Top-down trophic interactions related to forest tent caterpillar outbreaks in temperate hardwood and boreal mixed-wood forests in Quebec

Anne-Sophie Caron

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Signed by the final examining committee:

____Chair
Dr Erin Barker

____External Examiner
Dr Leah Flaherty

____Examiner
Dr Carly Ziter

____Examiner
Dr Jean-Philippe Lessard

____Co-supervisor
Dr Miguel Montoro Girona

____Thesis Supervisor
Dr Emma Despland

Approved by ____
Robert Weladji, Graduate Program Director

09/07/2023 (date of defense) ____________________________________
Pascal Sicotte
Faculty of Arts and Science

Abstract

Top-down trophic interactions related to forest tent caterpillar outbreaks in temperate hardwood and boreal mixed-wood forests in Quebec

Anne-Sophie Caron, Ph.D.
Concordia University, 2023

This thesis aims to investigate different trophic interactions related to the outbreaking cycles of the forest tent caterpillar (*Malacosoma disstria* Hübner, Lepidoptera: Lasiocampidae), both top-down and bottom-up, in two types of forests, the boreal and the temperate. Throughout field studies, we determined that forest tent caterpillar early-instar larvae were more susceptible to mortality due to pathogens and maternal effects in years after the outbreak than to predators. These results suggest delayed density dependence and contribute to low endemic levels between outbreak peaks. We also investigated the overwintering mortality of forest tent caterpillars at the egg stage. While larger egg masses tended to promote survival, this factor was not the only significant predictor. Mortality was also related to average winter temperature variation and cold spells. With increasingly unpredictable climate patterns, both factors could cause high mortality levels during the winter. Finally, with the high amount of organic material released during the outbreaks, we investigated the impact on potential predators, such as ants. We observed a shift in ant communities in the boreal forest but not in temperate forests, suggesting that disturbances caused by the forest tent caterpillar can alter less ecologically complex and redundant ecosystems. Forest tent caterpillars are important disturbance agents and participate in multiple trophic interactions during outbreaks, cementing the importance of a better understanding of their population dynamics.

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I want to thank Dr. Emma Despland for welcoming me into her lab and supporting me throughout the past few years, which have been very hectic, to say the least. I would also like to thank my co-supervisor, Dr. Miguel Montoro Girona, who stepped up halfway through my Ph.D. and welcomed me with arms open in his lab. I would also like to extend a huge thank you to Joshua Jarry, who collected a lot of the data used in this season during the summers of 2018 and 2019, as well as Gaspar Legendre for the 2015-2017 data. Thank you to my lab mates over the years, Pamela Yataco Marquez, Mahsa Hakimara, Éric Dexheimer, Bastien Bellemin-Noël and Sabina Noor, for your insight and support. A special thank you to my field assistants, Shannon Clarke, Mercy Harris, Emma Gillies, Gabrielle Ednie, Nia Krasteva, Tania Couture, Jessica Reid and Brittanny Talarico, for the great times through our gruelling field work, climbing trees and trekking through the forest. To my partner, David, and my best friend, Camille, who always supported me in good and bad times. To Mathilde, my fellow entomology grad student. Going through this process at the same time as you were one of the highlights of my Ph.D., and I am so glad it brought us together. To all my friends and the communities I am a part of in-person and online (especially the greenhouse), thank you for being there and allowing me to catch my breath and make me laugh. To my family, Maman, Papa and Evelyne, thank you for supporting my dreams, no matter what they are. I specifically want to honour my grandfather, Louis-George Périgny with this thesis. Along with my parents, he made sure we had the possibility of going to university, to follow our academic dreams, a chance he did not get.

A Ph.D. is possible only with the help of a wide scientific community. Lab work was done in part by undergraduates the lab, Andrew Cormier, April Mansfield, Colette Éthier, Sarah Fahrat and

Boriana Chopova, as well as Vanier College interns Angelika Gnanapragasam, Janella Snagg-Romeo and Katerina Lazaris. I want to thank my friend and colleague, Bella Richmond, for her help with data management and support. I would also like to thank Juanita Rodriguez of the Centre d'Étude de la Forêt for her help with the statistical analysis. I would also like to thank my committee, Dr. Carly Ziter and Dr. Jean-Philippe Lessard, for their help, feedback, and understanding of my many challenges during my Ph.D. I would also like to thank Dr. Chris MacQuarrie and Dr. Barry Cooke for their assistance at the beginning of my Ph.D. and for helping me get my head around the puzzle that is forest tent caterpillar population dynamics and Dr. Chris Law for his great help with the microphotography and the automation work.

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Perspective and Positionality

This research pertains to regions in Quebec which are located on the unceded Indigenous lands of the Abitibiwinni and Algonquin Anishinabeg people in the boreal forest as well as the Kanien’kehá:ka, Omàmìwininìwag (Algonquin) and Anishinabewaki in the temperate forest. Concordia University is situated in Tiohtià:ke, on the unceded territory of the Kanien’kehá:ka Nation.

For this project, I have conducted my research within the framework of Western science and forestry, which focuses on exploiting forest ecosystems and a Western notion of ecosystem disturbances and biodiversity. Society demands multiple and sometimes conflicting values from forests, such as wildlife habitat, recreation, biodiversity, and forest products. I acknowledge that the framework surrounding the economic aspect of forestry is very much centered on a utilitarian framework and that the forest provides much more benefits to humans and non-humans.

Contribution of Authors

I was the principal investigator for all the research work undertaken in this thesis under the supervision of Dr. Emma Despland and co-supervised by Dr. Benoit Lafleur at the beginning of my diploma and Dr. Miguel Montoro Girona at the end. Chapter 2 resulted in a manuscript which has been published in an international peer-reviewed journal, for which I was the main author. Chapter 3 also resulted in a manuscript and has been published in an international peer-reviewed journal. The species list presented in this paper might also be submitted as a micropublication in the journal *Specimens*. In the event that the manuscript is accepted for future publication, the authors will be credited in the following order: Caron, A-S, Montoro Girona M, Despland E. Finally, the experiments for Chapter 4 were conducted by me; in the event that the manuscript is accepted for future publication, the authors will be credited in the following order: Caron, A-S, Law C, Montoro Girona M, Despland E.

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Chapter 1 - General introduction

Insect outbreaks, like forest fires, are normal disturbances in natural ecosystems. However, the trajectory of such outbreaks is changing. A growing number of researchers are concerned that, with climate change, especially in temperate and boreal forests (Schlyter et al. 2006), these outbreaks will become more unpredictable (Dukes et al. 2009). Therefore, monitoring these outbreaks and understanding their impact on ecosystems is increasingly important.

Forest tent caterpillars (*Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae) (hereby referred to as FTC)) are early-spring defoliators attacking hardwood tree species, both in the temperate and mixed-wood boreal forests of Canada (Cooke and Lorenzetti 2006a; Man and Rice 2010). In temperate forests, FTC generally attack sugar maple trees (*Acer saccharum* Marsh.(Sapindaceae)) and, in the boreal forest, generally attack trembling aspens (*Populus tremuloides* Michx. (Salicaceae)). Forest tent caterpillars are univoltine, and the eggs are laid at the end of the summer. The eggs overwinter as eggs and emerge in April, growing through May and July, pupating in June and emerging as adults in July (Figure 1.1).

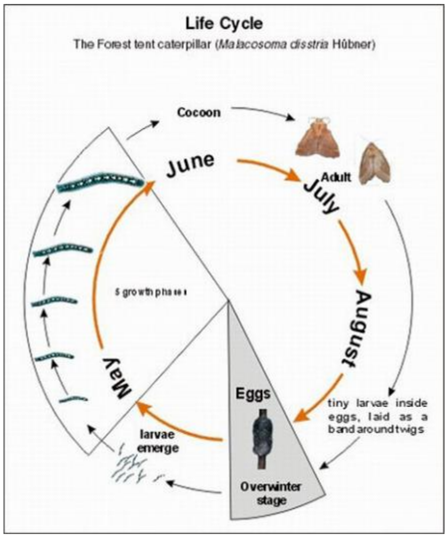


Figure 1.1 Life cycle of the forest tent caterpillars (Malacosoma disstria Hübner). Mark J. Primavera, Natural Resources Canada

Cyclical outbreaks of FTC have been recorded since the 1940s in Quebec (Fitzgerald 1995), and the pest is present across much of North America. In Quebec, the two regions more affected in the recent outbreaks were the Abitibi and Outaouais regions, the outbreak started in 2016 and finished in 2018 (MFFP 2016; 2019). Cooke and Lorenzetti (2006a) have demonstrated that FTC outbreaks vary in terms of periodicity, duration and intensity depending on the geographical location according to the separate populations. In the south of Quebec, outbreaks tend to be shorter and closer together, with peaks lasting around 1-2 years and occurring every 9 years, while in the north, they tend to be longer but at longer time intervals, with peaks lasting around 1-6 years and occurring every 10-13 years (Cooke and Lorenzetti 2006). Additionally, recent research by MacDonald et al. (2022) showed increased genomic variation depending on geographic distance and host tree, giving further evidence for those distinct populations.

The difficulty in predicting both the occurrence, duration, intensity and location of the outbreaks comes partly from the challenges in conducting studies on low-density, pre-outbreak populations. Indeed, at that stage, populations are not present in sufficient numbers to be sampled efficiently (Bouchard et al. 2018). While outbreaking populations vary dramatically in mortality rates, endemic populations are less visible and understood. This situation is also the case for many other outbreaking forest defoliators such as the spruce budworm (Bouchard et al. 2018) and the autumnal moth (Jepsen et al. 2008)-.

1.1 FTC population dynamics

Like other insect pests (Turchin, Taylor, and Reeves 1999), density dependence and delayed density dependence are thought to play a large role in controlling FTC population dynamics (Cooke and Lorenzetti, 2006). Density dependence refers to population growth rates varying according to population size and/or density. Delayed density dependence, as described in Turchin, Taylor, and Reeves (1999), often shows mortality to be negligible during a population growth phase, increasing at peak population and reaching a maximum as populations decline. Delayed density dependence can generate dramatic population cycles, such as with the spruce budworm. Bouchard et al. (2018) demonstrated that parasitism contributes to mortality in low-density populations and as a potential cause for sudden population fluctuations across large spatial scales.

Like most lepidopterans, FTC is r-selected and therefore governed by maximum reproductive capacities where many eggs are laid but with a low survival rate. Survival rates can change with population density in interaction with host plants and natural enemies (Despland 2017; Parmesan 2006; van Asch and Visser 2007; Boggs 2016). Parasitoids and diseases are often considered important in FTC outbreak crash as sources of delayed-density dependent mortality (Parry 1995; Parry, Spence, and Volney 1997; Hodson 1977).

Landscape heterogeneity in forests could increase FTC outbreaks' duration by reducing parasitoid flies' dispersal abilities (Roland and Taylor 1997). It could also impact the transmission of viruses such as nuclear polyhedrosis virus (NPV) (Stairs 1965; Roland and Kauppp 1995; L. D. Rothman and Roland 1998) which are associated with population density declines in FTC (Moulinier 2013). It is proposed that fragmented habitats and the consequent disruption of the host-parasitoid interactions can explain some spatial variations in FTC dynamics (Roland and Taylor 1997).

1.2 Trophic interactions and ecological repercussions of insect outbreaks

As defined by Ripple et al. (2016), after an extensive review, trophic cascades “are indirect species interactions that originate with predators and spread downward through food webs.” In our case, the consumption of FTC by diverse predators could trickle down and indirectly promote fewer inputs to soil ecosystems, as seen in Figure 1.2.

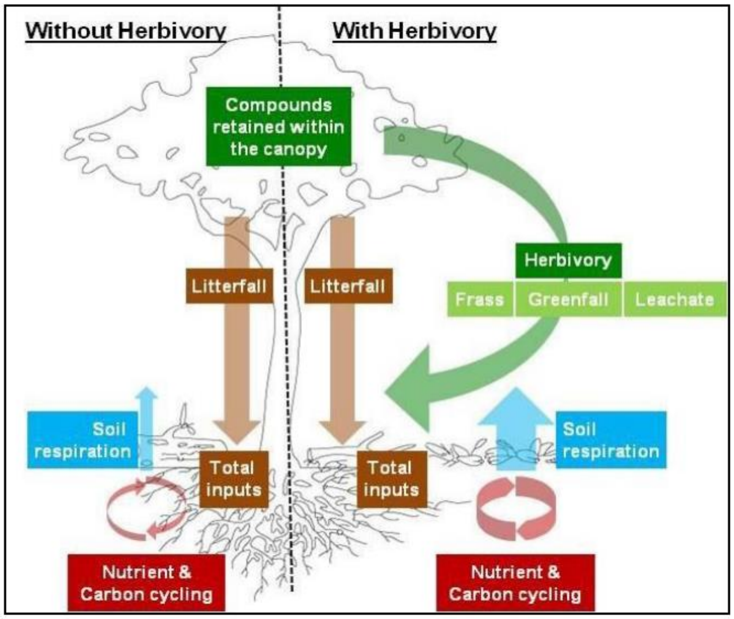


Figure 1.2 Trophic interactions in forested areas with and without herbivory (Metcalfe et al. 2014, 20).

During pest outbreaks, the effects of the pest can be felt at multiple scales in the trophic networks and have both positive and negative impacts (Figure 1.3). Outbreaks cause green fall and frass deposits, liberating nutrients retained in the canopy, which increases resources for belowground organisms in soil food webs as well as helping with nutrient availability for saplings. The presence of herbivores provides an influx of nitrogen-based resources with frass and greenfall. This has been shown in both temperate (Reynolds and Hunter 2001) and mixed-wood forests (Lewis and Likens 2007), where experimental manipulations of frass and greenfall have been shown to induce responses in soil respiration and soil nutrient cycling. In temperate and mixed-wood forests, pulses of nitrogen can alter the cycling of nitrogen and stimulate bacterial and fungal communities, indicating a potential nitrogen limitation can affect detrital communities (Yang 2006).

Additionally, Dansereau-Macias, Despland, and Handa (2023) found a significant decrease in microbial biomass in previously defoliated stands, suggesting carbon reallocation from the root exudates to foliage regeneration. The carbon-based substrate was markedly different following defoliation, but the ratio of fungal to total microbial activity was unchanged. These results suggest that major defoliation episodes can cause changes in soil chemistry and affect the microbial communities, influencing forest plant responses to those defoliation events.

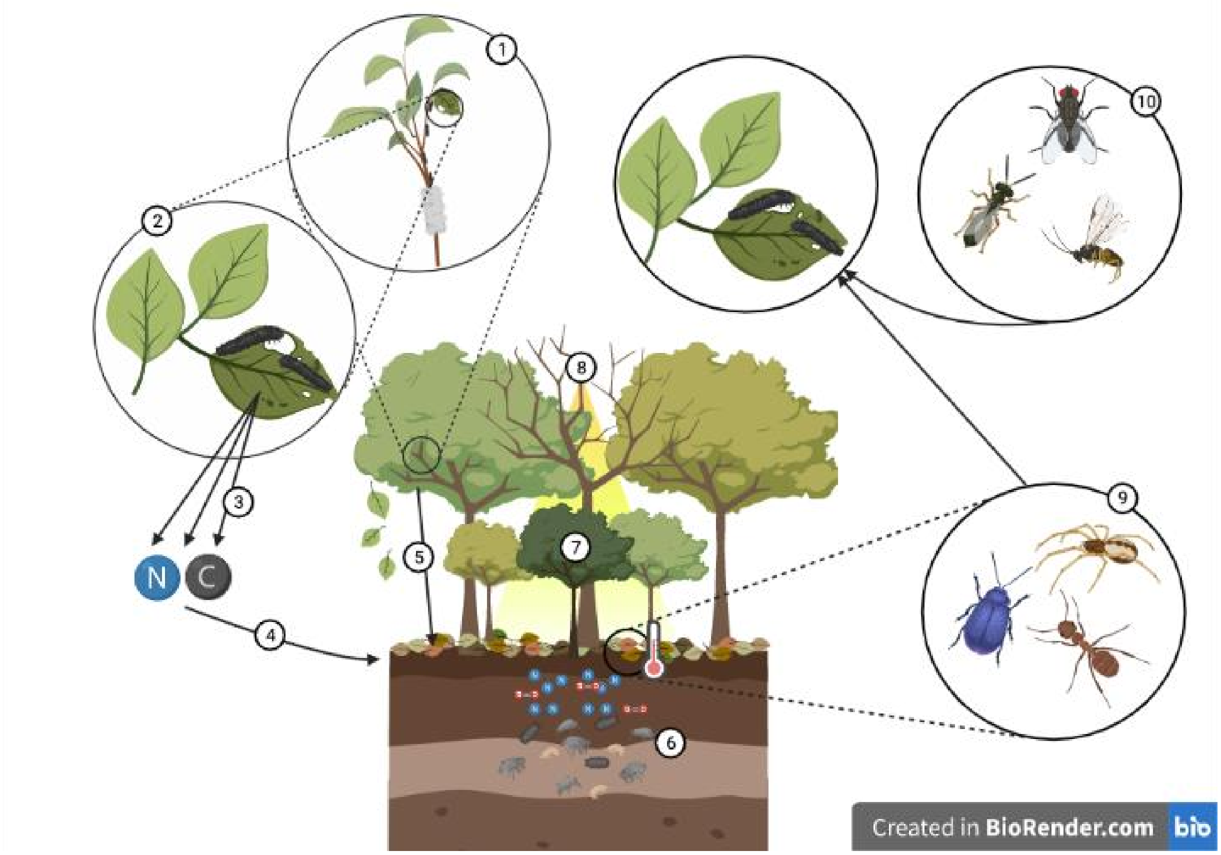


Figure 1.3 Trophic interactions related to the defoliation caused by forest tent caterpillar herbivory. 1) forest tent caterpillar egg mass in the tree around a branch, 2) herbivory by forest caterpillar, 3) nutrients leaching from the leaves, 4) nutrients leaching into the soil, 5) green fall, 6) microarthropods using the added nutrient resource, 7) saplings in the understory using the light available due to 8) a canopy opening, 9) ground-based natural enemies using microarthropods and other resources and attacking forest tent caterpillars along with 10) flying natural enemies.

However, the implications for succession might be drastically different in mixed-wood and temperate forests. In our case, the boreal mixed-wood forest sites are dominated by trembling aspen

(Populus tremuloides Michx, Salicaceae) and the temperate forest sites with sugar maple (*Acer saccharum* Marsh, 1785). In boreal mixed-wood forests, the overstory canopy decline is expected to release understory conifers and accelerate forest succession from hardwood to conifer dominance (Greene et al. 2002; Shepperd et al. 2001; Chen and Popadiouk 2002). This suggests that aspens can quickly respond to changes in canopy gaps caused by insect defoliation, similar to their response to overstory mortality by pathogens and wind (Hill, Mallik, and Chen 2005) or harvesting (Brais et al. 2004; Man et al. 2008). Understory shrubs, generally restricted by low light conditions (McCoy and Bell 1991), responded quickly to the foliage reduction of the overstory canopy by insect defoliation, likely due to increased light availability. However, this succession has not been investigated in maple-dominated temperate forests. FTC-caused defoliation might promote the competitive release of beech or young maples, but this remains to be investigated. The succession trajectory might drastically differ since sugar maples are shade-tolerant, whereas aspens are pioneer species.

Soil resource availability can shape the structure of local arthropod communities (Polis, Anderson, and Holt 1997). Food resource addition is likely to increase the abundance and species richness of ants (Kaspari 1996; McGlynn 2006; Arnan, Rodrigo, and Retana 2007), spiders (Chen and Wise 1999), beetles (Yang 2006), and microarthropods (Chen and Wise 1999; Halaj and Wise 2002). Indeed, Gagnon Koudji et al. (2023) found no significant difference in collembola abundance between defoliated and non-defoliated sites. However, they observed changes in the community one year after the outbreak. They bounced back to the communities found in non-defoliated sites two years after the outbreak, suggesting an ephemeral effect of added resources. The community composition of collembolas was linked to some soil nutrients (P, C, Mg, Mn) but not to microbial biomass.

Omnivores such as ants and predators such as spiders can increase indirectly in density, especially if the addition of resources increases the density of prey items like mites and collembolas, feeding on microbes in decaying material (Klironomos, Widden, and Deslandes 1992). Additionally, epigeic arthropods, such as ants and collembolas, may respond to soil characteristics such as ground cover and soil moisture more than they respond to overstory processes (Work et al. 2004; Vellend et al. 2013; Niemela et al. 1992). This can affect insect herbivore mortality (Riihimäki et al. 2005) if epigaeic predators ascend into the canopy to prey on the herbivores.

1.3 Natural enemies and causes of mortality

For lepidopterans and FTC specifically, sources of mortality rates vary throughout the life cycle because of different scaling properties (e.g., mandible size and strength, thermal mass, surface-to-volume ratio), metabolism, digestive physiology, sensory modalities (Hochuli 2001), and gut microbiota (Mason and Raffa 2014).The different instars are vulnerable to a myriad of variables influencing their survival rates such a predation, displacement and diseases (Despland 2017).

The first source of mortality through the FTC life cycle comes during their overwintering. Since eggs are deposited at the end of the summer (around August) and overwinter as pharate larvae, the larvae enter diapause in the fall, only hatching around April-May, around budburst (Fitzgerald 1995). FTC egg masses show several adaptations to promote winter survival. While laying the eggs, the female secretes a spumaline coat, dark and foamy in texture, that then hardens and serves as a first line of defence against environmental injuries to the egg (Parry, Goyer, and Lenhard 2001). For most of the winter, however, the mechanism truly protecting the eggs is the glycerol content in each egg, allowing it to reach its supercooling temperature (Fitzgerald 1995). This supercooling point allows the eggs to withstand cold temperatures where they would have frozen, allowing the water molecules to stay liquid instead of forming into ice (Uelmen, Duman, et al. 2016).

