Bottom-up pathways for arthropods and forest breeding birds in a southern Ontario forest.

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Abstract

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Long-term avian population declines, particularly for the avian insectivore guild, are a conservation concern. With widespread and continuing population trends, climate change and its negative effects on avian food resources is a plausible cross-species driver. My goal was to evaluate whether bottom-up trophic effects of climate change could be influencing avian populations. I used a space-for-time approach to assess the influence of snowpack and soil moisture variability on arthropods and subsequent effects on nest survival. In the 2010 and 2011 growing seasons, I sampled arthropods, soil moisture (soil volumetric water content; VWC), snowpack (snow water equivalent; SWE), forest floor depth (L, F, H layers) and soil texture in conifer plantations and mixed deciduous forest in Southern Ontario's Ganaraska Forest (~4, 400 ha). I used additive linear mixed effects models to assess the responses of arthropod groups' (e.g., order or class) relative biomass (g/day) and abundance (count/day) to those variables. Influences for each arthropod group's biomass and abundance were typically in the same direction. Maximum annual SWE significantly positively influenced most arthropod groups and annual relative difference in VWC positively influenced one quarter. In mixed directions, forest type influenced half of the groups and soil texture and forest floor depth each affected less than one quarter. I then used structural equation models to evaluate relationships between SWE, VWC, the biomass of three arthropod functional guilds, and logistic-exposure model calculated daily nest survival rates for American Robin (*Turdus* *migratorius*), Eastern Wood-Pewee (*Contopus virens*), Least Flycatcher (*Empidonax minimus*), Ovenbird (*Seiurus aurocapilla*), and Red-eyed Vireo (*Vireo olivaceus*). Arthropod guilds included diet-based food, predaceous arthropods and soil-dwelling bioindicators. SWE significantly positively influenced food biomass in all five models and negatively influenced predaceous arthropods in three models. Soil moisture had a mix of positive, negative, and null effects. Eastern Wood-Pewee and Red-eyed Vireo nest survival positively related to food and negatively related to predaceous arthropod biomass. American Robin, Least Flycatcher and Ovenbird nest survival did not appear to be related to arthropod biomasses. Through bottom-up relationships, predicted climate change-induced reductions in snowpack may cause food resource declines and negatively affect some forest breeding bird populations.

Keywords: Nest survival, path analysis, structural equation model, arthropods, biomass, food supply, snowfall, soil moisture, climate change

Preface

My thesis chapters 2 and 3 are formatted with the intent to be submitted for publication and they have been formatted differently to meet the submission guidelines for different target journals. Throughout my thesis, I use “we” to refer to myself, future co-authors, and field and lab technicians. My field technicians and I performed the fieldwork and laboratory analysis, I performed the statistical analysis and writing with my thesis committee members providing oversight, input, critical review, and editing.

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Chapter 1: General introduction

1.0. Background

1.0.1. Avian population declines

Widespread and long-term avian population declines have been identified and are cause for conservation concern. For example, North America's eastern forest breeding bird abundance has declined by more than 166 million since 1970, approximately a 17% loss with more than 65% of species in decline (Rosenberg et al. 2019). Some groups such as aerial insectivores have shown greater declines than others (Blancher et al. 2009, Nebel et al. 2010, Smith et al. 2015). Spatially extensive and continuing population declines for many species suggest that broad-scale factors that are species independent are causing the declines (Smith et al. 2015).

Some of the stressors for avian populations include insecticides, habitat degradation and loss, pollution, and climate change on both the breeding and wintering grounds (Nebel et al. 2010, Spiller and Dettmers 2019, Nebel et al. 2020). For instance, avian insectivore declines have been linked to neonicotinoid insecticides (Hallman et al. 2014) and agricultural intensification (Murphy 2003), Acadian Flycatcher (*Empidonax virescens*) reproduction has been linked to mercury (Hg) pollution (Rowse et al. 2014), and North American aerial insectivore populations can be explained by a composite climate index (Michel et al. 2021). With widespread arthropod declines across multiple habitat types (Siebold et al. 2019), and coincidental avian declines (Spiller and Dettmers 2019) such as the decline of aerial insectivores (Blancher et al. 2009), bottom-up trophic cascades may be a key driver (Tallamy and Shriver 2021, Pearce-Higgins and Morris 2022).

The bottom-up relationship may be particularly influential for temperate forest insectivorous birds that have the highest arthropod consumption rate among all global biomes (Nyffeler et al. 2018). A meta-analysis of the relationships between food resources and avian fecundity showed a positive relationship and that effects were greater for forest breeding insectivores than for other avian guilds (Grames et al. 2023). Given the spatial and temporal scales of declines of both birds and insects and climate change trends, the effects of climate change are a plausible unifying factor (Nebel et al. 2020, Pearce-Higgins and Morris 2022). Within the avian literature the effect of climate change has been generally focused on temperature increases and phenological mismatches (Radchuk et al. 2019, Samplonius et al. 2021), but climate change can alter arthropod communities, subsequently affecting higher trophic levels (Lister and Garcia 2018). Therefore, climate change could be affecting forest breeding bird food resources causing negative population effects.

1.0.2. Avian populations and food resources

Food resources affect avian populations by influencing nest survival probability and recruitment (Duguay et al. 2000, Visser et al. 2006, Ruffino et al. 2014, Tallamy and Shriver 2021, Bailey and Bonter 2022). Clutch sizes (Cody 1966, Hussell and Quinney 1987, Arcese and Smith 1988) and nestling numbers (Wiehn and Korpimäki 1997) and the likelihood of double brooding (Nagy and Homes 2005) have all been positively related to food resources. Additionally, higher provisioning rates increase nestling growth rate (Visser et al. 2006, Ruffino et al. 2014) which reduces fledgling nest residency and nest exposure time and therefore the probability of being depredated (Duguay et al. 2000) as well as increasing survivorship after fledging (Martin et al. 2018).

1.0.3. Avian food resources and climate

In temperate forests, net primary production (NPP) is influenced by temperature, and non-winter and winter precipitation (Murphy et al. 2022), supporting primary consumers that facilitate the bottom-up trophic cascade (Prather et al. 2020). The most influential factors and responses of climate change will be different among ecosystems, and in North America's eastern temperate forests, winter is a major annual alteration that requires significant adaptation to survive (Nielsen et al. 2022) but results in substantial ephemeral resources (Both et al. 2010). Recognition of the influences of the effects of winter and subsequent ecosystem alterations is necessary to adequately appraise the potential consequences of climate change (Williams et al. 2015).

Climate model predictions for southern Ontario suggest that winter precipitation is likely to increase (McDermid et al. 2015, Zhou et al. 2017) with a commensurate and already observed change to a greater proportion of winter precipitation as rainfall rather than snowfall (McCabe and Wolock 2010, Notaro et al. 2014, Ahmed et al. 2022). The change in winter rainfall to snowfall proportions coincides with increasing warming in the coldest periods (McKenney et al. 2010). The result would be shallower, denser snowpack with shortened residency and stronger coupling of winter air temperature with ground surface and soil temperatures (Hardy et al. 2001, Williams et al. 2015, Reinmann et al. 2019). Loss of subnivean insulation can expose organisms to greater temperature fluctuations and deeper soil freezing which can increase arthropod mortality due to freezing during diapause or after early exit from diapause (Bale and Hayward 2010).

Climate models also predict that non-winter annual precipitation will not change, but that there will be less frequent rainfall events with more intensity (McKenney et al. 2010, Wang et al. 2015, Zhou et al. 2017, Vincent et al. 2018) and maximum temperatures will increase (McKenney et al. 2010). Therefore, growing season soil moisture could decline due to fewer rainfall recharge events, greater loss of potential soil recharge as surface runoff due to precipitation rates exceeding infiltration rates and higher evapotranspiration (Sheffield and Wood 2008, Seneviratne et al. 2010, McDermid et al. 2015). Furthermore, areas of southern Ontario with highly permeable predominantly sandy soil and little water holding capacity such as the Oak Ridges Moraine (Buttle 2011) require continuous recharge events to maintain soil moisture. The sum of these effects will result in reduced soil moisture which subsequently reduces a site's viability for arthropod oviposition, egg survivorship, and suitability for metamorphosis (Huk and Kühne 1999, Holland et al. 2007, Johnson et al. 2010, Parr and Bishop 2022). Additionally, soil moisture contributes to aboveground vegetative growth (Newman et al. 2006) which benefits arthropod herbivores (Wimp et al. 2010, Prather et al. 2020) and their predators. As a result, reductions in soil moisture could negatively affect arthropod biomass and therefore negatively affect nest productivity.

1.0.4. Research goal

My goal was to assess the potential effects of predicted climate change on forest breeding birds using a space-for-time approach by modeling responses to empirical observations. My overarching hypothesis was that bottom-up abiotic controls influence breeding bird nest survival through a relationship that is mediated by food resources. To realize this goal in a short -term study, I sampled abiotic factors across a study area and used the gradients of their variation as temporal analogues.

To achieve my goal, I divided the research into two main objectives. The first objective (Chapter 2) was testing the hypothesis that factors including snowpack, soil moisture, forest floor depth, soil texture, and date are influential for arthropod relative biomass and abundance sampled using pitfall traps during the main neotropical migrant breeding period from early May to the beginning of September. For the second objective (Chapter 3), I used structural equation models to test my hypothesis that there is a pathway linking snowpack and soil moisture to arthropod biomass and forest breeding bird daily nest survival rates.

1.1. Study area

1.1.1. The Ganaraska Forest

Southern Ontario's forests can be classified into 5 main forest types: upland tolerant hardwoods, upland oaks, lowland hardwoods, lowland conifers, and plantations (Elliott 1998). Following extensive deforestation of Southern Ontario due to European colonization and subsequent agricultural and urban development, less than 30% of the original forest cover remains and Red Pine (*Pinus resinosa*) plantations used to stabilize soil erosion and facilitate natural regeneration contribute substantially to that area (McPherson and Timmer 2002, Parker et al. 2008). My study site was in the Ganaraska Forest, Ontario (44°05'N, 78°30'W; hereafter 'Forest'), a 4, 443 ha natural area owned by the Ganaraska Region Conservation Authority (Powell 2017) and one of the largest areas of continuous forest in southern Ontario (Buttle and Farnsworth 2012). The Forest is composed of 30% plantations and 30% upland oaks/upland tolerant hardwoods (Powell 2017), providing a suitably large study area to stratify sampling within forest types that area representative of major areas of southern Ontario forest.

Forest uses include year-round motorized and non-motorized recreation, hunting, and rotational annual timber harvests applying selective silvicultural systems (Powell 2017). The Ganaraska Forest is also a significant groundwater recharge zone for the headwaters of waterways extending southward to Lake Ontario including the Ganaraska River (Powell 2017) and associated urban and rural areas.

1.1.2. The Oak Ridges Moraine

The Forest is situated on the Oak Ridges Moraine (hereafter 'Moraine') a glacial feature that extends ~160 km east to west approximately 15 km north of Lake Ontario. The Moraine is composed of diamicton, and fining-upward silt, sand and gravel, and the Forest is on a deep formation of sand, and mostly coarse and gravelly sediment up to 150 m thick with sandy and sandy loam Pontypool series surface soils (Barnett et al. 1998, Powell 2017). The Moraine's coarse soils and topography result in its importance as a water recharge zone for aquifers that feed headwaters that start on the Moraine and extend underground beyond its topographic boundary (Gerber and Howard 2002).

1.1.3. Study area climate

The Forest is in the Mixedwood Plains Ecozone's Lake Simcoe-Rideau Ecoregion (6E), a moderate temperature ecoclimatic region (Crins et al. 2009). From 1981 to 2010 at the Peterborough Airport weather station (44°14'N, 78°22'W; ~19.8 km) the daily average temperature was 6.2°C, average annual rainfall was 712.5 mm and average annual snowfall was 151.2 cm (Government of Canada 2023). On the Moraine, snowfall is approximately 17% (± 5%) of total annual precipitation (Buttle 2011). During the study period, a summary of daily precipitation data from Tapley (44°10'N, 78°30'W; ~9.6 km) weather station and temperature data from Peterborough Airport and Trent University (44°21'N, 78°17'W; ~34.3 km; Sept. 23 to Dec. 31, 2011) weather stations (Government of Canada 2023), indicated that the study area had 203.9 mm more total rainfall and 95.5 cm more total snowfall in 2011 than 2010, but similar average daily mean temperatures between years (Table 1.1).

Table 1.1. Summaries of total rainfall (mm), snowfall (cm), and average daily mean temperature (°C) for during the 2010 and 2011 study years using precipitation data from the Tapley weather station (44°10'N, 78°30'W) and temperature data from the Peterborough Airport (2010 and 2011 with some supplementary data for 2011 (September 23 to December 31) from the Trent University weather station (Government of Canada 2023).

	2010	2011
Total rainfall	771.3 mm	975.2 mm
Total snowfall **(first and last snowfall of snow year)**	84.9 cm (Nov. 30, 2009, to Mar. 20, 2010)	180.4 cm (Nov. 27, 2010, to Mar. 12, 2011)
Average daily mean temperature	7.8°C	7.2°C

1.2. Study design: space-for-time approach

Study designs to investigate the effects of climate change on ecological networks include experimental manipulation, long -term observations, or inference based on observed responses to gradients. The spatial scale required to assess effects on avian nest survival precludes an experimental approach and a long-term study is feasible but requires significant resources and duration beyond the scope of most studies. Using a space-for-time approach in which models using natural gradients are used to infer responses to future scenarios (Fukami and Wardle 2005) is a prospective solution as it addresses some limitations of long-term study designs.

The Ganaraska Forest provides an ideal location to perform a space-for-time investigation as it is a large area where many samples can be collected, but not so large that there are spatially covarying natural changes in conditions (Fukami and Wardle 2005), particularly major variation in ecosite composition. Surface soils are consistently sand dominated with variations that include smaller proportions of silt and minor proportions of clay. Thus, soil is rapidly drained, and moisture is dependent on recent precipitation. Increasing amounts of smaller particles (i.e., silt and clay) slightly increase water holding capacity causing small gradients without major shifts in ecosystem composition. Also, although vegetation composition is similar throughout the study area, variation in understory densities results in variation in hydraulic conductivity (Greenwood and Buttle 2014). Finally, canopy cover varies because of the interspersion of blocks of conifer plantations, mostly Red Pine, among mixed deciduous forest. Afforestation using conifer plantations began in the 1940's to mitigate significant erosion caused by clearing and cropping of marginal and sub-marginal agricultural land (Buttle 2011). Differing proportions of coniferous to deciduous canopy influence interception during non-winter rains (Buttle and Farnsworth 2012) and winter snowfall (Greenwood and Buttle 2018), but due to complex forest tree species compositional texture, avian nest territories typically include areas of deciduous forest and coniferous plantations. Additionally, topographic characteristics such as aspect, elevation, and slope can control snow accumulation and melt (Pomeroy et al. 1998, Jost et al. 2007), so the topographic variation within my study area (Fig. 2.3) adds to variation in snowpack.

As there are generally similar ecological conditions within forest types across my study area, gradients in snowfall and soil moisture facilitate assessments that are not confounded by ecological covariates that would exist if greater geographic dispersion of study sites was used to capture gradients. Furthermore, the magnitude of variation within the plot-to-plot gradients of soil moisture and snowpack I measured are likely representative of near-future conditions. Greater variation, such as including sites with no winter snow cover, would represent a distant future time where assumptions of concurrent ecosystem reorganization would be more complex, although such sites would provide more similar higher temperatures.

1.3. Chapter 2 background: abiotic gradients and arthropods

In Chapter 2, I used linear mixed effect models to assess the influence of snowpack, soil moisture, forest floor depth, soil texture forest type and a quadratic effect of date on relative biomass and relative abundance of arthropods collected using pitfall traps. Models included additive effects of independent variables and random effects of plot nested in year. For snowpack, I re-measured depth and snow water equivalent throughout the winter and used maximum snow water equivalent from within a year for each plot used in my sampling design. For soil moisture, I measured soil water content multiple times during the non-winter period and calculated a mean annual relative difference (decimal value) to create a scaled ranking of a plot's soil moisture relative to all other plots. I sampled soil at each plot to calculate the composition of sand, silt, and clay as well as measured forest floor depth. Applying the observed responses of arthropods to the gradients of independent variables measured across the study area, I qualitatively interpreted how the effect of climate change through less snowpack and drier soils may influence arthropods.

1.4. Chapter 3 background: arthropod biomass and nest survival

In Chapter 3, I used structural equation modeling to assess relationships between abiotic variables, arthropod biomass, and daily nest survival rates of American Robin (*Turdus migratorius*), Eastern Wood-Pewee (*Contopus virens*), Least Flycatcher (*Empidonax minimus*), Ovenbird (*Seiurus aurocapilla*), and Red-eyed Vireo (*Vireo olivaceous*; Figure 1.1). Structural equation modeling allowed me to evaluate the strengths and directionalities of relational pathways for the influence of climate change on nest survival rates.

Structural equation modeling (SEM) is a recommended method for space-for-time for gradient analyses to investigate causal relationships based on empirical observations (Fukami and Wardle 2005). Structural equation models include exogenous (independent) variables used to model relationship pathways with endogenous (dependent) variables. As well, they can include mediator variables that are both endogenous and exogenous that facilitate linked pathways. My hypothesized model (Fig. 1.1) was analyzed separately for each focal bird species and included annual maximum snow water equivalent (SWE; cm) and mean annual relative difference in volumetric water content (VWC) as exogenous variables to evaluate the influence of snowpack and soil moisture, respectively. The snowpack and soil moisture pathways led to arthropod biomass (g/day dry weight) mediators which included three functional groups: foods consumed by focal avian species, soil bioindicators and predaceous arthropods. The mediating biomass group pathways led to the endogenous variable daily nest survival rate.

To calculate daily nest survival rates, I used logistic-exposure modeling (Shaffer 2004) to assess a suite of temporal models that included iterations of additive combinations of year, Julian date, quadratic Julian date and nest stage for each species. The best-fitting model from the temporal suite was selected using the lowest AICc value (Akaike's Information Criterion corrected for small sample sizes), an information theoretic approach that uses likelihood estimation for model fit and penalizes the number of variables in the model. The best-fitting model was then combined with my sample plot locations as a grouping factor and used to calculate daily nest survival rates for each nest monitoring interval (effective observations). To link abiotic variables and arthropod biomasses to daily nest survival rates, I created a mesh of Thiessen polygons where boundaries are assigned mid-way between plots. Nests within those polygons were assigned that polygon's abiotic and arthropod sampling data.

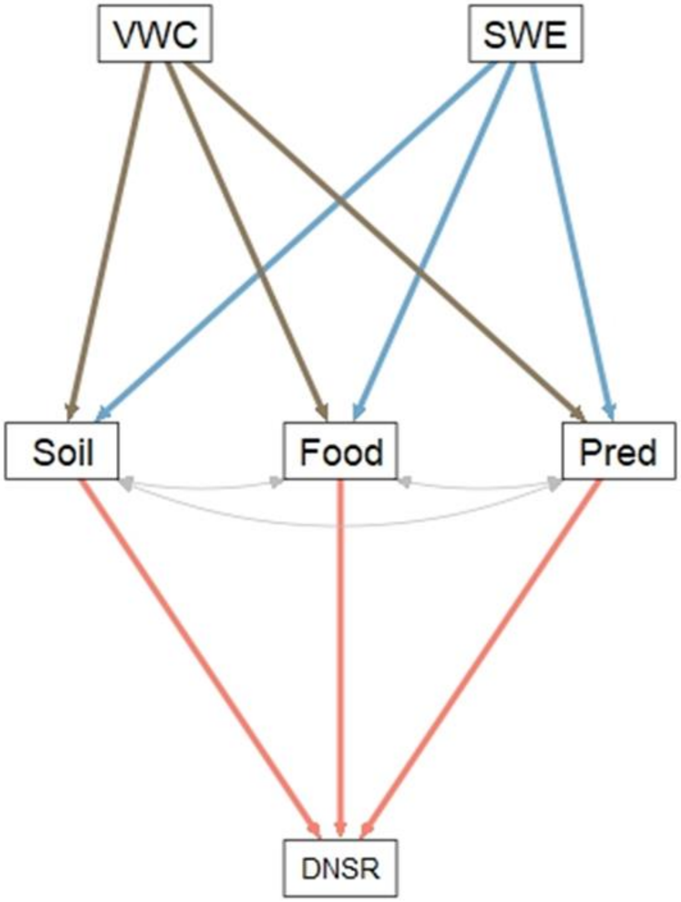

Figure 1.1. Diagram of structural equation model pathways used for daily nest survival rate analysis in Chapter 3. VWC = mean relative difference in soil volumetric water content (m^3 water / m^3 soil), SWE = maximum annual snow water equivalent (cm), Soil = biomass (g/day) of soil bioindicator arthropod functional group, Food= biomass (g/day) of arthropods in focal avian species diet, Pred= biomass (g/day) of predaceous arthropod functional group, DNSR = daily nest survival rate of focal avian species calculated using logistic-exposure modeling. Colours indicate pathways including specific variables to improve visualization (brown = VWC; blue = SWE; red = DNSR; grey= potential residual covariances).

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Chapter 2: Macroarthropods respond to climatic and habitat gradients in temperate conifer plantations and natural deciduous forest[1]

Keywords: Terrestrial macroarthropods, temperate forest, precipitation, snowfall, soil moisture, forest type, biomass, relative abundance, conifer plantation, deciduous forest

2.0. Abstract

2.0.1. Background

Climate change could alter ecosystem processes and trophic relationships. Arthropods which cycle nutrients, facilitate fungal and bacterial movement and resource availability, and are predators and prey could be affected by altered snowpack and soil moisture caused by predicted changes in precipitation and evaporation. From May to August 2010 and 2011, we used pitfall traps to sample macroarthropods in pine plantations and deciduous forest in the Ganaraska Forest (4, 443 ha) on the Oak Ridges Moraine, southern Ontario. We modeled arthropod relative biomass (g/day) and abundance (count/day), summed by order, family and composite total using additive combinations of forest type, soil texture, forest floor depth, snowpack (preceding year's maximum snow water equivalent), non-winter soil moisture (annual average relative difference in volumetric water content), and quadratic Julian date in linear mixed effect models.

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2.0.2. Results

Snowpack was the most influential variable, significantly affecting 10 out of 12 arthropod groups with positive effects for all but Acariformes. Soil moisture significantly positively influenced 4 out of 12 groups including total arthropods. Julian date was the second-most influential variable, affecting 9 out of 12 groups demonstrating a convex upward response of increase followed by decrease over the sampling period, except Collembola which increased over the sampling period. Forest type had a mix of influences for 7 of the 12 arthropod groups assessed with 4 arthropod groups having greater measures in deciduous forest and 3 having greater measures in coniferous forest. Soil texture and forest floor depth were the least influential variables (3 out of 12 groups each).

2.0.3. Conclusion

Climate trends and predictions in this study region suggest that winter precipitation will have an increased proportion of rain rather than snow and less persistent snowpack. Summer precipitation may increase but will occur in fewer and more intense rainfall events. In combination with higher summer temperatures causing greater evapotranspiration, the sandy soils of the study area may become drier. If these changes occur, the modeled responses to our observed gradients suggest potentially significant complex and negative effects for arthropod assemblages.

2.1. Introduction

Terrestrial arthropods influence forest ecosystems through their roles in herbivory, decomposition, mineralization, nutrient cycling, translocating organic matter, modifying soil structure, and altering microbial and fungal networks (Seastedt and Crossley 1984, Hassall et al. 1987, Zimmer 2002, Briones 2018, Brousseau et al. 2019, Menta and Remelli 2020). Arthropods are also predators and prey items, providing a significant source of nutrition to other arthropods, mammals, reptiles, amphibians, and birds while regulating lower trophic level populations (Polis et al. 1998).

Arthropod distribution and abundance are influenced by population-level controls such as prey and food availability (Brousseau et al. 2019), competitors, parasites, and predators (Polis et al. 1998, Ostfeld and Keesing 2000, Zhao et al. 2013) as well as habitat availability for hibernation, reproduction, and metamorphosis (Lövei and Sunderland 1996, Huk and Kühne 1999). Through ecological processes, arthropod community structure can also be attributed to bottom-up abiotic factors including air temperature, growing-season precipitation, relative humidity, snowpack depth and residency period, and soil texture (Williams et al. 2014, Torode et al. 2016, Briones 2018, Harris et al. 2019, Shao et al. 2021). Considering the wide array of ecological processes regulated by arthropods, spatial and temporal changes in community structure, abundance and biomass could significantly alter forest ecosystems in the face of current negative population and community trends (Harvey et al. 2022).

Misalignment between temperature and invertebrate thermal tolerance because of climate change has demonstrated the potential for severe vulnerability (Johansson et al. 2020). While more warm-acclimated species may benefit, increased temperatures may be detrimental for cold-acclimated species at the southern end of their geographic range (Fox et al. 2014). The results, especially in the short-term, can be de-stabilized community dynamics and not simply replacement of one species with another (Diamond et al. 2016). Although temperature has been a focal theme (VanDerWal et al. 2013), climate change will alter more than just mean, maximum and minimum annual temperatures, and envelope. Understanding the relationship of arthropods to other climatic factors such as winter and summer precipitation and concomitant snowpack and soil moisture in common temperate forest types will improve appraisal of the influence of less-studied climate metrics. Given the importance of arthropods to ecological processes and food webs, understanding the potential influence of additional climatic changes can improve inferred consequences for ecosystem dynamics.

In the northern Lake Ontario basin, annual precipitation and temperatures have been increasing (Zhou et al. 2017). In multiple climate model scenarios, summer precipitation is expected to decline or remain the same while current increases in summer temperatures are expected to continue (McDermid et al. 2015, Zhou et al. 2017). Summer precipitation is also becoming less frequent with more intense events resulting in lower infiltration and greater surface runoff (Wang et al. 2015, Zhou et al. 2017, Vincent et al. 2018). The result is that summer soil moisture is expected to decline (Sheffield and Wood 2008, Seneviratne et al. 2010).

Arthropod groups demonstrate sensitivity to changes in soil moisture (Seal and Tschinkel 2010, Brygadyrenko 2014, Torode et al. 2016). The directions of relationships are inconsistent as some responses are positive while others are negative and depending on the resolution of the modeling (e.g., species versus order) differences in abundance or biomass of arthropods may not be obvious. For instance, species with narrow habitat preferences may be replaced by generalists (Kirichenko-Babko et al. 2020) resulting in no evident change in biomass, abundance, or species richness. In some ecosystems, increased precipitation amounts can increase vegetation biomass and thus result in an increase in herbivores and their predators (Polis et al. 1998). As well, some invertebrates will select areas with high soil moisture for oviposition (Huk and Kühne 1999) and can require continuously moist soil to prevent desiccation (Parr and Bishop 2022), maintain egg viability (Johnson et al. 2010), and support emergence (Holland et al. 2007). In other situations, invertebrates may be more abundant at drier sites as they opportunistically feed on stressed vegetation (Berryman et al. 1987). For some arthropods, fluctuating soil moisture rather than increases or decreases alone may be the most important influence on abundance (Huhta and Hänninen 2001). Evidence of relationships may also be temporary as the relationship between wetness and herbivore arthropods may be strong until higher-level predators reduce and suppress those populations (Polis et al. 1998).

The Lake Ontario basin has been experiencing warmer winter temperatures, reduced cold periods, fewer frost-days and increased freeze-thaw days (Vincent et al. 2018). These trends, in addition to predicted unchanging or increasing amounts of winter precipitation, are expected to continue (McDermid et al. 2015, Zhou et al. 2017). Currently observed and projected continuing trends include substantial declines in annual snowfall, average snow depth and the number of days with snowpack as well as a shift to a greater proportion of winter precipitation as rain rather than snow (McCabe and Wolock 2010, Notaro et al. 2014, Ahmed et al. 2022). Increased temperatures and rain-on-snow events will cause reduced snowpack depth and denser snow (Penczykowski et al. 2017), resulting in poorer sub-nivean insulation.

Thermal insulation provided by the snowpack moderates sub-nivean temperature fluctuation associated with above snowpack air temperature and prevents colder soil temperatures, deeper frost depth, and freeze-thaw cycling (Hardy et al. 2001, Reinmann et al. 2019). Resultant exposure of forest floor arthropods to the loss of insulating snowpack may result in greater mortality and therefore reduced habitat availability. Effects may be more pronounced for species that exit diapause in response to higher temperatures and then are exposed to lethal temperatures without adequate biochemical preparation (Bale and Howard 2010). Cold-hardy species with high freeze tolerance are expected to benefit from earlier melt as they will have a longer active period, but biochemically cold tolerant species that use a freeze avoidance strategy may not realize the same benefits (Bale and Hayward 2010). Furthermore, lower snowpack depth and shortened duration of snow cover would result in less contribution of melt to initial growing season soil moisture (Hardy et al. 2011). Earlier timing of that melt contribution could also potentially cause a mismatch with food source phenology or life stage moisture requirements (Huk and Kühne 1999).

In addition to climatic influences, arthropod communities can be influenced by spatial and temporal covariates such as forest type, forest floor depth and soil texture for provision of food, hibernation, and oviposition sites. For instance, beetles (Order Coleoptera) are more abundant in deciduous forest than coniferous forest (Neuvonen et al., 2012 Ulyshen and Hanula 2009), whereas slugs (Order Gastropoda) have shown the opposite pattern (Kappes and Schilthuizen 2014) and some wasps (Order Hymenoptera) have not exhibited any relationship to different forest types (Ulyshen et al. 2011). For herbivores and decomposers, the effect of forest type could be due to differences in palatability (Brousseau et al. 2021) between the presence of considerably less lignin and somewhat less cellulose in the leaves of some deciduous species such as Sugar (*Acer saccharum*) and Red Maple (*Acer rubrum*) compared with the conifers such as Red and White Pine (*Pinus resinosa* and *Pinus strobus*; Aber et al. 1990). As leaf litter, these species become part of the forest floor's litter, fibric and humic components and part of the ground-level food web (Krishna and Mohan 2017) as well as contributing to moderating soil moisture evaporation (Harris et al. 2019). Soil texture and its associated water holding capacity is also an important regulator of soil moisture, but also influences habitat suitability for arthropods (Crawford 1988) by supporting arthropod movement or related vegetation. In addition to spatial covariates, temporal covariates can influence arthropod populations as abundance sampled using pitfall trapping have demonstrated increases followed by decreases over the growing season (Crowley et al. 2023).

