Effects of Climate Change on Midwestern Ecosystems: Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest

Suggested Citation

Ratcliffe, H., Charton, K., Siddons, T., Lyons, M.P. and LeDee, O. 2025. Effects of Climate Change on Midwestern Ecosystems: Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest. Midwest Climate Adaptation Science Center. (72 pages) Available: https://mwcasc.umn.edu

Acknowledgements

This work was supported by the U.S. Geological Survey (USGS) Midwest Climate Adaptation Science Center and included technical contributors from the Oak Ridge Institute for Science Education and the University of Minnesota, Twin Cities. We acknowledge the World Climate Research Programme's Working Group on Coupled Modelling, which is responsible for CMIP, and we thank the climate modeling groups for producing and making available their model output. For CMIP, the U.S. Department of Energy's Program for Climate Model Diagnosis and Intercomparison provides coordinating support and leads development of software infrastructure in partnership with the Global Organization for Earth System Science Portals. We thank the Midwest Association of Fish and Wildlife Agencies, Wildlife Diversity Technical Working Committee for their engagement.

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Table of Contents

Foreword 4
Series Overview 4
Process 4
Habitat Selection 4
Climate Exposure 4
Habitat Prioritization 5
Focal Wildlife Species 6
Focal Aquatic Systems 6
Literature Review 7
Taxonomic Conventions 7
Chapter Organization 7
Executive Summary 9
Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest 10
Key Climate Change Stressors 10
Warming 10
Milder Winters 10
Key Climate Change Impacts 14
Habitat Structure 14
Community Composition 17
Invasive Species 19
Pests and Pathogens 20
Herbivory 22
Climate Change Impacts by Habitat 23
Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest 23
Overview of Climate Projections 25
Key Climate Change Stressors 26
Key Climate Change Impacts 29
Focal Wildlife Species: American Marten 34
Focal Aquatic System: Pelican Lake 35
Work Cited 36
Appendix 1 71

Appendix 2 72

Foreword

Series Overview

The following is the seventh chapter of a multi-part series examining the vulnerability of natural habitats in the Midwest region to the impacts of climate change. This work was conceived as part of an interagency effort to facilitate the inclusion of climate change considerations into 2025 revisions of State Wildlife Action Plans (SWAPs). Although tailored to the needs of state agencies within the Midwest region, these assessments focus on habitats and species found throughout North America and are thus broadly relevant to regions and considerations beyond that of the Midwest.

This work was developed as a collaboration between the U.S. Geological Survey (USGS) Midwest Climate Adaptation Science Center (MW CASC) and natural resource agencies from Minnesota, Wisconsin, Michigan, Ohio, Indiana, Illinois, Iowa, and Missouri. During discussions on the needs and challenges of the 2025 SWAP revision process, collaborators identified habitat climate vulnerability as a key area requiring further exploration and deeper understanding.

Process

To assess the impact of climate change on habitats in the Midwest, the MW CASC developed a process comprised of the following steps: 1) potential habitat identification and delineation; 2) summarizing exposure to key climate change stressors; and 3) reviewing and synthesizing relevant scientific literature into qualitative summaries of climate change impacts to habitats.

Habitat Selection

We identified and defined habitats using the U.S. National Vegetation Classification database (USNVC, 2020), which provides a common lexicon of hierarchically classified and spatially referenced vegetation communities throughout the United States. Within this hierarchy, the Group level represents the finest resolution classification tier that is coupled with spatially referenced distributions. Hereafter, discrete “habitats” are synonymous with USNVC Groups and their corresponding lower-level community classifications (Alliance and Association). To enhance relevancy for the Midwest region, the lowest-level classifications for each group (i.e., Association) not occurring within the Midwest were excluded from this assessment.

Climate Exposure

To summarize climate exposure, we utilized a combination of Level II and Level III ecoregions (U.S. Environmental Protection Agency, 2013) to identify 12 ecologically relevant sub-regions of the Midwest that served as the spatial basis for summarizing climate exposure (Figure i). Climate projections are derived from the Coupled Model Intercomparison Project Phase 5 (CMIP5) and were statistically downscaled using the MACAv2-METDATA dataset, which applies the Multivariate Adaptive Constructed Analogs (MACA) method (Abatzoglou, 2013; van Vuuren and others, 2011). Projections are

presented under two greenhouse gas concentration pathways: RCP4.5, an emissions scenario assuming global mitigation efforts that lead to greenhouse gas emissions peaking mid-century and stabilizing by 2100, and RCP8.5, a high-emissions scenario that assumes continued growth in greenhouse gas emissions with limited mitigation. These scenarios represent a range of plausible future climate conditions and are commonly used to bracket moderate and high-end climate change trajectories. In-text references to climate projections primarily detail RCP8.5 estimates to highlight particularly severe outcomes, although all tables and figures report both RCP4.5 and RCP8.5 estimates.

Figure i. Distribution and names of 12 ecoregions within the larger Midwest region. Ecoregions represent a mixture of Level II and Level III EPA ecoregions (U.S. Environmental Protection Agency, 2013) and have been renamed following the Midwest Conservation Blueprint Ecoregions (Wright and others, 2022).

Habitat Prioritization

Seventy-seven natural Groups (i.e., habitats) occur in states comprising the Midwest region (Minnesota, Wisconsin, Michigan, Ohio, Indiana, Illinois, Iowa, and Missouri). To focus this assessment on a subset of these habitats, representatives from each state identified two or more habitats for each ecoregion

present in their respective state. We reconciled conflicting priorities to identify two habitats per ecoregion (hereafter identified as "priority habitats") for a total of 22 priority habitats that served as the focus of our analysis (Table i).

Table i. Priority habitats for each ecoregion. Analogous Level III EPA ecoregion numbers (U.S. Environmental Protection Agency, 2013) and U.S. National Vegetation Classification database Group numbers (USNVC, 2020) are provided for each ecoregion and priority habitat.

Ecoregion	Priority habitat
Appalachian Forest (8.4.3)	Appalachian-Central Interior Mesic Forest (G020)
	Central Appalachian-Northeast Oak Forest and Woodland (G650)
Central Irregular Plains (9.2.4)	Central Midwest Oak Openings and Barrens (G181)
	South Central-Appalachian-Northeast Floodplain Forest Group (G673)
Central Plains (8.2.1–8.2.4)	Midwest Floodplain Forest (G652)
	Central Interior-Great Lakes Flatwoods and Swamp Forest (G917)
Driftless Area (8.1.5)	North-Central Beech - Maple - Basswood Forest (G021)
	North-Central Oak - Hickory Forest and Woodland (G649)
Erie Drift Plains (8.1.1, 8.1.10)	North-Central Beech - Maple - Basswood Forest (G021)
	Appalachian-Northeast Mesic Forest (G742)
Interior Plateau (8.3.2, 8.3.3, 8.3.6, 8.5.2)	Bald-cypress - Tupelo Floodplain Forest (G033)
	Interior Low Plateau Oak Forest, Woodland and Savanna (G950)
Mixed Wood Plains (8.1.4)	Laurentian-Acadian Alkaline Swamp (G046)
	Eastern North American Freshwater Marsh (G125)
Northern Hardwood Forest (5.2.1, 5.2.2)	Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest (G048)
	Eastern North American Boreal-Subboreal Bog and Acidic Fen (G1172)
Northern Plains (9.2.1, 9.2.2)	Northern Tallgrass Prairie (G075)
	Midwest Wet Prairie, Wet Meadow, and Shrub Swamp (G770)
Ozarks (8.4.5)	Central Midwest Oak Openings and Barrens (G178)
	Oak - Shortleaf Pine Ozark-Ouachita Forest, Woodland and Savanna (G949)
Temperate Prairie (9.2.3)	North-Central Oak-Hickory Forest and Woodland (G059)
	Interior Low Plateau Oak Woodland Forest (G333)
Great Lakes Plains (8.1.6)	Midwest Prairie Alkaline Fen (G183)

Focal Wildlife Species

We include focal wildlife species to demonstrate how habitat impacts may influence wildlife responses to climate change. For each priority habitat (Table i), we review climate change impacts on one focal wildlife species, with specific attention paid to habitat considerations. We selected focal wildlife species based on consultation with state agencies, with the aim of choosing species listed by one or more state agency as a Species of Greatest Conservation Need (SGCN).

Focal Aquatic Systems

Because the USNVC is predominantly focused on terrestrial habitat types, we also include sections summarizing the impact of climate change on select focal aquatic systems. Unlike the focal wildlife species sections, which are associated with specific priority habitats (Table i), we selected one focal aquatic system for each ecoregion (Figure i). These selections were based on consultation with state agencies, with the aim of discussing a diverse set of aquatic system types. While focused on specific geographic areas, each section includes climate change impacts that are relevant to the broader aquatic system type.

Literature Review

For each priority habitat, we reviewed and synthesized available scientific literature. We used USNVC habitat descriptions and lists of dominant plant species provided for each Group and relevant sub-level to characterize each habitat and focus our literature search (Appendix 1). We searched for relevant literature related to these habitat characteristics and dominant species that either explicitly mentioned climate change or indirectly discussed climate-related topics. Lastly, to narrow our focus, we identified two particularly relevant climate-related stressors for each habitat to hone our literature search.

Taxonomic Conventions

Wherever possible, we follow the Integrated Taxonomic Information System database (Integrated Taxonomic Information System (ITIS), 2025) for common names, Latin names, and taxonomic authorities. Because many species have multiple common names, we defer to the PLANTS Database (USDA, NRCS, 2025) to select a single, consistent common name for each plant species. In cases where taxonomic resolution is lacking, such as for certain pests or pathogens not included in ITIS, we use the most widely accepted names from the primary scientific literature. To enhance clarity and usability, especially for readers consulting individual sections as standalone references, we define Latin names at first mention for each common name in each chapter subsection.

Chapter Organization

Each chapter in this series focuses on a subset of ecologically related priority habitats (Table ii). Because climate change impacts are frequently shared between similar habitat types, we first provide an overview of climate impacts to the broader system type before summarizing climate impacts for each specific habitat. The higher-level USNVC classification that links ecologically similar habitats (typically at the Macrogroup level and hereafter referred to as “ecosystem”) determines each broader system type into which chapters are organized. Among the seven chapters in the series, this chapter focuses solely on a single habitat and does not utilize the broader “ecosystem” classification.

Table ii. Series chapters and priority habitats. Habitats are organized by the series chapter in which they occur, with their corresponding U.S. National Vegetation Classification database Group numbers (USNVC, 2020).

Series chapter	Priority habitat
1. Temperate Flooded and Swamp Forest	Midwest Floodplain Forest (G652)
	South Central-Appalachian-Northeast Floodplain Forest Group (G673)
	Bald-cypress - Tupelo Floodplain Forest (G033)
	Central Interior-Great Lakes Flatwoods and Swamp Forest (G917)
	Laurentian-Acadian Alkaline Swamp (G046)
2. Appalachian-Interior-Northeast Mesic Forest	Appalachian-Central Interior Mesic Forest (G020)
	Appalachian-Northeast Mesic Forest (G742)
	North-Central Beech - Maple - Basswood Forest (G021)
3. North American Bog and Fen	Midwest Prairie Alkaline Fen (G183)
	Eastern North American Boreal-Subboreal Bog and Acidic Fen (G1172)
4. Eastern North American Temperate Freshwater Marsh, Wet Meadow and Shrubland	Eastern North American Freshwater Marsh (G125)
	Midwest Wet Prairie, Wet Meadow and Shrub Swamp (G770)
5. Central and Eastern North American Grassland and Shrubland	Central Tallgrass Prairie (G333)
	Northern Tallgrass Prairie (G075)
	Central Interior Acidic Open Glade and Barrens (G178)
	Eastern North American Ruderal Meadow and Shrubland (G059)
6. Central Interior Oak Forest, Woodland and Savanna	Interior Low Plateau Oak Forest, Woodland and Savanna (G950)
	Oak - Shortleaf Pine Ozark-Ouachita Forest, Woodland and Savanna (G949)
	Central Midwest Oak Openings and Barrens (G181)
	North-Central Oak - Hickory Forest and Woodland (G649)
	Central Appalachian-Northeast Oak Forest and Woodland (G650)
7. Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest	Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest (G048)

Executive Summary

The Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat occupies the cool, subboreal portion of the upper Midwest, Minnesota, Wisconsin, and Michigan, and is influenced by long, cold winters, persistent snowpack, and relatively short growing seasons. Across this region, temperatures are increasing in all seasons, driving longer growing seasons and higher maximum temperatures. Winter is warming most rapidly, leading to milder conditions characterized by less extreme minimum temperatures, reduced snowpack, and more frequent freeze-thaw cycles.

These changes may drive shifts in both habitat structure and community composition. During the growing season, warming can accelerate soil processes and increase nutrient availability; however, declining snowpack in winter can increase soil frost exposure and disrupt root function and nutrient uptake. Moreover, direct temperature changes are likely to disproportionately disadvantage boreal species adapted to cool conditions. As temperatures exceed physiological thresholds, boreal conifers such as balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*) are expected to decline, while heat-tolerant temperate hardwoods, including maples (*Acer* spp.) and birches (*Betula* spp.), are projected to increase. Although milder winters may reduce some forms of stress, these impacts vary among species and may further favor temperate hardwoods. Overall, these dynamics could increase habitat suitability for species near their northern (cold) range limits and decrease suitability for those near their southern (warm) limits, restructuring competitive dynamics among species.

Warming and milder winters may also increase plant invasion, pest and pathogen outbreaks, and herbivory – relaxing climatic constraints that typically limit these pressures. Warming can favor invasive species with high growth rates and phenological plasticity, accelerate pest and pathogen development and reproductive output, and weaken community resilience under stress. Milder winters may enable northward range expansion of invasive species and forest pests, such as bark beetles (*Dendroctonus* spp.), and increase phenological synchrony between insect emergence and host budburst, as observed for eastern spruce budworm (*Choristoneura fumiferana*). Herbivory, particularly by white-tailed deer (*Odocoileus virginianus*), is also expected to increase under milder winters, potentially suppressing regeneration of preferred species, including several boreal trees.

Proactive, flexible management that anticipates continued warming and winter change will be important to sustain this forest habitat. Potential strategies include maintaining climatic refugia, supporting regeneration of desired species, and reducing compounding stressors such as invasive species and herbivory.

Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest

Key Climate Change Stressors

Climate change is altering the temperature regimes that influence the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat across the Midwest. This forest system is shaped by long, cold winters, persistent snowpack, and relatively short growing seasons. Rapid warming, especially in winter, along with longer growing seasons and declining snow cover, is shifting these foundational conditions. As a result, the thermal and moisture dynamics that have historically maintained this forest type are changing.

Warming

Over the past century, average growing season temperatures have increased across the Midwest. In contrast, in the southern portions of the region (i.e., most of Iowa and Missouri, and southern portions of Illinois and Indiana), maximum temperatures in summer months have cooled slightly; this is likely due to cropland expansion and increased transpiration – a phenomenon referred to as the "warming hole" (Singh and others, 2023; Vose and others, 2017; Wilson and others, 2023). However, this cooling pattern is not uniform, with portions of the northern Midwest experiencing extreme heat and summer heat waves (Rastogi and others, 2023; Singh and others, 2023). By the end of the century, climate projections indicate additional warming, with longer growing seasons and consistently warmer summer months (Figure 1) (Ford and others, 2021a; Marvel and others, 2023; Xue and others, 2022). The moderating influence of land-use change on maximum temperatures will likely weaken, resulting in higher maximum summer temperatures, more days exceeding average summer temperatures, and more frequent and intense heatwaves (Liess and others, 2022; Matthews and others, 2018; Rastogi and others, 2023; Wobus and others, 2018; Wuebbles and Kunkel, 2026; Xie and others, 2021). Warming may also increase the number of growing degree days, resulting in longer growing seasons, but also days above 30°C (86°F), increasing the risk of plant heat stress (Matthews and others, 2018). Warming during the growing season can increase the magnitude and severity of drought; additionally, by increasing evaporative demand, aridity, and fuel drying, fire risk may increase (Alizadeh and others, 2020; Costanza and others, 2023; Donovan and others, 2023; Hoell and others, 2021; Kerr and others, 2018; Rastogi and others, 2023; Will and others, 2013; Wilson and others, 2023; Zhao and others, 2020).

Milder Winters

Winters are warming rapidly across the Midwest. The upper Midwest has historically been characterized by very cold minimum temperatures, prolonged and extensive snow cover, and short growing seasons (Contosta and others, 2019; Contosta and others, 2020; Kreyling, 2019; Rittenhouse and Rissman, 2015). Over the past century, winters have become milder, marked by less severe minimum temperatures, reduced snow depth and duration, earlier starts to the growing season, and an increase in freeze-thaw cycles (Contosta and others, 2019; Contosta and others, 2020; Ford and others, 2021b; Ford and others, 2022; Sinha and Cherkauer, 2010). These trends are expected to intensify in the coming decades, particularly as warming disproportionately occurs during winter, leading to warmer minimum temperatures (Figure 2), less snowfall, and longer growing seasons (Byun and others, 2019; Demaria and

others, 2016; Ford and others, 2021b; Ford and others, 2022; Liess and others, 2022; Liess and others, 2026).

As temperatures rise, a larger proportion of winter precipitation may fall as rain rather than snow, average snowpack depth will likely decline, snow will melt more often and earlier, and bare ground days will become more frequent (Contosta and others, 2019; Demaria and others, 2016; Ford and others, 2021b; Kreyling, 2019; Quante and others, 2021). In some portions of the upper Midwest, reduced ice cover on the Great Lakes may temporarily increase lake effect snowfall; however, the overall trend is toward less snow on the landscape, particularly as days above freezing become more common (Ford and others, 2021b; Ford and others, 2022; Wright and others, 2013). These shifts may also result in more rain-on-snow events in some places, which can accelerate snowmelt and promote ice formation at the soil surface (Aryal and others, 2025; Contosta and others, 2019; Ning and Bradley, 2015; Notaro and others, 2014). Since snowpack acts an important insulator, declining snow cover and more snow-free days can expose overwintering species to colder temperatures and more frequent freeze-thaw cycles, increasing cold stress even as winters warm on average (Contosta and others, 2019; Contosta and others, 2020; Contosta and others, 2024; Dey and others, 2019; Sanders-DeMott and others, 2018). Declining snow cover can also reduce spring soil moisture recharge, potentially increasing drought stress later in the growing season (Dymond and others, 2014; Mori and others, 2014). Milder winters may also raise the risk late spring frost events, or “false springs,” when earlier warm periods trigger emergence and growth that are later damaged by late frosts (Allstadt and others, 2015; Zohner and others, 2020).

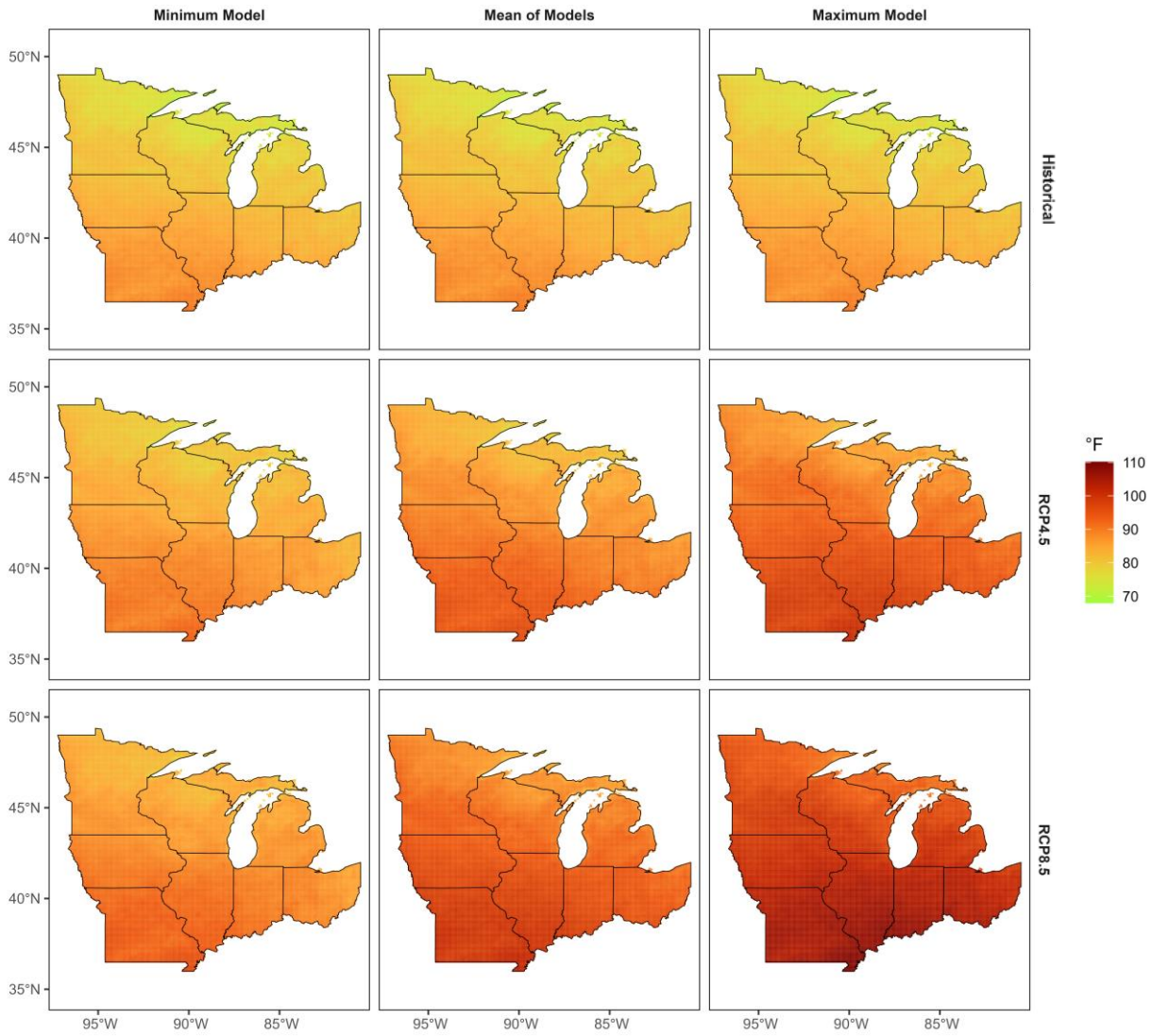

Figure 1. Projected changes in maximum summer temperature in the Midwest. Projections use gridded climate data obtained via the Climate Toolbox Climate Mapper at a 4-km resolution (Hegewisch and Abatzoglou, 2024) based on 20 CMIP5 climate models downscaled using MACAv2-METDATA for moderate- and high-emissions (RCP 4.5 and 8.5) scenarios (Abatzoglou, 2013; Abatzoglou and Brown, 2012). Values show average historical (1971–2000, top row) and projected (2070–2099) summer (June–August) maximum temperature (°F) for each emissions scenario (RCP 4.5, middle row; RCP 8.5, bottom row). To capture variation across climate models, models with the lowest (minimum model, left column) and highest (maximum model, right column) projected maximum summer temperature under RCP 8.5 are presented in addition to the mean of all models (middle column).

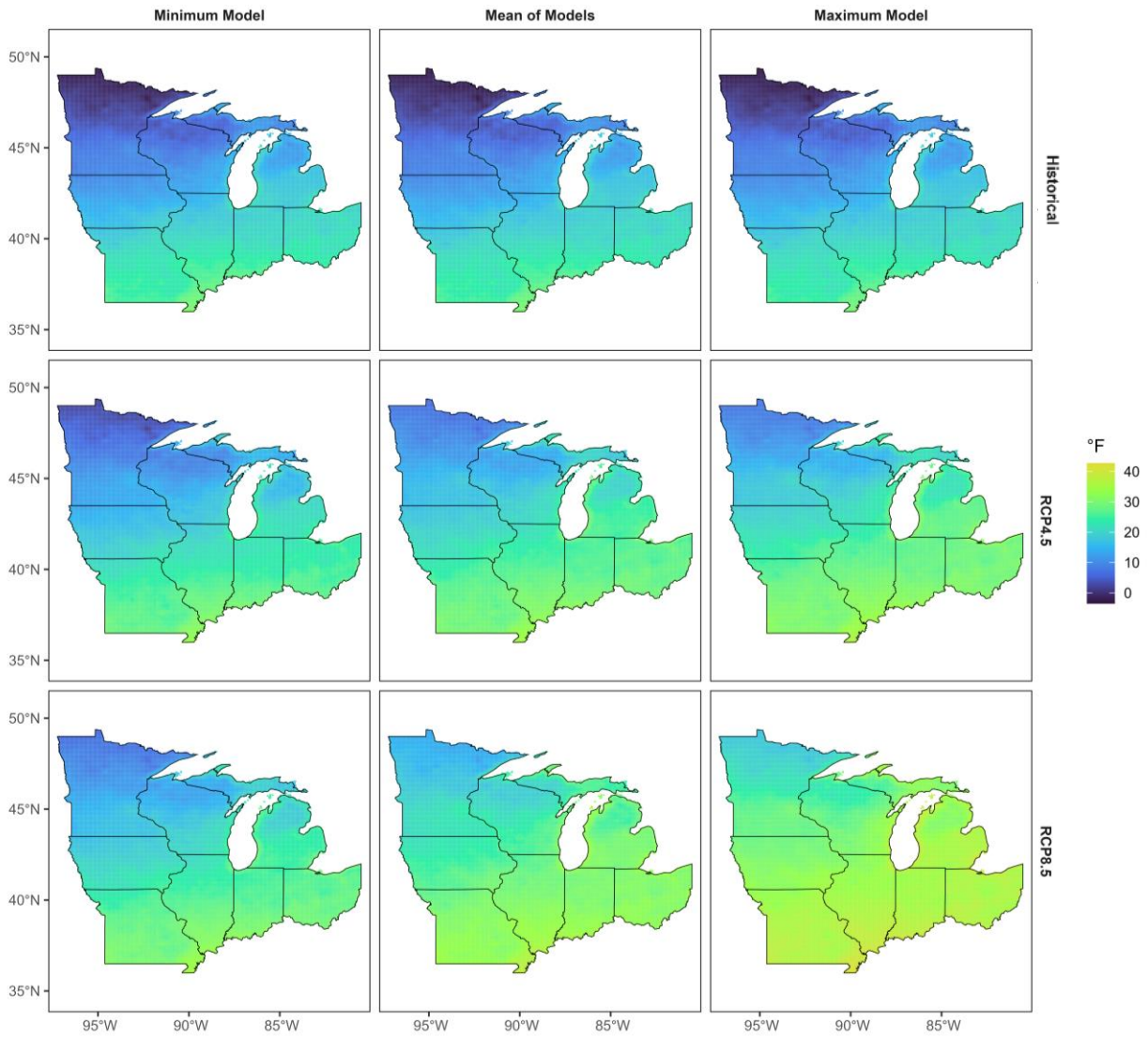

Figure 2. Projected changes in minimum winter temperature in the Midwest. Projections use gridded climate data obtained via the Climate Toolbox Climate Mapper at a 4-km resolution (Hegewisch and Abatzoglou, 2024) based on 20 CMIP5 climate models downscaled using MACAv2-METDATA for moderate- and high-emissions (RCP 4.5 and 8.5) scenarios (Abatzoglou, 2013; Abatzoglou and Brown, 2012). Values show average historical (1971–2000, top row) and projected (2070–2099) winter (December–February) minimum temperature (°F) for each emissions scenario (RCP 4.5, middle row; RCP 8.5, bottom row). To capture variation across climate models, models with the lowest (minimum model, left column) and highest (maximum model, right column) projected minimum winter temperature under RCP 8.5 are presented in addition to the mean of all models (middle column).