While accidents and failure to establish on plants make FTC vulnerable during the first instars (Despland 2017), predation and parasitism were traditionally thought to be more important in later larval instars (Hawkins, Cornell, and Hochberg 1997). However, research has shown that predation rates can be very high in early-instars (Zalucki, Clarke, and Malcolm 2002; Nixon and Roland 2012). Several arthropods are known to prey on forest tent caterpillars such as hemipteran stinkbugs (Evans 1982), beetles, especially of the genus *Calosoma* (Fitzgerald and Costa 1999), ants (Green and Sullivan 1950; Parry, Spence, and Volney 1998) as well as spiders, acting as generalist predators (McClure and Despland 2010; Ronnås et al. 2010). Many species of parasitoids attack the eggs and pupae of species of the *Malacosoma* genus, and a few families of parasitoids also attack the larval stage (see Fitzgerald (1995) and references therein; Williams, Parry, and Langor 1996).

Microbes, such as pathogens like the nuclear polyhedrosis virus (NPV), can also impact insect mortality (Fitzgerald 1995). The NPV is a baculovirus that can infect whole populations rapidly and often with population declines (Stairs 1965). NPV is spread horizontally after the death of an infected caterpillar and is density dependent (Myers and Cory 2013; Rothman and Myers 1996). There can also be sub-lethal effects and infection can be transmitted vertically to offspring infecting the population of the next growing season (Myers and Cory 2013; Rothman and Myers 1996).

However, for outbreaking insects, specialist enemies seem to cause very little mortality by predation in low-density populations (Dwyer, Dushoff, and Yee 2004; Turchin et al. 2003; Berryman 1996). Generalist enemies, on the other hand, seem to have a greater impact on low-density populations and populations can be maintained at endemic densities by predation.(Klemola et al. 2002; Gould, Elkinton, and Wallner 1990; Glasgow 2006; Bouchard et al. 2018).

It is suggested that the impacts of natural enemies, i.e. predators and parasitoids, on outbreaking insects will be greater in more diverse habitats, especially those with more plant species, since this would promote higher natural enemy abundance and diversity (Andow 1991; Russell 1989; Root 1973). It is generally accepted that more diverse habitats provide greater diversity of predator species and microhabitats for generalist natural enemies and a greater diversity of resources for adult parasitoids. This will also allow for a greater abundance of prey species refuges, allowing specialist enemy populations to persist (reviewed by Jactel, Brockerhoff, and Duelli (2005)).

Ants are significant predators in northern ecosystems. It has been shown multiple times that ants can play a role in controlling pest invertebrate species (Thunes, Gjerde, and Skartveit 2018; Folgarait 1998; Punttila, Niemelä, and Karhu 2004; Moya-Laraño and Wise 2007; Kilpeläinen et al. 2007; Petal 1978; Halaj and Wise 2002; Gibb and Hochuli 2003; Kilpeläinen et al. 2009; Mestre et al. 2013; Maňák et al. 2015). However, the extent to which they play a role in controlling FTC outbreaks has not been previously investigated.

Ants are considered ecosystem engineers and can affect carbon and nutrient pool sizes and fluxes (Risch et al. 2005). Wood ants' diet consists of elements from different trophic levels, including invertebrate prey from both the canopy and forest floor (Domisch, Finér, Neuvonen, Niemelä, et al. 2009; Finér et al. 2013; Rosengren 1991). Moreover, forest tent caterpillars have been reported as a food source for some species of wood ants, especially species from the *Camponotus* genus (Green and Sullivan 1950a; Parry, Spence, and Volney 1998). Despland and Lessard (2022) also found that ants could climb trees early in the spring, therefore being one of the only enemies present at budburst when FTC hatch. By using a recruitment-based social foraging strategy, ants are thus able to create heavy predation pressure on FTC and thus become a significant source of mortality for early-instar FTC. Ants could not only be an important source of mortality for FTC, but they could also cause a delayed density-dependent mortality response and contribute to outbreaking dynamics. At another level, canopy gaps and increased nutrient flow during outbreaks could increase ant abundance (Correa et al. 2016; Gotelli and Ellison 2002). This dynamic would create a feedback loop where ants and FTC can drive each other's populations.

1.4 Purpose

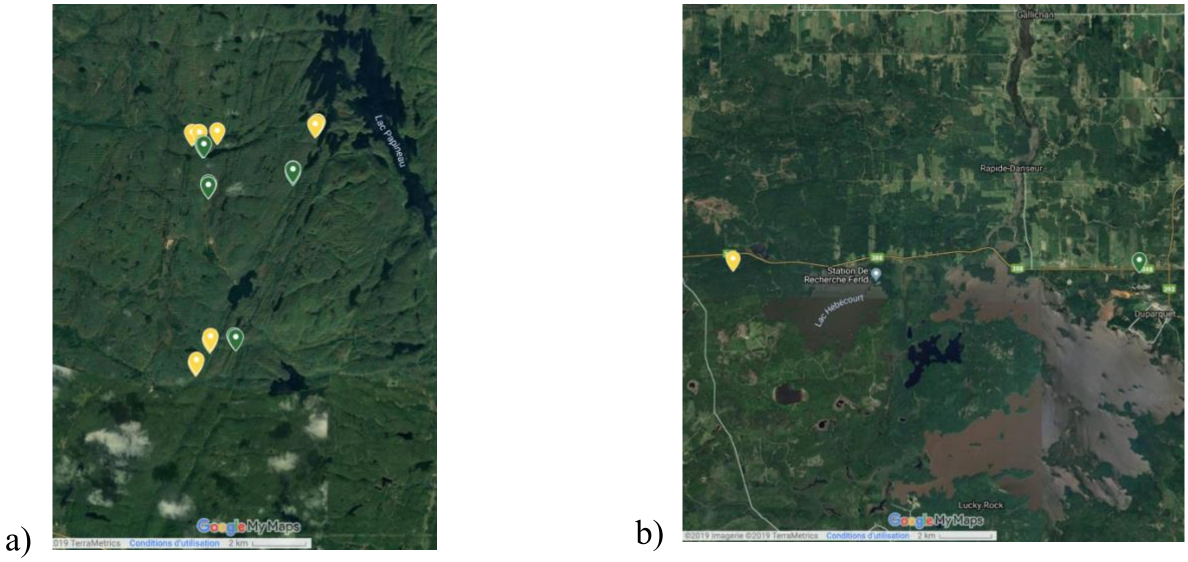


Figure 1.4 Site selected in a) the temperate forest and b) the boreal forest, The sites in yellow were not defoliated in the past outbreak (2016-2017) while the green ones where defoliated.

My research aims to examine the different trophic interactions related to the disturbance event that is an FTC outbreak in terms of both the effect of FTC on other arthropods in the ecosystem and the feedback response, especially in terms of FTC mortality. To answer these questions, we used two sets of sites, one in the temperate forest (Figure 1.4a) and one in the boreal forest (Figure 1.4b). This work provides novel contributions in examining mortality from different sources in endemic populations. In Chapter 1, I presented a literature review of the subject. In Chapter 2, I will characterize the different sources of mortality that FTC larvae are subjected to in endemic populations, test hypotheses of density dependence, and provide a new equation to quantify marginal mortality rates. In Chapter 3, I will examine the potential shifts in ant community composition in relation to the FTC outbreak and the direct and indirect drivers of these shifts. In Chapter 4, I will examine the effect of temperature variation and weather events on the overwintering mortality of FTC during and after the outbreak. This work will further our understanding of the different trophic interactions taking place during and after the peak of an FTC outbreak, especially those related to the increased mortality of FTC larvae during and after the crash of said outbreak.

Chapter 2 – Early-instar mortality of a forest pest caterpillar: which mortality sources increase during an outbreak crash?

The following chapter is based on the published manuscript: Caron, A. S., Jarry, J. J., & Despland, E. (2022). Early-instar mortality of a forest pest caterpillar: which mortality sources increase during an outbreak crash? *Entomologia Experimentalis et Applicata*, *170* (3), 268-276.

2.1 Abstract

Collapses of insect pest outbreaks are often attributed to delayed density dependence of predation. The forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), is an outbreaking pest species defoliating mixed wood boreal forests in eastern Canada. This species presents periodic population dynamics with peaks every ten years and outbreaks lasting 1–3 years, leading to stand die-back and occasionally mortality. We investigated the relative importance of various sources of early-instar caterpillar mortality during and after the crash of an outbreak, testing for density dependence. We used a triad set-up of complete predator exclusion, partial exclusion, and free colonies to distinguish between intrinsic mortality (caused by, e.g., pathogens) and mortality caused by flighted and walking natural enemies and compared defoliated outbreak sites with control sites.

Overall, survival was lowest in the free colonies and increased with partial and complete predator exclusion. Survival was also higher in control than in outbreak sites and higher in the final year of the outbreak than in the following year. During the outbreak collapse, we observed no changes in mortality from walking enemies but an increase in intrinsic mortality and mortality from flighted enemies in the year following the outbreak. This increase is consistent with the density dependence

of these mortality sources, but its occurrence in the control sites was also unexpected. These findings show that early-instar mortality from flighted natural enemies and intrinsic source increases after the outbreak but do not contribute to the population crash. However, they help maintain low endemic levels between epidemics.

2.2 Introduction

Eruptive population dynamics imply dramatic changes in mortality rates between the growth and decline phases of outbreaks. Large fluctuations in population density are associated with r-selection and type III survival curves (Watt 1960; Fowler 1981; Emlen 1984); when high numbers of eggs are laid, but survival in early instars is low, density dependence in larval mortality can generate eruptive dynamics. Indeed, density dependence of top-down mortality through predation, parasitism, and disease likely plays a large role in driving population dynamics of many outbreaking forest lepidopterans (Royama 1984; Myers 1993; Turchin, Taylor, and Reeves 1999; Cooke and Lorenzetti 2006b; Bouchard et al. 2018; Birch et al. 2019). This mortality can occur at different stages of the prey life cycle depending on the natural enemy involved, and we focus on agents of early-instar mortality since less is known about mortality at this stage in our study system (Despland 2018).

Effects of prey population density on predation can be grouped in three scenarios that generate different dynamics, as described in Turchin (1999): (1) predation does not vary with the prey population density; (2) predation exhibits direct density dependence and the highest contribution to prey mortality is during the peak year of an outbreak; this first-order process tends to stabilize population dynamics (Müller and Godfray 1999; Klemola et al. 2010; Bouchard et al. 2018; Bellone, Björkman, and Klapwijk 2019); and (3) if predation is delayed density-dependent, its contribution to prey mortality is low during prey population growth and reaches a maximum as prey populations decline; this second-order process amplifies prey population cycles. Mortality from natural enemies acting at different stages of the prey life cycle can follow either of these scenarios and thus interact to create complex population dynamics (Ferguson and Stiling 1996).

2.2.1 Natural history of forest tent caterpillars

The forest tent caterpillar (FTC) is a univoltine early-spring defoliator attacking hardwood trees across North America (Man and Rice 2010). Trembling aspen (Populus tremuloides Michx, Salicaceae) is FTC's main host tree species in the Canadian boreal forest. Cyclical outbreaks of FTC have been recorded since the 1940s and occur approximately every ten years (Fitzgerald 1995), lasting from 1 to 4 years (Cooke and Lorenzetti 2006). FTC moths lay eggs in masses in the mid to late summer. Eggs then overwinter and hatch the following spring, synchronizing with the host tree bud break (Fitzgerald 1995). FTC is a gregarious feeder that lives in colonies of up to several hundred individuals, maintaining cohesion for most of their development (Despland 2013).

Many generalist arthropod predators prey on FTC, such as stink bugs (Evans 1982), beetles (Fitzgerald and Costa 1999), ants (Green and Sullivan 1950b; Parry, Spence, and Volney 1998), and spiders (McClure and Despland 2010; Ronnås et al. 2010). Some birds have been reported to attack later instar caterpillars, but their overall impact is low (Fitzgerald 1995). Many species of parasitoids attack *Malacosoma* spp. eggs and pupae (Fitzgerald 1995; Williams, Parry, and Langor 1996), but parasitism of larvae is low (Nixon and Roland 2012). A viral pathogen plays an important role in FTC outbreak dynamics: the nuclear polyhedrosis virus (NPV) causes dramatic epizootic infections in larvae, destroying entire colonies. NPV mortality can exhibit both direct and indirect density dependence: horizontal virus transmission increases with population density, and vertical transmission leads to high mortality in the subsequent generation (Myers 1993, 199). Mortality can also occur due to poor nutritional resources or maternal condition (Ginzburg and Taneyhill 1994; Rossiter 1991).

A recent FTC upsurge in eastern Canada provided an opportunity to test for density responses of different larval mortality agents by comparing early-instar mortality rates in colonies in control and outbreak stands. In this study, we separated mortality into three sources: due to predation by walking or flighted natural enemies or intrinsic factors, including pathogens. A mortality source showing direct density dependence will show an increase in mortality in the outbreak in the outbreak's final year. In contrast, one exhibiting delayed density dependence will be highest in the outbreak stand in the subsequent year. This study is novel in its approach as its methods allow to decipher between complete and partial predator exclusion and thus provides more specific results as well using marginal rates of attacks in our calculations.

2.3 Materials and Methods

2.3.1 Study Sites

We conducted the study in and around the Forêt d'enseignement et de recherche du lac Duparquet (FERLD, N48.513, W79.369), within the boreal mixed-wood forests of eastern Canada, in post-fire (1923) regenerated stands dominated by trembling aspen (*P. tremuloides*). The region was affected by an FTC outbreak starting in 2015 (MFFP 2015) and continuing in 2016 and 2017 (MFFP 2016; 2017). No FTC defoliation was observed in the region in 2018 and 2019 (MFFP 2019).

We selected 14 sites in trembling aspen stands that were heavily defoliated in 2016, and 2017 (outbreak sites) and 14 control sites in similar age stands having escaped defoliation (B Lafleur, pers. obs.). Sites were at least 100-m from each other. The same sites were sampled during both years. To confirm defoliation history, we examined 20 trembling aspen saplings between 1 and 3 m tall in a 100-m radius around each site for FTC colonies from 2017 to 2019. We quantified sources of larval mortality at each site with a triad experimental design repeated in 2017, 2018, and 2019. We set up experimental egg masses in late May and left until late June when FTC reached the fourth instar. Each triad contained three enclosure treatments (Figure 2.1): (1) free: an egg mass is attached to a branch, making the emerging colony vulnerable to both flying and walking natural enemies. (2) Tanglefoot: the base of the branch on which the egg mass is placed is coated with Tanglefoot (Tanglefoot Company, Grand Rapids, MI, USA), a physical barrier made from a sticky non-drying resin. This barrier prevents crawling arthropods, not flying predators/parasitoids, from reaching the sentinel caterpillar colony. Moreover, (3) caged: a fine mesh cage encloses the branch on which the egg mass is placed, excluding all predators and parasitoids.

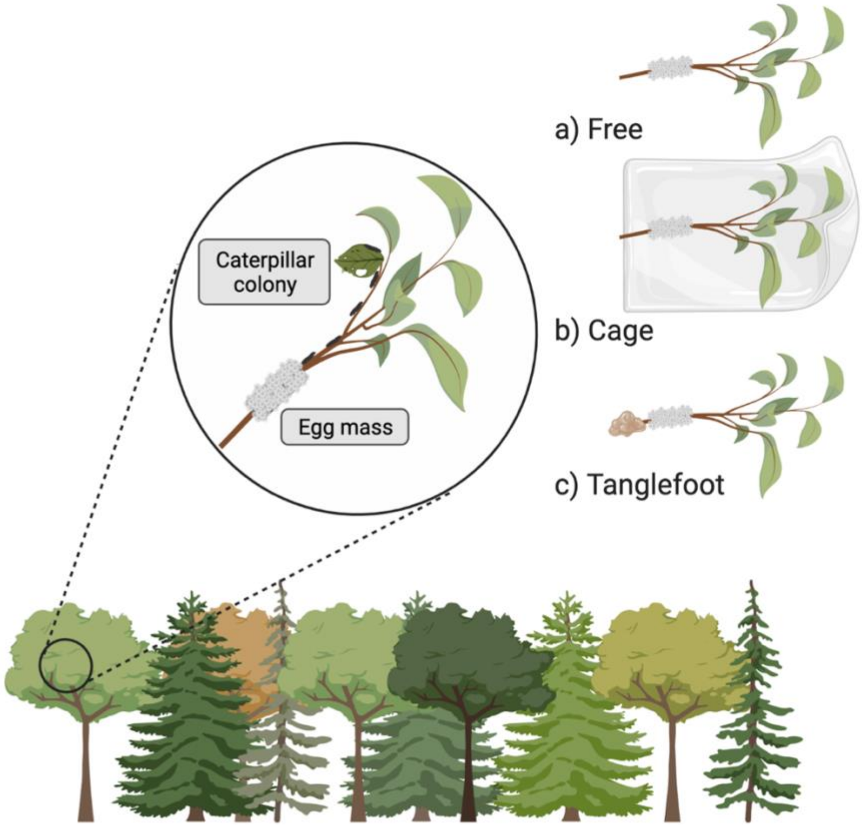


Figure 2.1 Experimental design; each site received the three enclosure treatments on different saplings: (A) free, (B) cage, and (C) tanglefoot

We collected egg masses in early spring in the outbreaking stand and stored them at 4 °C until they were installed in the trees shortly before bud burst (i.e., 23 May 2017, 28 May 2018, and 6 June 2019). Before being placed in the trees, the egg masses were sterilized with bleach to prevent the spread of pathogens (Grisdale 1968) from the sites where they were collected. This way, any NPV present would be from the ecosystem itself and not introduced through the egg masses.

In 2017 and 2018, we placed one triad of egg masses at each of the 28 sites (14 per defoliation level; control and outbreak). Egg mass collection in 2019 yielded very low numbers, as the outbreak had crashed throughout the region. Thus, we reduced replication to four sites per defoliation treatment (a total of eight trees). The 2019 data are presented but excluded from analyses.

2.3.2 Colony monitoring

We monitored colonies from hatching to the fourth larval stage when we collected all colonies and counted the surviving larvae. We also took down the empty egg masses to assess egg mortality. Each egg was visually scored as either hatched or unhatched (i.e., dead) using NIS-Elements Br 3.0 imaging software (Nikon, Tokyo, Japan) and FIJI imaging software (Schindelin et al. 2012). We then calculated the hatch rate by dividing the number of hatched eggs by the total number of eggs on the egg mass.

2.3.3 Marginal rates of mortality from different sources

We calculated larval survival rates as the number of observed live larvae at the end of the experiment divided by the number of hatched eggs (S_c = survival rate of caged colonies,

S_t = survival rate of tanglefoot colonies and S_f = survival rate of free colonies). Then, we converted this number into mortality rates by subtracting the survival rate from 1. We partitioned the effects of different causes of mortality by comparing mortality rates of colonies in caged, free, and tanglefoot colonies. This method assumes that the cages do not affect mortality factors other than predation and parasitism (Royama 2001). Our approach resembles that of Bouchard et al. (2018) but with the added complexity of the partial predator exclusion (tanglefoot) treatment.

We first had to define the following mortality types. (1) 'Intrinsic mortality' occurs because of factors intrinsic to the colony (e.g., pathogens, maternal effects). Any mortality inside the cages is considered intrinsic: $D_c = 1-S_c$. (2) 'Extrinsic mortality' is caused by factors external to the colony (e.g., predators, parasitoids). We computed, for each site, total mortality in the presence of all possible mortality sources minus mortality caused by intrinsic factors: $D_e = S_f-S_c$. Within this category, we can further describe two types of predation mortality: (2a) 'flighted mortality' is mortality caused by natural enemies that can reach the colony by flight (e.g., flies, wasps), and (2b) 'walking mortality' is mortality caused by predators that can only get to the colony with no obstacles to walking to reach their prey (e.g., spiders, ants).

We accounted for the overlap between intrinsic and extrinsic mortality by calculating marginal rates of flighted and walking predation as well as rates of infection. As mentioned by Bouchard et al. (2018), obtaining an unbiased estimation for mortality is difficult if an individual can be attacked by one natural enemy (e.g., disease) and then killed by another (e.g., a predator). Marginal rates provide a method to calculate rates of non-observable attacks and estimate overall mortality from each source without overlap (Royama 2001). We assume no overlap between walking and flighted mortality agents because most mortality in the early-instars is due to predators rather than parasitoids (Nixon and Roland 2012). Additionally, our method does not account for the potential non-consumptive effect of predators, such as predator-attempted attacks leading to escape and dispersal (McClure and Despland 2010). We also assume that an attack by one enemy does not increase the mortality rate from another source, i.e., parasitism or disease does not make caterpillars more vulnerable to predators (Royama 2001). We used the following equations based on Royama (2001) and Bouchard et al. (2018):

$$\mathrm{M_i} = \mathrm{D_c},$$

$$\mathrm{M_f} = \frac{\mathrm{D_t} - \mathrm{M_i}}{1 - \mathrm{M_i}},$$

$$\mathrm{M_e} = \frac{\mathrm{D_f} - \mathrm{M_i}}{1 - \mathrm{M_i}}, \text{ and}$$

$$\mathrm{M_g} = \mathrm{M_e} - \mathrm{M_f},$$

Equation 2.1 where D_c = mortality observed in caged colonies (= $1–S_c$), D_t = mortality observed in tanglefoot colonies (= $1–S_t$), D_f = mortality observed in free colonies (= $1−S_f$), M_i = marginal attack rate for intrinsic factors, M_e = marginal rate of predators (both flighted and walking), M_f = marginal rate of flighted predation, and M_g = marginal rate of walking predation.

