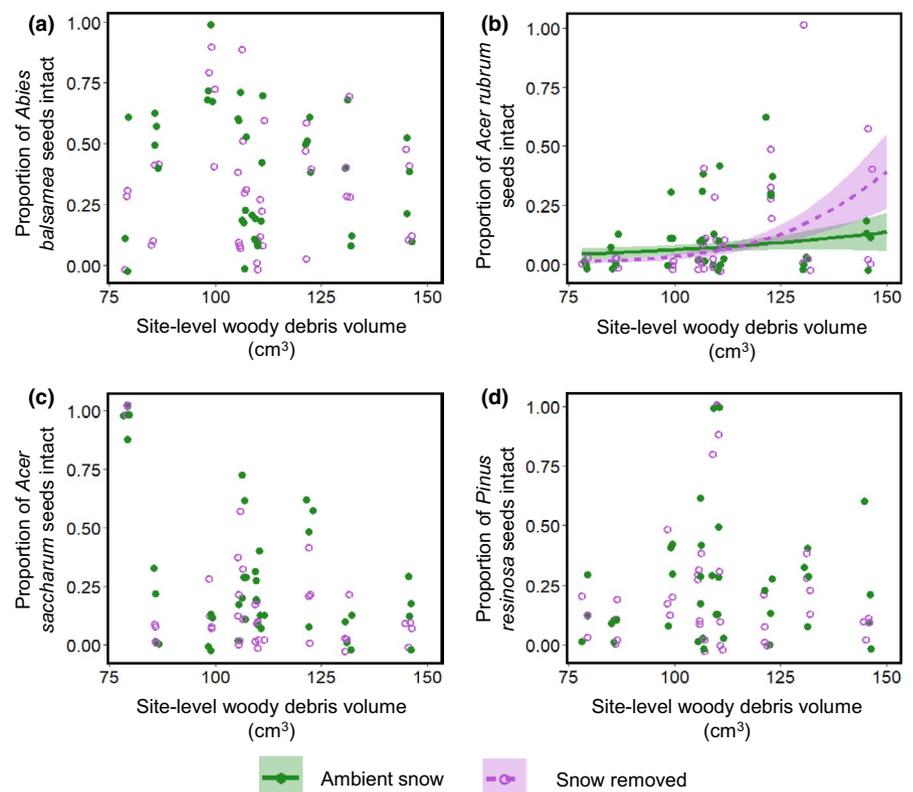


FIGURE 2 Effect of snow removal treatment (green closed circles, solid line: ambient snow depth, purple open circles, dashed line: snow removed) and site-level ambient woody debris volume (cm^3) on seed removal of (a) *Abies balsamea*, (b) *Acer rubrum*, (c) *Acer saccharum*, and (d) *Pinus resinosa*. Points represent observed data, and curves represent model predictions \pm one standard error for slopes significantly different from 0



mammals by providing thermal stability and reduced predation risk (Korslund & Steen, 2006; Kausrud et al. 2008). However, removing snow increased seed removal of *Acer saccharum* in both woody-debris treatments (Figure 1c) and increased seed removal of *Abies balsamea* in plots with no woody debris added (Figure 1b).

This supports the hypothesis that shallow snow may favor small-mammal foraging by increasing the apparency of small food items (Anderson, 1986; Guiden et al. 2019). Our results were likely driven by undocumented shifts in consumer activity during late winter (i.e., after our snow removal treatment), as there was no

effect of snow removal on the abundance or identity of seed predators foraging in our plots during early winter (Appendix S2, Guiden & Orrock, 2020).

Understanding how small mammals forage in northern temperate forests without snow is critical, because as temperate forests warm, more winter precipitation falls as rain rather than snow (Kreyling, 2010). Warmer temperatures are expected to shift the distribution of the woody species used in this study toward higher latitudes (Iverson et al. 2008), but few species are keeping pace with climate change (Zhu et al. 2012). One explanation for this failure to track climatic niches is that plant–consumer interactions may constrain plant migration. For example, seed predation can limit *Acer saccharum* seedling establishment (Brown & Vellend, 2014; Urli et al. 2016). Because reduced snow depth can amplify seed predation for some species (Figure 1), habitats with consistently deep snow could provide important refugia, and may be a high priority for conservation (Morelli et al. 2020). However, snow depth only affected seed removal of two of the four species examined here. Such selective seed removal might contribute to broad-scale patterns of change in community composition (Howe & Brown, 2000), such as replacement of *Acer saccharum* with *Acer rubrum* (Abrams, 1998; Iverson et al. 2008; Taylor et al. 2017). Winter climate change may accelerate this shift in some habitats, as decreased snow depth increased *Acer saccharum* seed removal (Figure 1c), but decreased *Acer rubrum* seed removal in sites with ambient woody debris (Figure 2b). Predicting climate-mediated compositional changes of northern temperate forests will therefore likely require identifying which species experience increased seed removal under projected climatic conditions, and how local-scale habitat structure moderates these changes (Maron et al. 2014).

