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ARTICLE

Ecology of Critical Zones

Snow refugia: Managing temperate forest canopies to maintain winter conditions

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Abstract

Climate change is reducing snowpack across temperate regions with negative consequences for human and natural systems. Because forest canopies create microclimates that preserve snowpack, managing forests to support snow refugia—defined here as areas that remain relatively buffered from contemporary climate change over time that sustain snow quality, quantity, and/or timing appropriate to the landscape—could reduce climate change impacts on snow cover, sustaining the benefits of snow. We review the current understanding of how forest canopies affect snow, finding that while closed-conifer forests and snow interactions have been extensively studied in western North America, there are knowledge gaps for deciduous and mixed forests with dormant season leaf loss. We propose that there is an optimal, intermediate zone along a gradient of dormant season canopy cover (DSCC; the proportion of the ground area covered by the canopy during the dormant season), where peak snowpack depth and the potential for snow refugia will be greatest because the canopy-mediated effects of snowpack sheltering (which can preserve snowpack)

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outweigh those of snowfall interception (which can limit snowpack). As an initial test of our hypothesis, we leveraged snowpack measurements in the northeastern United States spanning the DSCC gradient (low, <25% DSCC; medium, 25%–50% DSCC; and high, >50% DSCC), including from 2 sites in Old Town, Maine; 12 sites in Acadia National Park, Maine; and 30 sites in the northern White Mountains of New Hampshire. Medium DSCC forests (typically mature mixed coniferous–deciduous forests) exhibited the deepest peak snowpacks, likely due to reduced snowfall interception compared to high DSCC forests and reduced snowpack loss compared to low DSCC forests. Many snow accumulation or snowpack studies focus on the contrast between coniferous and open sites, but our results indicate a need for enhanced focus on mixed canopy sites that could serve as snow refugia. Measurements of snowpack depth and timing across a wider range of forest canopies would advance understanding of canopy–snow interactions, expand the monitoring of changing winters, and support management of forests and snow-dependent species in the face of climate change.

KEYWORDS
climate change, forest canopy, forest management, microclimate, mixed forest, snow refugia, snowpack, winter, climate refugia

INTRODUCTION

Seasonal snow cover is critical to the functioning of human, natural, and physical systems across the planet. It is also fundamental to winter recreation and tourism and enables transportation and resource extraction in places that are inaccessible during the growing season (Chugunkova & Pyzhev, 2020; Rittenhouse & Rissman, 2015), boosting rural and mountain economies (Dawson & Scott, 2013; Hagenstad et al., 2018). Accumulated snow (snowpack) is a key component of Earth's climate system that cools local and regional winter temperatures through its high albedo (Burakowski et al., 2018; Zhang, 2005) and provides water resources by recharging rivers, surface reservoirs, and groundwater during spring melt (Barnett et al., 2005; Hale et al., 2023; Immerzeel et al., 2020; Siirila-Woodburn et al., 2021). The thermal insulation generated by snow protects tree roots and seedlings from freezing damage (Batllori et al., 2009; Renard et al., 2016; Sanders-DeMott, McNellis, et al., 2018; Sanders-DeMott, Sorensen, et al., 2018), maintains soil water in liquid form (Decker et al., 2003; Hardy et al., 2001; Tatariw et al., 2017), and provides protection and habitat for wildlife species adapted to snowy environments (Shipley & Zuckerberg, 2023; Thompson et al., 2021; Zimova et al., 2016). Altogether, winter snowpack provides an array of benefits for ecosystems and humans.

However, in recent decades, climate change has reduced the depth and duration of seasonal snow cover in most regions (Aragon & Hill, 2024; Contosta et al., 2019, 2020; Gottlieb & Mankin, 2024; Grogan et al., 2020; Jia et al., 2023; Mudryk et al., 2020), with negative consequences for human, natural, and physical systems that rely on snowpack. Warmer winters have led to more precipitation falling as rain instead of snow (Feng & Hu, 2007; Huntington et al., 2004) and have increased the frequency of mid-winter thaws, changing the rate of snowmelt and altering hydrologic cycles (Harpold & Brooks, 2018; Henry, 2008; Musselman et al., 2017), with uncertain implications for streamflow (Gordon et al., 2022). These patterns have been documented in Northern Hemisphere mid-latitude regions and are expected to continue or accelerate with ongoing climate change (Aygün et al., 2019; Gottlieb & Mankin, 2024; Mudryk et al., 2020). However, impacts vary by emissions scenarios, as well as geographic factors like latitude and elevation (Burakowski et al., 2022).

One opportunity to reduce the influence of climate change on seasonal snow cover and ensure that the benefits provided by snow continue is to conserve and create snow refugia, which we define as areas that remain relatively buffered from contemporary climate change over time that sustain snow quality, quantity, and/or timing appropriate to the landscape. This definition of snow refugia expands that of Balantic et al. (2021) and Strickfaden et al. (2023) and provides more specificity to support management policies and guidelines for retaining the benefits of seasonal snowpack for ecosystems and people. The snow refugia concept includes preserving three important characteristics of snow, beyond being present or absent, that influence ecosystem functions: quality (e.g., texture, density), quantity (depth, accumulation), and timing (onset, persistence, and melt). Snow quality has implications for wildlife; for example, American marten (*Martes americana*) prefer areas with low-density snow, presumably to avoid predators (Sirén et al., 2017) or to easily access the subnivean layer (Pauli et al., 2013). Deep, powdery snow, on the other hand, can negatively impact species like white-tailed deer (*Odocoileus virginianus*) (Lefort et al., 2007) and coyotes (*Canis latrans*) (Sirén et al., 2017). Snow quantity affects biotic interactions such as competition and predation (Sirén et al., 2021; Williams et al., 2015; Zimova et al., 2016), winter timber harvests that rely on snowpack to minimize soil and root impacts from equipment (Chugunkova & Pyzhev, 2020), and outdoor recreational activities (Hagenstad et al., 2018; Hamilton et al., 2007). The timing of snow regulates the exposure of seedlings, tree roots, and soils to freezing conditions, with implications for forest health and productivity (Cleavitt et al., 2008; Reinmann et al., 2019), soil microbial communities, and biogeochemical cycles (Patel et al., 2021; Sanders-DeMott, Sorensen, et al., 2018). Thus, buffered areas—or snow refugia—that preserve the presence and local characteristics of snowpack will play a crucial role in maintaining ecosystem structure and function and supporting sociocultural values in cold regions.

Various ecosystem features and their interactions can generate and influence snowpack quality, quantity, and timing, and thus the possibility of snow refugia. These factors include topoclimate (e.g., cold-air pooling, wind), physiography (e.g., elevation, slope, aspect, proximity to water bodies), and biotic factors (e.g., canopy cover and vegetation structure). Here, we focus on the influence of forest canopy cover (the proportion of the ground area covered by the canopy) on snow characteristics that could produce snow refugia. This builds on the concept of ecosystem-protected refugia, where biological processes internal to an ecosystem can lead to decoupling from regional climate (Stralberg et al., 2020). Because most studies in North America exploring the effects of forest structure on snowpack have been focused on western coniferous forests and often compare open- and closed-canopy conditions (Varhola et al., 2010), such work has rarely captured the gradients of canopy structure, species composition, and phenological variability that exist in mixed coniferous–deciduous forest systems common in many eastern temperate and boreal regions (Penn et al., 2012). Focusing solely on open and closed conifer canopies or coniferous canopy gradients limits our understanding of how forest structural characteristics—and therefore various forms of forest management—impact the snow resource, particularly in regions such as the northeastern United States, where canopies can contain deciduous and/or coniferous constituents. For instance, most coniferous forest types, which have needles present year-round, affect snow dynamics in fundamentally different ways than deciduous or mixed forest types that lose all or part of their leaves during the snow (dormant) season (Nelson et al., 2013). Lacking direct, ground-based observations of snowpack under the canopy types that dominate northeastern forests can introduce uncertainty into models, such as snow hydrology models, that rely on accurate snow data to predict runoff or water availability. Additionally, the northeastern region is a globally important carbon sink (Dubayah et al., 2022; Jiang et al., 2022) and has relatively dense forest cover compared to other regions in the United States. The scale of northeastern forests also allows for management actions that are tractable and meaningful across the landscape, with a strong network of practitioners and land managers already engaged in forest climate adaptation (McGann et al., 2022; Schattman et al., 2024). Supporting the idea that management can enhance snow refugia, modeling in the Sierra Nevada Range of the western United States found that forest thinning generally increased snow water equivalent (SWE, the equivalent amount of liquid water stored in snowpack) and reduced sublimation loss in sheltered, presumably intermediate canopy cover sites (Harpold et al., 2020; Krogh et al., 2020), while thinning in dense, tall canopy sites led to even greater increases in snow persistence (Lewis et al., 2023). Consequently, we have the greatest potential to create, strengthen, and conserve snow refugia via guidelines and policies that involve the management of vegetation. Although we focus on the northeastern US region here, canopy–snow relationships observed in northeastern forests are relevant to other regions across the boreal-temperate ecotone, such as the upper Midwest of the United States and southern Ontario, Quebec, and the Maritime Provinces in Canada.