As we calculate the marginal rates using numbers from different egg masses placed at the same sites, some calculations resulted in negative numbers. To remedy this, we replaced any negative results with zeros.

2.3.4 Statistical analysis

We first tested for homogeneity of variance in the egg mass size and hatch rate using Levene's test and fit linear models for both egg mass size and hatch rate. Smaller egg masses and low hatch rates can imply poor maternal condition, and these offspring often have lower chances of survival (Hunter and Elkinton 2000). We next fitted a generalized linear model with a quasipoisson distribution for percentage survival as the data were overdispersed and contained many zeros. All three models consisted of the response variable against fixed effects of year, defoliation history, and enclosure treatment, including an interaction term for year and defoliation history. The analysis of egg mass size acted as a negative control to confirm the randomization of egg masses among treatments. Complete models including sites as a random factor where also tested, but only the simplified model was selected due to fit.

We then fitted generalized linear models with quasipoisson distribution to marginal rates of intrinsic, flighted, and walking mortality, as the data were overdispersed and contained many zeros. Models included fixed effects of year, defoliation history, and enclosure treatment, including the interaction term year*defoliation history. The model used was a reduced model as the addition of two and three way interaction did not improve model fit. We then used a Tukey post hoc test to compare the means within the models. All analyses were conducted in the R v.3.4 statistical computing environment (R Development Core 2017).

2.4 Results

2.4.1 Outbreak status

Surveys of FTC showed an average of 3.36 ± 1.86 (mean ± SD) colonies out of 20 saplings in 2017 in the outbreaking stand. However, we observed no wild colonies in the control stand in any of the three years of the study nor in the outbreaking stand in 2018 or 2019.

2.4.2 Egg mass size and hatch rate

Egg mass size did not differ significantly between defoliation history or year or their interaction

(Table 2.1). However, it varied between enclosure treatments ($F_{2,4} = 4.66$, p = 0.01). The difference between 'cage' and 'tanglefoot' colonies drove that relationship (Tukey test: p = 0.007). Hatch rates varied with defoliation history ($F_{1,6} = 9.73$, p = 0.002) and enclosure treatment ($F_{2,5} = 3.1$, p = 0.047). Most significantly, hatch rates decreased between years ($F_{2,5} = 22.79$, p = 0.001), decreasing from 0.74 ± 0.21 in 2017 to 0.53 ± 0.18 in 2018 (Tukey test: p<0.001). Hatch rates declined in 2019 to 0.52 ± 0.36, but we did not include these data in the analysis due to low replication.

Table 2.1 Summary statistics for the linear model on egg mass size (no. eggs in each egg band) and hatch rates (% eggs hatched per band) and generalized linear model for larval survival (%)

Response	Term	d.f.	SS	MS	F	P
No. eggs/egg band	Year of experiment	1	21105	10552.6	22.79	0.63
	Defoliation history	1	99	98.6	0.032	0.86
	Enclosure treatment	2	28468	14234.1	4.66	0.011
	Year*defoliation	1	10414	10413.7	3.41	0.067
% eggs hatched	Year of experiment	2	21105	10552.6	22.79	9.6e-07
	Defoliation history	1	4505	4505.1	9.73	0.002
	Enclosure treatment	2	2872	1435.9	3.10	0.048
	Year*defoliation	2	2197	1098.3	2.37	0.096
		d.f.	Deviance	Resid. d.f.	Resid. Dev.	Pr (> χ)
% larval survival	Null model			155	6202.6	
	Year of experiment	1	610.43	154	5592.2	9.6e-07
	Defoliation history	1	183.52	153	5408.6	0.0072
	Enclosure treatment	2	1538.53	151	3870.1	7.4e-14
	Year*defoliation	1	5.02	150	3865.1	0.66

2.4.3 *Overall larval survival*

As expected, larval survival was highest in the caged colonies, followed by the tanglefoot colonies and then the free colonies ($\chi^2 = 1538.53$, d.f. = 2, p<0.001) (Table 2.1; Figure 2.2). The three enclosure treatments differed (Tukey test: p<0.001). Survival varied significantly with defoliation history ($\chi^2 = 183.52$, d.f. = 1, p<0.001), being higher in the control than in the outbreak site (mean ± SD = 0.37 ± 0.34 vs. 0.25 ± 0.30; Tukey test: p<0.01). Survival also decreased from 2017 to 2018 ($\chi^2 = 610.43$, d.f. = 1, p<0.001). It was higher during the last year of the outbreak (2017) than in the following year (2018) (2017: 0.41 ± 0.36 vs. 2018: 0.154 ± 0.21; Tukey test: p<0.001). Survival increased slightly in 2019 (0.22 ± 0.22), but we did not include these data in the analysis due to low replication (n = 4 + 4). The interaction of year and defoliation history was not significant. These results suggest some delayed density dependence in mortality rates as the lowest survival rate was delayed a year compared to the peak density. However, contrary to expectation, this increased mortality was observed in both the control and defoliated sites.

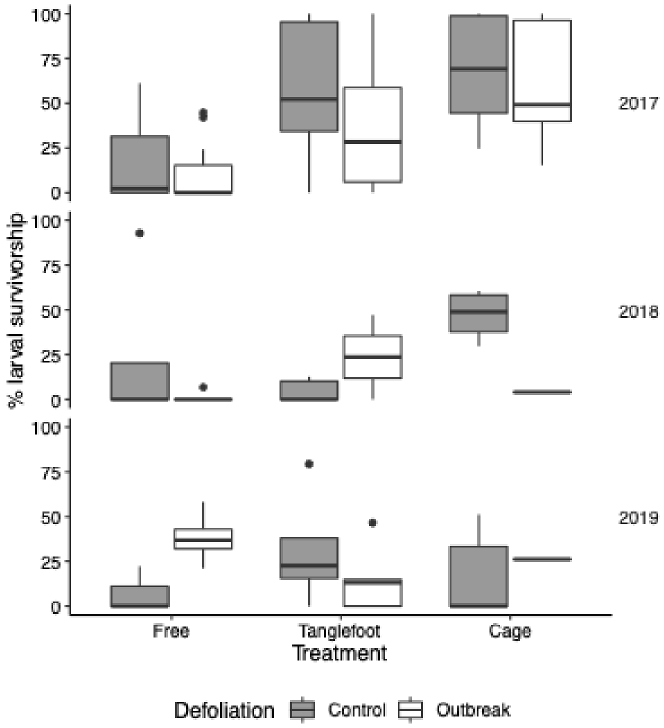


Figure 2.2 Overall survival (%) of forest tent caterpillar colonies in the three enclosure treatments: unprotected control (free), protected from walking predators (tanglefoot), and completely protected (cage). Colonies were observed in stands that had been previously defoliated (outbreak) or not (control) over three years: 2017 (n = 14 + 14), 2018 (n = 14 + 14), and 2019 (n = 4 + 4). In the box plots, the lower boundary of the box indicates the 25th percentile, the bold line within the box marks the median, and the upper boundary of the box indicates the 75th percentile. The whiskers indicate the 10th and 90th percentiles. Dots are outliers (>Q3 + 1.5 × interquartile range)

2.4.4 *Marginal rates of mortality*

Year affected the marginal rates of intrinsic mortality ($\chi^2 = 8.19$, d.f. = 1, p = 0.004) and of flighted predation ($\chi^2 = 17.77$, d.f. = 1, p= 0.042), but not on the marginal rate of mortality from walking predators ($M_g = 0.33 \pm 0.17$) (Table 2.2). There were no significant differences between control and outbreak stands. The marginal rates of flighted and intrinsic mortality were relatively low in 2017 ($M_f = 0.25$, $M_i = 0.42$) and increased dramatically in 2018 in both control and defoliated stands ($M_f = 0.45$, $M_i = 0.83$) (Figure 2.3). These results are consistent with those observed for the overall survival rates.

Table 2.2 Summary statistics for the test of the effects of experimental treatments on marginal rates of mortality from the three sources

		d.f.	Deviance	Resid. d.f.	Resid. dev.	Pr (> χ)
Intrinsic mortality	Null model			36	9.62	
	Year of experiment	1	1.42	35	8.19	0.0038
	Defoliation history	1	0.31	34	7.89	0.18
	Year*defoliation	1	0.10	33	7.78	0.44
Flighted mortality	Null model			36	19.56	
	Year of experiment	1	1.79	35	17.77	0.042
	Defoliation history	1	0.0023	34	17.77	0.94
	Year*defoliation	1	0.59	33	17.18	0.25
Walking mortality	Null model			36	15.061	
	Year of experiment	1	0.049	35	15.012	0.71
	Defoliation history	1	0.052	34	14.96	0.71
	Year*defoliation	1	0.51	33	14.45	0.24

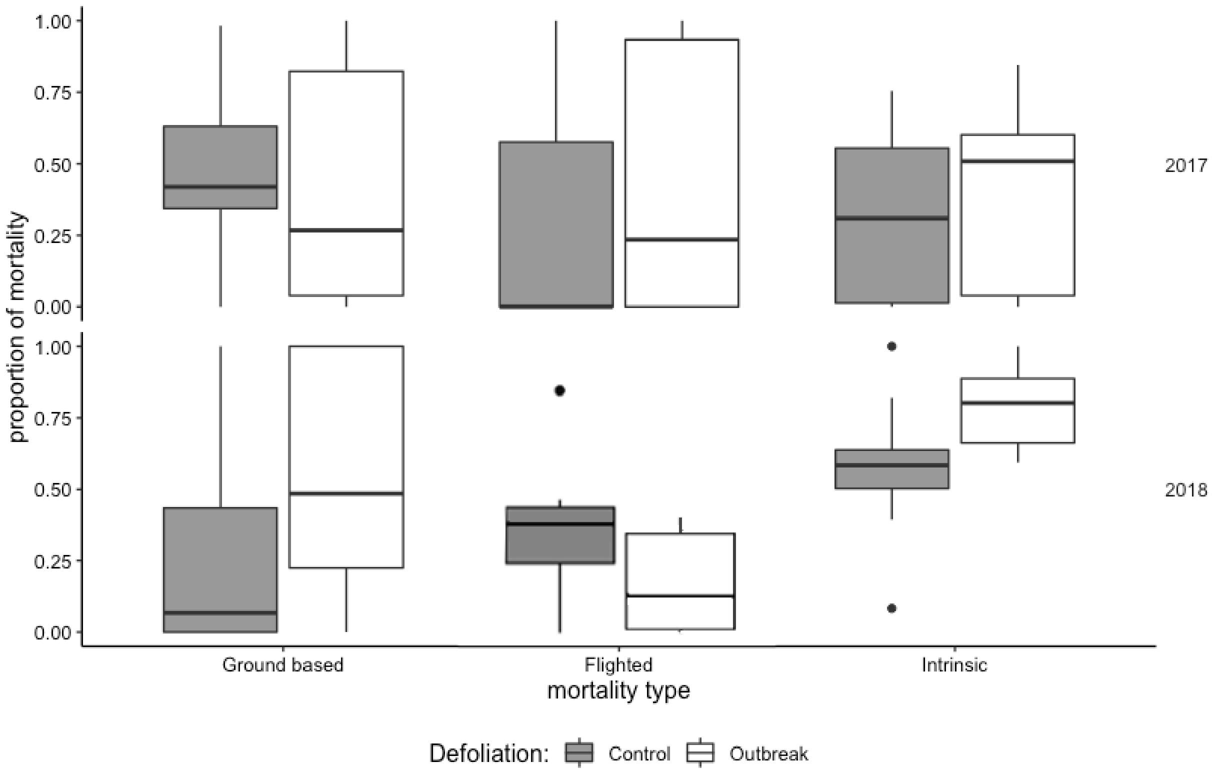


Figure 2.3 Marginal mortality rates of forest tent caterpillar colonies attributed to different sources of mortality: ground-based (walking mortality, M_g), flighted mortality (M_f), and intrinsic mortality (M_i). Colonies were observed in stands that had been previously defoliated (outbreak) or not (control) over two years: 2017 and 2018 (each n = 14). Box plot parts are as in Figure 2.2.

2.5 Discussion

As expected, larval survival increased with both protective treatments. Survival was lower in the outbreak than in control sites, linked to the crash of the outbreak. It also decreased from 2017 to 2018, consistent with the effects of delayed density-dependent mortality agents. Marginal attack rates showed increases between years in intrinsic and flighted mortality but not mortality from walking predators, suggesting these first two factors exhibit delayed density dependence.

2.5.1 Intrinsic mortality

Intrinsic mortality increased significantly in the year following the outbreak, following the delayed density dependence scenario. Egg hatch rates also decreased over the same period, and both these phenomena could be linked to pathogen infections. The notoriously virulent nuclear polyhedrosis virus (NPV) is vertically and horizontally transmitted. Its incubation period is approximately ten days, after which the infected animal's body liquefies, releasing virions to infect others. In addition, NPV can be transmitted directly to offspring through the eggs of sub-lethally infected females (Myers and Kuken 1995). The increase in intrinsic mortality and decrease in egg hatch rate observed in the present study are in line with previous observations of viral disease increasing with population density in tent caterpillars (Stelzer 1967; Bird 1969; Myers 1993; Kukan and Myers 1997; Rothman 1997). High infection rates in 2017 imply that many females laying eggs likely had sublethal infections, which, when transmitted vertically, led to mortality among their offspring in the second instar, approximately ten days after hatching. This scenario would explain the increased intrinsic mortality in 2018 in both outbreak and control sites because eggs from the outbreak stand were used in both locations. There could also be maternal effect of poor resources at the sites where the egg masses were collected since they were collected during the last year of the outbreak and we can assume that nutritional resources were low and the population crashing (Rossiter 1991; Ginzburg and Taneyhill 1994).

2.5.2 Natural enemies

Flighted enemies can include insect predators such as vespid wasps (McClure and Despland 2010), birds, and parasitoids (mostly flies and ichneumonid and braconid wasps). These parasitoids are much more specialized than predators in terms of the developmental stage they can attack.

Indeed, the most important source of parasitoid mortality was excluded from this study because it attacks late instars and pupae: the sarcophagid fly *Arachnidomyia aldrichi* Parker (Sippell 1962;

Witter and Kulman 2017; Parry 1995; Nixon and Roland 2012). Egg parasitoids were not included either, but FTC egg parasitism is generally quite low (Knight, Lavigne, and Pogue 1991).

Although some generalist parasitoids do attack earlier instars (Ives 1971, 19; Parry 1994), a study of mortality sources in low-density FTC populations in Alberta (western Canada) showed zero parasitism in the first and second instars, and only low rates in the third and fourth instars (Nixon and Roland 2012). In Nixon and Roland (2012)'s study, overall rates of parasitism were extremely variable. Between 0 and 100% of marginal larval mortality was due to parasitoids, but most occurred in the final instar or the pupal stage. The literature provides evidence that parasitoids are an important source of mortality in the collapse of FTC outbreaks, and these are mostly late-instar and pupal parasitoids (Parry 1994; Fitzgerald 1995). In our study, generalist predators are more likely sources of flighted mortality than parasitoids. Although we did not observe the predators in this study, they are likely similar to those observed by Nixon and Roland (2012), such as spiders, ants, beetles, and pentatomids.

Flighted mortality increased in the year following the outbreak peak, suggesting a delayed density-dependent response—the third scenario of Turchin (1999). The similar pattern observed in the control sites was unexpected; however, spatial autocorrelation of parasitism rates has been seen to be high over distances of hundreds of kilometres in another outbreaking forest pest, spruce budworm, *Choristoneura fumiferana* (Clemens) (Bouchard et al. 2018). This could explain the increased parasitism rates following the outbreak collapse, even in sites not directly affected by the outbreak.

Mortality from walking predators, on the other hand, did not respond to FTC density, exhibiting the neutral pattern in Turchin's (1999) first scenario. Walking natural enemies are mostly generalist predators that might not respond to FTC density if other factors limit their abundance (Bouchard et al. 2018). For instance, ant populations often depend on prey availability late in the growing season, long after FTC have completed their life cycle.

2.5.3 Density dependence

Marginal attack rates showed increases between years in intrinsic and flighted mortality but not mortality from walking predators, suggesting these first factors exhibit lagged density dependence. The three mortality sources thus showed different patterns concerning FTC density: intrinsic and flighted mortality appeared delayed density-dependent (Turchin’s third scenario), whereas walking mortality agents showed no response to density (Turchin’s first scenario). Lower early-instar survival in the year following the outbreak in recently defoliated sites is consistent with density dependence of mortality agents attacking this developmental stage. The similar increase in mortality in control sites confirms the resilience of forest lepidopteran outbreak cycles to experimental manipulation (Myers 1990). It appears linked to egg provenance (for intrinsic mortality) and spatial autocorrelation (for flighted mortality).

The design of our study does not permit us to confirm the direct density-dependent increase in parasitism reported in several outbreaking forest Lepidoptera (Gould, Elkinton, and Wallner 1990; Klemola et al. 2010), including FTC (Roland 1993). Our results, however, are concordant with results of delayed density dependence by Myers (1990), who showed that overall early larval mortality of congeneric western tent caterpillar, *Malacosoma californicum pluviale* (Dyar), increased in the year following the onset of decline. Myers (1990) attributed this delayed density-dependent mortality to NPV, and our results show a role for both disease and flighted predators.

Myers (1990) studied mortality sources over the outbreak cycle in western tent caterpillar, which shares similar life history with FTC (Fitzgerald 1995) and showed that mortality of late instars was high in the peak outbreak year (i.e., direct density dependence), and was mostly attributed to NPV infections and parasitoids. By contrast, early larval mortality was low in the peak year of the outbreak but increased in the following years (i.e., exhibited delayed density dependence). Myers (1990) and our results suggest that early and late instar mortality play different roles in outbreak dynamics. In their review of population cycles of outbreaking forest Lepidoptera, Myers and Cory (2013) outline that outbreaking dynamics require both a direct density-dependent mortality source that initiates the decline at peak density and delayed density-related mechanism(s) that prolongs the population decline. They also state that the mortality sources for the two processes should be different. Our results concur with previous research suggesting that early-instar mortality does not drive the collapse of tent caterpillar outbreaks, which is likely due to horizontally transmitted NPV and parasitoids acting on later instars (Myers 1990; Roland 1993; Myers and Cory 2013). However, our results and those of Myers (1990) show that early-instar mortality exhibits the delayed density dependence required to prolong collapse and likely occurs via vertically transmitted NPV and invertebrate predators. Predators have generally been overlooked in the study of forest Lepidoptera crashes (Myers and Cory, 2013), but classical population ecology predicts delayed density dependence. Modelling by Cooke and Lorenzetti (2006) showed that the oscillation pattern seen in FTC populations in Quebec indicates delayed density dependence of mortality from natural enemies. We provide empirical evidence for this delayed density-dependent mortality and show that it occurs in the early-instars.

2.6 Conclusion

This study shows that both intrinsic and flighted-predator mortality of young caterpillars increases in the years immediately after the end of an FTC epidemic. Previous work had highlighted the important role of direct density-dependent mortality in the late larval and pupal stages in the collapse of FTC outbreaks (Parry 1995; Williams, Parry, and Langor 1996; Parry, Spence, and Volney 1997; Nixon and Roland 2012), and our results suggest that early-instar mortality exhibits delayed density dependence and increases following outbreak collapse. Cooke and Lorenzetti (2006) argue that examination of FTC time series in eastern Canada suggests population regulation by delayed density dependence, and our results provide a mechanism for this density dependence. Early-instar mortality thus plays an important role in outbreak dynamics by accelerating population collapse and pushing post-outbreak populations to extremely low levels.

Chapter 3 - Forest Tent Caterpillar Outbreaks Drive Change in Ant Community in Boreal Forests

The following chapter is based on the published manuscript: Caron, A. S., Gagnon-Koudji, E. C., Handa, I. T., Girona, M. M., & Despland, E. (2023). Forest Tent Caterpillar Outbreaks Drive Change in Ant Communities in Boreal Forests, *Forests*, *14*(6), 1147.

3.1 Abstract

Insect outbreaks are major drivers of natural disturbances in forest ecosystems. Outbreaks can, directly and indirectly, affect the composition of soil arthropod communities through canopy opening, nutrient addition and predator-prey interactions. This study aimed to understand the impacts of forest tent caterpillar (*Malacosoma disstria*; FTC) outbreaks through cascading effects on ant communities in temperate and boreal forests in Canada. Pitfall traps and Berlese funnels were used to compare the ant communities and the surrounding arthropod communities between control and outbreak sites in boreal and temperate forests (in Quebec, Canada). Using the Sørensen dissimilarity index, we determined the alpha and beta diversity of the ant community. Other arthropods collected in the traps were counted to evaluate the richness and abundance of potential prey for the ants and other potential predators of the FTC.

We used an indicator species analysis to examine the species associated with sites defoliated by the outbreak. In the boreal forest, species composition varied significantly between control and outbreak sites. FTC outbreaks caused decreases in species richness and increases in the evenness of ant communities in defoliated sites due to the loss of rarer species. This pattern was driven in part by the presence of other predators. A similar but weaker pattern was observed in the temperate forest. Ant community beta diversity did not change in response to the outbreak in the boreal forest,

but in the temperate forest, it was lower in the outbreak than in the control sites. Ant species in the boreal forest showed stronger associations with either control or previously defoliated sites than did species in the temperate forest. Our study showed that disturbances such as insect outbreaks can drive changes in the ant community. While we only observed small effects of outbreaks, manipulation experiments using resource addition could help us validate the mechanisms behind these relationships.