Our objective was to model the influence of the climate-regulated abiotic variables snowpack (snow water equivalent) and soil moisture (volumetric soil water content), and covariates of forest type, soil texture, forest floor depth and date on arthropod relative abundance and biomass in two common Southern Ontario upland forest types (upland tolerant hardwoods and red pine plantations). We hypothesized that non-winter soil moisture and winter snowpack will influence arthropod relative abundance and biomass. Our modeling used the responses of coarse phylogenetic groups, as family-level arthropod groups have demonstrated differing responses to climate variables, including differing responses between habitats (Høye et al. 2021). We predict that arthropod relative biomass and abundance will be positively related to winter snowpack, modeled using annual maximum snow water equivalent, and growing season soil moisture, modeled as relative difference in soil volumetric water content. In addition to snow and soil moisture parameters, our models included soil texture, as a greater proportion of silt and clay increases water retention capacity and therefore results in prolonged moisture retention and may also be an influence on arthropod habitat suitability. We also included forest floor depth as it is an important control of invertebrate populations by moderating soil moisture fluctuation as well providing habitat and food and is identified as a variable that should be analyzed along with soil moisture (Harris et al. 2019).

2.2. Materials and methods

2.2.1. Study area

Our study was carried out from April through August in 2010 and 2011 in the Ganaraska Forest (hereafter 'Forest'), Ontario (44°05'N, 78°30'W; Fig. 2.1). The Forest is a 4, 443 ha natural area owned by the Ganaraska Region Conservation Authority and one of the largest blocks of continuous forest in southern Ontario (Buttle and Farnsworth 2012). The Forest is located on the Oak Ridges Moraine (hereafter 'moraine') which extends ~160 km east to west, parallel to Lake Ontario and is composed of diamicton and fining-upward silt, sand, and gravel. Within the moraine, the Forest is at the westernmost extent of the Pontypool Wedge, one of the Moraine's four wedge shaped bodies, composed of more coarse and gravelly sediment than other parts of the moraine (Barnett et al. 1998). The study area is composed of rapidly drained sand and is therefore very dry and soil moisture is largely controlled by recent soil wetting events (Buttle et al. 2014). The Forest is composed of 30% conifer plantations and 30% upland oaks/upland tolerant hardwoods (Powell 2017) with other forest types such as lowland hardwoods and conifer lowlands composing the remainder.

The Forest is in the Mixedwood Plains Ecozone's Lake Simcoe-Rideau Ecoregion (6E), a moderate temperature ecoclimatic region (Crins et al. 2009). From 1981 to 2010, the daily average temperature was 6.2°C, average annual rainfall was 712.5mm and average annual snowfall was 151.2 cm (Peterborough Airport weather station: 44°14'N, 78°22'W; Government of Canada 2023). During the study period, there was a similar average annual daily mean temperature between years (Table 2.1 and Fig. 2.2; Peterborough Airport and Trent University [44°21’N, 78°17’W; September 23 to December 31, 2011] weather stations; Government of Canada 2023). There was 203.9 mm more total rainfall (Fig. 2.2) and 95.5 cm more total snowfall (Fig. 2.3; Tapley weather station: 44°10’N, 78°30’W; Government of Canada 2023) in 2011 than 2010 (Table 2.1).

In the 2010 (May 10 to August 30) and 2011 arthropod sampling periods (May 17 to August 24), average daily mean temperatures were 18.7°C (range = 4.5°C – 26.2°C) and 18.9°C (range = 11.6°C – 24.4°C), respectively. Total rainfall during the arthropod sampling period (Fig. 2.2) was 377.3 mm in 2010 and 390.4 mm in 2011 and average rainfall per day on days with precipitation during that period was 9.7 mm (*SD* = 8.5 mm, *n*= 39) in 2010 and 10.0 mm in 2011 (*SD* = 13.8 mm, *n*= 39).

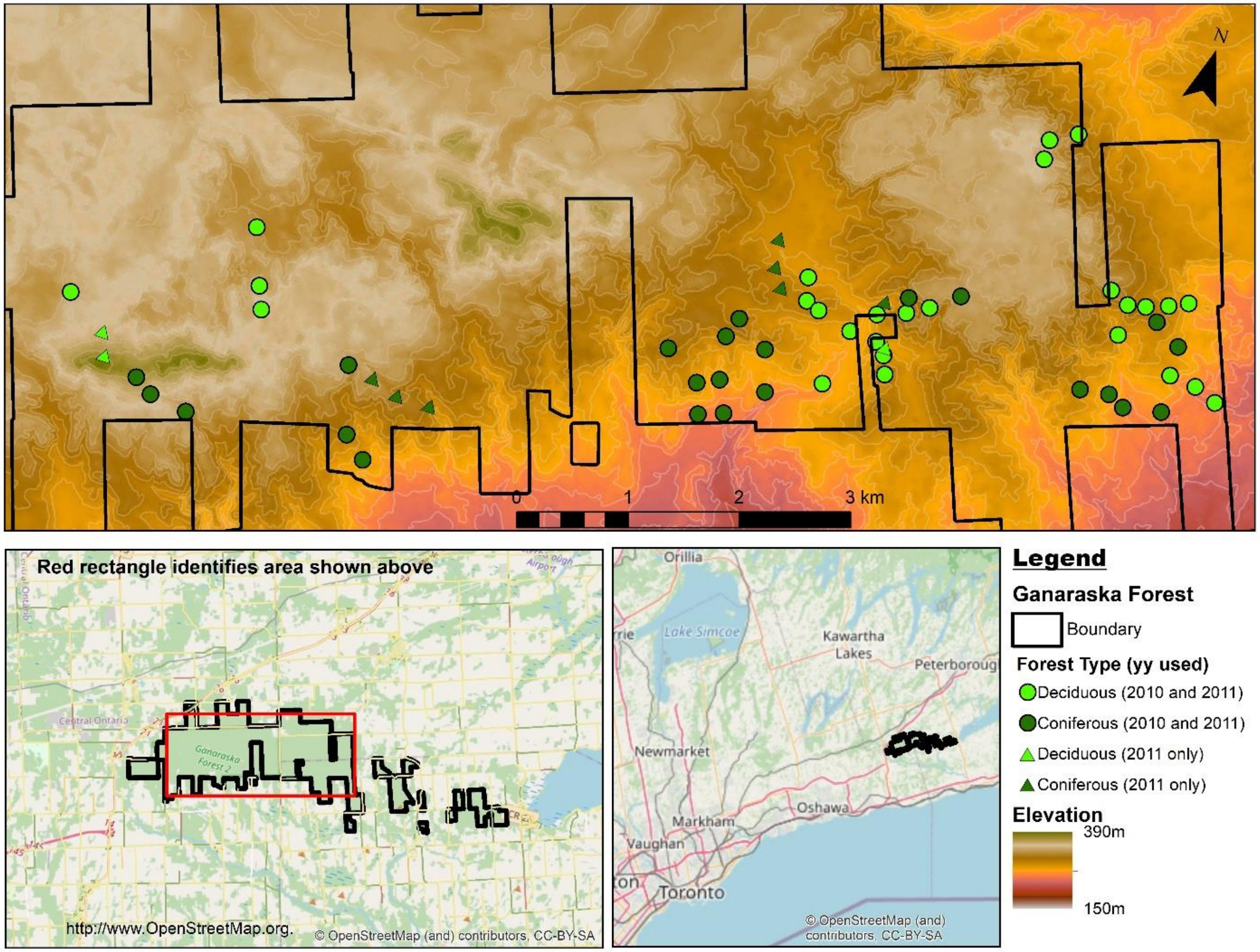

Figure 2.1. Location of the Ganaraska Forest study area as well as sample plot locations (see Fig. 2.4 for sampling layout) within the study area.

Table 2.1. Summaries of total rainfall (mm), snowfall (cm), and average daily mean temperature (°C) during the 2010 and 2011 study years using precipitation data from the Tapley weather station (44°10’N, 78°30’W) and temperature data from the Peterborough Airport (2010 and 2011 with some supplementary data for 2011 (September 23 to December 31) from the Trent University weather station (Government of Canada 2023).

	2010	**2011**
Total rainfall	771.3 mm	975.2 mm
Total snowfall **(first and last snowfall of snow year)**	84.9 cm (Nov. 30, 2009, to Mar. 20, 2010)	180.4 cm (Nov. 27, 2010, to Mar. 12, 2011)
Average daily mean temperature	7.8°C	7.2°C

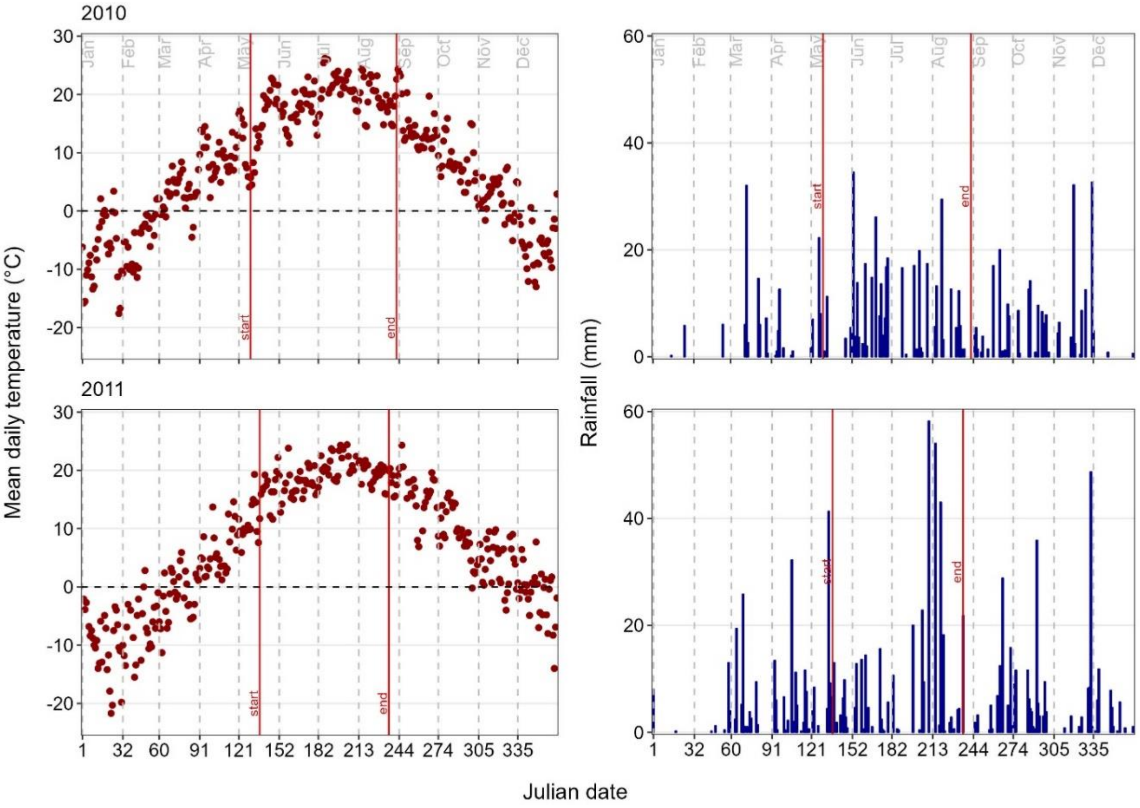

Figure 2.2. Mean daily temperature (°C; left) from the Peterborough Airport (44°14’N, 78°22’W) and Trent University (44°21’N, 78°17’W; September 23 to December 31, 2011) weather stations and total rainfall (mm; right) per day from the Tapley weather station (44°10’N, 78°30’W; Government of Canada 2023) in 2010 and 2011 (Julian day 1 = January 1). Red lines indicate start and end dates for that year’s arthropod pitfall trap sampling.

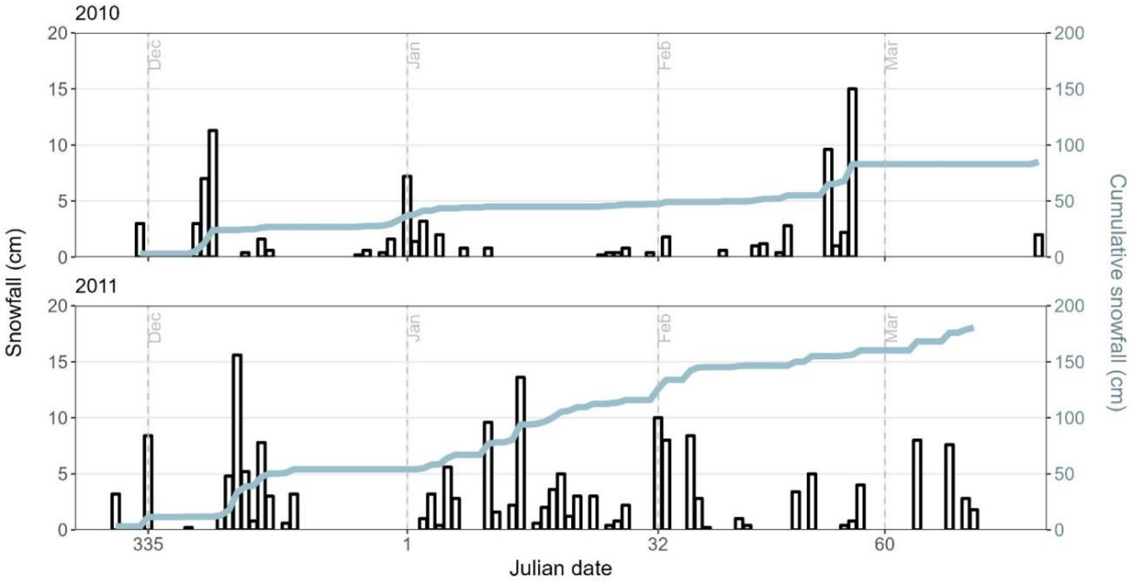

Figure 2.3. Total daily snowfall (cm; black hollow bars and left axis) and cumulative annual snowfall (cm; light blue line and right axis) for the winters of 2010 and 2011 (Julian day 1 = January 1) from the Tapley weather station (44°10’N, 78°30’W; Government of Canada 2023).

2.2.2. Sample sites

Sample sites (18 m x 18 m)were selected as triplets along an elevational gradient within a common slope and forest type. The original intent of this study design was that a topographically controlled moisture gradient would facilitate variation with the highest elevation of the triplet being drier and the lowest elevation being wetter, which would also require consideration for spatial autocorrelation. Data exploration prior to analysis showed no consistent topographic pattern; thus, we treated each sample site as distinct and not nested within a slope. Median distance to the nearest neighbouring plot (calculated using package spatstat.geom v3.0-6; Baddeley *et al.* 2023) was 212 m (range: 137 to 967 m) in 2010 and 214 m (range: 77 to 526 m) in 2011. Sample site elevations ranged from 215 m to 375 m a.s.l. We collected forest composition, forest floor depth, soil texture, snowpack, and soil moisture data (Fig. 2.4) at 50 sites (23 coniferous and 27 deciduous) in 2010 and 60 sites (30 of each coniferous and deciduous) in 2011 (Fig. 2.1). We measured 50 of the same sites in both years and 10 additional sites in 2011 to create an even number of sample sites.

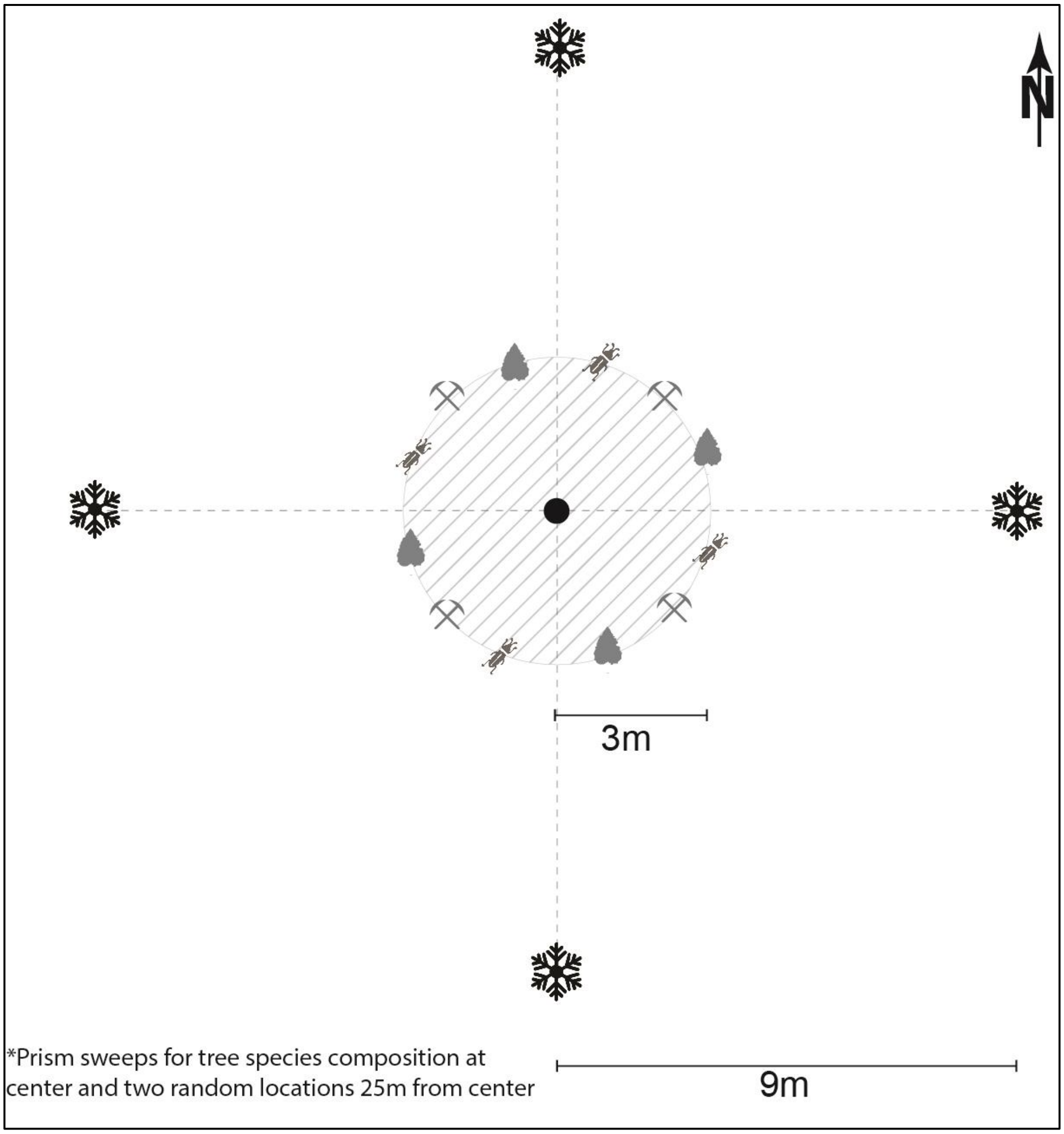

Figure 2.4. Sampling layout used for soil volumetric water content (black center circle), snowpack surveys (snowflake icons with dashed transect lines), and the area where random sampling for forest floor depth, soil texture and pitfall trapping was located (dashed circle filled diagonal lines and surrounded by leaf, beetle and pickaxe icons). Forest composition sampling using a basal prism was performed at the center point as well as 25m from the center point in two random directions.

2.2.3. Forest type

We used a 2X basal area angle prism (variable radius sampling) and averaged 3 samples (one at the site center and two at 25 m in random directions from the center) to calculate tree (> 10 cm diameter at breast height) species composition at each sample site. Dominant tree species (highest percent composition) at plots were Red Pine (n = 30 plots), White Pine (n = 1 plot), Sugar Maple (n = 11 plots), Red/Black Oak (*Quercus rubra*/*velutina*; n = 16 plots), Trembling Aspen (*Populus tremuloides*; n = 1 plot), and White Birch (*Betula papyrifera*; n = 1 plot).

There was a clear distinction in tree species composition between Red Pine plantations and deciduous sites, but we used Principal Components Analysis (PCA) with covariance matrix to assess distinctiveness and potential variable reduction of forest composition using proportions of dominant genera. Dominant genera additively included the percent composition of other species in that genus including Red/Black Oak, Bur Oak (*Quercus macrocarpa*), and White Oak (*Quercus alba*) in Oak spp., Sugar Maple and Red Maple in Maple spp., Red Pine, Scots Pine (*Pinus sylvestris*) and White Pine in Pine spp., Trembling Aspen and Largetooth Aspen (*Populus grandidentata*) in Poplar spp., and White Birch as Birch spp. We found that PC1 explained 75% of variation and PC2 explained 19% of variation. PC1 loadings differentiated between deciduous and coniferous groups (positive values indicated sites with more conifer), while PC2 loadings differentiated between oak and maple proportions (positive values indicated sites with more oak and less maple; Table 2.2). As we were trying to reduce the number of variables and simplify models, we recognized the strong influence of coniferous versus deciduous forest type on PC1 and therefore used them as model factor levels instead of PC scores.

Table 2.2. Components loadings from PC1 and PC2 which explained 75% and 19% of the variation, respectively, in basal area composition at plots in the Ganaraska Forest, Ontario.

Genus Group	PC1	PC2
Pine spp.	0.87	0.02
Oak spp.	-0.38	0.65
Maple spp.	-0.30	-0.76
Poplar spp.	-0.07	0.01
Birch sp.	-0.03	-0.00

2.2.4. Forest floor depth

We measured forest floor depth (mm; L,F,H organic matter layers) at three random locations within 3 m of each sample site's center one time from August through September. Depth from the top of the leaf litter layer to the top of mineral soil was measured at each corner of a 50 cm x 50 cm quadrat using a thin transparent ruler to the nearest mm and averaged for each site.

2.2.5. Soil texture

Soil texture was assessed at the same location as the first forest floor measurement quadrat by digging a pit with a 50 cm x 50 cm opening to the bottom of the A horizon. Four soil samples were collected from the exterior walls at approximately the middle depth of the A horizon using a 101.79 cm^3 (4.76 cm dia. opening x 5.72 cm length) metal cylinder inserted horizontally into the pit walls. Samples from each plot were combined and air dried and we averaged the composition of sand, silt, and clay (Heck et al. 2017) from 2 subsamples, measured using a laser particle size analyzer

(Horiba Partica LA-950V2, Japan). As clay was a minor component of soil texture (≤ 3.5% in all samples; Fig. 2.5), we used the percent composition of sand as an independent variable in tests.

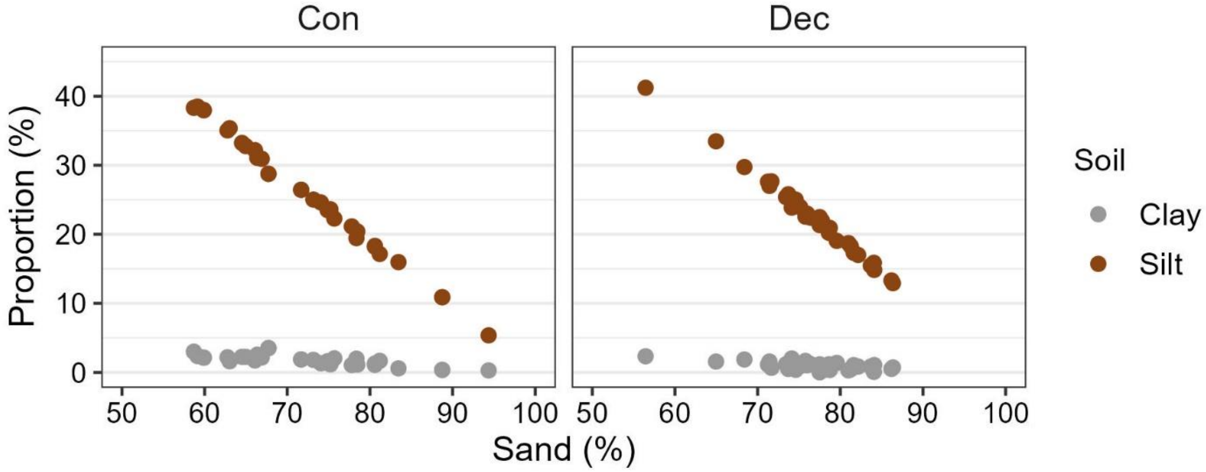

Figure 2.5. Proportions (%) of clay (grey), silt (brown) compared to sand (x-axis) in coniferous (Con) and deciduous (Dec) forest plot soil textures.

2.2.6. Snow water equivalent

We used a metric prairie snow sampler (Geo Scientific Ltd., Vancouver, BC, Canada) to measure snow depth (to nearest 0.5 cm) at 3, 6, and 9 m as well as snow water equivalent (SWE; cm) at 9 m from sample site centers in each cardinal direction. We calculated snow density (g/cm^3) using the 9 m samples. We ensured that previous sampling and traverses did not affect measurements by making minor adjustments to the sample point when necessary. We repeatedly measured snow throughout the winter season, particularly after major precipitation events from Jan 26 (Julian day 26) to March 18 (Julian day 77) in the 2010 snow year and December 21 (Julian day -10) to April 12 (102) in the 2011 snow year. We collected 94 (n = 376) and 232 (n=928) averaged measures at coniferous plots and 120 (n = 480) and 227 (n=908) averaged measures at deciduous sites in 2010 and 2011, respectively. We averaged each site's four measures of SWE and 12 measures of depth and tested the correlation between annual maximum measurements of depth and SWE. We found that annual maximum snow depth and maximum SWE were highly correlated in 2010 (r = 0.89, n = 50) and 2011 (r = 0.81, n = 60) and in both years combined (r = 0.90, n = 110). We selected maximum annual average SWE (cm; MaxSWE) as an independent variable in modeling as it is a commonly collected snow measure and provides a composite value of snow depth and density.

2.2.7. Soil moisture

We used a time domain reflectometry probe (Delta-T Devices Ltd. PR2 Profile Probe (Cambridge, England) to estimate subsurface volumetric soil water content (m^3 water/m^3 soil; VWC). Measurements were repeatedly collected at the same locations through permanently installed access tubes at the sample site centers. Volumetric water content for the upper 20 cm of the soil column was calculated by averaging measures from the 10 cm and 20 cm depth sensors. In 2010 and 2011, sampling was performed from May 4 (Julian day 124) to August 30 (Julian day 242).

Due to access tube ground contact errors and defective moisture sensors, we used fixed effects OLS estimation (R package ‘fixest', Bergé, 2022) to fill as many missing samples as possible. Using the best fitting singular and additive combinations of surface, 10 cm, 20 cm, and 30 cm deep measures and depending on available data (Table 2.3), we estimated 22 of 207 volumetric water content values in 2010 and 9 of 467 values for 2011. To collect surface data, we used a Delta-T Devices ML2 ThetaProbe, but we did not include it as an independent variable in models due to a strong correlation with subsurface measures (r = 0.90).

Table 2.3. Linear regressions used to estimate missing 2010 and 2011 VWC where the subscript number indicates the depth measurement location in cm and s indicates surface measurement.

Predicted value	Model variables	R^2	# predicted (2010)	# predicted (2011)
VWC_{10}	VWC_s	0.82	7	4
VWC_{10}	VWC_{20}	0.80	3	1
VWC_{10}	$VWC_s + VWC_{20}$	0.88	3	1
VWC_{20}	VWC_{30}	0.87	5	0
VWC_{20}	VWC_s	0.81	4	3

To reduce model complexity and improve interpretability, we scaled plot VWC's to provide a measure of a plot's moisture that was relative to all others. We first calculated a plot's relative difference in soil moisture within each month of the sampling period. Where the volumetric water content of a site is θ_S and the monthly average volumetric water content among all sites is $\theta_{\bar{x}}$, the monthly relative difference in soil moisture for each site was calculated using:

$$\frac{\theta_S - \theta_{\bar{x}}}{\theta_{\bar{x}}}$$

The resulting values were positive (above average moisture) and negative (below average moisture) and their size relates their comparative amount of wetness or dryness. Then, we calculated mean annual relative difference in volumetric water content (rdVWC) by averaging each site's values among all months within a year. We tested within-site pairwise correlations of each site's monthly and annual relative differences and found strong correlations between all month and year combinations ($r \geq 0.8$). Therefore, to reduce model complexity we retained rdVWC for each site within each year to use an independent variable and as there was moderate correlation of interannual rdVWC ($r = 0.67$) for sites sampled in both years, we used each year's annual average. In addition to providing readily comparable and interpreted relative soil moisture value for each site, rdVWC allowed for the analysis of a plot's arthropod data regardless of missing monthly moisture values due to sampling gaps.

2.2.8. Arthropod sampling

Arthropods were sampled using pitfall traps (clear plastic containers with 11.43 cm dia. opening) filled with water, a few drops of dishwashing soap to break the surface tension, and approximately 25% ethyl alcohol to reduce the potential for decay during the trapping period. In 2010, we installed 4 pitfall traps in random directions and a random distance within 3 m of the sample site center and sampled arthropods from May 10 (Julian day 130) to August 30 (Julian day 242). In 2011, we installed 3 traps per plot and sampled arthropods from May 17 (Julian day 137) to August 24 (Julian day 236). Counts were averaged among each site's pitfall traps per sampling period to correct for differences in the number of traps sampled within. Inconsistent trap numbers within a plot per period were the result of discarding samples from traps disturbed by wildlife or that had improperly set depth or soil contact around their opening at the time of collection. Macroarthropods were then transferred to storage bags and frozen in ethanol until laboratory identification.

Pitfall traps may be more of a reflection of activity rather than abundance or density (Williams et al. 2014), but our intent is a relative assessment of the influence of independent variables during the sample sampling period rather than reporting population predictions. We assessed 174 coniferous and 189 deciduous samples aggregated by sample site and sampling period in 2010 and 103 coniferous and 100 deciduous aggregate samples in 2011. Rounded to the nearest full day, traps were set for an average of 8 days (range 2 to 16 days) in 2010 and 7 days (range 5 to 13 days) in

2011. The mid-point of the trapping period was used as the Julian date in analyses with January 1 being Julian day 1 within each year.

Similar to Williams et al. (2014), samples were coarsely identified and grouped into the following classes: Chilopoda (Centipedes), Diplopoda (Millipedes), and Gastropoda (separated as Snails and Slugs), Symphyla (Pseudocentipedes), superorders: Acariformes (Mites), and orders: Araneae (spiders), Coleoptera (Beetle separated as adults and larva), Collembola (Springtails), Diptera (true flies separated as larva and adults), Haplotaxida (Earthworms), Hemiptera (True Bugs as larva and adults), Hymenoptera (Wasps and Sawflies) with family Formicidae (Ants) separated, Isopoda (Suborder Oniscidea: Woodlouse), Lepidoptera (Butterflies and Moths with larva and adults separated), Neuroptera (Net-winged insects), Opiliones (Harvestmen), Orthoptera (Crickets and Grasshoppers). For modeling, Chilopoda, Diplopoda, and Symphyla were combined into Subphylum Myriapoda due to morphological similarity (Fernández et al. 2016).

Each arthropod counted was classified into a length category, typically by 3 mm intervals up to 19 mm and then a single category for body lengths ≥20 mm. Biomass was calculated using oven-dried mass for each arthropod group’s body lengths measured for a previous unpublished study in the Ganaraska Forest (Walters 2008). Where a length and mass combination were unavailable, we used the average of the mass from immediately larger and smaller intervals or OLS estimation if averaging was not possible. As values had been converted to average relative abundance per plot day, biomass values represented relative average mass per plot per day (g/day).