Key Climate Change Impacts

Climate change is altering the conditions that maintain the structure and function of the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat. Warming and milder winters are likely to drive significant changes in habitat structure, community composition, and species interactions, as even modest disruptions to climatic conditions can have cascading effects.

Habitat Structure

Abiotic responses to warming and milder winters. Warming and milder winters may alter abiotic processes in the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat by changing nutrient cycling, snowpack dynamics, and soil temperature regimes. Warming accelerates soil biogeochemical processes, increasing soil respiration, nitrogen mineralization, and nitrification, which can raise availability of inorganic nitrogen (Mao and others, 2025; Melillo and others, 2002; Melillo and others, 2011; Rustad and others, 2001). Warming also accelerates soil organic matter decomposition and carbon dioxide release (Melillo and others, 2002; Melillo and others, 2011). These shifting patterns can alter nutrient balances between nitrogen and phosphorous, potentially shifting which nutrients are the most limiting (González de Andrés, 2019).

Milder winters can delay or reduce snow accumulation, diminishing the insulating capacity of snow, exposing soils to cold air, and increasing the frequency and depth of soil freezing (Brown and DeGaetano, 2011; Groffman and others, 2001; Kreyling, 2019; Mori and others, 2014; Sanders-DeMott and others, 2019). As snow cover declines, minimum soil temperatures may initially become colder and occur later in winter, particularly in northern portions of the region that historically had deep, persistent snowpack (Brown and DeGaetano 2011). Reduced snow depth may also increase soil frost depth, disrupting root function, reducing nitrogen uptake, and increasing nutrient losses through leaching (Campbell and others, 2014; Cleavitt and others, 2008; Hardy and others, 2001; Sanders-DeMott and others, 2019; Sorensen and others, 2016). Milder winters may also increase the frequency of winter precipitation falling as rain, including rain-on-snow events, further accelerating snowmelt. These events can increase runoff and sediment transport, shift nutrient export from spring snowmelt to earlier winter periods, and increase episodic nutrient losses through leaching (Casson and others, 2012; Ning and Bradley, 2015; Swanston and others, 2018). Collectively, these processes increase the risk of nutrient loss during milder winters (Caron and others, 2025; Groffman and others, 2001; Handler and others, 2014; Kreyling and others, 2020; Makoto and others, 2014). The magnitude of these changes will vary with local conditions – forests with greater canopy gaps or higher deciduous cover may experience larger reductions in snow cover than closed-canopy conifer stands due to greater solar exposure (Pastore and others, 2025). Over time, continued winter warming may raise soil temperatures across much of the region, even as snowpack declines, shortening the soil frost season and reducing total frost depth (Hardy and others, 2001; Janowiak and others, 2014; Sinha and Cherkauer, 2010).

Biotic responses to warming. Rising temperatures and more frequent heat extremes will likely impose direct physiological stress on plants in the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat. Excessive heat can increase plant photorespiration, disrupt transpiration and photosynthesis, and impair leaf development — particularly during spring leaf-out when tissues are highly sensitive (Filewod and Thomas, 2014; Teskey and others, 2015). Physiological sensitivity to heat stress (e.g., the temperature at which warming exceeds the photosynthetic optimum) varies widely among species. Boreal-associated trees such as balsam fir (*Abies balsamea*), white spruce (*Picea glauca*),

and arborvitae (*Thuja occidentalis*) often experience increasing stress as temperatures exceed those historically typical of hemiboreal regions; in contrast, temperate species such as red maple (*Acer rubrum*) and eastern white pine (*Pinus strobus*) tend to exhibit greater tolerance and may respond neutrally or positively to moderate warming (Housset and others, 2015; Kincaid, 2017; Münchinger and others, 2023; Reich and others, 2015; Teskey and others, 2015; Way and Oren, 2010). Due to physiological constraints and limited gene flow from warmer-adapted populations, species occurring near their southern (warm) range limits in this northern forest may have limited capacity to acclimate to further warming (D'Orangeville and others, 2023; Gagne and others, 2020; Ghannoum and Way, 2011; Gunderson and others, 2010; Hammer and others, 2025; Sendall and others, 2015). When temperatures and heat waves exceed plant tolerance, mortality increases, particularly for boreal species in younger stands where competition is high (Allen and others, 2010; Chaste and others, 2019; Frelich and others, 2021; Frelich and others, 2024; Luo and Chen, 2013; Reich and others, 2015). Warming, especially when paired with dry conditions, has been associated with increased mortality in species such as balsam fir (*Abies balsamea*), white spruce (*Picea glacua*), and paper birch (*Betula papyrifera*), while temperate species like red maple (*Acer rubrum*) often demonstrate higher survival and competitive performance (Boulanger and others, 2017; Girardin and others, 2016; Lapointe-Garant and others, 2010; Luo and Chen, 2015; Michaelian and others, 2011; Reich and others, 2022; Thom, 2023; Vaughn and others, 2021a). Warming may also alter reproduction; higher temperatures can increase flowering and seed production but can also reduce seedling establishment and survival through increased evaporative demand and thermal stress (Hanberry and others, 2024; Ibáñez and others, 2017). Overall, productivity is likely to increase for species near their northern (cold) range limits and decline for those near their southern (warm) limits, restructuring competitive dynamics and shifting growth advantages among species (Bernal-Escobar and others, 2022; Duveneck and others, 2014; Fusco and others, 2024; Reich and others, 2015; Reich and others, 2022; Stangler and others, 2016; Wang and others, 2023).

The effects of warming-related physiological stress are often modified by local conditions such as canopy structure and topography. Dense canopy cover, for example, can buffer understory temperatures (De Frenne and others, 2021; Haesen and others, 2023; Zellweger and others, 2020), whereas open canopies and reduced conifer dominance may amplify maximum ambient temperatures (Chen and others, 1999; De Frenne and others, 2021; Wang and others, 2023). Canopy thermal buffering of summer maximum temperatures may also be less effective at the southern (warm) edge of this forest type (Gilbert and others, 2022). High temperatures are often tolerable for plants when water availability is sufficient to support evaporative cooling; however warming becomes more detrimental under reduced soil moisture or elevated vapor pressure deficit, (i.e., constrained hydraulic function) (Hanberry and others, 2024; Handler and others, 2014; Teskey and others, 2015). In temperature and energy-limited northern forests, when moisture remains sufficient, warming can enhance growth – lengthening the growing season and increasing photosynthetic activity – particularly for species near their northern (cold) range limits (D'Orangeville and others, 2023; Fisichelli and others, 2014; Fusco and others, 2024; Reich and others, 2015; Wang and others, 2023; Way and Oren, 2010; Wotherspoon and others, 2024). However, if temperatures exceed physiological optima or if increased evapotranspiration intensifies moisture stress, these gains may be temporary (Canham and others, 2018; D'Orangeville and others, 2018; Wotherspoon and others, 2024). Warming may also differentially reduce productivity in boreal conifers such as balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and arborvitae (*Thuja occidentalis*), while increasing productivity for temperate hardwoods such as maples (*Acer* spp.) and some pines such as white pine (*Pinus strobus*) (Foster and others, 2016; Girardin and others, 2016; Kincaid, 2017; Reich and others, 2015; Reich and others, 2022). While the effect of warming on net ecosystem productivity remains uncertain, it is likely that the general trend of increasing productivity for species at the northern (cold) edge of their range and decreases for those at the southern (warm) edge

of their range in this northern forest habitat will restructure competitive dynamics and increasingly reorder productive hierarchies (Bernal-Escobar and others, 2022; Duveneck and others, 2014; Fusco and others, 2024; Reich and others, 2015; Reich and others, 2022; Stangler and others, 2016; Wang and others, 2023).

Biotic responses to milder winters. Winter conditions, including snowpack, soil freezing, chilling degree days, and seasonal timing, directly impact plant physiology and demography in the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat (Contosta and others, 2024; Ladwig and others, 2016; Mori and others, 2014). In some instances, milder winter conditions may reduce winter physiological stress. For example, fewer and shorter extreme cold events and reduced soil freezing where snow persists may decrease fine root mortality and improve plant performance (Cleavitt and others, 2008; Contosta and others, 2019; Fuss and others, 2016). These benefits will vary among species. Less severe winter minimum temperatures may promote establishment of more temperate species, such as maples (*Acer* spp.) and birches (*Betula* spp.), potentially at the expense of boreal species (e.g., balsam fir (*Abies balsamea*)) (Collier and others, 2022; Frelich and others, 2021; Taylor and others, 2020).

However, declining snow cover and extreme cold also introduces new stresses (Brandt, 2020; Contosta and others, 2019; Drescher and Thomas, 2013; Lesk and others, 2017). While single occurrences of frost damage may have minor or transient effects, persistent, deep soil freezing and more frequent freeze-thaw cycles may offset or even reverse productivity gains from warming (Conrad-Rooney and others, 2025; Kreyling, 2019; Makoto and others, 2014; Sorensen and others, 2018; Wipf and others, 2009; Yihan and others, 2025). Tissue damage resulting from shallower or intermittent snowpack may also lead to reduced nutrient uptake and suppressed growth (Campbell and others, 2014; Comerford and others, 2013; Kreyling, 2019; Reinmann and others, 2019; Stern and others, 2023; Tierney and others, 2001). More frequent rain-on-snow and midwinter thaw events can promote ice encasement, limiting oxygen availability and further increasing injury risk (Kreyling, 2019; Martz and others, 2016). Reduced snow cover may also lower post-winter germination and increase seed mortality for some species (Burns, 1990; Groffman and others, 2012; Janowiak and others, 2014; Kreyling, 2019; Weigel and others, 2021; Yihan and others, 2025).

As winters shorten, earlier spring warming and snowmelt may advance leaf-out, flowering, budburst, and ground-layer emergence (Brandt, 2020; Calinger and others, 2013; Morin and others, 2009; Rice, 2016; Rice and others, 2018; Vaughn and others, 2021a). In some species, such as red maple (*Acer rubrum*), earlier phenology may increase early-season carbon gain, providing a key competitive advantage (Dow and others, 2022; Vaughn and others, 2021b). However, earlier growth can also increase exposure to late spring frosts, particularly for species that initiate growth rapidly in response to warming, including many boreal species (Frelich and others, 2024). Late frost events following early budburst can damage buds, leaves, and shoots, reducing canopy development and annual growth (Augspurger, 2009; Frelich and others, 2024; Hufkens and others, 2012). Quaking aspen (*Populus tremuloides*), for example, may be particularly susceptible to frost injury, resulting in defoliation, tissue damage, and reduced productivity (Birch and others, 2023). For species that require a set number of chilling days, warmer winters may also increase the risk of frost damage by delaying leafout after budburst, thus extending the period of greatest frost risk (Chamberlain and Wolkovich, 2021). Inadequate winter chilling may also disrupt dormancy release, particularly near species' southern (warm) range limits, resulting in delayed or abnormal budburst, flowering, and leaf-out (Morin and others, 2007; Morin and others, 2009; Park and others, 2014).

Because phenological responses will vary among species, seasonal synchronicity may shift. For example, flowering richness may become more concentrated at seasonal margins, and the window for understory species to emerge before canopy leaf-out reduces light penetration may shorten (Landuyt and others, 2025; Montgomery and others, 2020; Ramirez-Parada and others, 2022; Rice and others, 2018). These incongruent shifts are likely to alter competitive relationships among species by altering relative regeneration success and growth rates (Calinger and others, 2013; Hufkens and others, 2012; Landuyt and others, 2025; Montgomery and others, 2020; Morin and Chuine, 2014) and may create phenological mismatches with interacting taxa such as insect pollinators (Makoto and others, 2014).

Community Composition

General community response to climate change. Situated along the boreal-temperate transition zone, the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat may be particularly vulnerable to long-term, biome-scale community reorganization. Many boreal species are expected to lose suitable habitat along their southern range limits, while temperate hardwoods may expand northward as conditions become more favorable (Handler and others, 2014; Janowiak and others, 2014; Prasad and others, 2020; Swanston and others, 2011; Wotherspoon and others, 2024). Boreal species such as balsam fir (*Abies balsamea*), spruces (*Picea* spp.), and aspens (*Populus* spp.) are likely to decline in relative importance, while oak-hickory hardwood groups, particularly maples (*Acer* spp.) and oaks (*Quercus* spp.), are projected to increase (Bakshi and others, 2025; Etterson and others, 2020; Fisichelli and others, 2014; Janowiak and others, 2014; Lucash and others, 2018; Qoronfleh, 2023; Vickers and others, 2021). In drier portions of the region, especially northwestern Minnesota, moisture limitations may instead favor transitions towards pine (*Pinus* spp.) forests, or alternatively, savannas, grasslands, or barrens (Frelich and others, 2024; Gonzalez and others, 2010; Prasad and others, 2020; Swanston and others, 2018; Toot and others, 2020; Wotherspoon and others, 2024). However, compositional change will likely proceed unevenly across space and time, as differences in dispersal capacity, fecundity, and seedling establishment limit the ability of some climatically favored species to occupy newly suitable areas (Aitken and others, 2008; Boisvert-Marsh and others, 2014; Boisvert-Marsh and others, 2022; Sharma and others, 2022). Existing forest structure may further slow transitions by inhibiting recruitment of temperate species beneath boreal overstories (Boisvert-Marsh and de Blois, 2021; Fisichelli and others, 2013; Henry and Walters, 2023; Solarik and others, 2020). Soil suitability, substrate type, and other site conditions can also constrain establishment even where climatic conditions have become favorable, potentially contributing to the persistence of mixed or transitional communities along the southern boreal margin (Beauregard and de Blois, 2016; Boisvert-Marsh and de Blois, 2021; Lafleur and others, 2010). Substantial compositional change may therefore require stand-replacing or novel disturbances to overcome these legacies and allow dominance shifts (Fisichelli and others, 2013; Frelich and others, 2024). As a result, biome-scale community reorganization may continue to lag behind shifting climate conditions (Boisvert-Marsh and de Blois, 2021).

Community responses to warming. Because boreal tree species are adapted to cool summer temperatures and short growing seasons, rising summer temperatures in the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat may erode their competitive advantage, particularly near the southern edge of their range. At the same time, warming summers may enhance growth and competitiveness of co-occurring temperate species that are typically better suited to warmer conditions (Bakshi and others, 2025; Boisvert-Marsh and others, 2019; Bolte and others, 2014; Brice and others, 2020; Fisichelli and others, 2012; Fisichelli and others, 2014; Frelich and others, 2024). Heat-tolerant temperate hardwoods such as red maple (*Acer rubrum*) and sugar maple (*Acer saccharum*), along with pines (*Pinus* spp.) and early successional species like paper birch (*Betula*

papyrifera) may increasingly replace boreal species, particularly mid- to late-successional conifers such as balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*) (Dobson and others, 2025; Hanberry and others, 2024; Luo and Chen, 2013). These predictions are also supported by paleo-ecological data which demonstrate that climate warming approximately 7,000 years ago converted boreal forests into oak-pine systems (Girardin and others, 2024). As these shifts occur, forests may trend toward younger, more homogeneous structures, with declining representation of old-growth, late-successional boreal stands (Apfelbaum and others, 2023). At larger magnitudes of warming, boreal species may be unable to persist even in locally favorable conditions, increasing the likelihood of landscape-scale loss of boreal forest (Astigarraga and others, 2024; Chalumeau and others, 2024; Frelich and others, 2024). Under these conditions, boreal species are more likely to be lost from these forests than maintained within mixed assemblages, lowering overall biodiversity, especially where repeated disturbances prevent recovery of late-successional species (Frelich and others, 2024; Reich and others, 2022; Stralberg and others, 2020; Xi and others, 2024).

The rate of community change can depend on disturbance dynamics. Shifts may be gradual where competitive and successional processes dominate but can occur rapidly following disturbance events. By weakening the conditions that favor boreal dominance, warming may make forests more susceptible to compositional change following disturbance or mortality events (Brice and others, 2020; Johnstone and others, 2016). Canopy gaps created by the loss of dominant boreal species may release advanced growth and regeneration of co-occurring temperate species, creating additional opportunities for compositional shifts (Boulanger and others, 2017; Brice and others, 2020; Knapp and others, 2019; Mccarthy, 2001; Soubeyrand and others, 2023). Interactions among warming, drought, and fire can further accelerate these changes by increasing mortality risk and favoring species capable of rapid resprouting or regeneration following disturbance. Hotter summers may increase drought-related mortality, particularly among conifers with limited resprouting capacity, increasing the likelihood of state shifts toward broadleaf-dominated forests or, in drier areas, grasslands (Allen and others, 2015; Anderegg, 2015; Boulanger and others, 2017; Choat and others, 2012; Frelich and Reich, 2010; Thom, 2023). Over time, these processes may allow stand-scale disturbances to accumulate into regional shifts in biome structure (Bolte and others, 2014; Hammond and others, 2022; Soubeyrand and others, 2023).

Community responses to milder winters. Milder winters may alter community composition in the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat by changing which species can sustain growth and regeneration under winter conditions (Contosta and others, 2019; Contosta and others, 2024). As winter minimum temperatures rise, survival and recruitment constraints on temperate species may relax, allowing species such as maples (*Acer* spp.) and birches (*Betula* spp.) to increase in abundance. As a result, recruitment advantages previously held by boreal species like balsam fir (*Abies balsamea*) may decline (Collier and others, 2022; Frelich and others, 2021; Hänninen, 2016; Körner, 2021; Sykes and Prentice, 1995; Taylor and others, 2020) or may be lost, gradually shifting composition away from fir-dominated stands (Astigarraga and others, 2024; Girardin and others, 2022; Hiura and others, 2019). Red maple (*Acer rubrum*) may be particularly well adapted to benefit from milder winter conditions and thus may become more abundant (Stern and others, 2023; Vaughn and others, 2021a).

Reduced snow cover is associated with lower post-winter germination and higher overwinter seed mortality for species that rely on snow for effective seed dispersal, such as yellow birch (*B. alleghaniensis*) (Burns, 1990; Drescher and Thomas, 2013; Groffman and others, 2012; Janowiak and others, 2014; Kreyling, 2019; Weigel and others, 2021; Yihan and others, 2025). Declining snow cover may also reduce sapling growth for species like sugar maple (*Acer saccharum*) (Henne and others, 2007). Conversely, declining snow cover may increase sapling survival for eastern white pine (*Pinus strobus*),

sugar maple (*Acer saccharum*), and paper birch (*Betula papyrifera*) compared to balsam fir, white ash *(Fraxinus americana*), white spruce (*Picea glauca*), and arborvitae (*Thuja occidentalis*) (Drescher and Thomas, 2013). Future community composition will likely be strongly influenced by this variation in snow cover impacts to species. Critically, species that may perform better in warmer winter temperatures may also be more vulnerable to freeze stress caused by those same warmer conditions, underscoring the complex species and life-stage dependent responses to changing snow conditions.

Changes in phenology associated with milder winters may also influence community composition. Species that respond rapidly to warming cues, such as red maple (*Acer rubrum*), may gain competitive advantages and become more dominant relative to less responsive species (Gu and others, 2022; Landuyt and others, 2025; Montgomery and others, 2020; Polgar and Primack, 2011; Wheeler and others, 2017; Wolkovich and Cleland, 2011). However, earlier development can also increase vulnerability to late frost events, particularly for species like sugar maple (*Acer saccharum*) and quaking aspen (*Populus tremuloides*), suggesting that repeated frost events may gradually favor more frost-resilient species over highly responsive competitors (Augspurger, 2009; Birch and others, 2023; Hufkens and others, 2012). Phenological responses may also depend on species-specific chilling requirements, as insufficient winter chilling can delay or disrupt dormancy release, particularly in boreal species, and create mismatches in the timing of growth among co-occurring species (Chamberlain and Wolkovich, 2021; Kreyling, 2019; Morin and others, 2009; Park and others, 2014; Solarik and others, 2020). These changes may also extend to the forest understory, where earlier canopy leaf-out may shorten high-light windows for shade-intolerant forest-floor plants (Landuyt and others, 2025; Rice and others, 2018). Conversely, spring ephemerals and other understory plants that respond to earlier warming may prematurely emerge or flower before frost risk has subsided, increasing their vulnerability to subsequent frost damage (Augspurger, 2013; Chamberlain and others, 2019; Inouye, 2022). Longer flowering seasons and increased co-flowering richness at seasonal margins may also modify competitive interactions among understory functional groups and influence relative abundance trajectories over time (Calinger and others, 2013; Gallinat and others, 2026; Ramirez-Parada and others, 2022).

Invasive Species

Invasive species responses to warming. Warming temperatures and milder winters may relax climatic constraints that have historically limited invasive species establishment and spread in the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat (Allen and Bradley, 2016; Evans and others, 2024; Finch and others, 2021; Wang and others, 2019). As a result, several invasive plants, including tree of heaven (*Ailanthus altissima*), garlic mustard (*Alliaria petiolata*), Amur honeysuckle (*Lonicera maackii*), common buckthorn (*Rhamnus cathartica*), Japanese barberry (*Berberis thunbergii*), and multiflora rose (*Rosa multiflora*), may continue to gain suitable habitat in the upper Midwest (Evans and others, 2024; Merow and others, 2017; Reinhardt and others, 2020). In some cases, invasive species may disproportionately benefit from warmer conditions relative to co-occurring native species. For example, glossy buckthorn (*Frangula alnus*), honeysuckles (*Lonicera* spp.), and common buckthorn can exhibit greater increases in growth rates under warmer temperatures than many native species, particularly boreal conifers, suggesting that rapid, resource exploitative growth strategies common to invasive species can provide a pronounced competitive advantage under future warming (Song and others, 2025). Earlier springs may also amplify the existing competitive advantage many of these invasive species already gain by leafing out earlier than many co-occurring native species (Harrington and others, 1989; Knight and others, 2007; McEwan and others, 2009; Smith, 2013; Wolkovich and Cleland, 2014). Other invasive species such as bishop's goutweed (*Aegopodium podagraria*), glossy buckthorn, and common St. John’s wort (*Hypericum perforatum*) are projected to lose suitable habitat in

the upper Midwest (Evans and others, 2024; Reinhardt and others, 2020). While predicting invasive species establishment and spread remains challenging, more frequent and severe disturbances combined with weakened native community stability are expected to increase the abundance of opportunistic invasive species (Dukes and others, 2009; Felton and Smith, 2017; Finch and others, 2021; Orbán and others, 2021; Potter and others, 2026). These trends may be exacerbated by interactions with other stressors such as deer herbivory, which can further cause invasive species proliferation due to the unpalatable nature of many invasive shrubs (Eschtruth and Battles, 2009; Knight and others, 2009).

Invasive species may also interact with warming to facilitate additional invasions. In northern Minnesota, for example, warming combined with invasive earthworms has been associated with increases in invasive understory plant species and declines in native plant diversity (Alexander and others, 2022; Eisenhauer and others, 2012; Holdsworth and others, 2007; Janowiak and others, 2014; Thouvenot and others, 2024). As warming allows earthworm populations to expand and increasing deciduous cover enhances litter palatability, cascading feedbacks may emerge that facilitate additional invasions and further alter compositional change (Eisenhauer and others, 2015; Frelich and others, 2019; Frelich and others, 2024; Singh and others, 2019).

Invasive species responses to milder winters. Introduced species often show greater phenological responsiveness to climate change than native species, which may confer competitive advantages as winters shorten and growing seasons lengthen in the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat (Fridley, 2012; Garretson and others, 2022; Hanberry and others, 2024; Wolkovich and others, 2013; Wolkovich and Cleland, 2014). Phenological shifts that disrupt germination of native species with narrow physiological requirements may benefit invasive species with broader germination niches (Hicks and others, 2019). As winter minimum temperatures rise and frost damage eventually becomes less frequent, constraints on northern (cold) range limits may weaken for species like garlic mustard (*Alliaria petiolata*), common buckthorn *(Rhamnus cathartica*), and multiflora rose (*Rosa multiflora*), potentially facilitating further northward spread (Kurtz, 2010; Moser and others, 2009; Reinhardt and others, 2020). However, as with warming, milder winters will not benefit all invasive species. Increasing freeze-thaw events can reduce seed survival in some introduced species, including honeysuckles (*Lonicera* spp.) and common buckthorn *(Rhamnus cathartica*) (Orrock and others, 2025).