Here, we first review the research conducted on forest–snow relationships and present a conceptual framework of how dormant season canopy cover (DSCC, the proportion of the ground area covered by the canopy during the dormant season) affects snowpack and snow refugia in northeastern forests. We then provide an initial test of our conceptual model using three case studies across the northeastern US region that uniquely consider a wide range of forest types and canopy conditions that have so far been overlooked. Each study maximized either temporal or spatial assessments, which together allowed us to explore how the forest canopy influences snow dynamics among a variety of canopy cover conditions and through time. Additionally, we discuss how our framework informs opportunities for experimental manipulations and tests of snow refugia development across natural gradients, enhanced monitoring networks, and co-created research related to forest management and climate adaptation practices.

DEVELOPING A CONCEPTUAL BASIS: FOREST EFFECTS ON SNOW THROUGHFALL AND PERSISTENCE

Forests in regions with seasonal snow cover host a diverse range of interrelated structural characteristics that collectively influence snow, such as differences in forest type and composition, canopy density and leaf area (López-Moreno & Latron, 2008; Sun et al., 2022), gap size and density (Currier & Lundquist, 2018; Mazzotti et al., 2019; Seyednasrollah & Kumar, 2014), and tree spatial arrangement (Schneider et al., 2019). Thus, the presence or absence of an overstory forest canopy and its structural characteristics can allow for a wide range of snow conditions even within a relatively small area or ecosystem. The forest canopy regulates several snowpack accumulation and ablation (reduction) processes, including canopy snow interception, snow deposition patterns, and the sub-canopy radiative balance (Varhola et al., 2010). In this section, we discuss characteristics of the forest canopy that influence snowpack depth and persistence as evidenced by previous research, noting that this research has primarily been conducted in areas of conifer-dominated forest conditions (Dickerson-Lange et al., 2017; Lundquist et al., 2013; Roth & Nolin, 2017; Strickfaden et al., 2023).

Forest type and composition

Forest type and composition (i.e., the variety and abundances of plant species in a community) can strongly influence snow interception rates. Deciduous forests generally exhibit lower interception rates than coniferous forests because they lose all or some of their leaves in the dormant season, which may lead to greater snow accumulation under deciduous canopies. Perhaps because many studies of snow hydrology focus on mountain "water tower" catchments that tend to be conifer-dominated, fewer studies of canopy snow interception have focused on deciduous canopies; however, studies that compared snow dynamics between deciduous and coniferous forest types show large variability in canopy snow interception or its inverse, throughfall, between stand types and among climatic regions. For conifer-dominated forests, the interception range of 28%–83% (Lundquist et al., 2013; Martin et al., 2013) encompasses values reported for Japan (Pomeroy et al., 1998) and western North America (Roth & Nolin, 2017; Storck et al., 2002). Interception in coniferous forests may decline in colder and boreal climates (Lundquist et al., 2013), which may be partly related to weaker snow grain cohesion at low temperatures (Roth & Nolin, 2019). For example, the interception range in pine and fir forests in Siberia and Russia was reported at 3%–58% (Pomeroy et al., 1998).

Despite limited studies in deciduous forests, there is compelling evidence that their interception rates are lower than those of coniferous forests, as is to be expected under canopies with dormant season leaf loss (Suzuki et al., 2008). Notably, Huerta et al. (2019) estimated canopy interception of snow as 23% in deciduous southern beech (*Nothofagus*) forests in the Southern Andes of Chile. In Maine, within the northeastern United States, snowpack depth was greater in deciduous and mixed stands than that in coniferous and open sites (by up to ~50 cm at peak snowpack) (Halpin & Bissonette, 1988). In nearby coastal New Hampshire, snowpack depth was greatest in deciduous-dominated sites compared to under coniferous and mixed canopies, as measured by magnaprobe and manual snow tubes (Proulx et al., 2023). SWE was ~1.7–2.8 times higher in deciduous aspen (*Populus* spp.) stands than in coniferous forests in Ontario, Canada, and was also higher under aspen canopies than under spruce (*Picea* spp.) and pine (*Pinus* spp.) stands or in open canopies in Saskatchewan, Canada (Pomeroy & Gray, 1995).

The influence of forest type on snowpack duration is unresolved. Research from Maine (Halpin & Bissonette, 1988) indicates that forest type may not strongly affect snowpack duration. By contrast, a study in western Montana, USA, found that snow persisted longer under a deciduous conifer species (*Larix occidentalis*) than under evergreen conifers (Schneider et al., 2019). A global meta-analysis of 21 plot-scale field studies, mostly conducted in western North America, indicated that in areas with mean winter temperatures exceeding −1°C, forest cover can shorten snowpack duration by 1–2 weeks, regardless of composition, compared to adjacent open areas via enhanced longwave radiation and snowmelt (Lundquist et al., 2013). Conversely, in cold regions where snowmelt occurs later in the season, canopy shielding against shortwave radiation generally outweighs increases in longwave radiation, reducing snowmelt and increasing snowpack duration (Dickerson-Lange et al., 2021). However, these patterns also depend on slope and aspect (Ellis et al., 2011; Safa et al., 2021) and have largely been studied in coniferous forest types.

Canopy density and leaf area

Canopy density, the amount of leaf area within the canopy, and other closely related canopy structural metrics (e.g., canopy occlusion, canopy closure, leaf area index, sky view fraction, crown completeness) determine the extent and thickness of canopy coverage and influence snowpack accumulation and persistence on the ground through the competing effects of snowfall interception and the protection of snowpack from solar radiation and wind (Hedstrom & Pomeroy, 1998; Lundberg & Halldin, 2001; Pomeroy et al., 1998; Pomeroy & Gray, 1995). For instance, in New Mexico, USA, coniferous forests with moderate (25%–40%) canopy density estimates, derived from National Land Cover Data (NLCD), had deeper snowpack than open areas or under denser (>40% cover) canopies (Veatch et al., 2009). A study in the Sierra Nevada Range of the western United States also indicated that maintaining moderate canopy density in coniferous forests promotes deeper snowpack, as thinning dense coniferous forests (>40% canopy cover) increased snow accumulation, whereas thinning moderate density coniferous forests decreased snow accumulation (Lewis et al., 2023). This was due to the negative effect of increased radiation, sublimation, and wind redistribution on snowpack when thinning forests with less than about 40% or 50% canopy cover (Lewis et al., 2023). However, SWE decreased roughly linearly with increasing canopy density across a wide range of canopy densities (25%–80% sky view fraction) in a mixed beech-fir forest in the Pyrenees of Spain (López-Moreno & Latron, 2008). These results were consistent with a study from New Hampshire, USA, where SWE decreased with increasing coniferous cover, which was associated with reduced sky view fraction (Penn et al., 2012). Deciduous canopies generally have lower winter canopy cover than coniferous canopies, reducing canopy snowfall interception while providing some shelter from solar radiation and wind (Varhola et al., 2010; Veatch et al., 2009). This balance may explain why snowpack depth was greatest in deciduous and, in some cases, mixed forest types in the northeastern studies described above (Halpin & Bissonette, 1988; Proulx et al., 2023). An important consideration is how and when canopy density is measured, which can vary across studies and may not always reflect winter conditions or the nuances of marcescent species such as American beech (*Fagus grandifolia*) or deciduous needle-leaved trees such as eastern larch (*Larix laricina*), which both occur in the northeastern United States.

