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# The Vulnerability of Overwintering Insects to Loss of the Subnivium

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## ABSTRACT

**Aim:** Winter climate change threatens the subnivium (i.e., the microhabitat that exists between the snowpack and the ground), and the community of species that depends on it for overwintering survival. One group of species that will likely exhibit an array of responses to subnivium loss is overwintering insects because they vary in their cold tolerance strategies and lower thermal limits. For an assemblage of eight insect species that range in their cold tolerance strategies and include both pollinators and pests, we investigated species-specific vulnerabilities to shifting subnivium conditions.

**Location:** Great Lakes region in the United States.

**Methods:** We applied information on each insect's supercooling point to spatially- and temporally-explicit models of minimum subnivium temperatures generated from active-warming experiments and comprising three scenarios: current conditions (i.e., control), +3°C and +5°C.

**Results:** Although species varied in their vulnerabilities, our predictions indicated that exposure to lethal temperatures generally decreased under warming of 3°C, but increased under warming of 5°C, indicating that once enough warming happens, a tipping point is reached. We also found that freeze-tolerant species (i.e., species that can survive at temperatures below their supercooling point) possess a more cryptic vulnerability to winter climate change because sustained below-freezing temperatures were sufficient to induce vulnerability (i.e., predicted mortality), even when temperatures were above the supercooling point.

**Main Conclusions:** This work provides a better understanding of the vulnerability of different insect species to winter climate change, which is critical because overwintering survival and the fitness consequences incurred during overwintering likely represent important bottlenecks for the population dynamics of subnivium-dependent species.

## 1 | Introduction

Global climate change disrupts a host of abiotic processes (Campbell et al. 2009; Gao et al. 2015) that together have altered the conditions in which species persist (Lehikoinen et al. 2011; Herrera et al. 2018). This is especially true for winter in temperate regions, where climate change has led to reductions in snow cover extent and duration (Lemke and Ren 2007; Serreze 2010), as well as extreme events (e.g., extreme cold outbreaks, polar vortices) (Vavrus et al. 2006; Kodra et al. 2011). Future climate scenarios predict continued reductions in snow cover due to the conversion of snowfall to rainfall and more frequent rain-on-snow events (Peacock 2012), which will result in shallower, denser and more variable snowpacks (Christopher et al. 2008). These changes give rise to one of the most critical consequences of winter climate change: the degradation of the subnivium, the microhabitat that exists between the snowpack and the ground (Pauli et al. 2013; Thompson et al. 2021).

Since the low thermal conductivity of snow traps heat released from the soil (Pruitt 2005), the subnivium provides a thermally stable refuge for a diversity of overwintering plants and animals (Pauli et al. 2013). Therefore, sufficient depths of low-density snow keep ground temperatures stably around 0°C regardless of fluctuations in ambient air temperature (Marchand 2013). Warmer winter temperatures, however, reduce the extent, duration and thermal stability of the subnivium (Thompson et al. 2018, 2021), leading to more variable ground temperatures and freeze–thaw cycles (Groffman et al. 2001; Brown and DeGaetano 2011; Grillakis et al. 2016). With reduced snow cover, ground temperatures are also more susceptible to prolonged cold from extreme cold outbreaks. Consequently, loss of the subnivium microhabitat could have severe ecological consequences for the community of species that depend on it for overwintering survival.

Although a compromised subnivium is more susceptible to colder and more variable winter temperatures that can reduce survival rates of species overwintering there (Korslund and Steen 2006; Bokhorst et al. 2012; O'Connor and Rittenhouse 2016), the effects of subnivium loss will not be uniform across taxa, given the wide diversity of adaptations to cold stress. Despite a growing focus in recent years on merging species distribution modelling with metabolic requirements and microclimate conditions (Kearney and Porter 2009; Lenoir et al. 2017; Briscoe et al. 2023), few studies have addressed overwintering species in the subnivium (but see Kearney 2020), and those that have tend to be single-species focused due to the amount of data and computation time required (e.g., Fitzpatrick et al. 2019). Since the effects of warmer winter temperatures and subnivium loss on overwintering survival are likely to be complex, understanding the relative impacts on assemblages of overwintering species is necessary for directing future research and conservation efforts.

One group of species that will likely exhibit an array of responses to subnivium loss are overwintering insects because they have a wide range of cold tolerance strategies, including freeze tolerance, freeze avoidance, chill tolerance and chill susceptibility (Lee 2010; Overgaard and MacMillan 2017). Freeze-tolerant species synthesise ice-nucleating agents in the winter, which enable conversion of up to 80% of their extracellular bodily fluids to ice at temperatures at or above −10°C (Brown et al. 2004; Lee 2010). This extracellular freezing protects organs and tissues by preventing the irreversible damage that would result from ice crystal formation inside cells (Toxopeus and Sinclair 2018). The temperature at which extracellular freezing occurs is known as the supercooling point (SCP) (Lee 2010), that is, the temperature at which insects can avoid ice formation in their cells and survive at sub-freezing temperatures (Dancau et al. 2018). After temperatures fall below the SCP, freeze-tolerant individuals can survive additional cooling, but there is a high amount of interspecific variation in the difference between the SCP and the temperature at which mortality occurs, known as the lower lethal temperature (LLT) (Bale and Worland 2005). In cases where the LLT is close to, but still below the SCP, species are considered weakly freeze tolerant; when the LLT is far below the SCP, species are strongly freeze tolerant (Hart and Bale 1998; Sinclair et al. 2015).

Contrary to freeze-tolerant species, freeze-avoidant species actively remove ice-nucleating agents from their bodies and produce cryoprotectants in their hemolymph that help them to remain in a liquid state at low temperatures without the formation of body ice (Neven et al. 1986; Brown et al. 2004). These cryoprotectants are effective up until the SCP, which in freeze-avoidant species is equivalent to the LLT. Temperature acclimation helps in these efforts, with brief exposure to nonlethal low temperatures triggering the accumulation of cryoprotectants in a process called rapid cold hardening (Kelty and Lee 1999). While freeze-avoidant species can survive cold temperatures as long as ice does not form in their bodies, for chill-susceptible species, mortality occurs at or around 0°C (Lee 2010; Sinclair et al. 2015). Chill-tolerant species are somewhat more robust; they can withstand cold temperatures, but mortality occurs at temperatures above their SCP (Overgaard and MacMillan 2017).

Prior research on insect cold tolerance and overwintering success has typically assumed a constant organismal response to the environment (Marshall and Sinclair 2012) or a constant environmental input for the organism (Beekman et al. 1998), yet both the environment and organismal responses to changes in the environment are highly variable. Additionally, although snow cover has been acknowledged as an important component of winter survival (Szabo and Pengelly 1973; Brown et al. 2004; Marshall and Sinclair 2012; Berzitis et al. 2017), many empirical studies have not used realistic values of subnivium temperatures, with experimental temperatures 3°C–4°C above the subnivium's characteristically stable temperature of 0°C (Mercader and Scriber 2008; Scriber et al. 2012; Woodard et al. 2019). Consequently, there is a gap in knowledge about the physiological limits imposed by the environment and the relative impacts of climate change for different insect species that reside in the subnivium.

Here we unveil a framework to better understand the relative effects of winter climate change using an assemblage of insect species that range in their cold tolerance strategies. We apply information on the supercooling points for this set of species to models of current and future subnivium conditions in the Great Lakes region of North America (hereafter Great Lakes region) to better understand the vulnerability of these species in the face of winter climate change (Thompson et al. 2021). By merging previously collected physiological data with a warming experiment that incorporates natural environmental variability and fine-scale drivers measured at a daily timescale and over a broad geographic extent, we quantify interspecific overwintering vulnerability across an entire winter season. Since the subnivium in the Great Lakes region is predicted to be fairly resilient to warming of 3°C (Thompson et al. 2021), we hypothesized that vulnerability across insect species would be roughly equivalent between current conditions and a warming scenario of 3°C, regardless of interspecific variation in supercooling points.

Alternatively, since warming of 5°C is predicted to result in drastic reductions in subnivium extent and duration in all areas except those with lake-effect snow (Thompson et al. 2021), we expected the vulnerability of insect species to follow a similar geographic pattern, with high vulnerability in interior areas away from lakes and low vulnerability in areas downwind of lakes. Further, for species with lower SCPs, we hypothesized that the extent of their vulnerability would not be as widespread as those with higher SCPs.