Pests and Pathogens

Pest and pathogen responses to warming. Warming may modify pest and pathogen pressure in the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat through both direct effects on pest and pathogen organisms and indirect effects on host susceptibility and vulnerability. Warmer temperatures may accelerate insect growth rates and increase reproductive output, elevating the risk of more frequent or severe outbreaks. These effects may be particularly pronounced for species historically constrained by short growing seasons such as phloem feeding insects (*Hemiptera* spp.), butterflies and moths (*Lepidoptera* spp.), and bark beetles (*Scolytidae* spp.) (Dukes and others, 2009; Flower and Gonzalez-Meler, 2015; Pureswaran and others, 2018; Schebeck and others, 2024; Stanturf and others, 2024). Elevated temperatures can accelerate larval development in invasive wood-boring insects including the Asian long-horned beetle (*Anoplophora glabripennis*) and emerald ash borer (*Agrilus planipennis*), potentially increasing population growth rates and the frequency of damaging outbreaks (Fusco and others, 2024; Keena and Moore, 2010; Meng and others, 2015; Pureswaran and others, 2018). Warming may also exacerbate pest pressure by compromising host resistance. Physiological stress and altered nutrient allocation under higher temperatures can weaken plant

defenses, making trees more susceptible to insect attack (Cole and others, 2021; Dukes and others, 2009; Harvey and others, 2020; Simler-Williamson and others, 2019).

Pathogen responses to warming vary considerably, but evidence suggests warming will increase the activity and impact of several forest pathogens in northern systems. As climatic limitations relax in historically cold regions, the number of pathogens capable of producing consequential tree mortality is expected to increase (Dukes and others, 2009; Janowiak and others, 2014; Sturrock and others, 2011; Venäläinen and others, 2020). Many fungal pathogens are sensitive to narrow temperature ranges, suggesting that seasonal warming could alter outbreak frequency and severity (Agrios, 2005; Coakley and others, 1999; Dudney and others, 2021; Dukes and others, 2009; Garrett and others, 2016; Guégan and others, 2023; Pautasso and others, 2012; Williams and others, 2000). For example, warmer temperatures have been associated with outbreaks of white pine needle damage pathogens (including *Bifusella linearis*, *Lecanosticta acicula*, *Lophophacidium dooksii*, and *Septorioides strobi*) and widespread defoliation events (Frumhoff and others, 2007; Wyka and others, 2018; Wyka and others, 2018). Warming, particularly if accompanied by wetter conditions, may also increase sporulation, dispersal, and infectivity of foliar pathogens (Coakley and others, 1999; Kliejunas, 2011; Sturrock and others, 2011). Several wood-decay and root pathogens such as root rot (*Armillaria* spp.), for example, may become more virulent as warmer temperature extend optimal conditions for growth and spore formation, particularly where host defenses are weakened by climate stress (Dukes and others, 2009; Klopfenstein and others, 2009; Kubiak and others, 2017; Sturrock and others, 2011).

Pest and pathogen responses to milder winters. Milder winters in the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat, including less extreme cold, warmer minimum temperatures, and shorter cold periods, can substantially reduce winter mortality for many forest insects, including spongy moths (*Lymantria dispar*) and forest tent caterpillars (*Malacosoma disstria*) (Dukes and others, 2009; Flower and Gonzalez-Meler, 2015; Harvey and others, 2020; Klapwijk and others, 2016; Neuvonen and others, 1999; Pureswaran and others, 2018; Simler-Williamson and others, 2019). Observed declines in winter “kill days” indicate that milder winters are already relaxing historical climatic constraints on pest survival (Contosta and others, 2019). As these constraints weaken, several pest species, such as bark beetles (e.g., southern pine beetle (*Dendroctonus frontalis*), and mountain pine beetle (*Dendroctonus ponderosae*)), may expand northward and eastward into the forests of the upper Midwest, increasing the potential for outbreaks (Bentz and Jönsson, 2015; Lesk and others, 2017; Preisler and others, 2012; Pureswaran and others, 2018; Simler-Williamson and others, 2019). Wamer winters and longer growing seasons may also increase insect populations by allowing additional brood cycles per season, particularly for wood-boring species (Finch and others, 2021; Pureswaran and others, 2018; Tobin and others, 2014).

However, milder winters may also negatively impact some pests. Declining snow depth and duration can expose overwintering diapausing insects to greater cold stress by reducing insulation from snowpack, thus depleting energy reserves as warming increases metabolic rates (Harvey and others, 2020; Pureswaran and others, 2018). For example, although warmer winters may increase overwinter survival of forest tent caterpillar larvae (*Malacosoma disstria*), late frost events can cause spring larval mortality, potentially moderating outbreak potential (Cooke and Roland, 2018; Dukes and others, 2009; Schowalter, 2017). Similarly, rising winter temperatures may increase mortality in eastern spruce budworm (*Choristoneura fumiferana*) along the southern edge of its range, where warmer conditions disrupt completion of its annual life cycle (Boulanger and others, 2025; Collier and others, 2022; Gray and others, 2013; Pureswaran and others, 2018; Régnière and others, 2012).

Changing seasonal timing may also alter pest-host synchrony. Because insect development and host phenology do not always advance at the same rate, mismatches between insect emergence and optimal feeding windows can reduce outbreak severity for some pest species (Bracalini and others, 2024; Harvey and others, 2020; Lehmann and others, 2020; Mironidis and Savopoulou-Soultani, 2010; Ren and others, 2020; Rice and others, 2021; Stanturf and others, 2024). However, for many species like eastern spruce budworm (*Choristoneura fumiferana*), warming may increase synchrony between insect emergence and budburst of its hosts balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*), potentially increasing outbreak risk (Boulanger and others, 2025; Portalier and others, 2022; Ren and others, 2020). This variability pest-host synchrony changes underscores how milder winters can simultaneously promote pest persistence and expansion while introducing new sources of mortality and instability, producing nonlinear and species-specific responses across northern forest ecosystems.

For pathogens, warmer winter temperatures may reduce cold-induced mortality and lengthen periods when pathogens are metabolically active, increasing disease pressure in systems historically constrained by cold winters (Balla and others, 2021; Dukes and others, 2009; Sturrock and others, 2011). Wood-decay and root pathogens such as root rot (*Armillaria* spp.) and tree decay fungi (*Heterobasidion* spp.) may benefit from longer periods of suitable temperatures that allow sustained physiological function for a greater portion of the year (Balla and others, 2021; Dukes and others, 2009; Kubiak and others, 2017). Warmer winters may also increase overwinter survival of white pine needle damage pathogens (including *Bifusella linearis*, *Lecanosticta acicula*, *Lophophacidium dooksii*, and *Septorioides strobi*), leading to more frequent mass defoliation events in eastern white pine (*Pinus strobus*) (Wyka and others, 2018). As winters become milder, additional pathogens historically constrained by cold temperatures, including several water molds (e.g., *Phytophthora* spp.) that afflict maples (*Acer* spp.), pines (*Pinus* spp.), and oaks (*Quercus* spp.), may expand their ranges into the Midwest (Burgess and others, 2017; Contreras-Cornejo and others, 2023; Kliejunas, 2011; Sturrock and others, 2011; Teshome and others, 2020). Perhaps most significantly, milder winters may facilitate the establishment and spread of previously unknown or novel pathogens in these forests (Nnadi and Carter, 2021).

Herbivory

Herbivory responses to warming and milder winters. Climate change may amplify herbivory pressure on some species in the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat, particularly from white-tailed deer (*Odocoileus virginianus*). Warmer winters and reduced snowpack are expected to increase access to forage and improve deer survival, contributing to higher deer populations across much of the Midwest (Côté and others, 2004; Felton and others, 2024; MDNR, 2016; Patton and others, 2021; Weiskopf and others, 2019). At high densities, chronic browsing can disproportionately suppress regeneration of browse-preferred species and drive long-term shifts in forest composition (Miller and others, 2023). Species such as yellow birch (*Betula alleghaniensis*), eastern white pine (*Pinus strobus*), quaking aspen (*Populus tremuloides*), red oak (*Quercus rubra*), and arborvitae (*Thuja occidentalis*) are particularly vulnerable to browsing pressure and may face additional regeneration challenges under milder winter conditions (Côté and others, 2004; Dahlberg and Guettinger, 1956; Harris and others, 2025; Henry and Walters, 2023; Patton and others, 2021). As snowpack decreases, deer may access a broader range of species and forage more heavily on saplings of red maple (*Acer rubrum*) and sugar maple (*Acer saccharum*) (Harris and others, 2025), potentially slowing anticipated climate-driven increases in their dominance. In addition, if reduced snow cover increases sapling exposure to cold stress, saplings may be less tolerant of browsing in the subsequent growing season (Champagne and others, 2021).

Climate Change Impacts by Habitat

Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest

The Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat occupies the cool, subboreal portion of the northern Great Lakes region, extending from northeastern Minnesota through northern Wisconsin and Michigan to northern New England and parts of southern Canada (Figure 3) (Cohen and others, 2015; Cohen and others, 2025; Faber-Langendoen and others, 2020; Gawler, 2009; USNVC, 2025). In the Midwest, these forests occur primarily north of the climatic tension zone and are strongly associated with landscapes shaped by glaciation, including glacial lakeplains and moraines, scoured bedrock uplands, and till and outwash plains (Cohen and others, 2015; Cohen and others, 2025; Gawler, 2009; Minnesota Department of Natural Resources, 2003b; Minnesota Department of Natural Resources, 2003a; Sims, 1997; Zoladeski and others, 1995). Site conditions span gradients in soil texture, depth, and drainage, with typically thin loamy, silt, or clay soils (Cohen and others, 2015; Cohen and others, 2025; Minnesota Department of Natural Resources, 2003b; Minnesota Department of Natural Resources, 2003a; Sims, 1997; USNVC, 2025; Zoladeski and others, 1995). Proximity to the Great Lakes moderates temperature extremes and increases snowfall relative to more interior regions (Albert, 1995; Gawler, 2009).

Vegetation structure is characterized by tall, closed-canopy forests dominated by boreal conifers and mixed boreal hardwoods (Table 1) (Cohen and others, 2015; Cohen and others, 2025; Faber-Langendoen and others, 2020; Gawler, 2009; USNVC, 2025). Across the habitat, gradients in soil moisture, soil types, topography, and disturbance regimes drive shifting dominance among conifers and hardwoods (Cohen and others, 2015; Cohen and others, 2025; Faber-Langendoen and others, 2020; Gawler, 2009; Minnesota Natural Heritage Program (MNNHP), 1993; USNVC, 2025). Canopy-opening disturbances and gap dynamics promote temporary dominance by early-successional hardwoods such as paper birch (*Betula papyrifera*) and quaking aspen (*Populus tremuloides*), while temperate northern hardwoods such as sugar maple (*Acer saccharum*) are less common. Understory communities vary with canopy structure and include a mix of shrubs and herbaceous species (Faber-Langendoen, 2007; Faber-Langendoen and others, 2020; USNVC, 2025). Natural disturbance regimes are dominated by windfall, insect defoliation, and infrequent catastrophic fire, while logging has become a major anthropogenic disturbance across much of the region (Gawler, 2009; Kost and others, 2007; Shifley and others, 2014).

Current threats to this habitat include ongoing logging pressure, land-use change, and chronic herbivory (Gawler, 2009; Kost and others, 2007; Shifley and others, 2014). Invasive species are generally less widespread than in many other habitats of the Midwest, but problematic invasive plants include Norway maple (*Acer platanoides*), garlic mustard (*Alliaria petiolata*), Japanese barberry (*Berberis thunbergii*), autumn olive (*Elaeagnus umbellata*), honeysuckles (*Lonicera* spp.), buckthorns (*Rhamnus cathartica* and *Frangula alnus*), and multiflora rose (*Rosa multiflora*) (Kost and others, 2007).

Table 1. Plant species common to the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat. Taxonomic authority, common name, growth habit, and native status are determined according to the PLANTS Database (USDA, NRCS, 2025).

Species	Common name	Growth habit
Abies balsamea (L.) Mill.	Balsam fir	Tree
Acer rubrum L.	Red maple	Tree
Betula papyrifera Marshall	Paper birch	Tree
Picea glauca (Moench) Voss	White spruce	Tree
Pinus strobus L.	Eastern white pine	Tree
Populus balsamifera L.	Balsam poplar	Tree
Populus tremuloides Michx.	Quaking aspen	Tree
Thuja occidentalis L.	Arborvitae	Tree
Eurybia macrophylla (L.) Cass.	Bigleaf aster	Forb

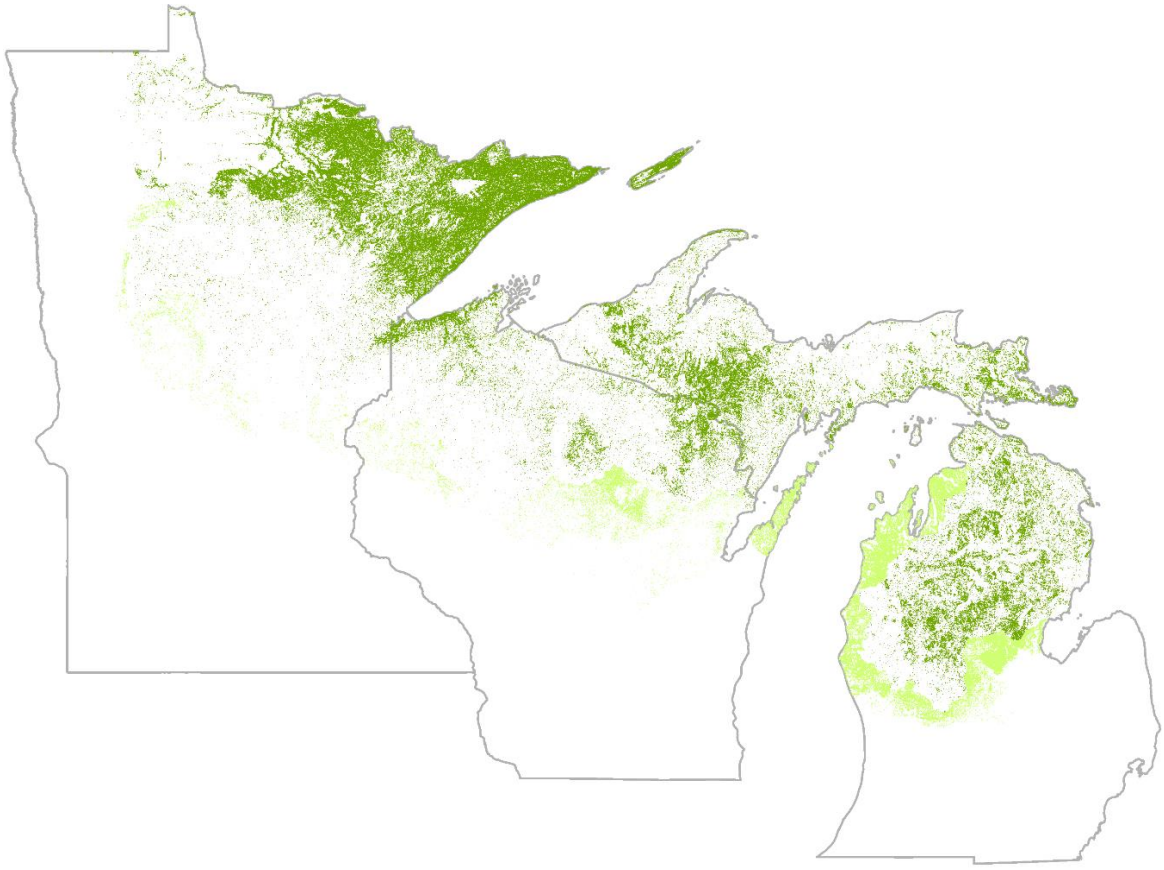

Figure 3. Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat distribution. Geographic distribution of the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat (Group Code: G048) in the Midwest (USNVC, 2025). Dark green areas indicate Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat in the Northern Hardwood Forest ecoregion, while light green areas mark additional

locations throughout the Midwest. Habitat boundaries have been enlarged to enhance visibility and do not reflect true proportions.

Overview of Climate Projections

The Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat is prioritized for the Northern Hardwood Forest ecoregion (Table i), and climate projections for this area largely reflect regional trends. Both average and extreme temperatures are expected to rise throughout the coming century, with model projections indicating a 11.1°F increase by the end of the century under the high emissions scenario (RCP 8.5; Table 2) (Clarke and others, 2022; Marvel and others, 2023; Masson-Delmotte and others, 2021). Most models also project an increase in annual precipitation, averaging 3.2 additional inches per year, although some indicate a slight decline (Table 3) (Marvel and others, 2023). However, precipitation is expected to become more variable, with more extreme events and notably drier summers despite the overall increase (Dollan and others, 2022; Liess and others, 2022; Marvel and others, 2023; Polasky and others, 2021).

Table 2. Projected changes in annual temperature in the Northern Hardwood Forest ecoregion. Projections use data obtained via the Climate Toolbox Climate Mapper (Hegewisch and Abatzoglou, 2024) based on 20 CMIP5 climate models downscaled using MACAv2-METDATA for moderate- and high-emissions (RCP 4.5 and 8.5) scenarios (Abatzoglou, 2013; Abatzoglou and Brown, 2012). Values show average historical (1971–2000) and projected annual mean temperature (°F) by mid- (2040–2069) and end of the century (2070–2099), as well as the absolute change relative to the historical value (in parentheses), for each emissions scenario. To capture variation across climate models, models with the lowest (minimum model) and highest (maximum model) projected temperature under RCP 8.5 are presented in addition to the mean of all models.

	1971–2000	2040–2069		2070–2099	
	Historical	RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5
Minimum model	41.3°F	43.9°F (2.6)	45.5°F (4.2)	44.3°F (3.0)	47.9°F (6.6)
Mean of models	41.1°F	46.3°F (5.2)	47.9°F (6.8)	47.4°F (6.3)	52.2°F (11.0)
Maximum model	41.2°F	49.5°F (8.3)	51.2°F (10.0)	51.2°F (10.0)	57.2°F (15.9)

Table 3. Projected changes in annual precipitation in the Northern Hardwood Forest ecoregion. Projections use data obtained via the Climate Toolbox Climate Mapper (Hegewisch and Abatzoglou, 2024) based on 20 CMIP5 climate models downscaled using MACAv2-METDATA for moderate- and high-emissions (RCP 4.5 and 8.5) scenarios (Abatzoglou, 2013; Abatzoglou and Brown, 2012). Values show average historical (1971–2000) and projected annual precipitation (inches) by mid- (2040–2069) and end of the century (2070–2099), as well as the percent change relative to the historical value (in parentheses), for each emissions scenario. To capture variation across climate models, models with the lowest (minimum model) and highest (maximum model) projected precipitation under RCP 8.5 are presented in addition to the mean of all models.

	1971–2000	2040–2069		2070–2099	
	Historical	RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5
Minimum model	29.5 in	29.6 in (0%)	29.3 in (-1%)	30.7 in (4%)	28.7 in (-3%)
Mean of models	29.5 in	31.5 in (7%)	32.0 in (8%)	31.8 in (8%)	32.7 in (11%)
Maximum model	29.7 in	33.8 in (14%)	36.1 in (22%)	33.1 in (12%)	36.6 in (24%)

Key Climate Change Stressors

Warming and milder winters. Across the Northern Hardwood Forest ecoregion, the plant heat-tolerance zone is projected to increase by approximately 108% above historical conditions by the end of the century under the high emissions scenario, equivalent to more than three additional tolerance zones (RCP 8.5; Table 4). The highest values are expected in the southwestern part of the region, while the lowest are expected in the northeastern areas, particularly the Upper Peninsula of Michigan and North Shore of Minnesota (Figure 4). A higher plant heat-tolerance zone indicates that conditions suitable for species adapted to warmer climates may expand across much of the region, potentially reducing the climatic advantage of boreal species and favoring temperate hardwoods. Annual number of freeze free days is also projected to increase by approximately 35% above historical conditions by the end of the century under the high emissions scenario, adding more than 63 additional days or roughly two months of freeze-free conditions each year (RCP 8.5; Table 5). The greatest number of freeze free days is projected in the southeastern part of the region, particularly the Lower Peninsula of Michigan, while the fewest is expected in the northwestern part of the region in Minnesota (Figure 5). Increasing freeze-free days may reflect milder winters, earlier spring onset, and longer growing seasons, potentially enhancing growth and productivity but also altering phenology, increasing frost exposure, and favoring temperate species, pests, and invasive plants over boreal species.

Table 4. Projected changes in plant heat-tolerance zone in the Northern Hardwood Forest Ecoregion. Projections use data obtained via the Climate Toolbox Climate Mapper (Hegewisch and Abatzoglou, 2024) based on 20 CMIP5 climate models downscaled using MACAv2-METDATA for moderate- and high-emissions (RCP 4.5 and 8.5) scenarios (Abatzoglou, 2013; Abatzoglou and Brown, 2012). Values show average historical (1971–2000) and projected annual heat-tolerance zones (average annual number of days in which the maximum daily temperature is greater than 86°F) by mid- (2040–2069) and end of the century (2070–2099), as well as the percent change relative to the historical value (in parentheses), for each emissions scenario. To capture variation across climate models, models with the lowest (minimum model) and highest (maximum model) projected average plant heat-tolerance zone under RCP 8.5 are presented in addition to the mean of all models.

	1971–2000	2040–2069		2070–2099	
	Historical	RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5
Minimum model	3.3	3.8 (14%)	4.3 (30%)	4.2 (28%)	4.6 (39%)
Mean of models	3.3	4.7 (44%)	5.4 (65%)	5.2 (60%)	6.8 (108%)
Maximum model	3.3	5.4 (63%)	6.2 (87%)	6.4 (94%)	7.7 (132%)

Table 5. Projected changes in annual freeze free days in the Northern Hardwood Forest Ecoregion. Projections use data obtained via the Climate Toolbox Climate Mapper (Hegewisch and Abatzoglou, 2024) based on 20 CMIP5 climate models downscaled using MACAv2-METDATA for moderate- and high-emissions (RCP 4.5 and 8.5) scenarios (Abatzoglou, 2013; Abatzoglou and Brown, 2012). Values show average historical (1971–2000) and projected total annual days in which the minimum temperature remains above freezing (32°F) by mid-century (2040–2069), as well as the percent change relative to the historical value (in parentheses), for each emissions

scenario. To capture variation across climate models, models with the fewest (minimum model) and most (maximum model) projected annual freeze free days under RCP 8.5 are presented in addition to the mean of all models.

	1971–2000	2040–2069		2070–2099	
	Historical	RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5
Minimum model	183.6	200.5 (9%)	204.1 (11%)	200.3 (9%)	219.4 (20%)
Mean of models	183.3	211.1 (15%)	220.7 (20%)	218.2 (19%)	246.6 (35%)
Maximum model	184.8	238.4 (29%)	247.0 (34%)	248.2 (34%)	285.0 (54%)

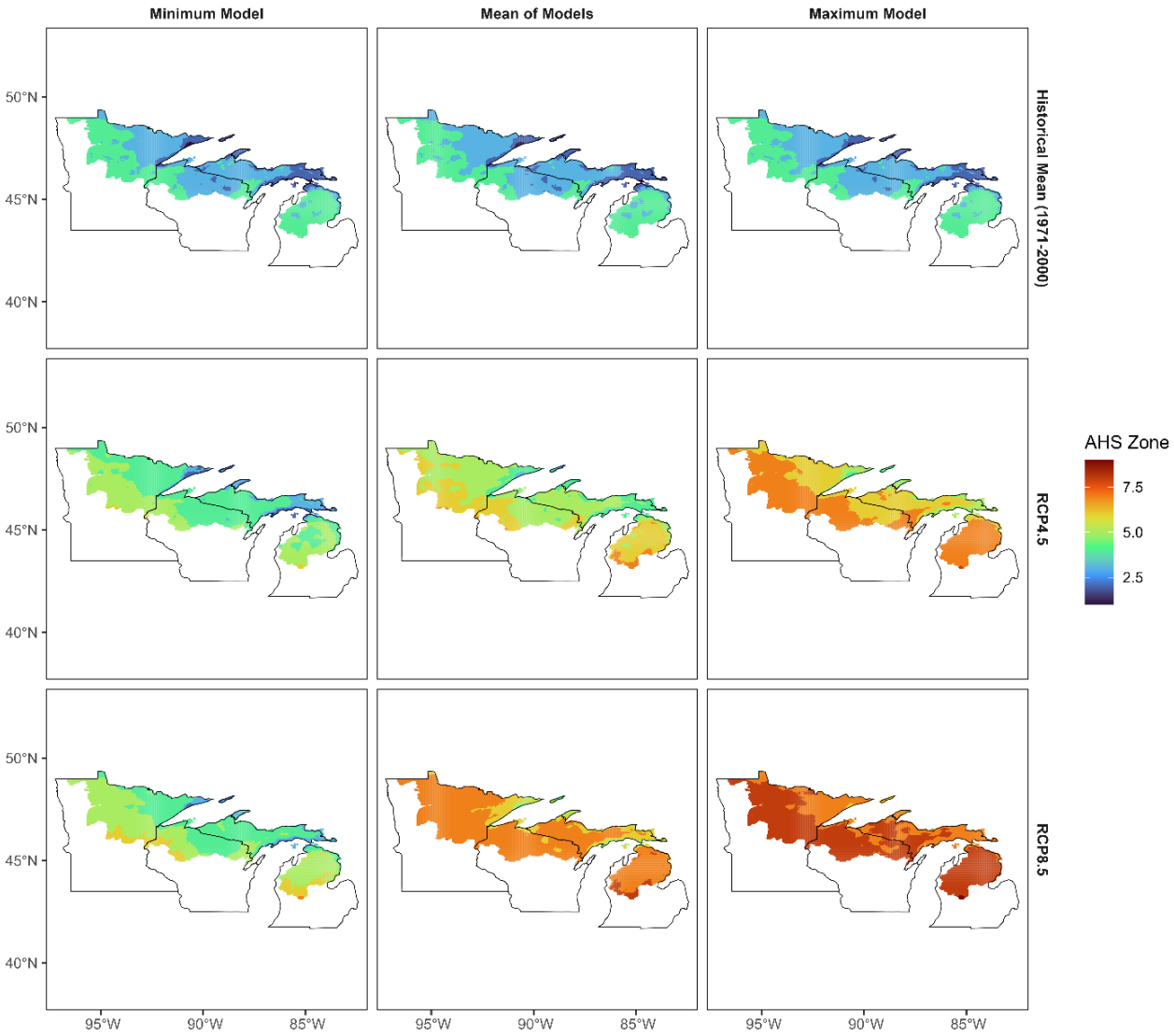

Figure 4. Projected annual plant heat-tolerance zone for the Northern Hardwood Forest ecoregion. Projections use gridded climate data obtained via the Climate Toolbox Climate Mapper at a 4-km resolution (Hegewisch and Abatzoglou, 2024) based on 20 CMIP5 climate models downscaled using MACAv2-METDATA for moderate- and high-emissions (RCP 4.5 and 8.5) scenarios (Abatzoglou, 2013; Abatzoglou and Brown, 2012). Values show average

historical (1971–2000, top row) and projected (2070–2099) annual heat-tolerance zones (average annual number of days in which the maximum daily temperature is greater than 86°F) for each emissions scenario (RCP 4.5, middle row; RCP 8.5, bottom row). To capture variation across climate models, models with highest (minimum model, left column) and lowest (maximum model, right column) average heat-tolerance zone under RCP 8.5 are presented in addition to the mean of all models (middle column).