We tested models for groups encountered on more than 25% of sampling (i.e., average of > 0 individuals/plot/trapping period) as well as a total for all groups combined. Models included (% of samples encountered), Coleoptera Adults (98%), Diptera Adults (91%), Collembola (88%), Gastropoda – Slugs (83%), Hymenoptera – Ants (77%), Araneae (67%), Coleoptera Larva (59%), Gastropoda – Snails (55%), Chilopoda (55%), Diplopoda (55%), Acari (54%), Hymenoptera- non-Ant (43%), Orthoptera (41%), and Haplotaxida (26%). We did not test models of Lepidoptera Adults (13%), Lepidoptera Larva (13%), Opiliones (13%), Hemiptera Adults (12%), Isopoda (7%), Hemiptera Larva (5%), Symphyla (3%), Diptera Larva (1%), Neuroptera Adults (1%), or Neuroptera Larva (< 1%) as they did not meet this threshold.

2.2.9. Statistics

We assessed the additive influence of forest type, rdVWC, forest floor depth, soil texture, MaxSWE and the quadratic effect of Julian date (Julian date + Julian date^2) on arthropod relative biomass (g/day) and relative abundance (count/day) using a linear mixed effect model (package lme4 v1.1.28; Bates *et al.* 2022) with REML estimation. Prior exploratory visual analysis of trends within and between independent and dependent variables did not suggest any interactions. Most trends appeared linear, but we included a quadratic term of Julian date as there appeared to be some convex upward patterns in the abundance of some arthropod groups with mid-summer peaks related to date. We used the lmerTest package (v3.1-3; Kuznetsova et al. 2022) to evaluate *p* values for *t* test statistics using Statterthwaite's method of approximation for calculating mixed effect model degrees of freedom (Kuznetsova et al. 2017). We also extracted parameter coefficients and confidence intervals using the broom.mixed package (Bolker and Robinson 2022) and fitted those estimates using the ciTools package (Haman and Avery 2020). We considered *p* values < 0.05 statistically significant and performed all analyses were using the R statistical software version 4.1.00 (R Core Team, 2021) in RStudio version 1.4.1717 (RStudio Team, 2021).

We included year and site nested in year as random effects to partition unmeasured interannual causes of variance and to account for unexplained within site variation from repeated sampling of the same trap locations. Random terms were modeled as unobserved sources of variation where each factor level had its own intercept with pooled variance (Bates et al. 2015). We included year as a random effect even though it had 2 levels as it could contribute additional unexplained variation and was not an *a priori* selected fixed effect. When random effect singularity occurred, we removed year and retained site as a sole random factor as the small number of levels for year did not contribute to variation among pooled intercepts (Oberpriller et al. 2022).

We visually assessed residuals for normality, homogeneity of variance and homoscedasticity using histograms, q-q plots, and plots of predicted versus observed residuals (Zuur et al. 2009) for each model. Residuals were often skewed due to the large number of zeroes or small counts, so we transformed dependent variables using $\log_{10}$ + 0.01 to 0.00001 depending on the biomass values and $\log_{10}$ + 0.1 for relative abundance. Models of Coleoptera larva, Orthoptera, non-ant Hymenoptera, Diplopoda, Araneae, and Haplotaxida failed to meet the assumptions of variance normality and homoscedasticity after transformations, so they were not tested. Chilopoda and Snails were only modeled using relative abundance as biomass model residuals did not meet statistical assumptions.

2.3. Results

2.3.1. Summary of independent variables

Among forest types, we found a significant difference in forest floor depth and a non-significant difference in soil texture. Forest floor was significantly deeper ($t = 4.15$, df = 58.0, $p < 0.001$) in coniferous forest than deciduous forest (Fig. 2.6). Deciduous forest soils had a slightly greater, but non-significant ($t = -1.94$, df = 50.9, $p = 0.058$) average proportion of sand than coniferous forest (Fig. 2.6).

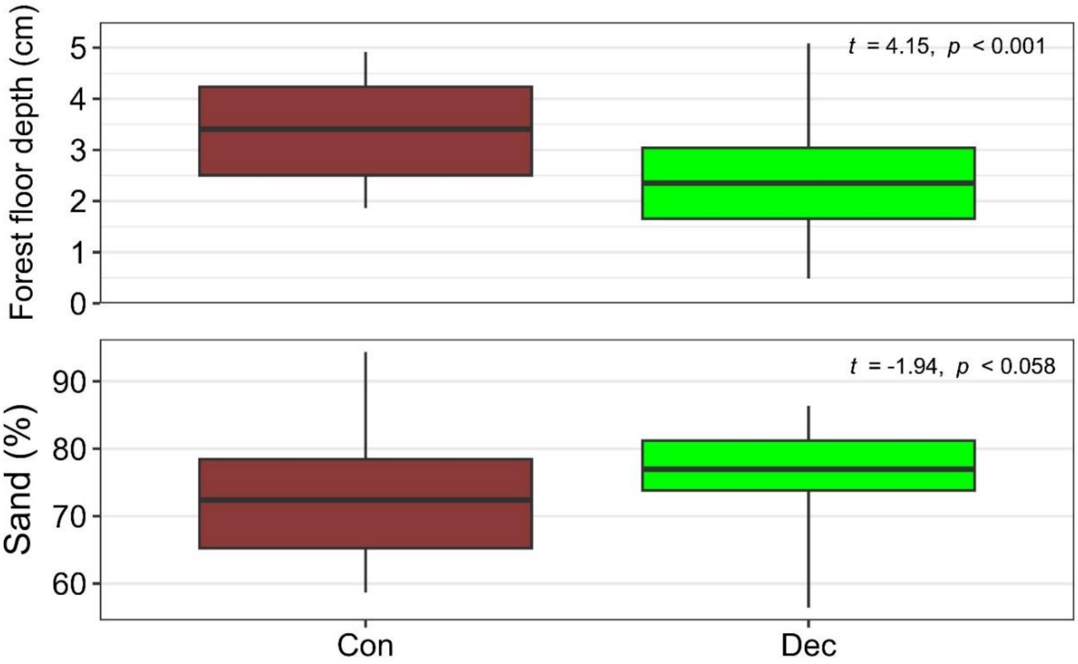

Figure 2.6. Comparisons of forest floor depth (cm; top figure) and percent sand composition (%; bottom figure) between coniferous (Con; brown) and deciduous (Dec; green) forest sites. Boxplot horizontal lines are medians, box limits are first and third quartiles and vertical lines are minimum and maximum range. Results of *t*-tests between forest types are shown.

Between May 1 and August 31, average volumetric water content was somewhat higher in deciduous forest compared to coniferous forest within years although there was less of an absolute difference in 2011 (Table 2.4). Within forest type variability (standard deviation) was nearly the same within years. The patterns for rdVWC are similar, although median relative difference values show that coniferous sites had generally below average soil moisture in 2010 (median = -0.093, range = -0.660 – 0.570, *n* = 23) whereas deciduous forest median soil moisture was slightly above the 2010 average (median = 0.032, range = -0.683 – 0.708, *n* = 27; Fig. 2.7). In 2011, median coniferous (median = 0.012, range = -0.644 – 0.660, *n* = 30) and deciduous (median = 0.070, range = -0.689 – 0.565, *n* = 30) soil moistures were both above and closer to the overall average (Fig 2.7). Linear modeling of the additive effects of year, forest type, and cubic Julian date terms suggested that there was no significant difference in VWC between years ($p = 0.18$) or forest types ($p = 0.07$), although there were significant polynomial (cubic) effects of Julian date (estimate = -0.3884, $p < 0.001$), Julian date^2 (estimate = 0.3024, $p < 0.001$) and Julian date^3 (estimate = 0.2354, $p < 0.001$) with soil moisture highest in May, declining into July and then increasing through August (Fig. 2.8). These patterns were more obvious in 2011 measurements (Fig. 2.8 c,d) than those from 2010 (Fig. 2.8 a,b) and their strength was likely a reflection of sampling effort. As patterns were similar between forest types within years, our use of averaged mean monthly relative difference in VWC (rdVWC) provided us with a scaled value where variance was independent of the relationship with time but captured among plot relative VWC. The large range of variation and between month consistency of VWC at our plots in both years confirms that there was a suitable moisture gradient to allow for interpretation of influence.

Table 2.4. Summary of average volumetric water content (x̄VWC; m^3 water/m^3 soil) and standard deviation (SD; ± m^3/m^3) measured during the arthropod sampling period in coniferous (Con) and deciduous (Dec) forest in 2010 and 2011.

	2010		**2011**	
	Con	**Dec**	**Con**	**Dec**
x̄VWC (m^3/m^3)	0.136	0.154	0.154	0.160
SD (± m^3/m^3)	0.059	0.059	0.062	0.064
No. of samples	104	103	250	217

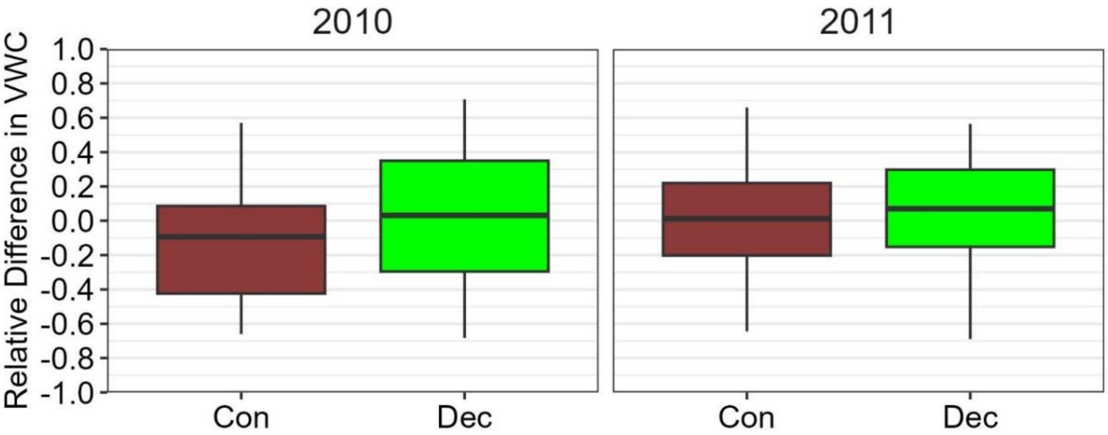

Figure 2.7. Comparisons of annual relative difference in volumetric water content (rdVWC) from the mean of all plots in the upper 20 cm of soil among plots in coniferous (Con; brown) and deciduous (Dec; green) forest in 2010 (left) and 2011 (right). Horizontal lines are medians, box limits are first and third quartiles and vertical lines are minimum and maximum ranges.

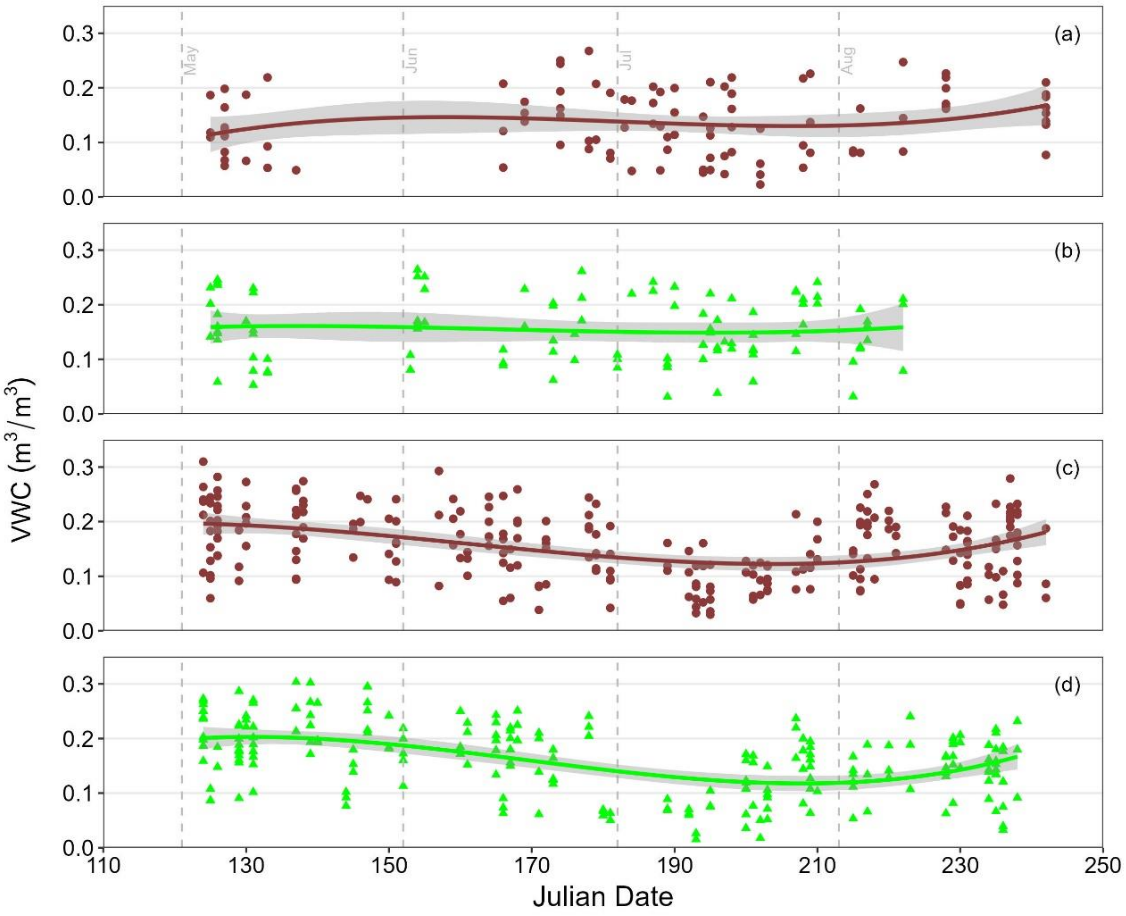

Figure 2.8. Volumetric water content (VWC; m^3/m^3) in the upper 20 cm of soil measured at coniferous (a and c; brown circles) and deciduous (b and d; green triangles) forest sites in 2010 (a and b) and 2011 (c and d). Fits (lines) of linear additive models of year, forest type and quadratic effect of Julian date (date + $date^2$) with standard errors (envelopes) are shown.

MaxSWE was significantly greater (Fig. 2.9) in deciduous forest (2010 mean = 7.8 cm, SD = ±1.1 cm, $n = 27$; 2011 mean = 13.0 cm, SD = ±2.1 cm, $n = 30$) than in pine plantations (2010 mean = 5.5 cm, SD = ±1.3 cm, $n = 23$; 2011 mean = 9.3 cm, SD = ±2.4 cm, $n = 30$) in 2010 ($t = -6.69$, df = 43.8, $p < 0.001$) and 2011 ($t = -6.36$, df = 57.0, $p < 0.001$), as would be expected due to greater canopy interception in the latter. Like soil moisture, snowpack temporal patterns were similar between forest types (Fig. 2.10) and there was a range in variation within forest types providing a suitable gradient for modeling. SWE was strongly positively correlated with snow depth ($r = 0.85$) and less strongly positively correlated with snow density ($r = 0.68$), although both contribute to SWE. Therefore, we suggest that our use of MaxSWE is a suitable indicator of the snowpack's insulative qualities.

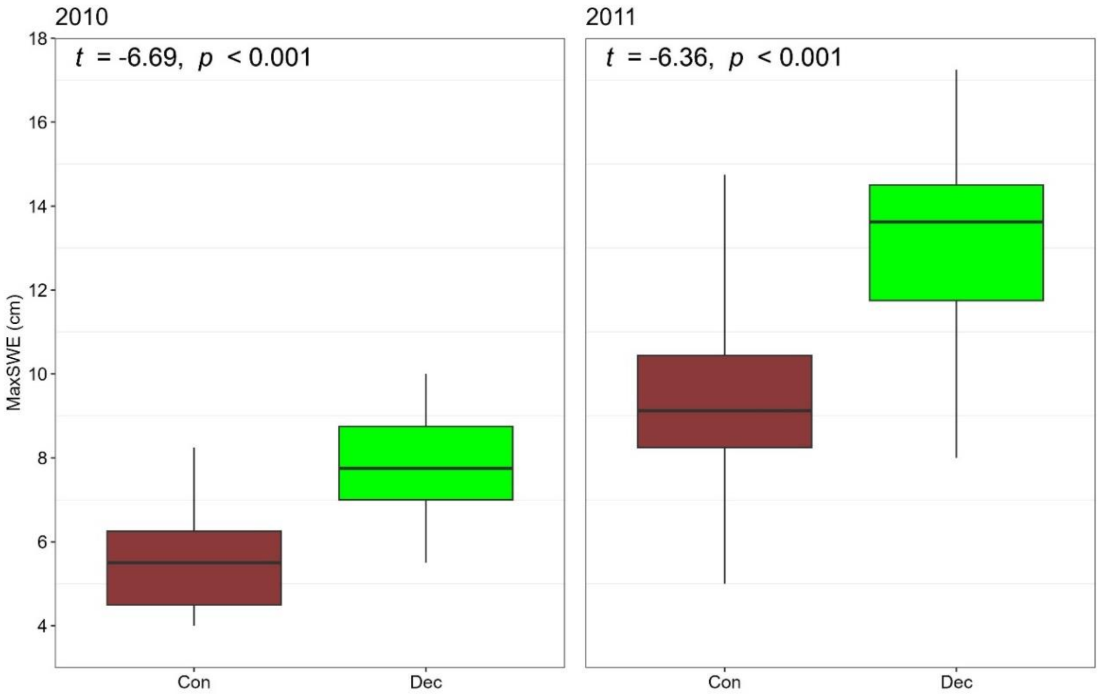

Figure 2.9. Differences in Max SWE (cm) between coniferous (Con; brown) and deciduous (Dec; green) forest in 2010 (left) and 2011 (right). Boxplot horizontal lines are medians, box limits are first and third quartiles and vertical lines are minimum and maximum ranges.

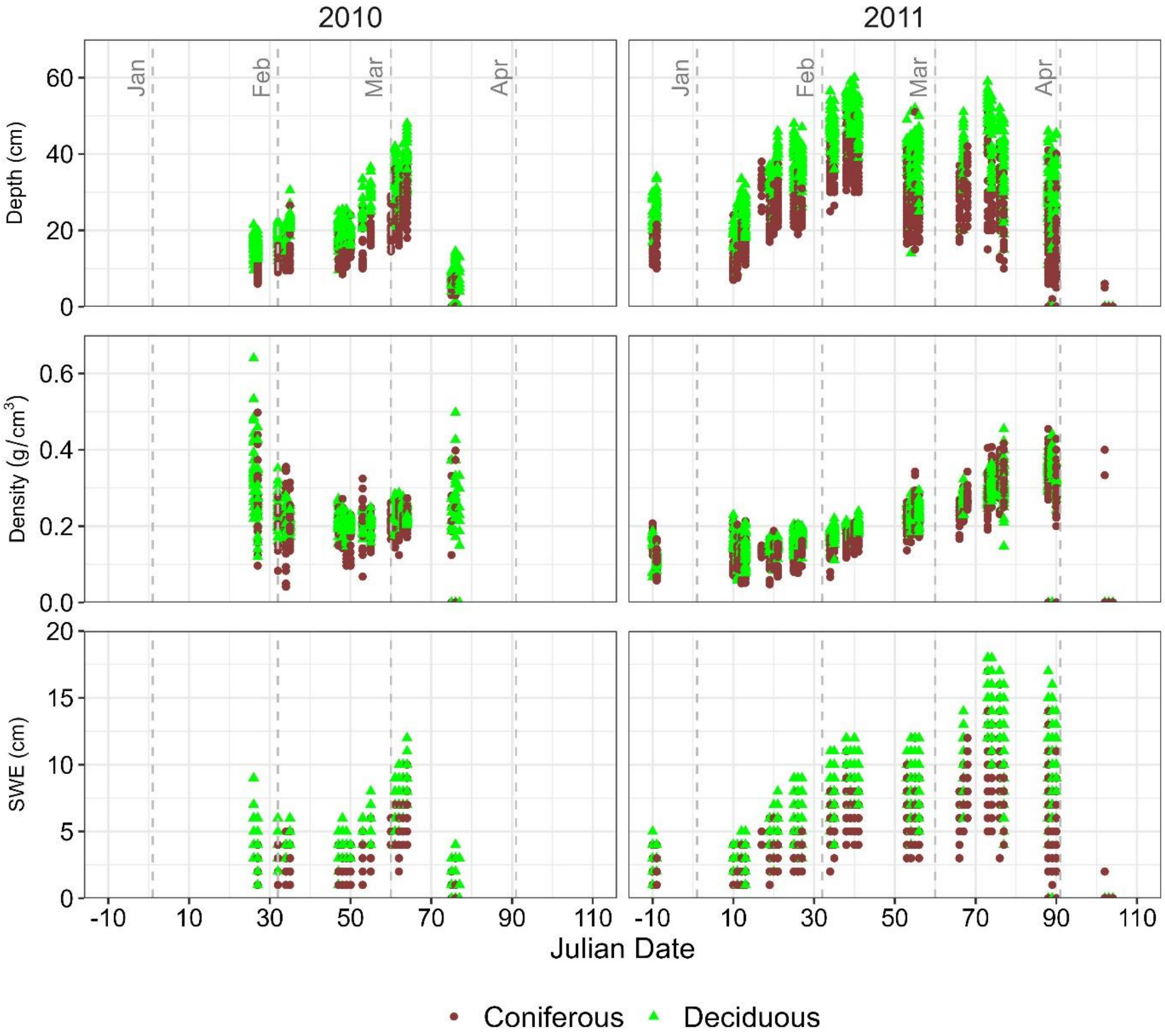

Figure 2.10. Measurements of snow depth (cm), snow density (g/cm^3) and snow water equivalent (SWE; cm) from the winter prior to 2010 (left) and 2011 (right) arthropod sampling seasons in coniferous (brown circles) and deciduous (green triangles) plots in the Ganaraska Forest.

2.3.2. Arthropods

There were mixed responses of relative biomass (Tables 2.5, 2.6) and relative abundance (Table 2.5, 2.7) among arthropod groups and composite totals to the influence of climatic, habitat and temporal variables. All models included at least one statistically significant ($p < 0.05$) parameter and the most commonly recurring significant parameter was MaxSWE (Table 2.5). rdVWC was less influential among group abundances and biomasses but had a significant positive effect on total arthropod relative biomass and abundance (Tables 2.5 - 2.7). Forest type had a mix of significant positive and negative effects but did not significantly influence total arthropod relative biomass or abundance, and forest floor depth and soil texture had the least recurring influence (Tables 2.5 - 2.7). Overall, there were generally significant quadratic effects of Julian date (Tables 2.5 - 2.7). Typically, where effects were observed for an arthropod group, the effects were significant and in the same direction for relative biomass and abundance (Table 2.5).

Table 2.5. Summary of significant ($p < 0.05$) additive linear mixed effects models of the effects of forest type (Forest= forest type as factor; positive indicates greater in deciduous, negative indicates greater in coniferous), percent sand composition (Sand; %), forest floor depth (Floor; cm), maximum annual snow water equivalent (MaxSWE; cm), mean relative difference in soil volumetric water content (rdVWC) and quadratic effect of Julian date (Julian + Julian^2) on arthropod relative biomass and relative abundance. Positive and negative relationships are indicated by plus (+) and minus (-) symbols, respectively, μ indicates significant estimates for biomass only and N indicates significant estimates for abundance only. Arthropod groups with a † indicates that only relative abundance was tested due to assumptions of normality.

	Forest	Sand	Floor	MaxSWE	rdVWC	Julian	Julian^2
Total Arthropods				+	+	+	−
Acariformes				−	+		
Chilopoda†			+	+		+	−
Collembola	$+^{\mu}$						$+^{N}$
Coleoptera (ad)	+			$+^{\mu}$		+	−
Coleoptera (ad+lar)	+			+		+	−
Diptera (ad)	$+^{\mu}$			+	+	+	−
Gastropoda (slug)	−			+	+	$+^{\mu}$	−
Gastropoda (snail)†		+					
Hymenoptera (ant)	−	$-^{\mu}$	−	+		+	−
Hymenoptera (total)	−	−	−	+		+	−
Myriapoda				+			

Table 2.6. Linear mixed effect model parameter estimates (*b*) and t values (* = $p < 0.05$) for the relationship between arthropod relative biomass (g/day; log10 + group superscript numbers transformed) and the additive effects of forest type (Forest; positive values indicate greater in deciduous forest and negative values indicate greater in coniferous forest), percent sand composition (Sand; %), forest floor depth (Floor; cm), annual maximum snow water equivalent (MaxSWE; cm), annual average relative difference of volumetric water content in top 20cm of soil (rdVWC) and quadratic effect of Julian date (Julian + Julian^2). Statistically significant parameter estimates are shown in bold and t values are denoted by *. An ^{a} indicates that an estimate was significant for abundance and biomass models while a ^{b} indicates an estimate that was only significant for abundance or biomass models.

	b_0	**Forest**	**Sand**	**Floor**	**MaxSWE**	**rdVWC**	**Julian**	**Julian^2**
Total Relative Arthropod Biomass$^{+0.01}$								
b	**-3.3140**	-0.0778	0.0029	0.0219	**0.0412**	**0.1242**	**0.0200**	**-0.0001**
t	-4.97*	-1.50	1.11	0.98	6.99^{*a}	2.29^{*a}	2.96^{*a}	-3.12^{*a}
Acariformes$^{+0.00001}$								
b	**-6.2288**	0.0871	0.0008	-0.0288	**-0.0514**	**0.1235**	0.0164	-0.0000
t	-7.18*	1.76	0.34	-1.41	-7.10*^{b}	2.30*^{a}	1.81	-1.23
Collembola$^{+0.00001}$								
b	**-3.968**	**0.1973**	-0.0063	0.0023	0.0149	0.0697	-0.0071	0.0000
t	-3.77*	2.29^{*b}	-1.68	0.07	0.92	0.81	-0.66	1.54^{b}
Coleoptera (Adult)$^{+0.01}$								
b	**-5.5778**	**0.0902**	-0.0012	0.0080	**0.0112**	0.0687	**0.0431**	**-0.0001**
t	-10.21*	2.16^{*a}	-0.58	0.45	2.32^{*a}	1.57	7.77^{*a}	-7.87^{*a}
Coleoptera (Adult and Larva)$^{+0.01}$								
b	**-5.8901**	**0.0763**	-0.0009	-0.0053	**0.0129**	0.0478	**0.0467**	**-0.0001**
t	-10.66*	1.80^{b}	-0.43	-0.29	2.64^{*a}	1.07	8.33^{*a}	-8.41^{*a}
Diptera (Adult)$^{+0.0001}$								
b	**-6.7132**	**0.1432**	-0.0028	-0.0115	**0.0278**	**0.1592**	**0.0403**	**-0.0001**
t	-5.63*	2.09^{*b}	-0.85	-0.40	2.79^{*a}	2.14^{*a}	3.12^{*a}	-3.32^{*a}
Gastropoda (Slug)$^{+0.01}$								
b	**-2.9562**	**-0.3012**	0.0013	0.0160	**0.0279**	**0.1264**	**0.0184**	**-0.0001**
t	-5.39*	-6.35^{*a}	0.67	0.91	3.13^{*a}	2.68^{*a}	3.32^{*b}	-4.41^{*a}
Hymenoptera (Ant)$^{+0.0001}$								
b	**-6.1497**	**-0.3039**	**-0.0087**	**-0.0884**	**0.0399**	-0.0857	**0.0361**	**-0.0001**
t	-7.59*	-3.81^{*a}	-2.53^{*a}	-2.97^{*a}	2.72^{*a}	-1.01	4.48^{*a}	4.37^{*a}
Hymenoptera (Total)$^{+0.0001}$								
b	**-4.3303**	**-0.2792**	**-0.0126**	**-0.1180**	**0.0464**	-0.0472	**0.0219**	**-0.0001**
t	-4.51*	-3.32^{*a}	-3.42^{*a}	-3.76^{*a}	2.96* ^{a}	-0.56	2.25^{*a}	-2.25^{*a}
Myriapoda $^{+0.01}$								
b	**-2.5834**	0.0782	0.0024	0.0406	**0.0291**	0.1007	0.0031	0.0000
t	-2.71*	1.02	0.61	1.22	3.45*^{a}	1.27	0.33	-0.02

Table 2.7. Linear mixed effect modeling of arthropod relative abundance (count/day). Table terminology and symbology are explained in Table 2.4. Lack of superscript letter beside a significant t value indicates that only relative abundance models were evaluated for that group.

	b_0	**Forest**	**Sand**	**Floor**	**MaxSWE**	**rdVWC**	**Julian**	**Julian^2**
Total Relative Abundance$^{+0.1}$								
b	-0.8125	-0.0523	-0.0014	0.0041	**0.0230**	**0.1425**	**0.0145**	**-0.0000**
t	-1.34	-1.31	-0.72	0.25	4.01^{*a}	3.24^{*a}	2.33^{*a}	-2.18^{*a}
Acariformes$^{+0.1}$								
b	-1.5163	-0.0360	0.0011	-0.0204	**-0.0097**	**0.1170**	0.0056	-0.0000
t	-1.99	-0.77	0.55	-1.18	-1.04^{b}	2.56^{*a}	0.70	-0.23
Chilopoda$^{+0.1}$								
b	**-10.115**	0.0502	0.0058	**0.1110**	**0.0902**	0.0511	**0.0782**	**-0.0002**
t	-6.66*	-0.44	1.12	2.52^{*}	4.43^{*}	0.43	4.98^{*}	-4.87^{*}
Collembola$^{+0.1}$								
b	0.7922	0.1221	-0.0035	-0.0006	0.0049	0.0852	-0.0172	**0.0001**
t	0.88	1.71	-1.61	-0.039	0.91	1.17	-1.87	2.77^{*b}
Coleoptera (Adult)$^{+0.1}$								
b	**-6.4925**	**0.1442**	-0.0042	-0.0065	**0.0270**	0.0666	**0.0726**	**-0.0002**
t	-8.50^{*}	2.45^{*a}	-1.39	-0.26	4.00^{*a}	1.08	9.38^{*a}	-9.63^{*a}
Coleoptera (Adult and Larva)$^{+0.1}$								
b	**-6.3630**	**0.1253**	-0.0036	-0.0155	**0.0277**	0.0532	**0.0711**	**-0.0002**
t	-8.59^{*}	2.22^{*b}	-1.25	-0.64	4.24^{*a}	0.90	9.45^{*a}	-9.66^{*a}
Diptera (Adult)$^{+0.1}$								
b	**-4.0521**	0.0326	-0.0020	0.0040	**0.0311**	**0.1464**	**0.0382**	**-0.0001**
t	-5.11^{*}	0.73^{b}	-0.93	0.216	4.72^{*a}	3.02^{*a}	4.62^{*a}	-4.53^{*a}
Gastropoda (Slug)$^{+0.1}$								
b	-1.044	**-0.4427**	0.0024	0.0122	**0.0367**	**0.1799**	0.0138	**-0.0001**
t	-1.39	-6.79^{*a}	0.83	0.50	3.02^{*a}	2.77^{*a}	1.82^{b}	-3.03^{*a}
Gastropoda (Snail)$^{+0.1}$								
b	-0.7181	0.0213	**0.0043**	0.0178	0.0114	0.0681	-0.0019	0.0000
t	-1.56	0.55	3.40^{*}	1.20	1.63	1.71	-0.40	0.29
Hymenoptera (Ant)$^{+0.1}$								
b	**-2.676**	**-0.2758**	**-0.0073**	**-0.0725**	**0.0352**	-0.0528	**0.0285**	**-0.0001**
t	-3.974^{*}	-4.16^{*a}	-2.52^{*a}	-2.92^{*a}	2.89^{*a}	-0.79	4.25^{*a}	4.13^{*a}
Hymenoptera (Total)$^{+0.1}$								
b	**-2.253**	**-0.2483**	**-0.0089**	**-0.0814**	**0.0333**	-0.0477	**0.0260**	**-0.0001**
t	-3.32^{*}	-3.91^{*a}	-3.24^{*a}	-3.43^{*a}	2.84^{*a}	-0.75	3.82^{*a}	-3.68^{*a}
Myriapoda $^{+0.1}$								
b	**-1.8011**	0.0388	0.0026	0.0310	**0.0329**	0.1152	0.0050	0.0000
t	-2.00*	0.50	0.66	0.91	4.10^{*a}	1.46	0.55	-0.13

2.3.3. Forest type

Forest type influenced arthropods groups in different directions, with some groups having greater relative biomass and abundance in deciduous forest than in conifer plantations suggesting assemblages differed between forest types. Total relative arthropod biomass (Table 2.6, Fig. 2.11) and relative abundance (Table 2.7) were not different between forest types. Slugs, Ants and total Hymenoptera had significantly greater relative biomass (Table 2.6, Fig. 2.11) and abundance (Table 2.7) in coniferous forest. As Ants contributed only 46% of Hymenoptera biomass, it suggests that non-Ant Hymenoptera biomass and abundance, which could not be tested separately due to model assumptions, were also greater in coniferous forest. Coleoptera adult, Collembola and Diptera adult relative biomasses were significantly greater in deciduous forest (Table 2.6, Fig. 2.11). Total Coleoptera (adult and larva) relative abundance was also significantly greater in deciduous forest (Table 2.7).