3.2 Introduction

Insect outbreaks cause major natural disturbance events in forests and have had an impact on these ecosystems for a long time (Aakala et al. 2023; Montoro Girona, Navarro, and Morin 2018; Navarro et al. 2018). Defoliation, or feeding on leaves, by insect herbivores not only slows tree growth but can also promote nutrient cycling and accelerate succession (Lavoie et al. 2021). In addition, caterpillars are prey, and their population explosions affect trophic webs (De Grandpré et al. 2022; Caron, Jarry, and Despland 2022). Ecosystem effects of insect outbreaks can happen through various direct and indirect mechanisms: leaf removal increases light and temperature on the forest floor; exploding caterpillar populations increase prey availability for many predators; and frass, insect corpses and dropped foliage constitute nutrient transfers from trees to soils (De Grandpré et al. 2022; Swank et al. 1981; Hunter 2001; Metcalfe et al. 2014; 2016; Lovett et al. 2002). Together, these effects can stimulate decomposition, enhance nutrient mineralization, increase soil respiration, promote plant growth and alter brown food webs, defined by the consumption of decaying biomass by detritivores (Gravel, Albouy, and Thuiller 2016; Barnes et al. 2018; Kristensen, Metcalfe, and Rousk 2018; Lovett and Ruesink 1995; Debaly, Marchand, and Girona 2022; Odum 1970). However, the full complexity of underground food webs, referring to any trophic interaction taking place in and under the layer of litter, remains poorly understood, and the role of soil arthropods in mediating the effects of leaf-eating insect outbreaks on ecosystem functioning is not clear (Calderón-Sanou et al. 2021).

Caldéron-Sanou et al. (2021) found that the direct and indirect effects of caterpillar outbreaks increase the diversity of other arthropods in the underground food web at different trophic levels. They showed that the magnitude of the impacts of defoliation did not decrease at higher trophic levels, contrary to what was assumed. The researchers expected the effect of defoliation to be diluted the higher the trophic level. Instead, they observed a more diverse food web and a greater proportion of high-trophic level taxa in defoliated than in control forests. Because so many of the species making up the soil community are responsible for structural and functional characteristics of the ecosystem, a change in their assemblage could have a large impact on ecosystems (Bardgett and Caruso 2020; De Ruiter, Neutel, and Moore 1995; Estes et al. 2011; Saravesi et al. 2015; Vindstad, Laksforsmo et al. 2014; Sandén et al. 2020). The functional roles of ants are also important to consider, as they will modulate the ants' responses to perturbations, even in the environment (Hoffmann and Andersen 2003).

Ants are particularly important in forests since they are one of the few large-scale ecological engineers (Jurgensen et al. 2008; Risch and Jurgensen 2008; Domisch, Finér, Neuvonen, Niemelä, et al. 2009). Ants make up a large part of the insect biomass. They can play multiple ecological roles, such as predators, soil engineers, nutrient cyclers and regulators of plant growth and reproduction (Del Toro, Ribbons, and Pelini 2012; Folgarait 1998; Hölldobler and Wilson 1990; Wardle et al. 2011), thus shaping both in-ground and above-ground trophic webs. In these northern forests, ants play a crucial role in arthropod communities (Laine and Niemelä 1980; Punttila, Niemelä, and Karhu 2004) and nutrient fluxes (Finér et al. 2013; Wardle et al. 2011). The social organization of ant colonies means they can respond rapidly and dramatically to environmental changes and hence can mediate ecosystem effects of disturbance (Andersen 2019).

The prey availability for ants can increase with defoliator outbreaks, both directly due to the presence of caterpillars and indirectly due to the stimulation of brown food webs. Indeed, soil detrivores and fungivores respond to an increase in microbial biomass and activity induced by high-quality inputs, leading to increased soil respiration and nutrient cycling, especially if the nutrient inputs are sustained for a few years (De Grandpré et al. 2022; Kaukonen et al. 2013; Mikola et al. 2001; Pitman, Vanguelova, and Benham 2010; Chapman et al. 2003). Many of these soil microarthropods, such as collembola, Acarina and Isopoda, can be prey for ants (Moya-Laraño and Wise 2007; Çakır 2019), but this is not the only way in which changes in brown food webs can influence ants. Indeed, ants are deeply interconnected with boreal and temperate forest trophic webs (Laine and Niemelä 1980; Punttila, Niemelä, and Karhu 2004), but their responses to changes in these communities are poorly understood. For instance, increases in other arthropod predators could constrain ant responses. Ants are well-understood to exert significant predation pressure on forest defoliators (Karhu and Neuvonen 1998; Way and Khoo 1992; Tilman 1978; Gösswald 1990). However, the reverse, namely the effects of outbreaks on ant communities, has received less attention. Considering the keystone role of ants, this knowledge gap constrains our understanding of the cascading effects of defoliator outbreaks.

The impacts of forest canopy opening on ants have mostly been studied through the effects of forest management (Carvalho and Vasconcelos 1999; Maeto and Sato 2004; Palladini et al. 2007; Ewers et al. 2015). Multiple studies have shown an increase in ant abundance and diversity with moderate management intensity, where there is some increase in clearing area, canopy opening and edges (Palladini et al. 2007; Punttila et al. 1994; Véle, Holuša, and Horák 2016). The main driver appears to be a change in the forest floor microclimate from the canopy opening. Grevé et al. (2018) found that forest management (with a moderate proportion of harvested tree volume and even-aged stands) increases abundance, species richness and functional diversity in ant communities in temperate forests and that this was due to reduced canopy cover and stand structural complexity. They also found that shade-intolerant ant species (pioneer or gap species needing environments with high availability of light to establish and grow (Farji-Brener 2001)) were more likely to be favoured and that this was likely due to warm conditions in the stands. In Japanese temperate forests, both open habitat specialists and generalists were abundant in managed forests, but shade-tolerant species (persistent or mature forest species, able to thrive in shaded environments (Farji-Brener 2001)) declined (Maeto and Sato 2004; Yamamoto 2000). In boreal forests, similar trends have been observed in Europe (Punttila et al. 1994; 1991). Open habitats in temperate and boreal forests affect ant diversity and abundance positively. A decrease in shade-tolerant ant species was especially correlated with lower canopy coverage in European studies (Punttila et al. 1991; 1994; Schall et al. 2018).

The forest tent caterpillar (*Malacosoma disstria* Hübner, 1820) is an important forest defoliator of hardwoods across much of North America. Outbreaks usually last 3–5 years and slow the growth of host trees, sometimes leading to stand dieback (Fitzgerald 1995). During forest tent caterpillar outbreaks, defoliation increases canopy openness, increasing sun exposure to the forest floor, resulting in higher soil temperatures, drier soil, and increased growth of saplings and understory plants (Moulinier 2013). Similar canopy opening has increased ant abundance and species richness in managed or recovering forests (Punttila et al. 1994; Palladini et al. 2007).

However, unlike most forest management practices, insect outbreaks also involve an increase in prey abundance for ants, both directly from the outbreaking caterpillars and indirectly via the stimulation of brown food webs. Indeed, ants are common predators of caterpillars (Lach, Parr, and Abbott 2010) and have been shown to have substantial impacts on the abundance of caterpillars (Montllor and Bernays 1993; Karhu and Neuvonen 1998; Piñol et al. 2010) and other leaf-chewing herbivores (Clark et al. 2016). Ant predation has been suggested to show a density-dependent response to caterpillar availability, increasing during an outbreak and playing a role in controlling the outbreak (Green and Sullivan 1950b; Despland and Lessard 2022). Ants could alter trophic cascades by lowering herbivory damage (Rosumek et al. 2009; Romero, Antiqueira, and Koricheva 2011; Moreira et al. 2012). While thinking of trophic cascades, it is also important to consider that ants prey on soil micro-organisms, such as springtails (Collembola) as well, with certain groups, such as the ground-dwelling Dacetini (Myrmicinae) being specialized predators (Cerdá and Dejean 2011), thus acting on different parts of the food web associated with caterpillar outbreaks.

This study investigated the dynamics between ant communities and defoliation at the ecosystem level in both a boreal and a temperate forest. Specifically, we evaluated the effects of a forest tent caterpillar outbreak on ant communities, examining drivers related to environmental conditions on the forest floor and changes in soil arthropod communities. We hypothesized that canopy opening, high numbers of caterpillars, and increased soil arthropods driven by nutrient inputs would lead to higher ant species diversity. Increased energy and nutrient flow, combined with increased heterogeneity of the forest floor, was predicted to open niches, thus promoting higher ant diversity. In terms of evenness, there are two possibilities: either many species are favoured, thus leading to a more homogenous community (higher evenness), or only a few species can take advantage of novel conditions, thus leading to a more heterogenous community (lower evenness). We also examined associations of the ant species with control or outbreak sites. Finally, we evaluated the role of three potential drivers related to outbreaks that could affect ant populations, namely canopy opening, increased soil microarthropod populations (using collembolas as a representative group) that can provide food resources for ants, and changes in soil arthropod predator populations.

3.3 Materials and Methods

3.3.1 Study Area and Experimental Design

This study was conducted in two forest stands affected by the most recent FTC outbreak. In both regions, an FTC outbreak was detected in 2016 (MFFP 2016) and continued in 2017 (MFFP 2017), but no defoliation was observed in 2018 or 2019.

The Forêt d'enseignement et de recherche du lac Duparquet (FERLD; N48.513, W79.369) is within the boreal mixed-wood forests of eastern Canada, in post-fire (1923) regenerated stands dominated by mature trembling aspen (*Populus tremuloides* Michx, 1803) 10–15 m tall. Due to the vertical structure of aspens (very few branches until the canopy), the trees are closer together and thus at a relatively high density. The climate is cold-temperate, with a (1961–1990) mean annual temperature of 0.9°C and mean annual precipitation of 642 mm of rain and 215 mm of snow. Fire drives the disturbance regime, and large, even-age trembling aspen stands arise from post-fire regeneration (Bergeron 2000). The soils are Grey Luvisols (Canada 2013) from glaciolacustrine clay deposits (Vincent and Hardy 1977). The region was affected by an FTC outbreak for three years, starting in 2015 (MFFP 2015) and continuing in 2016 and 2017 (MFFP 2016; 2017). No FTC defoliation was observed in either 2018 or 2019 (MFFP 2019). Spruce budworm (*Choristoneura fumiferana* Clemens, Lepidoptera: Torticidae) (Morin, Laprise, and Bergeron 1993) attack the conifers in the area, and the birch tube maker (*Acrobasis betulella* Hulst, Lepidoptera: Pyralidae) and the lesser-eyed sallow (*Enargia infumata* Grote, Lepidoptera: Noctuidae) (Dubuc 1996) can also defoliate deciduous trees in this forest.

The Kenauk Nature Reserve (N45.712, W74.887) is within a temperate deciduous forest composed of stands dominated by mature sugar maple (*Acer saccharum* Marsh, 1785) and American beech (*Fagus grandifolia* Ehrh, 1787). Since maple trees tend to have branches along the trees, the density was slightly lower than for aspen forests. The climate is cold-temperate, with a mean annual temperature of 5°C, and has a mean total annual rainfall of 807.4 mm and a total annual snowfall of 178.1 cm (Environment Canada 2017). The disturbance regime is driven by a mix of insect pests, mostly defoliators such as the FTC and, more recently, the spongy moth (*Lymantria dispar dispar* Linnaeus, Lepidoptera:Erebidae), and weather events. The soils in the study area are classified as Dystric Brunisols with a moder-type humus (Lajoie 1967; Canada 2013).

3.3.2 Experimental Design

The sites were classified as outbreak or control using both data from the MFFP reports cited previously, as well as from on-site observations from other researchers. Both sampled sites are part of research institutes that host various forest and insect monitoring projects whose information we used in site selection. The variable representing outbreak and control sites will be referred to as defoliation history for the rest of the study. In both regions, each site was characterized by a focal tree around which we sampled the arthropod fauna. The arthropod sampling was conducted within 5 m of the focal tree at each site. We sampled all sites twice per field season over two years. We then pooled the traps, sampling period and year for each site.

In the boreal forest, we selected 28 sites in trembling aspen-dominated stands (generally over 50% of aspen and where other trees were conifers), including 14 that were heavily defoliated in 2016–2017 (outbreak sites) and 14 control sites. The sites were described in Chapter 2. These sites were sampled both during (2016-2017) and after (2018-2019) the outbreak. The focal trees remained the same during all years of sampling.

In the temperate forest, twelve (12) sites in sugar maple stands that were heavily defoliated in 2016 and 2017 (outbreak sites) and 12 control sites in similar age stands having escaped defoliation were sampled in 2018 and 2019.

3.3.3 Environmental Variables

To confirm the defoliation history of control and outbreak sites, we examined twenty saplings of the respective focus tree species in each region, between 1 and 3 m tall in a 100 m radius around the focal tree, for forest tent caterpillar colonies in 2017, 2018 and 2019. At each site, we also measured canopy openness using a densiometer in 2018 and 2019 (every two weeks during May, June and July) and used an average of four measurements, rotating 90º on oneself, as per the methodology recommended by the tool. We then averaged over all measurements per site taken at the different sampling dates. Unfortunately, the 2017 data used in this study came from the dataset of a previous student and did not contain the canopy data.

3.3.4 Ant Survey

Ants were sampled in control stands at FERLD in 2016 by Despland and Lessard (Despland and Lessard 2022), and these data were only included in the species list (Table S3.1). Since the sampling method was quite different from the ones used the following year, we could not use these data in the analysis; however, they helped us obtain a description of the ant fauna. Standardized ant sampling in control and outbreak sites was conducted in 2017–2019 at FERLD and 2018–2019 at Kenauk.

At each site, five pitfall traps, 50 mm in diameter, filled with propylene glycol and one drop of both ethanol and unscented liquid soap, were set in the ground for 48 h (Bestelmeyer et al. 2000). Pitfall traps in cold temperate climates usually attract bigger ants but are readily used to sample ants of most functional groups (Mahon, Campbell, and Crist 2017). Pitfall traps were positioned in a radius around the focal tree, 5 m from one another and left for 48h. The process was repeated two times, once in late May and once in late June, to coincide with the FTC larval period. Note that ants are not very active in May, but late June is near the peak activity period.

All ants sampled in the pitfall traps were identified to species level (Francœur 2001; Ellison et al. 2012) and a subsample was confirmed by Dr. André Francoeur, Dominic Ouellette and Dr. Jean-Philippe Lessard. Specimens that were either too deteriorated or could not be identified were omitted from further analysis. Ant abundance was transformed to presence-absence data to account for bias from nest proximity. Ant occurrence was evaluated as the number of traps in which a given ant species was collected. We pooled data from all the traps at each site for further analysis. We calculated ant species richness as the number of ant species found per plot.

3.3.5 Survey of Other Arthropods

We collected collembolas to use as a proxy of other potential food resources for ants beyond the FTC larvae. Collembolas were also sampled in a subset (N = 8) of outbreak and control sites. The samples were taken within a diameter of 1 m around the focal tree. At each tree, two replicates of litter were taken within a 20 × 20 cm quadrant, two soil samples from 0–5 cm and two samples from 5–10 cm, using a 5 cm corer. The two replicates for each sampling type were combined and conserved at 4 °C and extracted less than 48 h after collecting in the laboratory. The soil fauna was extracted using Berlese–Tullgren extractors running for seven days, with temperatures gradually increasing from 20 °C to 50 °C. The specimens were conserved in 70% ethanol and sorted to separate collembolas from other soil organisms. Collembolas were prepared and identified using published keys (Hopkin 2007; Fjellberg 1998; 2007; Christiansen and Bellinger 1980)**,** collembola.org and ecotaxonomy.org. If possible, the specimens were identified to the lowest taxonomic level but were at least identified to family. The samples were also grouped into morphospecies for hard-to-identify species (Gagnon Koudji et al. 2023). Only collembolas from these samples were considered, not by-catch from pitfall traps.

Additionally, all other potential predators and parasitoids found in the pitfall traps were counted, such as spiders, wasps, beetles and stinkbugs, that have been previously defined as predators and parasitoids of the forest tent caterpillar (Evans 1982; Fitzgerald and Costa 1999; McClure and Despland 2010; Ronnås et al. 2010; Cobbold et al. 2005), and the total predator abundance was included in statistical analyses.

3.3.6 Statistical Analysis

An ANOVA was performed to evaluate the effect of defoliation history (independent variable) on ant species richness and evenness (dependent variables). All the years were pooled together in each region (2017–2019 for the boreal forest and 2018–2019 for the temperate forest) in all analyses since a preliminary analysis showed no effect or interaction of year.

To investigate the differences in community composition between sites with different defoliation histories, we calculated a dissimilarity matrix based on the Sørensen dissimilarity index (Sorensen 1948; Jaccard 1901). This index was used for the community analysis (for both ordination and beta diversity analyses) because it is one of the widely used indices for presence-absence datasets. It examines the number of species shared by two sites and the number of species unique to each. The maximum and minimum values of Sørensen are 0 (the same species composition) and 1 (no shared species). To visualize the dissimilarity matrices, we used nonparametric multidimensional scaling (NMDS) plots via the metaMDS function in the vegan package for R Champ (Oksanen et al. 2010). Then, we tested the differences in the taxonomic position of the community centroids (multivariate location) between defoliation histories using 'Permutational Multivariate Analysis of Variance' (PERMANOVA), the adonis2 function in the vegan package, with 999 permutations. These vectors of our chosen variables (defoliation history, canopy openness, predator abundance, prey abundance and prey species richness) were tested for significant effects in shaping the observed ant communities. Since we could not use AICs or similar methods for model selection with PERMANOVAs, we retained variables with an R^2 of more than 0.02 when conducting a PERMANOVA in our analysis.

We performed an indicator species analysis to further explore the community's changes due to the different defoliation regimes (Dufrêne and Legendre 1997). This method allows us to quantitatively assess the association of specific species of ants to either of our two groups, in this case, the control and outbreak sites. It assesses the predictive values of species as indicators of the conditions prevailing under different defoliation regimes (De Caceres and Jansen 2016). Component 'A' is a conditional probability referring to the positive predictive value of the species as an indicator of the defoliation history. Component 'B' is another conditional probability referring to the likelihood of finding a species in sites experiencing the defoliation history. Both components vary from 0 to 1

(Dufrêne and Legendre 1997). All analyses were carried out using R version 4.2.0 (R Development Core 2017).

3.4 Results

We collected and identified a total of 2940 individual worker ants belonging to 37 species and morphospecies from 2 subfamilies and 8 genera across our 28 sites in the boreal forest (Table S3.1) and 24 sites in the temperate forest (Table S3.2).

Ants were absent in some pitfall traps, even though other arthropods were collected. From the sites sampled in the boreal forest, we collected ants from 100% of the control and 92% of the outbreak sites. In the temperate forest, we collected ants from 83% of the control and 50% of the outbreak sites. Species accumulation curves validated our experimental species sampling design for defoliation histories and regions (Figure S3.1 and S3.2).. Abundance tended to be slightly higher in control sites.

Forest tent caterpillar colonies were observed in 2017 in the outbreak sites (3.36 ± 1.86 (mean ± SD) colonies of 20 saplings) but not in the control sites, and none were observed at all in 2018 and 2019 in the boreal forest. In the temperate forest, we observed colonies both in the outbreak sites (5.5 ± 2.85 (mean ± SD) colonies of 20 saplings) and in the control sites (4.01 ± 2.50 (mean ± SD) colonies of 20 saplings).

3.4.1 Species Richness and Evenness

Three species were shared between the two regions. We found a total of 21 species in the boreal forest sites, with the species occurring most often being *Camponotus novaeboracensis* (Fitch, 1855)

(23% of traps), *Myrmica alaskensis* (Wheeler, 1917) and *Formica subaenescens* (Emery 1893). In the temperate forest sites, we found a total of 16 species, with the species occurring most often being *Aphaenogaster picea* (Wheeler, 1908) (25% of traps), *Lasius americanus* (Emery 1893) and *Stenamma diecki* (Emery 1895). Many rare species, with only one occurrence, were observed. However, a single occurrence of a species can imply multiple individuals in the same trap.

In the boreal forest, we observed significantly lower species richness (df =1, $F_{1,2} = 9.91$, $p = 0.003$) and significantly higher evenness in the outbreak than in the control sites (df = 1, $F_{1,2} = 9.41$, $p = 0.004$). We identified similar trends in the temperate forest sites; however, the high proportion of traps that did not collect ants (90%) reduced the sample size and, hence, the power of the analyses. In many cases, at least one trap per site had ants; therefore, when pooling traps at each site, we observed ants in 83% of the outbreak sites and 50% of the control sites. In the temperate forest, the species richness (df = 1, $F_{1,2} = 0.84$, $p = 0.372$) and evenness (df = 1, $F_{1,2} = 3.87$, $p = 0.085$) did not differ significantly between the control and outbreak sites (Figure 3.1).