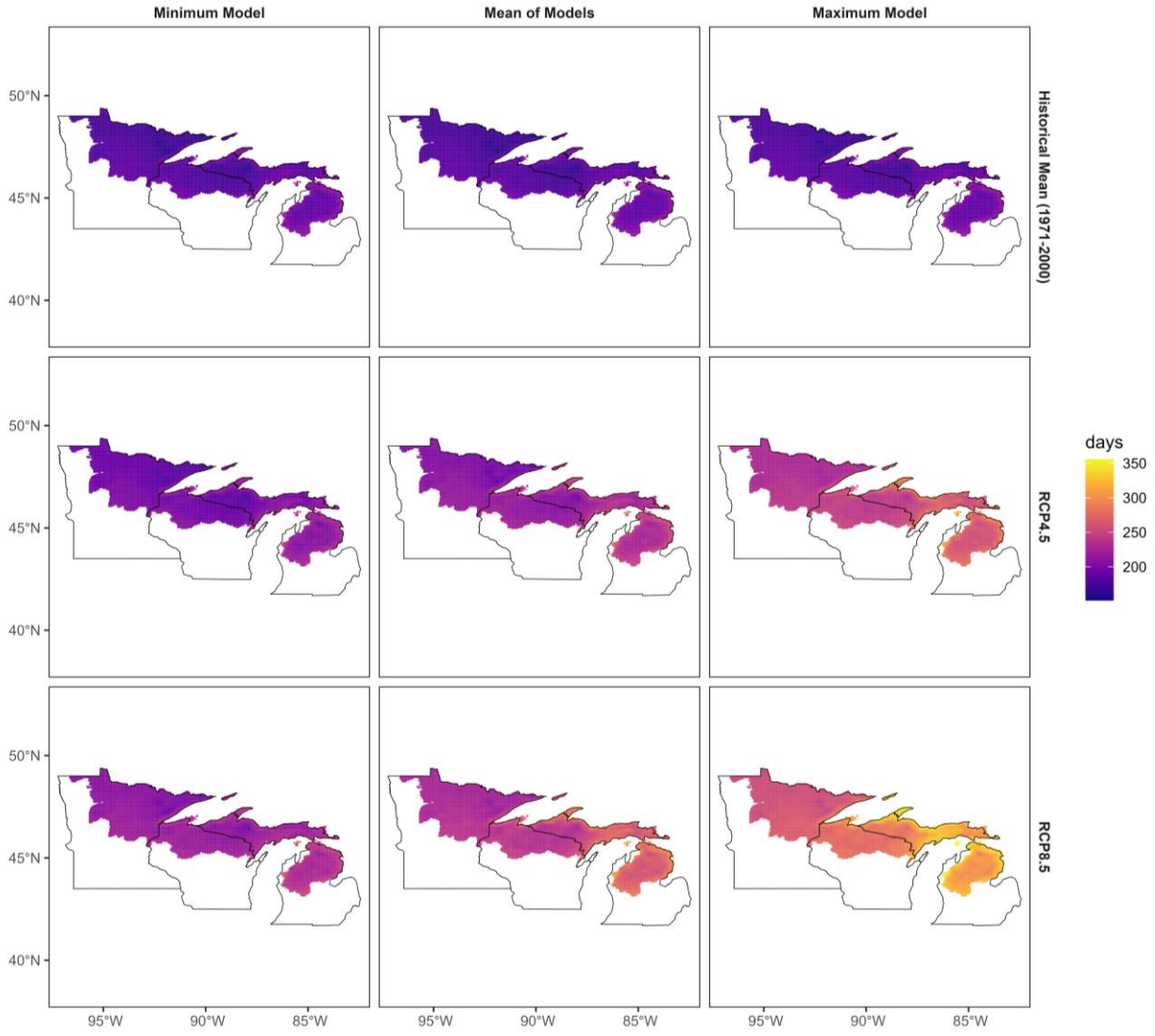

Figure 5. **Projected annual freeze free days for the Northern Hardwood Forest ecoregion**. Projections use gridded climate data obtained via the Climate Toolbox Climate Mapper at a 4-km resolution (Hegewisch and Abatzoglou, 2024) based on 20 CMIP5 climate models downscaled using MACAv2-METDATA for moderate- and high-emissions (RCP 4.5 and 8.5) scenarios (Abatzoglou, 2013; Abatzoglou and Brown, 2012). Values show average historical (1971–2000, top row) and projected (2070–2099) total annual days in which the minimum temperature remains above freezing (32°F) for each emissions scenario (RCP 4.5, middle row; RCP 8.5, bottom row). To capture variation across climate models, models with the fewest (minimum model, left column) and most (maximum model, right column) projected freeze free days under RCP 8.5 are presented in addition to the mean of all models (middle column).

Key Climate Change Impacts

This section summarizes how climate change is impacting the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat, including the specific effects of warming and milder winters (Table 6). The bullet points below provide a concise overview of these impacts on habitat structure, community composition, invasive species, pests and pathogens, and herbivory.

Habitat structure:

- Warming and milder winters may speed up soil processes (e.g., mineralization, nitrification, soil respiration), increasing nitrogen availability during the growing season but reducing it in winter through more frequent leaching and runoff (Campbell and others, 2009; Rustad and others, 2001; Melillo and others, 2002; Mao and others, 2025; Kreyling and others, 2019; Swanston and others, 2018; Sanders-DeMott and others, 2019; Campbell and others, 2014).
- Milder winters may reduce snowpack depth and duration, increasing soil frost depth and exposure to cold, though snowfall may increase locally due to enhanced lake-effect precipitation from reduced ice cover (Brown and DeGaetano 2011; Groffman and others, 2001; Kreyling and others, 2019; Mori and others, 2014; Sanders-DeMott and others, 2019).

Community Composition:

- Climate change may shift the boreal-temperate ecotone northward, decreasing habitat suitability for boreal species such as balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and aspens (*Populus* spp.) at their southern range limits and increasing suitability for temperate hardwoods such as maples (*Acer* spp.) and oaks (*Quercus* spp.) (Bakshi and others, 2025; Etterson and others, 2020; Fisichelli and others, 2014; Handler and others, 2014; Janowiak and others, 2014; Lucash and others, 2018; Prasad and others, 2020; Qoronfleh, 2023; Swanston and others, 2018; Vickers and others, 2021; Wotherspoon and others, 2024).
- In northwestern Minnesota, limited moisture may inhibit temperate forest expansion, instead favoring transitions to pine-dominated forests or grasslands (Frelich and others, 2024; Gonzalez and others, 2010; Swanston and others, 2011; Toot and others, 2020; Wotherspoon and others, 2024).
- Warming may exceed physiological thresholds for boreal conifers like balsam fir (*Abies balsamea*) and white spruce (*P. glauca*), increasing the abundance of heat-tolerant hardwoods like red maple (*Acer rubrum*), sugar maple (*A. saccharum*), yellow birch (*Betula alleghaniensis*), and paper birch (*Betula papyrifera*) and woody invasives such as honeysuckles (*Lonicera* spp.) (Table 6) (Bakshi and others, 2025; Boisvert-Marsh and others, 2019; Brice and others, 2020; Chalumeau and others, 2024; Dobson and others, 2025; Frelich and others, 2021; Frelich and others, 2024; Hanberry and others, 2024; Hanberry, 2024; Luo and Chen, 2013; Reich and others, 2015; Song and others, 2025; Soubeyrand and others, 2023).
- Interactions among warming, drought, and fire may intensify disturbance, increasing tree mortality, and favoring early-successional species with rapid resprouting or post-disturbance regeneration, leading to compositional shifts (Allen and others, 2015; Bolte and others, 2014; Boulanger and others, 2017; Brice and others, 2020; Soubeyrand and others, 2023; Thom, 2023).
- Milder winters may benefit regeneration of maples (*Acer* spp.) and birches (*Betula* spp.) over balsam fir (*Abies balsamea*), though reduced snow cover may counteract these benefits by

increasing exposure to soil freezing and frost damage (Table 6) (Burns, 1990; Collier and others, 2022; Drescher and Thomas, 2013; Frelich and others, 2021; Janowiak and others, 2014; Kreyling, 2019; Stern and others, 2023; Taylor and others, 2020; Vaughn and others, 2021a; Weigel and others, 2021).

- Milder winters may reshape competitive dynamics and drive compositional shifts by shortening winters and advancing springs, potentially favoring phenologically responsive species like red maple (*Acer rubrum*) and disadvantaging species with specific chilling requirements, such as balsam fir (*Abies balsamea*) and quaking aspen (*Populus tremuloides*) (Table 6) (Chamberlain and Wolkovich, 2021; Gu and others, 2022; Kreyling, 2019; Landuyt and others, 2025; Montgomery and others, 2020; Morin and others, 2009; Park and others, 2014; Polgar and Primack, 2011; Solarik and others, 2020; Wheeler and others, 2017; Wolkovich and Cleland, 2011).
- Earlier growth under milder winters may increase exposure to late frosts, potentially negatively impacting responsive but frost-sensitive species such as sugar maple (*Acer saccharum*) and quaking aspen (*Populus tremuloides*) (Table 6) (Augspurger, 2009; Birch and others, 2023; Hufkens and others, 2012).

Invasive species:

- Warming and milder winters may relax environmental constraints that typically limit invasion, creating favorable conditions for species such as tree of heaven (*Ailanthus altissima*), garlic mustard (*Alliaria petiolata*), Amur honeysuckle (*Lonicera maackii*), common buckthorn (*Rhamnus cathartica*), and multiflora rose (*Rosa multiflora*), while decreasing suitability for some species at their southern range limits like bishop's goutweed (*Aegopodium podagraria*) (Allen and Bradley, 2016; Evans and others, 2024; Finch and others, 2021; Reinhardt and others, 2020; Song and others, 2025; Wang and others, 2019).
- Warming, combined with expanding invasive earthworm populations, may facilitate plant invasion and reduce native plant diversity, particularly where increasing deciduous dominance enhances litter palatability for earthworms (Alexander and others, 2022; Eisenhauer and others, 2012; Eisenhauer and others, 2015; Frelich and others, 2019; Holdsworth and others, 2007; Janowiak and others, 2014; Singh and others, 2019; Thouvenot and others, 2024).
- Milder winters and more variable seasonal timing may favor invasive species over natives by extending the growing season and amplifying the advantages of their germination breadth and phenological plasticity (Fridley, 2012; Garretson and others, 2022; Hanberry and others, 2024; Hicks and others, 2019; Wolkovich and others, 2013; Wolkovich and Cleland, 2011; Zettlemoyer and others, 2019).
- More frequent freeze-thaw cycles under milder winters may reduce seed survival for some invasive species, including honeysuckles (*Lonicera* spp.) and common buckthorn (*Rhamnus cathartica*) (Dukes and others, 2009; Felton and Smith, 2017; Finch and others, 2021; Orbán and others, 2021; Orrock and others, 2025; Potter and others, 2026).

Pests and pathogens:

- Climate change may amplify pest and pathogen pressure by directly increasing populations and indirectly increasing host susceptibility (Dukes and others, 2009; Jactel and others, 2012;

Stanturf and others, 2024; Sturrock and others, 2011; Teshome and others, 2020; Vose and others, 2013; Weed and others, 2013).

- Warming may increase pest pressure by accelerating development, increasing reproduction, and elevating outbreak potential for taxa such as phloem-feeding insects (*Hemiptera* spp.), some butterflies and moths (*Lepidoptera* spp.), and bark beetles (*Scolytidae* spp.), while also increasing host stress and reducing plant defenses (Cole and others, 2021; Dukes and others, 2009; Flower and Gonzalez-Meler, 2015; Fusco and others, 2024; Harvey and others, 2020; Keena and Moore, 2010; Pureswaran and others, 2018; Schebeck and others, 2024; Simler-Williamson and others, 2019; Stanturf and others, 2024).
- Warming may lengthen periods favorable for pathogen growth, increasing the virulence of wood-decay and root pathogens such as root rot (*Armillaria* spp.) and tree decay fungi (*Heterobasidion* spp.) and foliar pathogens such as white pine needle damage (including *Bifusella linearis*, *Lecanosticta acicula*, *Lophophacidium dooksii*, and *Septorioides strobi*) (Balla and others, 2021; Dukes and others, 2009; Kliejunas and others, 2009; Kliejunas, 2011; Kubiak and others, 2017; Sturrock and others, 2011; Wyka and others, 2018).
- Milder winters may reduce overwinter mortality for forest insects such as bark beetles (*Dendroctonus frontalis*, *Dendroctonus ponderosae*), spongy moth (*Lymantria dispar*), and forest tent caterpillar (*Malacosoma disstria*), potentially facilitating northward and eastward range expansion into the upper Midwest (Bentz and Jönsson, 2015; Contosta and others, 2019; Dukes and others, 2009; Flower and Gonzalez-Meler, 2015; Lesk and others, 2017; Preisler and others, 2012; Pureswaran and others, 2018; Simler-Williamson and others, 2019).
- Shifts in seasonal timing under milder winters may enhance synchrony between pests like eastern spruce budworm (*Choristoneura fumiferana*) and hosts such as balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*), elevating outbreak risk (Boulanger and others, 2025; Bracalini and others, 2024; Portalier and others, 2022; Ren and others, 2020; Rodenberg and others, 2024; Schwartzberg and others, 2014).
- Milder winters may reduce overwinter mortality for pathogens such as root rot (*Armillaria* spp.) tree decay fungi (*Heterobasidion* spp.), white pine needle damage (including *Bifusella linearis*, *Lecanosticta acicula*, *Lophophacidium dooksii*, and *Septorioides strobi*), and water molds (*Phytophthora* spp.), increasing disease pressure and the risk of novel pathogen establishment (Balla and others, 2021; Contreras-Cornejo and others, 2023; Dukes and others, 2009; Nnadi and Carter, 2021; Sturrock and others, 2011; Teshome and others, 2020; Wyka and others, 2018).
- Some climate changes may reduce pests and pathogens impacts by increasing parasitism such as for spongy moth (*Lymantria dispar*), creating phenological mismatches between some hosts and pests such as with forest tent caterpillar (*Malacosoma disstria*), or reducing overwintering survival of species dependent on snow insulation such as the spruce budworm (*Choristoneura fumiferana*) (Boulanger and others, 2025; Bracalini and others, 2024; Cooke and Roland, 2018; Harvey and others, 2020; Portalier and others, 2022; Pureswaran and others, 2018; Ren and others, 2020; Rice and others, 2021; Rodenberg and others, 2024; Schwartzberg and others, 2014; Stanturf and others, 2024).

Herbivory:

- Warming and milder winters may increase forage access and improve survival of white-tailed deer (*Odocoileus virginianus*), contributing to higher deer densities and amplifying browsing

pressure (Côté and others, 2004; Felton and others, 2024; MDNR, 2016; Patton and others, 2021; Weiskopf and others, 2019).

- Selective deer browsing may suppress regeneration of browse-preferred species such as sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), eastern white pine (*Pinus strobus*), quaking aspen (*Populus tremuloides*), and arborvitae (*Thuja occidentalis*), while simultaneously promoting unpalatable invasive shrubs (Bradshaw and Waller, 2016; Champagne and others, 2021; Dahlberg and Guettinger, 1956; Frerker and others, 2014; Harris and others, 2025; Henry and Walters, 2023; Patton and others, 2021).
- Mild winters may reduce sapling tolerance to browsing by increasing exposure to cold stress as snow cover declines, but may also reduce herbivory by small mammals dependent on snow cover for winter foraging (Champagne and others, 2021; Sanders-DeMott and others, 2018).

Table 6. Summary of impacts from key climate change stressors on Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat species. Some species appear in contradictory impacts (e.g., showing both high and low tolerance to warming), reflecting conflicting findings in the literature.

Stressor	Impact	Affected Species
Warming	When thermal tolerance is low, decreased performance, growth, and/or abundance	*Abies balsamea*[1,2,3,4,5,6] *Acer rubrum*[7] *Betula papyrifera*[4,8] *Frangula alnus*[5] *Picea glauca*[1,3,4,5,9,10] *Pinus strobus*[4,5] *Thuja occidentalis*[11,12]
	When thermal tolerance is high, increased performance, growth, and/or abundance	*Abies balsamea*[13] *Acer rubrum*[1,4,6,13,14] *Acer* spp.[3] *Betula papyrifera*[1,4,5,13] *Frangula alnus*[1] *Lonicera* spp.[1] *Picea glauca*[15] *Populus tremuloides*[5,13] *Rhamnus cathartica*[3,5,16] *Rhamnus* spp.[1]
Milder winters	When sensitivity to freeze and frost stress is high, heightened susceptibility to damage, disturbances, reduced productivity, and regeneration failure	*Abies balsamea*[17] *Acer rubrum*[17,18,19] *Betula papyrifera*[17,20] *Picea glauca*[17] *Pinus strobus*[17] *Populus tremuloides*[21] *Thuja occidentalis*[17]
	When sensitivity to freeze and frost stress in low, potential for competitive advantage	*Acer rubrum*[22,23,24,25] *Betula papyrifera*[17] *Picea glauca*[17] *Pinus strobus*[17] *Thuja occidentalis*[17]
Seasonal shifts	When phenological shifts are well-matched to changing seasonality, potential for competitive advantage	*Acer platanoides*[30] *Acer rubrum*[30,31] *Betula papyrifera*[31]

	Frangula alnus[32] *Hypericum perforatum*[33] *Lonicera maackii*[31] *Lonicera* spp.[32] *Populus balsamifera*[31] *Populus tremuloides*[26,31] *Rhamnus cathartica*[31] *Rosa multiflora*[31]
When chilling requirements are unmet or phenological responses are inadequate, higher rates of trophic mismatches, competitive exclusion, and regeneration failure	*Abies balsamea*[28,29] *Acer platanoides*[29] *Acer rubrum*[26] *Ailanthus altissima*[29] *Betula papyrifera*[29] *Eurybia macrophylla*[27] *Frangula alnus*[29] *Lonicera maackii*[29] *Picea glauca*[26,29] *Pinus strobus*[26,29] *Thuja occidentalis*[29]

[1]Dobson and others (2025); [2]Raney and others (2016); [3]Reich and others (2015); [4]Reich and others (2022); [5]Song and others (2025); [6]Vaughn and others (2021); [7]Ibáñez and others (2017); [8]Perillo (2017); [9]Billah and Goldblum (2019); [10]Frelich and Reich (2010); [11]Housset and others (2015); [12]Kincaid (2017); [13]Wang and others (2023); [14]Soubeyrand and others (2023); [15]Bernal-Escobar and others (2022); [16]Fisichelli and others (2014); [17]Drescher and Thomas (2013); [18]Byard and others (2010); [19]Sanders-DeMott and others (2018b); [20]Chamberlain and Wolkovich (2021); [21]Birch and others (2023); [22]Peters and others (2020); [23]Morin and Chuine (2014); [24]Stern and others (2023); [25]Vaughn and others (2021); [26]Montgomery and others (2020); [27]Bertin (2017); [28]Collier and others (2022); [29]USDA, NRCS (2025); [30]Miller and others (2023); [31]Gallinat and others (2025); [32]Fridley (2012); [33]Zettlemoyer and others (2019)

Focal Wildlife Species: American Marten

The American marten (*Martes americana)* is a small mustelid distributed across northern North America. Martens occupy both deciduous and coniferous forests, with higher occupancy in structurally complex, mature forests with dense canopies and coarse woody debris (Viau and others, 2024). At a microhabitat scale, martens prefer large diameter trees and snags (Kirk and Zielinski, 2009) that provide structural and thermal heterogeneity for thermoregulation and survival, particularly given their limited fat reserves and thin fur. In winter, martens prefer subnivean sites (Taylor and Buskirk, 1994), a seasonal refuge below the snow where much of their winter prey base reside. Climate change may threaten these habitats, as reduced snow depth and more variable winter conditions can alter the stability of the subnivium (Pauli and others, 2013).

Given their wide distribution, marten responses to climate change will likely vary with climatic and landscape conditions. In Alaska, marten distributions have expanded (Baltensperger and others, 2017), and in the Great Lakes region martens have recolonized portions of their historical range following reintroductions (Smith and Pauli, 2024). Interspecific interactions may also influence marten response to climate change and their future distributions. Snow is a significant driver of both marten and fisher (*Pekania pennanti*) distribution, so future changes in snow conditions and development may increase niche overlap, increase competition with fishers, and contribute to local extirpation of marten (Manlick and others, 2020).

As a harvested furbearer, monitoring, assessment, and harvest management remain important tools for managing American marten populations (Skalski and others, 2011). Another important tool in marten conservation is maintaining landscape connectivity to increase habitat complexity (e.g., woody debris) and reduce fragmentation (Druin and others, 2025). As climate change drives loss in connectivity (e.g., Lake Superior ice bridges) and declines in long-lived coarse woody debris, human intervention may be needed to preserve genetic diversity and support marten resilience to climate change (Chagnon and others, 2022; Smith and Pauli, 2024).

Focal Aquatic System: Pelican Lake

Pelican Lake is a large, deep glacial seepage lake in Crow Wing County, Minnesota, within the Pine River watershed of the Northern Lakes and Forests ecoregion (Minnesota Pollution Control Agency, 2016; RMB Environmental Laboratories, Inc., 2013). The lake reaches a maximum depth of approximately 104 feet and stratifies seasonally, creating cold, well-oxygenated deepwater habitat during portions of the year (RMB Environmental Laboratories, Inc., 2013). Long-term monitoring indicates that Pelican Lake has maintained oligotrophic conditions, high water clarity, and an extensive littoral zone supporting diverse native aquatic vegetation and a cool-water fish assemblage including cisco (*Coregonus artedi*), a species sensitive to changes in temperature and dissolved oxygen (RMB Environmental Laboratories, Inc., 2013; Simon and Perleberg, 2010). While the lake currently maintains high water quality and supports cold-water species, projected warming and changing precipitation patterns are likely to increase stress on deepwater and nearshore habitats over time, particularly where shoreline alteration or nutrient inputs compound climatic effects (Fang and others, 2025; Jacobsen and others, 2019; Sharma and others, 2021). Substantial shoreline development and recreational use place ongoing pressures on nearshore habitat and water quality (Division of Fish and Wildlife, Section of Fisheries, 2015; RMB Environmental Laboratories, Inc., 2013).

Because the lake's ecological condition is closely linked to seasonal ice cover, thermal stratification, groundwater inputs, and shoreline integrity, projected changes in air temperature, ice duration, and precipitation patterns have direct implications for deepwater oxygen availability, littoral habitat extent, and overall water quality (Dadaser-Celik and Stefan, 2007; Fang and others, 2025; Jacobsen and others, 2019; Sharma and others, 2021). Lakes across the upper Midwest are already experiencing measurable shifts in ice cover, including later freeze-up, earlier ice-out, and shorter ice seasons (Sharma and others, 2021). Midwestern lakes are projected to lose an additional 18 to 43 days of ice cover by late century, with deeper lakes particularly sensitive to delayed freeze-up (Blagrave and Sharma, 2023). For deep, stratified lakes, longer open-water seasons are expected to lengthen or intensify seasonal stratification, which can reduce vertical mixing and limit replenishment of oxygen to deep waters (Blagrave and Sharma, 2023; Sharma and others, 2021). Warming temperatures, particularly when combined with increasing nutrient inputs, can increase metabolic oxygen demand in bottom waters and reduce the availability of cold, well-oxygenated habitat required by species such as cisco (*Coregonus artedi*) (Fang and others, 2025; Tingley and others, 2019).

Work Cited

Abatzoglou, J.T., 2013, Development of gridded surface meteorological data for ecological applications and modelling: International Journal of Climatology, v. 33, no. 1, p. 121–131, at https://doi.org/10.1002/joc.3413.

Abatzoglou, J.T., and Brown, T.J., 2012, A comparison of statistical downscaling methods suited for wildfire applications: International Journal of Climatology, v. 32, no. 5, p. 772–780, at https://doi.org/10.1002/joc.2312.

Agrios, George N., 2005, Plant pathology: Elsevier.

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., and Curtis-McLane, S., 2008, Adaptation, migration or extirpation: climate change outcomes for tree populations: Climate change outcomes for tree populations: Evolutionary Applications, v. 1, no. 1, p. 95–111, at https://doi.org/10.1111/j.1752-4571.2007.00013.x.

Albert, D.A., 1995, Regional Landscape Ecosystems of Michigan, Minnesota, and Wisconsin: A Working Map and Classification: USDA Forest Service, North Central Forest Experiment Station, at https://doi.org/10.2737/NC-GTR-178.

Alexander, G., Almendinger, J., and White, P., 2022, The long-term effects of invasive earthworms on plant community composition and diversity in a hardwood forest in northern Minnesota: Plant-Environment Interactions, v. 3, no. 2, p. 89–102, at https://doi.org/10.1002/pei3.10075.

Alizadeh, M.R., Adamowski, J., Nikoo, M.R., AghaKouchak, A., Dennison, P., and Sadegh, M., 2020, A century of observations reveals increasing likelihood of continental-scale compound dry-hot extremes: Science Advances, v. 6, no. 39, p. eaaz4571, at https://doi.org/10.1126/sciadv.aaz4571.

Allen, J.M., and Bradley, B.A., 2016, Out of the weeds? Reduced plant invasion risk with climate change in the continental United States: Biological Conservation, v. 203, p. 306–312, at.