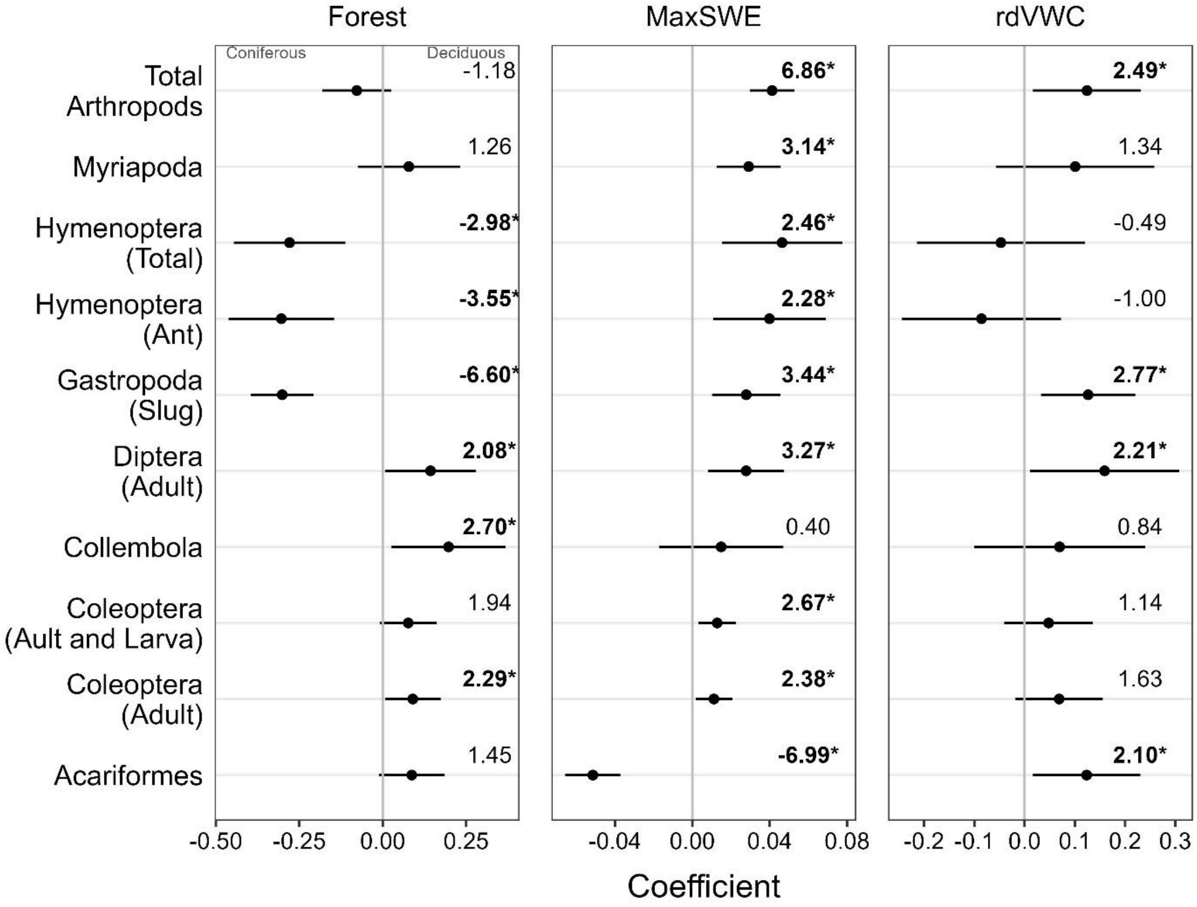

Figure 2.11. Parameter coefficients (circles), 95% confidence intervals (lines) and *t* values (right hand size of each plot) for forest type (Forest; positive coefficient indicates greater biomass in deciduous and negative is greater biomass in coniferous; left), annual maximum snow water equivalent (MaxSWE; cm; middle) and mean annual relative difference in volumetric water content (rdVWC; right) from additive linear mixed effect models of arthropod relative biomass. Significant *t* values ($p < 0.05$) are indicated with an * and bold font.

2.3.4. Soil texture (Percent sand)

Soil texture was one of the least influential model parameters with significant effects for 2 out of 10 (Table 2.6) arthropod groups' relative biomass and 3 out of 12 groups' relative abundance (Table 2.7). Total Hymenoptera and Ant-only relative biomass and abundance were significantly negatively related to percent sand composition of soil. Also, Snail relative abundance was positively related to the percent of sand in soil (Table 2.7). Therefore, Total Hymenoptera and Ants-only had greater relative abundance and biomass at plots with soils containing more silt and less sand, whereas snails were more abundant in soils with less silt and more sand.

2.3.5. Forest floor depth

Forest floor depth was influential for the relative biomass of 2 out of 10 arthropod groups (Table 2.6) and for the relative abundance of 3 out of 12 arthropod groups (Table 2.7). For relative biomass, forest floor depth was only influential for the order Hymenoptera, with significant negative effects on both total Hymenoptera and Ant-only relative biomass (Table 2.6). Forest floor depth was also a significant negative influence for Hymenoptera and Ant-only relative abundances and was a significant positive influence for Chilopoda relative abundance (Table 2.7).

2.3.6. Snow water equivalent

MaxSWE was the most recurring significantly influential factor affecting arthropods, with significant relationships in 9 out of 10 models of relative biomass (Table 2.6, Fig. 2.11) and 9 out of 12 models of relative abundance (Table 2.7). Non-significant relationships with MaxSWE were observed for Collembola relative biomass and abundance as well as Snail and Acariformes relative abundances. Acariformes were also the only group to have negative parameter estimates for MaxSWE, including both relative abundance and biomass, although only the biomass parameter estimate was significant. The positive influence of MaxSWE was the only significant variable parameter estimate in the Myriapoda relative abundance model.

2.3.7. Soil moisture

Soil moisture (rdVWC) was a minor influence on arthropod relative biomass and abundance and no models included a significant negative relationship with rdVWC. rdVWC was a significant positive influence for the relative biomass (Table 2.6) and abundance (Table 2.7) of Total Arthropods, Acariformes, Diptera Adults and Slugs (Fig. 2.11).

2.3.8. Date

Julian date was a significant influence on arthropod biomass and abundance, with most groups having similar responses. Relative biomass and abundance were significantly related to date for 7 of 10 (Table 2.6) and 9 of 12 (Table 2.7) group models, respectively. Most significant relationships were a quadratic effect of Julian date with positive base parameter estimates and negative squared parameter estimates which model a convex upward pattern of increasing, then decreasing values over the sampling period (Fig. 2.12). Slug relative biomass and abundance models did not follow the same convex upward pattern, declining from the start of the sampling period (Fig. 2.12, Table

2.6). Only Collembola relative abundance had a statistically significant increase over the sampling period (Fig. 2.13, Table 2.7).

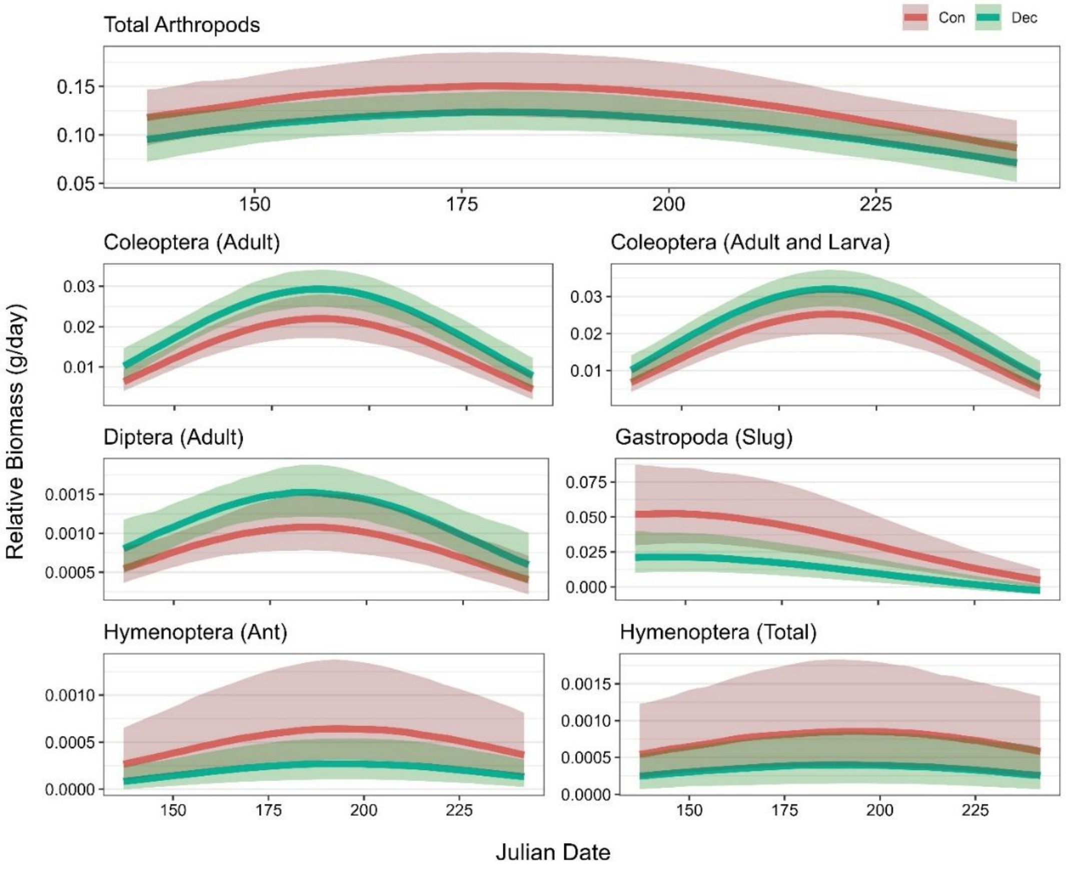

Figure 2.12. Global model estimations of mean relative arthropod biomass per day (g/day; backtransformed values) with 95% confidence intervals in coniferous (Con) and deciduous (Dec) forest for all models with significant effects of date. Covariates were held constant at average measured values (MaxSWE=10.625 cm, Litter = 2.8 cm, sand=74.9%, rdVWC=0.009).

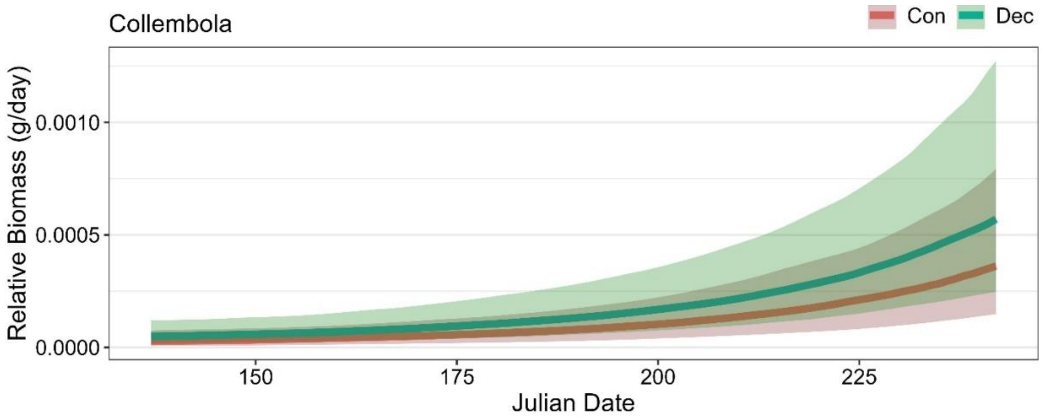

Figure 2.13. Global model estimation of mean Collembola relative biomass per day. Symbology and model parameters as described in Fig. 2.11.

2.4. Discussion

We found that two parameters, snowpack modeled using maxSWE and the effect of date were significantly influential in 83% (10 of 12) and 75% (9 of 12) of the models, respectively. As well, measures of relative arthropod biomass and abundance responded similarly within each group. We predominantly found that relative biomass and abundance generally increased with increasing snowpack (MaxSWE) increased until approximately mid-July followed by a decline to the end of our sampling periods near the end of August. These patterns were observed for all groups including total arthropods, except for Acariformes (Mites), Collembola (Springtails) and Snails (Gastropoda).

2.4.1. Habitat covariates: forest type, soil texture, forest floor depth

Among habitat covariates forest type was more influential than soil texture or forest floor depth on arthropod biomass and abundance. Unlike MaxSWE and date, forest type affected arthropod groups in different directions, thus being the main contributor to differences in arthropod assemblages across our two forest types. The effects of deciduous versus coniferous forest types on arthropod groups have been observed elsewhere and can be attributed to variation in resource filters (Gossner et al. 2014) such as soil pH, coarse woody debris and herbaceous cover providing for necessities such as egg laying (Kappes 2006).

The effects we observed among arthropod groups both confirmed previously published results for some arthropod groups and contrasted with published results for others. As previously observed using aerial malaise trapping in the same Forest (Falconer and Nol 2020), forest type did not influence total relative arthropod biomass. We found that Coleoptera were more abundant in deciduous forest than coniferous forest which has been reported in other studies (Ulyshen and Hanula 2009, Neuvonen et al. 2012). We also found that there was no difference in Collembola relative abundance between the two different forest types, as was reported in a comparison of Collembola in Beech (*Fagus sylvatica*), Spruce (*Picea abies*), and mixed forests in Germany (Salamon et al. 2008). By contrast, we found the opposite results for Slugs (Gastropoda) than that observed in an extensive European study which more Slug abundance in deciduous compared to coniferous forest (Kappes and Schilthuizen 2014). Also contrasting with our results, a study by Ulyshen et al. (2011) found no significant differences in Hymenoptera between forest types, whereas we found greater abundance in coniferous than deciduous forest. Thus, our results support that forest type is an important factor in the arthropod assemblage at our study area, but that responses vary geographically and are likely confounded by other factors such as vegetation species composition, soil texture and chemistry, climate among others.

Soil texture and forest floor depth negatively influenced Hymenoptera (total and Ant-only) relative abundance and biomass, and forest floor depth positively influenced Chilopoda relative abundance. The positive relationship between percent sand and Snail relative abundance was the only relationship observed for that group and this effect was the only model which had a single significant variable. This may reflect a trait-based ability to survive dry periods or a lack of humidity preference rather than a habitat relationship (Astor et al. 2017).

2.4.2. Climatic variables: SWE and VWC

MaxSWE was significantly influential for a greater proportion of arthropod groups than rdVWC. In almost all models where maxSWE and rdVWC were significantly influential, their effects on total arthropod relative biomass and abundance were positive. The responses of organisms to changes in snow depth are not well understood (Christenson et al. 2017) yet the prevalence and consistency of the influence of MaxSWE on arthropods we report demonstrates strength of that relationship and suggests that snowpack reductions either induce mortality or reduce habitat suitability. These findings generally support the results of previous studies. For instance, in northern tolerant hardwood forest in New Hampshire, snow depth and cover persistence positively influenced ground beetle capture rates in the growing season (Harris et al. 2019) and reduced snowpack depth resulted in negative effects for total litter arthropod and Hymenoptera abundance (Templer et al. 2012). The responses of arthropods to snowpack reductions reported by Templer et al. (2012) that differed from our results were the lack of effects on Chilopoda, adult Diptera, Diplopoda and larval Coleoptera abundances whereas we observed significant positive effects. However, we did not test Diplopoda or larval Coleoptera independently as we included them in Myriapoda and Coleoptera regardless of life stage.

The main arthropod groups to deviate from the predominantly positive relationships with snowpack we observed were the soil and litter dwelling Collembola and Acariformes which had null and negative responses respectively as well as Snails which were also not significantly impacted by snowpack . Our results for those groups add to the body of literature that reports mixed responses to the impacts of snowpack on arthropod abundance. For example, Templer et al. (2012) observed a positive relationship between snowpack and abundance for Collembola and no effect for Acariformes, which are opposite to our results. Christenson et al. (2017) observed a similar result to ours with a negative response of Acariformes abundance to snow depth. However, in contrast to our results, they also observed a negative response for Collembola. The lack of response by Collembola and Snails could be due to life-history strategies to mitigate cold-induced mortality (Templer et al. 2012). The negative response to snowpack by Acariformes is not likely to be related to cold-induced stresses and could be the result of sub-nivean predation (Merriam et al. 1983) or habitat alteration, particularly due to altered vegetation and soil organic matter due to fine root mortality that occurs with reduced insulation from snow (Kreyling et al. 2007).

Despite hypothesized relationships, we found little evidence that soil moisture influenced the relative biomass or abundance of most arthropod groups, although it did influence the total of all groups. Our results generally contrast with those from studies elsewhere such as the positive influences of soil moisture on Collembola (Tsiafouli et al. 2004, Torode et al. 2016, Christenson et al. 2017), Coleoptera (Huk and Kühne 1999), and Diplopoda (Wytwer and Tracz 2003). The positive relationship between soil moisture and Acariformes we report, however, corresponds with results from other studies (Taylor and Wolters 2005, Lindo and Winchester 2008, Christenson et al. 2017) and is likely due to the significant risk posed to this group by desiccation during summer dry periods (Eissfeller et al. 2013). Hymenoptera was the only group for which we observed a negative, albeit non-significant, relationship with soil moisture, particularly for Ants, and this relationship has been reported previously by other studies (Seal and Tschinkel 2010, Brygadyrenko 2014). Among other groups, the lack of relationships with soil moisture could have resulted from a small range of soil moisture variability across our study sites. Arthropod communities in our study area may also be composed of drought-adapted species that are resilient to soil moisture fluctuation in this rapidly drained, sandy, and often dry environment, although persistent lengthy dryness may overwhelm any adaptations (David and Handa 2010).

2.4.3. Julian date

Nearly all arthropod group relative biomasses and abundances significantly increased and then decreased annually over the study period (May to end of August) in a convex upward pattern. Collembola was the only group to demonstrate a very different pattern where they increased exponentially over the sampling period. Acariformes and Myriapoda relative biomass and abundance as well as Snail (Gastropoda) relative abundance were not influenced by date. A similar convex upward temporal pattern over the same sampling period to what we modeled has been observed in other studies including for total arthropods (Crowley et al. 2023), total biomass (Tulp and Schekkerman 2008, Busse et al. 2022), Coleoptera (Harris et al. 2019), Collembola (Templer et al. 2012, Christenson et al. 2017), and Hymenoptera (Templer et al. 2012). Our results differed from a study which found that Acariformes abundance followed the same convex upward temporal pattern (Templer et al. 2017), whereas we did not observe any pattern for that group.

Compared to other sampling methods, we found a different temporal pattern in total arthropods than those collected using aerial malaise traps in prior years in the same Forest (Falconer and Nol 2020). Our temporal patterns also differed from the results of sampling using canopy beating but were like the results of sampling using pitfall, malaise and understory beating in that same study (Crowley et al. 2023). Additionally, sampling methods including ground malaise traps and light traps only collecting at night (Busse et al. 2022) and window traps collecting beetles (Harris et al. 2019) produced similar results to ours.

Temporal changes in arthropods during the growing season are generally related to photoperiod and availability of food sources such as host plants causing exit and entrance into diapause as well as obligate stages of metamorphosis (Denlinger et al. 2017). The consistency of our results substantiates the importance of including covariate temporal effects when assessing arthropod biomass and abundance. Furthermore, the similarity of our results to the temporal patterns reported in previously published studies using different trapping methods and sampling different species and groups suggests that the pattern is widespread.

2.4.4. Potential effects of climate change

The positive effect of snowpack was the most important and nearly universal influence on arthropod relative biomass and abundance in our study. Based on our results, temperate forest ecosystems, mediated through arthropods, are potentially facing a serious negative effect of climate change related to winter precipitation. The potential for decline in arthropod biomass can have significant upward and downward cascading effects (Lister and Garcia 2018, Pureswaran et al. 2018). For example, increases in groups such as Ants could have negative trophic effects for their prey and potentially positive trophic effects for their predators. Destabilized arthropod communities will have serious consequences to ecosystem structure and function as well as the provision of ecosystem services (Harvey et al. 2022).

Total winter precipitation is predicted to increase in our study region north of Lake Ontario but is likely to change in its proportions with less snow and more rain (McCabe and Wolock 2010). The result will be reduced snowpack as well as a change in snow cover phenology with a shortened snow cover residency period (Chen et al. 2015). Insulation provided by snow decouples temperatures below and above the snowpack and its loss can increase arthropod mortality due to exposure to deeper frost and colder ground surface temperatures, leading to cryo-stress (Bale and Hayward 2010) as well as freeze thaw cycles that increase mortality compared to stable cold exposure (Bale et al. 2001, Marshall and Sinclair 2014). Furthermore, mid-winter melts increase mortality due to early warmth exposure causing premature diapause emergence and vulnerability to resumption of freezing temperatures as well exposure to melted water that can subsequently freeze and cause ice encasement (Bale and Howard 2010). Given that predictions for this region are increases in freeze-thaw events, reduced snowfall with increased winter precipitation as rainfall rather than snow (McCabe and Wolock 2010), our results show that reduced maxSWE, which can occur because of less initial depth and greater loss of water from melting, highlight significant potential for negative consequences. In our study area, total arthropod relative biomass and abundance as well as the biomass and abundance of many arthropod groups could experience decline, except for possible increases in Acariformes biomass and abundance, no changes in biomass or abundance for Collembola, and no changes in abundance for Snails (Gastropoda). This is particularly concerning as we measured snow in a year where the area's total snowfall (2011: 180.4 cm) was only slightly above the average annual snowfall (151 cm) and a year with much lower total snowfall (2010: 84.9 cm), thus demonstrating the potential for effects. Given the variation in responses found elsewhere, further investigation of responses should be undertaken in other geographic locations with differing climate and habitat conditions.

The effects we observed and consequent inferences do not likely provide long-term predictions for arthropod community structure as changes will interact with range shifts and immigration of species adapted to regionally novel conditions (David and Handa 2010, Halsch et al. 2021). As well, top-down, and bottom-up effects do not act in isolation (Hunter and Price 1992) and it is possible that resource increases and pulses that would be observed over a greater time scale will result in increased predators and greater top-down controls (Ostfeld and Keesing 2000), especially with an associated time lag. Nonetheless, our observations modeled across the gradients we measured suggest the potential for a future climatic-based restructuring phase (Bartley et al. 2019) and therefore instability in the maintenance of ecological processes in both temperate deciduous forest and conifer plantations.

2.4.5. Scale refinement recommendation

The coarseness of species groupings in modeling potentially allows for broader scale extrapolation of results; however, undesirable assumptions in model interpretation are likely to persist (Botkin et al. 2007) as demonstrated by the inconsistency in results among comparative studies. On the other hand, species-scale models may provide more specificity, but likely need refined variables and are unlikely to provide results that can be generalized and applied to ecosystems (Botkin et al. 2007). Our results provide a coarse-level approach to understanding the effects of climatic and habitat variables on arthropods but are likely limited to our study region. Future analyses could refine the approach we used for groupings and scale down to families, trait-based categories, or functional groups (Williams et al. 2014, Astor et al. 2017, Brousseau et al. 2019, Halsch et al. 2021). In some cases, where no effect for an order was observed it is possible that, for example, predators from that group were influenced in one direction, whereas herbivores were affected in another or that the response of predators may lag in time as their populations respond to prey amounts. This may allow for better interpretation of results or improve interpretability of comparison of the results of other studies. As well, further habitat variable delineation could be used. As we wanted to reduce model complexity, we did not pursue modeling continuous variability between forest composition as an independent variable, particularly within deciduous-dominated forest types. When stratifying plots, our goal was to use mature deciduous forest with a high composition of maple, but many plots had high variability in contributions by oak and poplar. Future research could pursue analyses that consider finer scale definition of plot forest composition.

2.5. Conclusion

We performed a multi-variable approach to modeling the influence of habitat and climatic gradients on arthropod relative biomass and relative abundance in coniferous plantation and natural deciduous forest types. We found pervasive significant negative effects of maximum annual snow water equivalent and a convex upward pattern of increase followed by decrease across the sampling period for most arthropod groups and combined totals. Forest type was the next most influential factor on community assemblage and there was less consistency in the direction of its effects compared to snowpack and date with groups differing in abundance between deciduous forest and conifer plantations. The least influential factors were soil moisture, soil texture and forest floor depth which mainly influenced Hymenoptera. Soil moisture was, however, significantly positively influential for total arthropod relative biomass and abundance which could have significant effects for their predators. Considering the strong effect of snowpack on arthropods that we observed, predicted snowpack depletion resulting from climate change could have significant negative effects of arthropod assemblages and associated ecological processes.

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Chapter 3: Arthropods as food and competitors mediate ecoclimatic effects on nest survival for some temperate breeding songbirds[2]

Keywords: Nest survival rate, arthropod biomass, path analysis, structural equation model, snow, soil moisture, Least Flycatcher, Eastern Wood-Pewee, American Robin, Ovenbird, Red-eyed Vireo

3.0. Abstract

Food availability through bottom-up ecosystem productivity limits insectivorous breeding bird clutch size, nestling growth, and nest survival and as climate can influence arthropod biomass, climate change could affect avian fecundity. Southern Ontario is predicted to experience warmer winters, more winter rainfall rather than snow, hotter summers, and less frequent, more summer rainfall events of higher intensity resulting in shallower and denser snowpack and drier non-winter soil. We used structural equation modeling in a space-for-time approach to investigate if snowfall and soil moisture changes could influence avian populations for five common and wide-ranging forest breeding insectivorous species in the Ganaraska Forest on the Oak Ridges Moraine in southern Ontario. American Robin (*Turdus migratorius*), Eastern Wood-Pewee (*Contopus virens*), Least Flycatcher (*Empidonax minimus*), Ovenbird (*Seiurus aurocapilla*) and Red-eyed Vireo (*Vireo olivaceus*) nest survival rates were calculated using logistic-exposure modeling and then included in assessments of pathway relationships with composites of food, predator, and soil bioindicator arthropod functional group biomasses, snowpack measured as snow water equivalent, and soil moisture measured

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as soil water content. Eastern Wood-Pewee and Red-eyed Vireo nest success were positively related to food biomass and negatively related to predaceous arthropods suggesting a putative competitive prey depression. American Robin, Least Flycatcher and Ovenbird nest survival appeared to be more strongly related to top-down nest predator effects. Relationships between soil moisture and arthropods were inconsistent whereas snowpack consistently and positively influenced arthropod prey and mostly negatively affected predaceous arthropods. Predicted future declines in snowfall could negatively affect avian insectivore populations by reducing food resources and cause declines in nest survival for some species.

3.1. Introduction

Widespread and long-term avian population declines are a conservation concern. For example, North America's eastern forest breeding bird abundance has declined by more than 166 million since 1970, approximately a 17% loss with more than 65% of species in decline (Rosenberg et al. 2019). Some groups such as aerial insectivores have shown greater declines than others (Blancher et al. 2009, Nebel et al. 2010, Smith et al. 2015).

Causes of avian population declines are varied or uncertain (Thompson et al. 2009). Spatially extensive and continuous effects among many species suggest that broad-scale, species-independent factors (Smith et al. 2015) such as pesticides, pollution, land alteration, invasive species, and climate change could be causes of decline (Şekercioğlu et al. 2004, Spiller and Dettmers 2019, Nebel et al. 2020, Møller et al. 2021). For instance, insectivore declines have been linked to neonicotinoid insecticides (Hallman et al. 2014) and agricultural intensification (Murphy 2003), and Acadian Flycatcher (*Empidonax virescens*) reproduction has been linked to mercury pollution from food sources (Rowse et al. 2014). As well, North American aerial insectivore populations, most of which are declining, are strongly related to climate indices (Michel et al. 2021) and earlier diapause emergence of arthropod prey has advanced and shortened avian nesting periods (Dunn and Winkler 1999, Visser et al. 2006, Murphy et al. 2022).

Nest (Smith et al. 2011, Roos et al. 2018) and fledgling (Sunde 2005) survival are significant regulators of avian fitness and populations (Wilcove 1985, Martin 1993, Thompson 2007). Songbird nest survival is a combination of top-down and bottom-up controls where both predation on eggs and young (top-down) and the ability of adults to acquire sufficient food to provision nestlings (bottom-up) can affect populations (Zanette et al. 2006). However, predation cannot occur without the existence of nests and those nests rely first on bottom-up resources that provide nutrition for breeding birds, for their existence and persistence.