## 2 | Methods

### 2.1 | Study Area

The climate of the Great Lakes region is temperate, with warm summers and cold winters (ranging from approximately 8°C to 29°C and −22°C to 3°C, respectively) that vary according to latitude and proximity to the Great Lakes (Andresen et al. 2014; PRISM Climate Group 2020). This area experiences strong temperature variability across its area in the winter months, and the coldest overall temperatures occur in northern interior areas, away from the Great Lakes (Andresen et al. 2014). Areas in the lake effect zone (i.e., downwind of the lakes) typically have more moderate climates with larger amounts of snowfall (Changnon and Jones 1972; Scott and Huff 1996; Burnett et al. 2003).

### 2.2 | Species Selection

We surveyed the literature to find insect species that could be affected by changes in subnivium conditions using different combinations of key terms (e.g., insect, pollinator, pest, snow, overwintering, supercooling point and Great Lakes) in Web of Science and by checking the citations of the articles found through the keyword search. We selected species that: (1) have distributional ranges in all or part of the Great Lakes region; (2) overwinter in the subnivium or just under the soil surface (i.e., approximate subnivium); and (3) have published information on their supercooling points in the literature. Since the cold tolerance strategies of freeze tolerance and freeze avoidance are more common in temperate areas like the Great Lakes region (Overgaard and MacMillan 2017), we focused on species with these strategies. Based on these criteria we selected eight species: the rusty patched bumblebee (*Bombus* (*Bombus*) *affinis*, freeze-avoidant pollinator), the yellow-banded bumblebee (*Bombus* (*Bombus*) *terricola*, freeze-avoidant pollinator), the diamondback moth (*Plutella xylostella*, freeze-avoidant pest), the Canadian tiger swallowtail (*Papilio canadensis*, freeze-avoidant pollinator), the Eastern tiger swallowtail (*Papilio glaucus*, freeze-avoidant pollinator), the woolly bear caterpillar (*Pyrrharctia isabella*, freeze-tolerant pollinator), the bean leaf beetle (*Cerotoma trifurcata*, freeze-tolerant pest), and the hoverfly (*Syrphus ribesii*, freeze-tolerant pollinator). Further details on the characteristics of each species are supplied in the Methods S1.

### 2.3 | Extraction of Species Data

Supercooling point data on bumblebees (*Bombus* spp.) and hoverflies (*Syrphus ribesii*) were extracted directly from published tables, while for all other species we used the software xyscan to extract data from published figures (Ullrich 2020). For the two bumblebee species (*B. affinis* and *B. terricola*), we used *Bombus terrestris*, a species in the same subgenus as *B. affinis* and *B. terricola* as a proxy due to the paucity of data on supercooling points in bumblebees and evidence that thermal tolerance is conserved across evolutionary lineages (Methods S1) (Cameron et al. 2007; Leiva et al. 2019). From the SCP values obtained for all species, we selected the lowest and highest reported SCP (highest/lowest mean ± SE/CI), to use in the analysis as a measure of the best- and worst-case scenario for each species (Table 1). For example, Kukal et al. (1991) reported an SCP for the Canadian tiger swallowtail (*Papilio canadensis*) of −24.0°C ± 0.9°C, so for this species we used −23.1°C and −24.9°C as the best- and worst-case scenario, respectively.

For bean leaf beetles (*Cerotoma trifurcata*, freeze-tolerant pest), we also extracted information on the median survival time for individuals held at a constant temperature of 0°C (Lam and Pedigo 2000). Median survival time corresponds to the time required for 50% mortality in a sample population. To find this value, we fit a quadratic regression model to survival data published in Lam and Pedigo (2000). We then extracted the number of days corresponding to 50% mortality, as well as the associated confidence interval using the fitted regression line.

### 2.4 | Active-Warming Experiments

To represent the range of variation in current and future winter conditions in the Great Lakes region, we installed active-warming greenhouses with automated, retractable roofs at nine sites throughout Minnesota, Wisconsin and Michigan in the fall of 2016 (Figure S1). Sites spanned a broad latitudinal gradient (42.9°–46.8° N) and three habitat types: deciduous forest, coniferous forest and open areas. At each site, we installed three greenhouses, each with a different temperature treatment: the control ($GH_{control}$, internal temperature = ambient temperature), 3°C warmer than ambient ($GH_{+3°C}$), and 5°C warmer than ambient ($GH_{+5°C}$). We chose these treatments to capture the variability in the Coupled Model Intercomparison Project's (CMIP5) emission scenarios, which predict warmer winter temperatures ranging from approximately 3.5°C–6°C in the Great Lakes region (Notaro et al. 2014).

We also monitored the environment external to all greenhouses to capture current conditions. From December 2016 to March 2017, for each greenhouse and the external environment, we monitored ambient temperatures and wind speed at 1-min intervals and subnivium temperature and snow depth at 5-min intervals. In each greenhouse, subnivium temperatures were measured with 16 temperature probes that were 0.3 m apart and affixed to the ground in a four-by-four grid. In the external environment, we affixed 4 probes, also separated by 0.3 m, to the ground outside of each greenhouse for a total of 12 external subnivium temperature measurements.

To capture real-time precipitation and temperature, we paired each greenhouse with an external weather station that included a heated rain gauge and an ambient temperature sensor. Communication between the instruments inside the greenhouse

**TABLE 1** | Species characteristics and supercooling points (SCP) extracted from published literature.

| Species | Cold tolerance strategy | Overwintering strategy | Ecosystem (dis) service | Caste | Developmental stage | Included RCH | Sample size | Mean supercooling point (°C) | Study | SCP values used in analysis (°C) |
|---|---|---|---|---|---|---|---|---|---|---|
| *Bombus terrestris*[a] | Freeze avoidant | Diapause | Pollinator | queen | Adult | No | 20 | −7.0 ± 0.3 | Owen et al. 2013 | −6.7, −7.3 |
| *Plutella xylostella* | Freeze avoidant/ chill susceptible | Quiescence | Pest | NA | Pupa | No | 12 | −10.8 ± 0.4 | Park and Kim 2014 | −9.6, −12.8 |
| | | | | | Pupa | Yes | 12 | −12.6 ± 0.2 | Park and Kim 2014 | |
| | | | | | Adult | No | 12 | −10.1 ± 0.5 | Park and Kim 2014 | |
| | | | | | Adult | Yes | 12 | −10.1 ± 0.1 | Park and Kim 2014 | |
| *Papilio Canadensis* | Freeze avoidant | Diapause | Pollinator | NA | Pupa | No | 4–8 | −24.0 ± 0.9 | Kukal et al. (1991) | −23.1, −24.9 |
| *Papilio glaucus* | Freeze avoidant | Diapause | Pollinator | NA | Pupa | No | 4–8 | −23.0 ± 1.2 | Kukal et al. 1991 | −21.8, −24.2 |
| *Pyrrharctia isabella* | Freeze tolerant | Diapause | Pollinator | NA | Final instar larva | No | 69–111 | −10.7 ± 0.1[b] | Marshall and Sinclair 2011 | |
| | | | | | Final instar larva | No | 69–111 | −7.6 ± 0.1[c] | Marshall and Sinclair 2011 | −6.3, −10.8 |
| | | | | | Final instar larva | No | 4–8 | −6.6 ± 0.3 | Layne et al. 1999 | |
| *Cerotoma trifurcata* | Freeze tolerant | Diapause | Pest | NA | Adult | No | 29 | −8.0 [−7.0, −9.3][d] | Carrillo et al. 2005 | −7.0, −9.3 |
| | | | | | Adult | No | 19 | −8.9 [−8.4, −9.3][e] | Carrillo et al. 2005 | |
| | | | | | Adult | No | 14 | −8.8 [−7.0, −9.2][f] | Carrillo et al. 2005 | |

(Continues)

**TABLE 1** | (Continued)

| Species | Cold tolerance strategy | Overwintering strategy | Ecosystem (dis) service | Caste | Developmental stage | Included RCH | Sample size | Mean supercooling point (°C) | Study | SCP values used in analysis (°C) |
|---|---|---|---|---|---|---|---|---|---|---|
| *Syrphus ribesii* | Freeze tolerant | Diapause | Pollinator | NA | Third instar larva | No | 24 | −7.6 ± 0.4 | Brown et al. 2004 | −4.8, −8.0 |
| | | | | | Third instar larva | No | 24 | −6.8 ± 0.1[g] | Hart and Bale 1998 | |
| | | | | | Third instar larva | No | 24 | −6.7 ± 0.1[h] | Hart and Bale 1998 | |
| | | | | | Third instar larva | No | 24 | −6.5 ± 0.1[i] | Hart and Bale 1998 | |
| | | | | | Third instar larva | No | 24 | −6.3 ± 0.4[j] | Hart and Bale 1998 | |
| | | | | | Third instar larva | No | 24 | −5.1 ± 0.3[k] | Hart and Bale 1998 | |

*Note:* We used the highest and lowest values (SCP ± standard error or confidence interval) in our analyses to represent a best and worst case for each species, respectively. Caste is specific to *Bombus* spp. and refers to the caste that overwinters in the subnivium. Developmental stage refers to the life stage (e.g., egg, larva, pupa and adult) during which overwintering occurs. Included RCH refers to whether each study included an acclimation period, otherwise known as rapid cold hardening.