Allen, C.D., Breshears, D.D., and McDowell, N.G., 2015, On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene: Ecosphere, v. 6, no. 8, p. art129, at https://doi.org/10.1890/ES15-00203.1.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., and others, 2010, A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests: Forest Ecology and

Management, v. 259, no. 4, p. 660–684, at https://doi.org/10.1016/j.foreco.2009.09.001.

Allstadt, A.J., Vavrus, S.J., Heglund, P.J., Pidgeon, A.M., Thogmartin, W.E., and Radeloff, V.C., 2015, Spring plant phenology and false springs in the conterminous US during the 21st century: Environmental Research Letters, v. 10, no. 10, p. 104008, at https://doi.org/10.1088/1748-9326/10/10/104008.

Anderegg, W.R.L., 2015, Spatial and temporal variation in plant hydraulic traits and their relevance for climate change impacts on vegetation: New Phytologist, v. 205, no. 3, p. 1008–1014, at https://doi.org/10.1111/nph.12907.

Apfelbaum, S.I., and Haney, A., 2023, Fire and climate change in the North American Great Lakes pine transition forest, *in* Zhang, L, Wang S., and Liangying, L. eds, Mitigated Global Climate Change – Enhancing Adaptation, Evaluation, and Restoration or Mountain Ecosystems: IntechOpen, at https://doi.org/ 10.5772/intechopen.110734.

Aryal, Y., Ficklin, D.L., and Myers, D.T., 2025, Projected changes in rain-on-snow events and their impacts on summer low streamflow in the Great Lakes basin: Environmental Modelling & Software, v. 193, p. 106612, at https://doi.org/10.1016/j.envsoft.2025.106612.

Astigarraga, J., Esquivel-Muelbert, A., Ruiz-Benito, P., Rodríguez-Sánchez, F., Zavala, M.A., Vilà-Cabrera, A., Schelhaas, M.-J., Kunstler, G., Woodall, C.W., Cienciala, E., Dahlgren, J., Govaere, L., König, L.A., Lehtonen, A., and others, 2024, Relative decline in density of Northern Hemisphere tree species in warm and arid regions of their climate niches: Proceedings of the National Academy of Sciences, v. 121, no. 28, p. e2314899121, at https://doi.org/10.1073/pnas.2314899121.

Augspurger, C.K., 2009, Spring 2007 warmth and frost: phenology, damage and refoliation in a temperate deciduous forest: Functional Ecology, v. 23, no. 6, p. 1031–1039, at https://doi.org/10.1111/j.1365-2435.2009.01587.x.

Augspurger, C.K., 2013, Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing: Ecology, v. 94, no. 1, p. 41–50, at https://doi.org/10.1890/12-0200.1.

Bakshi, B., Polasky, S., and Frelich, L.E., 2025, Predicting the impact of climate change on forest composition, deer, and outdoor recreation using structural equation modeling (SEM) in northeastern Minnesota: Journal of Environmental Management, v. 392, p. 126695, at https://doi.org/10.1016/j.jenvman.2025.126695.

Balla, A., Silini, A., Cherif-Silini, H., Chenari Bouket, A., Moser, W.K., Nowakowska, J.A., Oszako, T., Benia, F., and Belbahri, L., 2021, The threat of pests and pathogens and the potential

for biological control in forest ecosystems: Forests, v. 12, no. 11, p. 1579, at https://doi.org/10.3390/f12111579.

Beauregard, F., and de Blois, S., 2016, Rapid latitudinal range expansion at cold limits unlikely for temperate understory forest plants: Ecosphere, v. 7, no. 11, p. e01549, at https://doi.org/10.1002/ecs2.1549.

Bentz, B.J., and Jönsson, A.M., 2015, Chapter 13 - Modeling Bark Beetle Responses to Climate Change, *in* Vega, F.E. and Hofstetter, R.W. eds., Bark Beetles: Academic Press, San Diego, p. 533–553.

Bernal-Escobar, M., Zuleta, D., and Feeley, K.J., 2022, Changes in the climate suitability and growth rates of trees in eastern North America: Ecography, v. 2022, no. 9, p. e06298, at https://doi.org/10.1111/ecog.06298.

Bertin, R.I., 2017, Climate change and flowering phenology in Franklin County, Massachusetts: The Journal of the Torrey Botanical Society, v. 144, no. 2, p. 153–169, at https://doi.org/10.3159/TORREY-D-16-00019R2.

Billah, M.M., and Goldblum, D., 2019, Radial growth of Picea glauca and Picea engelmannii across Canada and USA: monthly climate, decadal oscillations, and climate change: Physical Geography, v. 40, no. 6, p. 503–520, at https://doi.org/10.1080/02723646.2019.1599482.

Birch, J.D., Chikamoto, Y., DeRose, R.J., Manvailer, V., Hogg, E.H., Karst, J., Love, D.M., and Lutz, J.A., 2023, Frost-associated defoliation in *Populus tremuloides* causes repeated growth reductions over 185 years: Ecosystems, v. 26, no. 4, p. 843–859, at https://doi.org/10.1007/s10021-022-00799-w.

Blagrave, K., and Sharma, S., 2023, Projecting climate change impacts on ice phenology across Midwestern and Northeastern United States lakes: Climatic Change, v. 176, no. 9, p. 119, at https://doi.org/10.1007/s10584-023-03596-z.

Boisvert-Marsh, L., and de Blois, S., 2021, Unravelling potential northward migration pathways for tree species under climate change: Journal of Biogeography, v. 48, no. 5, p. 1088–1100, at https://doi.org/10.1111/jbi.14060.

Boisvert-Marsh, L., Pedlar, J.H., de Blois, S., Le Squin, A., Lawrence, K., McKenney, D.W., Williams, C., and Aubin, I., 2022, Migration-based simulations for Canadian trees show limited tracking of suitable climate under climate change: Diversity and Distributions, v. 28, no. 11, p. 2330–2348, at https://doi.org/10.1111/ddi.13630.

Boisvert-Marsh, L., Périé, C., and de Blois, S., 2014, Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes: Ecosphere, v. 5, no. 7, p. art83, at https://doi.org/10.1890/ES14-00111.1.

Boisvert-Marsh, L., Périé, C., and de Blois, S., 2019, Divergent responses to climate change and disturbance drive recruitment patterns underlying latitudinal shifts of tree species: Journal of Ecology, v. 107, no. 4, p. 1956–1969, at https://doi.org/10.1111/1365-2745.13149.

Bolte, A., Hilbrig, L., Grundmann, B.M., and Roloff, A., 2014, Understory dynamics after disturbance accelerate succession from spruce to beech-dominated forest—the Siggaboda case study: Annals of Forest Science, v. 71, no. 2, p. 139–147, at https://doi.org/10.1007/s13595-013-0283-y.

Boulanger, Y., Desaint, A., Martel, V., Marchand, M., Tonye, S.M., Saint-Amant, R., and Régnière, J., 2025, Recent climate change strongly impacted the population dynamic of a North American insect pest species: PLOS Climate, v. 4, no. 2, p. e0000488, at https://doi.org/10.1371/journal.pclm.0000488.

Boulanger, Y., Taylor, A.R., Price, D.T., Cyr, D., McGarrigle, E., Rammer, W., Sainte-Marie, G., Beaudoin, A., Guindon, L., and Mansuy, N., 2017, Climate change impacts on forest landscapes along the Canadian southern boreal forest transition zone: Landscape Ecology, v. 32, no. 7, p. 1415–1431, at https://doi.org/10.1007/s10980-016-0421-7.

Bracalini, M., Balacenoiu, F., and Panzavolta, T., 2024, Forest health under climate change: impact of insect pests: iForest - Biogeosciences and Forestry, v. 17, no. 5, p. 295, at https://doi.org/10.3832/ifor4520-017.

Bradshaw, L., and Waller, D.M., 2016, Impacts of white-tailed deer on regional patterns of forest tree recruitment: Forest Ecology and Management, v. 375, p. 1–11, at https://doi.org/10.1016/j.foreco.2016.05.019.

Brandt, L., 2020, Climate as a driver of change in U.S. forests: *in*: Dockry, M.J., Bengston, D.N., Westphal, L.M., comps. 2020. Drivers of change in U.S. forests and forestry over the next 20 years. Gen. Tech. Rep. NRS-P-197., p. 7, at https://doi.org/10.2737/NRS-GTR-P-197-paper2.

Brice, M.-H., Vissault, S., Vieira, W., Gravel, D., Legendre, P., and Fortin, M.-J., 2020, Moderate disturbances accelerate forest transition dynamics under climate change in the temperate–boreal ecotone of eastern North America: Global Change Biology, v. 26, no. 8, p. 4418–4435, at https://doi.org/10.1111/gcb.15143.

Brown, P.J., and DeGaetano, A.T., 2011, A paradox of cooling winter soil surface temperatures in a warming northeastern United States: Agricultural and Forest Meteorology, v. 151, no. 7, p. 947–956, at https://doi.org/10.1016/j.agrformet.2011.02.014.

Burgess, T.I., Scott, J.K., Mcdougall, K.L., Stukely, M.J.C., Crane, C., Dunstan, W.A., Brigg, F., Andjic, V., White, D., Rudman, T., Arentz, F., Ota, N., and Hardy, G.E.St.J., 2017, Current and projected global distribution of *Phytophthora cinnamomi* , one of the world's worst

plant pathogens: Global Change Biology, v. 23, no. 4, p. 1661–1674, at https://doi.org/10.1111/gcb.13492.

Burns, R.M., and Honkala, B. H. tech. coords. 1990, Silvics of North America: 2. Hardwoods: Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC vol. 2, 877 pp.

Byard, S., Wisniewski, M., Li, J., and Karlson, D., 2010, Interspecific analysis of xylem freezing responses in *Acer* and *Betula*: HortScience, v. 45, no. 1, p. 165–168, at https://doi.org/10.21273/HORTSCI.45.1.165.

Byun, K., Chiu, C.-M., and Hamlet, A.F., 2019, Effects of 21st century climate change on seasonal flow regimes and hydrologic extremes over the Midwest and Great Lakes region of the US: Science of The Total Environment, v. 650, p. 1261–1277, at https://doi.org/10.1016/j.scitotenv.2018.09.063.

Calinger, K.M., Queenborough, S., and Curtis, P.S., 2013, Herbarium specimens reveal the footprint of climate change on flowering trends across north-central North America: Ecology Letters, v. 16, no. 8, p. 1037–1044, at https://doi.org/10.1111/ele.12135.

Campbell, J.L., Socci, A.M., and Templer, P.H., 2014, Increased nitrogen leaching following soil freezing is due to decreased root uptake in a northern hardwood forest: Global Change Biology, v. 20, no. 8, p. 2663–2673, at https://doi.org/10.1111/gcb.12532.

Canham, C.D., Murphy, L., Riemann, R., McCullough, R., and Burrill, E., 2018, Local differentiation in tree growth responses to climate: Ecosphere, v. 9, no. 8, p. e02368, at https://doi.org/10.1002/ecs2.2368.

Caron, S.B., Campbell, J., Driscoll, C.T., Groffman, P.M., Leonardi, B., Reinmann, A., Rustad, L., Wilson, G., and Templer, P.H., 2025, Shallow snowpack and early snowmelt reduce nitrogen availability in the northern hardwood forest: Biogeochemistry, v. 168, no. 3, p. 49, at https://doi.org/10.1007/s10533-025-01239-2.

Casson, N.J., Eimers, M.C., and Watmough, S.A., 2012, Impact of winter warming on the timing of nutrient export from forested catchments: Hydrological Processes, v. 26, no. 17, p. 2546–2554, at https://doi.org/10.1002/hyp.8461.

Chagnon, C., Moreau, G., Bombardier-Cauffopé, C., Barrette, J., Havreljuk, F., and Achim, A., 2022, Broad-scale wood degradation dynamics in the face of climate change: A meta-analysis: GCB Bioenergy, v. 14, no. 8, p. 941–958, at https://doi.org/10.1111/gcbb.12951.

Chalumeau, A., Bergeron, Y., Bouchard, M., Grondin, P., Lambert, M.-C., and Périé, C., 2024, Anticipated impacts in habitat of diagnostic species of potential natural vegetations due to climate change at the ecotone between temperate and boreal forests: Climate Change Ecology, v. 8, p. 100089, at https://doi.org/10.1016/j.ecochg.2024.100089.

Chamberlain, C.J., Cook, B.I., García de Cortázar-Atauri, I., and Wolkovich, E.M., 2019, Rethinking false spring risk: Global Change Biology, v. 25, no. 7, p. 2209–2220, at https://doi.org/10.1111/gcb.14642.

Chamberlain, C.J., and Wolkovich, E.M., 2021, Late spring freezes coupled with warming winters alter temperate tree phenology and growth: New Phytologist, v. 231, no. 3, p. 987–995, at https://doi.org/10.1111/nph.17416.

Champagne, E., Raymond, P., Royo, A.A., Speed, J.D.M., Tremblay, J.-P., and Côté, S.D., 2021, A review of ungulate impacts on the success of climate-adapted forest management strategies: Current Forestry Reports, v. 7, no. 4, p. 305–320, at https://doi.org/10.1007/s40725-021-00148-5.

Chaste, E., Girardin, M.P., Kaplan, J.O., Bergeron, Y., and Hély, C., 2019, Increases in heat-induced tree mortality could drive reductions of biomass resources in Canada's managed boreal forest: Landscape Ecology, v. 34, no. 2, p. 403–426, at https://doi.org/10.1007/s10980-019-00780-4.

Chen, J., Saunders, S.C., Crow, T.R., Naiman, R.J., Brosofske, K.D., Mroz, G.D., Brookshire, B.L., and Franklin, J.F., 1999, Microclimate in forest ecosystem and landscape ecology: Variations in local climate can be used to monitor and compare the effects of different management regimes: BioScience, v. 49, no. 4, p. 288–297, at https://doi.org/10.2307/1313612.

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., and others, 2012, Global convergence in the vulnerability of forests to drought: Nature, v. 491, no. 7426, p. 752–755, at https://doi.org/10/gbb398.

Clarke, B., Otto, F., Stuart-Smith, R., and Harrington, L., 2022, Extreme weather impacts of climate change: an attribution perspective: Environmental Research: Climate, v. 1, no. 1, p. 012001, at https://doi.org/10.1088/2752-5295/ac6e7d.

Cleavitt, N.L., Fahey, T.J., Groffman, P.M., Hardy, J.P., Henry, K.S., and Driscoll, C.T., 2008, Effects of soil freezing on fine roots in a northern hardwood forest: Canadian Journal of Forest Research, v. 38, no. 1, p. 82–91, at https://doi.org/10.1139/X07-133.

Coakley, S.M., Scherm, H., and Chakraborty, S., 1999, Climate change and plant disease management: Annual Review of Phytopathology, v. 37, no. 1, p. 399–426, at https://doi.org/10.1146/annurev.phyto.37.1.399.

Cohen, J.G., Kost, M.A., Slaughter, B.S., and Albert, D.A., 2015, A Field Guide to the Natural Communities of Michigan: Michigan State University Press, East Lansing, Michigan, USA, 362 pp.

Cohen, J.G., Kost, M.A., Slaughter, B.S., Albert, D.A., Lincoln, J.M., Kortenhoven, A.P., Wilton, C.M., Enander, H.D., Anderson, M.E., Parr, M.R., Bassett, T.J., and Korroch, K.M., 2025, Michigan Natural Community Classification, Michigan Natural Features Inventory, Michigan State University Extension, Lansing, MI: Accessed June 25, 2026, at https://mnfi.anr.msu.edu/communities/classification.

Cole, C.T., Morrow, C.J., Barker, H.L., Rubert-Nason, K.F., Riehl, J.F.L., Köllner, T.G., Lackus, N.D., and Lindroth, R.L., 2021, Growing up aspen: ontogeny and trade-offs shape growth, defence and reproduction in a foundation species: Annals of Botany, v. 127, no. 4, p. 505–517, at https://doi.org/10.1093/aob/mcaa070.

Collier, J., MacLean, D.A., D'Orangeville, L., and Taylor, A.R., 2022a, A review of climate change effects on the regeneration dynamics of balsam fir: The Forestry Chronicle, v. 98, no. 1, p. 54–65, at https://doi.org/10.5558/tfc2022-005.

Comerford, D.P., Schaberg, P.G., Templer, P.H., Socci, A.M., Campbell, J.L., and Wallin, K.F., 2013, Influence of experimental snow removal on root and canopy physiology of sugar maple trees in a northern hardwood forest: Oecologia, v. 171, no. 1, p. 261–269, at https://doi.org/10.1007/s00442-012-2393-x.

Conrad-Rooney, E., Reinmann, A.B., and Templer, P.H., 2025, Declining winter snowpack offsets carbon storage enhancement from growing season warming in northern temperate forest ecosystems: Proceedings of the National Academy of Sciences of the United States of America, v. 122, no. 28, p. e2412873122, at https://doi.org/10.1073/pnas.2412873122.

Contosta, A.R., Arndt, K.A., Baulch, H.M., Casson, N.J., Harpold, A., Morelli, T.L., Sirén, A.P.K., and Templer, P.H., 2024, Threshold changes in winter temperature and precipitation drive threshold responses across nine global climate zones and associated biomes: Annual Review of Ecology, Evolution, and Systematics, v. 55, no. 1, p. 271–300, at https://doi.org/10.1146/annurev-ecolsys-110421-102101.

Contosta, A.R., Casson, N.J., Garlick, S., Nelson, S.J., Ayres, M.P., Burakowski, E.A., Campbell, J., Creed, I., Eimers, C., Evans, C., Fernandez, I., Fuss, C., Huntington, T., Patel, K., and others, 2019, Northern forest winters have lost cold, snowy conditions that are important for ecosystems and human communities: Ecological Applications, v. 29, no. 7, p. e01974, at https://doi.org/10.1002/eap.1974.

Contosta, A.R., Casson, N.J., Nelson, S.J., and Garlick, S., 2020, Defining frigid winter illuminates its loss across seasonally snow-covered areas of eastern North America: Environmental Research Letters, v. 15, no. 3, p. 034020, at https://doi.org/10.1088/1748-9326/ab54f3.

Contreras-Cornejo, H.A., Larsen, J., Fernández-Pavía, S.P., and Oyama, K., 2023, Climate change, a booster of disease outbreaks by the plant pathogen *Phytophthora* in oak forests: Rhizosphere, v. 27, p. 100719, at https://doi.org/10.1016/j.rhisph.2023.100719.

Cooke, B.J., and Roland, J., 2018, Early 20th century climate-driven shift in the dynamics of forest tent caterpillar outbreaks: American Journal of Climate Change, v. 7, no. 2, p. 253–270, at https://doi.org/10.4236/ajcc.2018.72017.

Costanza, J.K., Koch, F.H., and Reeves, M.C., 2023, Future exposure of forest ecosystems to multi-year drought in the United States: Ecosphere, v. 14, no. 5, p. e4525, at https://doi.org/10.1002/ecs2.4525.

Côté, S.D., Rooney, T.P., Tremblay, J., and others, 2004, Ecological impacts of deer overabundance: Annual Review of Ecology, Evolution, and Systematics, v. 35, p. 113–147, at https://doi.org/10.2307/annurev.ecolsys.35.021103.30000006.

Dadaser-Celik, F., and Stefan, H.G., 2007, Lake level response to climate in Minnesota: University of Minnesota, Project Report No. 502.

Dahlberg, B.L., and Guettinger, R.C., 1956, The white-tailed deer in Wisconsin: Game Management Division, Wisconsin Conservation Department., at https://digital.library.wisc.edu/1711.dl/HG5ONPR67GYVL8J

De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B.R., Zellweger, F., Aalto, J., Ashcroft, M.B., Christiansen, D.M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., and others, 2021, Forest microclimates and climate change: Importance, drivers and future research agenda: Global Change Biology, v. 27, no. 11, p. 2279–2297, at https://doi.org/10.1111/gcb.15569.

Demaria, E.M.C., Roundy, J.K., Wi, S., and Palmer, R.N., 2016, The Effects of Climate Change on Seasonal Snowpack and the Hydrology of the Northeastern and Upper Midwest United States: Journal of Climate, v. 29, no. 18, p. 6527–6541, at https://doi.org/10.1175/jcli-d-15-0632.1.

Dey, D.C., Knapp, B.O., Battaglia, M.A., Deal, R.L., Hart, J.L., O'Hara, K.L., Schweitzer, C.J., and Schuler, T.M., 2019, Barriers to natural regeneration in temperate forests across the USA: New Forests, v. 50, no. 1, p. 11–40, at https://doi.org/10.1007/s11056-018-09694-6.

Division of Fish and Wildlife, Section of Fisheries, 2015, Crow Wing County lakes prioritization and screening: Minnesota Board of Soil and Water Resources, 39 pp., at https://wrl.mnpals.net/islandora/object/WRLrepository%3A3408.

Dobson, K., Zhu, K., Song, Y., Zhu, J., Adler, P., Stemkovski, M., Montgomery, R., Stefanski, A., Worm, K., and Reich, P., 2025, A few key species drive community thermophilization under experimental warming: accessed March 17, 2026, at, https://www.researchsquare.com/article/rs-8050401/latest.

Dollan, I.J., Maggioni, V., Johnston, J., Coelho, G. de A., and Kinter, J.L., 2022, Seasonal variability of future extreme precipitation and associated trends across the Contiguous U.S.: Frontiers in Climate, v. 4, at https://doi.org/10.3389/fclim.2022.954892.

Donovan, V.M., Crandall, R., Fill, J., and Wonkka, C.L., 2023, increasing large wildfire in the eastern United States: Geophysical Research Letters, v. 50, no. 24, p. e2023GL107051, at https://doi.org/10.1029/2023GL107051.

D'Orangeville, L., Maxwell, J., Kneeshaw, D., Pederson, N., Duchesne, L., Logan, T., Houle, D., Arseneault, D., Beier, C.M., Bishop, D.A., Druckenbrod, D., Fraver, S., Girard, F., Halman, J., and others, 2018, Drought timing and local climate determine the sensitivity of eastern temperate forests to drought: Global Change Biology, v. 24, no. 6, p. 2339–2351, at https://doi.org/10.1111/gcb.14096.

D'Orangeville, L., St-Laurent, M.-H., Boisvert-Marsh, L., Zhang, X., Bastille-Rousseau, G., and Itter, M., 2023, Current symptoms of climate change in boreal forest trees and wildlife, *in* Girona, M.M., Morin, H., Gauthier, S., and Bergeron, Y. eds., Boreal Forests in the Face of Climate Change: Sustainable Management: Springer International Publishing, Cham, p. 747–771.

Dow, C., Kim, A. Y., D'Orangeville, L., Gonzalez-Akre, E. B., Helcoski, R., Herrmann, V., Harley, G. L., Maxwell, J. T., McGregor, I. R., McShea, W. J., McMahon, S. M., Pederson, N., Tepley, A. J., & Anderson-Teixeira, K. J., 2022, Warm springs alter timing but not total growth of temperate deciduous trees: Nature, v. 608, no. 7923, p. 552–557, at https://doi.org/10.1038/s41586-022-05092-3

Drescher, M., and Thomas, S.C., 2013, Snow cover manipulations alter survival of early life stages of cold-temperate tree species: Oikos, v. 122, no. 4, p. 541–554, at https://doi.org/10.1111/j.1600-0706.2012.20642.x.

Druin, L.M., Gilbert, J.H., Woodford, J.E., and Pauli, J.N., 2025, Movement corridors reveal conservation opportunities, challenges, and indigenous roles in the recovery of American Martens (Waabizheshi; *Martes americana*) in the upper Great Lakes region: Biological Conservation, v. 302, p. 111005, at https://doi.org/10.1016/j.biocon.2025.111005.

Dudney, J., Willing, C.E., Das, A.J., Latimer, A.M., Nesmith, J.C.B., and Battles, J.J., 2021, Nonlinear shifts in infectious rust disease due to climate change: Nature Communications, v. 12, no. 1, p. 5102, at https://doi.org/10.1038/s41467-021-25182-6.

Dukes, J.S., Pontius, J., Orwig, D., Garnas, J.R., Rodgers, V.L., Brazee, N., Cooke, B., Theoharides, K.A., Stange, E.E., Harrington, R., Ehrenfeld, J., Gurevitch, J., Lerdau, M., Stinson, K., and others, 2009, Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? Canadian Journal of Forest Research, v. 39, no. 2, p. 231–248, at https://doi.org/10.1139/X08-171.

Duveneck, M.J., Scheller, R.M., White, M.A., Handler, S.D., and Ravenscroft, C., 2014, Climate change effects on northern Great Lake (USA) forests: A case for preserving diversity: Ecosphere, v. 5, no. 2, p. art23, at https://doi.org/10/gfvcw2.

Dymond, S.F., Kolka, R.K., Bolstad, P.V., and Sebestyen, S.D., 2014, Long-term soil moisture patterns in a northern Minnesota forest: Soil Science Society of America Journal, v. 78, no. S1, accessed October 11, 2023, at https://doi.org/10.2136/sssaj2013.08.0322nafsc.

Eisenhauer, N., Fisichelli, N.A., Frelich, L.E., and Reich, P.B., 2012, Interactive effects of global warming and 'global worming' on the initial establishment of native and exotic herbaceous plant species: Oikos, v. 121, no. 7, p. 1121–1133, at https://doi.org/10.1111/j.1600-0706.2011.19807.x.

Eisenhauer, N., Stefanski, A., Fisichelli, N.A., Rice, K., Rich, R., and Reich, P.B., 2015, Warming shifts 'worming': Effects of experimental warming on invasive earthworms in northern North America: Scientific Reports, v. 4, no. 1, p. 6890, at https://doi.org/10/gjpr2c.

Eschtruth, A.K., and Battles, J.J., 2009, Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion: Ecological Monographs, v. 79, no. 2, p. 265–280, at https://doi.org/https://doi.org/10.1890/08-0221.1.

Etterson, J.R., Cornett, M.W., White, M.A., and Kavajecz, L.C., 2020, Assisted migration across fixed seed zones detects adaptation lags in two major North American tree species: Ecological Applications, v. 30, no. 5, p. e02092, at https://doi.org/10.1002/eap.2092.