With widespread arthropod declines across multiple habitat types (Sánchez-Bayo and Wyckhuys 2019, Siebold et al. 2019), and coincidental avian declines (Spiller and Dettmers 2019) such as the decline of aerial insectivores (Blancher et al. 2009), bottom-up trophic cascades may be a key driver (Tallamy and Shriver 2021, Pearce-Higgins and Morris 2022). Declining arthropod diversity, abundance, and biomass can alter trophic balances (Siebold et al. 2019) and the relationship between food resources and measures of fecundity appears to be stronger in forests than in other habitats (Grames et al. 2023). Furthermore, arthropod prey consumption rates by insectivorous avifauna in temperate forests are among the highest of all global biomes (Nyffeler et al. 2018).

From a bottom-up perspective, food resources mediate avian populations by supporting nest productivity in a variety of ways. Prey availability positively influences clutch size (Cody 1966, Hussell and Quinney 1987, Ruffino et al. 2014), nestling growth (Visser et al. 2006, Ruffino et al. 2014, Grames et al. 2023), parental nest defense (Duguay et al. 2000, Vafidis et al. 2018, Murphy et al. 2022), re-nesting (Arcese and Smith 1988), double-brooding (Nagy and Holmes 2005), nest survival rates (Stodola et al. 2010, Tallamy and Shriver 2021, Bailey and Bonter 2022), and post-fledging survivorship (Vitz and Rodewald 2011, Martin et al. 2018). Earlier prey availability also supports earlier egg laying (Visser et al. 2006) which facilitates more nesting attempts following nest loss. Thus, bottom-up drivers are a significant mediator of breeding season productivity (Wiehn and Korpimäki 1997, Seagle and Sturtevant 2005).

In addition to consumption as prey, arthropods influence bottom-up forces by facilitating energy transfer from basal resources, modifying habitats, and competing for consumption of the same prey. For example, Acariformes (mites) and Collembola (springtails) are dominant soil arthropod groups that are often used as bioindicators because they respond to environmental properties such as leaf litter and soil quality and nutrients, have low dispersal rates, and are critical to soil processes (Behan-Pelletier 1999, Yang et al. 2015, Zhang et al. 2023) that influence bottom-up trophic processes. As well, predaceous arthropods are significant consumers of other arthropods. Araneae and Opiliones are generally obligate invertebrate consumers (Nyffeler et al. 2023), and the large amounts of invertebrate biomass they consume, particularly in temperate forests (Nyffeler and Birkhofer 2017), are augmented by other predaceous arthropods such as some species of Coleoptera and Myriapoda (Chen and Wise 1999, Nyffeler et al. 2018). Although rarely reported, predaceous arthropods can compete with birds for resources (Wirta et al. 2015) to the extent of affecting fitness (Aho et al. 1999).

Whereas top-down and bottom-up pressures are both important factors for nest survival and arthropod populations and productivity, the strength of their influence depends on the nature of the ecosystem under study (Preston and Rotenberry 2006). Net primary production is a major bottom-up control of arthropods and is the result of a combination of climatic variables including temperature, non-winter precipitation, and winter precipitation and can, in turn, influence nest productivity (Murphy et al. 2022). In the Great Lakes St. Lawrence Forest Region's temperate forests, seasonal changes are critical to facilitating arthropod productivity that provides the energetic needs of migratory breeding birds. Changes in winter and summer climate have the potential to modify arthropod biomasses (Wagner 2020, Chapter 2) and could result in bottom-up trophic cascades (Lister and Garcia 2018) subsequently affecting breeding birds.

In our study area, winter precipitation is expected to, and has begun to, increase (McDermid et al. 2015, Zhou et al. 2017) with an increasing proportion of winter precipitation as rainfall rather than snowfall (McCabe and Wolock 2010, Notaro et al. 2014, Ahmed et al. 2022). The result is a shallower, denser snowpack with contracted residency and stronger coupling of winter air temperature with subnivean ground surface and soil temperatures (Hardy et al. 2001, Reinmann et al. 2019). Loss of insulation from snow will cause exposure to greater temperature fluctuations and deeper freezing which can increase arthropod mortality due to overwinter freezing and exposure after early exit from diapause (Bale and Hayward 2010).

While non-winter total annual precipitation is not generally predicted to change in southern Ontario, it is expected that there will be fewer and more intense periods of rainfall (Wang et al. 2015, Zhou et al. 2017, Vincent et al. 2018). As well, summer temperatures are expected to increase, and with the fewer and more intense rainfall events, this may result in in less opportunity for soil water recharge, greater loss of potential recharge to runoff, and increased drying due to evapotranspiration (Sheffield and Wood 2008, Seneviratne et al. 2010, McDermid et al. 2015, Padrón et al. 2020). The sum of these effects would be reduced summer soil moisture which can reduce a site's viability for invertebrate oviposition, egg survivorship, and suitability for metamorphosis (Huk and Kühne 1999, Holland et al. 2007, Johnson et al. 2010, Parr and Bishop 2022).

We used structural equation modeling to evaluate mediated path analyses (Fan et al. 2016) of the indirect effects of abiotic variables on songbird daily nest survival rates, mediated by arthropods. The benefit of using structural equation modeling is that it controls for multiple covariances among many potential multivariate combinations (Kline 2004) and is solved using simultaneous maximum likelihood estimation of all pathways to best reproduce the observed variance-covariance matrix. Therefore, we assessed the relative influences of multiple processes within a network (Grace et al. 2010), including unobserved effects through inclusion of residual covariances

(Maruyama 1998) given all effects within the model. This approach allowed us to elucidate indirect, offsetting, and suppressed effects (Laughlin and Grace 2019) producing better inference about how nest survival rates may respond to the potential effects of climate change through the influence of snowpack and soil moisture on arthropods in our study area.

Structural equation models include exogenous variables which influence another variable, mediator variables which are both influenced by and have an influence on other variables, and an endogenous variable influenced by the mediator variables (Eisenhauer et al. 2015). We did not include any unmediated pathways between abiotic variables and daily nest survival as we did not want to infer unsuspected mechanisms and wanted to use the strength of *a priori* model identification (Eisenhauer et al. 2015). Our models estimated the strength of pathways between the exogenous variables snowpack, using annual maximum snow water equivalent, and soil moisture, modeled using relative difference in volumetric water content, and relative biomass (g/day) of three composite arthropod groups as mediator variables and between the mediator variables and the endogenous variable daily nest survival rate. The three composite arthropod biomass groups included food based on species-specific diets rather than total trapped biomass (after Grames et al. 2023), soil bioindicators comprised of Collembola and Acariformes, and predaceous arthropods including Araneae, Opiliones and Coleoptera. We applied this model to American Robin (*Turdus migratorius*), Eastern Wood-Pewee (*Contopus virens*), Least Flycatcher (*Empidonax minimus*), Ovenbird (*Seiurus aurocapilla*), and Red-eyed Vireo (*Vireo olivaceus*). These species breed throughout our study area, predominantly feed on arthropods during the breeding period, and provide a cross-section of genera, foraging strategies, and diets.

American Robin is a medium-sized thrush that consumes a wide variety of foods including Annelida, Lepidoptera larva, Coleoptera, Hemiptera, and Ants (Hymenoptera) as well as fruit (Swihart and Johnson 1986, Wheelwright 1986). In a widespread study of American Robin diets, Coleoptera, particularly Carabidae, Curculionidae and Scarabaeidae families, represented approximately 40% of invertebrates in the diet by frequency (Wheelwright 1986). American Robins nest at heights ranging from ~1.5 – 22 m (this study) and lay a clutch of 3 to 4 eggs with 12 to 14-d incubation and approximately 13-d nestling rearing periods (Vanderhoff et al. 2020).

Eastern Wood-Pewee is a small aerial insectivore that forages in the sub- and lower-canopy in forests through use of aerial flights from and to an exposed perch, particularly using sallying where they fly out and return to the same perch when capturing prey (Hartung and Brawn 2005). Eastern Wood-Pewees nest in trees at heights ranging from ~7 – 25 m (this study), lay a clutch of 2 to 3 eggs and have approximately 14-d incubation and 16-d nestling periods (Falconer and Nol 2020). Their diet includes Hymenoptera, Diptera, Lepidoptera, Coleoptera, Homoptera, Orthoptera and Araneae (Sample et al. 1993).

Least Flycatchers typically nest in aggregated clusters (Tarof and Ratcliffe 2004, Geboers and Nol 2009). They nest in trees with nest heights from ~1 – 26 m high (this study) and typically lay a clutch of 4 eggs (Darveau et al. 1993) with average incubation and nestling periods of approximately 12 and 15-d, respectively (Briskie and Sealy 1989). Least Flycatcher diet includes Coleoptera, Diptera, Hemiptera, Hymenoptera, Homoptera, Lepidoptera larva, Mecoptera, Araneae, Orthoptera, Odonata and Gastropoda (Sherry 1979, Robinson and Holmes 1982, Darveau et al. 1993, Tarof and Briskie 2020) and they mostly use hovering foraging tactics and, to a lesser extent, will hawk and glean insects (Sherry 1979).

Ovenbird is a ground-nesting warbler that mostly forages within 0.2 m of the substrate surface, focusing on ground litter and foliage using probing, gleaning, and hovering (Holmes and Robinson 1988). Ovenbirds lay a clutch of 2 to 6 eggs, incubate for approximately 12-d, and fledge 7 to 10-d after hatching (Stenger and Falls 1959, Stodola et al. 2010). Ovenbird diet can be interannually variable and include mostly adult Coleoptera, Lepidoptera larvae, Hymenoptera, Diptera adults and smaller amounts of Gastropoda, Hemiptera, Araneae, and Lepidoptera adults (Stenger 1958, Holmes and Robinson 1988, Streby et al. 2013).

Red-eyed Vireos nest in pendulant cups in tree branches from ~0.5 – 25 m high (this study) and incubate an average clutch of 3 eggs for 12 to 14-d and have a nestling period of 10 to 12-d (Cimprich et al. 2020). Red-eyed Vireos hover, glean, and hawk when foraging, preferring to forage in the leaves at the ends of branches (James 1976, Maurer and Whitmore 1981) in the upper canopy (Hartung and Brawn 2005), although females forage more in lower forest layers (Williamson 1971). Their diet includes Coleoptera, Lepidoptera larva and adults, Diptera, Hymenoptera, Hemiptera, Homoptera, Orthoptera, Araneae and, in late summer, fruit (Williamson 1971, Robinson and Holmes 1982, Sample et al. 1993).

Given predicted climate change-induced alterations in snowpack and summer soil moisture and potentially negative resultant consequences for arthropods, we sought to assess whether bottom-up trophic pathways could affect breeding bird nest survival rates. We hypothesized that there would be strong moderating relationships between the biomass of multiple arthropod guilds, snowpack, soil moisture and breeding bird nest survival rates. We expected that the biomass of avian arthropod diets, predaceous arthropods, and soil bioindicators would be positively influenced by maximum annual snow water equivalent and soil water content. We also expected that there would be strong positive relationships between both arthropod food biomass and soil bioindicator biomass and daily nest survival rate and weaker negative effects between predaceous arthropod biomass and daily nest survival rate because these arthropod predators could suppress populations of arthropod prey.

3.2. Methods

3.2.1. Study area and plots

Our study was carried out from January 2010 to August 2011 in the Ganaraska Forest, Ontario (44°05’N, 78°30’W). The forest is in the Mixedwood Plains Ecozone’s Lake Simcoe-Rideau Ecoregion (6E) of the Great Lakes-St. Lawrence Forest region, a moderate temperature ecoclimatic region (Crins et al. 2009). From 1981 to 2010, the daily average temperature was 6.2°C, average annual rainfall was 712.5 mm and average annual snowfall was 151.2 cm (Peterborough Airport weather station: 44°14’N, 78°22’W; Government of Canada 2023). During the study period, there was a similar average annual daily mean temperature between years (Table 3.1 and Figure 3.1; Peterborough Airport and Trent University [44°21’N, 78°17’W; September 23 to December 31, 2011] weather stations; Government of Canada 2023). As well, there was 203.9mm more total rainfall (Figure 3.1) and 95.5cm more total snowfall (Figure 3.2; Tapley weather station: 44°10’N, 78°30’W; Government of Canada 2023) in 2011 than in 2010 (Table 3.1).

In the 2010 (May 10 to August 30) and 2011 arthropod sampling periods (May 17 to August 24), which coincide closely with the nest monitoring periods (May 21 to September 1, 2010, and May 19 to August 26, 2011), average daily mean temperatures were 18.7°C (range = 4.5°C – 26.2°C) and 18.9°C (range = 11.6°C – 24.4°C), respectively. Total rainfall during the arthropod sampling period (Fig. 2.1) was 377.3 mm in 2010 and 390.4 mm in 2011 and average rainfall per day on days with precipitation during that period was 9.7 mm (*SD* = 8.5 mm, *n*= 39) in 2010 and 10.0 mm in 2011 (*SD* = 13.8 mm, *n*= 39).

Table 3.1. Summaries of total rainfall (mm), snowfall (cm), and average daily mean temperature (°C) for 2010 and 2011 using precipitation data from the Tapley weather station (44°10’N, 78°30’W) and temperature data from the Peterborough Airport (2010 and 2011) with some supplementary data for 2011 (September 23 to December 31) from the Trent University weather station (Government of Canada 2023).

	2010	**2011**
Total rainfall	771.3 mm	975.2 mm
Total snowfall (first and last snowfall of snow year)	84.9 cm (Nov. 30, 2009, to Mar. 20, 2010)	180.4 cm (Nov. 27, 2010, to Mar. 12, 2011)
Average daily mean temperature	7.8°C	7.2°C

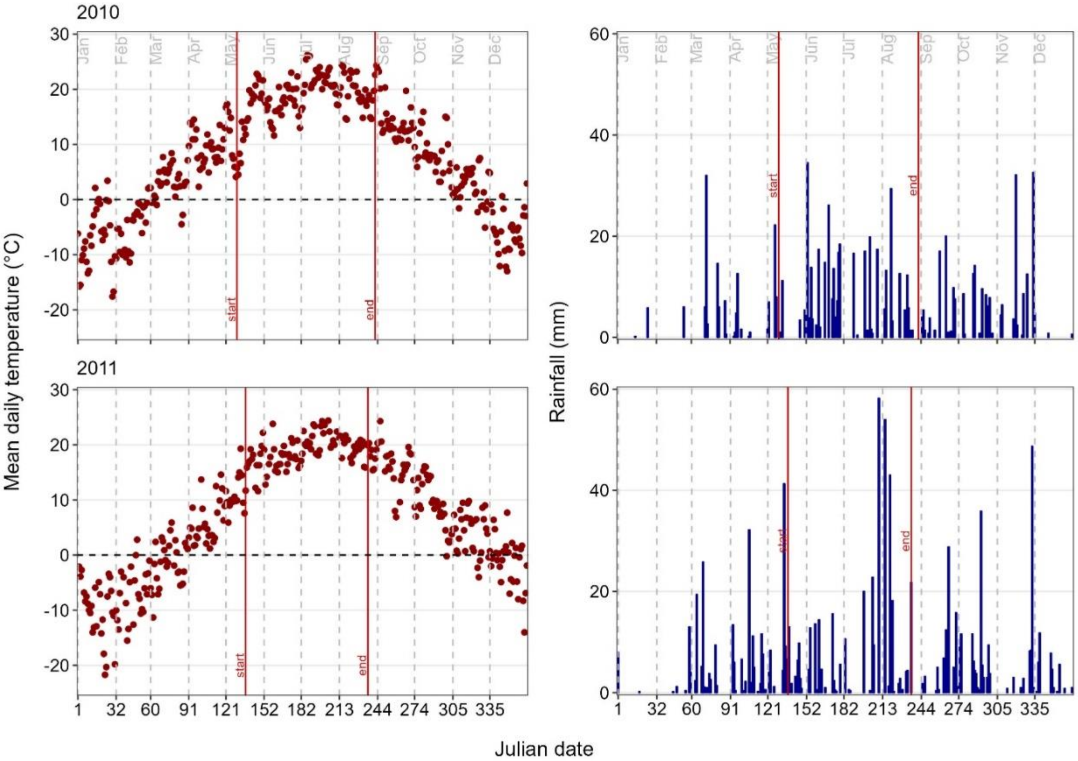

Figure 3.1. Mean daily temperature (°C; left) from the Peterborough Airport (44°14’N, 78°22’W) and Trent University (44°21’N, 78°17’W; September 23 to December 31, 2011) weather stations and total rainfall (mm; right) per day from the Tapley weather station (44°10’N, 78°30’W; Government of Canada 2023) in 2010 and 2011 (Julian day 1 = January 1). Red lines indicate start and end dates for that year’s nest monitoring.

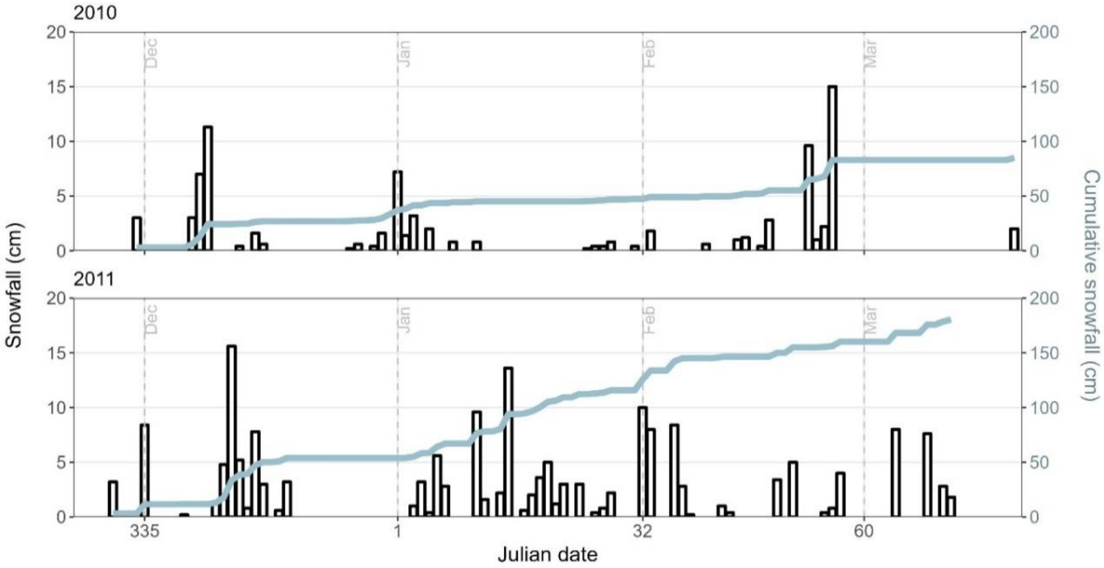

Figure 3.2. Total daily snowfall (cm; black hollow bars and left axis) and cumulative annual snowfall (cm; light blue line and right axis) for the winters of 2010 and 2011 (Julian day 1 = January 1) from the Tapley weather station (44°10’N, 78°30’W; Government of Canada 2023).

The Forest is almost equally comprised of coniferous plantation and mixed hardwoods. Coniferous plantations are dominated by red pine (*Pinus resinosa*) with smaller areas of white pine (*Pinus strobus*), Scots pine (*Pinus sylvestris*), jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), European larch (*Larix decidua*), and American larch (*Larix laricina*). Mixed hardwoods are dominated by red oak (*Quercus rubra*), sugar maple (*Acer saccharum*), and poplar (*Populus spp*.; Tedford 1978) and include some bitternut hickory (*Carya cordiformis*).

Sampling used in this study involved a plot center defined by a soil moisture access tube, snow sampling transects oriented by cardinal directions and arthropod pitfall sampling randomly spaced within 3 m of the center (Figure 3.3). We sampled snowfall, soil moisture and arthropods at 50 plots in 2010 and 60 plots in 2011, with all 2010 plots being remeasured in 2010 and an additional plots added in 2010. Plot elevations ranged from 215 m to 375 m a.s.l.

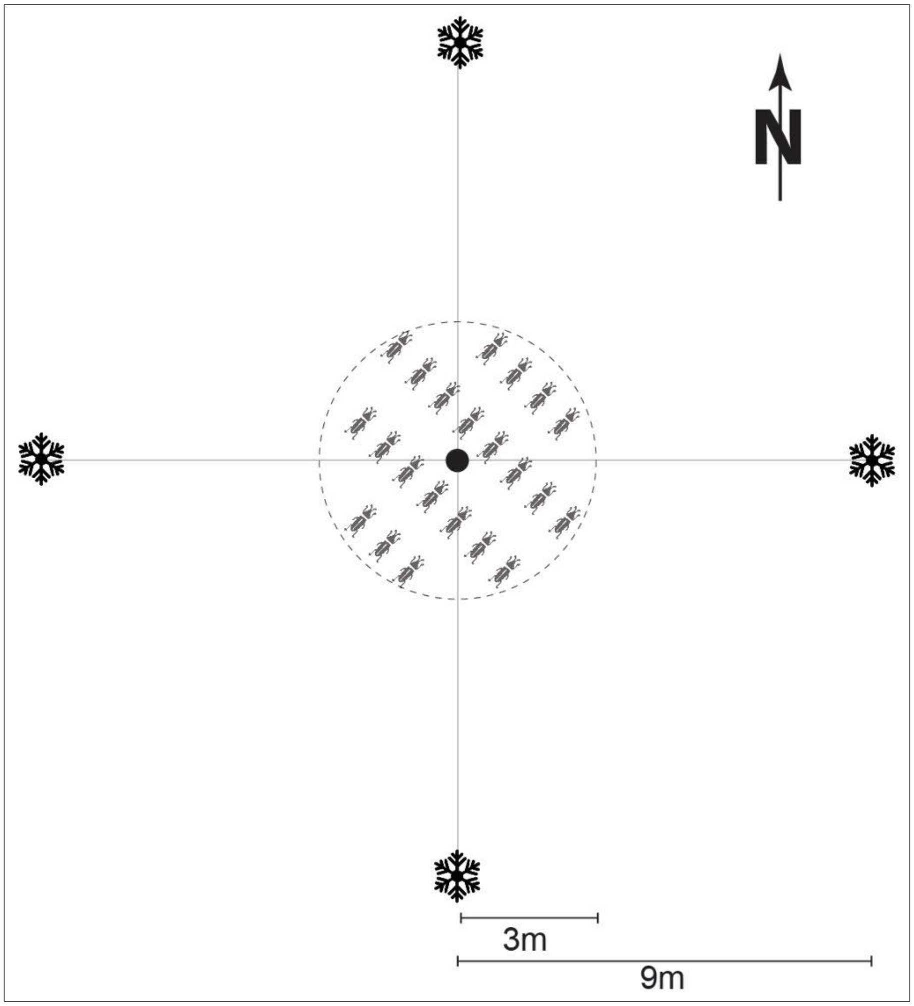

Figure 3.3. Sampling layout used for soil volumetric water content (black center circle), snow water equivalent surveys (snowflake icons), and area where pitfall traps were randomly located (dashed circle filled by beetle icons).

3.2.2. Soil volumetric water content

We used a time domain reflectometry probe (Delta-T Devices Ltd. PR2 Profile Probe (Cambridge, England) to estimate subsurface volumetric soil water content (m^3/m^3; VWC). Measurements were repeatedly collected at the same locations through permanently installed access tubes and volumetric water content for the upper 20 cm of the soil column was calculated by averaging the 10 cm and 20 cm depth sensor measures. In 2010 and 2011, sampling was performed from May 4 (Julian day 124) to August 30 (Julian day 242). Due to access tube ground contact errors and defective moisture sensors, we used fixed effects OLS estimation (R package 'fixest'; Bergé 2022) to fill as many missing measures as possible. Using the best fitting singular and additive combinations of surface, 10 cm, 20 cm, and 30 cm and depending on available data from a plot at a sample time, we estimated 22 of 207 volumetric water content values in 2010 and 9 of 467 values for 2011.

To reduce model complexity and improve interpretability, we scaled plot soil moistures to provide a measure of a plot's moisture that was relative to that of all others. We first calculated a plot's relative difference in soil moisture within each month of the sampling period. Where the volumetric water content of a site is θ_S and the monthly average volumetric water content among all sites is $\theta_{\bar{x}}$, the monthly relative difference in soil moisture for each site can be calculated as:

$$\frac{\theta_S - \theta_{\bar{x}}}{\theta_{\bar{x}}}$$

The resulting values can be positive (above average moisture) and negative (below average moisture) and their size relates to the comparative amount of wetness or dryness.

Then, we calculated mean annual relative difference in volumetric water content (rdVWC) by averaging each plot's values within each sampling month per year. We tested within-site pairwise correlations of each plot's monthly and annual relative differences and found strong correlations between all month and year combinations ($r \geq 0.8$). Therefore, to reduce model complexity we retained mean annual relative difference in VWC for each plot within each year. As there was weak correlation of interannual relative differences ($r = 0.67$) for plots sampled in both years, we used the applicable year's annual average.

3.2.3. Snow water equivalent

We used a metric prairie snow sampler (Geo Scientific Ltd., Vancouver, BC, Canada) to measure snow water equivalent (cm) at 9 m from the plot center in each cardinal direction. We ensured that trampling from previous sampling did not affect measurements by making minor adjustments to the sample point when necessary. We repeatedly recorded SWE throughout the winter season, particularly after major precipitation events, and averaged each plot's four measures. We repeatedly recorded snow water equivalent throughout the winter season, particularly after major precipitation events from Jan 26, 2010 (Julian day 26) to March 18, 2010 (Julian day 77) in the 2010 snow year, and December 21, 2010 (Julian day -10) to April 12, 2011 (Julian day 102) in the 2011 snow year. We calculated each plot's annual maximum snow water equivalent (cm; SWE) using 214 (*n* = 856) and 459 (*n*=1836) averaged measures from 2010 and 2011, respectively.

We used a metric prairie snow sampler (Geo Scientific Ltd., Vancouver, BC, Canada) to measure snow depth (to nearest 0.5 cm) at 3, 6, and 9 m as well as snow water equivalent (SWE; cm) at 9 m from sample site centers in each cardinal direction. We calculated snow density (g/cm^3) using the 9 m samples. We ensured that previous sampling and traverses did not affect measurements by making minor adjustments to the sample point when necessary. We repeatedly recorded snow water equivalent throughout the winter season, particularly after major precipitation events from Jan 26, 2010 (Julian day 26) to March 18, 2010 (Julian day 77) in the 2010 snow year, and December 21, 2010 (Julian day -10) to April 12, 2011 (Julian day 102) in the 2011 snow year. We calculated each plot's annual maximum snow water equivalent (cm; SWE) using 214 (*n* = 856) and 459 (*n*=1836) averaged measures from 2010 and 2011, respectively. We averaged each site's four measures of SWE and 12 measures of depth and tested the correlation between annual maximum measurements of depth and SWE. We found that overall depth and SWE were highly correlated in 2010 ($r = 0.89$, $n = 50$) and 2011 ($r = 0.81$, $n = 60$) and in both years combined ($r = 0.90$, $n = 110$). We selected maximum annual average SWE (cm; MaxSWE) as an independent variable in modeling as it is a commonly collected snow measure and provides a composite value of snow depth and density.

3.2.4. Arthropod sampling

Arthropods were sampled using pitfall traps (clear plastic cups with a 11.43 cm dia. opening) filled with water, a few drops of dishwashing soap to break the surface tension and approximately 25% ethyl alcohol to reduce decay during the trapping period. In 2010, we installed 4 pitfall traps in random directions and a random distance within 3 m of the plot center and sampled arthropods from May 10 (Julian day 130) to August 30 (Julian day 242). In 2011, we installed three traps per plot and sampled arthropods from May 17 (Julian day 137) to August 24 (Julian day 236). Counts were averaged among the pitfall traps collected at each plot per sampling period to correct for differences in the number of traps sampled within a period. Inconsistent trap numbers per period were the result of discarding samples from traps disturbed by wildlife, that were set too shallow or that had discontinuous soil contact around their opening. Macroarthropod samples were transferred to storage bags and frozen in ethanol until later identification in the laboratory. We analyzed 363 samples aggregated by plot and sampling period in 2010 and 203 aggregate samples in 2011. Traps were set for an average sampling period of 8 days (range 2 to 16 days) in 2010 and 7 days (range 5 to 13 days) in 2011. For each plot we averaged relative biomass by month, with a sample's date based on the mid-point of the trapping period.

Samples were identified and grouped into the following: subphylum Myriapoda (includes classes Chilopoda (centipedes), Diplopoda (millipedes), Symphyla (pseudocentipedes)), class Gastropoda (snails and slugs), superorder Acariformes (mites), and orders: Araneae (spiders), Coleoptera (beetle), Collembola (springtails), Diptera (true flies), Haplotaxida (earthworms), Hemiptera (true bugs), Hymenoptera (wasps, sawflies and ants), Isopoda (Suborder Oniscidea: woodlouse), Lepidoptera (butterflies and moths), Opiliones (harvestmen), and Orthoptera (crickets and grasshoppers). Samples were also classified based on length, typically by 3 mm intervals up to 19 mm and then a single category for body lengths ≥20mm. Biomass was calculated using oven-dried weights for body lengths measured for an unpublished study in the Ganaraska Forest (Walters 2008). Where a length and weight combination were unavailable, we used the average of the weights from immediately larger and smaller intervals or OLS estimation if averaging was not possible. As values had been converted to average relative abundance per plot day, biomass values represented relative average dry mass per plot per day (g/day).

3.2.5. Nest monitoring

In 2010 and 2011, we searched for nests around our plot centers and found active American Robin, Eastern Wood-Pewee, Least Flycatcher, Ovenbird and Red-eyed Vireo nests by visually searching potential nest habitat and observing parental behavior. Nests were found from 0 m to 270 m from the nearest plot centre with a median distance of 102 m. To link nests with abiotic and arthropod variables, we created a mesh of Thiessen polygons where boundaries are assigned mid-way between plots. Nests within a plot's Thiessen polygon were assigned the soil moisture and snowpack data for that plot (Fig. 3.4). This approach which is required to facilitate grouping for logistic-exposure modeling assumes that measures for that polygon such as food and abiotic variables are the strongest influences for the nest as they are from the nearest sample site, regardless of proximity to other sample sites.

We found and monitored nests from May 21 (Julian day 141) to September 1 (Julian day 244) in 2010 and from May 19 (Julian day 139) to August 26 (Julian day 238) in 2011. We monitored active nests every 4 days on average (*SE* = 0.04 days; Range 1 – 12 days) until a nest failed or fledged young. When a nest was empty near the predicted fledging date, we searched the vicinity for fledglings, displays by adults, and assessed other signs of successful fledging such as nest condition and fecal matter in the nest (Burhans and Thompson 2006). Nest failure was assumed when signs of predation were present (e.g., disturbed nest cup) or if the nest was empty prior to the minimum expected fledging date.

Nests were categorized by incubation and nestling stages. Nests that transitioned between stages during a visit interval (American Robin: 22.8%; Eastern Wood-Pewee: 15.5%; Least Flycatcher: 6.6%; Ovenbird: 15.5%; Red-eyed Vireo: 8.8%) were assigned to the incubation stage as we did not expect the influence of begging or provisioning to have as much of an effect in early nestling stages as in late nestling stages. We did not include any nests of unknown outcome or with unknown contents (and therefore unknown stage) in analyses.