[a]Used as a proxy for *Bombus* (*Bombus*) *affinis* and *Bombus* (*Bombus*) *terricola*.

[b]Year 1 of study: 2008–2009.

[c]Year 2 of study: 2009–2010.

[d]SCP measured in December, brackets indicate 25th and 75th percentiles.

[e]SCP measured in February, brackets indicate 25th and 75th percentiles.

[f]SCP measured in March, brackets indicate 25th and 75th percentiles.

[g]Held at a constant 20°C.

[h]Acclimation of 15°C for 2 days, 10°C for 12 days and 5°C for 12 days.

[i]Acclimation of 15°C for 8 days, 10°C for 2 days and 5°C for 20 days.

[j]Acclimation of 15°C for 2 days, 10°C for 10 days, 5°C for 8 days and 0°C for 13 days.

[k]Acclimation of 15°C for 8 days, 10°C for 2 days, 5°C for 20 days and 0°C for 20 days.

and this weather station allowed us to capture both precipitation events and future climate conditions. When a precipitation event was registered by the heated rain gauge, the retractable roof of the greenhouse opened to allow the snow or rain to fall inside. When the roof was closed, precise temperature control for each treatment was achieved through the near continuous measurements of ambient temperature from each weather station and the temperature measured from inside each greenhouse. For further details on the experimental design and the equipment used, please see the Methods S1.

## 2.5 | Statistical Analysis

### 2.5.1 | Subnivium Temperature

To derive a daily subnivium temperature for each treatment, we extracted the daily minimum ground temperature from each sensor for the period of 1 December 2016 to 31 March 2017 and then calculated the mean of those minimum temperatures for each treatment (environmental control, $n=12$; greenhouse treatments, $n=16$) and each day. We characterised subnivium conditions using daily minimum temperatures because these temperatures allow us to quantify the lower limit of what insects would have to endure during their overwintering, while averaging across all the temperature probes for a given treatment limits the impact of outliers.

### 2.5.2 | Boosted Regression Trees

To generate regional predictions of ground temperatures, we followed the methodology of Thompson et al. (2021) and used boosted regression trees (BRT) to model daily minimum ground temperatures, with each treatment (external environment, $GH_{control}$, $GH_{+3°C}$, $GH_{+5°C}$) modelled separately (Breiman 2001). Our predictors included daily maximum air temperature, daily minimum air temperature, daily median snow depth, daily mean snow density, daily mean wind speed and habitat type. We selected these predictors because maintenance of the subnivium habitat (i.e., sustaining temperatures between the ground and the snowpack of ~0°C) depends on a balance between air temperature, snow depth and snow density (Thompson et al. 2018), with ideal subnivium conditions occurring with sub −0°C air temperatures, deep snow and low snow density. At the same time wind and land cover can disrupt this balance through redistribution and interception of snow cover, respectively (Pomeroy et al. 1998; Varhola et al. 2010).

After identifying the optimal settings and number of iterations for the models (Methods S1), we ran each model 50 times using the R package *dismo* (Hijmans et al. 2011; R Core Team 2022). In each iteration, the data was split into training and testing sets (70% and 30% of the data, respectively), allowing us to account for both the stochasticity intrinsic to boosted regression tree models (Elith et al. 2008) and the variability in our collected data. While the maximum possible observations for each treatment was 1089 (i.e., 9 sites × 121 days), each treatment (and by extension each model) had slightly less observations due to minor equipment problems that caused missing values for a small sample of days. However, all treatments had at least 95% of the total maximum possible observations available to split into training and testing sets (Table S4). To assess the predictive performance of the models, we calculated predictive deviance and root mean square error for each iteration, and visually assessed plots of observed and predicted values, as well as plots of residual and predicted values.

While software packages like NicheMapR represent the current state-of-the-art in microclimate and biophysical modelling (Kearney and Porter 2017), we found that the boosted regression tree models we trained with experimentally generated climate data provided higher predictive accuracy. Fitzpatrick et al. (2019) used NicheMapR to predict subnivium temperatures in the Great Lakes region for the winter of 2016–2017 and the resulting vulnerability of overwintering wood frogs (Fitzpatrick et al. 2019). To validate their models, they used data generated from the subnivium temperature sensors located external to the active-warming greenhouses described herein, and found root mean square errors ranging from 2.15°C to 3.83°C. Since the boosted regression tree models provided lower root mean square errors (see Section 3), we elected to continue with this modelling framework.

### 2.5.3 | Spatial Predictions

To predict subnivium temperatures across the broader Great Lakes region, we obtained spatially explicit data on air temperature, snow depth and density, wind speed and land cover (Methods S1). We predicted minimum ground temperatures across the Great Lakes region for each day of our study period (1 December 2016 to 31 March 2017) at a 1-km resolution for the environment external to the greenhouses, $GH_{control}$, $GH_{+3°C}$ and $GH_{+5°C}$, with 50 bootstrap samples for each day/treatment combination. By comparing the predictions generated for the environment external to the greenhouses to those generated for $GH_{control}$, we also identified an offset, or correction factor, so that the ground temperature predictions would be unbiased by any effects of the greenhouse structure (Methods S1). We applied the correction factor to the predictions produced for $GH_{+3°C}$ and $GH_{+5°C}$, which left us with 50 predictive surfaces of minimum daily ground temperature for each of three scenarios: no winter warming, warming of 3°C, and warming of 5°C. Finally, we summarised the predictions for each scenario by finding the mean of the predicted minimum ground temperatures across the 50 predictive surfaces.

### 2.5.4 | Quantifying Insect Vulnerability

To quantify the effect of future winter temperatures on the vulnerability of insects overwintering in the subnivium, we used the highest and lowest SCPs extracted from the literature for each selected species as a threshold and to represent the worst and best cases, respectively, for overwintering survival. Higher supercooling points indicate that a species is relatively more sensitive to cold temperatures since the species would experience either extracellular freezing (freeze-tolerance) or mortality (freeze-avoidant) before other species with lower supercooling points. We present the results for the highest SCP (i.e., worst case) here and direct the reader to the supplemental materials for results on the lowest SCP (i.e., best case). We applied each species-specific SCP as a threshold to the predictive surfaces generated for each climate scenario and assigned a 1 to cells with ground temperature values lower than the threshold (1 cell = 1 $km^2$). Then, across each climate scenario and for each cell, we summed these instances to represent the number of days in the winter season that the minimum daily ground temperature fell below the species' SCP. For the entire region, we also summed the cells that fell below each species' threshold to represent the extent of vulnerability for each day in the winter season.

Although the number of days below the SCP provides a common metric with which to compare freeze-avoidant and freeze-tolerant species, the correlation between the number of days below the SCP and the vulnerability of freeze-tolerant species may not be as strong as in freeze-avoidant species, since freeze-tolerant species can survive at temperatures below their supercooling point (Bale and Worland 2005). Therefore, we also used data on the number of days until 50% mortality in bean leaf beetles (*C. trifurcata*, a freeze-tolerant pest) held at a constant temperature of 0°C. This mortality information provides an additional measure of vulnerability for this species, as well as a means of assessing the ability of the number of days below SCP to serve as a reliable indicator of vulnerability in a freeze-tolerant species. For the predictive surfaces generated for each climate scenario, we calculated the maximum consecutive days of daily minimum ground temperatures at or below 0°C in each grid cell. We then used the time until 50% mortality that was observed in a sample of *C. trifurcata* (± confidence interval) (Lam and Pedigo 2000) as a threshold to determine the spatial distribution of consecutive below-freezing days that were below, within, and above the range of consecutive days that *C. trifurcata* could withstand. Then, to compare the SCP-based vulnerability estimates with the mortality-based vulnerability estimates, we examined how the distribution of days with temperatures below the species' SCP and the extent of vulnerability overlapped with these lower lethal ranges.