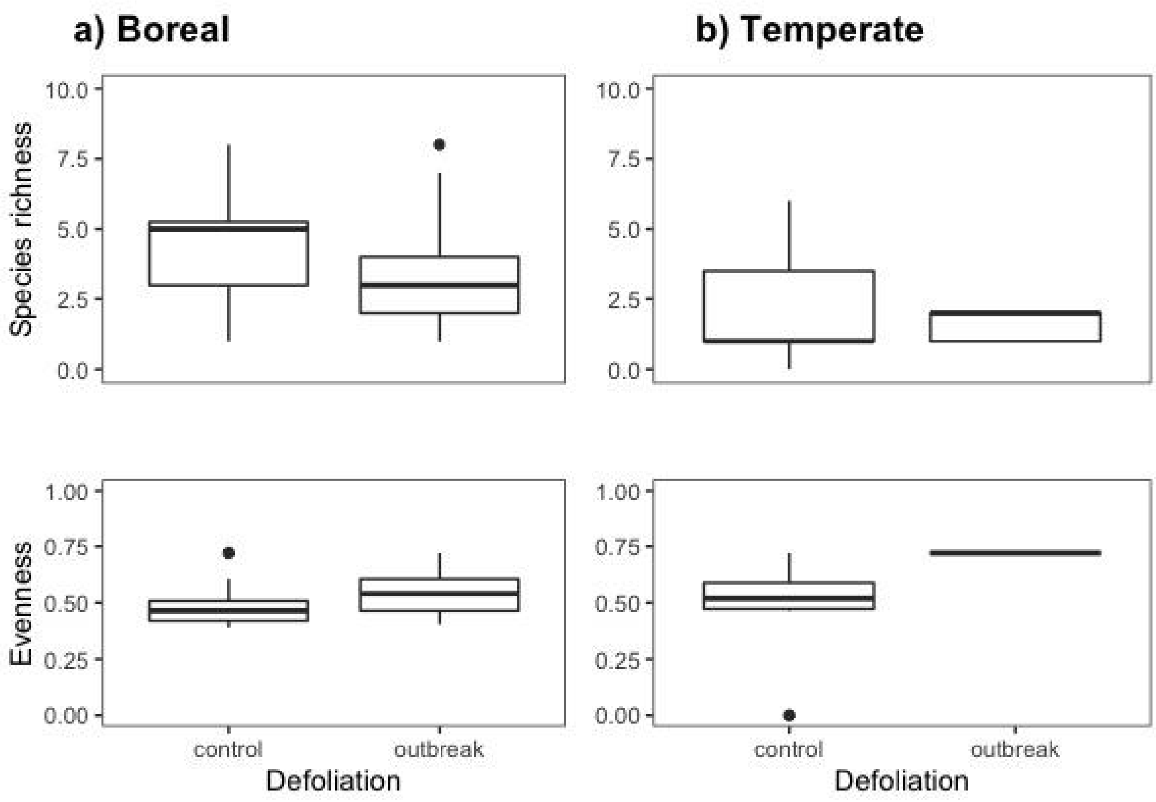


Figure 3.1 Species richness and evenness. The two panels on the right refer to the boreal forest data, while the two on the left refer to the temperate forest data. Box plots represent data from pitfall traps only and from a subset of years for the boreal forest samples (2017-2018) to limit the variation in sampling methods from 2016 and 2019, respectively. In the box plots, the lower boundary of the box indicates the 25th percentile, the bold line within the box marks the median, and the upper boundary of the box indicates the 75th percentile. The whiskers indicate the 10th and 90th percentiles. Dots are outliers (>Q3 + 1.5 × interquartile range).

3.4.2 Species Composition

The species composition in the boreal forest sites varied significantly between control and outbreak sites ($F_{1,52} = 5.39$, $p = 0.002$, $R2 = 0.091$ df = 1) (Figure 3.2; Table 3.1) but with an obvious overlap. Canopy openness, collembola abundance and diversity all aligned with defoliation, showing that they all increased with increased defoliation but did not contribute significantly to predicting ant communities. Predator abundance also increased with defoliation and were significantly associated with changes in the ant community.

In the temperate forest, however, while the control and outbreak sites tended to cluster away from each other, this clustering was not significant. Additionally, no other factors in the analysis significantly affected ant community composition (Table 3. 1).

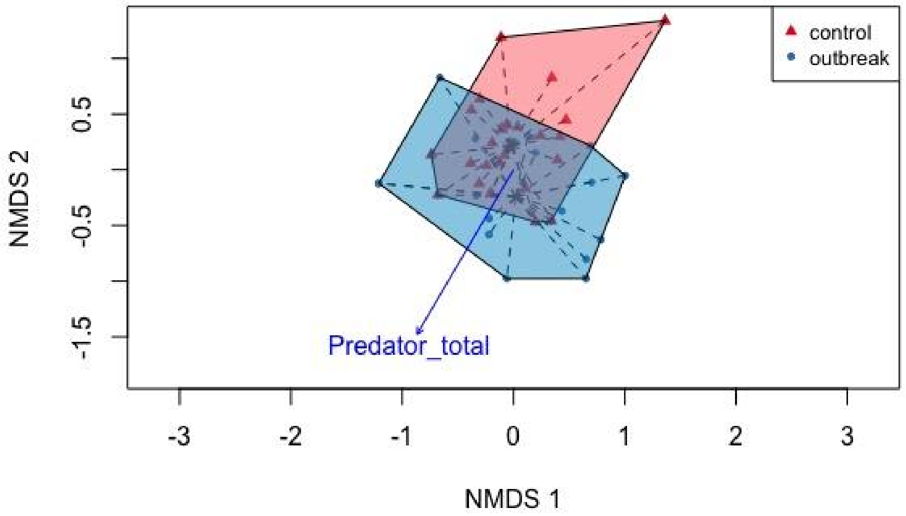


Figure 3.2 NMDS ordination of boreal forest sites within control and outbreak stands based on the Sørensen dissimilarity index using taxonomic data. The abundance of predators was the only covariate aligned significantly with the ant community composition.

Table 3.1 Summary of statistics for PERMANOVAs of the effect of defoliation history on taxonomic compositional turnover of ant communities. Significant values ($p < 0.05$) are highlighted in bold.

	Boreal forest					**Temperate forest**			
	df	F	R^2	p-value		df	F	R^2	p-value
Defoliation history	1	4.62	0.080	**0.001**	Defoliation history	1	1.45	0.10	0.23
Canopy openness	1	1.24	0.021	0.33	Canopy openness	1	0.38	0.027	0.84
Predators	1	3.22	0.056	**0.017**	Predators	1	0.78	0.055	0.56
Collembola (abundance)	1	0.389	0.0066	0.78	Collembola (abundance)	1	1.64	0.11	0.18
Collembola (species richness)	1	1.18	0.021	0.35					
Residuals	47		0.82			14		0.70	

3.4.3 *Beta Diversity*

The taxonomic multivariate dispersion (i.e., homogenization) did not differ significantly between defoliation histories in the boreal forest ($F_{1,2} = 2.026$, df = 1, p = 0.1607), but did in the temperate forest ($F_{1,2}$ = 7.31, df = 1, p = 0.009) (Figure 3.3). However, it is important to note that homogenization was quite low (i.e., beta diversity was high) between sites since the distance to the centroid was high above the null expectation.

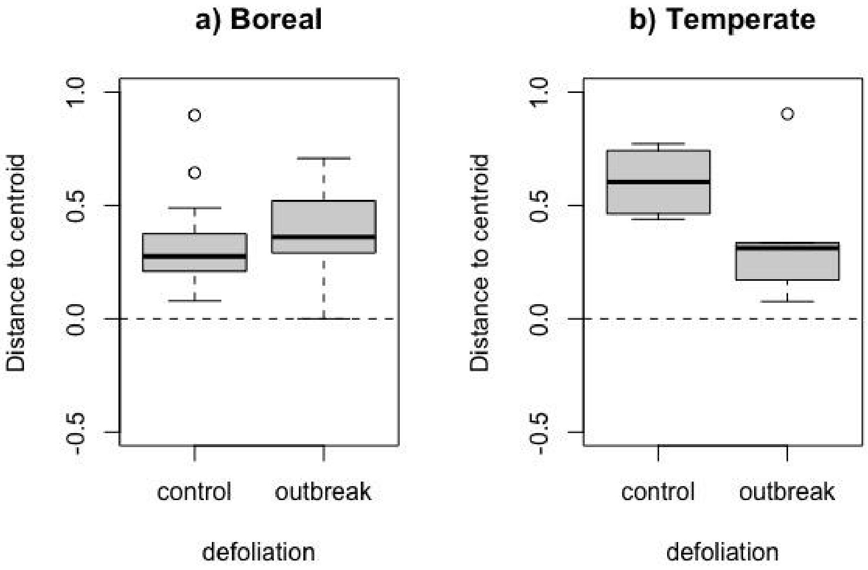


Figure 3.3 Boxplot of the standardized effect size of each site's distance to multivariate space centroid (SES Dcentroid) in a) boreal and b) temperate forests. The black dashed line represents null expectations. In the box plots, the lower boundary of the box indicates the 25th percentile, the bold line within the box marks the median, and the upper boundary of the box indicates the 75th percentile. The whiskers indicate the 10th and 90th percentiles. Dots are outliers (>Q3 + 1.5 × interquartile range).

3.4.4 Indicator Species

The indicator value (IndVal) index measures the association between a species and a site group, such as the defoliation history. Out of the 21 species found in the selected sites in the boreal forest, 3 species were significantly associated with one group, with 2 representing the control sites and 1 representing the outbreak sites (Table 3.2); another four species were found to be as likely to occur in both groups.

Table 3.2 Indicator species analysis for the boreal forest data only at alpha = 0.05. The "Indicator value index" measures the association between a species and a site group. "A" is the positive predictive value of the species as an indicator of the site group, and "B" is the sensitivity of the species as an indicator of the target site group.

Groups	Species	A	B	IVI*	p-value
Control	*Camponotus herculeanus*	0.78	0.57	0.67	0.008
	Myrmica detritinodis	0.89	0.32	0.54	0.004
Outbreak	*Formica integra*	1.0	0.2	0.45	0.018

* Indicator Value Index

In the temperate forest, however, we found no significant pattern of association with the defoliation history groups. Of the 17 species found in the selected sites in the temperate forest, 4 species were as likely to occur in both groups. However, even for others who preferred one of the two groups, none was strong enough to be considered an indicator.

3.5 Discussion

Contrary to our hypothesis that disturbance would increase ant diversity at defoliated sites by creating new ecological niches, the sites where the outbreak occurred did not contain a more diverse ant community. In the boreal forest, defoliation slightly lowered the ant alpha diversity but did not alter the beta diversity or the proportion of singletons. The increase in evenness was due to no species being overwhelmingly dominant. The only significant trend identified in the temperate forest was decreased beta diversity with defoliation. In the boreal forest, observed changes in ant communities were not significantly linked to changes in canopy openness, prey abundance or diversity. However, they did correlate with an overall increase in predator abundance in the defoliated sites. In the boreal forest, two ant species were identified as indicators of the control sites and one as an indicator of the outbreak sites.

3.5.1 Ant Community Responses to Disturbance

In both the temperate and boreal forests, the sites that had experienced defoliation due to an outbreak were more even and less species-rich than the control sites; however, this effect only attained statistical significance in the boreal forest. Disturbances generally impact arthropod communities more in structurally simple habitats than in complex ones (Broza and Izhaki 1997; Gardner et al. 1995). The MFFP protocol of outbreak detection and damages categorized stands as having light (defoliation on only the top of the canopy in some trees), moderate (defoliation on the top 2/3 in most of the trees) or severe (defoliation on most of the branches in most of the trees) (MFFP 2016). In our case, the intensity of the disturbance was moderate.

Ants are typically impacted indirectly by disturbances through effects on habitat structure, microclimate, resource availability and competitive interactions (Bardgett and Van Der Putten 2014; Bardgett et al. 2005; Hedlund et al. 2004; Anderson et al. 2012; Souza et al. 2015; Frizzo, Campos, and Vasconcelos 2012; Silveira et al. 2016; Vasconcelos, Maravalhas, and Cornelissen 2017). In our study, we knew (Lafleur, pers. obs. (boreal) and Nowell, pers. obs. (temperate)) that there was an increase in light reaching the understory during the outbreak, therefore creating a disturbance in the light regime. Unfortunately, we did not have the canopy openness deployed during the outbreak and thus do not have data to support these observations. Outbreaks of species such as the FTC are what could be considered a moderate chronic disturbance (Calizza et al. 2019), meaning that an outbreak event in itself causes moderate damage in an area; this is because leaves can reflush during the summer and that the epidemic cycle is relatively short (10 years), in contrast to the timescale on which a forest operates. However, since these outbreaks are not static geographically (Cooke, Sturtevant, and Robert 2022), the impacts may be less dramatic, especially since changes in ant communities are mostly driven by long-term disturbance regimes (Andersen et al. 2009; York 2000; Parr et al. 2004; Maravalhas and Vasconcelos 2014; Vasconcelos, Maravalhas, and Cornelissen 2017). While FTC outbreaks are part of this disturbance regime and can alter forest succession in the boreal forest (Moulinier 2013), they are relatively short-lived compared to those of the spruce budworm (Johns et al. 2019).

Research suggests that ant foraging in temperate regions is sensitive to sun exposure on the forest floor (Andersen 2019). This influence on foraging could translate to changes in communities, as foraging and competition are some of the main drivers of community assemblage (Lessard, Dunn, and Sanders 2009; Despland and Lessard 2022). Canopy openness was higher in defoliated sites, but it was not a significant contributor to predicting the ant communities in our study. This suggests that the observed canopy opening was not significant enough to affect the ant communities directly. However, it is important to mention that we did not have the canopy openness data for the years of the outbreak; thus, this measure relates to the canopy 1- and 2 years post-outbreak. Therefore, we do not know if canopy opening during the outbreak influenced the establishment of ant nests.

Additionally, aspens and maples can reflush during the same summer; hence, our measurement represents long-term canopy loss due to defoliation events. In the boreal region, rarer shade ant species were excluded from the outbreak sites and replaced with more common species. Therefore, while canopy openness was not retained as an indicator in our model, we nonetheless saw a change in the community consistent with a role for increased sunlight to the forest floor. Our study system, therefore, resembled uneven-aged forest management with a strong vertical structure and small gaps that closed quickly. These small gaps were less favourable to shade-intolerant ants than large open areas created by forest harvesting.

3.5.2 Indicator Species

Taxa that favour open habitats, such as the generalist Myrmicinae, usually do well in disturbed habitats; groups that prefer closed habitats, such as specialist predators, are often at a disadvantage (Hoffmann and Andersen 2003; Fotso Kuate et al. 2015; Leal et al. 2012; Solar et al. 2016). In our study, the species that were only present in the outbreak sites are associated with more open habitats such as managed forests, bogs, shrublands or disturbed areas (Fairweather et al. 2020; Milford 1999; Ellison, Farnsworth, and Gotelli 2002; Francoeur 1986; Francoeur 1973; Francoeur 2011).

In the boreal forest, *Camponotus novaeboracensis* was the species that occurred most often in both the control and defoliated stands. *C. novaeboracensis* is a behaviorally dominant ant (Oberg, Del Toro, and Pelini 2012). It has been observed to successfully attack forest tent caterpillars during the outbreak preceding our study (Despland and Lessard 2022). However, our results did not show this species becoming more dominant in the outbreak sites.

The main species retained as indicators of control sites in the boreal forest were *Camponotus herculeanus* (Linnaeus, 1758) and *Myrmica detritinodis* (Emery, 1921). *Camponotus herculeanus* is a widespread species in boreal forests (Wheeler, Wheeler et al. 1963; MacKay and Mackay 2002). *Myrmica detritinodis* is a shade species that prefers shelter under moss and lichens, preferably in high-moisture conditions (Sirois 1993). It was expected to prefer a high canopy cover. *C. herculeanus* was more surprising since it was seen to be previously associated with either closed or open habitats (Wheeler, Wheeler, et al. 1963; MacKay and Mackay 2002). In our system, we concluded that they may be more associated with closed habitats, but this may depend on other environmental characteristics.

One species associated with the outbreak sites is *Formica integra* (Nylander, 1856), but limited information is available on their ecology due to their low occurrences. However, they are part of the *Formica rufa* group (red wood ants), whose ecology has been well-studied in European boreal and temperate forests. In particular, red wood ants feed on invertebrate prey from both the canopy and forest floor (Rosengren 1991; Domisch, Finér, Neuvonen, Niemelä, et al. 2009; Hölldobler and Wilson 1990) and have been suggested to have the potential to control outbreaks of insect pests (Parmentier, Dekoninck, and Wenseleers 2014). They also build large mounds on the forest floor for their nests. The distribution of these mounds is governed by multiple factors (climate, ecosystem productivity, food resources) (Kilpeläinen et al. 2007; Serttaş et al. 2020), but light availability stood out as the most important factor (Stockan, Rao, and Pakeman 2010), signifying the importance of canopy openness. In our study, their increase in the outbreak sites suggests that this ant species is uniquely positioned to benefit from a short-term canopy opening and resource pulse associated with a defoliator outbreak to carry it over temporally. Since these mounds concentrate nutrients and can affect the biotic and abiotic components of the surrounding forest, they can increase the presence of associated species (e.g., spiders, beetles and millipedes) living near them, such as parasites, predators and scavengers, as they provide a stable habitat with consistently higher temperatures than the rest of the environment (Rosengren et al. 1987).

Several *Formica* and *Camponotus* species have been observed to attack lepidopteran caterpillars in eastern Canada (Despland and Lessard 2022). While studying ants' predation of the spongy moth, Weseloh (1989) found that both *Formica* and *Camponotus* spp. workers attacked caterpillars, especially at the first instar, and this decreased as the larvae grew. Thus, using forest tent caterpillars as prey could contribute to populations of *F. integra* and *C. novaeboracensis* in outbreak sites.

In the temperate forest, the species that occurred most were smaller-bodied ants from the *Aphaenogaster* and *Lasius* genera. However, no species were found to be indicators of either the control or outbreak sites. *Aphaenogaster* species from the species complex *A. picea* are omnivorous feeders and generally feed on small invertebrates and some mushrooms (Mokadam 2021). *Lasius americanus* is omnivorous and feeds on seeds and live and dead insects (Ellison et al. 2012). Both the *Aphaenogaster* and *Lasius* genera were widely distributed in the sites studied, but their distribution did not appear to be influenced by a defoliation history.

3.5.3 Prey, Predators, and Outbreaks

The results from Grevé et al. (2018) support our finding that overall prey abundance did not influence ant species composition through increased food resources during the outbreak. However, our results show a positive relationship between ants and other predators in the boreal forests; the basis for this relationship is unclear. These arthropods could be responding to a disturbance, similarly to ants, but without any direct trophic interactions between them (Grevé et al. 2018). Generalist predators tend to increase slowly in response to increased prey availability during a caterpillar outbreak, thus showing up as delayed density-dependent scenarios (Sabelis 1992). Thus, high numbers can be maintained in the year following an outbreak crash (Settle et al. 1996; Symondson, Sunderland, and Greenstone 2002).

Previous research also confirmed that increased prey abundance does not drive ant community responses to disturbance (Grevé et al. 2018) and that ants do not respond to resource pulses of arthropod prey (Yang 2006). Resource pulses tend to satiate predators and aboveground consumers (Karban 1982; Sweeney and Vannote 1982; Williams, Smith, and Stephen 1993). This pulse can also change the structure and dynamics of communities (Yang et al. 2010). This phenomenon is particularly present in boreal forest communities affected by spruce budworm outbreaks. This outbreak and the resulting pulse increase the relative abundance of mobile predators and parasitoids (Eveleigh et al. 2007). It is, however, important to note that spruce budworm outbreaks, such as the ones in the cited studies, last much longer than the FTC. Therefore, it is not surprising that the effects are larger. The decrease in ant diversity at our outbreak sites did correlate with an increase in other arthropod predators, suggesting that these predators may have been more effective than ants in responding to the prey pulse generated by the insect outbreak (Grevé et al. 2018). This trend may have emphasized an indirect effect of other predators on the ant population, but this was not directly studied. To do so, we would have to do studies with different sampling methods, focusing on ant nests and being able to characterize them in detail (how recent, size, substrate) as well as closeness to FTC colonies. We could then use those nests and perform exclusion experiments with the other predators to observe more direct links.

3.6 Conclusion

Changes in the ant community were only observed in the boreal forest sites. Indeed, less ecologically complex ecosystems are often less resilient to disturbances such as FTC defoliation (Grevé et al. 2018). In the boreal forest, the ant community composition did differ depending on the defoliation history, albeit with the opposite effect that we expected, with lower species richness and no clear association with increased sunlight or prey availability. The increase in other potential predators of the FTC suggested support for the resource pulse hypothesis since this functional group also increased with defoliation.

Further research exploring microclimatic changes and resources related to FTC outbreaks and ants is needed to decipher the mechanisms at play, especially ones where manipulation of the resources associated with FTC outbreaks (canopy openness, nutrient addition, …) could be controlled instead of the observations done in this context. Resource addition studies have been done frequently in regard to ant communities (such as Lessard et al. 2011)) and thus the methods and framework already exist. More natural history knowledge for specific ant species is also required to be able to elucidate these mechanisms. Additionally, as mentioned by Kristensen, Rousk, and Metcalfe (2020), distinguishing between low-intensity chronic herbivory and intense pulses such as those present during outbreaks would be beneficial in deciphering the underlying mechanisms structuring food webs.

3.7 Supplementary material

Table S.3.1 Species list and occurrence in traps of ants in the boreal forest sites along with functional traits and shade-tolerance. Functional traits were determined using several sources, from published descriptions, field guides and previous studies (Fairweather et al. 2020; Andersen 2019; Ellison 2012; Banschbach and Herbers 1999; Francoeur 1973, 1983; 1986; 1997; 2011). Using the same sources, shade tolerance was determined as either low (marked preference for open habitats), moderate (found in both open and closed habitats), high (marked preference for closed habitats), unknown (if the species was not studied enough to make a determination) and NA if it was a morphospecies.