We modeled daily nest survival rate (DNSR; the probability that a nest survives one day to the next) with a logistic-exposure model using a generalized linear model with a modified logit link (Shaffer 2004). As generalized linear models with custom link functions cannot be included in current structural equation model R packages, we calculated DNSR using separate modeling and used the predicted values for each nest observation interval as the response variable in subsequent structural equation modeling.

To account for temporal effects on daily nest survival rates (Thompson 2007), we compared a suite of models using Akaike's Information Criterion corrected for small samples (AICc). We constructed 7 models that included a null model, as well as additive combinations of year, nest stage as a factor, Julian date with day 1 on January 1, and quadratic Julian date (Date + Date^{2}). We used the model with the lowest AICc value added to plot as a grouping factor to predict DNSR for each nest observation interval.

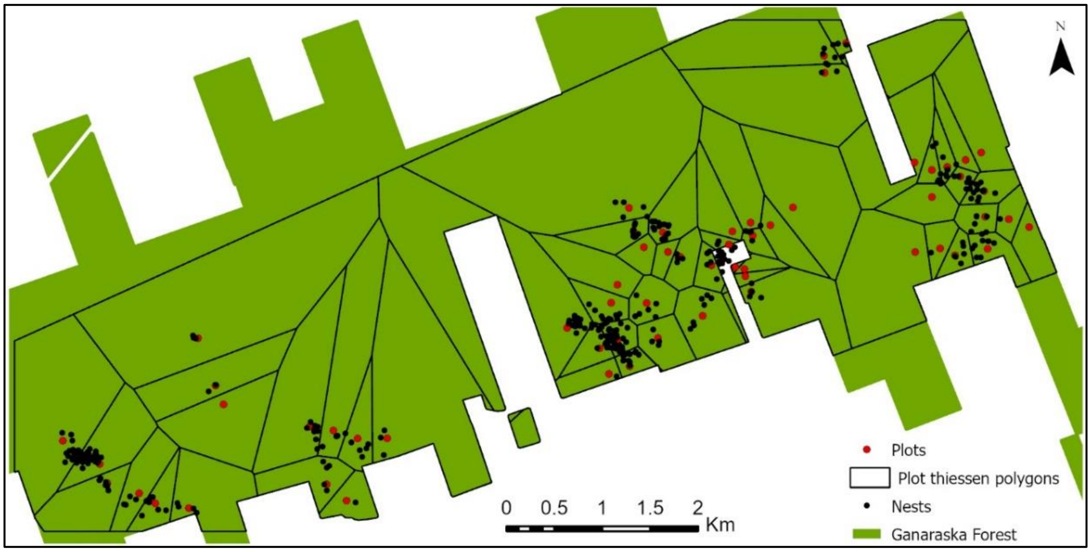

Figure 3.4. Map showing plot locations (red circles), associated Thiessen polygons (delineated by black lines), all monitored nests used in analyses regardless of species (black circles), and a portion of the Ganaraska Forest that included the entire extent of the study area (green polygon).

3.2.6. Structural equation modeling

We evaluated structural equation models using lavaan package 0.6.15 (Rossel 2012). Our model structure was a three-level, full mediation path analysis without latent variables (Figure 3.5). The soil bioindicator arthropod group (hereafter 'Soil') biomass was composed of the sum of Acariformes and Collembola biomass. The predaceous arthropod group (hereafter 'Pred') biomass was composed of the total biomass of Araneae, Coleoptera, and Opiliones. The food resource group (hereafter 'Food') biomass was composed using species-appropriate arthropod prey items (Table 3.2). We included Gastropoda, albeit including Slugs, in all food totals, even if not documented in their diet because of the importance of snails in providing calcium to nesting birds (Graveland and van der Wal 1996, Pabian and Brittingham 2011, Pintar and Olsen 2022). Biomass totals were negatively skewed, so we log-transformed the data adding 0.1 to food, 0.01 to predators, and 0.0001 to soil bioindicators to facilitate transformation of 0 values. We tested multivariate normality for all models using the Mardia test and univariate Shapiro-Wilk tests in package mvnormalTest 1.0.0 (Zhang et al. 2020). In all cases, data failed multivariate normality tests, so we used the "MLM" maximum likelihood estimator with robust standard errors and robust measures of model fit. We continued to use log-transformed data in our models as non-transformed data resulted in multiple models failing to converge and log-transformation improved linearity.

We constructed structural equation models to have the smallest ratio of observations to free parameters as possible, as a minimum 5:1 ratio is recommended but a greater ratio such as 10:1 is recommended when distributions are non-normal

(Bentler and Chou 1987). In our base structural equation model, there were 13 potential free parameters (individual linear combinations) made up of two exogenous variables, three arthropod groups as mediators and a single endogenous response variable. If all mediator groups were also identified to have residual covariance due to an unmeasured effect, then the number of free parameters would be a maximum of 16. We included only those residual covariances required to improve model fit (significant relationships) to minimize the number of free parameters used.

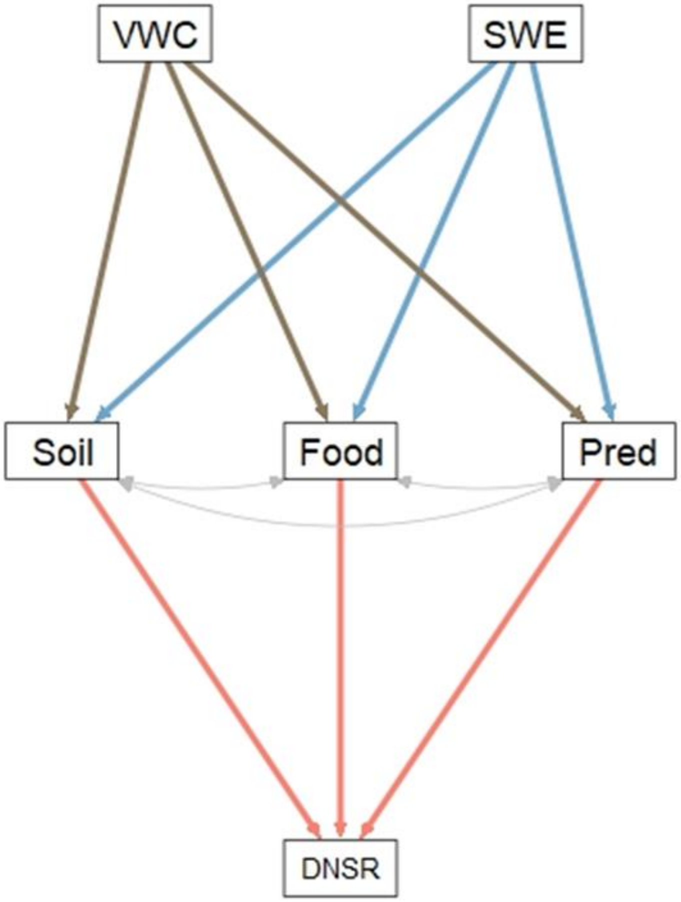

Figure 3.5. Diagram of structural equation model pathways used for daily nest survival rate analysis in Chapter 3. VWC = mean relative difference in soil volumetric water content (m^3 water / m^3 soil), SWE = maximum annual snow water equivalent (cm), Soil = biomass (g/day) of soil bioindicator arthropod functional group, Food= biomass (g/day) of arthropods in focal avian species diet, Pred= biomass (g/day) of predaceous arthropod functional group, DNSR = daily nest survival rate of focal avian species calculated using logistic-exposure modeling.

Table 3.2. Arthropod groups included in biomass totals for food sampled using pitfall trapping for American Robin (*Turdus migratorius*), Eastern Wood-Pewee (*Contopus virens*), Least Flycatcher (*Empidonax minimus*), Red-eyed Vireo (*Vireo olivaceus*), and Ovenbird (*Seiurus aurocapilla*) based on published diets as reviewed in the introduction.

American Robin	**Eastern Wood-Pewee / Least Flycatcher / Red-eyed Vireo**	**Ovenbird**
• Araneae	• Araneae	• Araneae
• Coleoptera	• Coleoptera	• Coleoptera
• Diptera	• Diptera	• Diptera
• Gastropoda	• Gastropoda	• Gastropoda
• Haplotaxida	• Hemiptera	• Hemiptera
• Hemiptera	• Hymenoptera	• Hymenoptera
• Hymenoptera	• Lepidoptera	• Lepidoptera
• Lepidoptera	• Opiliones	• Opiliones
• Opiliones	• Orthoptera	
• Orthoptera		

Measures of structural equation model fit are sensitive to misspecification in different areas (e.g., covariances versus loadings) and small sample sizes (*N* values ≤ 200), so we used combinational assessments of model fit (Hu and Bentler 1999). To assess the fit of our models, we used recommended minimum values of 0.95 for robust comparative fit index (rCFI), 0.9 for robust Tucker-Lewis index (rTLI) and maximum values of 0.06 for robust root mean square error of approximation (rRMSEA) and 0.09 for standardized root mean square residual (rSRMR; Hu and Bentler 1999, Fan et al. 2016).

American Robin, Eastern Wood-Pewee and Ovenbird models passed goodness-of-fit tests (Table 3.3). Least Flycatcher and Red-eyed Vireo models' rTLI and rRMSEA tests did not meet thresholds and rCFI was slightly below the threshold for Red-eyed Vireo (Table 3.3). Structural equation model goodness-of-fit indices are descriptive and based on rules of thumb, which are often not considered rigid, but arbitrarily defined approximate thresholds (Schermelleh-Engel et al. 2003, Hu and Bentler 1999). As the rCFI for Red-eyed Vireo was within 0.01 of the threshold, and an RMSEA of 0.10 could be considered an "adequate fit" (Schermelleh-Engel et al. 2003) we did not consider these fits problematic. We accepted the fits given the overall achievement of goodness-of-fit and because we controlled free parameter ratios, specified models *a priori*, greater sample sizes are methodically challenging, and no rule of thumb applies to all situations (Schermelleh-Engel et al. 2003).

We considered results statistically significant at a 95% confidence level, but we also report on strong relationships with parameter estimate confidence intervals that slightly overlapped 0 and $p > 0.05$ and $p < 0.10$. We report unstandardized coefficients to allow comparison of parameter estimate across models and standardised coefficients for within model contribution of pathway strengths. We caution that standardized coefficients are based on standard deviation and therefore a normal distribution (Grace et al. 2010); however, skewness often persisted after transformation of our data due to the large number of zeros in arthropod biomasses. Statistical analyses were performed using the R statistical package version 4.2.3 (R Core Team, 2023) in RStudio version 2023.03.0 (RStudio Team, 2023). Spatial analyses were performed using ArcGIS Pro 2.5.0 (ESRI Inc 2020) with NAD1983 UTM 17N datum projection.

Table 3.3. Model specifications and goodness of fit test results for American Robin (*Turdus migratorius*), Eastern Wood-Pewee (*Contopus virens*), Least Flycatcher (*Empidonax minimus*), Ovenbird (*Seiurus aurocapilla*), and Red-eyed Vireo (*Vireo olivaceus*) structural equation models. Values beyond acceptable thresholds (below test names) are shown in bold. N. Obs.= effective number of observations; N. Param. = number of model free parameters used; rCFI = robust comparative fit index, rTLI= robust Tucker-Lewis index, rRMSEA= robust root mean square error of approximation and rSRMR= robust standardized root mean square residual.

	N. Obs..	***N. Param.***	**rCFI** (> 0.95)	**rTLI** (> 0.9)	**rRMSEA** (< 0.06)	**rSRMR** (< 0.09)
American Robin	147	14	0.99	0.95	0.05	0.04
Eastern Wood-Pewee	624	16	1.00	1.02	0.00	0.00
Least Flycatcher	211	16	0.96	**0.70**	**0.13**	0.04
Ovenbird	137	15	1.00	1.06	0.00	0.03
Red-eyed Vireo	272	15	**0.94**	**0.74**	**0.10**	0.05

3.3. Results

3.3.1. Abiotic variables

Each species had nests distributed across gradients of maximum SWE (Figure 3.6) and relative difference in non-winter VWC (Figure 3.7) in both years. We found more Eastern Wood-Pewee nests in areas which had lower SWE in 2010, but this pattern was not evident in 2011. Similarly, we monitored more Least Flycatcher nests in areas that had higher SWE in 2010, but not in 2011. Nests were more frequently found at wetter sites overall in 2011, but nests were found at sites with below average VWC for most species (Figure 3.7). The greater number of Least Flycatcher nests at sites with higher-than-average soil moisture in both years was the only apparent species-based pattern for VWC.

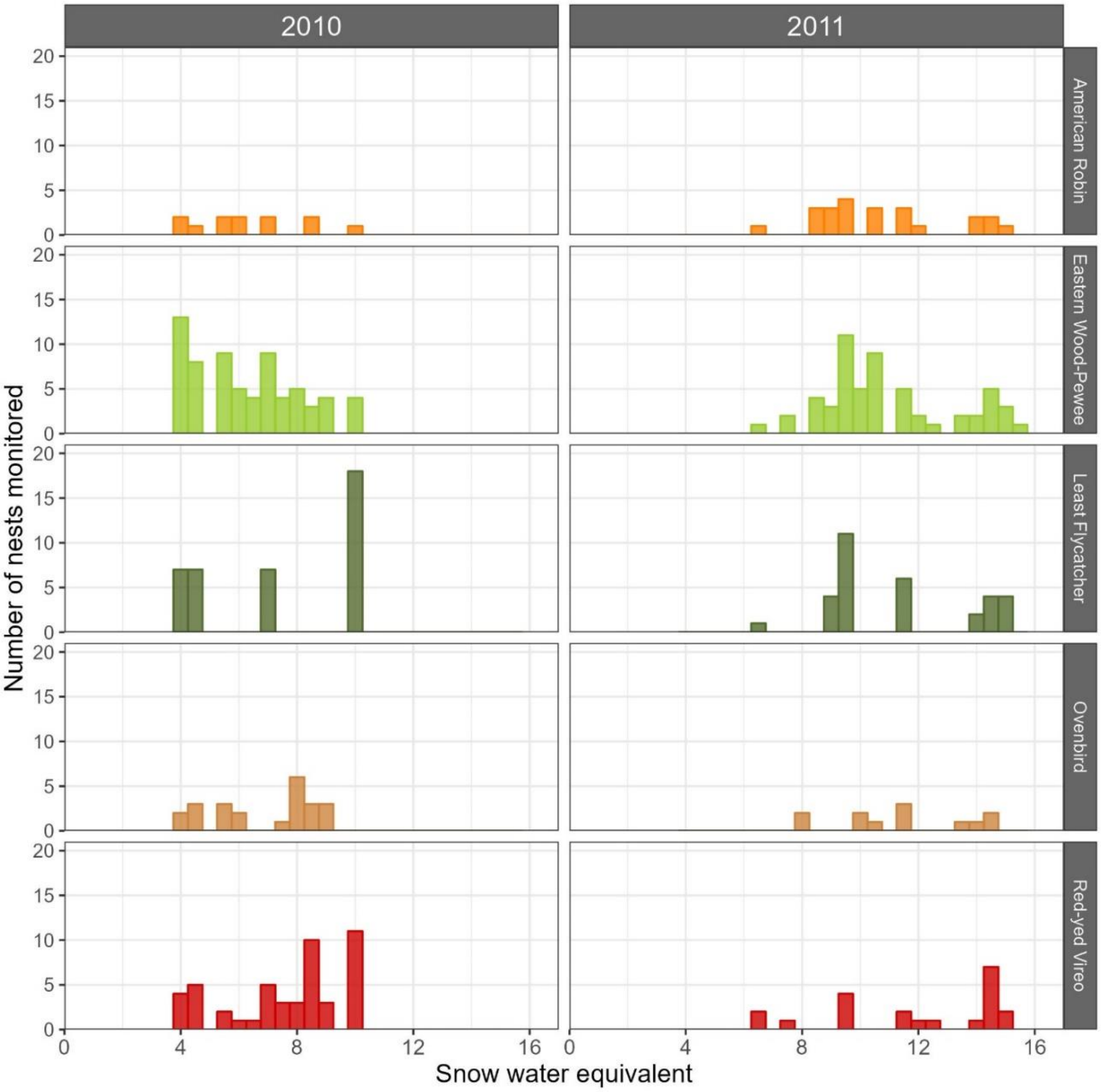

Figure 3.6. The number of nests monitored and used in analysis among gradients of snow water equivalent (SWE; cm) for focal species in 2010 and 2011 in the Ganaraska Forest, Ontario.

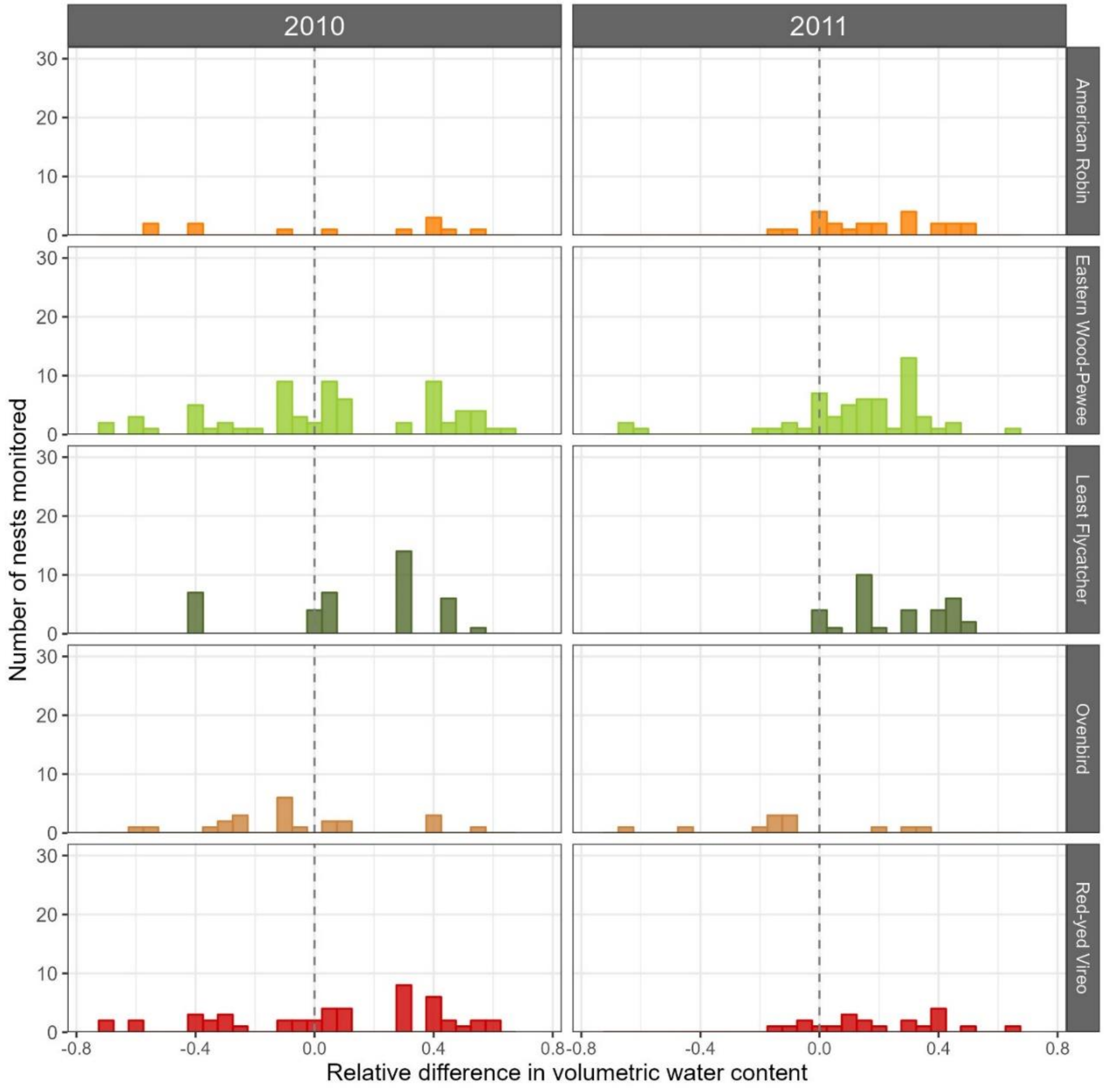

Figure 3.7. The number of nests monitored and used in analysis among gradients of relative difference in soil volumetric water content (VWC; m^3 water / m^3 soil) for focal species in 2010 and 2011 in the Ganaraska Forest, Ontario. The dotted line indicates the overall mean relative difference in volumetric water content (VWC).

3.3.2. Daily nest survival rates

Mean annual daily nest survival rates were variable among species (Table 3.4). American Robin generally had higher average DNSR than the other species with the second highest rate in 2010 (0.970) and highest rate in 2011 (0.986). Least Flycatcher generally had lower average DNSR than the other species, with the second lowest rate in 2010 (0.965) and the lowest rate in 2011 (0.946). Ovenbird had the most interannual variation in average DNSR, having the highest average rate in 2010 (0.980) and the second lowest rate in 2011 (0.947).

To improve estimates of nest-specific daily nest survival rates we included a preliminary suite of temporal covariates. We found that daily nest survival rates for all species were best modeled by a combination of temporal effects rather than an intercept-only model (Table 3.5). Nest survival increased from 2010 to 2011 for American Robin, Least Flycatcher and Red-eyed Vireo, but not Eastern Wood-Pewee and Ovenbird (Table 3.6). For all species except American Robin, nest stage was an important factor and the incubation stage had higher DNSR than the nestling stage. American Robin DNSR increased linearly with date, whereas Ovenbird DNSR rate declined. DNSRs for Eastern Wood-Pewee and Least Flycatcher had quadratic effects of date with DNSR first declining then increasing later in the nesting period.

Table 3.4. Mean annual daily nest survival rates (DNSR) with upper and lower 95% confidence intervals (CI), percentage of successful nests (% Success), effective number of observations (Effective *N*), total nests monitored (*N*), and total number of nest exposure days (Exposure days) for American Robin, Eastern Wood-Pewee, Least Flycatcher, Ovenbird, and Red-eyed Vireo nests monitored in the Ganaraska Forest, Ontario in 2010 and 2011.

	American Robin	**Eastern Wood-Pewee**	**Least Flycatcher**	**Ovenbird**	**Red-eyed Vireo**
2010					
DNSR	0.970	0.966	0.965	0.980	0.956
CI	0.938 – 0.989	0.954 – 0.976	0.945 – 0.979	0.961 – 0.991	0.938 – 0.970
% Success	58%	28%	33%	52%	35%
Effective *N*	48	325	120	96	180
N	12	68	39	23	48
Exposure days	177	1207	482	360	704
2011					
DNSR	0.986	0.973	0.946	0.947	0.972
95%CI	0.971 – 0.994	0.962 – 0.982	0.918 – 0.967	0.903 – 0.975	0.951 – 0.987
% Success	70%	32%	25%	17%	48%
Effective *N*	99	299	91	41	92
N	23	56	32	12	21
Exposure days	436	1121	368	163	342
Total *N*	35	124	71	35	69

Table 3.5. Akaike's information criterion (AICc) results and difference from the lowest value (ΔAICc) for logistic-exposure models of daily nest survival. Lowest value AIC was selected as the best fitting model and used for predicted daily nest survival rates used for subsequent structural equation models unless the null model was within 2 AIC points.

	American Robin		Eastern Wood-Pewee		Least Flycatcher		Ovenbird		Red-eyed Vireo	
Model	**AICc**	**ΔAICc**	**AICc**	**ΔAICc**	**AICc**	**ΔAICc**	**AICc**	**ΔAICc**	**AICc**	**ΔAICc**
Null	77.00	2.35	439.85	16.61	178.07	4.80	96.30	8.48	218.74	2.83
Year	77.65	3.00	440.92	17.69	178.52	5.25	94.81	7.00	219.04	3.13
Year+Stage	79.40	4.75	423.88	0.65	180.40	7.13	87.91	0.10	**215.90**	**0.00**
Year+Date	**74.65**	**0.00**	437.90	14.66	177.50	4.23	91.92	4.10	220.77	4.87
Year++Date+Date^2	76.76	2.10	433.25	10.02	175.26	1.99	93.49	5.68	221.12	5.21
Year+Stage+Date	75.37	0.72	425.84	2.61	176.35	3.08	**87.82**	**0.00**	217.91	2.01
Year+Stage+Date+Date^2	77.5	2.84	**423.23**	**0.00**	**173.27**	**0.00**	89.86	2.04	219.06	3.16

Table 3.6. Temporal logistic-exposure model parameter estimates with standard error (in parentheses below estimate) for American Robin (AMRO), Eastern Wood-Pewee (EAWP), Least Flycatcher (LEFL), Ovenbird (OVEN), Red-eyed Vireo (REVI) additive models with the lowest AICc. Values indicate parameters included in a species model include model intercept (b_0), the year 2011 (Year2011) as a factor (2010 parameter estimate is 0), the nestling stage ($Stage_{Nestling}$) as a factor (incubation stage parameter estimate is 0), Julian date (Date) where January 1st is day 1, and Julian date squared ($Date^2$).

Species	**b_0**	**$Year_{2011}$**	**$Stage_{Nestling}$**	**Date**	**$Date^2$**
AMRO	-15.960 (8.925)	1.040 (0.647)		0.053 (0.024)	
EAWP	26.444 (12.560)	0.228 (0.254)	-0.941 (0.279)	-0.251 (0.124)	0.001 (0.0003)
LEFL	73.572 (35.007)	-0.643 (0.359)	-0.912 (0.441)	-0.791 (0.410)	0.002 (0.001)
OVEN	23.461 (6.923)	-1.434 (0.579)	-1.497 (0.590)	-0.027 (0.017)	
REVI	-1.161 (4.002)	0.461 (0.389)	-0.759 (0.337)		

3.3.3. Structural equation model pathways

Among the species modeled, there were variable responses in the directions of pathway relationships between DNSR, arthropod group biomasses, snowpack, and soil moisture. There were significant positive relationships between food biomass and DNSR for Eastern Wood-Pewee and Red-eyed Vireo (Table 3.7). There was also a positive non-significant (*p* = 0.12) relationship between food biomass and DNSR for American Robin. Eastern Wood-Pewee and Red-eyed Vireo DNSR was also strongly, but not significantly (*p* = 0.057) negatively related to predaceous arthropod biomass. Least Flycatcher DSNR was negatively related to food biomass. Also, the soil bioindicator arthropod group had a significant positive influence on Least Flycatcher DNSR and a strong, but non-significant (*p* = 0.096) negative influence on American Robin DNSR.

There were generally variable combinations of responses of arthropod group biomasses to SWE and VWC among species models. Soil bioindicator biomass showed variable responses throughout species models with no abiotic influences in the American Robin, Ovenbird and Red-eyed Vireo models. Soil bioindicator biomass was positively influenced by VWC in Least Flycatcher and Eastern Wood-Pewee models and was negatively influenced by SWE in the Eastern Wood-Pewee model. Predaceous arthropods were influenced by different combinations of the effects of SWE and VWC among all species' models. SWE influenced predaceous arthropod biomass negatively in three of five models and positively in two of five models. Where there were negative relationships with SWE, predaceous arthropod biomass relationships with VWC were positive in one model, negative in one model and not related in one model. Where there were positive effects of SWE on predaceous arthropod biomass, one model had a positive relationship with VWC, and one had a negative relationship with VWC. The significant positive relationship between SWE and food biomass for all species was the most consistent influence between arthropods and abiotic factors. With these positive relationships, VWC was either negatively (two of five models) or not related (three of five models) to food biomass.

Table 3.7. Summary of structural equation model pathway relationships between daily nest survival rate (DNSR), maximum annual snow water equivalent (SWE; cm) and mean annual relative difference in soil volumetric water content (VWC) and relative biomass (g/day) of Soil bioindicator (Soil), Predator (Pred) and Food arthropod groups. Modeling was performed separately for American Robin, Eastern Wood-Pewee, Least Flycatcher, Ovenbird and Red-eyed Vireo. A red negative (—) symbol indicates a significant negative relationship and black plus symbol (+) indicates a significant positive relationship. Non-significant but strong relationships ($p > 0.05$ and $p \leq 0.1$) are indicated by the same symbols, but coloured grey.

		DNSR	**SWE**	**VWC**
American Robin	**Soil**	—		
	Pred		—	+
	Food		+	
Eastern Wood-Pewee	**Soil**		—	+
	Pred	—	+	+
	Food	+	+	
Least Flycatcher	**Soil**	+		+
	Pred		—	
	Food	—	+	—
Ovenbird	**Soil**			
	Pred		+	—
	Food		+	
Red-eyed Vireo	**Soil**			
	Pred	—	—	—
	Food	+	+	—

3.3.3.i. American Robin

American Robin DNSR was not significantly related to the biomass of any arthropod group (Figures 3.8 and 3.9), but there was a strong (p = 0.096) negative relationship (b = -0.041, LCI = -0.090, UCI = 0.007) with soil bioindicator biomass. DNSR was not related to food (b = 0.028, LCI = -0.007, UCI = 0.063) or predaceous arthropod biomasses (b = 0.019, LCI = -0.009, UCI = 0.047). The negative relationship between soil bioindicator biomass and DNSR had the largest standardized estimate (β = -0.209, LCI = -0.413, UCI = -0.005) whereas the standardized estimates for food biomass (β = 0.101, LCI = -0.036, UCI = 0.238) and predaceous arthropod biomass (β = 0.097, LCI = -0.040, UCI = 0.235) were smaller and similar.

The soil bioindicator biomass was not related to SWE or VWC. Food biomass was significantly positively related to SWE (b = 0.021, LCI = 0.012, UCI = 0.030) and not related to VWC. Predaceous arthropod biomass was significantly negatively related to SWE (b = -0.046, LCI = -0.062, UCI = -0.029) and significantly positively related to VWC (b = 0.178, LCI = 0.078, UCI = 0.277). The standardized coefficient for the negative effect of SWE (β = -0.595) on predaceous arthropod biomass was larger than the VWC (β = 0.284) coefficient.