## 3 | Results

The boosted regression tree models performed well with predictive deviances ranging from 1.93–2.49 and the error between actual and predicted values (i.e., root mean square error) ranging from 1.39°C–1.58°C (Tables S5 and S6). While predicted values generally tracked observed values, we found that the models tended to underestimate temperature extremes, especially at low temperatures (Figures S8–S11). This indicates, however, that our results regarding insect vulnerability are likely to be more conservative. We also examined the residuals of each model and found that while they exhibited random scatter around the zero line, across all models there was less variance when fitted values were between −5°C and 0°C (Figure S12). Though usually this heteroscedasticity would represent a fit issue, boosted regression trees are generally robust to heteroscedasticity due to their nonparametric nature.

Overall, we found that compared to current conditions, the total number of days below the SCP decreased for most species under warming of 3°C (Figure 1, Figure S13, Tables S7 and S8). This was especially true in northwestern areas of the study region, where there were about 20 less days of sub-SCP conditions in the +3°C scenario, even though region-wide reductions ranged only from 1.4 to 6.3 days (Figures 1 and 2, Figure S14). Under warming of 5°C, the total number of days with temperatures below the species' SCPs returned to those found under current conditions in central and southern areas, and surpassed those found under current conditions in northern regions, with species experiencing on average between 1.6 and 3.9 more days of sub-SCP conditions (Figure 2, Figure S14, Tables S7 and S8). Notably, the low supercooling points of the two butterfly species (*P. canadensis* and *P. glaucus*, both freeze-avoidant pollinators) did not result in any days below the SCP in any of the warming scenarios (Figure 1, Figure S13).

We found that the mean extent of vulnerability in the Great Lakes region improved under warming of 3°C, but expanded beyond the extents found under current conditions when warming reached 5°C (Tables S9 and S10). This increase in the extent of vulnerability between current conditions and warming of 5°C ranged from approximately 10,000 additional $km^2$ for bumblebees (*B. affinus* and *B. terricola*, freeze-avoidant pollinators), woolly bear caterpillars (*P. isabella*, freeze-tolerant pollinator), and bean leaf beetles (*C. trifurcata*, freeze-tolerant pest) to 25,000 additional $km^2$ for diamondback moths (*P. xylostella*, freeze-avoidant pest) and 80,000 additional $km^2$ for hoverflies (*S. ribesii*, freeze-tolerant pollinator). Daily extents of vulnerability were highly variable throughout the winter season with many peaks and valleys (Figure 3, Figure S15). In fact, despite the general pattern in which the mean extent of vulnerability increased under warming of 5°C, five species were predicted to experience a maximum daily extent of vulnerability under current conditions (*B. affinus*, *B. terricola*, *P. isabella*, *C. trifurcata* and *S. ribesii*, Figure 3).

The mean number of days until 50% mortality in a sample of bean leaf beetles held at a constant temperature of 0°C was 34.6 days [28.9, 41.3] (Figure S16; Lam and Pedigo 2000). Comparing this length of time to the number of consecutive days across the Great Lakes region with predicted daily minimum ground temperatures below 0°C revealed additional areas of vulnerability for this species, as well as additional areas of improvement beyond those predicted by the SCP analysis (Figure 4). While current conditions throughout much of the western portion of the study area exceeded the number of below-freezing days *C. trifurcata* could withstand, the central and southern portions of these western states dramatically improved in the +3°C and +5°C scenarios. Despite local variation, the extent of vulnerability increased drastically across all warming scenarios when accounting for the consecutive number of below-freezing days, with an additional 310,000 $km^2$ of vulnerability under current conditions, an additional 135,000 $km^2$ under warming of 3°C, and an additional 162,000 $km^2$ under warming of 5°C (Figure 4, Table S11).

Comparing the distribution of total sub-SCP days with the lower lethal durations of sub −0°C temperatures under current conditions and the +3°C climate scenario revealed considerable overlap between the three types of lower lethal durations (most favourable scenario: consecutive sub −0°C days below the duration that resulted in 50% mortality, moderate scenario: consecutive sub −0°C days within the duration that resulted in 50% mortality, and least favourable scenario: consecutive sub −0°C days above the duration that resulted in 50% mortality) when the total number of sub-SCP days ranged from 0 to 20 (Figure 5, Figure S17). This indicates that mortality in bean leaf beetles is possible even when the number of days in which the temperature falls below the species SCP is low or zero. In the +5°C scenario, there was a marked increase in the number of sub-SCP days, leading to a concurrent increase in the number of