Species	**Functional groups**	**Shade tolerance**
Camponotus herculeanus	Dominant, non agressive omnivore, cold tolerant	Moderate
Camponotus nearcticus	Subordinate, honeydew, extrafloral and gall nectar, sap fluxes, bird and reptile droppings, and occasional insect or spider prey	Moderate
Camponotus novaeboracensis	Subordinate, honeydew, extrafloral and gall nectar, sap fluxes, and occasional insect or spider prey	Moderate
Camponotus caryae	Unclear since rare	Unknown
Formica aserva	Facultative slavemaker, honeydew	Moderate
Formica glacialis	Cold-climate specialist, opportunists, honeydew	Unknown
Formica integra	Opportunist, Cold-climate specialist	High
Formica neogagates	Dominant, Cold-climate specialist	Moderate
Formica neorufibarbis	Dominant, opportunists, Cold-climate specialist	Moderate
Formica podzolica	Cold-climate specialist, Honeydew, opportunists	Moderate
Formica rubicunda	Cold-climate specialist, facultative slavemakers, honeydew	Moderate
Formica subaenescens	Cold-climate specialist, predators	Moderate
Formica lasioides	Tend to aphids, predators	High
Lasius americanus	Omnivorous, seeds, live insects and carcasses of dead ones and honeydew	Low
Leptothorax canadensis	Boreal forest specialist	Moderate
Leptothorax retractus	Cold-climate specialist, forested habitats	High
Myrmica alaskensis	Cold-climate specialist, dead wood, honeydew from aphids	Moderate
Myrmica detritinodis	Dominant, scavenger	High
Myrmica nearctica	Cold-climate specialist	High
Myrmica pinetorum	Opportunist	High
Tapinoma sessile	Opportunist	Moderate

Table S.3.2 Species list and occurrence in traps of ants in the temperate forest sites along with functional traits and shade-tolerance. Functional traits were determined using several sources, from published descriptions, field guides and previous studies (Fairweather et al. 2020; Andersen 2019; Ellison 2012; Banschbach and Herbers 1999; Francoeur 1973, 1983; 1986; 1997; 2011). Using the same sources, shade tolerance was determined as either low (marked preference for open habitats), moderate (found in both open and closed habitats), high (marked preference for closed habitats), unknown (if the species was not studied enough to make a determination) and NA if it was a morphospecies.

Species	**Functional groups**	**Shade tolerance**
Aphaenogaster picea	Opportunist, omnivorous scavenger and disperser of seeds of woodland herbs	Moderate
Camponotus pennsylvanicus	Honeydew, extrafloral nectaries, dead insects	High

Formica rubicunda	Cold-climate specialist, facultative slavemaker, honeydew	Moderate
Lasius americanus	Omnivorous species, seeds, live insects and carcasses of dead ones and honeydew	Low
Lasius aphidicola	Social parasite, honeydew	Moderate
Lasius neoniger	Opportunist, polyphagous, insects and nectar	Low
Lasius umbratus	Temporary social parasite, polyphagous, insect and nectar	Low
Leptothorax AF-can	Cryptic species	Unknown
Leptothorax AF-erg	Cryptic species	Unknown
Myrmica incompleta	Cold-climate specialist, honeydew	High
Myrmica punctiventris	Opportunist, generalist scavenger	High
Myrmica rubra	Opportunist, honeydew, extrafloral and gall nectar, sap and seeds.	Low
Stenamma diecki	Cryptic species, predates on collembolas	Moderate
Stenamma impar	Cryptic species	High
Temnothorax longispinosus	Cryptic species, honeydew, plant nectar, tiny insects.	High

Table S.3.3 Table of raw abundance of ant species in the boreal forest

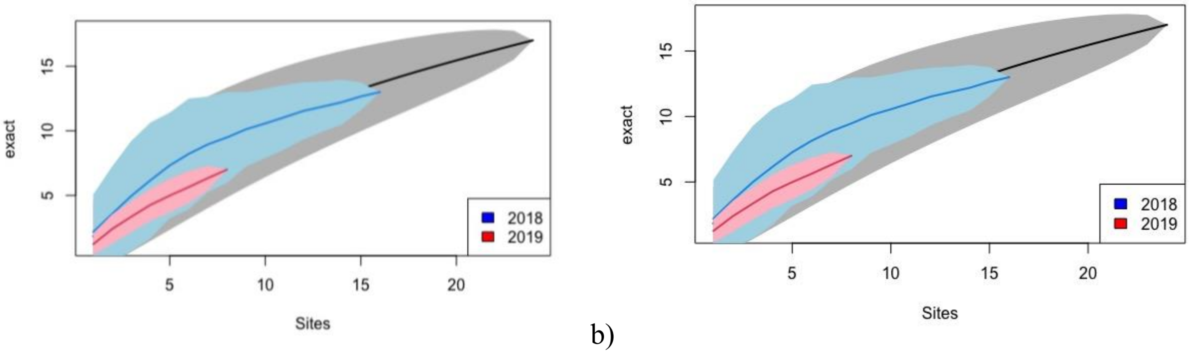
	2016		2017		2018		2019		
Species	control	outbreak	control	outbreak	control	outbreak	control	outbreak	Total
Camponotus herculeanus			57	8	15	2			82
Camponotus nearcticus			2						2
Camponotus novaeboracensis	56	107	172	136	38	25	20	2	556
Camponotus caryae					1				1
Formica aserva	42								42
Formica glacialis	121	3		2					126
Formica integra	1	1	41	29					72
Formica neorufibarbis	27	30	59	18	3	2			139
Formica neogagates	12	49	57	1	5	3			127
Formica podzolica	212	218	8	3	12	1			454
Formica subaenescens		5	193	55	44	28			325
Lasius americanus	5	2		11	10	14	2	2	46
Leptothorax canadensis	1			5					6
Leptothorax retractus	5	1	13	3					22
Myrmica alaskensis	44	19	72	137	38	28			338
Myrmica podzolica				1					1
Myrmica subaenescens				1					1
Myrmica pinetorum	3								3
Myrmica detritinodis		6	127		6	1			140
Myrmica nearctica		3							3
Tapinoma sessile	7	2		7					16
Total	536	446	801	417	172	104	22	4	2502

Table S.3.4 Table of raw abundance of ant species in the temperate forest

	2018		2019		
Species	control	outbreak	control	outbreak	Total
Aphaenogaster picea	51	13	1	1	66
Camponotus pennsylvanicus	5				5
Camponotus herculeanus	1				1
Formica rubicunda	2				2
Formica rubra			1		1
Lasius neoniger			1		1
Lasius umbratus	1				1
Lasius americanus	10		6		16
Lasius aphidicola			1		1
Leptothorax AF-can	1				1
Leptothorax AF-erg				1	1
Myrmica incompleta	1				1
Myrmica punctiventris	2				2
Stenamma diecki	3	3			6
Stenamma impar	3	1			4
Temnothorax longispinosus	4	1			5
Total	84	18	10	2	114

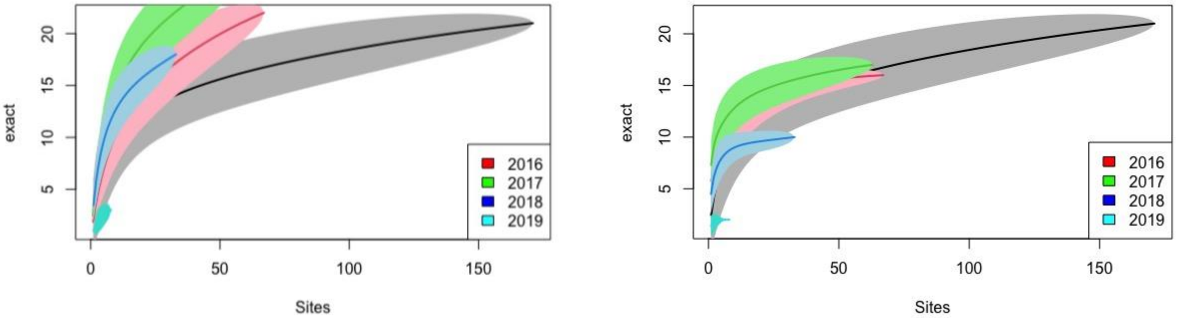
Table S.3.5 Abundance of arthropods that can be considered potential predator of FTC, collected from pitfall traps.

Forest	**Defoliation history**	**Spiders**	**Beetles**	**Flies**	**Wasps**	**True bugs**
Boreal	Control	194	168	327	102	23
	Outbreak	264	182	275	117	27
Temperate	Control	210	329	485	83	17
	Outbreak	195	312	414	90	24



a) b)

Figure S 4.1 Rarefaction curve for the temperate sites per year with a) species occurrence and b) species raw abundance. The y-axis represents the number of species and the x-axis the number of samples taken at each site combined.



a) b)

Figure S 5.2 Rarefaction curve for the boreal forest sites per year with a) species occurrence and b) species raw abundance. The y-axis represents the number of species and the x-axis the number of samples taken at each site combined.

Chapter 4 – Factors involved in overwintering mortality of forest tent caterpillar egg masses

4.1 Abstract

Global warming is expected to increase severity of insect outbreaks and that one of the key mechanisms in increased overwinter survival. With outbreaking herbivorous insects causing important damage in forest ecosystems through the defoliation of trees and their subsequent vulnerability to dieback, understanding the sources of mortality is essential. Overwintering insects such as the forest tent caterpillar can be especially subjected to temperature changes and increasingly extreme weather events that could impact their outbreaking dynamics. In this study, we evaluate the impact of climate factors (winter average daily temperature, winter average daily temperature variation, number of days below a cold threshold of -20°C, number of days above 0°C, the longest period below -20°C and -30°C as well as fall degree days) on larval emergence from forest tent caterpillars egg masses during and after an outbreak in the boreal and temperate forests. Egg mass size is also included as an index of maternal condition to evaluate potential changes in intrinsic factors during the outbreak crash. We found that emergence varied significantly between years and forest types. We also found that egg mass size is the main predictor of emergence in the boreal forest, suggesting a role for maternal sublethal infection status or nutrition as a determinant of egg overwinter survival. However, our research shows that there is both a stochastic extrinsic effect (cold) and a delayed-density dependent intrinsic effect (represented by egg mass size) that interact to determine overwintering mortality.

4.2 Introduction

Herbivorous insects are major disturbances that modify the structure and function of forest ecosystems (Lavoie et al. 2021; Aakala et al. 2023). For more than 20 years, scientists have been studying the impact of climate change on insects (Volney and Fleming 2000). It is expected that the frequency and severity of insect pest damage will increase under climate change, particularly in high-latitude boreal forests (Girona et al. 2023; Lehmann et al. 2020; Jactel, Koricheva, and Castagneyrol 2019). Weather is a major driver in the biological cycle and survival of pest species and can greatly impact the damage they cause (Subedi et al. 2023; Debaly, Marchand, and Girona 2022). For example, with the mountain pine beetle (*Dendroctonus ponderosae* Hopkins, 1902) (MPB), their range has been expanding due to lower winter mortality under climate warming (Carroll et al. 2003), resulting in unprecedented outbreaks in terms of density and severity (Taylor et al. 2006). This has led to increasing harm to trees and the release of immense amounts of carbon, leading to a regime shift in the ecology of the affected regions (Kurz et al. 2008).

The current climate disruptions affect the intensity and frequency of extreme climatic events such as cold spells (Cohen et al. 2012; Francis and Vavrus 2012; Overland and Wang 2015) and winter thaws (Williams, Henry, and Sinclair 2015). Both could seriously affect insect overwinter mortality, such as outbreaking lepidopterans in Canadian forests and have great implications for forest pest management. To withstand cold temperatures during the winter, insects use one of two strategies: freeze tolerance (surviving internal ice formation) or freeze avoidance (maintaining body fluids in a liquid, supercooled state at temperatures below their melting point). Both processes use hydrophilic cryoprotectants to protect macromolecules and act as anti-freeze to the water droplets (Lee 2010). Of those, glycoproteins are some of the most associated with cold tolerance and have been studied extensively in insects (Doucet, Walker, and Qin 2009; Duman 2015; Bar Dolev, Braslavsky, and Davies 2016).

One of the species using the mechanism of freeze-avoidance is the forest tent caterpillar (FTC) (*Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae)), an outbreaking pest insect in deciduous forests of North America, following a population cycle of around 10 years with peaks generally lasting 1-6 years (Cooke and Lorenzetti 2006). FTC egg masses are laid at the end of the summer around twigs and branches where they overwinter. They then emerge at budburst in the spring of the following year (Cooke and Lorenzetti 2006) (Figure 1.1).

Forest tent caterpillars enter diapause as pharate larvae within eggs and, during that state, lower their metabolic rate, stop most developmental processes, and lower energy consumption (Hahn and Denlinger 2007; 2011). Several protective mechanisms promote winter survival: a protective spumaline coating around the egg mass (Parry, Goyer, and Lenhard 2001) and glycerol content present in the eggs, which allows for their supercooling ability (Fitzgerald 1995). The supercooling point (SCP) is the temperature where freezing occurs, and eggs die, and it varies depending on species and populations (Knight 1986; Uelmen, Duman, et al. 2016). Glycerol content in the forest tent caterpillar is relatively low for most of the year but triples from December to February before decreasing again in March (Hanec 1966). The eggs can withstand temperatures between -20°C and -40°C depending on their geographical provenance (Uelmen, Duman, et al. 2016).

Repeated cold events, involving spells of a few days at cold temperatures (threshold depending on the population) with warmer days in between (Marshall and Sinclair 2015), can impact survival in FTC. Exposure to low temperatures can provoke what is referred to as chilling injuries, meaning that they are not directly related to freezing but to the duration and intensity of cold exposure (Nedvěd, Lavy, and Verhoef 1998; Chen and Walker 1994). Repeated chilling injuries overwintering insects can cause sublethal effects such as reduced reproductive output and growth rate (Bale, Worland, and Block 2001; Sinclair and Chown 2005; Marshall and Sinclair 2010). Winterkill can be influenced not only by the acute effect of low daily temperatures but also by the degree of physiological preconditioning before exposure to cold and by the length of exposure (Cooke and Roland 2003). Marshall and Sinclair (2012) have shown that repeated short cold exposures resulted in high survival in overwintering insects compared to prolonged cold exposure.

It has also been known for several decades that extremely cold temperatures close to the emergence of FTC larvae can cause mortality (Wetzel, Kulman, and Witter 1973) as glycerol content in eggs decreases as spring approaches. It is important to note that the glycerol content can also vary due to the temperature variability of the overwintering microhabitat due to phenotype variation in response to temperature fluctuations in the microhabitats (Sinclair 2015). Jensen's inequality (Denny 2017) shows that high-temperature variation in the fall and spring can lead to higher than normal lipid consumption (Williams et al. 2012) which could be lethal in the spring since the lipid reserve is likely depleted (Uelmen, Duman, et al. 2016).

Previous studies have explored the factors influencing overwintering mortality in FTC across the northern part of its distribution range, such as host species, forest heterogeneity and phenology. In Alberta, Cooke and Roland (2003) focused on the influence of forest heterogeneity on outbreak duration. They found it a relatively good predictor but noted other predictors, such as winter temperature, spring degree-day accumulation, and elevation, relatively weakly associated with outbreak duration. In Québec, Trudeau et al. (2010) looked at the impact of host species on FTC performance, comparing the trembling aspen and the sugar maple. FTC reared on aspens generally had shorter, higher pupal weights, fecundity, and larger and heavier eggs. However, glycerol content was lower in aspen-reared caterpillars. It is also important to note that investment in spumaline does not decrease with poor diets (Colasurdo, Gélinas, and Despland 2009). Susceptibility to cold can be linked to density-dependent factors related to fitness and thus might decrease with higher populations due to a lack of nutritional resources (Cooke and Roland 2003). This susceptibility could translate into delayed density-dependence with the fitness of the parents being seen in the following generation (Myers and Cory 2013).

In this study, we explored the effect of winter climate and delayed density dependence on overwinter mortality in two different FTC populations in Quebec: one on sugar maple in the temperate forest and one on trembling aspen in the boreal zone. We use egg mass size (number of eggs in a mass) as an index of maternal condition and predict that egg survival rate should increase with egg mass size (Myers and Cory 2013) and that egg mass size should decrease between years as the outbreak progresses. Survival is expected to decrease with colder temperatures and longer durations of cold spells. Winter thaws (periods of above 0°C temperatures) might lower survival. Finally, we hypothesize that higher fall degree-day accumulation will increase mortality. The relative roles of these different factors, density-dependent (intrinsic) and stochastic (extrinsic) processes, in determining overwintering survival are likely to differ between the colder boreal and the milder temperate sites.

4.3 Materials and Methods

4.3.1 Study sites

This study used egg masses collected in and around two forest areas affected by the most recent FTC outbreak (2015-2017) (Figure 4.1). In both regions, an FTC outbreak was detected in 2015 (MFFP 2016) and continued until 2017 (MFFP 2017), but no defoliation was observed in 2018 or 2019. In the boreal zone, eggs were collected in the Abitibi region from the Forêt d'enseignement et de recherche du Lac Duparquet (FERLD; N48.513, W79.369) and around the Rouyn-Noranda airport (N48.209312, W78.838757) from mature aspen (*Populus tremuloides* Michx, 1803) stands in the boreal mixed-wood forests of eastern Canada. Fire drives the disturbance regime, and large, even-age trembling aspen stands arise from post-fire regeneration (Bergeron 2000). The studied stands regenerated post-fire (1923) and are mostly made up of mature trees reaching 10–15 m. Due to the vertical structure of aspens (very few branches until the canopy), the trees are closer together and thus at a relatively high density. The climate is cold-temperate, with a (1961–1990) mean annual temperature of 0.9 °C and mean annual precipitation of 642 mm of rain and 215 mm of snow. The region was affected by an FTC outbreak for three years, starting in 2015 (MFFP 2015) and continuing in 2016 and 2017 (MFFP 2016; 2017). The temperate forest sites are in the Outaouais region, including and around The Kenauk Nature Reserve (N45.712, W74.887), in mature stands dominated by sugar maple (*Acer saccharum* Marsh, 1785) and American beech (*Fagus grandifolia* Ehrh, 1787). The climate in the area is cold-temperate, with a mean annual temperature of 5 °C, a mean annual rainfall of 807.4 mm and a total annual snowfall of 178.1 cm (Environment Canada 2017). The disturbance regime is driven by a mix of insect pests, mostly defoliators such as the forest tent caterpillar and, more recently, the spongy moth, and weather events.

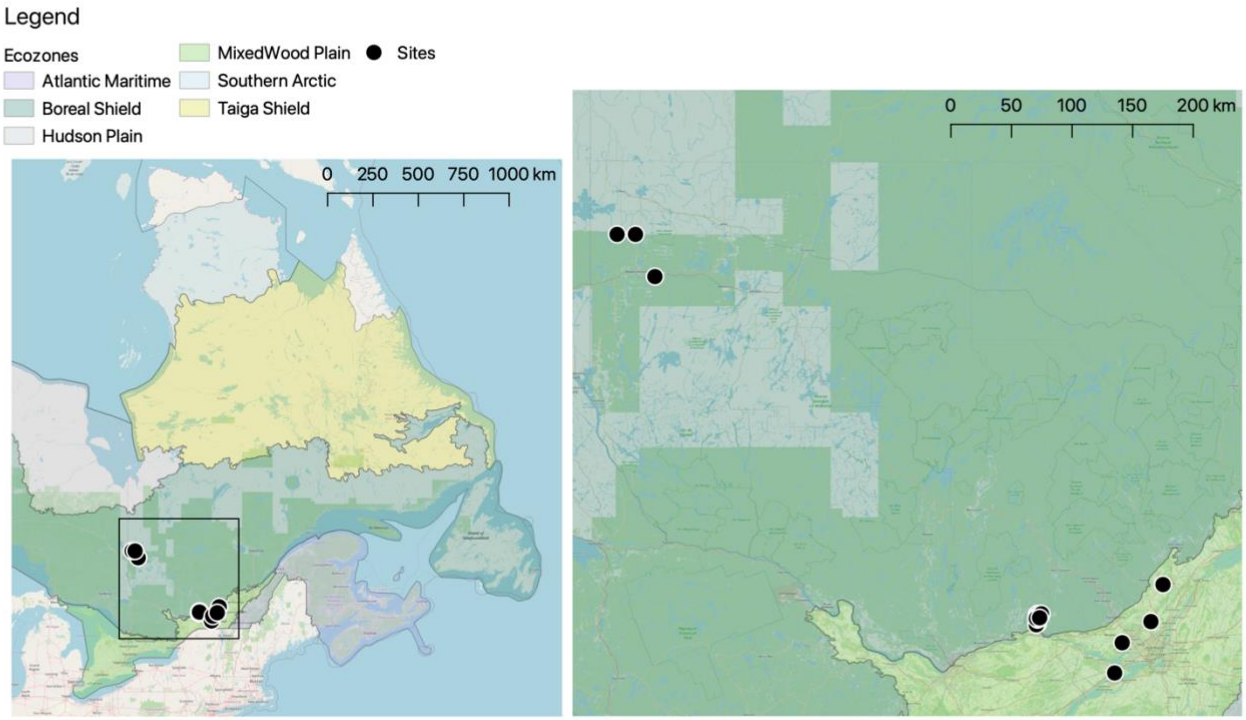


Figure 4.1 Map of collection sites in the boreal and temperate forests along with the ecozones in which they stand. Note that the temperate sites at the southeast border of the boreal shield are in the mixed wood plain ecozone and are populated by mostly deciduous trees.

4.3.2 *Experimental design and sampling*

To collect egg masses, we conducted surveys of the trees in March-April of 2016-2019, when the snow cover was still present. Egg masses were sorted according to weathering to distinguish between current-year eggs (spumaline intact) and previous-year eggs (spumaline damaged).