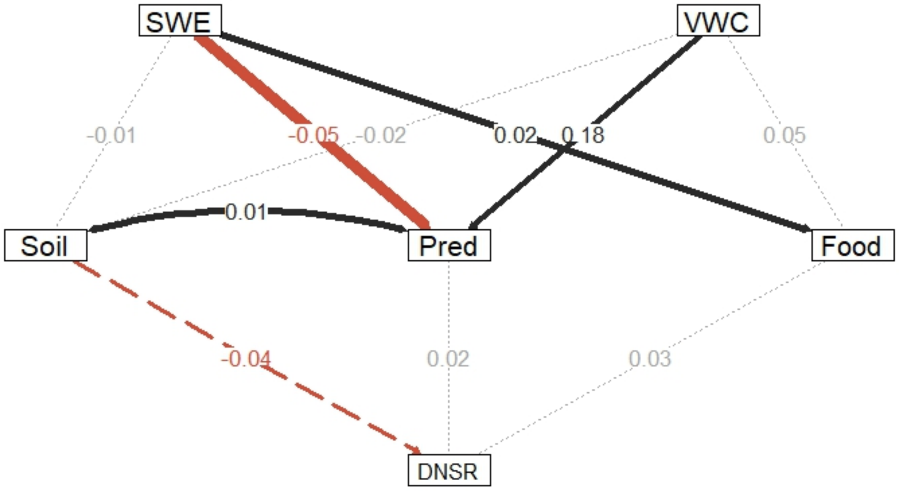

Figure 3.8. Structural equation model pathways for American Robin daily nest survival rate (DNSR) related to arthropod group biomasses (g/day; Soil = soil bioindicator arthropods, Pred= predaceous arthropods, Food= arthropods in American Robin diet), maximum annual snow water equivalent (SWE; cm) and annual relative difference in volumetric water content (VWC). Line colour and thickness are relative to standardized estimate size and direction (black= positive; red=negative). Unstandardized estimates shown on lines. Solid lines are significant relationships ($p < 0.05$), long dashed lines indicate p value between 0.05 and 0.1 and dotted grey lines indicate $p > 0.1$.

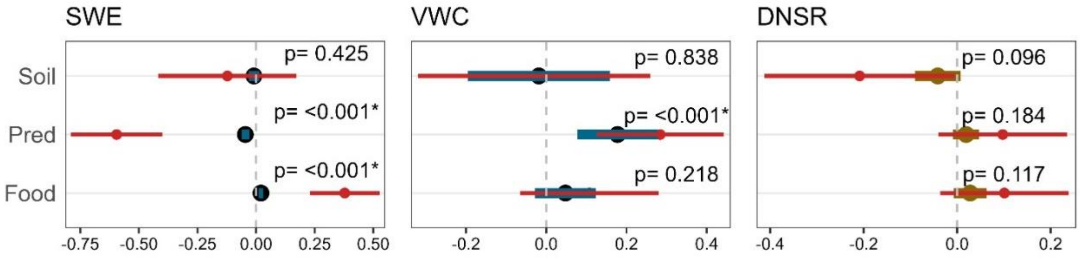

Figure 3.9. Standardized (red and thin) and unstandardized (all other colours and thick) parameter estimates (point) and 95% confidence intervals (line) for pathway relationships between maximum snow water equivalent (SWE; cm), relative difference in volumetric water content (VWC), mean relative biomass of soil arthropods (Soil), predaceous arthropods (Pred) and arthropod food items (Food) and American Robin daily nest survival rate (DNSR). p values of unstandardized estimates are shown.

3.3.3.ii. Eastern Wood-Pewee

Eastern Wood-Pewee DNSR was significantly related to food and predaceous arthropod biomass, but not soil bioindicator biomass. Food biomass significantly positively influenced DNSR (*b* = 0.035, LCI = 0.005, UCI = 0.065) and significantly negatively related to predaceous arthropod biomass (*b* = -0.023, LCI = -0.045, UCI = -0.001; Figures 3.10 and 3.11). The relationship with food biomass had a larger standard estimate (β = 0.109, LCI = 0.022, UCI = 0.195) than the relationship with predaceous arthropod biomass (β = -0.097, LCI = -0.186, UCI = -0.007), although the confidence interval values were overlapping, so there is some uncertainty in the relative strengths of the effects.

All arthropod groups biomasses were significantly related to SWE although the soil bioindicator group was a negative relationship whereas the other relationships were positive. Changes in SWE had a greater effect on food biomass (β = 0.438, LCI = 0.385, UCI = 0.490) than predaceous arthropod biomass (β = 0.095, LCI = 0.015, UCI = 0.174). There were significant positive relationships between VWC and predaceous arthropod biomass and soil bioindicator biomass, but no relationship with food biomass. For predaceous arthropods, changes in VWC (β = 0.131, LCI = 0.044, UCI = 0.218) would have greater effects than changes in SWE, but there was overlap in their confidence intervals.

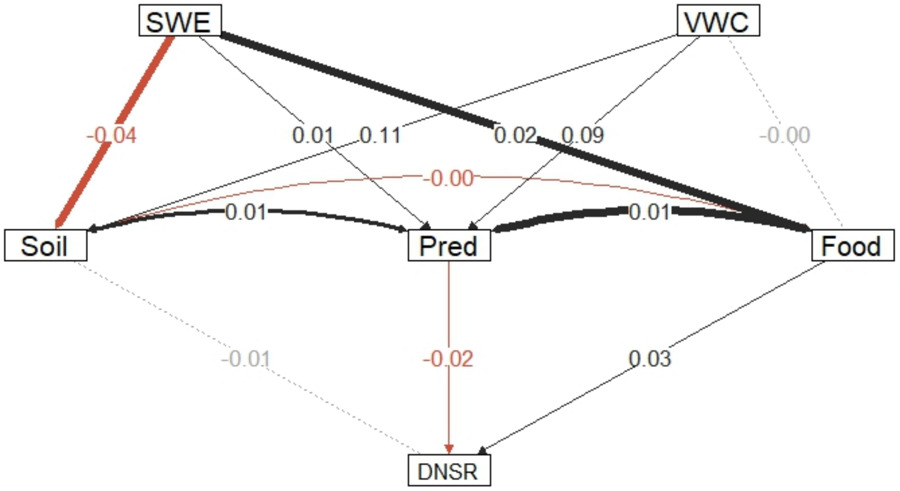

Figure 3.10. Structural equation model pathways for Eastern Wood-Pewee daily nest survival rate (DNSR) related to arthropod group biomasses (g/day; Soil = soil bioindicator arthropods, Pred= predaceous arthropods, Food= arthropods in Eastern Wood-Pewee diet), maximum annual snow water equivalent (SWE; cm) and annual relative difference in volumetric water content (VWC). Line colour and thickness are relative to standardized estimate size and direction (black= positive; red=negative). Unstandardized estimates shown on lines. Solid lines are significant relationships ($p < 0.05$), long dashed lines indicate *p* value between 0.05 and 0.1 and dotted grey lines indicate $p > 0.1$.

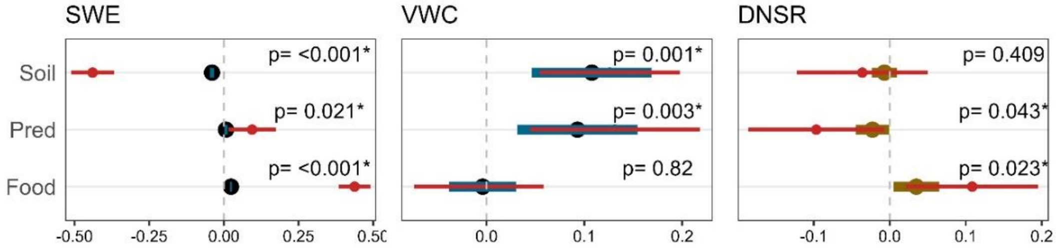

Figure 3.11. Standardized (red and thin) and unstandardized (all other colours and thick) parameter estimates (point) and 95% confidence intervals (line) for pathway relationships between maximum snow water equivalent (SWE; cm), relative difference in volumetric water content (VWC), mean relative biomass of soil arthropods (Soil), predaceous arthropods (Pred) and arthropod food items (Food) and Eastern Wood-Pewee daily nest survival rate (DNSR). *p* values of unstandardized estimates are shown.

3.3.3.iii. Least Flycatcher

Least Flycatcher DNSR was significantly influenced by food biomass and soil bioindicator biomass. DNSR was significantly negatively related to food biomass (*b* = -0.094, LCI = -0.154, UCI = -0.034) and significantly positively related to soil bioindicator biomass (*b* = 0.026, LCI = 0.002, UCI = 0.049; Figures 3.12 and 3.13). There was a weakly (*p* = 0.14) negative trend with predaceous arthropod biomass (*b* = -0.016) with confidence intervals overlapping 0 (LCI = -0.037, UCI = 0.005). The negative effect of food biomass on DNSR (β = -0.269, LCI = -0.420, UCI = -0.119) had greater strength than the positive effect of soil bioindicators (β = 0.162, LCI = 0.018, UCI = 0.305), although there was some overlap in standardized estimate confidence intervals.

VWC had a significant negative relationship with food biomass (*b* = -0.062, LCI = -0.119, UCI = -0.004) and a non-significant positive relationship with soil bioindicator biomass (*b* = 0.165, LCI = -0.010, UCI = 0.340). Food biomass also had a significant positive relationship with SWE (*b* = 0.019, LCI = 0.014, UCI = 0.023).

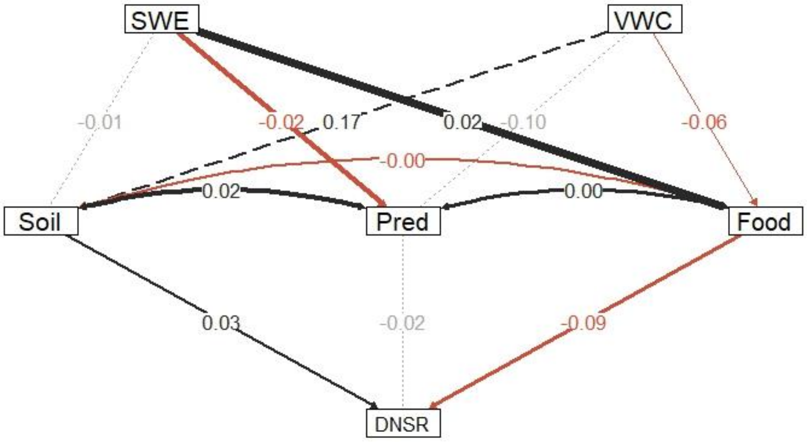

Figure 3.12. Structural equation model pathways for Least Flycatcher daily nest survival rate (DNSR) related to arthropod group biomasses (g/day; Soil = soil bioindicator arthropods, Pred= predaceous arthropods, Food= arthropods in Least Flycatcher diet), maximum annual snow water equivalent (SWE; cm) and annual relative difference in volumetric water content (VWC). Line colour and thickness are relative to standardized estimate size and direction (black= positive; red=negative). Unstandardized estimates shown on lines. Solid lines are significant relationships (*p* < 0.05), long dashed lines indicate *p* value between 0.05 and 0.1 and dotted grey lines indicate *p* > 0.1.

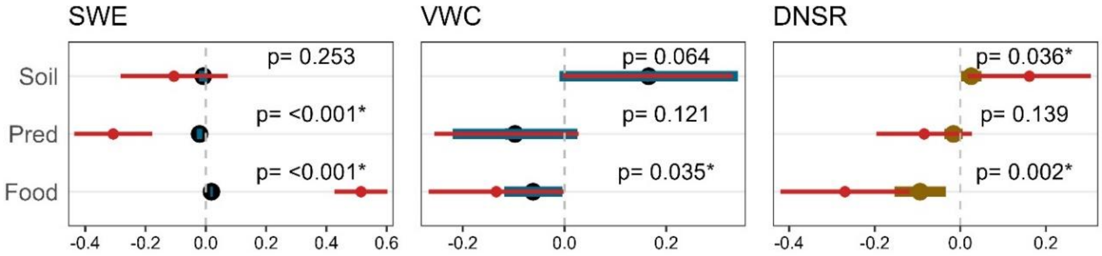

Figure 3.13. Standardized (red and thin) and unstandardized (all other colours and thick) parameter estimates (point) and 95% confidence intervals (line) for pathway relationships between maximum snow water equivalent (SWE; cm), relative difference in volumetric water content (VWC), mean relative biomass of soil arthropods (Soil), predaceous arthropods (Pred) and arthropod food items (Food) and Least Flycatcher daily nest survival rate (DNSR). *p* values of unstandardized estimates are shown.

3.3.3.iv. Ovenbird

Ovenbird DNSR was not related to the biomass of any arthropod groups (Figure 3.14 and 3.15). Among the arthropod groups, food biomass was significantly positively related to SWE (*b* = 0.019, LCI = 0.008, UCI = 0.030) and predaceous arthropods were significantly negatively related to VWC (*b* = -0.277, LCI = -0.391, UCI = -0.163) and strongly positively related to SWE (*b* = 0.011, LCI = -0.001, UCI = 0.024).

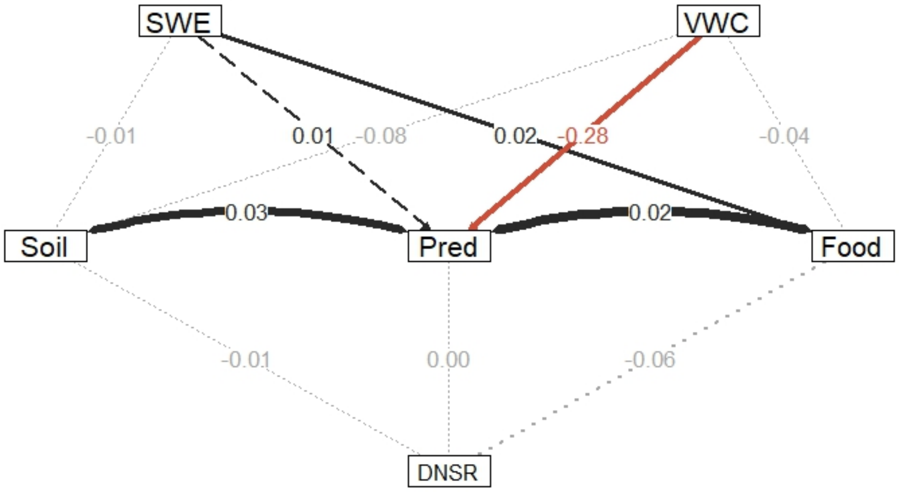

Figure 3.14. Structural equation model pathways for Ovenbird daily nest survival rate (DNSR) related to arthropod group biomasses (g/day; Soil = soil bioindicator arthropods, Pred= predaceous arthropods, Food= arthropods in American Robin diet), maximum annual snow water equivalent (SWE; cm) and annual relative difference in volumetric water content (VWC). Line colour and thickness are relative to standardized estimate size and direction (black= positive; red=negative). Unstandardized estimates shown on lines. Solid lines are significant relationships (*p* < 0.05), long dashed lines indicate *p* value between 0.05 and 0.1 and dotted grey lines indicate *p* > 0.1.

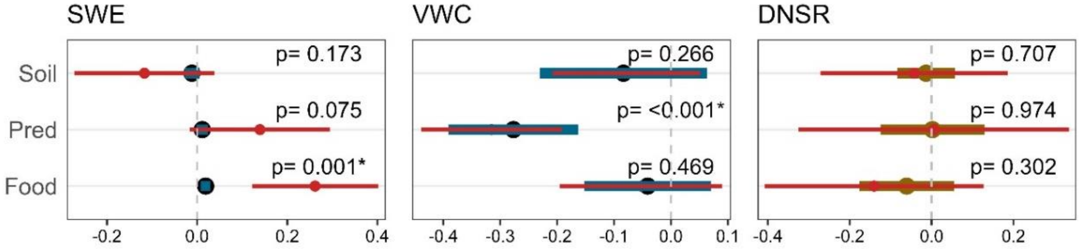

Figure 3.15. Standardized (red and thin) and unstandardized (all other colours and thick) parameter estimates (point) and 95% confidence intervals (line) for pathway relationships between maximum snow water equivalent (SWE; cm), relative difference in volumetric water content (VWC), mean relative biomass of soil arthropods (Soil), predaceous arthropods (Pred) and arthropod food items (Food) and Ovenbird daily nest survival rate (DNSR). *p* values of unstandardized estimates are shown.

3.3.3.v. Red-eyed Vireo

Red-eyed Vireo DNSR was significantly influenced by food biomass and predaceous arthropod biomass, but not soil bioindicator biomass. DNSR was significantly positively related to food biomass (*b* = 0.084, LCI = -0.018, UCI = 0.150) and strongly, but not significantly (*p* = 0.057), negatively related to predaceous arthropod biomass (*b* = -0.049, LCI = -0.099, UCI = 0.001; Figures 3.16 and 3.17). There was no relationship with soil bioindicator biomass.

Food biomass was significantly positively related to SWE (*b* = 0.015, LCI = 0.010, UCI = 0.021) and negatively related to VWC (*b* = -0.123, LCI = -0.186, UCI = -0.060). Predaceous arthropod biomass was significantly negatively related to SWE (*b* = -0.019, LCI = -0.029, UCI = -0.009) and non-significantly, but strongly negatively related to VWC (*b* = -0.079, LCI = -0.168, UCI = 0.010).

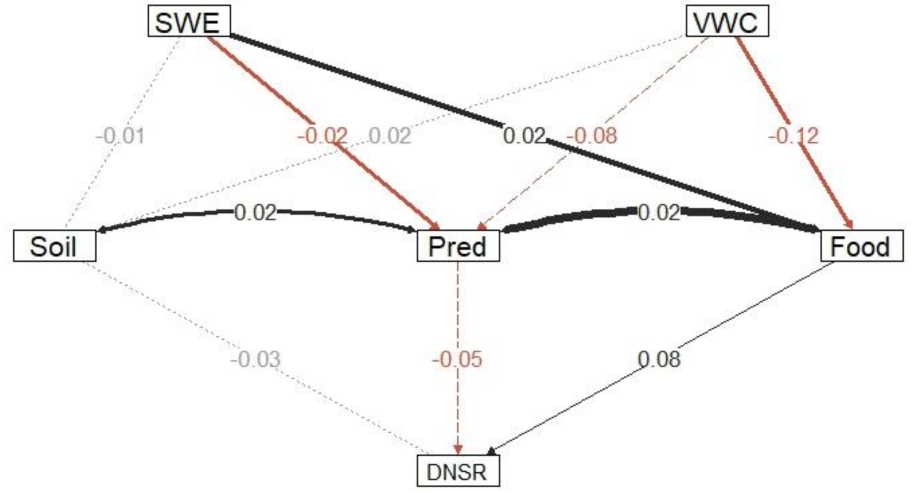

Figure 3.16. Structural equation model pathways for Red-eyed Vireo daily nest survival rate (DNSR) related to arthropod group biomasses (g/day; Soil = soil bioindicator arthropods, Pred= predaceous arthropods, Food= arthropods in Red-eyed Vireo diet), maximum annual snow water equivalent (SWE; cm) and annual relative difference in volumetric water content (VWC). Line colour and thickness are relative to standardized estimate size and direction (black= positive; red=negative). Unstandardized estimates shown on lines. Solid lines are significant relationships (*p* < 0.05), long dashed lines indicate *p* value between 0.05 and 0.1 and dotted grey lines indicate *p* > 0.1.

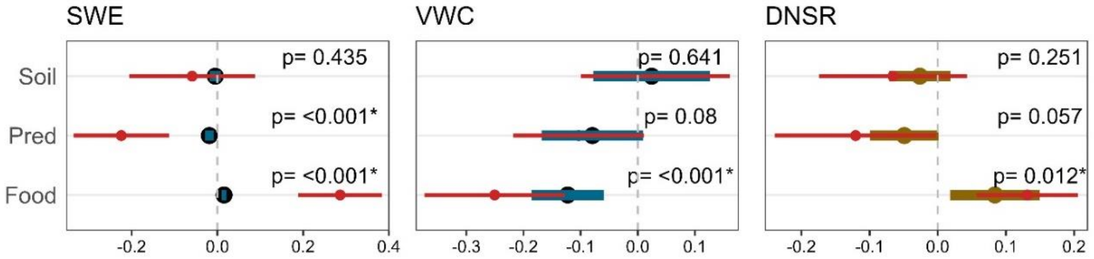

Figure 3.17. Standardized (red and thin) and unstandardized (all other colours and thick) parameter estimates (point) and 95% confidence intervals (line) for pathway relationships between maximum snow water equivalent (SWE; cm), relative difference in volumetric water content (VWC), mean relative biomass of soil arthropods (Soil), predaceous arthropods (Pred) and arthropod food items (Food) and Red-eyed Vireo daily nest survival rate (DNSR). *p* values of unstandardized estimates are shown.

3.4. Discussion

Relationships linking soil moisture, snowpack and arthropod biomass with daily nest survival were mixed among five common breeding birds of southern Ontario forests. Our hypothesis that bottom-up ecological relationships influence nest survival rates was supported for two (Eastern Wood-Pewee and Red-eyed Vireo) of five species, but not evident for the three others. We did not find parallel effects among species as we hypothesized, but factors influencing avian populations can be species-specific (Smith et al. 2015) and climatic effects have been demonstrated to vary among avian families (Michel et al. 2021). Other multi-species studies have also found distinct influences of food and habitat among different species of nesting birds (e.g., Schmidt and Ostfeld 2003, Ruhl et al. 2020). We recognize that we test models using arthropod biomasses collected in the same vertical location as the typical foraging of our focal species. We did attempt to collect arthropods using methodologies other than pitfall sampling, such as aerial traps, but these traps were ineffective and often did not collect any invertebrates. We did, however, sample many of the groups reported in focal species diets and patterns of arthropod biomass and abundance can be very similar among sampling in different vertical with greater biomass generally found at the ground level (e.g., Preisser et al. 1998, Lister and Garcia 2018, Blaise 2022, Crowley et al. 2023, Nell et al. 2023) and with similar temporal patterns of relative abundance among arthropod guilds at different vertical layers (Yoshida et al. 2021). Given the likelihood for bottom-up effects to influence arthropods in similar directions throughout vertical forest layers, our sampling provides a corresponding measure to test these relationships.

3.4.1. Nest survival rates

The beneficial effect of bottom-up productivity through food resources on nest survival was limited to Eastern Wood-Pewee and Red-eyed Vireo. American Robin, Least Flycatcher and Ovenbird nest survival was evidently more likely influenced by top-down effects, although we did not model predation pressure directly. Thus, we found evidence for the positive link between food and avian fecundity (Grames et al. 2023) for some species, but rather than being a universal relationship, the effects varied among species.

Bottom-up relationships for Red-eyed Vireo have not previously been observed, but Eastern Wood-Pewee studies have shown mixed evidence for bottom-up and top-down regulation. For instance, in an experimental food reduction study, measures of Red-eyed Vireo fecundity did not show any response (Marshall et al. 2002), although only Lepidoptera were altered resulting in partial diet reduction. Another previous study did, however, demonstrate top-down control of Red-eyed Vireo populations by linking nest survival rate to predator populations (Schmidt and Ostfeld 2003). At a broad population-level Eastern Wood-Pewee have been shown to be related to lake-based emergent invertebrates (Manning and Sullivan 2021) demonstrating some prior evidence of bottom-up regulation. Although contrasting with our results, Eastern Wood-Pewee nest survival has been demonstrated to be more influenced by top-down controls. Falconer and Nol (2020) observed higher Eastern Wood-Pewee nest survival rates in deciduous compared to coniferous forest (confidence intervals overlapping) despite there being no difference in invertebrate biomass, but squirrel abundance correlated negatively to nest survival.

The positive relationship between Least Flycatcher and soil bioindicator biomass suggests a potential bottom-up relationship, but the unexpected negative relationship with food biomass and low nest survival rates (apparent nest survival calculated using 27-day nest period: 37% in 2010 and 22% in 2011) likely indicates stronger top-down pressure. Previously published studies also found no demonstration of bottom-up relationships for Least Flycatcher. For instance, Least Flycatcher breeding cluster site selection was not related to arthropod biomass (Tarof and Ratcliffe 2004). Additionally, in a study comparing declining and healthy maple stands, which represented influences on food availability, there was no significant difference in nest survival rate between the sites (Darveau et al. 1993). That study also showed that adults were adaptively managing food resources by increasing the number of provisioning trips to nests (Darveau et al. 1993), thus mitigating the potential influence of bottom-up effects on fledgling growth rates and survival.

The lack of any relationships with the arthropod groups we tested for Ovenbird also supports a strong top-down relationship. This result was unexpected given that Ovenbird forages low to the ground and therefore most proximately to pitfall sampling and there is also evidence for bottom-up controls from previous studies. For instance, Burke and Nol (1998) found that Ovenbird nest survival was positively related to food resources. Furthermore, a study in the eastern US demonstrated a pathway linking forest productivity using site index with litter invertebrates and Ovenbird fledging success (Seagle and Sturtevant 2005). Ovenbird habitat use has also been demonstrated to be related to arthropod biomass (Ruhl et al. 2020) and nest survival has been shown to not be influenced by top-down pressures when other species were (Schmidt and Ostfeld 2003). Our results for Ovenbird, however, are consistent with a study that showed the increases in arthropod biomass that relate to forest recovery did not influence apparent adult survival rates suggesting that there were not greater interannual return rates due to higher nesting success (Vernouillet et al. 2014).

American Robin was included as a species that is regulated by top-down pressure, but the influences of arthropod biomass were less clear than other species with a non-significant positive relationship with food biomass and a strong, but non-significant negative relationship with soil bioindicator biomass. Previous evidence for top-down regulation of American Robin has been found. American Robin nest survival in an urban area was demonstrated to be related to the relative abundance of American Crows (*Corvus brachyrhynchos*; Malpass et al. 2017). In that study, however, American Crows were attracted to the area and therefore more abundant due to supplemental feeding which is not typically an antagonistic factor for predation pressure and risk in natural environments.

In general, we found that our results contrasted with prior evidence for multiple species as bottom-up effects were not previously demonstrated for Red-eyed Vireo and only broadly shown in Eastern Wood-Pewee. As well, bottom-up effects tended to influence Ovenbird populations in other studies and locations, where we observed no relationship. For Least Flycatcher and American Robin, our results supported previous evidence of the absence of a relationship to food biomass and top-down regulation by predators, respectively. We do, however, highlight that published studies of the relationship between arthropods and nest survival for these species, except Ovenbird, are scant and therefore comparisons are limited. There were no obvious patterns or reasons for our contrasting results with other studies or the variation in results among species in our study. There were no obvious differences among foraging types such as aerial insectivores versus gleaners, vertical foraging layers such as canopy foragers versus ground-foragers or short-distance versus long-distance migrants. Furthermore, our results contrast with those of other studies undertaken within a close geographic range. One of the main differences between our study and others is that we used diet-specific biomasses rather than total biomass of all trapped arthropods as recommended by Grames et al. (2023). Future investigation using species-specific dietary information and using additional vertical trapping methods could help resolve our findings.

3.4.2. Predaceous arthropods

In the Eastern Wood-Pewee and Red-eyed Vireo models, we observed a negative relationship between predaceous arthropod biomass and daily nest survival rate suggesting a possible competitive suppression of those species' food biomass. The relationship between predaceous arthropods and birds has typically focused on the suppressive effect of birds (Rogers et al. 2012). Top-down relationships between avian insectivores and arthropods are usually expected to be a trophic cascade where consumption of intermediate predators (i.e., predaceous arthropods) dampens negative effects on herbivorous arthropod abundance, although equal effects for both arthropod trophic levels have been reported (Mooney et al. 2010). Increases of predaceous arthropods under declining top-down pressure by birds has been reported in numerous (Rogers et al. 2012), but not all (Mestre et al. 2012), exclusion studies. However, if there was a release on predaceous arthropods, a simultaneous release should be observed for lower trophic level arthropods (Mooney et al. 2010) where DNSR would be negatively related to food biomass, but the relationships with food biomass we observed for Eastern Wood-Pewee and Red-eyed Vireo were positive.

We instead suggest that there was a horizontal rather than vertical trophic effect where intermediate arthropod predators exerted competitive pressure for food resources with birds during the nesting period. Arthropods have been reported to alter habitat suitability (Loss et al. 2012) but reports of negative effects of predaceous arthropods on birds are rare. Spiders have been observed to kill birds through entrapment in webs (Brooks 2012) and ectoparasites can worsen body condition and cause mortality (López-Rull and Garcia 2015). As well, spiders can be a vector for toxicity transfer to birds (Beaubien et al. 2020). Negative effects of arthropods on birds, particularly because of direct competition with predaceous arthropods, are scarce. Competition has been linked between invertebrates and birds for cones (Christensen and Whitham 1993), nectar (Gill et al. 1982) and general interference of foraging (Haemig 1996). An extensive study of an arctic food web demonstrated competition between birds and spiders for arthropods (Wirta et al. 2015). The consequences of competition are rarely extended to effects on fecundity, but Aho et al. (1999) observed that red wood ant (*Formica rufa*) consumption of mutual food resources resulted in significant negative effects on the number of Eurasian Treecreeper (*Certhia familiaris*) fledglings and their body condition.

From the arthropod that we collected in samples, the groups that could be contributing to the negative influence on DNSR and presumed competition with insectivorous birds that we observed including Araneae, Coleoptera, Myriapoda and Opiliones. Araneae and Opiliones are generalist predators that consume similar total arthropod biomass as birds (Nyffeler et al. 2018). Prey items such as Araneae, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, and Orthoptera (Birkhofer and Wolters 2012) overlap with our focal avian species diets. These arthropod groups can significantly influence the strength of bottom-up controls (Welti et al. 2020). Furthermore, Araneae have a competitive advantage over insectivorous birds, especially those that are provisioning young, as they can fast when food resources are not available (Michalko et a. 2019). Coleoptera and Myriapoda are not solely composed of predators (Digel et al. 2014) but include higher trophic level arthropod predators that can affect arthropod populations (Ferlian et al. 2012, Julian et al. 2019). Furthermore, individuals of these groups may not play a large role as avian food resources as they live in leaf litter and under coarse woody debris, potentially reducing the likelihood of encounters with avian predators (Stenger 1958). We note that we did not include Myriapoda in our predaceous arthropod biomass to be conservative as we included all Coleoptera which we recognize would also include non-predators. As we could not find other examples of this presumptive competitive pathway, we recommend that further investigation is needed to disentangle and substantiate this relationship.

3.4.3. Soil bioindicator arthropods

We did not find strong evidence to support a role of soil bioindicator arthropods as indicators of bottom-up controls on nest survival rates. We included soil bioindicators in our models to provide analogues for soil conditions and nutrients and resultant benefits to primary productivity (DeMott et al. 2017, Li et al. 2017). The negative and positive relationships between soil bioindicators and American Robin and Least Flycatcher DNSR, respectively, are difficult to interpret as relationships were in different directions, with different effect strengths and differently influenced by exogenous abiotic variables, including none. Therefore, we do not recommend including this variable comprised of Acariformes and Collembola in future modeling. A bioindicator group that is more inclusive of other species or groups and created as a latent variable to indicate ecological productivity could be a useful tool for avian nest survival rate prediction.

3.4.4. Potential effects of climate change

Our main goal in this study was to use a space-for-time approach to model the relationship between climate-based variables on arthropods to infer how climate change could influence nest survival rates and forest breeding bird populations. The most evident mediating relationship was the positive relationship between the food biomasses of all species and maximum annual snow water equivalent which we also observed as a common relationship among arthropod groups in Chapter 2. This relationship, however, only significantly mediated pathways for Eastern Wood-Pewee and Red-eyed Vireo nest survival.