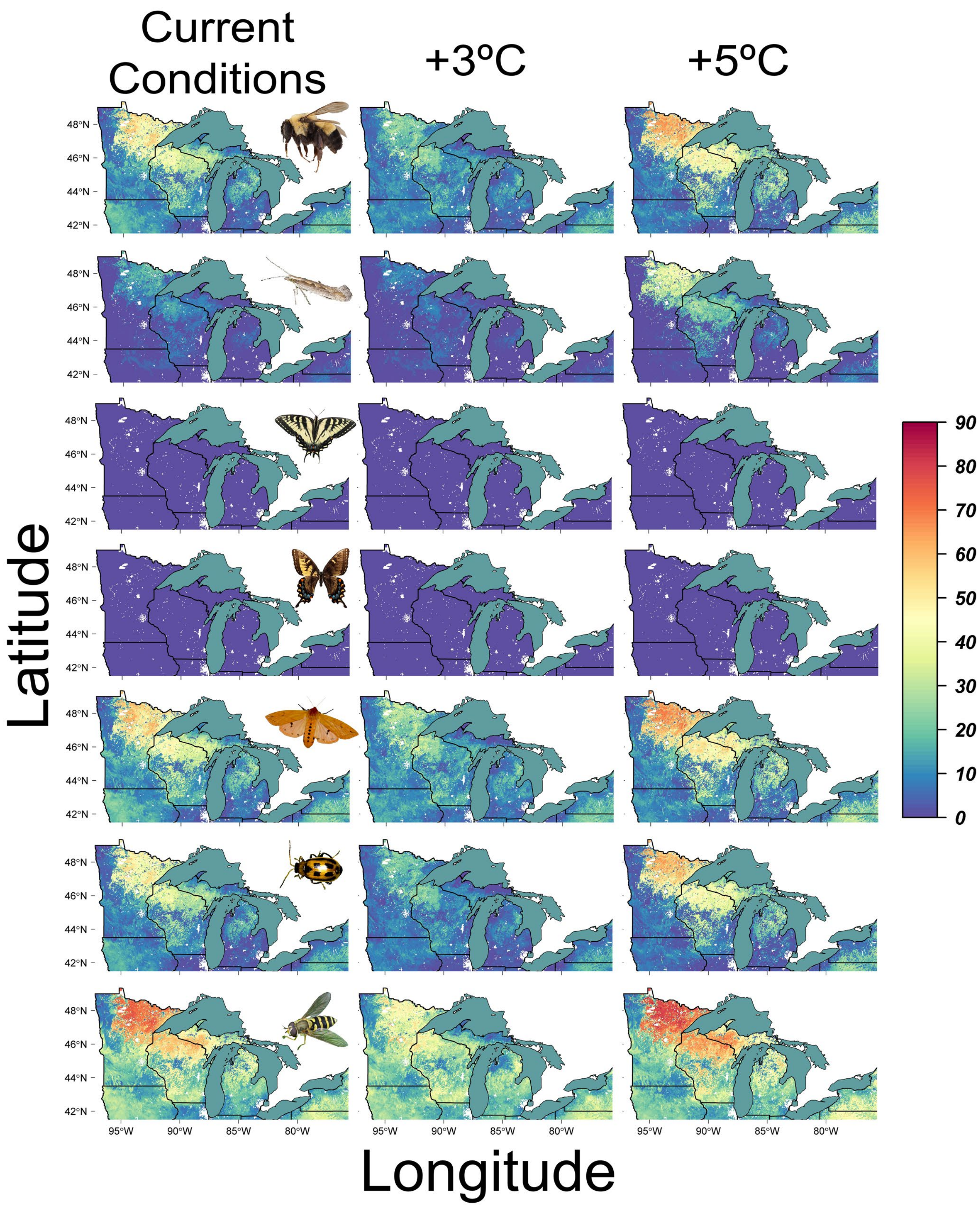


**FIGURE 1** | Legend on next page.

**FIGURE 1** | Total number of days in the winter season (1 December 2016 to 31 March 2017) below the highest published supercooling point (i.e., worst case) for insect species differing in their cold tolerance strategies under current, 3°C warmer and 5°C warmer conditions. From top to bottom: Buff-tailed bumblebee (*Bombus* (*Bombus*) *terrestris*), used a proxy for the Rusty patched bumblebee (*Bombus* (*Bombus*) *affinis*) and the yellow-banded bumblebee (*Bombus* (*Bombus*) *terricola*), freeze-avoidant pollinators; Diamondback moth (*Plutella xylostella*), freeze-avoidant pest; Canadian tiger swallowtail (*Papilio canadensis*), freeze-avoidant pollinator; Eastern tiger swallowtail (*Papilio glaucus*), freeze-avoidant pollinator; Woolly bear caterpillar (*Pyrrharctia isabella*), freeze-tolerant pollinator; Bean leaf beetle (*Cerotoma trifurcata*), freeze-tolerant pest; and Hoverfly (*Syrphus ribesii*), freeze-tolerant pollinator. Images of insects adapted from: *Rusty-patched bumblebee queen* by Miklasevskaja, M., 1971, https://val.vtecostudies.org/projects/vtbees/bombus-affinis/ Copyright 2024 by Vermont Center for Ecostudies; *Diamondback moth* 2006, https://en.wikipedia.org/wiki/Diamondback_moth; *Papilio canadensis* by Mdf, 2008, https://en.wikipedia.org/wiki/Papilio_canadensis; *Mosaic Gynandromorphs*, *Eastern Tiger Swallowtail* (*Papilio glaucus*) by Grace, K., 1979, https://www.floridamuseum.ufl.edu/100-years/object/eastern-tiger-swallowtail/ Copyright 2024 by Florida Museum of Natural History; *Pyrrharctia isabella* by Reago, A. and McClarren C., 2014 https://en.wikipedia.org/wiki/Pyrrharctia_isabella; *Adult bean leaf beetle* by University of Nebraska-Lincoln, 2024, https://cropwatch.unl.edu/soybean-management/insects-bean-leaf-beetle Copyright 1869–2024 by University of Nebraska-Lincoln; *Syrphus ribesii* by Aiwok, 2010, https://en.wikipedia.org/wiki/Syrphus_ribesii.

consecutive sub −0°C days that were beyond what *C. trifurcata* could withstand (Figure 5, Figure S17).

## 4 | Discussion

Warming winter temperatures are associated with a reduction in snow cover extent and a higher likelihood of rain-on-snow events, which in turn reduces the insulating capacity of snow cover (Zuckerberg and Pauli 2018). Consequently, even with warmer air temperatures, ground temperatures become paradoxically colder due to the lack of insulation (Brown and DeGaetano 2011). Despite this general phenomenon, prior work on the impact of winter warming on the spatial and temporal patterns of the subnivium demonstrated little to no change in extent or duration under warming of 3°C (Thompson et al. 2021). Therefore, we hypothesized that species' vulnerabilities would be roughly equivalent between the +3°C scenario and current conditions. Surprisingly, our results indicated that subnivium temperatures under warming of 3°C are likely to increase relative to current conditions, leading to reductions in the number of sub-SCP days and the mean extent of vulnerability for most insect species (Figures 1–3). We suspect that rather than disrupting the balance of air temperature, snow depth and snow density required for ideal subnivium conditions, warming of +3°C actually facilitated maintenance of this balance, with warmer, but still below-freezing air temperatures that prevented melting and refreezing events that decrease snow depth and increase snow density. Given that warming of 3°C does not seem to involve deleterious effects for either the subnivium microhabitat or the insects that depend on it (Thompson et al. 2021), efforts to reduce global emissions and limit warming should not exceed this value when setting benchmarks for conserving the subnivium and communities of overwintering insects in seasonally snow-covered environments across the Northern Hemisphere.

Under warming of 5°C, ground temperatures throughout the Great Lakes region decreased below those found in current conditions, which generally caused insect vulnerabilities to increase (Figures 1–3). There was considerable spatial variation in the magnitude of the change in vulnerability, however, with the northern areas of our study region becoming especially exposed to higher thermal extremes, while central and southern areas experienced more modest increases in vulnerability (Figure 1). Consequently, given both localised increases and decreases, the difference between the mean number of sub-SCP days for each species in the 5°C warming scenario and current conditions across the entire study region was low (Figure 2). Despite this geographic variation, the mean extent of variability between current conditions and warming of 5°C increased for all but the two butterfly species (*P. glaucus* and *P. canadensis*), indicating that warming of 5°C likely represents a tipping point at which exposure to lethal temperatures becomes much more difficult to avoid (Figure 3).

Notably, since prior work on the effects of winter climate change in lake-effect areas predicted high probabilities of subnivium occurrence and long subnivium durations under warming of 5°C (Thompson et al. 2021) due to reduced lake ice and more lake-effect snow (Notaro et al. 2015), we expected low insect vulnerability in the northern areas surrounding the Great Lakes. Contrary to our hypotheses, these areas demonstrated some of the highest levels of vulnerability for insects under warming of 5°C (Figures 1 and 4). Our results show that although continued lake-effect snow may partially safeguard subnivium extent and duration in these areas, warming of 5°C is likely to increase temperature variability within this microhabitat, thereby leading to increased vulnerability for overwintering insects.

Despite these general trends, species responses did not converge according to their cold tolerance strategies. For example, our predictions show that two freeze-avoidant butterfly species (*P. canadensis* and *P. glaucus*) could remain relatively buffered to changing subnivium conditions even under warming of 5°C due to their extremely low supercooling points (Figure 1). Similarly, the diamondback moth (*P. xylostella*), a freeze-avoidant pest species, demonstrated extremely low sensitivity to both current conditions and warming of 3°C, although warming of 5°C was sufficient to increase its vulnerability in northern areas of our study region (Figures 1, 3). Alternatively, the situation appears bleaker for bumblebees (*Bombus* spp.) and hoverflies (*S. ribesii*) under both current conditions and warming of 5°C, despite the modest reductions in vulnerability under 3°C warming (Figures 1 and 3).

Freeze-tolerant species have been regarded as more uniform in their responses to cold, since mortality occurs at temperatures below their supercooling point (Bale and Worland 2005). Critically, however, these species are not immune to an unlimited range of temperatures, nor are they necessarily able