Seed traits, such as seed size, may in part explain the strong interspecific variation in seed removal in this experiment (Lichti et al. 2014; Linabury et al. 2019). In the largest seed we analyzed, *Acer saccharum*, seed removal consistently increased with snow removal (Figure 2c). In smaller seeds (*Acer rubrum* and *Abies balsamea*), the effect of snow removal on seed predation depended on woody debris (Figures 1a and 2b). This may indicate that winter climate change will have a more consistent negative effect on large seeds, which are typically preferred by seed predators (Dylewski et al. 2020). Conversely, the effect of winter climate change on small or intermediate-sized seeds may be more context-dependent on local habitat features, such as woody debris, which are known to affect foraging decisions. In addition to seed size, other seed traits such as chemical defenses or seed hardness may provide additional dimensions that influence seed predator preferences in novel winter climates (Schmidt, 2000; Wang & Chen, 2009; Lobo, 2014).

4.2 | Woody debris may provide a tool to control seed removal during winter

We predicted that in the absence of snow, woody debris would decrease predation risk perceived by small mammals and consequently increase seed removal. We made this prediction because

small mammals extensively use woody debris as a predation refuge in forests across the world (Loeb, 1999; McCay, 2000; Bowman et al. 2001; Guiden & Orrock, 2017). However, both our woody-debris addition and high site-level woody-debris volume led to changes in seed removal (Figures 1 and 2). This may reflect that woody debris is used by mustelid predators during winter to access subnivean habitat (Buskirk et al. 1989), which can elevate the predation risk perceived by small mammals (Andruskiw et al. 2008). However, the manner in which small mammals use woody debris may depend on woody-debris age, shape, or aggregation (Orrock et al. 2000; Zollner & Crane, 2003; Sullivan et al. 2012; Malo et al. 2013). Our experimental design allowed us to control for natural variation in these characteristics and add woody-debris pieces of average size. However, small mammals may respond strongest to smaller or larger than average pieces of woody debris, or clusters of woody debris, that provide important air pockets under snow or structural complexity to hide from predators (Orrock et al. 2000; Sullivan et al. 2012). Future experiments that manipulate characteristics of woody debris, and not just its presence or absence, might help identify habitats where small mammals concentrate seed predation around woody debris (Malo et al. 2013; Guiden & Orrock, 2017).

While individual land managers often cannot directly mitigate climate change, they can manipulate the local context in which climate change plays out. Woody-debris manipulations are already commonly used to manipulate small-mammal abundance or diversity following disturbances such as logging (e.g., Sullivan et al. 2012). Land managers could also decrease woody-debris volume to reduce seed predation on some woody species, such as *Acer saccharum*, although this may increase seed predation on other species, such as *Acer rubrum* (Figure 2). However, it will be necessary to weigh the potential benefits of woody-debris removal against its costs, as woody debris provides critical habitat for seeds and seedlings (O'Hanlon-Manners & Kotanen, 2004), insects (Grotsky et al. 2018), and small mammals (Sullivan et al. 2012) while also influencing carbon storage and nutrient cycling (Kim et al. 2006; Gonzalez-Polo et al. 2013). Additionally, woody debris addition or removal treatments may depend on the amount of woody debris present at a site (Table 1), perhaps indicating that small mammals require a threshold volume of woody debris before it provides predation refuge (Guiden & Orrock, 2017). Woody debris manipulations may therefore provide managers with an important tool to influence foraging decisions made by cryptic seed predators, particularly in habitats where seed predation may limit seedling establishment of great ecological or economic importance (Schnurr et al. 2002; Brown & Vellend, 2014; Rittenhouse & Rissman, 2015).

5 | CONCLUSION

Northern temperate forests will increasingly have warmer winters characterized by less snow (Notaro et al. 2011). Our results show that reduced snow may increase top-down effects of small-mammal seed removal on some woody species, but not others, and may depend on local context such as the presence or volume of woody debris.

While such context dependency is common in seed removal studies (Willson & Whelan, 1990; Manson & Stiles, 1998; Maron et al. 2014), our work highlights several directions for future research. For example, seed production is highly variable for many masting temperate tree species, which can have a strong effect on seed predation and fate (Schnurr et al. 2002; Lichti et al. 2014; Zwolak et al. 2016). Replicating this experiment in high-mast vs low-mast years may identify important temporal variation in the strength of snow removal or woody debris effects on seed predation. Additionally, giving-up density studies might help ecologists disentangle the role of woody debris in shaping perception of small-mammal predation risk vs other foraging costs, such as metabolic costs (Orrock & Danielson, 2009). By understanding the relative strength of regional climate trends and local heterogeneity in modifying habitat structure and shaping trophic interactions, ecologists may be able to better anticipate shifts in forest ecosystems in the coming decades.

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DATA AVAILABILITY STATEMENT

All data and code are publicly available on FigShare (Guiden, <https://doi.org/10.6084/m9.figshare.12834899>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Study area map

Appendix S2. Supplemental results and data analysis

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