Climate predictions for our study area suggest that winter precipitation will increase in the future, but that due to warmer temperatures there will be an increase in the proportion of precipitation falling as rain and a decrease in the proportion of snowfall (McCabe and Wolock 2010, Notaro et al. 2014, McDermid et al. 2015). The resulting loss of ground insulation during winter (Hardy et al. 2001, Reinmann et al. 2019) due to decreased snowpack depth, increased snow density and shorter or more discontinuous snowpack residency could result in increased arthropod mortality (Bale and Hayward 2010). These effects could explain the effects we observed in this study and Chapter 2. Based on our results and climate predictions, we can infer that food biomass will decline for all our avian study species. The effects of this decline would translate into lower daily nest survival rates for Red-eyed Vireo and Eastern Wood-Pewee. This is particularly concerning for Eastern Wood-Pewee which has a declining population (Watt et al. 2020) and is a listed species at risk (special concern) federally (Government of Canada 2015) and provincially in Ontario (Ontario Ministry of the Environment, Conservation and Parks 2021). Red-eyed Vireo on the other hand has a stable population (Cimprich et al. 2020), but declining nest productivity in the temperate forest region could negatively affect populations.

Extrapolation of our results suggests significant negative effects on some forest breeding birds in the absence of adaptations and shifts by consumers and prey. Shifts in predatory strategy and food consumption is a regular response to seasonal prey item availability but can be at the expense of body condition from lower nutritional quality (Sample et al. 1993) and potentially requiring more parental provisioning effort (Senécal et al. 2021). Arthropods adapted to future conditions may immigrate to the area, particularly in northward shifts (Breed et al. 2013), and migratory birds demonstrate diet shifts throughout the year (Wheelwright 1986, Gagnon and Hobson 2009) as well as during alterations of food resources (Sample et al. 1993). For example, during southward migration, the nesting birds that we monitored are required to rely on different arthropod species including those that could move northward. Thus, trophic networks may successfully restructure (Tylianakis and Morris 2017) in response to alterations.

3.4.5. Structural equation modeling

We demonstrated the implementation of structural equation modeling in analyzing relationships with nest survival which is a rarely used assessment method in avian literature. Assessments used in similar studies to ours have typically been single variable assessment of arthropod biomass and nest survival (e.g., Duguay et al. 2000) or more complex approaches like Seagle and Sturtevant (2005) where the effect of soil moisture on invertebrate biomass was modeled and then related to a subsequent second model linking biomass to fledging success. Structural equation modeling, however, allows for evaluation of a model that simultaneously considers effects among many linked relationships.

Previously published examples of the use of structural equation modeling in assessing avian fecundity have been limited to models that used the number of fledged young (Le Tortorec et al. 2013) and logistic regression of nest success (Van de Ven et al. 2020) as endogenous variables. We extended these approaches using logistic-exposure model calculated daily nest survival rates (Shaffer 2004) as the endogenous variable. The major limitation of this approach is the need for many observations relative to free parameters (between 5:1 and 10:1; Bentler and Chou 1987) which can be difficult to attain in nest monitoring studies, although this is eased by using effective observation numbers in logistic-exposure models. Even with finding and monitoring many nests, models are likely to be limited in the number of exogenous parameters that can be used. We suggest that avian researchers continue to extend the use of structural equation modeling in nest studies and integrate other approaches such as piecewise structural equation modeling (Lefcheck 2015) which, in the context of our study, could not integrate logistic-exposure modeling in the computer application used at the time of this assessment.

3.5. Conclusion

We found a mix of results among species suggesting support for bottom-up effects for Eastern Wood-Pewee and Red-eyed Vireo populations and top-down effects for American Robin, Least Flycatcher and Ovenbird populations. Bottom-up effects were predominantly the positive influence of food biomass and negative influence of predaceous arthropod biomass on daily nest survival. The pathways linking positive effects between snowpack, arthropod biomass and daily nest survival rate suggest that declining snowpack will have significant negative effects on breeding bird fecundity. Our results add some evidence to the growing body of concerning ecological effects resulting from climate change, demonstrating a rarely assessed effect of non-breeding season climate on fecundity for two of five focal species. We demonstrate additional pathways for climate change mechanisms affecting avian insectivore populations beyond the more typically studied influences of temperature, precipitation, and insect phenology.

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Chapter 4: General Discussion

4.0. Summary

My research goal was to use a space-for-time approach to assess the response of breeding birds and arthropods to variables that could be used to infer the effects of climate change in a large southern Ontario forest. In Chapter 2, I modeled the relationships of the ecoclimatic variables snowpack and soil moisture, habitat covariates of forest type, soil texture, and forest floor depth and the temporal covariate of Julian date as a quadratic effect with arthropod biomass and abundance in mature deciduous forest and conifer plantations. Then, using structural equation modeling in Chapter 3, I assessed the pathway relationships of snowpack and soil moisture on daily nest survival rates mediated by composite biomass of three arthropod functional groups (food from species-specific diets, predators, and soil bioindicators) for five forest nesting passerines: American Robin (*Turdus migratiorius*), Eastern Wood-Pewee (*Contopus virens*), Least Flycatcher (*Empidonax minimus*), Ovenbird (*Seiurus aurocapilla*) and Red-eyed Vireo (*Vireo olivaceus*).

4.1. Chapter 2: Macroarthropods respond to climatic and habitat gradients in temperate conifer plantations and natural deciduous forest

4.1.1. Summary of Results

The predominant effects on relative biomass and abundance of ground-dwelling arthropod groups were the positive effect of snowpack (annual maximum snow water equivalent: MaxSWE) and the quadratic effect of Julian date whereby an increase was followed by a decrease midway through the sampling period (convex upward pattern). For both variables, two arthropod groups showed opposite patterns from the prevalent results with Acariformes responding negatively to snowpack and Collembola increasing exponentially over the sampling period (May through August). Forest type was the next most influential variable on arthropod abundance, with effects in different directions representing different arthropod assemblages between deciduous forest and red pine plantations. Forest type did not, however, affect total arthropod abundance. Soil moisture (measured as annual average relative difference in volumetric water content: rdVWC), forest floor depth and soil texture had comparably minor influences, with each variable significantly affecting only a few groups, although soil moisture significantly positively affected total arthropods and was only a positive effect where significant influences were measured.

4.1.2. Arthropod responses to climate change

Based on climate predictions described in Chapter 2, the predominantly positive influence of snowpack on almost all arthropod groups is concerning for alterations of ecological structure and function. When snowfall amounts decline, especially when replaced by rainfall and concurrent with increasing winter temperatures

(McCabe and Wolock 2010, Notaro et al. 2014, McDermid et al. 2015) we can expect shallower snow depth, shorter snow cover residency and higher snow density. These changes would result in less snowpack insulation and less ablation-based soil moisture recharge (Hardy et al. 2001, Reinmann et al. 2019). For almost all the arthropod groups that I tested, including total arthropods, the effects of predicted climate change could be:

1. Greater probability of mortality due to exposure to cold temperatures including deeper and harder soil freezing.
2. Greater probability of early exit from diapause and subsequent mortality from exposure to fluctuating and freezing temperatures.
3. Reduced soil water recharge from the protracted meltwater needed for egg survival, hatching and metamorphosis.

The potential for drier summer soils because of less infiltration from more runoff during rain events and greater evapotranspiration (Sheffield and Wood 2008, Seneviratne et al. 2010) could make the study area's rapidly drained sandy soil drier and less hospitable for arthropods. Drier soils can negatively affect egg survival, hatching and instar metamorphosis (Huk and Kühne 1999, Holland et al. 2007, Johnson et al. 2010, Parr and Bishop 2022). Even though the study area is typically dry due to the sandy soils and likely inhabited by species adapted to those conditions, I detected no relationships where arthropods benefited from drier soils.

During my study period, there was large interannual variation in snowfall that is representative of future climate change, although did not include confounding factors such as rain on-snow events, air temperature and freeze-thaw cycling. The average annual total snowfall for the area is 151.2 cm (Government of Canada 2023) and in 2010, the total annual snowfall was 66.3 cm less than average (84.9 cm) and in 2011, the total snowfall was 29.2 cm greater (180.4 cm) than average. This interannual variation, in addition to site level variation, provided a seemingly appropriate gradient to model the responses to a future decline in snowpack. Therefore, I infer from my results that future climate is likely to significantly disrupt arthropod biomass and abundance for most arthropod groups and total arthropods combined. Even if arthropods that are better suited to new conditions replace climate-induced losses, there will be a period of community disorganization and the prospect of reaching and maintain a stable equilibrium seems tenuous.

4.1.3. Potential ecosystem effects

Arthropods play key roles in ecosystem processes such as, but not limited to, nutrient cycling, decomposition, herbivory, and as predators and prey. Forest breeding birds have been experiencing significant population declines (Rosenberg et al. 2019) and coincidental declines in arthropod prey are a possible cause (Spiller and Dettmers 2019, Møller et al. 2021) as they can influence fecundity through nest productivity and survival (Wilcove 1985, Martin 1993, Thompson 2007). Thus, the relationships that I observed and potential subsequent responses of arthropod biomass to climate change predictions could have significant implications for forest breeding bird populations.

4.2. Chapter 3: Arthropods as food and competitors mediate ecoclimatic effects on nest survival for some temperate breeding songbirds

4.2.1. Summary of results

The influence of abiotic variables on arthropod biomass and their mediating effects for nest survival were inconsistent among focal species (Table 3.7). The positive influence of snowpack on food biomass was found in all species' models and there were no consistent relationships between snowpack and predaceous arthropod or soil bioindicator biomasses or soil moisture with any arthropod group. I found bottom-up effects on nest survival for Eastern Wood-Pewee and Red-eyed Vireo, both of which were positively related to food biomass and negatively related to predaceous arthropod biomass. Predaceous arthropods are presumably competitively suppressing avian food resources, a rarely reported effect (Gill et al. 1982, Christensen and Whitham 1993, Haemig 1996, Wirta et al. 2015), and only previously demonstrated to negatively affect Eurasian Treecreeper fecundity (*Certhia familiaris*; Aho et al. 1999). American Robin nest survival also appeared to relate positively to food biomass and snowpack, but due to the non-significant relationship ($p = 0.12$), I did not include it as a species regulated through bottom-up processes.

Like my results and inferences from Chapter 2, I suggest that, particularly due to changing snowpack, there may be significant future consequences for arthropods, especially as prey resources for forest birds. Among the species I modeled, this is a particular concern for Eastern Wood-Pewee which has a declining population and is a species at risk (Special Concern: Government of Canada 2015, Ontario Ministry of Environment, Conservation and Parks 2021). Red-eyed Vireo populations are stable (Cimprich et al. 2020) and are therefore not as much of an immediate concern but ensuring that common species remain common is also a necessary conservation approach.

An additional conservation concern evident in my results is that food biomass of all species was positively related to snowpack and therefore could translate into a common stressor among forest breeding passerines. Although variation in food biomass was not influential for the nest survival of all species, I only assessed a small number of species that nest in southern Ontario forests. As I observed similar responses for two of five species, that represents effects on 40% of species investigated and if that proportion translated to all forest breeding species, the ecological consequences would be substantial.

4.3. Recommendations

4.3.1. Arthropod sampling

A criticism of food resource sampling and nest modeling is that there may be a disconnect between the arthropods sampled and the foods found and consumed (Grames et al. 2023). Our approach of assigning arthropods to functional groups recognizes the relationships and contributions of arthropods as food, competition, and facilitators. This approach is an improvement over using total biomass as it recognizes that there are different effects among arthropods and that not all arthropods contribute in the same way for each avian species, but I suggest several improvements for further study.

The first improvement would be more refined assignment of arthropods to functional groups. I did not include some arthropods to a group where they likely should have been included, but either did not have the *a priori* evidence or the resolution (species identification) needed. For example, Myriapoda or Isopoda were not included in American Robin diets as there was no published evidence to suggest including them. American Robin, however, are generalists (Vanderhoff et al. 2020) and although Myriapoda and Isopoda are chitinous, they would provide substantial amounts of food biomass. Myriapods and Isopods are not often encountered as they live within the leaf litter and soil and under rocks and logs, but they have been observed to be consumed by other thrushes (Holmes and Robinson 1988). Further empirical research is needed to classify all food items, identify geographically appropriate food items, and provide the most up-to-date knowledge about diets. The most recent diets for focal species were published at least 30 years ago (Table 4.1), but insectivore declines have been related to dietary changes in response to anthropogenic stressors on invertebrates (Nocera et al. 2012, Pomfret et al. 2012). Model parameterization, therefore, would be improved by recent and local diet data.

Model parameterization could be further improved by including a priori knowledge of the contribution importance of different arthropods to avian diets. My current models assume that contribution to diet is the same as pitfall trap capture rates, thus disregarding foraging, and resource harvesting strategies as well as prey discovery probability. It is unlikely, however, that species with specific prey finding strategies would encounter all arthropods at the same rate and may avoid some arthropods at certain times. For example, as I do not have evidence to the contrary, a scenario could be that an Eastern Wood-Pewee captures a 7 cm long myriapod the day after its young have hatched. Presumably the food item would not be suitable for nestling provisioning as it would not fit in the young's mouth and may be indigestible to them. The adult may consume that individual or a portion of it if they require food at that time, otherwise it may be disregarded. If two or three of those items are captured in sampling, they would disproportionally contribute to total biomass, despite not contributing a significant proportion to diet. Identification of the proportions of food harvested by each species would allow biomass to be weighted by dietary importance. Biomass totals would then better represent the capacity to provide adequate forage although this would entail significant observation of provisioning birds or other indirect analyses like using DNA metabarcoding on fecal pellets.

As my results indicate that predaceous arthropods are competitors for food resources, similar refinement could improve inferences about those effects as well. The predaceous arthropod group did not include relevant predators such as Ants and some Myriapoda because coarseness of my identification would have required including non-predators from those groups. To be conservative, I did not want excessive contributions of non-predaceous arthropods to that group's biomass. Coleoptera were included and I recognized that not all are predaceous, but that a large number including their larvae are. I expected that the error caused by including non-predaceous Coleoptera could be somewhat balanced by not including the biomass of other predators. Furthermore, predaceous arthropods may be more appropriately modeled using relative abundance, consumption rates, or metabolic rates. Use of biomass as I did in this study could be the result of many small spiders or a few large ones, both which have implications for the degree of competition for food resources.

Table 4.1. Summary of publication dates for references used in diet compilations for the “Birds of the World” species accounts.

Species	Reference publication date	Reference
American Robin	1915, 1986, 1990	Vanderhoff et al. 2020
Eastern Wood-Pewee	1970, 1993	Watt et al. 2020.
Least Flycatcher	1912, 1971, 1993	Tarof and Briskie 2020
Ovenbird	1958, 1988	Porneluzi et al. 2020
Red-eyed Vireo	1925, 1945, 1971, 1982, 1990	Cimprich et al. 2020

4.0.2. Trapping methods

As I concentrated on bottom-up effects, a focus of my discussion will be on improving food resource sampling in future research. I used one sampling method in my analyses but attempted three trapping methods for sampling arthropods in different vertical layers: pitfall traps on the forest floor, sticky bands installed on tree trunks in the sapling layer and aerial traps suspended immediately below the canopy, with two different iterations of the latter. The only data used in my analyses were from pitfall trapping as it was the most effective sampling method with the least concern for sampling error bias.

Pitfall trapping is not a completely accurate sampling method for species-specific avian diets as it is not ideal for sampling Lepidoptera (Streby et al. 2013) or flying insects. As well, invertebrate relative abundance samples may be higher in forest floor traps than canopy layer traps, but they often show similar patterns of abundance and biomass (e.g., Preisser et al. 1998, Lister and Garcia 2018, Yoshida et al. 2021, Blaise 2022, Crowley et al. 2023, Nell et al. 2023). A sampling strategy recognizing that food sources are variable vertically, horizontally, and temporally, including shifts in importance, would be the best approach for accurate modeling, but would require multi-faceted, repetitive sampling. For instance, Lepidoptera larvae are often identified as a key avian food source (Robinson and Holmes 1982, Streby et al. 2013, Nyffeler et al. 2018, Tallamy and Shriver 2021) including for aerial insectivores (Sample et al. 1993), so it would be ideal to include sampling techniques in addition to ground sampling to better sample those items. The following provides discussion on the other trapping methods that I attempted.

As a second sampling method, we installed sticky band traps (Tanglefoot® insect glue painted onto plastic food wrap) at breast height (1.3 m from the ground) on tree boles. The main problem with the sticky band traps was that the plastic wrap did not lay flush against tree, especially depending on bark roughness and bark furrow depth which caused differential trapping efficiency by allowing invertebrates to travel beneath the traps. As well, arthropods and wildlife were attracted to the sticky band traps for foraging and other life history needs. For example, we observed bagworm moth cases (Order Lepidoptera, family Psychidae) attached to some traps which suggested there was an attraction to the traps, potentially for their ability to support attachment of the case. Opiliones were attracted to the traps, likely for foraging on trapped insects with individuals often observed grouped along the outside edges of the trap as well as moving on the trapping portion thereby modifying samples. Additionally, we observed multiple instances of woodpeckers and nuthatches foraging on trapped insects, with some samples containing Hairy Woodpecker (*Dryobates villosus*) and Northern "Yellow-shafted" Flicker (*Colaptes auratus*) feathers. The sampling error created by bark inconsistency, attraction and predator foraging could not be quantified and corrected, and as a result I did not include this sampling method in analyses.

I also tried a modified tow net to sample flying invertebrates immediately below the canopy. The net (a butterfly net bag) was installed on a pvc frame that had a vertical rope running through a portion of it which allowed the trap to spin 360° and orient its opening into the wind like a windsock (Fig. 4.2a). Unfortunately, this trap design was not effective and often resulted in few or no insects captured. Tow nets have been used to successfully capture insects for use in nest analysis (i.e., Quinney and Ankney 1985), but they were installed in open habitats that would provide greater wind transport of invertebrates, thus likely better trapping efficiency. To overcome the trapping deficiency and collect samples from a greater vertical height, I modified the design to a hanging malaise-style trap with perpendicular interception panels at the base and an upward mesh funnel leading to a collection unit (Fig. 4.2b). These traps also had poor trapping efficiency, so sampling was discontinued.

One suggestion for the relationship between food resources and breeding birds is that changes in prey quality rather than abundance are influencing fecundity (Spiller and Dettmers 2019). To improve prey quality assessment and interpretation of non-biomass indicators, future analyses would be improved by greater resolution in arthropod identification. I identified arthropod groups to higher identification levels such as class, superorder and order as the focus was on overall biomass and not specific arthropod qualities. The coarseness of the identification was beneficial for maintaining as much simplicity as possible within already complex models, but limits interpretation.

My results demonstrate that many complex processes are occurring, and that nest survival rate could not be simply modeled as a path where abiotic variables influence total biomass and total biomass influences nest survival. Concurrent to needing better identification resolution, analyses would be improved through greater knowledge of prey selection by focal species. Understanding prey preferences would help elucidate what the most beneficial, and therefore highest relative quality, food resources are. Future modeling would benefit from advances using this resolution, path complexity and *a priori* knowledge about food supply.

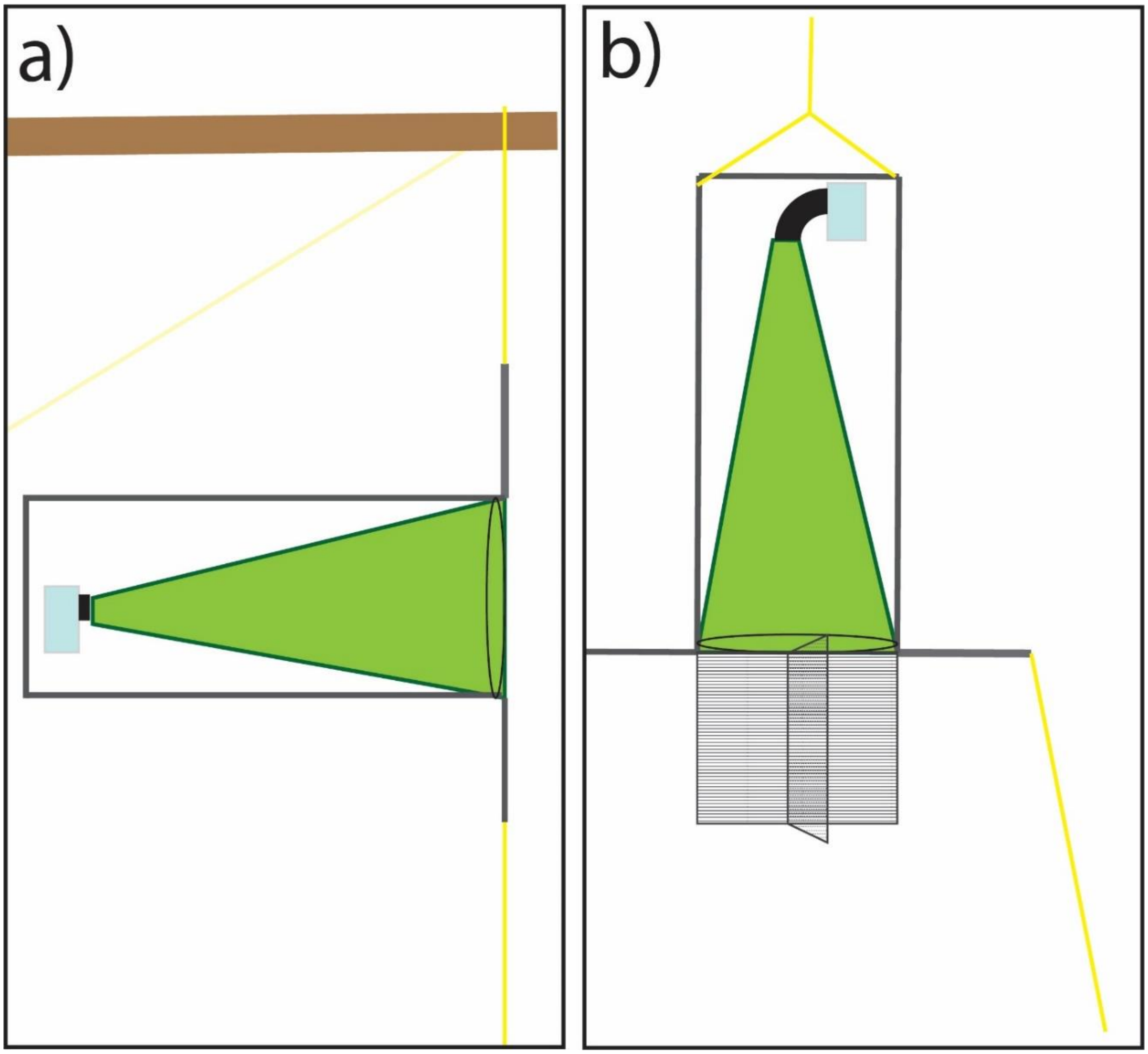

Figure 4.1. Aerial insect trap designs used to sample lower canopy invertebrates in the Ganaraska Forest with horizontal tow net-style traps in (a) and hanging malaise-style traps in (b). Green indicates a butterfly net nylon mesh, patterned grey rectangles indicate 1 mm window screen, solid blue rectangles were collection bottles with water and ethanol, dark grey lines were PVC conduit frames, yellow lines were ropes used to raise, lower, and hold traps, and the thick brown line demonstrates how a canopy limb was used to suspend the trap.

4.0.3. Study design

To further improve analysis in addition to better arthropod data, the overall study design could be improved. As insects are mobile, especially insects that live off the forest floor, capturing an insect does not necessarily confirm the relationship to local conditions. For instance, aerial insect traps could capture aquatic macroinvertebrates which were laid in, developed, and emerged from a nearby waterway and are basically unrelated to the location they are found. This dispersal could be more related to winds that carried the arthropods to that location.

More appropriate approaches would be annual re-measurement of variations in climate, arthropods, and daily nest survival over a larger local area, such as the entire Ganaraska Forest, and then assessing responses to interannual variation. Such a study design would provide the best analysis, but long-term data sets such as this are resource-demanding and logistically complex. Another option is to extend the use of gradients as analogs for change as I did in this study, but across a greater geographic scale such as measuring an area known for high snowfall (e.g., lake effect snow) and an area where snowfall is generally lower. Variables that would be difficult to control in an analog study design, but necessary to account for as covariates, include microclimate, vegetation, soil type, and forest management approaches as well as biotic adaptations and interactions. Nonetheless, if two comparable areas can be used, it would help overcome some of the challenges of long-term data collection.

4.0.4. Modeling

My use of structural equation models with logistic-exposure model calculated daily nest survival rate (Shaffer 2004) demonstrates the potential to extend generalized linear models in analyzing daily nest survival with a flexible and informative multivariate approach. I combined multiple pathways with a mediator into a single model which allows for interpretation of a system rather than individualized model fitting comparisons.

The best approach would be to incorporate logistic-exposure modeling directly into a structural equation model as a pathway rather than using it to calculate daily nest survival rates for each exposure interval and then using each interval rate as an observation. An example of this could be incorporating logistic-exposure modeling into a function such as piecewise structural equation modeling implemented using the R package piecewiseSEM (Lefcheck 2015). I attempted to blend these modeling methods, but the custom logit link function coding of logistic-exposure modeling does not allow for the exposure days component (a vector) to be called within the piecewise structural equation model function. The benefit of being able to perform this analysis would be that the arthropod mediators could be included with other moderator variables while maintaining daily nest survival rate as the right-hand side endogenous variable without it being a prior-fitted prediction.

4.1. Conclusion

I found that nest survival for two out of five (40%) forest breeding bird species including the Eastern Wood-Pewee, a species at risk, are significantly influenced by snowpack through the mediating effect of food resources. These results were reinforced modeling of relative biomass and abundance of various arthropod groups (e.g., orders and classes) and total arthropods which showed that snowpack was the most predominant and consistent influence among the ecoclimatic, habitat and temporal covariates I tested. These results partially supported my hypotheses that snowpack and soil moisture influence arthropods and that those influences mediate avian nest survival rates as soil moisture was not a consistent influence on arthropod measures and not all avian species' nest survival rates were affected. As well, I used a time-for-space study design to assess responses to empirical gradients to allow for inference against predicted climate change. My results suggest that given expected declines in snowpack, there may be significant disruption to current arthropod assemblages and associated ecological processes including declines in avian food resources which in turn could affect fecundity rates and populations. Long-term ecosystems changes that will confound these results include species range shifts and immigration and trophic rewiring which cannot be observed through this study design.

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Appendix A. Structural equation model example code

The following provides an example of the structural equation model code used in Chapter 3 analyses (mediated path analysis) as well as the code to modify and create the plots. The analyses were performed with the R statistical package version 4.2.3 in RStudio version 2023.03.0 and used the R packages lavaan 0.6-15 (analysis) and semPlot 1.1.6 (plotting). Note that all code is in blue and notes are in red preceded and followed by ***.

The following code assumes that there is a data frame with the following vectors:

- dnsr – fitted values of interval (i.e., effective observations) daily nest survival rates calculated using logistic exposure modeling
- Soil.mass – average daily dry weights of Collembola and Acariformes
- Pred.mass - average daily dry weights of Araneae, Opiliones, and Coleoptera
- Food.mass - average daily dry weights of arthropods from the diet of the focal species
- SWE – maximum annual snow water equivalent
- VWC – relative difference in volumetric water content
- DNSR.PA – creates the model structure for testing

```
***read in appropriate packages***
library(lavaan)
library(semPlot)

***create model for testing***

DNSR.PA <- '
          soil.mass ~ SWE + VWC
          pred.mass ~ SWE + VWC
          food.mass ~ SWE + VWC

dsr ~ soil.mass + pred.mass + food.mass

***Identify residual covariances if necessary. These are best identified using
modification indices (high indices) and then check the significance of the covariances
after as non-significant covariances will reduce model fit. The following code suggests
that there are significant covariances among all mediator variables. Remove any
unneeded combinations***
pred.mass ~~ soil.mass + food.mass
soil.mass ~~ food.mass
'
```

*** fits the model using structural equation model analysis using “MLM” estimator for robust standard errors***

```
DNSR.PA.fit<-sem(DNSR.PA, data= dataframe, estimator="MLM", check.gradient=F)
```

provides the modification indices for the model fit

```
print(modindices(DNSR.PA.fit))
```

provides a summary of the structural equation model that includes a section of all of the different measures of model fit

```
summary(DNSR.PA.fit, fit.measures=T)
```

provides a printout of all parameter estimates for the model

```
DNSR.PA.fit.est<-parameterEstimates(DNSR.PA.fit, standardized=F)

DNSR.PA.fit.est
```

provides a printout of all standardized estimates for the model

```
DNSR.PA.fit.std<-standardizedsolution(DNSR.PA.fit, type= "std.all", se=T, zstat=T, pvalue=T, ci=T)
DNSR.PA.fit.std
```

the following lines can be all combined into a single R chunk and run together. This will create vectors that will change the symbology of the plot

makes line width relative to the size of the standardized estimate

```
DNSR.PA.fit.std$new.width<-abs(DNSR.PA.fit.std$est)*10
```

line types become solid [1], long-dash [5], dotted [3] based on estimate p value. Must remain in this order

```
DNSR.PA.fit.est$new.line[DNSR.PA.fit.est$pvalue < 0.05]<-1
DNSR.PA.fit.est$new.line[DNSR.PA.fit.est$pvalue > 0.05]<-5
DNSR.PA.fit.est$new.line[DNSR.PA.fit.est$pvalue > 0.1]<-3
```

changes the colours of the lines to black for positive standardized estimates, red for negative standardized estimates and grey for standardized estimates that are non-significant. Must remain in this order

```
DNSR.PA.fit.std$new.colour[DNSR.PA.fit.std$est > 0]<-"#292929"
DNSR.PA.fit.std$new.colour[DNSR.PA.fit.std$est < 0]<-"#CD4F39"
DNSR.PA.fit.std$new.colour[DNSR.PA.fit.std$pvalue >0.1]<-"grey65"
```

changes the arrowhead size based on the p values to help with visualization

```
DNSR.PA.fit.est$new.asize[DNSR.PA.fit.est$pvalue < 0.1]<-2
```

```
DNSR.PA.fit.est$new.asize[DNSR.PA.fit.est$pvalue > 0.1]<-0
```

This will create the plot layout used in Chapter 3

```
DNSR.PA.plot<-semPaths(DNSR.PA.fit,curve=-1,what="std", fade=F, sizeMan=8,
sizeMan2=3, layout="tree3", centerLevels=T, rotation=1, exoCov=F, residuals=F,
whatLabels = "est", edge.label.cex=1)
```

This will apply the symbology changes

```
DNSR.PA.plot$graphAttributes$Edges$color<-DNSR.PA.fit.std$new.colour
DNSR.PA.plot$graphAttributes$Edges$width<-DNSR.PA.fit.std$new.width
DNSR.PA.plot$graphAttributes$Edges$lty<-DNSR.PA.fit.est$new.line
DNSR.PA.plot$graphAttributes$Edges$asize<-DNSR.PA.fit.est$new.asize

plot(DNSR.PA.plot)
```