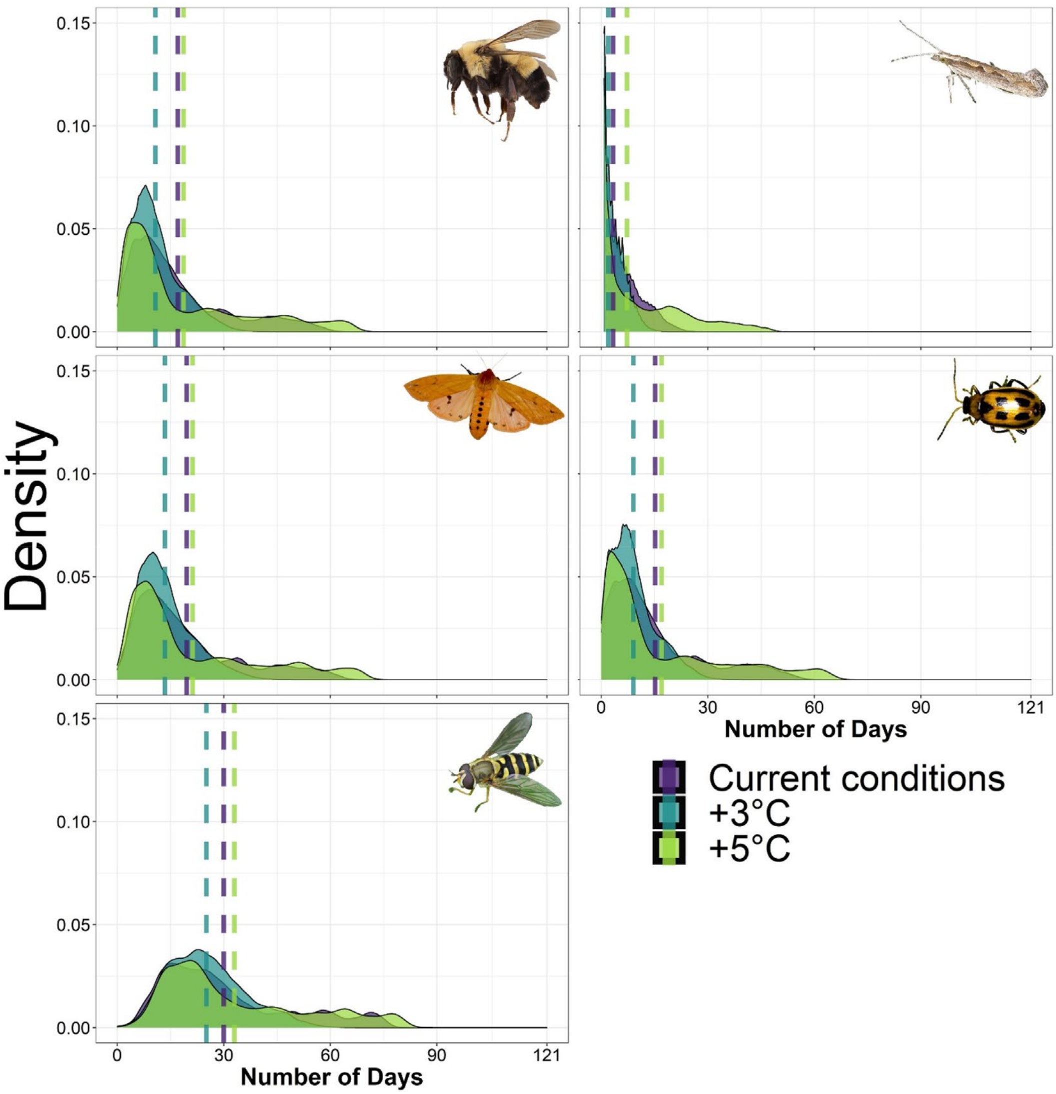


**FIGURE 2** | Density plots showing the distributions of the total number of days in the winter season (1 December 2016 to 31 March 2017) below the highest published supercooling point (i.e., worst case) for insect species differing in their cold tolerance strategies under current, 3°C warmer and 5°C warmer conditions. Dotted lines represent the mean number of days in each warming scenario. Top row: Buff-tailed bumblebee (*Bombus* (*Bombus*) *terrestris*), used a proxy for the Rusty patched bumblebee (*Bombus* (*Bombus*) *affinis*) and the yellow-banded bumblebee (*Bombus* (*Bombus*) *terricola*), freeze-avoidant pollinators, and the Diamondback moth (*Plutella xylostella*), freeze-avoidant pest. Middle row: Woolly bear caterpillar (*Pyrrharctia isabella*), freeze-tolerant pollinator and Bean leaf beetle (*Cerotoma trifurcata*), freeze-tolerant pest. Bottom row: Hoverfly (*Syrphus ribesii*), freeze-tolerant pollinator. The two butterfly species (Canadian tiger swallowtail (*Papilio canadensis*)) and Eastern tiger swallowtail (*Papilio glaucus*, both freeze-avoidant pollinators) are not pictured because under each climate scenario the total days below each of their SCPs was zero. Images of insects adapted from: *Rusty-patched bumblebee queen* by Miklasevskaja, M., 1971, https://val.vtecostudies.org/projects/vtbees/bombus-affinis/ Copyright 2024 by Vermont Center for Ecostudies; *Diamondback moth* 2006, https://en.wikipedia.org/wiki/Diamondback_moth; *Pyrrharctia isabella* by Reago, A. and McClarren C., 2014 https://en.wikipedia.org/wiki/Pyrrharctia_isabella; *Adult bean leaf beetle* by University of Nebraska-Lincoln, 2024, https://cropwatch.unl.edu/soybean-management/insects-bean-leaf-beetle Copyright 1869–2024 by University of Nebraska-Lincoln; *Syrphus ribesii* by Aiwok, 2010, https://en.wikipedia.org/wiki/Syrphus_ribesii.

to survive extended periods of exposure to cold (Layne and Blakeley 2002). For example, although woolly bear caterpillars (*P. isabella*) can endure subzero temperatures, they are still susceptible to prolonged extreme cold outbreaks and demonstrate higher mortality during repeated freeze–thaw events (Layne et al. 1999; Marshall and Sinclair 2011). Similarly, the freeze-tolerant bean leaf beetle (*C. trifurcata*) can only survive constant temperatures of 0°C for 29–41 days (Lam and Pedigo 2000), despite having a supercooling point around −8°C (Carrillo et al. 2005). Our comparison of vulnerability in bean leaf beetles between this lower lethal limit (0°C for 29–41 days) and the number of days below its SCP (Figures 4 and 5) corroborated this idea of a more cryptic vulnerability that is likely typical of other freeze-tolerant species since sustained below-freezing temperatures even at temperatures above the SCP were sufficient to induce vulnerability (i.e., predicted mortality). We found more areas of vulnerability for bean leaf beetles using the lower lethal limit than we did with the number of sub-SCP days, as well as overlap between the least favourable and moderate scenarios (i.e., consecutive sub