Canopy gaps and tree spatial arrangement

Openings within the forest canopy (gaps) have been shown to increase snow accumulation, although the influences of the shapes and sizes of gaps on accumulation are disputed (Dickerson-Lange et al., 2023; Golding & Swanson, 1978; Sun et al., 2018) and other factors such as wind can interact with forest edges to create a "snow fence" effect, accumulating redistributed snow (Dickerson-Lange et al., 2021). Snowpack accumulation within gaps varies widely; even within a small (~1.5 km^2) domain, a process-based model in the Alps indicated variance of up to 200 mm of SWE in gaps or open areas, which can reflect meteorological and topographic controls (Mazzotti et al., 2023). In a homogenous lodgepole pine (*Pinus contorta*) forest in Alberta, Canada, canopy gaps of two to three tree heights in diameter had the greatest snow accumulation, while canopy gaps of one tree height in diameter had the least snow ablation (Golding & Swanson, 1978). Similarly, a study in a mixed coniferous forest in Montana, USA, indicated that widely spaced single trees and small gaps promoted deep and persistent snowpack compared to denser canopies by reducing interception and longwave radiation (Schneider et al., 2019). Additionally, forest edges influence snow accumulation and persistence, partly by disrupting wind and allowing blowing snow scoured from the open to accumulate near or within forested areas (Dickerson-Lange et al., 2021); for example, Currier and Lundquist (2018) found that differences in snowpack depth between various forest-edge classifications (e.g., leeward vs. windward) can be equally as important as differences in snowpack depth between open areas and forest-covered areas. Wind sheltering provided by vegetation and terrain (Marks et al., 2002) can produce drifts that result in outsized contributions to snowmelt hydrologic flux (Marshall et al., 2019).

A CONCEPTUAL MODEL OF SNOW DYNAMICS AND REFUGIA ACROSS A DSCC GRADIENT

The forest canopy acts as a mesofilter that modifies the characteristics influencing snowpack (climate, topography), thereby generating sub-canopy microclimates (De Frenne et al., 2013) and potentially snow refugia (Balantic et al., 2021; Keppel et al., 2024). Yet, the ways in which forest canopies affect the timing, quality, and quantity of snow in mixed and deciduous temperate forests, particularly in the northeastern United States, are poorly understood. Studies that have previously explored these relationships occurred largely in coniferous forests and adjacent open areas or canopy gaps. Many have also taken place in semi-arid climates such as the Mountain West of North America. This current state of knowledge raises questions about how forest canopies influence snowpack and the functions they provide in more mesic, temperate systems relevant to the northeastern region, underscoring the benefit of a research framework that is inclusive across forest canopies.

We therefore present a conceptual model of how a gradient in DSCC regulates snowpack and potentially provides snow refugia, as canopy cover measurements reflect the integration of several interrelated forest characteristics that can influence snow dynamics (e.g., forest type and species composition, canopy density, leaf area, canopy gaps, and tree spatial arrangement, as described above) (Figure 1). The interplay among these forest characteristics determines where a given stand or forest falls along the continuous DSCC gradient and thus, the model is inclusive across northeastern forest types. As there are no consistent thresholds for canopy cover classifications, we define the low zone of the DSCC gradient (Figure 1a) as <25% DSCC, which could span, for example, open canopies (e.g., <2-m tall vegetation, after recent harvest or disturbance) to deciduous forests with no

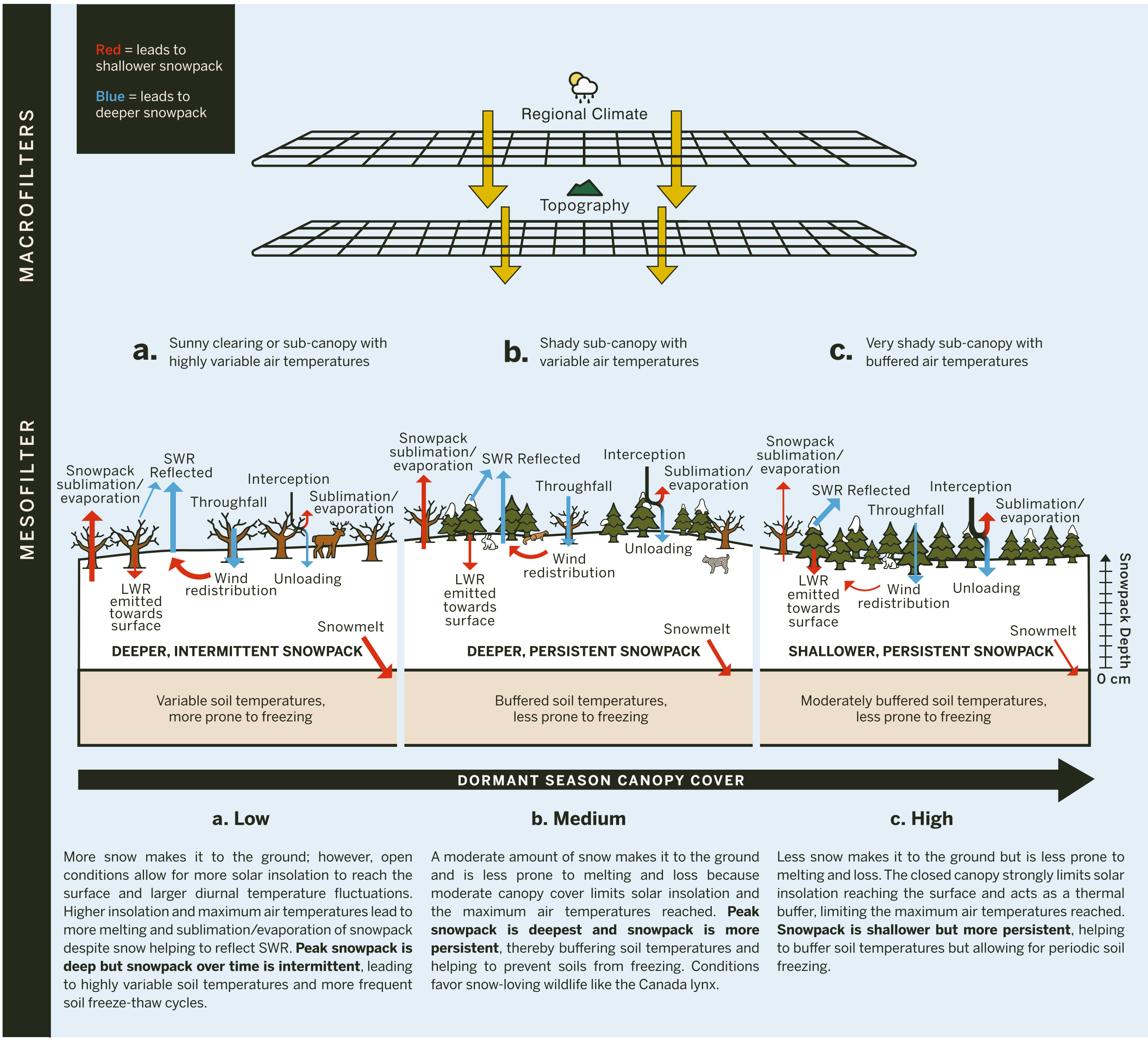

FIGURE 1 Conceptual diagram of the mechanisms driving differences in snowpack along a continuous gradient of dormant season canopy cover (DSCC). Macrofilters such as regional climate and topographical characteristics (e.g., elevation, slope, and aspect) determine base conditions, which are modified by the interrelated vegetation mesofilter characteristics that determine canopy cover (e.g., forest type/species composition, canopy density, leaf area, spatial arrangement, gap distributions/sizes). Red arrows indicate processes that lead to shallower snowpack, and blue arrows represent processes that lead to deeper snowpack; arrow sizes represent relative strength of the fluxes. Differences in snowpack depth among forest types over time are shown in Figure 2. LWR, longwave radiation; SWR, shortwave radiation. Illustration credit: Marissa Wandrey.