Evans, A.E., Jarnevich, C.S., Beaury, E.M., Engelstad, P.S., Teich, N.B., LaRoe, J.M., and Bradley, B.A., 2024, Shifting hotspots: Climate change projected to drive contractions and expansions of invasive plant abundance habitats: Diversity and Distributions, v. 30, no. 1, p. 41–54, at https://doi.org/10.1111/ddi.13787.

Faber-Langendoen, D., 2007, Field Guide to the plant community types of Voyageurs National Park: US Geological Survey.

Faber-Langendoen, D., Edinger, G., Lundgren, J., Nichols, B., Puryear, K., Schlawin, J., Shappell, L., Sneddon, L., Sorenson, E., Walz, K., Zaino, B., and Zimmerman, E., 2020, Revisions to the vegetation types in the Northeastern states: An expert review of USNVC groups and alliances and their relation to state natural community types: Proceedings of the U.S. National Vegetation Classification, v. USNVC-Proc-XX, at.

Fang, X., Jacobson, P.C., Jiang, L., Herb, W.R., Stefan, H.G., Pereira, D.L., and Johnson, L.B., 2025, Understanding effects of climate change and eutrophication on fish habitat in glacial lakes of the Midwest states and management strategies, *in* Lackner, M., Sajjadi, B., and Chen, W.-Y. eds., Handbook of Climate Change Mitigation and Adaptation: Springer

Nature Switzerland, Cham, p. 81–149, at https://doi.org/10.1007/978-3-031-84483-6_16.

Felton, A.J., and Smith, M.D., 2017, Integrating plant ecological responses to climate extremes from individual to ecosystem levels: Philosophical Transactions of the Royal Society B: Biological Sciences, v. 372, no. 1723, p. 20160142, at https://doi.org/10.1098/rstb.2016.0142.

Felton, A.M., Wam, H.K., Borowski, Z., Granhus, A., Juvany, L., Matala, J., Melin, M., Wallgren, M., and Mårell, A., 2024, Climate change and deer in boreal and temperate regions: From physiology to population dynamics and species distributions: Global Change Biology, v. 30, no. 9, p. e17505, at https://doi.org/10.1111/gcb.17505.

Filewod, B., and Thomas, S.C., 2014, Impacts of a spring heat wave on canopy processes in a northern hardwood forest: Global Change Biology, v. 20, no. 2, p. 360–371, at https://doi.org/10.1111/gcb.12354.

Finch, D.M., Butler, J.L., Runyon, J.B., Fettig, C.J., Kilkenny, F.F., Jose, S., Frankel, S.J., Cushman, S.A., Cobb, R.C., Dukes, J.S., Hicke, J.A., and Amelon, S.K., 2021, Effects of climate change on invasive species, *in* Poland, T.M., Patel-Weynand, T., Finch, D.M., Miniat, C.F., Hayes, D.C., and Lopez, V.M. eds., Invasive Species in Forests and Rangelands of the United States: Springer International Publishing, Cham, p. 57–83.

Fisichelli, N., Frelich, L.E., and Reich, P.B., 2012, Sapling growth responses to warmer temperatures 'cooled' by browse pressure: Global Change Biology, v. 18, no. 11, p. 3455–3463, at https://doi.org/10.1111/j.1365-2486.2012.02785.x.

Fisichelli, N.A., Frelich, L.E., and Reich, P.B., 2013, Climate and interrelated tree regeneration drivers in mixed temperate–boreal forests: Landscape Ecology, v. 28, no. 1, p. 149–159, at https://doi.org/10.1007/s10980-012-9827-z.

Fisichelli, N.A., Frelich, L.E., and Reich, P.B., 2014, Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures: Ecography, v. 37, no. 2, p. 152–161, at https://doi.org/10.1111/j.1600-0587.2013.00197.x.

Flower, C.E., and Gonzalez-Meler, M.A., 2015, Responses of temperate forest productivity to insect and pathogen disturbances: Annual Review of Plant Biology, v. 66, no. Volume 66, 2015, p. 547–569, at https://doi.org/10.1146/annurev-arplant-043014-115540.

Ford, T.W., Budikova, D., and Wright, J.D., 2022, Characterizing winter season severity in the Midwest United States, Part I: Climatology and recent trends: International Journal of Climatology, v. 42, no. 6, p. 3537–3552, at https://doi.org/10.1002/joc.7431.

Ford, T.W., Chen, L., and Schoof, J.T., 2021a, Variability and transitions in precipitation extremes in the Midwest United States: Journal of Hydrometeorology, v. 22, no. 3, p. 533–545, at https://doi.org/10.1175/jhm-d-20-0216.1.

Ford, C.M., Kendall, A.D., and Hyndman, D.W., 2021b, Snowpacks decrease and streamflows shift across the eastern US as winters warm: Science of The Total Environment, v. 793, p. 148483, at https://doi.org/10.1016/j.scitotenv.2021.148483.

Foster, J.R., Finley, A.O., D'Amato, A.W., Bradford, J.B., and Banerjee, S., 2016, Predicting tree biomass growth in the temperate–boreal ecotone: Is tree size, age, competition, or climate response most important? Global Change Biology, v. 22, no. 6, p. 2138–2151, at https://doi.org/10.1111/gcb.13208.

Frelich, L.E., Blossey, B., Cameron, E.K., Dávalos, A., Eisenhauer, N., Fahey, T., Ferlian, O., Groffman, P.M., Larson, E., Loss, S.R., Maerz, J.C., Nuzzo, V., Yoo, K., and Reich, P.B., 2019, Side-swiped: ecological cascades emanating from earthworm invasions: Frontiers in Ecology and the Environment, v. 17, no. 9, p. 502–510, at https://doi.org/10.1002/fee.2099.

Frelich, L.E., Johnstone, J., and Kuuluvainen, T., 2024, Chapter 11 - Boreal forests, *in* McNulty, S.G. ed., Future Forests: Elsevier, p. 221–242.

Frelich, L.E., Montgomery, R.A., and Reich, P.B., 2021, Seven ways a warming climate can kill the southern boreal forest: Forests, v. 12, no. 5, p. 560, at https://doi.org/10.3390/f12050560.

Frelich, L.E., and Reich, P.B., 2010, Will environmental changes reinforce the impact of global warming on the prairie–forest border of central North America? Frontiers in Ecology and the Environment, v. 8, no. 7, p. 371–378, at https://doi.org/10.1890/080191.

Frerker, K., Sabo, A., and Waller, D., 2014, Long-term regional shifts in plant community composition are largely explained by local deer impact experiments: PLoS ONE, v. 9, no. 12, p. e115843, at https://doi.org/10.1371/journal.pone.0115843.

Fridley, J.D., 2012, Extended leaf phenology and the autumn niche in deciduous forest invasions: Nature, v. 485, no. 7398, p. 359–362, at https://doi.org/10.1038/nature11056.

Frumhoff, P.C., McCarthy, J.J., Melillo, J.M., Moser, S.C., and Wuebbles, D.J., 2007, Confronting climate change in the US Northeast: A report of the northeast climate impacts assessment. Union of Concerned Scientists, Cambridge, Massachusetts, p. 47–61, at.

Fusco, E., Halofsky, J.E., Reilly, M., Prendeville, H.R., and Sousa-Silva, R., 2024, Chapter 9 - Temperate forests, *in* McNulty, S.G. ed., Future Forests: Elsevier, p. 177–202.

Fuss, C.B., Driscoll, C.T., Groffman, P.M., Campbell, J.L., Christenson, L.M., Fahey, T.J., Fisk, M.C., Mitchell, M.J., Templer, P.H., Durán, J., and Morse, J.L., 2016, Nitrate and dissolved organic carbon mobilization in response to soil freezing variability: Biogeochemistry, v. 131, no. 1, p. 35–47, at https://doi.org/10.1007/s10533-016-0262-0.

Gagne, M.A., Smith, D.D., and McCulloh, K.A., 2020, Limited physiological acclimation to recurrent heatwaves in two boreal tree species: Tree Physiology, v. 40, no. 12, p. 1680–1696, at https://doi.org/10.1093/treephys/tpaa102.

Gallinat, A.S., Schwartz, M.D., Donnelly, A., Li, X., and Crimmins, T.M., 2026, Combined volunteer and ecological network observations show broad-scale temperature-sensitivity patterns for deciduous plant flowering and leaf-out times across the eastern USA: Journal of Ecology, v. 114, no. 1, p. e70165, at https://doi.org/10.1111/1365-2745.70165.

Garretson, A., Feldsine, N., Napoli, M., Long, E.C., and Forkner, R.E., 2022, Networks of phenological synchrony reveal a highly interconnected ecosystem and potential vulnerability to climate-driven mismatches: bioRxiv 2002.07.11.499341, accessed October 27, 2023, at https://doi.org/10.1101/2022.07.11.499341.

Garrett, K.A., Nita, M., De Wolf, E.D., Esker, P.D., Gomez-Montano, L., and Sparks, A.H., 2016, Plant Pathogens as Indicators of Climate Change, *in* Letcher, T. M. eds. Climate Change (Second Edition): Elsevier, p. 325–338, at http://dx.doi.org/10.1016/B978-0-444-63524-2.00021-X.

Gawler, S.C., 2009, Laurentian-Acadian northern hardwood forest: Federal Geographic Data Committee, accessed December 30, 2024 at https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.723040/Laurentian-Acadian_Northern_Hardwood_Forest.

Ghannoum, O., and Way, D.A., 2011, On the role of ecological adaptation and geographic distribution in the response of trees to climate change: Tree Physiology, v. 31, no. 12, p. 1273–1276, at https://doi.org/10.1093/treephys/tpr115.

Gilbert, N.A., Anich, N.M., Worland, M., and Zuckerberg, B., 2022, Microclimate complexities at the trailing edge of the boreal forest: Forest Ecology and Management, v. 524, p. 120533, at https://doi.org/10.1016/j.foreco.2022.120533.

Girardin, M.P., Gaboriau, D.M., Ali, A.A., Gajewski, K., Briere, M.D., Bergeron, Y., Paillard, J., Waito, J., and Tardif, J.C., 2024, Boreal forest cover was reduced in the mid-Holocene with warming and recurring wildfires: Communications Earth & Environment, v. 5, no. 1, p. 1–12, at https://doi.org/10.1038/s43247-024-01340-8.

Girardin, M.P., Guo, X.J., Gervais, D., Metsaranta, J., Campbell, E.M., Arsenault, A., Isaac-Renton, M., and Hogg, E.H., 2022, Cold-season freeze frequency is a pervasive driver of subcontinental forest growth: Proceedings of the National Academy of Sciences, v. 119, no. 18, p. e2117464119, at https://doi.org/10.1073/pnas.2117464119.

Girardin, M.P., Hogg, E.H., Bernier, P.Y., Kurz, W.A., Guo, X.J., and Cyr, G., 2016, Negative impacts of high temperatures on growth of black spruce forests intensify with the

anticipated climate warming: Global Change Biology, v. 22, no. 2, p. 627–643, at https://doi.org/10.1111/gcb.13072.

González de Andrés, E., 2019, Interactions between Climate and Nutrient Cycles on Forest Response to Global Change: The Role of Mixed Forests: Forests, v. 10, no. 8, p. 609, at https://doi.org/10.3390/f10080609.

Gonzalez, P., Neilson, R.P., Lenihan, J.M., and Drapek, R.J., 2010, Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change: Global Ecology and Biogeography, v. 19, no. 6, p. 755–768, at https://doi.org/10/fcgfx3.

Gray, M.J., Hagy, H.M., Nyman, J.A., and Stafford, J.D., 2013, Management of wetlands for wildlife, *in* Anderson, J.T. and Davis, C.A. eds., Wetland Techniques: Springer Netherlands, Dordrecht, p. 121–180.

Groffman, P.M., Driscoll, C.T., Fahey, T.J., Hardy, J.P., Fitzhugh, R.D., and Tierney, G.L., 2001, Colder soils in a warmer world: A snow manipulation study in a northern hardwood forest ecosystem: Biogeochemistry, v. 56, no. 2, p. 135–150, at https://doi.org/10.1023/A:1013039830323.

Groffman, P.M., Rustad, L.E., Templer, P.H., Campbell, J.L., Christenson, L.M., Lany, N.K., Socci, A.M., Vadeboncoeur, M.A., Schaberg, P.G., Wilson, G.F., Driscoll, C.T., Fahey, T.J., Fisk, M.C., Goodale, C.L., and others, 2012, Long-term integrated studies show complex and surprising effects of climate change in the Northern Hardwood Forest: BioScience, v. 62, no. 12, p. 1056–1066, at https://doi.org/10.1525/bio.2012.62.12.7.

Gu, H., Qiao, Y., Xi, Z., Rossi, S., Smith, N.G., Liu, J., and Chen, L., 2022, Warming-induced increase in carbon uptake is linked to earlier spring phenology in temperate and boreal forests: Nature Communications, v. 13, p. 3698, at https://doi.org/10.1038/s41467-022-31496-w.

Guégan, J.-F., de Thoisy, B., Gomez-Gallego, M., and Jactel, H., 2023, World forests, global change, and emerging pests and pathogens: Current Opinion in Environmental Sustainability, v. 61, p. 101266, at https://doi.org/10.1016/j.cosust.2023.101266.

Gunderson, C.A., O'hara, K.H., Campion, C.M., Walker, A.V., and Edwards, N.T., 2010, Thermal plasticity of photosynthesis: The role of acclimation in forest responses to a warming climate: Global Change Biology, v. 16, no. 8, p. 2272–2286, at https://doi.org/10.1111/j.1365-2486.2009.02090.x.

Haesen, S., Lenoir, J., Gril, E., De Frenne, P., Lembrechts, J.J., Kopecký, M., Macek, M., Man, M., Wild, J., and Van Meerbeek, K., 2023, Microclimate reveals the true thermal niche of forest plant species: Ecology Letters, v. 26, no. 12, p. 2043–2055, at https://doi.org/10.1111/ele.14312.

Hammer, J.M., Dusenge, M.E., Bither, N., Cook, A., Duarte, A.G., Lee, K., Murphy, B.K., Pastore, M.A., Schmiege, S.C., Swartman, R., Bermudez, R., Hüner, N.P.A., Reich, P.B., and Way, D.A., 2025, Photosynthetic capacity is reduced by warming but unaffected by elevated CO_2 in seedlings of five boreal tree species: Plant Physiology, v. 199, no. 1, p. kiaf380, at https://doi.org/10.1093/plphys/kiaf380.

Hammond, W.M., Williams, A.P., Abatzoglou, J.T., Adams, H.D., Klein, T., López, R., Sáenz-Romero, C., Hartmann, H., Breshears, D.D., and Allen, C.D., 2022, Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests: Nature Communications, v. 13, no. 1, p. 1761, at https://doi.org/10.1038/s41467-022-29289-2.

Hanberry, B.B., 2024, Tree species distributions in the United States and Canada under climate from 20,000 years ago to year 2100: Trees, Forests and People, v. 17, p. 100612, at https://doi.org/10.1016/j.tfp.2024.100612.

Hanberry, B.B., Abrams, M.D., and Nowacki, G.J., 2024, Potential interactions between climate change and land use for forest issues in the eastern United States: Land, v. 13, no. 3, at https://doi.org/10.3390/land13030398.

Handler, S., Duveneck, M.J., Iverson, L., Peters, E., Scheller, R.M., Wythers, K.R., Brandt, L., Butler, P., Janowiak, M., Shannon, P.D., Swanston, C., Eagle, A.C., Cohen, J.G., Corner, R., and others, 2014, Michigan forest ecosystem vulnerability assessment and synthesis: a report from the Northwoods Climate Change Response Framework project: U.S. Department of Agriculture, Forest Service, Northern Research Station NRS-GTR-129, NRS-GTR-129 pp., accessed October 27, 2023, at https://doi.org/10.2737/NRS-GTR-129.

Hänninen, H., 2016, Boreal and Temperate Trees in a Changing Climate: Springer Netherlands, Dordrecht.

Hardy, J.P., Groffman, P.M., Fitzhugh, R.D., Henry, K.S., Welman, A.T., Demers, J.D., Fahey, T.J., Driscoll, C.T., Tierney, G.L., and Nolan, S., 2001, Snow depth manipulation and its influence on soil frost and water dynamics in a northern hardwood forest: Biogeochemistry, v. 56, no. 2, p. 151–174, at https://doi.org/10.1023/A:1013036803050.

Harrington, R.A., Brown, B.J., and Reich, P.B., 1989, Ecophysiology of exotic and native shrubs in Southern Wisconsin: Oecologia, v. 80, no. 3, p. 356–367, at https://doi.org/10.1007/BF00379037.

Harris, L.B., Pastore, M.A., and D'Amato, A.W., 2025, Effects of browsing by white-tailed deer on tree regeneration vary by ontogeny and palatability in forests of the northeastern USA: Forest Ecology and Management, v. 593, p. 122906, at https://doi.org/10.1016/j.foreco.2025.122906.

Harvey, J.A., Heinen, R., Gols, R., and Thakur, M.P., 2020, Climate change-mediated temperature extremes and insects: From outbreaks to breakdowns: Global Change Biology, v. 26, no. 12, p. 6685–6701, at https://doi.org/10.1111/gcb.15377.

Hegewisch, K.C., and Abatzoglou, J.T., 2024, Climate Mapper web tool: accessed January 2, 2025, at https://climatetoolbox.org/.

Henne, P.D., Hu, F.S., and Cleland, D.T., 2007, Lake-effect snow as the dominant control of mesic-forest distribution in Michigan, USA: Journal of Ecology, v. 95, no. 3, p. 517–529, at https://doi.org/10.1111/j.1365-2745.2007.01220.x.

Henry, C.R., and Walters, M.B., 2023, Tree species size class patterns portend compositional shifts and low resilience in managed northern hardwood forests: Ecosphere, v. 14, no. 7, at https://doi.org/10.1002/ecs2.4621.

Hicks, R.N., Wang, F., Hidayati, S.N., and Walck, J.L., 2019, Seed germination of exotic and native winter annuals differentially responds to temperature and moisture, especially with climate change scenarios: Plant Species Biology, v. 34, no. 4, p. 174–183, at https://doi.org/10.1111/1442-1984.12250.

Hiura, T., Go, S., and Iijima, H., 2019, Long-term forest dynamics in response to climate change in northern mixed forests in Japan: A 38-year individual-based approach: Forest Ecology and Management, v. 449, p. 117469, at https://doi.org/10.1016/j.foreco.2019.117469.

Hoell, A., Ford, T.W., Woloszyn, M., Otkin, J.A., and Eischeid, J., 2021, Characteristics and predictability of Midwestern United States drought: Journal of Hydrometeorology, v. 22, no. 11, p. 3087–3105, at https://doi.org/10.1175/JHM-D-21-0052.1.

Holdsworth, A.R., Frelich, L.E., and Reich, P.B., 2007, Effects of earthworm invasion on plant species richness in northern hardwood forests: Conservation Biology: The Journal of the Society for Conservation Biology, v. 21, no. 4, p. 997–1008, at https://doi.org/10.1111/j.1523-1739.2007.00740.x.

Housset, J.M., Girardin, M.P., Baconnet, M., Carcaillet, C., and Bergeron, Y., 2015, Unexpected warming-induced growth decline in Thuja occidentalis at its northern limits in North America: Journal of Biogeography, v. 42, no. 7, p. 1233–1245, at https://doi.org/10.1111/jbi.12508.

Hufkens, K., Friedl, M.A., Keenan, T.F., Sonnentag, O., Bailey, A., O'Keefe, J., and Richardson, A.D., 2012, Ecological impacts of a widespread frost event following early spring leaf-out: Global Change Biology, v. 18, no. 7, p. 2365–2377, at https://doi.org/10.1111/j.1365-2486.2012.02712.x.

Ibáñez, I., Katz, D.S.W., and Lee, B.R., 2017, The contrasting effects of short-term climate change on the early recruitment of tree species: Oecologia, v. 184, no. 3, p. 701–713, at https://doi.org/10.1007/s00442-017-3889-1.

Inouye, D.W., 2022, Climate change and phenology: WIREs Climate Change, v. 13, no. 3, p. e764, at https://doi.org/10.1002/wcc.764.

Jacobsen, P.C., Hansen, G.J.A., Olmanson, L.G., Wehrly, K.E., Hein, C.L., and Johnson, L.B., 2019, Loss of coldwater fish habitat in glaciated lakes of the Midwestern United States after a century of land use and climate change: American Fisheries Society Symposium v. 90, p. 141–157.

Jactel, H., Petit, J., Desprez-Loustau, M.-L., Delzon, S., Piou, D., Battisti, A., and Koricheva, J., 2012, Drought effects on damage by forest insects and pathogens: a meta-analysis: Global Change Biology, v. 18, no. 1, p. 267–276, at https://doi.org/10.1111/j.1365-2486.2011.02512.x.

Janowiak, M.K., Iverson, L.R., Mladenoff, D.J., Peters, E., Wythers, K.R., Xi, W., Brandt, L.A., Butler, P.R., Handler, S.D., Shannon, P.D., Swanston, C., Parker, L.R., Amman, A.J., Bogaczyk, B., and others, 2014, Forest ecosystem vulnerability assessment and synthesis for northern Wisconsin and western Upper Michigan: a report from the Northwoods Climate Change Response Framework project: U.S. Department of Agriculture, Forest Service, Northern Research Station NRS-GTR-136, NRS-GTR-136 pp., accessed April 12, 2021, at https://doi.org/10.2737/NRS-GTR-136.

Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., Mack, M.C., Meentemeyer, R.K., Metz, M.R., Perry, G.L., Schoennagel, T., and Turner, M.G., 2016, Changing disturbance regimes, ecological memory, and forest resilience: Frontiers in Ecology and the Environment, v. 14, no. 7, p. 369–378, at https://doi.org/10.1002/fee.1311.

Keena, M.A., and Moore, P.M., 2010, Effects of temperature on *Anoplophora glabripennis* (Coleoptera: Cerambycidae) larvae and pupae: Environmental Entomology, v. 39, no. 4, p. 1323–1335, at https://doi.org/10.1603/EN09369.

Kerr, G.H., DeGaetano, A.T., Stoof, C.R., and Ward, D., 2018, Climate change effects on wildland fire risk in the Northeastern and Great Lakes states predicted by a downscaled multi-model ensemble: Theoretical and Applied Climatology, v. 131, no. 1, p. 625–639, at https://doi.org/10.1007/s00704-016-1994-4.

Kincaid, J., 2017, The effects of climate on radial growth of disjunct northern white cedar (*Thuja occidentalis* L.) in Virginia: Virginia Journal of Science, v. 68, no. 3, at https://doi.org/10.25778/WGGY-JY81.

Kirk, T.A., and Zielinski, W.J., 2009, Developing and testing a landscape habitat suitability model for the American marten (*Martes americana*) in the Cascades mountains of California: Landscape Ecology, v. 24, no. 6, p. 759–773, at https://doi.org/10.1007/s10980-009-9349-5.

Klapwijk, M.J., Bylund, H., Schroeder, M., and Björkman, C., 2016, Forest management and natural biocontrol of insect pests: Forestry: An International Journal of Forest Research, v. 89, no. 3, p. 253–262, at https://doi.org/10.1093/forestry/cpw019.

Kliejunas, J.T., 2011, A risk assessment of climate change and the impact of forest diseases on forest ecosystems in the Western United States and Canada: General Technical Report PSW-GTR-236. Albany, CA: USDA-Forest Service, Pacific Southwest Research Station. 70 p., v. 236, p. 1–70, at https://doi.org/https://doi.org/10.2737/PSW-GTR-236.

Kliejunas, J.T., Geils, B.W., Glaeser, J.M., Goheen, E.M., Hennon, P., Kim, M.-S., Kope, H., Stone, J., Sturrock, R., and Frankel, S.J., 2009, Review of literature on climate change and forest diseases of western North America: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station PSW-GTR-225, accessed December 20, 2024, at https://doi.org/10.2737/PSW-GTR-225.

Klopfenstein, N.B., Kim, M.-S., Hanna, J.W., Richardson, B.A., Lundquist, J., and Rocky Mountain Research Station, 2009, Approaches to predicting potential impacts of climate change on forest disease: an example with Armillaria root disease: Research paper RMRS ; RP-76, U.S. Dept. of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, at https://doi.org/10.2737/RMRS-RP-76.

Knapp, S.P., Webster, C.R., and Kern, C.C., 2019, The composition and height of saplings capturing silvicultural gaps at two long-term experiments in managed Northern Hardwood Forests: Forests, v. 10, no. 10, p. 855, at https://doi.org/10.3390/f10100855.

Knight, T.M., Dunn, J.L., Smith, L.A., Davis, J., and Kalisz, S., 2009, Deer facilitate invasive plant success in a Pennsylvania forest understory: Natural Areas Journal, v. 29, no. 2, p. 110–116, at https://doi.org/10.3375/043.029.0202.

Knight, K.S., Kurylo, J.S., Endress, A.G., Stewart, J.R., and Reich, P.B., 2007, Ecology and ecosystem impacts of common buckthorn (*Rhamnus cathartica*): a review: Biological Invasions, v. 9, no. 8, p. 925–937, at https://doi.org/10.1007/s10530-007-9091-3.

Körner, C., 2021, The cold range limit of trees: Trends in Ecology & Evolution, v. 36, no. 11, p. 979–989, at https://doi.org/10.1016/j.tree.2021.06.011.

Kost, M.A., Albert, D.A., Cohen, J.G., Slaughter, B.S., Schillo, R.K., Weber, C.R., and Chapman, K.A., 2007, Natural Communities of Michigan: Classification and Description: Michigan Natural Features Inventory Report Number 2007-21, 314 pp.

Kreyling, J., 2019, The Ecological Importance of Winter in Temperate, Boreal, and Arctic Ecosystems in Times of Climate Change, *in* Cánovas, F. M., Lüttge, U., Leuschner, C., and . Risueño, M.-C. eds, Progress in Botany:., v. 81, p. 377–399, at https://doi.org/10.1007/124_2019_35.

Kreyling, J., Schumann, R., and Weigel, R., 2020, Soils from cold and snowy temperate deciduous forests release more nitrogen and phosphorus after soil freeze–thaw cycles than soils from warmer, snow-poor conditions: Biogeosciences, v. 17, no. 15, p. 4103–4117, at https://doi.org/10.5194/bg-17-4103-2020.