Egg masses collected in boreal forests were collected on trembling aspen seedlings and adult trees where we could reach the branches using a pruner that had a 3-meter reach. In contrast, those in the temperate forest were mostly collected on sugar maple using the same sampling method. However, it is important to note that, in the temperate forest, we encountered many more egg masses laid on various deciduous trees and shrubs (e.g. blueberry bush (*Vaccinium corymbosum* L.), American beech (*Fagus grandifolia* Ehrh.,)) than in the boreal forest, even if shrubs are quite widespread in boreal forests. Since females only lay one egg mass (Fitzgerald 1995), we consider all egg masses statistically independent. The host tree on which the egg mass was found was not considered since it does not necessarily reflect the tree on which larval development occurred.

4.3.3 Automation of egg mass counts

We developed an automated method to distinguish rapidly between unhatched and hatched eggs on the egg masses. We first cleaned the egg masses using Grisdale's (1985) protocol. Once they were clean, the egg masses were sectioned into 3 to 5 sections, depending on the diameter, allowing for a clear view and focus of the eggs to be photographed using the NIS-Elements Br 3.0 imaging software (Nikon, Tokyo, Japan) attached to a dissecting microscope. We then used Labelbox and Roboflow to develop a neural network (full details in Supplementary information; Figure S4.1). Using our automation method, we counted each egg mass and got precise valueof the hatching rate for each egg mass. Since counting individual egg mass is tedious and work intensive, few studies with this number of specimens and this level of precision have been done before. However, we could not account for parasitism since it is hard to visually diagnose, can be confused with weatehring and often requires dissection.

4.3.4 Climate data

Climate data was collected from the closest Environment Canada (Environment and Climate Change Canada 2023) weather station that offered daily temperature monitoring during the winters (from December to March inclusively): Notre-Dame-de-la-Paix (Climate ID 7035666) (2017-2018) in the temperate and Rouyn (Climate ID 7086716) (2015-2018) in the boreal zone. These were the closest to our sites, being in a 20km radius. Here, we define winter as the months from December to March, as they are the months with snow and freezing temperatures both in Abitibi and

Outaouais. We calculated the average of the daily winter temperature variation through the winter months (difference between daily maximum and daily minimum), the longest period of temperature under -20°C and -30°C, the number of winter days below a threshold temperature (-20°C), the number of winter days above 0°C as well as fall degree days. -20°C was chosen as a threshold, as is the temperature at which forest tent caterpillar egg morality started to be observed in the lab. At -30°C, the mortality reached significant levels (Uelmen, Duman, et al. 2016).

4.3.5 Statistical analysis

To answer our questions regarding the difference in overwintering mortality within and between the different regions, we used a beta regression using the betareg package (Cribari-Neto and Zeileis, 2010) to account for the sample size variation between the two regions after testing for assumptions. Those assumptions were being link appropriateness ("deviance residuals vs. indices of observation", at least for the logit link, homogenous residuals ("deviance residuals vs. linear predictor"), normality ("half-normal plot of deviance residuals") and no outliers ("Cook's distance to determine outliers"). Beta regression allows for differing sample size by using simulated data to reach a similar sample size to other samples in order to be able to compare them directly. Therefore, it was used to see if the two regions were statistically different from each other even with variying sample sizes. In this model, our dependent variable was the emergence rates of the egg masses, and we tested it against the independent variables of region and year (year being considered as a factor). Sites were also considered, but dropped since they were the more complex model was not as good a fit as the simplified model. In terms of the years sampled, due to the very low number of specimens for 2015, we omitted it from further analyses.

Next, we analysed emergence data for the two regions separately, using ANOVAs based on a log transformation of the emergence rates. We then performed Tukey post hoc tests to determine the difference in emergence between the years.

We then used a linear model with log-transformed data to test the relationship between emergence and egg mass size in each region. Finally, we used linear models with log-transformed data to test the relationship between emergence and the climate variables described earlier. All variables are considered as continuous. We tested all variables independently at first. We then combined a list of possible biologically comprehensive models and tested for the best-fit model using AICs. We computed the effect size using Partial Eta Squared for each best-fit model. All analyses were carried out using R version 4.2.0 (R Development Core 2017).

4.4 Results

4.4.1 Sampling effort

We collected and counted 609 egg masses, with 568 from the boreal forest (2015 = 16, 2016 = 94, 2017 = 256, 2018 = 202) and 69 from the temperate forest (2017 = 28, 2018 = 41). Since many of these egg masses were collected before this project started and were intended to be used in different studies, we do not have the same number of egg masses in the two regions. In addition, egg masses were harder to find in temperate forest sites, even with similar sampling efforts.

4.4.2 Difference in emergence between regions and years

The beta regression analyses showed significant effects of year (df =1, X^2=28.35 $p < 0.0001$) (Table 4.1) and region (df =1, X^2=32.50, $p = 1.19^{-8}$) (Table 4.2) on the proportion of eggs that survived overwinter and emerged successfully.

Survival was overall higher in the temperate forest (80.67% ±0.49 (weighted average)) than in the boreal. In the boreal forest, survival was at its lowest in the year before the outbreak, peaking in the first year of the outbreak and decreasing in subsequent years (Table 4.3).

Table 4.1 Beta Reg Analysis of Deviance Table (Type II tests) of percent emergence of the egg masses in the years (treated as covariates)

	Df	Chi Square	P value	Pseudo R-Squared
Year (as covariate)	1	28.35	**1.01^{-7}**	0.031

Table 4.2 Beta Reg Analysis of Deviance Table (Type II tests) of percent emergence of the egg masses in the different forests

	Df	Chi Square	P value	Pseudo R-Squared
Region	1	32.50	**1.19^{-8}**	0.079

Table 4.3 Mean percent emergence of the egg masses in the different forests and years. The years noted represent the year in which they were laid.

Region	**Year**	**Mean**	**SD**
Temperate	2017	0.81	0.16
	2018	0.93	0.086
Boreal	2016	0.85	0.11
	2017	0.84	0.15
	2018	0.75	0.15

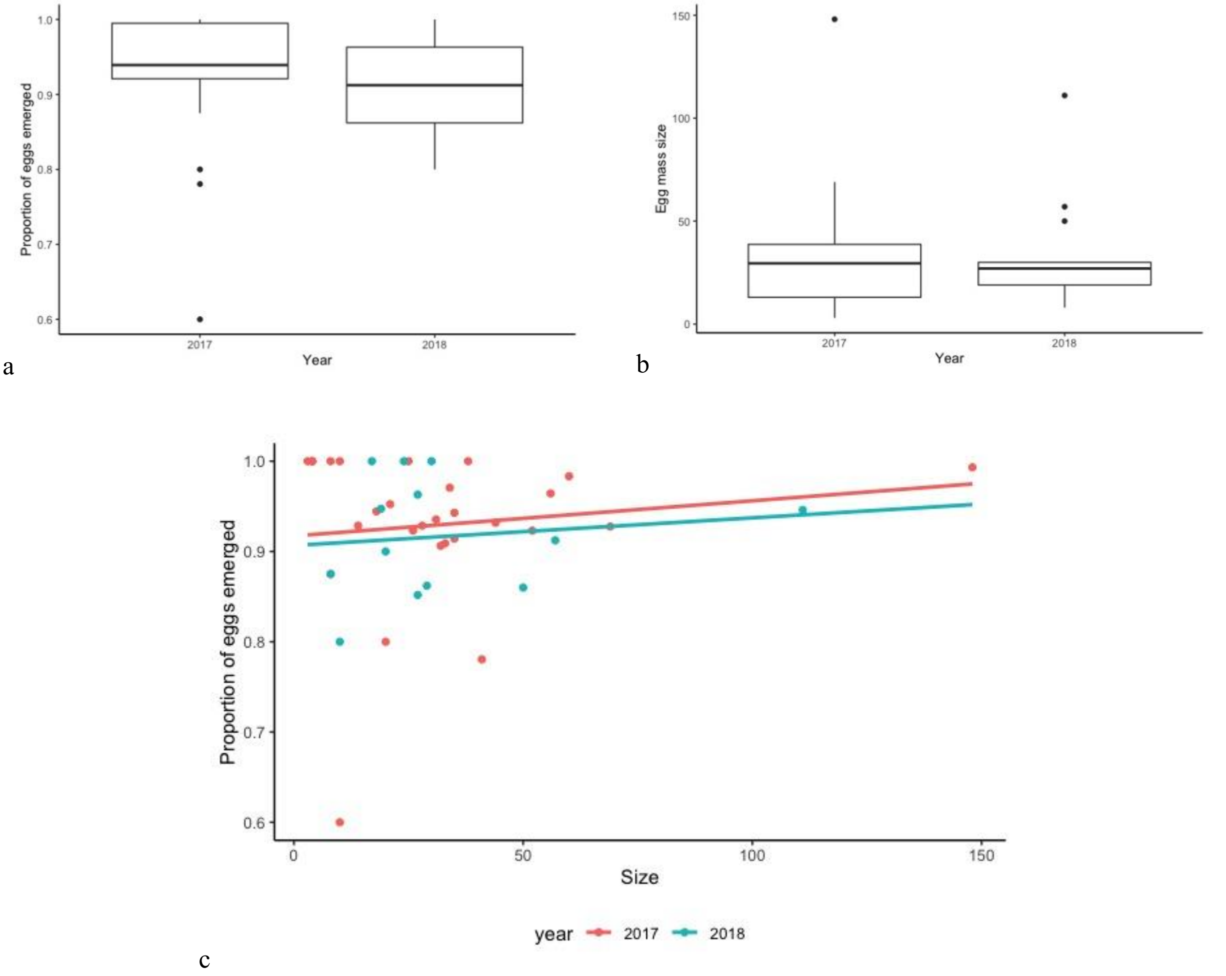
In the temperate forest, emergence rates testes using the beta regression did not differ between 2017 and 2018 (p=0.7199142). In the boreal forest, 2016, 2017 and 2018 were all significantly different from one another according to the Tukey test (2016-2017: p=0.008, 2017-2018: p<0.001, 2016-2018: p<0.001).

4.4.3 Egg mass size

In the temperate forest, egg mass size did not vary significantly between years, nor was it related to percent emergence (Figure 4.2C, Table 4.4). We, however, observed that many of the observed trends between the two years were what was hypothesized (Table 4.5).

Table 4.4 Replicated regression testing differences in egg mass size between years (treated as covariates)

		Df	Sum Square	Mean Sq	F value	P value
Temperate forest	Year	1	3	3.3	0.004	0.95
	Residuals	39	31	799.6		
Boreal forest	Year	1	17926	17926	4.97	**0.026**
	Residuals	566	2040034	3604		



a

b

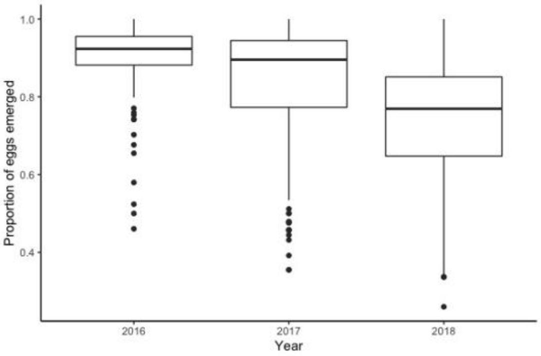
c

Figure 4.2 Summary plots of the temperate forest dataset. A) proportion of eggs that emerged per egg mass according to year, B) Number of eggs per egg mass for each year of the study, C) Proportion of eggs that emerged per egg mass according to egg mass size, Pink represents the 2017 data and blue the 2018 data. nkpi In the box plots, the lower boundary of the box indicates the 25th percentile, the bold line within the box marks the median, and the upper boundary of the box indicates the 75th percentile. The whiskers indicate the 10th and 90th percentiles. Dots are outliers (>Q3 + 1.5 × interquartile range)

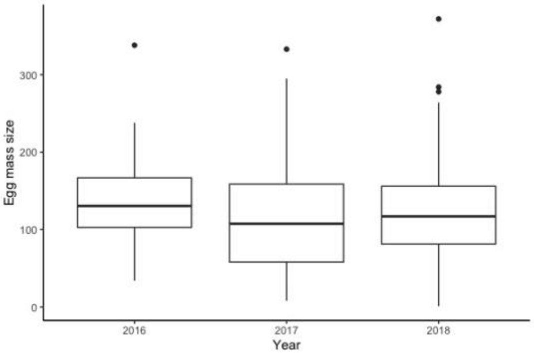
Table 4.5 Summary of the direction of the trends observed for the temperate forest data. None of the relationships were significant when tested using ANOVAs. The bolded signs represent the expected relationship.

		Direction of relationship (from 2017 to 2018)
Emergence ~	Average temperature	**+**
Emergence ~	Average temperature variation	**-**
Emergence ~	Longest period below -20C	**-**
Emergence ~	Longest period below -30C	**-**
Emergence ~	Total days below -20C	**-**
Emergence ~	Total number of days above 0C	+

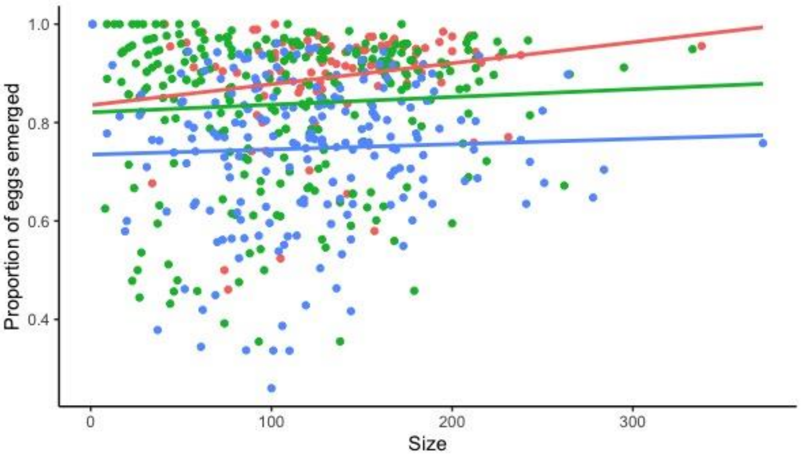
In the boreal forest, egg mass size significantly decreased as the years progressed (df=1, $F_{1,566}$=4.974, p=0.0261), and size of the egg mass was a good predictor of emergence rate (Table 4.6, Figure 4.3C).


Proportion of eggs emerged
1.0
0.8
0.6
0.4
2016
2017
2018
Year

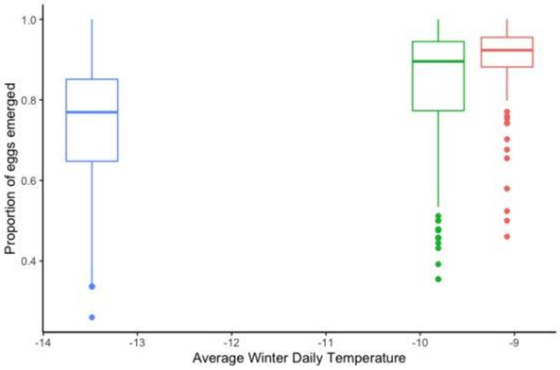
a


Egg mass size
300
200
100
0
2016
2017
2018
Year

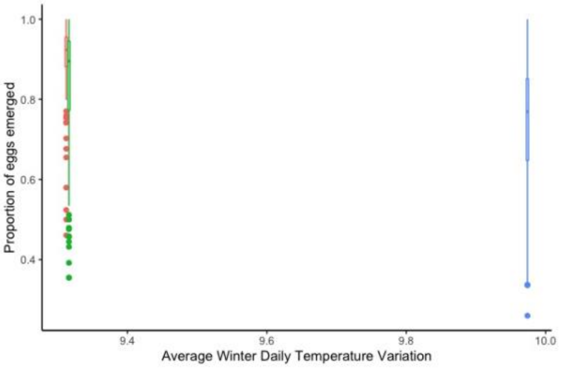
b


Proportion of eggs emerged
1.0
0.8
0.6
0.4
0
100
200
300
Size

c


Proportion of eggs emerged
1.0
0.8
0.6
0.4
-14
-13
-12
-11
-10
-9
Average Winter Daily Temperature

d


Proportion of eggs emerged
1.0
0.8
0.6
0.4
9.4
9.6
9.8
10.0
Average Winter Daily Temperature Variation

e

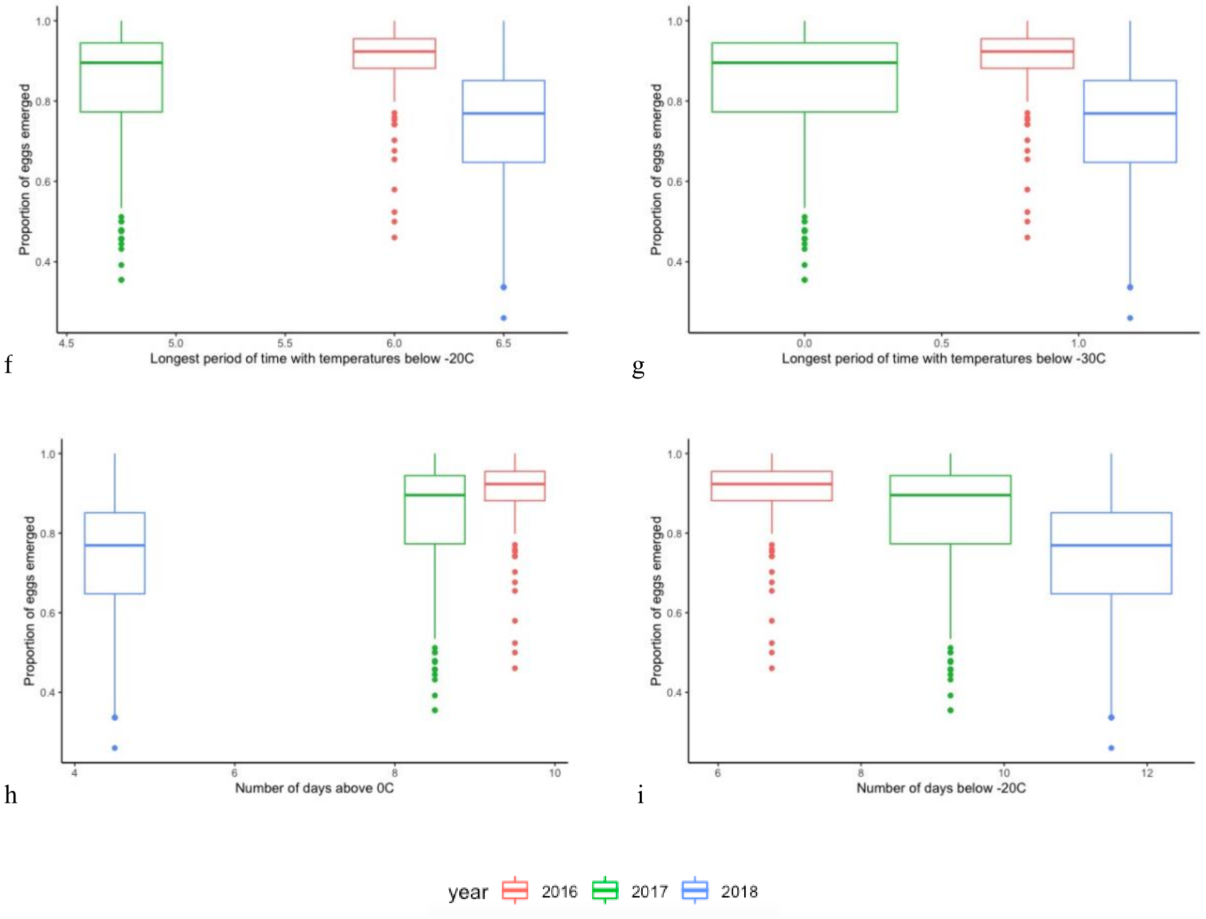


Figure 4.3 Summary plots of the boreal forest dataset. A) proportion emergence per year, B) egg mass size per year, C) scatterplot of emergence rate by egg mass size (lines represent best fit linear regressions for each year), D-I: boxplots showing proportion of larval emergence against different predictor variables D) by average winter daily temperature, E) by average winter daily temperature variation, F) by longest period of days below -20℃, G) by longest period of days below -30℃, H) by longest period of days above 0℃ and I) by number of days below -20℃. In plots C-I, pink refers to 2016, green to 2017 and blue to 2017. In the box plots, the lower boundary of the box indicates the 25th percentile, the bold line within the box marks the median, and the upper boundary of the box indicates the 75th percentile. The whiskers indicate the 10th and 90th percentiles. Dots are outliers (>Q3 + 1.5 × interquartile range)

Table 4.6 For boreal forest data, summary statistics for replicated regression of egg emergence rate against egg mass size and individual linear models for egg emergence rate vs environmental predictors. The best-fit linear model combining several *predictors is also shown; the associated effect size is 0.1802 (Wherry).*

Models						
		Df	**Sum Square**	**Mean Sq**	**F value**	**P value**
Emergence ~	Intercept	1	0.22	0.22	3.97	0.047 *
	Total egg mass size	566	30.84	0.05		
			Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
Emergence ~	Intercept		4.88	0.05	98.27	<2e-16 ***
	Average temperature		0.046	0.0044	10.35	<2e-16 ***
Emergence ~	Intercept		6.22	0.20	31.67	<2e-16 ***
	Average temperature variation		-0.19	0.020	-9.43	<2e-16 ***
Emergence ~	Intercept		4.78	0.050	95.64	< 2e-16 ***
	Longest period below -20C		-0.072	0.0086	-8.39	3.95e-16 ***
Emergence ~	Intercept		4.41	0.014	314.36	< 2e-16 ***
	Longest period below -30C		-0.069	0.018	-3.93	9.39e-05 ***
Emergence ~	Intercept		4.85	0.042	114.75	<2e-16 ***
	Total days below -20C		-0.049	0.0042	-11.51	<2e-16 ***
Emergence ~	Intercept		4.08	0.031	130.51	<2e-16 ***
	Total number of days above 0C		0.039	0.0041	9.59	<2e-16 ***
Emergence ~	Intercept		4.39	0.015	297.19	<2e-16 ***
	Fall degree days		-0.10	0.070	-1.44	0.15

Emergence ~	Random effects	**Variance**	**Std. Dev.**		
	Year	0.0073	0.085		
	Residuals	0.043	0.21		
	Fixed	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
	Intercept	5.31	0.52	10.14	0.00065 *
	Total egg mass size	0.00034	0.00015	2.22	0.027 *
	Average winter temperature variation	-0.050	0.053	-0.95	0.38
	Longest period below -20C	0.083	0.015	-5.69	4.98^{-7} ***

4.4.4 *Climate variables*

Since the previous beta regression showed a significant difference between the temperate and boreal region (Table 4.2), we tested the two regions separately.