dormant season leaf area; followed by the medium zone with 25%–50% DSCC (Figure 1b), such as mature mixed coniferous–deciduous forests; and finally, the high zone with >50% DSCC (Figure 1c), such as dense closed-canopy coniferous forests. We emphasize that while we use discrete classifications for ease of discussion and illustration, DSCC is a continuous gradient from 0% to 100% and different forests belonging to the same broad forest type could fall at different points along the gradient depending on developmental stage and how their particular characteristics shape their DSCC. We offer examples here as a guide. Although many other studies have focused on coniferous forests and near the endpoints of the DSCC gradient (i.e., comparisons between open-canopy vs. dense, coniferous forests), we also consider the many forest types and canopy conditions in between and how those characteristics influence snowpack. The goal of our conceptual model is to produce a testable hypothesis that will motivate research in the northeastern region inclusive of more points along the DSCC gradient.

Our hypothesis builds on the work of others (e.g., Halpin & Bissonette, 1988; Veatch et al., 2009) and asserts that there is an intermediate DSCC zone where peak snowpack depth and the potential for snow refugia will be greatest largely because of an optimal balance between the opposing canopy-mediated effects of snowfall interception (which can limit snowpack) and snowpack sheltering (which can preserve snowpack) (Figure 2). For instance, a low DSCC forest (e.g., open or deciduous canopy with no dormant season leaf area) will accumulate the most sub-canopy snowpack (Figure 2b) because of low snowfall interception (high throughfall) (Figure 1a; Boon, 2007; López-Moreno & Latron, 2008; Proulx et al., 2023). However, this will be at least partly offset by high snowpack loss for a given point in time (Figure 2c) via snowmelt, wind redistribution, sublimation, and evaporation despite some reflection of shortwave radiation from the snow surface when present (Figure 1a; Lewis et al., 2023). Thus, snow cover may be more intermittent, particularly in the early and late snow season.

By contrast, a high DSCC forest (e.g., dense, multi-aged coniferous) will accumulate the least sub-canopy snowpack (Figure 2b) because of high snowfall interception (low throughfall) (Figure 1c; Boon, 2007; López-Moreno & Latron, 2008) but may also lose the least snowpack and retain persistent snow cover (Figure 2c) because of canopy sheltering from incoming solar radiation and wind (Figure 1c; Veatch et al., 2009). However, canopy shading may be less important for snow storage in warmer regions (e.g., lower Mid-Atlantic and lower Midwest of the United States) that experience early snow disappearance (i.e., before solar radiation is high enough for shading to influence snowpack) (Dickerson-Lange et al., 2021; Lundquist et al., 2013). Moreover, in those regions, high-density canopies may increase longwave radiation reaching the snow surface and thereby enhance snowmelt (Dickerson-Lange et al., 2021; Lundquist et al., 2013; Safa et al., 2021). We expect that in the Northeast, where winter temperatures are cold and snowmelt occurs relatively late in the season, the effect of canopy shading against solar radiation on snow storage outweighs the effects of canopy-mediated

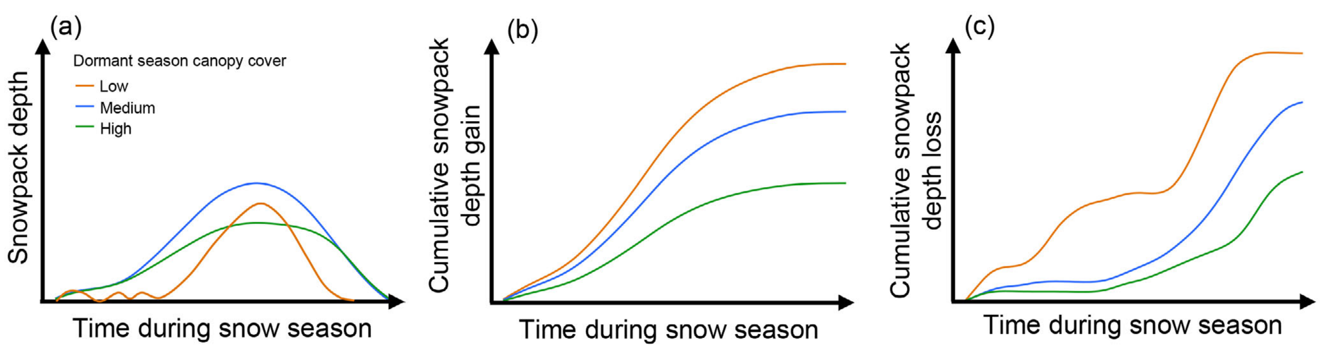

FIGURE 2 (a) Hypotheses of how differences in dormant season canopy cover (DSCC) affect sub-canopy snowpack depth and snow cover duration during the snow season. At a given point in time, snowpack depth is the difference between (b) cumulative snowpack depth gain (i.e., snow that reaches the surface) and (c) cumulative snowpack depth loss (i.e., losses from sub-canopy snowpack). Differences in cumulative gain among levels of DSCC are driven by differences in snow throughfall and sublimation/evaporation from intercepted canopy snow. Differences in cumulative loss among levels of DSCC are driven by differences in snowpack melt, sublimation, and evaporation. DSCC is illustrated with discrete categories here for simplification but is a continuous gradient. We hypothesize that there is an optimal zone where peak snowpack depth will be highest; here, this is illustrated as medium DSCC, which could represent a vertically stratified mixed coniferous–deciduous forest, for example. Low DSCC could represent a recently disturbed area with even-aged regenerating seedlings/saplings and little to no dormant season leaf area, while high DSCC could represent a dense coniferous forest with multiple age classes. See Figure 1 for an illustration of the mechanisms corresponding to each of the three levels of DSCC. SWE, snow water equivalent.

increases in longwave radiation, but this balance may tip in the other direction in warmer regions (Lundquist et al., 2013), particularly along steep south-facing slopes (Safa et al., 2021) or as climate warms. Thus, sunny south-facing slopes in warm winter regions may be an exception to our conceptual model, with higher rates of snowmelt in high DSCC forests than in the open.

In a medium DSCC forest, we expect snowpack accumulation and losses to be intermediate (Figure 2b,c), leading to the deepest maximum snowpack and, relative to low DSCC forests, more persistent snow cover (Figure 1b; Halpin & Bissonette, 1988; Pomeroy & Gray, 1995; Veatch et al., 2009), possibly allowing these forests to serve as snow refugia. This optimal zone may shift toward the low–medium end of the DSCC gradient in warmer regions because of canopy effects on the net radiative balance that we describe above (Safa et al., 2021). Therefore, although studies comparing open (Figure 1a) versus dense coniferous (Figure 1c) stands conclude that the presence of a forest canopy reduces snowpack (Broxton et al., 2015; Golding & Swanson, 1986; Storck et al., 2002), studies that consider intermediate canopy cover (Figure 1b) may find deeper snowpack compared to open canopies and/or that the presence of a forest canopy preserves snowpack throughout the season (Halpin & Bissonette, 1988; Lewis et al., 2023; Pomeroy & Gray, 1995; Veatch et al., 2009).