Kubiak, K., Żółciak, A., Damszel, M., Lech, P., and Sierota, Z., 2017, Armillaria Pathogenesis under Climate Changes: Forests, v. 8, no. 4, p. 100, at https://doi.org/10.3390/f8040100.

Kurtz, C.M., 2010, Effects of site and climate characteristics on forest invasibility by non-native plants in the Midwest.: accessed October 26, 2023, at, http://conservancy.umn.edu/handle/11299/93629.

Ladwig, L.M., Ratajczak, Z.R., Ocheltree, T.W., Hafich, K.A., Churchill, A.C., Frey, S.J.K., Fuss, C.B., Kazanski, C.E., Muñoz, J.D., Petrie, M.D., Reinmann, A.B., and Smith, J.G., 2016, Beyond arctic and alpine: the influence of winter climate on temperate ecosystems: Ecology, v. 97, no. 2, p. 372–382, at https://doi.org/10.1890/15-0153.1.

Lafleur, B., Paré, D., Munson, A.D., and Bergeron, Y., 2010, Response of northeastern North American forests to climate change: Will soil conditions constrain tree species migration? Environmental Reviews, v. 18, p. 279–289, at https://doi.org/10.1139/A10-013.

Landuyt, D., Lorer, E., Blondeel, H., De Frenne, P., and Verheyen, K., 2025, Sensitivity of understorey phenology to warming depends on forcing time window: Agricultural and Forest Meteorology, v. 372, p. 110733, at https://doi.org/10.1016/j.agrformet.2025.110733.

Lapointe-Garant, M.-P., Huang, J.-G., Gea-Izquierdo, G., Raulier, F., Bernier, P., and Berninger, F., 2010, Use of tree rings to study the effect of climate change on trembling aspen in Québec: Global Change Biology, v. 16, no. 7, p. 2039–2051, at https://doi.org/10.1111/j.1365-2486.2009.02048.x.

Lehmann, P., Ammunét, T., Barton, M., Battisti, A., Eigenbrode, S.D., Jepsen, J.U., Kalinkat, G., Neuvonen, S., Niemelä, P., Terblanche, J.S., Økland, B., and Björkman, C., 2020, Complex responses of global insect pests to climate warming: Frontiers in Ecology and the Environment, v. 18, no. 3, p. 141–150, at https://doi.org/10.1002/fee.2160.

Lesk, C., Coffel, E., D'Amato, A.W., Dodds, K., and Horton, R., 2017, Threats to North American forests from southern pine beetle with warming winters: Nature Climate Change, v. 7, no. 10, p. 713–717, at https://doi.org/10.1038/nclimate3375.

Liess, S., Twine, T. E., Snyder, P. K., Hutchison, W. D., Konar-Steenberg, G., Keeler, B. L., and Brauman, K. A., 2022, High-resolution climate projections over Minnesota for the 21st century: Earth and Space Science, v. 9, no. 3, e2021EA001893, at https://doi.org/10.1029/2021EA001893.

Liess, S., Roop, H.A., Twine, T.E., Clark, S., Coffman, D., Dolma, D., Farris, A., Fernandez, A., Gorman, J., and Meyer, N., 2026, County-scale climate projections over Minnesota and the effects of lakes: Water Resources Research, v. 62, no. 2, p. e2025WR040415, at https://doi.org/10.1029/2025WR040415.

Lucash, M.S., Scheller, R.M., Sturtevant, B.R., Gustafson, E.J., Kretchun, A.M., and Foster, J.R., 2018, More than the sum of its parts: how disturbance interactions shape forest dynamics under climate change: Ecosphere, v. 9, no. 6, p. e02293, at https://doi.org/10.1002/ecs2.2293.

Luo, Y., and Chen, H.Y.H., 2013, Observations from old forests underestimate climate change effects on tree mortality: Nature Communications, v. 4, p. 1655, at https://doi.org/10.1038/ncomms2681.

Luo, Y., and Chen, H.Y.H., 2015, Climate change-associated tree mortality increases without decreasing water availability: Ecology Letters, v. 18, no. 11, p. 1207–1215, at https://doi.org/10.1111/ele.12500.

Makoto, K., Kajimoto, T., Koyama, L., Kudo, G., Shibata, H., Yanai, Y., and Cornelissen, J.H.C., 2014, Winter climate change in plant–soil systems: summary of recent findings and future perspectives: Ecological Research, v. 29, no. 4, p. 593–606, at https://doi.org/10.1007/s11284-013-1115-0.

Manlick, P.J., Windels, S.K., Woodford, J.E., and Pauli, J.N., 2020, Can landscape heterogeneity promote carnivore coexistence in human-dominated landscapes? Landscape Ecology, v. 35, no. 9, p. 2013–2027, at https://doi.org/10.1007/s10980-020-01077-7.

Mao, C., Wang, Y., Ran, J., Wang, C., Yang, Z., and Yang, Y., 2025, Effects of warming and precipitation change on soil nitrogen cycles: a meta-analysis: Journal of Plant Ecology, v. 18, no. 3, p. rtaf051, at https://doi.org/10.1093/jpe/rtaf051.

Martz, F., Vuosku, J., Ovaskainen, A., Stark, S., and Rautio, P., 2016, The snow must go on: Ground ice encasement, snow compaction and absence of snow differently cause soil hypoxia, CO_2 accumulation and tree seedling damage in boreal forest: PLOS ONE, v. 11, no. 6, p. e0156620, at https://doi.org/10.1371/journal.pone.0156620.

Marvel, K., Su, W., Delgado, R., Aarons, S., Chatterjee, A., Garcia, M.E., Hausfather, Z., Hayhoe, K., Hence, D.A., Jewett, E.B., Robel, A., Singh, D., Tripati, A., and Vose, R.S., 2023, Climate trends, *in* (Crimmins, A. R., Avery, C. W., Easterling, D. R., Kunkel, K. E., Stewart, B. C., and Maycock, T. K., eds., Fifth National Climate Assessment: at https://doi.org/10.7930/NCA5.2023.CH2.

Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., and Gomis, M.I., 2021, Climate change 2021: the physical science basis:

Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change, v. 2, no. 1, p. 2391, at https://doi.org/https://doi.org/10.1017/9781009157896.

Matthews, S.N., Iverson, L.R., Peters, M.P., and Prasad, A., 2018, Assessing potential climate change pressures across the conterminous United States: mapping plant hardiness zones, heat zones, growing degree days, and cumulative drought severity throughout this century: U.S. Department of Agriculture, Forest Service, Northern Research Station NRS-RMAP-9, NRS-RMAP-9 pp., accessed February 13, 2026, at https://doi.org/10.2737/NRS-RMAP-9.

Mccarthy, J., 2001, Gap dynamics of forest trees: A review with particular attention to boreal forests: Environmental Reviews, v. 9, p. 1–59, at https://doi.org/10.1139/er-9-1-1.

McEwan, R.W., Birchfield, M.K., Schoergendorfer, A., and Arthur, M.A., 2009, Leaf phenology and freeze tolerance of the invasive shrub Amur honeysuckle and potential native competitors: The Journal of the Torrey Botanical Society, v. 136, no. 2, p. 212–220, at https://doi.org/10.3159/08-RA-109.1.

MDNR, 2016, Michigan Deer Management Plan: Michigan Department of Natural Resources, accessed December 16, 2024, at https://www.michigan.gov/dnr/managing-resources/wildlife/deer.

Melillo, J.M., Butler, S., Johnson, J., Mohan, J., Steudler, P., Lux, H., Burrows, E., Bowles, F., Smith, R., Scott, L., Vario, C., Hill, T., Burton, A., Zhou, Y.-M., and others, 2011, Soil warming, carbon–nitrogen interactions, and forest carbon budgets: Proceedings of the National Academy of Sciences, v. 108, no. 23, p. 9508–9512, at https://doi.org/10.1073/pnas.1018189108.

Melillo, J.M., Steudler, P.A., Aber, J.D., Newkirk, K., Lux, H., Bowles, F.P., Catricala, C., Magill, A., Ahrens, T., and Morrisseau, S., 2002, soil warming and carbon-cycle feedbacks to the climate system: Science, v. 298, no. 5601, p. 2173–2176, at https://doi.org/10.1126/science.1074153.

Meng, P.S., Hoover, K., and Keena, M.A., 2015, Asian longhorned beetle (Coleoptera: Cerambycidae), an introduced pest of maple and other hardwood trees in North America and Europe: Journal of Integrated Pest Management, v. 6, no. 1, p. 4, at https://doi.org/10.1093/jipm/pmv003.

Merow, C., Bois, S.T., Allen, J.M., Xie, Y., and Silander, J.A., 2017, Climate change both facilitates and inhibits invasive plant ranges in New England: Proceedings of the National Academy of Sciences, v. 114, no. 16, p. E3276–E3284, at https://doi.org/10.1073/pnas.1609633114.

Michaelian, M., Hogg, E.H., Hall, R.J., and Arsenault, E., 2011, Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest: Global Change Biology, v. 17, no. 6, p. 2084–2094, at https://doi.org/10.1111/j.1365-2486.2010.02357.x.

Miller, K.M., Perles, S.J., Schmit, J.P., Matthews, E.R., Weed, A.S., Comiskey, J.A., Marshall, M.R., Nelson, P., and Fisichelli, N.A., 2023, Overabundant deer and invasive plants drive widespread regeneration debt in eastern United States national parks: Ecological Applications, v. 33, no. 4, p. e2837, at https://doi.org/10.1002/eap.2837.

Minnesota Department of Natural Resources, 2003a, Field Guide to the Native Plant Communities of Minnesota: The Laurentian Mixed Forest Province: Minnesota Department of Natural Resources, St. Paul, MN.

Minnesota Department of Natural Resources, 2003b, Minnesota's Native Plant Community Classification: A Statewide Classification of Terrestrial and Wetland Vegetation Based on Numerical Analysis of Plot Data: Minnesota Department of Natural Resources Technical Report, at https://www.dnr.state.mn.us/npc/classification.html.

Minnesota Natural Heritage Program (MNNHP), 1993, Minnesota's Native Vegetation: A Key to Natural Communities: Minnesota Department of Natural Resources, Natural Heritage Program, 110 pp.

Minnesota Pollution Control Agency, 2016, Pine River Watershed Monitoring and Assessment Report: Minnesota Pollution Control Agency wq-ws3-07010105.

Mironidis, G.K., and Savopoulou-Soultani, M., 2010, Effects of heat shock on survival and reproduction of *Helicoverpa armigera* (Lepidoptera: Noctuidae) adults: Journal of Thermal Biology, v. 35, no. 2, p. 59–69, at https://doi.org/10.1016/j.jtherbio.2009.11.001.

Montgomery, R.A., Rice, K.E., Stefanski, A., Rich, R.L., and Reich, P.B., 2020, Phenological responses of temperate and boreal trees to warming depend on ambient spring temperatures, leaf habit, and geographic range: Proceedings of the National Academy of Sciences, v. 117, no. 19, p. 10397–10405, at https://doi.org/10.1073/pnas.1917508117.

Mori, A.S., Fujii, S., and Kurokawa, H., 2014, Ecological consequences through responses of plant and soil communities to changing winter climate: Ecological Research, v. 29, no. 4, p. 547–559, at https://doi.org/10.1007/s11284-013-1091-4.

Morin, X., Augspurger, C., and Chuine, I., 2007, Process-based modeling of species' distributions: what limits temperate tree species' range boundaries? Ecology, v. 88, no. 9, p. 2280–2291, at https://doi.org/10.1890/06-1591.1.

Morin, X., and Chuine, I., 2014, Will tree species experience increased frost damage due to climate change because of changes in leaf phenology? Canadian Journal of Forest Research, v. 44, no. 12, p. 1555–1565, at https://doi.org/10.1139/cjfr-2014-0282.

Morin, X., Lechowicz, M.J., Augspurger, C., O'Keefe, J., Viner, D., and Chuine, I., 2009, Leaf phenology in 22 North American tree species during the 21st century: Global Change Biology, v. 15, no. 4, p. 961–975, at https://doi.org/10.1111/j.1365-2486.2008.01735.x.

Moser, W.K., Hansen, M.H., Nelson, M.D., and McWilliams, W.H., 2009, Relationship of invasive groundcover plant presence to evidence of disturbance in the forests of the upper Midwest of the United States. Chapter 3.: *in* Kohli, R. K., Jose, S., Singh, H. P., Batish, D. R., eds., Invasive plants and forest ecosystems. Boca Raton, FL: CRC Press: 29-58., accessed March 17, 2026, at, https://research.fs.usda.gov/treesearch/19531.

Münchinger, I.K., Hajek, P., Akdogan, B., Caicoya, A.T., and Kunert, N., 2023, Leaf thermal tolerance and sensitivity of temperate tree species are correlated with leaf physiological and functional drought resistance traits: Journal of Forestry Research, v. 34, no. 1, p. 63–76, at https://doi.org/10.1007/s11676-022-01594-y.

Neuvonen, S., Niemelä, P., and Virtanen, T., 1999, Climatic change and insect outbreaks in boreal forests: the role of winter temperatures: Ecological Bulletins, no. 47, p. 63–67, at https://www.jstor.org/stable/20113228.

Ning, L., and Bradley, R.S., 2015, Snow occurrence changes over the central and eastern United States under future warming scenarios: Scientific Reports, v. 5, no. 1, p. 17073, at https://doi.org/10.1038/srep17073.

Nnadi, N.E., and Carter, D.A., 2021, Climate change and the emergence of fungal pathogens: PLOS Pathogens, v. 17, no. 4, p. e1009503, at https://doi.org/10.1371/journal.ppat.1009503.

Notaro, M., Lorenz, D., Hoving, C., and Schummer, M., 2014, Twenty-first-century projections of snowfall and winter severity across central-eastern North America: Journal of Climate, v. 27, no. 17, p. 6526–6550, at https://doi.org/10/gfvddw.

Orbán, I., Szitár, K., Kalapos, T., and Körel-Dulay, G., 2021, The role of disturbance in invasive plant establishment in a changing climate: insights from a drought experiment: Biological Invasions, v. 23, no. 6, p. 1877–1890, at https://doi.org/10.1007/s10530-021-02478-8.

Orrock, J.L., Lindley, E., and Zirbel, C.R., 2025, Freeze–thaw events differently affect survival of seeds of two native and two invasive woody species: Canadian Journal of Forest Research, v. 55, p. 1–6, at https://doi.org/10.1139/cjfr-2024-0276.

Park, A., Puettmann, K., Wilson, E., Messier, C., Kames, S., and Dhar, A., 2014, Can boreal and temperate forest management be adapted to the uncertainties of 21st century climate

change? Critical Reviews in Plant Sciences, v. 33, no. 4, p. 251–285, at https://doi.org/10.1080/07352689.2014.858956.

Pastore, M.A., Nelson, S.J., Burakowski, E.A., Contosta, A.R., D'Amato, A.W., Garlick, S., Lindsey, E., Lutz, D.A., Morelli, T.L., Sirén, A.P.K., Smith, G.A., and Weiskittel, A., 2025, Snow refugia: Managing temperate forest canopies to maintain winter conditions: Ecosphere, v. 16, no. 7, p. e70302, at https://doi.org/10.1002/ecs2.70302.

Patton, S.R., Russell, M.B., Windmuller-Campione, M.A., and Frelich, L.E., 2021, White-tailed deer herbivory impacts on tree seedling and sapling abundance in the Lake States Region of the USA: Annals of Forest Science, v. 78, no. 4, at https://doi.org/10.1007/s13595-021-01108-6.

Pauli, J.N., Zuckerberg, B., Whiteman, J.P., and Porter, W., 2013, The subnivium: a deteriorating seasonal refugium: Frontiers in Ecology and the Environment, v. 11, no. 5, p. 260–267, at https://doi.org/10.1890/120222.

Pautasso, M., Döring, T.F., Garbelotto, M., Pellis, L., and Jeger, M.J., 2012, Impacts of climate change on plant diseases—opinions and trends: European Journal of Plant Pathology, v. 133, no. 1, p. 295–313, at https://doi.org/10.1007/s10658-012-9936-1.

Perillo, H., 2017, Investigating tree growth responses to drought, temperature, and precipitation among *Betula papyrifera, Betula alleghaniensis*, *Pinus resinosa*, and *Tsuga canadensis*: accessed March 2, 2025, at https://underc.nd.edu/assets/254068/fullsize/perillo2017.pdf.

Peters, M.P., Prasad, A.M., Matthews, S.N., and Iverson, L.R., 2020, Climate change tree atlas, Version 4: at https://www.nrs.fs.fed.us/atlas.

Polasky, A.D., Evans, J.L., Fuentes, J.D., and Hamilton, H.L., 2021, Statistical climate model downscaling for impact projections in the Midwest United States: International Journal of Climatology, v. 42, no. 5, p. 3038–3055, at https://doi.org/10.1002/joc.7406.

Polgar, C.A., and Primack, R.B., 2011, Leaf-out phenology of temperate woody plants: from trees to ecosystems: New Phytologist, v. 191, no. 4, p. 926–941, at https://doi.org/10.1111/j.1469-8137.2011.03803.x.

Portalier, S.M.J., Candau, J.-N., and Lutscher, F., 2022, A temperature-driven model of phenological mismatch provides insights into the potential impacts of climate change on consumer–resource interactions: Ecography, v. 2022, no. 8, p. e06259, at https://doi.org/10.1111/ecog.06259.

Potter, K.M., Iannone, B.V., Riitters, K.H., Guo, Q., Pandit, K., and Oswalt, C.M., 2026, United States forests are increasingly invaded by problematic non-native plants: Forest Ecology and Management, v. 599, p. 123281, at https://doi.org/10.1016/j.foreco.2025.123281.

Prasad, A., Pedlar, J., Peters, M., McKenney, D., Iverson, L., Matthews, S., and Adams, B., 2020, Combining US and Canadian forest inventories to assess habitat suitability and migration potential of 25 tree species under climate change: Diversity and Distributions, v. 26, no. 9, p. 1142–1159, at https://doi.org/10.1111/ddi.13078.

Preisler, H.K., Hicke, J.A., Ager, A.A., and Hayes, J.L., 2012, Climate and weather influences on spatial temporal patterns of mountain pine beetle populations in Washington and Oregon: Ecology, v. 93, no. 11, p. 2421–2434, at https://doi.org/10.1890/11-1412.1.

Pureswaran, D.S., Roques, A., and Battisti, A., 2018, Forest insects and climate change: Current Forestry Reports, v. 4, no. 2, p. 35–50, at https://doi.org/10.1007/s40725-018-0075-6.

Qoronfleh, H., 2023, Modeling the effects of climate change on forest succession in Northern Michigan: accessed September 27, 2024, at https://doi.org/10.7302/21881.

Quante, L., Willner, S.N., Middelanis, R., and Levermann, A., 2021, Regions of intensification of extreme snowfall under future warming: Scientific Reports, v. 11, no. 1, p. 16621, at https://doi.org/10.1038/s41598-021-95979-4.

Ramirez-Parada, T.H., Park, I.W., and Mazer, S.J., 2022, Herbarium specimens provide reliable estimates of phenological responses to climate at unparalleled taxonomic and spatiotemporal scales: Ecography, v. 2022, no. 10, p. e06173, at https://doi.org/10.1111/ecog.06173.

Raney, P.A., Leopold, D.J., Dovciak, M., and Beier, C.M., 2016, Hydrologic position mediates sensitivity of tree growth to climate: Groundwater subsidies provide a thermal buffer effect in wetlands: Forest Ecology and Management, v. 379, p. 70–80, at https://doi.org/10.1016/j.foreco.2016.08.004.

Rastogi, D., Trok, J., Depsky, N., Monier, E., and Jones, A., 2023, Historical evaluation and future projections of compound heatwave and drought extremes over the conterminous United States in CMIP6: Environmental Research Letters, v. 19, no. 1, p. 014039, at https://doi.org/10.1088/1748-9326/ad0efe.

Régnière, J., St-Amant, R., and Duval, P., 2012, Predicting insect distributions under climate change from physiological responses: spruce budworm as an example: Biological Invasions, v. 14, no. 8, p. 1571–1586, at https://doi.org/10.1007/s10530-010-9918-1.

Reich, P.B., Bermudez, R., Montgomery, R.A., Rich, R.L., Rice, K.E., Hobbie, S.E., and Stefanski, A., 2022, Even modest climate change may lead to major transitions in boreal forests: Nature, v. 608, no. 7923, p. 540–545, at https://doi.org/10.1038/s41586-022-05076-3.

Reich, P.B., Sendall, K.M., Rice, K., Rich, R.L., Stefanski, A., Hobbie, S.E., and Montgomery, R.A., 2015, Geographic range predicts photosynthetic and growth response to warming in co-occurring tree species: Nature Climate Change, v. 5, no. 2, p. 148–152, at https://doi.org/10.1038/nclimate2497.

Reinhardt, J.R., Russell, M.B., Senay, S., and Lazarus, W., 2020, Assessing the current and potential future distribution of four invasive forest plants in Minnesota, U.S.A., using mixed sources of data: Scientific Reports, v. 10, no. 1, p. 12738, at https://doi.org/10.1038/s41598-020-69539-1.

Reinmann, A.B., Susser, J.R., Demaria, E.M.C., and Templer, P.H., 2019, Declines in northern forest tree growth following snowpack decline and soil freezing: Global Change Biology, v. 25, no. 2, p. 420–430, at https://doi.org/10.1111/gcb.14420.

Ren, P., Néron, V., Rossi, S., Liang, E., Bouchard, M., and Deslauriers, A., 2020, Warming counteracts defoliation-induced mismatch by increasing herbivore-plant phenological synchrony: Global Change Biology, v. 26, no. 4, p. 2072–2080, at https://doi.org/10.1111/gcb.14991.

Rice, K.E., 2016, Phenological responses of herbaceous plants, shrubs, and tree seedlings to experimental climate change conditions in northern Minnesota: accessed October 16, 2023, at https://www.proquest.com/docview/1830753688/abstract/1F6B6996C3AE424EPQ/1.

Rice, K.E., Montgomery, R.A., Stefanski, A., Rich, R.L., and Reich, P.B., 2018, Experimental warming advances phenology of groundlayer plants at the boreal-temperate forest ecotone: American Journal of Botany, v. 105, no. 5, p. 851–861, at https://doi.org/10.1002/ajb2.1091.

Rice, K.E., Montgomery, R.A., Stefanski, A., Rich, R.L., and Reich, P.B., 2021, Species-specific flowering phenology responses to experimental warming and drought alter herbaceous plant species overlap in a temperate–boreal forest community: Annals of Botany, v. 127, no. 2, p. 203–211, at https://doi.org/10.1093/aob/mcaa156.

Rittenhouse, C.D., and Rissman, A.R., 2015, Changes in winter conditions impact forest management in north temperate forests: Journal of Environmental Management, v. 149, p. 157–167, at https://doi.org/10.1016/j.jenvman.2014.10.010.

RMB Environmental Laboratories, Inc., 2013, Pelican Lake (18-0308-00 CROW WING COUNTY): Lake Water Assessment:, accessed October 1, 2024, at https://www.crowwing.gov/DocumentCenter/View/4746/Pelican-Lake-Assessment?bidId=.

Rodenberg, C.A., Hajek, A.E., Nadel, H., Stefanski, A., Reich, P.B., and Haynes, K.J., 2024, Rising temperatures may increase fungal epizootics in northern populations of the invasive spongy moth in North America: NeoBiota, v. 95, p. 291–308, at https://doi.org/10.3897/neobiota.95.126311.

Rustad, L., Campbell, J., Marion, G., Norby, R., Mitchell, M., Hartley, A., Cornelissen, J., Gurevitch, J., and GCTE-NEWS, 2001, A meta-analysis of the response of soil respiration,

net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming: Oecologia, v. 126, no. 4, p. 543–562, at https://doi.org/10.1007/s004420000544.

Sanders-DeMott, R., Campbell, J.L., Groffman, P.M., Rustad, L.E., and Templer, P.H., 2019, Chapter 10 - Soil warming and winter snowpacks: Implications for northern forest ecosystem functioning, *in* Mohan, J.E. ed., Ecosystem Consequences of Soil Warming: Academic Press, p. 245–278.

Sanders-DeMott, R., McNellis, R., Jabouri, M., and Templer, P.H., 2018, Snow depth, soil temperature and plant–herbivore interactions mediate plant response to climate change: Journal of Ecology, v. 106, no. 4, p. 1508–1519, at https://doi.org/10.1111/1365-2745.12912.

Schebeck, M., Lehmann, P., Laparie, M., Bentz, B.J., Ragland, G.J., Battisti, A., and Hahn, D.A., 2024, Seasonality of forest insects: why diapause matters: Trends in Ecology & Evolution, v. 39, no. 8, p. 757–770, at https://doi.org/10.1016/j.tree.2024.04.010.

Schowalter, T., 2017, Biology and management of the forest tent caterpillar (Lepidoptera: Lasiocampidae): Journal of Integrated Pest Management, v. 8, no. 1, p. 24, at https://doi.org/10.1093/jipm/pmx02.

Schwartzberg, E.G., Jamieson, M.A., Raffa, K.F., Reich, P.B., Montgomery, R.A., and Lindroth, R.L., 2014, Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees: Oecologia, v. 175, no. 3, p. 1041–1049, at https://doi.org/10.1007/s00442-014-2960-4.

Sendall, K.M., Reich, P.B., Zhao, C., Jihua, H., Wei, X., Stefanski, A., Rice, K., Rich, R.L., and Montgomery, R.A., 2015, Acclimation of photosynthetic temperature optima of temperate and boreal tree species in response to experimental forest warming: Global Change Biology, v. 21, no. 3, p. 1342–1357, at https://doi.org/10.1111/gcb.12781.

Sharma, S., Andrus, R., Bergeron, Y., Bogdziewicz, M., Bragg, D.C., Brockway, D., Cleavitt, N.L., Courbaud, B., Das, A.J., Dietze, M., Fahey, T.J., Franklin, J.F., Gilbert, G.S., Greenberg, C.H., and others, 2022, North American tree migration paced by climate in the West, lagging in the East: Proceedings of the National Academy of Sciences, v. 119, no. 3, p. e2116691118, at https://doi.org/10.1073/pnas.2116691118.