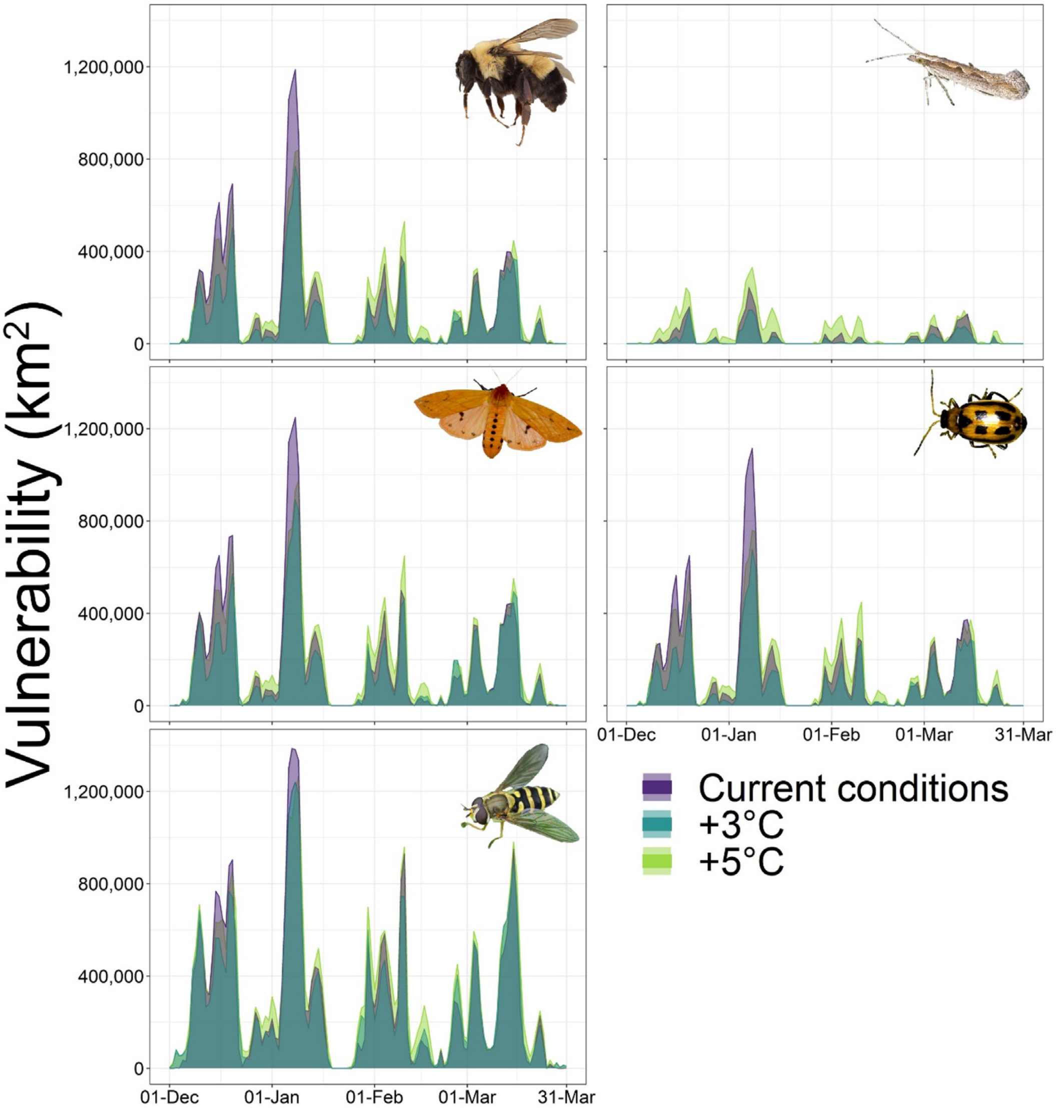


**FIGURE 3** | Daily extent of vulnerability (i.e., square kilometres where predicted ground temperatures were below the highest published supercooling point (i.e., worst case)) for insect species differing in their cold tolerance strategies under current, 3°C warmer and 5°C warmer conditions. Top row: Buff-tailed bumblebee (*Bombus* (*Bombus*) *terrestris*), used a proxy for the Rusty patched bumblebee (*Bombus* (*Bombus*) *affinis*) and the yellow-banded bumblebee (*Bombus* (*Bombus*) *terricola*), freeze-avoidant pollinators, and the Diamondback moth (*Plutella xylostella*), freeze-avoidant pest. Middle row: Woolly bear caterpillar (*Pyrrharctia isabella*), freeze-tolerant pollinator and Bean leaf beetle (*Cerotoma trifurcata*), freeze-tolerant pest. Bottom row: Hoverfly (*Syrphus ribesii*), freeze-tolerant pollinator. The two butterfly species (Canadian tiger swallowtail (*Papilio canadensis*)) and Eastern tiger swallowtail (*Papilio glaucus*, both freeze-avoidant pollinators) are not pictured because under each climate scenario the total days below each of their SCPs was zero. Images of insects adapted from: *Rusty-patched bumblebee queen* by Miklasevskaja, M., 1971, https://val.vtecostudies.org/projects/vtbees/bombus-affinis/ Copyright 2024 by Vermont Center for Ecostudies; *Diamondback moth* 2006, https://en.wikipedia.org/wiki/Diamondback_moth; *Pyrrharctia isabella* by Reago, A. and McClarren C., 2014 https://en.wikipedia.org/wiki/Pyrrharctia_isabella; *Adult bean leaf beetle* by University of Nebraska-Lincoln, 2024, https://cropwatch.unl.edu/soybean-management/insects-bean-leaf-beetle Copyright 1869–2024 by University of Nebraska-Lincoln; *Syrphus ribesii* by Aiwok, 2010, https://en.wikipedia.org/wiki/Syrphus_ribesii.

−0°C days above 41 days and within 29–41 days, respectively) and the number of winter season days below the bean leaf beetle's SCP (worst-case SCP: −7.0°C, best-case SCP −9.3°C). Critically, this indicates that individuals of this species could experience mortality even in the absence of any days below their SCP (Figure 5, Figure S17). These results echo those of Berzitis et al. (2017), who found extremely low overwintering survival rates of bean leaf beetles across experimental treatments in southern Canada that included warming of 4°C, complete snow removal with no warming, and intact snow cover with no warming, even though consecutive subfreezing days were uncommon in all but the snow removal treatment.

These nuances in interspecific vulnerability are especially important given the ecosystem services and disservices provided by insects, and the subsequent implications for both ecological processes and economic systems. Numerous insects provide critical pollination services, which contribute to the maintenance of genetic diversity in plant populations (Kearns et al. 1998) and increase the yield of cultivated crops, with economic valuations

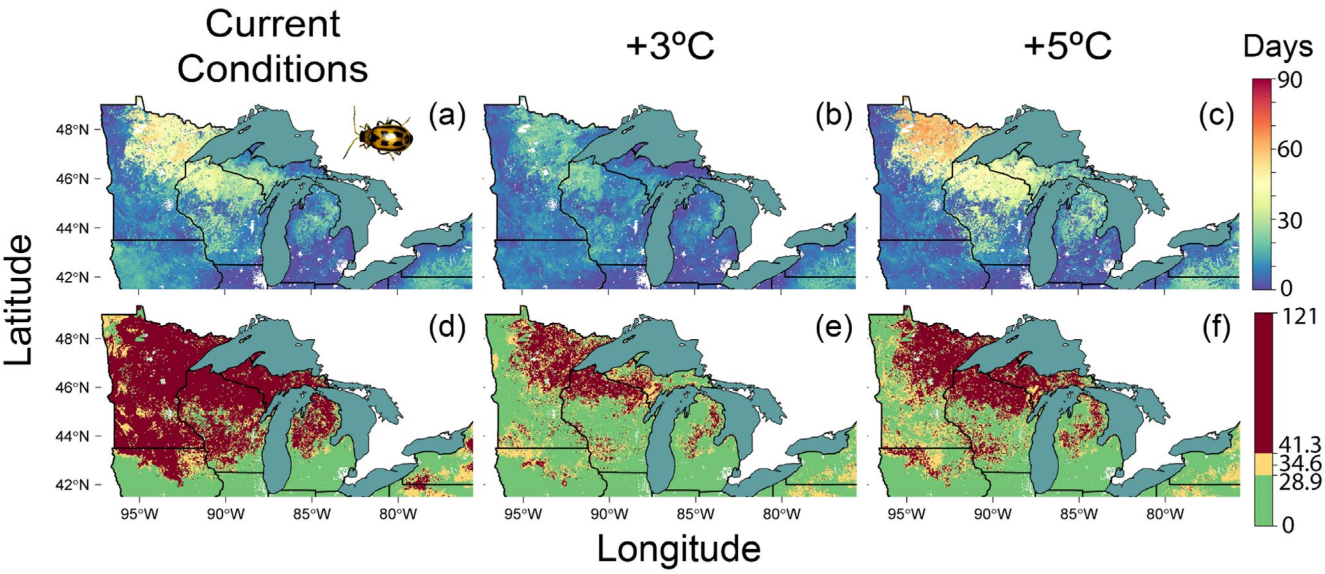


**FIGURE 4** | For three warming scenarios: Current conditions (i.e., no warming, a and d), warming of 3°C (b and e) and warming of 5°C (c and f), comparison between the total number of days in the winter season (1 December 2016 to 31 March 2017) with ground temperatures below the highest published supercooling point (−7.0°C, i.e., worst case) for bean leaf beetles (*Cerotoma trifurcata*, freeze-tolerant pest; a–c) and mortality expectations based on experimental data extracted from Lam and Pedigo (2000) (d–f), who found that the mean number of days until 50% mortality in a sample of *C. trifurcata* at constant temperatures of 0°C was 34.6 days [28.9, 41.3]. For (d–f) areas in red represent consecutive sub −0°C days exceeding the upper confidence limit of what *C. trifurcata* can withstand (i.e., least favourable scenario), areas in yellow represent consecutive sub −0°C days within the reported range for 50% mortality (i.e., moderate scenario), and areas in green represent sub −0°C days below the lower confidence limit of what *C. trifurcata* can withstand (i.e., most favourable scenario). Image of insect adapted from *Adult bean leaf beetle* by University of Nebraska-Lincoln, 2024, https://cropwatch.unl.edu/soybean-management/insects-bean-leaf-beetle Copyright 1869–2024 by University of Nebraska-Lincoln.