In our conceptual model, DSCC also influences other ecosystem components via impacts on snow. In lower DSCC forests that may experience substantial daytime solar insolation, nighttime radiative cooling, and more intermittent snowpack, diurnal changes in soil temperature may be larger, and soil freeze–thaw cycles may be frequent (Hardy et al., 2001). Repeated soil disturbances from freeze–thaw cycles could affect soil structure (Oztas & Fayetorbay, 2003; Xiao et al., 2019), roots (Kreyling et al., 2012; Sanders-DeMott, McNellis, et al., 2018; Sanders-DeMott, Sorensen, et al., 2018), microbes (Pastore et al., 2023; Sorensen et al., 2018; Yanai et al., 2004), and biogeochemical cycles (Nielsen et al., 2001; Song et al., 2017; Urakawa et al., 2014). By contrast, medium DSCC forests may experience the most insulated and stable soil temperatures by sustaining the deepest and most persistent snowpack. High DSCC forests may experience shallower but more persistent snowpack with less solar insolation and radiative cooling at the ground/snow surface, helping to buffer soil temperatures. Both instances could be considered snow refugia depending on the species of interest.

Wildlife distributions and habitat use patterns are shaped by many factors, but species that rely on the presence of snowpack may favor medium and high DSCC forests (e.g., snowshoe hare, *Lepus americanus*; Sirén et al., 2023; Figure 1b,c), with the species that need the deepest snowpack often using medium DSCC forests (e.g., Canada lynx, *Lynx canadensis*; Fuller et al., 2007, marten; Sirén et al., 2017; Figure 1c). Deer may be most abundant in areas with shallow, intermittent snowpack, found more often in low DSCC forests (Figure 1a), but they also use high DSCC forests that provide sheltered conditions and shallow snowpack (Lefort et al., 2007).

DSCC-DEPENDENT PATTERNS IN SNOW REFUGIA: NORTHEASTERN FOREST EXAMPLES

Given limited attention to studies of snow accumulation, depth, and persistence in varied DSCC contexts in the northeastern United States, we sought existing data that encompassed aspects of our conceptual drivers to provide an initial test of the influence of DSCC as shown in Figure 1 in this region. We present data from three case studies that span the three climate divisions present in northern New England and that measured snow accumulation, depth, and/or penetrability across forests with different DSCC types (Tables 1 and 2, Figures 3 and 4; Appendix S1: Figures S1–S7). These case studies include

TABLE 1 Characteristics of each regional case study location.

Characteristic	Old Town, ME	Acadia National Park, ME	White Mountains, NH
Coordinates	44.935, −68.666	44.343, −68.247	44.795, −71.316
Elevation (m asl)	40	152–442	619–1050
Climate division	Maine southern interior	Maine coastal	New Hampshire northern
Mean annual temperature (°C)	12.2[a]	7.6[b]	2.3[c]
Mean total annual precipitation (mm)	1130[a]	1430[b]	1769[c]

Abbreviations: asl, above sea level; ME, Maine; NH, New Hampshire.
[a]Data from 1991 to 2020; nearby weather station (Palecki et al., 2021).
[b]Data from 1999 to 2022; temperature data from Acadia National Park NPS Gaseous Monitoring Program, Station ID: ACAD-MH, https://ard-request.air-resource.com/; precipitation data from Acadia National Park NADP rain gauge, Site ID: ME98, https://nadp.slh.wisc.edu/precipitation/.
[c]Data from 1991 to 2022; Daymet (Thornton et al., 2022).

TABLE 2 Characteristics among dormant season canopy cover (DSCC) classes for each regional case study location.

	Old Town		Acadia			White Mountains			
Characteristic	Medium	High	Low	Medium	High	Open	Low	Medium	High
No. sites	1	1	6	4	2	8	4	8	10
Forest type	Mixed	Coniferous	Northern hardwood	Mixed, coniferous, or northern hardwood	Coniferous	Northern hardwood	Northern hardwood	Mixed	Coniferous
Dominant species	*Fgra*, *Tcan*	*Tcan*, *Pstr*	*Apen*/*Bpap*	*Apen*/*Bpap*, *Arub*, *Abal*, *Prub*	*Abal*, *Prub*	*Ball*, *Asac*	*Ball*, *Asac*	*Ball*, *Asac*, *Prub*, *Abal*	*Prub*, *Abal*
Forest age (years)	~80	~80	~60 to >200	~60 to >200	~60 to >200	~10	>100	>100	>100
Land-use history	Single-tree selection harvest in the past 10 years	Thinned in the past 25 years	One watershed burned 1947[a]	One watershed burned 1947[a]	One watershed burned 1947[a]	Harvested in the past 10 years	Harvested >100 years ago	Harvested >100 years ago	Harvested >100 years ago
Mean slope (°)[b]	2.4	0.9	14.5	11.5	20.3	10.3	7.7	9.4	10.4
Mean northness[b,c]	0.98	0.96	−0.51	−0.22	−0.58	−0.35	−0.58	−0.03	0.25
Mean eastness[b,d]	−0.2	0.27	0.16	−0.14	−0.65	−0.31	0.19	−0.29	−0.34

Abbreviations: Fgra, *Fagus grandifolia*; Tcan, *Tsuga canadensis*; Pstr, *Pinus strobus*; Apen, *Acer pensylvanicum*; Bpap, *Betula papyrifera*; Arub, *Acer rubrum*; Abal, *Abies balsamea*; Prub, *Picea rubens*; Ball, *Betula alleghaniensis*; Asac, *Acer saccharum*.

[a]One watershed burned in 1947, and one watershed has been undisturbed for >200 years; both watersheds contained sites in each DSCC class (see Schauffler et al., 2007).

[b]Value for each individual site is shown in Appendix S1: Table S1.

[c]Northness is cosine(aspect), calculated with aspect in radians; northness ranges from −1 at 180° (south) to 1 at 0° (north).

[d]Eastness is sine(aspect), calculated with aspect in radians; eastness ranges from −1 at 270° (west) to 1 at 90° (east).

2 adjacent forest sites in Old Town, Maine; 12 forest sites in Acadia National Park, Maine; and 30 forest sites in the northern White Mountains of New Hampshire (Tables 1 and 2; Appendix S1: Figure S1; methods and results are described in Appendix S1: Case study details).

These three regional case studies support our prediction that the greatest maximum snowpack depth occurs in medium DSCC forests (Figure 1), which here include mixed coniferous–deciduous forest types and those with about 25%–50% DSCC, underscoring their potential as snow refugia. For example, in the White Mountains, we found that in early winter, the lowest DSCC sites with open canopies accumulated the most snow, whereas high DSCC sites with dense canopies accumulated the least snow (Figure 4c) likely due to differences in interception and albedo. However, despite substantial early snow accumulation under the open canopies, those areas were likely more vulnerable to snow loss processes (e.g., snowmelt, wind redistribution, sublimation, and evaporation), limiting peak snowpack depth and potential as snow refugia. Thus, medium DSCC sites achieved and then maintained the deepest snowpack (Figure 4c). Although forests in Acadia National Park accumulated similar amounts of snow early in the season, snowpack accumulation among sites quickly diverged and followed our prediction (Figure 2a) with the deepest snowpack in medium DSCC forests, moderate snowpack in low DSCC forests, and the shallowest snowpack in high DSCC forests until the late snow season, when snowpack depth under low DSCC declined (Figure 4b). Although there was variability among sites, medium DSCC sites had ~2–2.5 cm higher SWE, on average, than low DSCC sites by mid-winter, and high