Sharma, S., Richardson, D.C., Woolway, R.I., Imrit, M.A., Bouffard, D., Blagrave, K., Daly, J., Filazzola, A., Granin, N., Korhonen, J., Magnuson, J., Marszelewski, W., Matsuzaki, S.S., Perry, W., and others, 2021, Loss of ice cover, shifting phenology, and more extreme events in northern hemisphere lakes: Journal of Geophysical Research: Biogeosciences, v. 126, no. 10, p. e2021JG006348, at https://doi.org/10.1029/2021JG006348.

Shifley, S.R., Moser, W.K., Nowak, D.J., Miles, P.D., Butler, B.J., Aguilar, F.X., DeSantis, R.D., and Greenfield, E.J., 2014, Five anthropogenic factors that will radically alter forest conditions and management needs in the Northern United States: Forest Science, v. 60, no. 5, p. 914–925, at https://doi.org/10.5849/forsci.13-153.

Simler-Williamson, A.B., Rizzo, D.M., and Cobb, R.C., 2019, interacting effects of global change on forest pest and pathogen dynamics: Annual Review of Ecology, Evolution, and Systematics, v. 50, no. 1, p. 381–403, at https://doi.org/10.1146/annurev-ecolsys-110218-024934.

Simon, S., and Perleberg, D., 2010, Aquatic vegetation of Pelican Lake (DOW 18-0308-00), Crow Wing County, Minnesota, 2010: Minnesota Department of Natural Resources, Ecological and Water Resources Division, 25 pp.

Sims, R.A., 1997, Field guide to the forest ecosystem classification for northwestern Ontario: Thunder Bay: Ontario Ministry of Natural Resources, Northwest Science ….

Singh, J., Schädler, M., Demetrio, W., Brown, G.G., and Eisenhauer, N., 2019, Climate change effects on earthworms - a review: Soil organisms, v. 91, no. 3, p. 114–138, at https://doi.org/10.25674/so91iss3pp114.

Singh, J., Sippel, S., and Fischer, E.M., 2023, Circulation dampened heat extremes intensification over the Midwest USA and amplified over Western Europe: Communications Earth & Environment, v. 4, no. 1, p. 432, at https://doi.org/10.1038/s43247-023-01096-7.

Sinha, T., and Cherkauer, K.A., 2010, Impacts of future climate change on soil frost in the midwestern United States: Journal of Geophysical Research: Atmospheres, v. 115, no. D8, accessed April 13, 2021, at https://doi.org/10.1029/2009jd012188.

Skalski, J.R., Millspaugh, J.J., Clawson, M.V., Belant, J.L., Etter, D.R., Frawley, B.J., and Friedrich, P.D., 2011, Abundance trends of American martens in Michigan based on statistical population reconstruction: The Journal of Wildlife Management, v. 75, no. 8, p. 1767–1773, at https://doi.org/10.1002/jwmg.227.

Smith, L. m., 2013, Extended leaf phenology in deciduous forest invaders: mechanisms of impact on native communities: Journal of Vegetation Science, v. 24, no. 6, p. 979–987, at https://doi.org/10.1111/jvs.12087.

Smith, M.M., and Pauli, J.N., 2024, Small but connected islands can maintain populations and genetic diversity under climate change: Ecography, v. 2024, no. 7, p. e07119, at https://doi.org/10.1111/ecog.07119.

Solarik, K.A., Cazelles, K., Messier, C., Bergeron, Y., and Gravel, D., 2020, Priority effects will impede range shifts of temperate tree species into the boreal forest: Journal of Ecology, v. 108, no. 3, p. 1155–1173, at https://doi.org/10.1111/1365-2745.13311.

Song, Y., Zhu, K., Chen, Y., Stefanski, A., Bermudez, R., Montgomery, R.A., and Reich, P.B., 2025, Warming makes 20 boreal species grow earlier but not always taller: p. 2025.11.30.691420, accessed January 29, 2026, at https://doi.org/10.64898/2025.11.30.691420.

Sorensen, P.O., Finzi, A.C., Giasson, M.-A., Reinmann, A.B., Sanders-DeMott, R., and Templer, P.H., 2018, Winter soil freeze-thaw cycles lead to reductions in soil microbial biomass and activity not compensated for by soil warming: Soil Biology and Biochemistry, v. 116, p. 39–47, at https://doi.org/10.1016/j.soilbio.2017.09.026.

Sorensen, P.O., Templer, P.H., Christenson, L., Duran, J., Fahey, T., Fisk, M.C., Groffman, P.M., Morse, J.L., and Finzi, A.C., 2016, Reduced snow cover alters root-microbe interactions and decreases nitrification rates in a northern hardwood forest: Ecology, v. 97, no. 12, p. 3359–3368, at https://doi.org/10.1002/ecy.1599.

Soubeyrand, M., Gennaretti, F., Blarquez, O., Bergeron, Y., Taylor, A.R., D'Orangeville, L., and Marchand, P., 2023, Competitive interactions under current climate allow temperate tree species to grow and survive in boreal mixedwood forest: Ecography, v. 2023, no. 5, p. e06525, at https://doi.org/https://doi.org/10.1111/ecog.06525.

Stangler, D.F., Hamann, A., Kahle, H.-P., and Spiecker, H., 2016, A heat wave during leaf expansion severely reduces productivity and modifies seasonal growth patterns in a northern hardwood forest: Tree Physiology, v. 37, no. 1, p. 47–59, at https://doi.org/10.1093/treephys/tpw094.

Stanturf, J.A., Conner, W., Coyle, D.R., and Goodrick, S., 2024, Chapter 7 - Forest disturbances, *in* McNulty, S.G. ed., Future Forests: Elsevier, p. 125–150.

Stern, R.L., Schaberg, P.G., Rayback, S.A., Hansen, C.F., Murakami, P.F., and Hawley, G.J., 2023, Growth trends and environmental drivers of major tree species of the northern hardwood forest of eastern North America: Journal of Forestry Research, v. 34, no. 1, p. 37–50, at https://doi.org/10.1007/s11676-022-01553-7.

Stralberg, D., Arseneault, D., Baltzer, J.L., Barber, Q.E., Bayne, E.M., Boulanger, Y., Brown, C.D., Cooke, H.A., Devito, K., Edwards, J., Estevo, C.A., Flynn, N., Frelich, L.E., Hogg, E.H., and others, 2020, Climate-change refugia in boreal North America: what, where, and for how long? Frontiers in Ecology and the Environment, v. 18, no. 5, p. 261–270, at https://doi.org/10.1002/fee.2188.

Sturrock, R.N., Frankel, S.J., Brown, A.V., Hennon, P.E., Kliejunas, J.T., Lewis, K.J., Worrall, J.J., and Woods, A.J., 2011, Climate change and forest diseases: Plant Pathology, v. 60, no. 1, p. 133–149, at https://doi.org/10.1111/j.1365-3059.2010.02406.x.

Swanston, C., Brandt, L.A., Janowiak, M.K., Handler, S.D., Butler-Leopold, P., Iverson, L., Thompson III, F.R., Ontl, T.A., and Shannon, P.D., 2018, Vulnerability of forests of the

Midwest and Northeast United States to climate change: Climatic Change, v. 146, no. 1–2, p. 103–116, at https://doi.org/10.1007/s10584-017-2065-2.

Swanston, C., Janowiak, M., Iverson, L., Parker, L., Mladenoff, D., Brandt, L., Butler, P., St. Pierre, M., Prasad, A., Matthews, S., Peters, M., Higgins, D., and Dorland, Avery., 2011, Ecosystem vulnerability assessment and synthesis: a report from the Climate Change Response Framework Project in northern Wisconsin: U.S. Department of Agriculture, Forest Service, Northern Research Station NRS-GTR-82, NRS-GTR-82 pp., accessed October 26, 2023, at https://doi.org/10.2737/NRS-GTR-82.

Sykes, M.T., and Prentice, I.C., 1995, Boreal forest futures: Modelling the controls on tree species range limits and transient responses to climate change: Water, Air, and Soil Pollution, v. 82, no. 1, p. 415–428, at https://doi.org/10.1007/BF01182851.

Taylor, S.L., and Buskirk, S.W., 1994, Forest microenvironments and resting energetics of the American marten *Martes americana*: Ecography, v. 17, no. 3, p. 249–256, at https://doi.org/10.1111/j.1600-0587.1994.tb00100.x.

Taylor, A.R., Endicott, S., and Hennigar, C., 2020, Disentangling mechanisms of early succession following harvest: Implications for climate change adaptation in Canada's boreal-temperate forests: Forest Ecology and Management, v. 461, p. 117926, at https://doi.org/10.1016/j.foreco.2020.117926.

Teshome, D.T., Zharare, G.E., and Naidoo, S., 2020, The threat of the combined effect of biotic and abiotic stress factors in forestry under a changing climate: Frontiers in Plant Science, v. 11, p. 601009, at https://doi.org/10.3389/fpls.2020.601009.

Teskey, R., Wertin, T., Bauweraerts, I., Ameye, M., Mcguire, M.A., and Steppe, K., 2015, Responses of tree species to heat waves and extreme heat events: Plant, Cell & Environment, v. 38, no. 9, p. 1699–1712, at https://doi.org/10.1111/pce.12417.

Thom, D., 2023, Natural disturbances as drivers of tipping points in forest ecosystems under climate change – implications for adaptive management: Forestry, v. 96, no. 3, p. 305–315, at https://doi.org/10.1093/forestry/cpad011.

Thouvenot, L., Ferlian, O., Craven, D., Johnson, E.A., Köhler, J., Lochner, A., Quosh, J., Zeuner, A., and Eisenhauer, N., 2024, Invasive earthworms can change understory plant community traits and reduce plant functional diversity: iScience, v. 27, no. 3, p. 109036, at https://doi.org/10.1016/j.isci.2024.109036.

Tierney, G.L., Fahey, T.J., Groffman, P.M., Hardy, J.P., Fitzhugh, R.D., and Driscoll, C.T., 2001, Soil freezing alters fine root dynamics in a northern hardwood forest: Biogeochemistry, v. 56, no. 2, p. 175–190, at https://doi.org/10.1023/A:1013072519889.

Tingley, R.W., Paukert, C., Sass, G.G., Jacobson, P.C., Hansen, G.J.A., Lynch, A.J., and Shannon, P.D., 2019, Adapting to climate change: guidance for the management of inland glacial

lake fisheries: Lake and Reservoir Management, v. 35, no. 4, p. 435–452, at https://doi.org/10.1080/10402381.2019.1678535.

Tobin, P.C., Gray, D.R., and Liebhold, A.M., 2014, Supraoptimal temperatures influence the range dynamics of a non-native insect: Diversity and Distributions, v. 20, no. 7, p. 813–823, at https://doi.org/10.1111/ddi.12197.

Toot, R., Frelich, L.E., Butler, E.E., and Reich, P.B., 2020, Climate-biome envelope shifts create enormous challenges and novel opportunities for conservation: Forests, v. 11, no. 9, p. 1015, at https://doi.org/10.3390/f11091015.

USDA, NRCS, 2025, The PLANTS Database: National Plant Data Team, accessed March 6, 2025 at http://plants.usda.gov.

USNVC, 2025, USNVC Database Version 3.0, Science Analytics and Synthesis (SAS) Program, U.S. Geological Survey. (Federal Geographic Data Committee, Vegetation Subcommittee). Washington D.C:, accessed March 26, 2025 at https://usnvc.org.

Vaughn, W.R., Taylor, A.R., MacLean, D.A., D'Orangeville, L., and Lavigne, M.B., 2021a, Climate change experiment suggests divergent responses of tree seedlings in eastern North America's Acadian Forest Region over the 21st century: Canadian Journal of Forest Research, v. 51, no. 12, p. 1888–1902, at https://doi.org/10.1139/cjfr-2021-0047.

Vaughn, W.R., Taylor, A.R., MacLean, D.A., D'Orangeville, L., and Lavigne, M.B., 2021b, Climate change experiment suggests divergent responses of tree seedlings in eastern North America's Acadian Forest Region over the 21st century: Canadian Journal of Forest Research, v. 51, no. 12, p. 1888–1902, at https://doi.org/10.1139/cjfr-2021-0047.

Venäläinen, A., Lehtonen, I., Laapas, M., Ruosteenoja, K., Tikkanen, O., Viiri, H., Ikonen, V., and Peltola, H., 2020, Climate change induces multiple risks to boreal forests and forestry in Finland: A literature review: Global Change Biology, v. 26, no. 8, p. 4178–4196, at https://doi.org/10.1111/gcb.15183.

Viau, J.-P., Sigouin, D., and St-Laurent, M.-H., 2024, Seasonal shifts in the habitat selection patterns of male American Marten (*Martes americana*) at a fine spatial scale: Journal of Mammalogy, v. 105, no. 4, p. 740–751, at https://doi.org/10.1093/jmammal/gyae048.

Vickers, L.A., Knapp, B.O., Kabrick, J.M., Kenefic, L.S., D'Amato, A.W., Kern, C.C., MacLean, D.A., Raymond, P., Clark, K.L., Dey, D.C., and Rogers, N.S., 2021, Contemporary status, distribution, and trends of mixedwoods in the northern United States: Canadian Journal of Forest Research, v. 51, no. 7, p. 881–896, at https://doi.org/10.1139/cjfr-2020-0467.

Vose, R.S., Easterling, D.R., Kunkel, K.E., LeGrande, A.N., and Wehner, M.F., 2017, Ch. 6: Temperature Changes in the United States. Climate Science Special Report: Fourth National Climate Assessment, Volume I, *in* Wuebbles, D.J., Fahey, D.W., Hibbard, K.A., Dokken, D.J., Stewart, B.C., and Maycock, T.K. eds., Climate science special report:

Fourth national climate assessment, volume I: U.S. Global Change Research Program, Washington, D.C., p. 185–206.

Vose, J., Peterson, D., and Patel-Weynand, T., 2013, Effects of Climatic Variability and Change on Forest Ecosystems: A Comprehensive Science Synthesis for the U.S. Forest Sector: U.S. Department of Agriculture, Pacific Northwest Research Station General Technical Report, accessed September 5, 2023, at https://www.fs.usda.gov/pnw/pubs/pnw_gtr870/pnw_gtr870.pdf.

van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G.C., Kram, T., Krey, V., Lamarque, J.-F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S.J., and others, 2011, The representative concentration pathways: an overview: Climatic Change, v. 109, no. 1, p. 5, at https://doi.org/10.1007/s10584-011-0148-z.

Wang, J., D'Orangeville, L., and Taylor, A.R., 2023, Tree species growth response to climate warming varies by forest canopy position in boreal and temperate forests: Global Change Biology, v. 29, no. 18, p. 5397–5414, at https://doi.org/10.1111/gcb.16853.

Wang, W.J., Thompson III, F.R., He, H.S., Fraser, J.S., Dijak, W.D., and Jones-Farrand, T., 2019, Climate change and tree harvest interact to affect future tree species distribution changes: Journal of Ecology, v. 107, no. 4, p. 1901–1917, at https://doi.org/10.1111/1365-2745.13144.

Way, D.A., and Oren, R., 2010, Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data: Tree Physiology, v. 30, no. 6, p. 669–688, at https://doi.org/10.1093/treephys/tpq015.

Weed, A.S., Ayres, M.P., and Hicke, J.A., 2013, Consequences of climate change for biotic disturbances in North American forests: Ecological Monographs, v. 83, no. 4, p. 441–470, at https://doi.org/10.1890/13-0160.1.

Weigel, R., Henry, H.A.L., Beil, I., Gebauer, G., Jurasinski, G., Klisz, M., van der Maaten, E., Muffler, L., and Kreyling, J., 2021, Ecosystem processes show uniform sensitivity to winter soil temperature change across a gradient from central to cold marginal stands of a major temperate forest tree: Ecosystems, v. 24, no. 6, p. 1545–1560, at https://doi.org/10.1007/s10021-021-00600-4.

Weiskopf, S.R., Ledee, O.E., and Thompson, L.M., 2019, Climate change effects on deer and moose in the Midwest: The Journal of Wildlife Management, v. 83, no. 4, p. 769–781, at https://doi.org/10/gjpr28.

Wheeler, J.A., Gonzalez, N.M., and Stinson, K.A., 2017, Red hot maples: *Acer rubrum* first-year phenology and growth responses to soil warming: Canadian Journal of Forest Research, v. 47, no. 2, p. 159–165, at https://doi.org/10.1139/cjfr-2016-0288.

Will, R.E., Wilson, S.M., Zou, C.B., and Hennessey, T.C., 2013, Increased vapor pressure deficit due to higher temperature leads to greater transpiration and faster mortality during drought for tree seedlings common to the forest–grassland ecotone: New Phytologist, v. 200, no. 2, p. 366–374, at https://doi.org/10.1111/nph.12321.

Williams, D.W., Long, R.P., Wargo, P.M., and Liebhold, A.M., 2000, Effects of climate change on forest insect and disease outbreaks, *in* Mickler, R.A., Birdsey, R.A., and Hom, J. eds., Responses of Northern U.S. Forests to Environmental Change: Springer New York, New York, NY, p. 455–494.

Wilson, A.B., Baker, J.M., Ainsworth, E.A., Andresen, J., Austin, J.A., Dukes, J.S., Gibbons, E., Hoppe, B.O., LeDee, O.E., Noel, J., Roop, H.A., Smith, S.A., Todey, D.P., Wolf, R., and others, 2023, Chapter 24: Midwest. Fifth National Climate Assessment: U.S. Global Change Research Program, accessed April 15, 2025, at https://doi.org/10.7930/NCA5.2023.CH24.

Wipf, S., Stoeckli, V., and Bebi, P., 2009, Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing: Climatic Change, v. 94, no. 1, p. 105–121, at https://doi.org/10.1007/s10584-009-9546-x.

Wobus, C., Zarakas, C., Malek, P., Sanderson, B., Crimmins, A., Kolian, M., Sarofim, M., and Weaver, C.P., 2018, Reframing future risks of extreme heat in the United States: Earth's future, v. 6, no. 9, p. 1323–1335, at https://doi.org/10.1029/2018EF000943.

Wolkovich, E.M., and Cleland, E.E., 2011, The phenology of plant invasions: a community ecology perspective: Frontiers in Ecology and the Environment, v. 9, no. 5, p. 287–294, at https://doi.org/10.1890/100033.

Wolkovich, E.M., and Cleland, E.E., 2014, Phenological niches and the future of invaded ecosystems with climate change: AoB PLANTS, v. 6, accessed October 12, 2020, at https://doi.org/10.1093/aobpla/plu013.

Wolkovich, E.M., Davies, T.J., Schaefer, H., Cleland, E.E., Cook, B.I., Travers, S.E., Willis, C.G., and Davis, C.C., 2013, Temperature-dependent shifts in phenology contribute to the success of exotic species with climate change: American Journal of Botany, v. 100, no. 7, p. 1407–1421, at https://doi.org/10.3732/ajb.1200478.

Wotherspoon, A.R., Achim, A., and Coops, N.C., 2024, Assessing future climate trends and implications for managed forests across Canadian ecozones: Canadian Journal of Forest Research, v. 54, no. 3, p. 278–289, at https://doi.org/10.1139/cjfr-2023-0058.

Wright, D.M., Posselt, D.J., and Steiner, A.L., 2013, Sensitivity of lake-effect snowfall to lake ice cover and temperature in the Great Lakes Region: Monthly Weather Review, v. 141, no. 2, p. 670–689, at https://doi.org/10.1175/mwr-d-12-00038.1.

Wuebbles, D.J., and Kunkel, K.E., 2026, Our changing climate is presenting major challenges to the Great Lakes Region: JAWRA Journal of the American Water Resources Association, v. 62, no. 1, p. e70078, at https://doi.org/10.1111/1752-1688.70078.

Wyka, S.A., Munck, I.A., Brazee, N.J., and Broders, K.D., 2018, Response of eastern white pine and associated foliar, blister rust, canker and root rot pathogens to climate change: Forest Ecology and Management, v. 423, p. 18–26, at https://doi.org/10.1016/j.foreco.2018.03.011.

Xi, Y., Zhang, W., Wei, F., Fang, Z., and Fensholt, R., 2024, Boreal tree species diversity increases with global warming but is reversed by extremes: Nature Plants, v. 10, no. 10, p. 1473–1483, at https://doi.org/10.1038/s41477-024-01794-w.

Xie, F., Erler, A.R., Chandan, D., and Peltier, W.R., 2021, Great Lakes Basin heat waves: an analysis of their increasing probability of occurrence under global warming: Frontiers in Water, v. 3, accessed February 13, 2026, at https://doi.org/10.3389/frwa.2021.782265.

Xue, P., Ye, X., Pal, J.S., Chu, P.Y., Kayastha, M.B., and Huang, C., 2022, Climate projections over the Great Lakes Region: using two-way coupling of a regional climate model with a 3-D lake model: Geoscientific Model Development, v. 15, no. 11, p. 4425–4446, at https://doi.org/10.5194/gmd-15-4425-2022.

Yihan, C., Templer, P.H., and Makoto, K., 2025, Unveiling responses of plant performance and vegetation cover to shifting snow regimes: a meta-analysis: Climatic Change, v. 178, no. 6, p. 116, at https://doi.org/10.1007/s10584-025-03955-y.

Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., Baeten, L., Hédl, R., Berki, I., Brunet, J., Van Calster, H., Chudomelová, M., Decocq, G., Dirnböck, T., and others, 2020, Forest microclimate dynamics drive plant responses to warming: Science, v. 368, no. 6492, p. 772–775, at https://doi.org/10.1126/science.aba6880.

Zettlemoyer, M.A., Schultheis, E.H., and Lau, J.A., 2019, Phenology in a warming world: differences between native and non-native plant species: Ecology Letters, v. 22, no. 8, p. 1253–1263, at https://doi.org/10.1111/ele.13290.

Zhao, C., Brissette, F., Chen, J., and Martel, J.-L., 2020, Frequency change of future extreme summer meteorological and hydrological droughts over North America: Journal of Hydrology, v. 584, p. 124316, at https://doi.org/10/gm6gmg.

Zohner, C.M., Mo, L., Renner, S.S., Svenning, J.-C., Vitasse, Y., Benito, B.M., Ordonez, A., Baumgarten, F., Bastin, J.-F., Sebald, V., Reich, P.B., Liang, J., Nabuurs, G.-J., de-Miguel, S., and others, 2020, Late-spring frost risk between 1959 and 2017 decreased in North America but increased in Europe and Asia: Proceedings of the National Academy of Sciences, v. 117, no. 22, p. 12192–12200, at https://doi.org/10.1073/pnas.1920816117.

Zoladeski, C.A., Wickware, G.M., Delorme, R.J., Sims, R.A., and Corns, I.G.W., 1995, Forest ecosystem classification for Manitoba: field guide: Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta. Special Report 2. 205 pp.

Appendix 1

Table iii. Woody plant species common to the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat. Key species were identified using USNVC floristic descriptions (USNVC, 2020), filtered by associations occurring within the Midwest that collectively comprise the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat. Taxonomic authority, common name, growth habit, and native status are determined according to the PLANTS Database (USDA, NRCS, 2025).

Species	Common name	Growth habit	Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest
Abies balsamea (L.) Mill.	Balsam fir	Tree	×
Acer rubrum L.	Red maple	Tree	×
Betula papyrifera Marshall	Paper birch	Tree	×
Picea glauca (Moench) Voss	White spruce	Tree	×
Pinus strobus L.	Eastern white pine	Tree	×
Populus balsamifera L.	Balsam poplar	Tree	×
Populus tremuloides Michx.	Quaking aspen	Tree	×
Thuja occidentalis L.	Arborvitae	Tree	×

Table iv. Non-woody plant species common to the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat. Key species were identified using USNVC floristic descriptions (USNVC, 2020), filtered by associations occurring within the Midwest that collectively comprise the Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest habitat. Taxonomic authority, common name, growth habit, and native status are determined according to the PLANTS Database (USDA, NRCS, 2025).

Species	Common name	Growth habit	Laurentian Subboreal Mesic Balsam Fir - Spruce - Hardwood Forest
Eurybia macrophylla (L.) Cass.	Bigleaf aster	Forb	×

Appendix 2

Climate projections are derived from the Coupled Model Intercomparison Project Phase 5 (CMIP5) and include model outputs from 20 unique models.

CMIP5 Models:

- bcc-csm1-1
- bcc-csm1-1-m
- CNRM-CM5
- CSIRO-Mk3-6-0
- GFDL-ESM2M
- HadGEM2-CC365
- HadGEM2-ES365
- inmcm4
- IPSL-CM5A-LR
- PSL-CM5A-MR
- MIROC5
- MIROC-ESM
- MIROC-ESM-CHEM
- MRI-CGCM3
- NorESM1-M
- IPSL-CM5B-LR
- CanESM2
- CCSM4
- GFDL-ESM2G
- BNU-ESM

To capture variation across CMIP5 climate models, models with the lowest (minimum model) and highest (maximum model) projected values under the RCP8.5 scenario are presented in addition to the mean of all models. Table v includes a list of all minimum and maximum models selected for each region and climate variable.

Table v. Climate Projection Minimum and Maximum Models. For each region and climate variable, minimum and maximum models were determined by averaging each climate variable projection for the RCP8.5 end of the century (2070–2099) scenario across each region.

Ecoregion	Climate Variable	Season	Minimum Model	Maximum Model
Northern Hardwood Forest	Plant Heat Tolerance Zone	Annual	inmcm4	HadGEM2-CC365
Northern Hardwood Forest	Freeze Free Days	Annual	GFDL-ESM2M	MIROC-ESM-CHEM
Northern Hardwood Forest	Precipitation	Annual	IPSL-CM5A-MR	GFDL-ESM2G
Midwest Region	Mean Maximum Temperature	Annual	MRI-CGCM3	HadGEM2-CC365
Northern Hardwood Forest	Mean Temperature	Annual	GFDL-ESM2M	MIROC-ESM-CHEM
Midwest Region	Mean Minimum Temperature	Annual	GFDL-ESM2M	HadGEM2-CC365