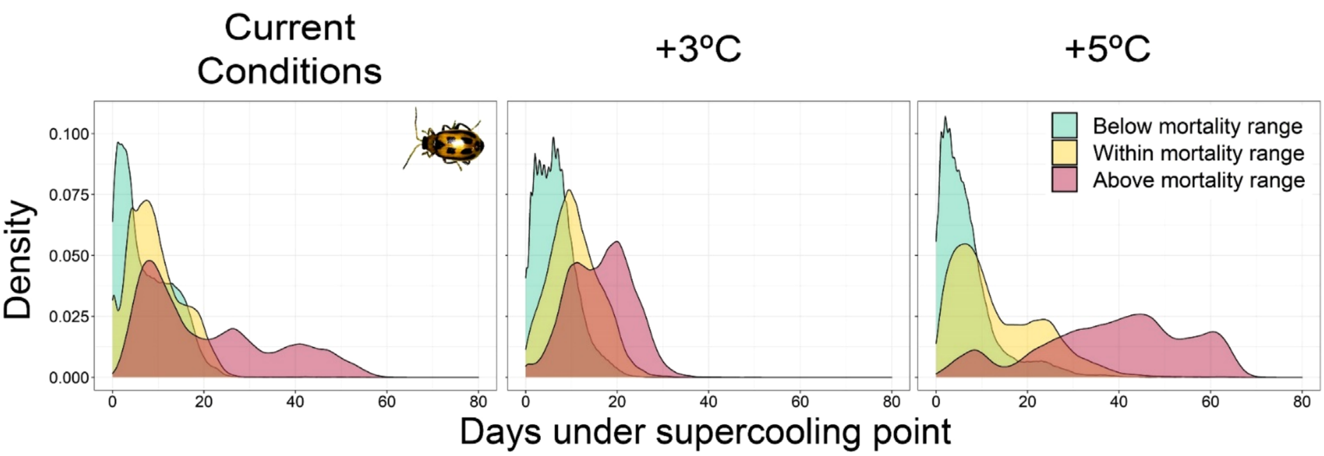


**FIGURE 5** | For three warming scenarios: Current conditions (i.e., no warming), warming of 3°C and warming of 5°C, density plots showing the overlap between the number of days during the winter season (1 December 2016 to 31 March 2017) with ground temperatures under the highest published supercooling point (−7.0°C, i.e., worst case) for bean leaf beetles (*C. trifurcata*) and the duration of consecutive days with ground temperatures at or below 0°C that would lead to 50% mortality based on experimental data extracted from Lam and Pedigo (2000). Lam and Pedigo (2000) found that the mean number of days until 50% mortality in a sample of *C. trifurcata* held at constant temperatures of 0°C was 34.6 days [28.9, 41.3]. 'Above mortality range' corresponds to consecutive sub −0°C days above this upper confidence limit of what *C. trifurcata* can withstand (i.e., least favourable scenario), 'Within mortality range' corresponds to consecutive sub −0°C days within the reported range for 50% mortality (i.e., moderate scenario), and 'Below mortality range' corresponds to sub −0°C days below the lower confidence limit of what *C. trifurcata* can withstand (i.e., most favourable scenario). Image of insect adapted from *Adult bean leaf beetle* by University of Nebraska-Lincoln, 2024, https://cropwatch.unl.edu/soybean-management/insects-bean-leaf-beetle Copyright 1869–2024 by University of Nebraska-Lincoln.

in the hundreds of billions of dollars (Gallai et al. 2009; Porto et al. 2020). Some pollinator species additionally help to control populations of pest species through predation (Hart and Bale 1998). Alternatively, pest species cause billions of dollars in damage to crops annually (Zalucki et al. 2012), with biocontrol efforts like pesticide applications causing declines in other animals, including insect pollinators (Raine and Gill 2015).

Decreases in pollinator populations have been well-studied, with pesticides, parasites and pathogens, habitat fragmentation and climate change among the most cited reasons for species declines (Cameron and Sadd 2020; Dicks et al. 2021). Similarly, the drivers of insect pest outbreaks have also received considerable attention and are most often attributed to land-use change (e.g., conversion to monoculture agriculture, urbanisation) and climate change (Dale and Frank 2017). For both pollinators and pests, however, studies on the effects of climate change have focused primarily on the impacts of heat waves and drought (Ju et al. 2015; Brown et al. 2016), rather than the consequences of a deteriorating subnivium (but see for example Marshall and Sinclair 2012; Berzitis et al. 2017; Huang 2017). Filling this gap in our knowledge is critical because overwintering survival and the fitness consequences incurred during overwintering likely represent important bottlenecks for the population dynamics of subnivium-dependent species (Woodard et al. 2019).

## 5 | Caveats

Our experimental approach for the collection of climate data focused on utilising active-warming greenhouses that were able to capture natural environmental variability in both winter precipitation (i.e., through the retractable roofs) and temperature (i.e., through communication between internal and external temperature sensors) (Thompson et al. 2021). While this method offered advantages, our ability to capture climate variability was constrained by our observation period: the winter season of 2016–2017. Although there is a high degree of uncertainty surrounding the expected frequency of extreme winter events like polar vortices in the future (Screen et al. 2018), it is possible that warming of 3°C could lead to increased variability in temperature and precipitation beyond the scope of our experimental design (Schimanke et al. 2013). Consequently, while our findings indicate a positive outlook for overwintering insects under warming of 3°C with reduced exposure to temperatures below their supercooling points, these results depend on the assumption that winter climate variability would resemble what was observed during the 2016–2017 season.

Our predictions also do not account for phenotypic plasticity. Thermal tolerance can be plastic (Schou et al. 2017); therefore, species with higher phenotypic plasticity in their thermal tolerance may be able to mitigate their responses to colder and more variable subnivium temperatures (Rodrigues and Beldade 2020). At the same time, evidence suggests that the magnitude of climate warming is likely to exceed the slightly broader tolerance ranges gained through phenotypic plasticity (Gunderson and Stillman 2015). Accordingly, phenotypic plasticity will likely not be wholly sufficient to buffer overwintering insects from changes in the subnivium.

## 6 | Conclusion

Cold tolerance is an essential component of insect fitness and one of the best determinants of species distributions (Sinclair et al. 2015); however, insect species exhibit considerable variation in their cold tolerance and overwintering strategies, as well as in their supercooling points and lower lethal temperatures (Sinclair et al. 2003). Consequently, despite the general trends we found of reduced vulnerability under warming of 3°C and increased vulnerability under warming of 5°C, interspecific variation in response to shifting subnivium temperatures still exists. This variation in overwintering vulnerability under different climate change scenarios will impact conservation plans for pollinators and mitigation plans for pests. Uncovering these species-specific responses will require additional data on the lower range of insect thermal tolerances, since currently this information—especially for some critical pollinators (e.g., *Bombus* spp.)—is limited (Sinclair et al. 2015). Equally important is the capacity to link thermal tolerance data with fine-scale data on microclimatic conditions. Through these efforts we can gain a better understanding of overwintering vulnerability for the diverse array of subnivium-dependent insects.

### Author Contributions

**Kimberly L. Thompson:** conceptualization, data collection, data curation, methodology, investigation, project administration, formal analysis, visualization, writing – original draft preparation, writing – review and editing. **Jonathan N. Pauli:** funding acquisition, resources, conceptualization, methodology, project administration, formal analysis, visualization, writing – review and editing. **Benjamin Zuckerberg:** funding acquisition, resources, conceptualization, methodology, project administration, formal analysis, visualization, writing – review and editing.


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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

Data to generate the spatial predictions of winter ground temperatures in the Great Lakes Region are publicly available, however, we provide all the data used in our analyses in a Dryad repository (https://doi.org/10.5061/dryad.4j0zpc8pk). Daily air temperature data were downloaded from Daymet (https://daymet.ornl.gov/); land cover data were downloaded from the United States Geological Survey's National Land Cover Database (https://www.usgs.gov/centers/eros/science/national-land-cover-database); daily snow depth and snow water equivalent data were downloaded from the National Snow and Ice Data Center's Snow Data Assimilation System Product (SNODAS, https://nsidc.org/data/g02158/versions/1#anchor-data-access-tools); and daily wind speed data were downloaded from the National Centers for Environmental Protection's North American Regional Reanalysis product (NARR, https://psl.noaa.gov/data/gridded/data.narr.html). Data on insect cold tolerances were extracted from published literature and are summarized in Table 1. Finally, the code to reproduce the analyses herein are available via the following link: https://github.com/kimberlylthompson/Overwintering-Insects_Publication.git.

### Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.70050.

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## Supporting Information

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