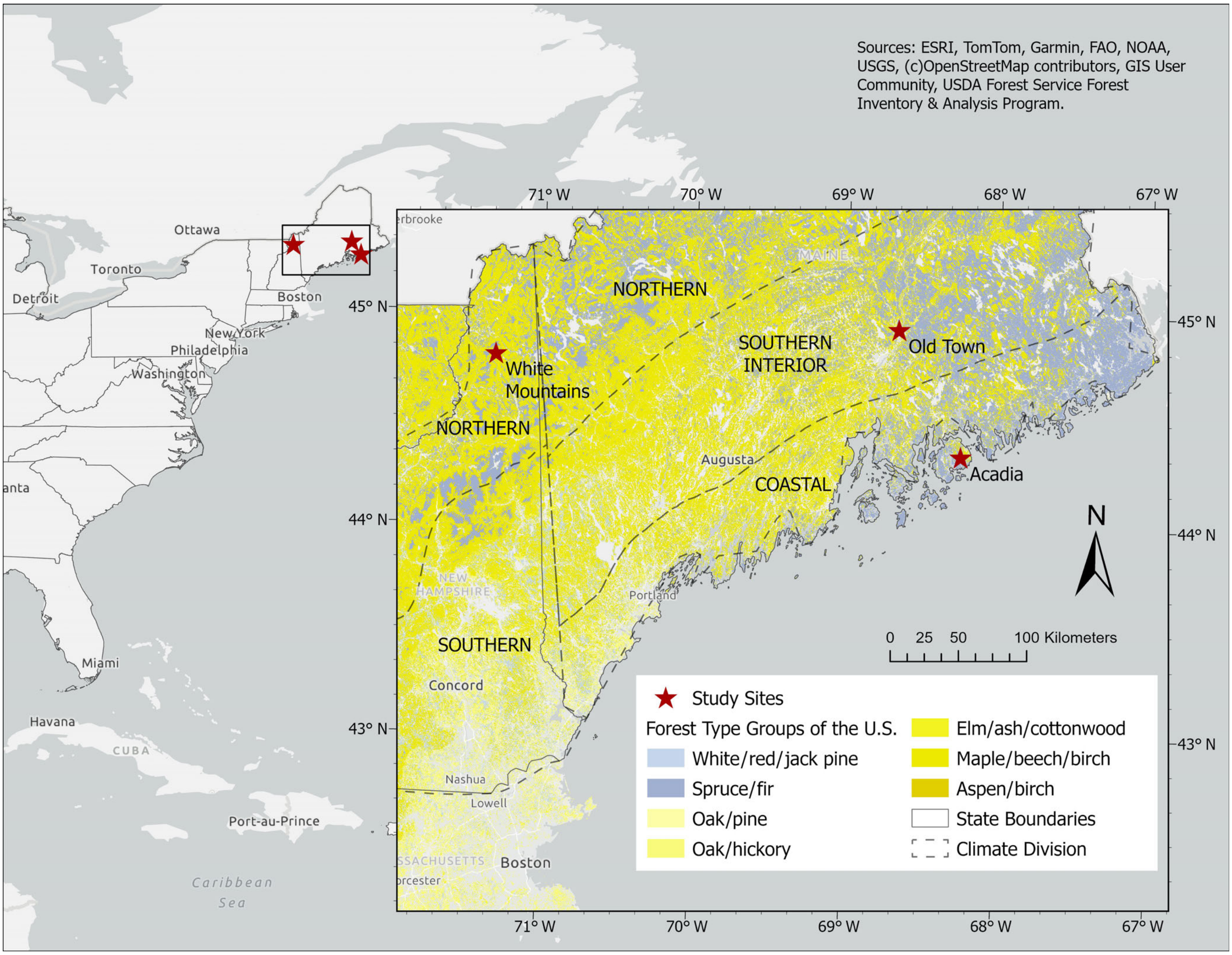

FIGURE 3 Map of study locations relative to climate divisions and forest type groups. The climate division within which each study resides appears in uppercase. Climate division data source: National Climatic Data Center, 1991, US Geological Survey, Reston, Virginia, https://water.usgs.gov/GIS/dsdl/climate_div_shp.zip. Forest types for the study region are from USDA Forest Service Forest Inventory & Analysis Program: Science by Barry T. Wilson (USFS); cartography by Emily Meriam (ESRI). Maps of each study's specific forest sites with dormant season canopy cover indicated are in Appendix S1: Figure S1.

DSCC sites had as much as ~3 cm less SWE than low DSCC sites (Appendix S1: Figure S3). In Old Town, maximum snowpack depth was, on average, 15 cm greater in the medium DSCC forest stand than in the high DSCC forest stand (Figure 4a).

Results from Old Town (Figure 4a; Appendix S1: Figure S4) also hint at temporal differences in snowpack dynamics among forest types, underscoring the benefit of long-term studies that investigate snow dynamics across the DSCC gradient. Notably, the date of peak snowpack depth at Old Town was, in some years, later in the medium DSCC forest than in the high DSCC forest by a few days to more than 1 month (Figure 4a; Appendix S1: Figure S4). Such differences in the timing of peak snowpack depth are important to hydrological cycles, soil biogeochemistry, wildlife, and recreation. Placing this finding within the context of current understanding of how forest canopies can influence the date of maximum snowpack depth is difficult because relevant literature is sparse. Some studies have used the standard date of April 1 as an index to compare maximum snowpack depth or SWE across sites or years (Bohr & Aguado, 2001; Kapnick & Hall, 2012; Varhola et al., 2010). As noted in Bohr and Aguado (2001), use of this date can lead to underestimation of peak SWE, and given the timing of peak snowpack one or more months earlier than April 1 depending on the year at these northeastern sites, the April 1 index is not appropriate here. In the absence of other examples against which to compare, we speculate that the large discrepancy in the timing of maximum snowpack depth between the medium and high DSCC forest stands during the winter of 2022–2023 was due to the outsized role that canopy

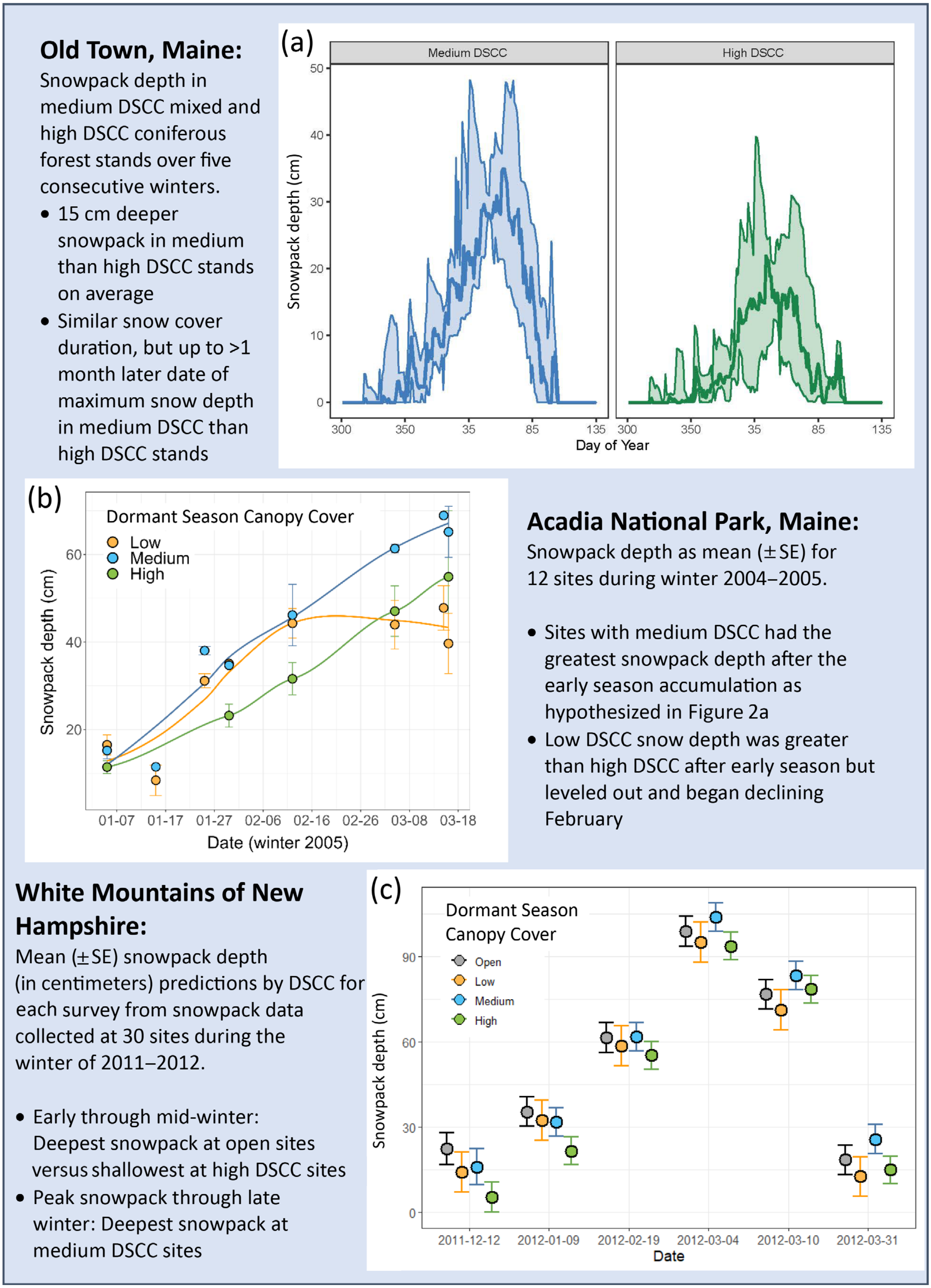

FIGURE 4 Legend on next page.

interception can play when snowfall occurs in tandem with relatively warm air temperatures (Lundquist et al., 2013; Roth & Nolin, 2019). This may have been the case in early March 2023, when air temperatures during a snowfall event were mild enough (about −1°C) to drive substantial canopy interception due to high snow grain cohesion (Roth & Nolin, 2019). Historical and projected trends for winter air temperatures in the northeastern United States (Burakowski et al., 2022; Contosta et al., 2020) indicate an increase in snowfall events during warm (≥2°C) or mild (−2.4 to 0.2°C; Roth & Nolin, 2019) conditions. The data from Old Town indicate that DSCC could substantially influence the accumulation of snow falling in warm or mild conditions that may become more common as the climate warms.

In our conceptual model, we also suggest that DSCC influences other ecosystem components such as soil biogeochemistry and wildlife via impacts on snow. Although we did not investigate those cascading effects here, we did observe a substantial influence of DSCC on soil temperature at Old Town. Notably, soil temperatures reached sub-zero much less often in the medium DSCC forest stand than in the high DSCC forest stand. The overlap in daily average air temperature and similarities in diurnal variability of air and soil temperatures between stands (Appendix S1: Figure S5) suggest that differences in canopy radiative balance between stands did not drive differences in soil temperature. Instead, the Old Town data indicate that deeper snowpack in the medium DSCC forest stand buffered soil from fluctuating air temperatures more than the shallower snowpack in the higher DSCC forest stand (Appendix S1: Figure S6). Prior studies have indicated that 15–45 cm of snow is needed to protect soil from fluctuating air temperatures (Brooks et al., 1997; Liptzin et al., 2009; Zhang, 2005), although the exact threshold depends on local site conditions such as snowpack density, SWE, and ambient air temperature (Liptzin et al., 2009; Zhang, 2005). At Old Town, we found that snowpack depth in the medium DSCC forest reached a minimum depth of 15 cm more frequently (~50% of each winter) than that in the high DSCC forest (0–30 days depending on year). Additionally, in the White Mountains, DSCC affected snow penetrability, a marker of snow density, which could have implications for wildlife and recreation (Appendix S1: Figure S7). The lower density snow observed at medium DSCC sites in the White Mountains may explain why certain mammals such as American marten select mixed forests during winter, as deep and powdery snow provides efficient subnivean access to resting, denning, and foraging sites (Pauli et al., 2013; Sirén et al., 2016).

By investigating snow dynamics in forests along the DSCC gradient, we reveal important patterns in northeastern forests that may be missed in studies limited to coniferous forests or low versus high DSCC contrasts, and we identify the potential importance of medium DSCC forests in creating potential snow refugia. Had we only compared low to high DSCC here, we would have concluded that the presence of a forest canopy reduces snowpack when it is influential. Instead, we found a more complex relationship between the forest canopy and snow, including an optimal zone in which the medium DSCC canopy allows snow accumulation while also protecting snowpack from loss mechanisms, a balance that has long been recognized but rarely tested across forest types or DSCC gradients (Halpin & Bissonette, 1988; Lewis et al., 2023; Varhola et al., 2010; Veatch et al., 2009). Overall, our case studies across the Northeast region indicate that medium DSCC forests could serve as snow refugia that will help to sustain the benefits provided by snow as climate change continues. Further studies that test our conceptual model by characterizing snow dynamics along DSCC gradients may help to guide management and improve model predictions in the northeastern US region and perhaps others along the boreal-temperate ecotone.

MANAGEMENT IMPLICATIONS AND FUTURE DIRECTIONS

In summary, our concept of snow refugia and model for how diverse forest canopies impact snow dynamics (Figures 1 and 2) offer a framework to guide research investigating forest management strategies for preserving snowpack and its benefits in northeastern forests amidst ongoing climate change. Our regional studies included a range of canopy conditions and support our concept that forests with moderate canopy cover in the dormant season promote the deepest snowpack, in contrast to results

FIGURE 4 Snowpack depth over time in forests spanning the dormant season canopy cover (DSCC) gradient at (a) Old Town, Maine; (b) Acadia National Park, Maine; and (c) White Mountains, New Hampshire. (a) Graphs show median (thick line), minimum (bottom thin line), and maximum (top thin line) of daily mean snowpack depths within each forest stand across the snow season for all five consecutive winters. Patterns for each individual winter are shown in Appendix S1: Figure S4. (b) Sites were categorized as low (<25%), medium (25%–50%), and high (>50%) DSCC. DSCC was quantified using fisheye photos and image analysis as documented in Nelson (2007). (c) Open, 8 harvested sites; low DSCC, 4 unharvested northern hardwood forest sites; medium DSCC, 8 unharvested mixed forest sites; and high DSCC, 10 unharvested coniferous forest sites.

from studies limited to coniferous forests or comparisons between open versus closed canopies. These linkages between forest canopy cover and snowpack (Figure 1) indicate tangible, site-level forest structural and compositional conditions that managers could encourage as part of climate adaptation actions, such as developing snow refugia for sustaining cold-dependent species and ecosystem functions in the face of climate change. Potential tactics, including supplementing or restoring or even creating snow refugia, could help protect snow-dependent species and functions even as temperatures warm (Keppel et al., 2024). However, increased manipulative and natural canopy–snow experiments, improved observational networks across a wider range of forest canopies, and manager involvement including the co-creation of research in the context of decision-support needs would allow us to better understand canopy–snow relationships and support forest ecosystem management in the northeastern United States.

Manipulative and natural canopy–snow experiments

Given the importance of snowpack to hydrological processes, drought, and water supply in the western United States, considerable recent research has explored the contributions of coniferous forest canopies to snowpack depth and duration in forests throughout the region (O'Donnell et al., 2021; Schneider et al., 2019; Stevens, 2017). Comparatively, the literature on the influence of deciduous and mixed forest canopies on snowpack depth and duration in northeastern temperate forests is much less developed and has been for over a decade (Penn et al., 2012). Thus, experiments in temperate forests that identify clear mechanisms of how understudied zones of the DSCC gradient affect wintertime snowpack depth and duration would be useful, especially given the potential importance of medium DSCC forests as snow refugia suggested by our regional studies (Figure 4) and associated conceptual model (Figure 1).

These experiments could leverage existing gradients in DSCC or create DSCC gradients through silvicultural treatments. Leveraging DSCC gradients that are attributable to differing stand ages and forest developmental stages could enhance understanding of which forest types most effectively promote snowpack in regenerating forests, patterns that may differ from those of the predominantly older-aged forests tested in our case studies. For example, DSCC differences among forest types could be less pronounced in younger stands (e.g., 15-year-old regenerating spruce-fir vs. beech stands) than those observed in older stands with developed canopies and sub-canopies, leading to less pronounced forest-type differences in snowpack. Documenting snowpack variability across a wider range of DSCC gradients would allow for assessment of management methods based on ecological models of silviculture that encourage a range of canopy gap sizes, retention of living and dead trees or patches, and multiple canopy layers, which represent strategies that generate medium to high DSCC, particularly in mixed forest and conifer-dominated systems (Raymond et al., 2023; Figure 1). Partial harvesting strategies, like selection and shelterwood methods, have become the predominant form of management across ownerships in the northeastern US region, indicating the operational and financial feasibility of these strategies for managing snow refugia (Bose, 2021). At the same time, increasing conifer cover in some areas may incur a cost if mature seed sources are not present and planting is necessary to restore this component. Gap closure rates for forests in this region suggest that small canopy openings created to enhance snow accumulation would last about 10–30 years depending on gap size and species composition, which overlaps with typical harvest entries for these forest types, allowing for the creation of new openings as initial areas no longer function as snow refugia (Rentch et al., 2010; Webster & Lorimer, 2005). Further research into how to prioritize sites for these silvicultural treatments, including the topographic settings and local climate regimes that may best support snow refugia and enhance connectivity across the landscape, is critical to ensure adaptive treatments are occurring in the portions of a given landscape with the greatest long-term potential for sustaining snow refugia. Such research is timely because increasing droughts and fires in the Northeast in recent years amplify the threat of declining snowpack (Burakowski et al., 2022) and highlight that new experimental efforts focused on snowpack retention in the northeastern United States would be beneficial to inform forest management.

Manipulative and natural canopy–snow experiments would also provide key benchmarks and thresholds for snow-dependent species, ecosystem functions, and human activities. For example, research that details how populations of wildlife species respond to snowpack depth (e.g., Evans & Mortelliti, 2022; Shipley & Zuckerberg, 2023) and change their behavior or survivorship may provide thresholds that relate to DSCC as outlined in the conceptual model (Figure 1) and by which snow-related forest management can be guided. Studies that leverage natural gradients in canopy structural characteristics and/or climate, experimental manipulations, and long-term forest monitoring plots in the Northeast could help define canopy structural thresholds to manage key ecosystem processes and functions linked to snow dynamics, such as soil carbon and nutrient cycling.

Improved observational networks

Collections of snowpack depth, duration, and timing of melt would advance understanding of canopy–snow relationships and help to identify snow refugia across a wide range of forest canopies found in the northeastern United States and across the boreal-temperate ecotone. The use of climatological sensor networks such as the Natural Resources Conservation Service's Snow Telemetry (SNOTEL) where gradients in forest canopy cover exist has led to a more comprehensive understanding of these relationships across the western US landscape (Sun et al., 2022), and a feasibility study focused on initiating such a network in the eastern United States is underway. Given the many long-term forest inventory plots located at research forests throughout the region, the addition of snowpack monitoring capabilities at these and other regional locations would expand our capacity to establish firm relationships between canopy characteristics and snow phenology. Advances in networks of snow data measurements (Sirén et al., 2018) and, in the case of wildlife, camera trap technology (Soininen et al., 2015) may also help the development of snowpack depth metrics and thresholds for different species and ecosystem processes. Although recent efforts to use unpiloted aerial systems equipped with light detection and ranging (lidar) have materialized (Jacobs et al., 2021; Proulx et al., 2023), considerable work remains to be done. Sites with paired lidar data and under-canopy snow metrics from sensors or manual measurements that could provide a robust design for testing the DSCC conceptual model (Figure 1) are sparse or absent at the northeast regional scale and would provide a rich opportunity for further research and modeling.

A critical consideration for where to locate new snow sensing networks would be the inclusion of actively managed forests. Although thinning of conifer species has often been referred to as a key strategy to influence snowpack in western North America (Harpold et al., 2020), the influences of site-specific climatology and topography can be dominant (Lundquist et al., 2013). Furthermore, canopy gaps and edges, which become more prevalent in forest management prescriptions such as patch cuts, group selection, and shelterwood harvests, have complex but important impacts on snowpack mass and timing (Broxton et al., 2021; Currier & Lundquist, 2018; Sun et al., 2022).

Manager involvement

Managers have identified changing winter conditions as one of the primary challenges to sustaining forest conditions in the northeastern US region (Schattman et al., 2024). At the same time, there has been an increasing focus of management activities on multi-aged and mixed species approaches that may minimize the impacts of changing climate regimes and a growing prevalence of non-indigenous insects and pathogens (McGann et al., 2022). Nevertheless, the linkages between these approaches and opportunities for enhancing snow refugia have been under explored. Current forest and site conditions will influence the relative degree to which canopy cover, the proportion of ground area covered by the canopy, can be managed to restore and maintain medium and high DSCC to enhance snow refugia. Given the unique role of mixed coniferous–deciduous forests in providing deep and persistent snowpack, as we assert in the conceptual model (Figure 1) and as indicated by the case studies, restoration of these once predominant forest types to areas historically supporting these assemblages could be a priority (Kenefic et al., 2021; Keppel et al., 2024). Similarly, conifer species provide a unique function overall in generating cold conditions at microscales, so strategies to sustain coniferous species, including protecting advance regeneration (i.e., seedlings/saplings that established naturally in the understory) during harvests (Bourque et al., 2022), ensuring suitable seedbed conditions are present (Weaver et al., 2009), and supplementing natural regeneration of coniferous species with planted seedlings representing future-climate-adapted genotypes (Palik et al., 2022) could be integrated into strategies for sustaining cold conditions.

Decision support tools for forest managers from western North America have been designed to estimate the combined influence of forest structure, aspect, and climatic conditions on snow accumulation (Dickerson-Lange et al., 2021), but these relationships may be more complex in forests with deciduous and coniferous elements. In the Northeast, regional (e.g., Northern Institute of Applied Climate Science) and statewide (e.g., Maine Adaptive Silviculture Network) practitioner-focused networks collaborate with researchers and agencies to co-create decision support resources such as climate change workbooks (e.g., Janowiak et al., 2014), providing a robust model for co-creating such tools focused on DSCC management for snow refugia development.

Finally, it will be important to understand how forest management for snow refugia relates to other objectives, including promoting resilience of spruce-fir forests, maintaining canopy cover or structure for wildlife requirements, promoting soil carbon accumulation and storage, and increasing tree vigor to minimize forest health concerns. In the northeastern United States, where the majority of forested lands are privately owned (Butler et al., 2021; Hoover & Riddle, 2021; Sass et al., 2020), studies assessing private landowners' attitudes toward snow persistence as a management objective may also be helpful for future practice. In addition, diversifying outreach efforts to highlight the important linkages between snow and forests, particularly in the context of changing winters, can potentially improve large-scale management.

AUTHOR CONTRIBUTIONS

This manuscript was collaboratively developed, written, and edited. All authors made substantial contributions to this work, including conceptualization, writing, contributing data, and interpreting or synthesizing results. All authors reviewed and edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Contosta, 2025; Nelson, 2025; Sirén, 2025) are available on Zenodo as follows: Acadia case study: https://doi.org/10.5281/zenodo.15282804, Old Town case study: https://doi.org/10.5281/zenodo.15303330, and White Mountains case study: https://doi.org/10.5281/zenodo.15306801.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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