None of the predictor variables had significant effects in the temperate forest, individually or in a combined model (Figure 4.2), but we did observe the trends (Figure 4.3). The effect size of the only variable in the best-fit model (total egg mass size) was of 0.02 (95% CI [0.025, 0.975]).

In the boreal forest, all the climatic variables significantly affected the emergence rate when tested individually (Table 4.6 and Figure 4.3). We see a positive relationship between emergence and higher average temperatures. We see a negative significant relationship with emergence in terms of the average winter temperature variation; average temperature variation increased, and emergence decreased. We see a significant negative relationship when looking at the longest consecutive number of days below the -20°C and -30°C threshold. In terms of total number of days below -20°C during the winter, we see a pattern of lower emergence along with the number of days below the threshold. Finally, we see a significant relationship between the number of days above 0°C and higher survival.

The best-fit model in the boreal showed that total egg mass size and the longest period below -20°C significantly affected the emergence rate (Table 4.6). The effect size for the independent variables in the best-fit models are stated in Table 4.7.

Table 4.7 Effect size of the best-fit model in the boreal forest using Partial Eta Squared

Parameter	**Eta^2 (partial)**	**95% CI**
Total egg mass size	0.87	[0.00, 1.00]
Average winter temperature variation	0.13	[0.00, 1.00]
Longest period below -20C	0.37	[0.21, 1.00]

4.5 Discussion

Our results show that, in the boreal forest, egg survival increased with egg mass size; winter weather, especially duration of periods below -20°C, also decreased overwinter survival. No significant differences in emergence rate were detected in the temperate forest. It is important to note that the temperate zone sample size was much lower and that the effect size provides evidence that variation is in part related to variables we have not sampled in this study. These could include more precise temperature data from the sites where the egg masses were collected, snow cover, position of the egg on the tree, wind speed, as well as the precise laying period of the different egg masses.

The results from the boreal forest imply both delayed density-dependent variation in egg survival, which would tend to amplify outbreak dynamics, and a density-independent influence of winter weather, which introduces a stochastic element to population dynamics. The interaction of these factors can lead to complex dynamics.

4.5.1 Maternal effects

The total egg mass size had a weak positive relationship with the emergence rate. When taken chronologically (excluding 2015), the egg mass size did show a decreasing trend with years, in accordance with what Wellington et al. (1975) predicted with the western tent caterpillar.

This decrease in fecundity (egg mass size) is not the only manifestation of decreased individual condition with outbreak progression. Ginzburg and Taneyhill (1994) showed that, in forest Lepidoptera (*Choristoneura fumiferana*, *Hyphantria cunea*, *Lymantria dispar*, *Epirrita autumnata*, *Bupalus piniaria* and *Acleris variana*), delayed density dependence was in part caused by the transmission of quality through generations via maternal effects, directly relating the average quality of individuals to population abundance. The role of individual condition and its impact on the subsequent generation through maternal effects was first proposed in the western tent caterpillar (WTC) (*Malacosoma pluviale)*. In work done by Wellington (1957; 1960; Wellington et al. 1975), egg overwinter survival was directly linked to the amount of yolk provided by the laying female.

This represents environmentally-based maternal effects where the condition of the mother can significantly influence offspring dispersal potential, growth rate, or fecundity, which can be sen through offspring numbers, through the quantity or quality of egg provisions (Rossiter 1991). The impact on offspring fecundity can have repercussions for several years, leading to delayed density dependence effects. Several studies (Cooke and Roland 2003; Prentice 1954; Gautreau 1964; J. Witter, Mattson, and Kulman 1975) have observed that egg mortality was high only after populations had reached epidemic levels, suggesting a link between overwintering mortality and population density (Wellington 1957; 1960). While the previous references are for the Western Tent Caterpillar, the similarities between the population cycles and physiology of the two species have been established (Lait and Hebert 2018; Ginzburg and Taneyhill 1994). Therefore, there is good evidence that maternal effect could play a role in the results we observed.

4.5.2 Overwinter survival and outbreak dynamics

It is also proposed that cold-weather anomalies might select the most cold-adapted individuals. Thus, the surviving population may better survive the winter, leading to nonstationary dynamic effects (Royama and Royama 1992). The effects on cold hardiness could then contribute to the observed density dependence effect associated with the cycling dynamic of the FTC. We did not see evidence for increased cold hardiness through the different years from 2016 to 2019, contrary to what Cooke and Roland (2003) observed in their study. While they observed higher survival as the years went on, we saw a slight decrease in survival from 2016-2019. This supports the hypothesis of lower maternal fitness related to density dependence effects instead of natural selection of cold-hardier eggs. With denser populations, nutrition becomes less adequate, rendering caterpillars more vulnerable, lowering maternal fitness and thus laying smaller egg masses and lower emergence rates during the following year (Ginzburg and Taneyhill 1994). Such a mechanism could lead to important nonstationary dynamic effects (Royama and Royama 1992) and thus contribute to the observed cyclical outbreak in FTC. These effects are in relation to stochastic weather events that can precipitate the crash of an outbreak Cooke and Roland (2003).

4.5.3 Climate variables and phenology

According to our best-fit model, total egg mass size was not the only predictor of emergence, showing the impact of temperature-related factors on the survival of FTC eggs. Changes in winter climate variability are challenging to predict, even when considering the likelihood of extreme events (Easterling et al. 2000). Organisms have experienced recurring cold spells similar to, or more severe than, those in the past, despite an overall trend of winter warming (Gloning, Estrella, and Menzel 2013).

An increase in variation of temperatures can disrupt the predictability of winter events and thus affect evolved cold-tolerance physiological mechanisms (Bale and Hayward 2010). Especially in species such as the FTC that have seasonally programmed responses where a certain warm temperature threshold being surpassed for a certain number of days kickstarts physiological processes to initiate emergence (Fitzgerald 1995), an increase in temperature could cause sub-lethal impacts (e.g. Marshall and Sinclair 2010), lower survival (e.g. (Régnière and Bentz 2007) and overwinter energetics (e.g. (Williams, Henry, and Sinclair 2015; Bale and Hayward 2010; Sinclair et al. 2013). Increasing mean winter temperatures could trap the insect in a freeze-thaw cycle where they would have to transition at the threshold much more often than previously, experiencing cold injuries and increased energy expenditure (Marshall and Sinclair 2012). This is likely cumulative in most overwintering insects (Williams, Henry, and Sinclair 2015). While average daily temperature variation, in the best-fit model, did not significantly impact emergence, we believe it is still an important factor to consider. More fine-scale data on temperature variation throughout the egg part of the FTC life cycle could illuminate more impacts of temperature variation seen in other related species as well as other variables such as variation in daily minimum and maximum temperatures. Because metabolic rate is generally slowed down during most of the colder parts of the winter, most of the lipid consumption seems to happen during periods of relatively warm conditions and early spring and late autumn when insects are not feeding but are subject to elevated metabolic rates during warm spells (Sinclair and Marshall 2018). Metabolites analysis by Trudeau et al. (2010) showed a U-shaped trend for glucose and glycogen throughout the winter and an inverse trend for glycerol. While we know that this pattern is consistent, between-year comparison through differing warming or temperature variation regime could help us better understand the lipid consumption and metabolic habits of forest tent caterpillars, especially in the face of a warming climate.

Another aspect to consider is the timing of diapause related to the climate. Since we did not follow the egg masses through the whole process, it is hard to determine when the eggs were laid and, thus, when diapause started. Imagos are generally seen in July in the boreal forest (personal communications and iNaturalist 2023) and live from 5-10 days. We can therefore assume the eggs are being laid around mid to late July. In spruce budworms, it has been shown that delaying diapause initiation by a few weeks relative to the usual timing resulted in higher overwintering mortality and the inability to accumulate enough glycerol to be able to survive lethal temperatures (Han and Bauce 1995). Additionally, Delisle, Bernier-Cardou, and Labrecque (2022) showed that early winter frosts could present similar challenges. Since it is likely that, under future climate change scenarios, the occurrence and severity of early winter frost or very later summer will increase (Gloning, Estrella, and Menzel 2013), this aspect needs to be considered when looking at the overwintering mortality of pest insects.

4.5.4 Forest types

Trembling aspen (*Populus tremuloides* Michx.) is the FTC's preferred host in the boreal zone, but sugar maple (*Acer saccharum* Marsh.) is the most commonly used host in the temperate area of our study (Witter 1979; Grisdale 1985; Martineau 1985). Sugar maple is known to be a less suitable host for FTC (Fortin and Mauffette 2002; Colasurdo, Dussutour, and Despland 2007), raising the possibility that differences in host plant quality could affect our findings. In a previous study (Trudeau et al. 2010), eggs laid by moths that fed on aspen had higher pupal weight and produced more eggs. Still, those who fed on maple had higher glycerol and glycogen levels and thus a lower supercooling point (Trudeau et al. 2010), which implies higher overwinter survival. The higher winter survival we observed in the temperate zone could thus be linked to host plants and milder winters. Genomic studies show small genetic differences between boreal FTC populations in aspen forests and temperate FTC populations in maple stands (MacDonald et al. 2023). They could further be investigated in terms of cold hardiness.

4.6 Conclusion

In this study, we demonstrate that emergence differed significantly between the two foci of the FTC outbreak ranging from 2015-2019 and that emergence followed a slight pattern of density dependence using emergence rates of the egg masses. Additionally, we showed that total egg mass size was important in predicting emergence, especially in the boreal region, but climate variables also played a significant role. These results align with Cooke and Roland (2003), who suggested that weather variables correlated with mortality are density-independent, but the factors mediating their impact, such as maternal condition, are density dependent. This important relationship between stochastic and density-dependent factors is crucial to predicting the future of FTC outbreaks.

Our results also suggest that the observed increase in the average temperature throughout the years related to the lower survival of FTC eggs. While 2-3 years is quite short to say the average temperature is increasing, we know from climate change projections that temperature is projected to increase in the next decades (Gloning, Estrella, and Menzel 2013). With this coinciding with an increase of days below the -20°C threshold, we expect that especially in the northern range of the FTC, with a likely increase of extreme winter events through global warming (Gloning, Estrella, and Menzel 2013), we will also see an increase in mortality of the FTC. Climate changes will likely cause an increase in average temperatures in the temperate forest, which could cause the dispersal of the local population towards the north of their distribution (Uelmen, Duman, et al. 2016). Climate change will likely facilitate the northward expansion of other insect species in north temperate zones. Therefore, the inclusion of maternal effects as well as climate is necessary to better predict the future of FTC outbreaks and their impact on the ecosystem.

4.7 Supplementary information

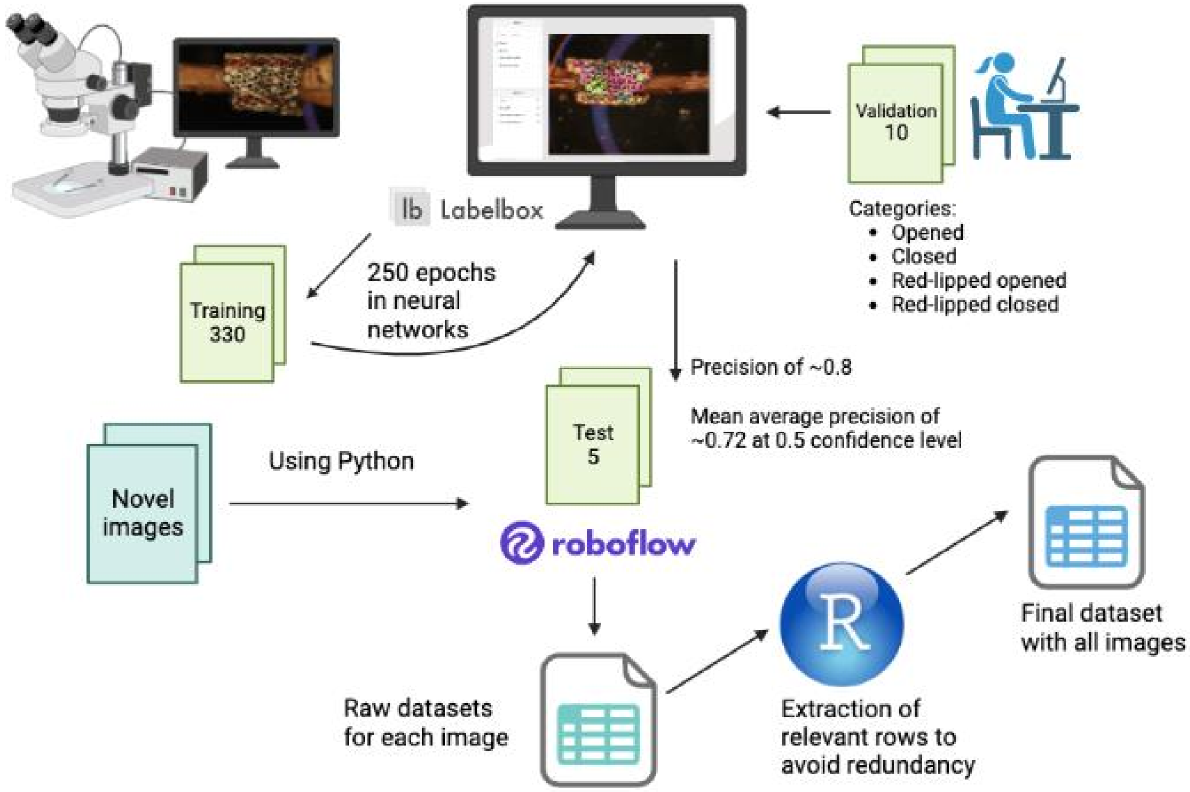


Figure S4.1 Diagram of automation process. Created with BioRender.com

We used a subset of 345 images of egg masses to train the model using the Labelbox web GUI (April 2020). This subset was split into training (330 images, some of which were transformed versions of existing images to increase the diversity of the input data), validation (10 images) which a trained observer manually counted to identify the different types of egg masses present and test (5 images) datasets. These images were presented to the Roboflow Object Detection trainer web GUI, which is a "you-only-look-once" (YOLO) network (Redmon et al. 2016) (roboflow.com, 2021/07/03). Egg casings were classified as open, closed, red-lipped open and red-lipped closed, and the YOLO network is trained to identify each of these object types with a certain degree of confidence. We were training the network with labelled images as training data teaches it to identify differences between the different classes, refined by a validation step that checks if the labels predicted by the current iteration of the network match the labels on the validation dataset. The training/validation cycle ran through 250 epochs, reaching a precision of ~0.8 and a mean average precision of ~0.72 at a 0.5 confidence level. Predictions on novel data were obtained using a Python script which uploaded the image to the Roboflow servers to be labelled by the model and then returned predictions in CSV files for each image. Data was then extracted using R. We used a loop to go through each file, grouping subsequent clusters of the four categories (opened, red-lipped opened, closed, red-lipped closed). When a set of non-red-lipped categories bigger than the red-lipped categories was detected, we used the last row of the red-lipped cluster as a cutoff for the new subset. Then, the remaining rows were added to a new CSV file, identifying the line with the name of the image. We ended up with a CSV with all the data associated with the images, which was then cleaned for analysis.

Chapter 5 - General Discussion

5.1 Thesis objectives and results

This thesis explored the top-down and bottom-up trophic interactions related to FTC outbreaks in Quebec in two populations across its range in eastern Canada. Throughout our different studies, we found that FTC had the potential to influence its environment through major defoliation events but also responded in a density-dependent way throughout its cycle, especially during the low-density endemic period between outbreaks.

In Chapter 2, we detected a pattern of density dependence following an outbreak related to two specific sources of mortality: intrinsic and from flighted natural enemies at an early instar. Predation and parasitism against FTC are usually studied at later instars. According to our study, predation did not make up for most of the mortality at the first instar. Our findings suggest that mortality from flighted enemies and intrinsic sources do not contribute to the crash of the outbreak but maintain these populations at low endemic levels between outbreaks.

In Chapter 3, we found that that defoliation history had an impact on ant species diversity with richness decreasing and ant evenness increasing with the presence of defoliation compared to non-defoliated sites. There was no significant difference in beta diversity between outbreak and control sites in the boreal forest, but there was a decrease of beta diversity in defoliated sites in the temperate forest. Additionally, species composition varied significantly between the control and outbreak sites. One of the major results from this chapter is that boreal ants tend to be more indicative of either control or outbreak sites than ants in temperate forests. We also provide the most up-to-date ant species list of the Forêt d'enseignement et de recherche du lac Duparquet (FERLD) and the

Abitibi region. Boreal ants remain a poorly studied fauna even though efforts have been made in recent years to catch up and provide an updated species list of the area, often providing new distribution records (Glasier et al. 2019; Ibarra-Isassi, Handa, and Lessard 2023 as well as work by André Francoeur, Jürgen Heinze and Jean-Philippe Lessard).

In Chapter 4, we were able to detect the influence of climate on the mortality occurring in egg masses during the overwintering period of the FTC life cycle. In this case, the low winter temperatures and temperature variation correlate with lower survival. Egg mass size correlated significantly with survival in our study. We observed an effect of the year, which, along with previous research, suggests a maternal effect by lowering the egg mass quality and, thus, increasing mortality due to winter conditions. These results are significant considering the likelihood of more erratic temperature variation and intense cold spells in boreal regions, even with rising global temperatures due to climate change (Cohen et al. 2012; Francis and Vavrus 2012; Overland and Wang 2015; Williams, Henry, and Sinclair 2015).

5.2 Future publications

During my thesis, especially for Chapter 4, I developed an automation tool with Dr. Chris Law from the Centre for Microscopy and Cell Imaging at Concordia University to help characterize forest tent caterpillar egg masses using a machine learning tool. While it has been described in the methods of Chapter 4 to present the resulting dataset, we will likely be writing a technical paper along with the code to share the tool more widely. Through the study of forest insect pests, we often encounter an immense amount of data which is time intensive to sort through. Having a better tool, at least for forest tent caterpillars and other species with similar egg masses such as the eastern and western tent caterpillars and potentially stink bugs such as the brown marmorated stink bugs, to help provide datasets of emergence will help with asking more precise questions on the matter without sacrificing the quality of the data to the time necessary for it. Additionally, because the model is trained on specific datasets, this tool could be adapted for other caterpillars and insects that share similarly arranged egg masses, such as stinkbugs.

5.3 Implication for sylvicultural practices related to pest insects

This thesis shows the importance of different sources of mortality and their link to the FTC outbreak cycle. It highlights the need to consider the whole ecosystem while aiming for sylvicultural practices to reduce or even contain the ecological and economic impacts of the outbreaks.

There are multiple reasons to manage pests within a forest ecosystem, whether for economic reasons, such as sustainable timber yields or environmental ones, such as emulating natural disturbance ecology. In both cases, having a clear long-term picture of insect disturbances is crucial (Cooke and Lorenzetti 2006). Pest impact assessments are regularly used to assess a pest's ecological and economic impact. However, these impacts are often hard to disentangle from ecosystem processes or the effect of other pest species (Swank et al. 1981; Reynolds, Hunter, and Crossley Jr 2000; Lovett et al. 2002; Lewis and Likens 2007). To do so, cumulative impact needs to be considered in terms of its effects on individuals (e.g. reproductive success, growth), populations (e.g. genetics, population dynamics), communities (e.g. species diversity, species composition), ecosystems (e.g. nutrient cycling), and regions (Parker et al. 1999; Ricciardi et al. 2013). Forests are also great reservoirs of biodiversity and provide multiple ecosystem services (Brockerhoff et al. 2017). Therefore, in recent years, the use of insecticides and pesticides has been diminished (Schowalter 2017), and management practices are shifting to a more integrated framework.

Since the forest tent caterpillars are native to the ecosystems, the goal is not necessarily eradicating them. As mentioned previously (Chapter 1), herbivory does not have strictly detrimental effects on forest ecosystems. Indeed, it can provide an input of nutrients to the soil and the plants and microorganisms living in it (Metcalfe et al. 2014). Additionally, the damage caused to trees is often non-lethal, even if it can accentuate the vulnerability of trees to other pathogens and disturbances (Fitzgerald 1995). Using an integrated pest management (IPM) approach is especially important in the case of the forest tent caterpillar. IPM is "an ecosystem-based strategy that focuses on long-term prevention of pests or their damage through biological control, habitat manipulation, modification of cultural practices, and use of resistant varieties. Pesticides are used only after monitoring indicates they are needed according to established guidelines, and treatments are made to remove only the target organism. Pest control materials are selected and applied to minimize risks to human health, beneficial and non-target organisms, and the environment" (University of California Davis 2015). The two basic strategies to reduce the negative impacts of pest insects are prevention (reduce probability and severity of future infestations by manipulating the stand, forest or landscape) and suppression (reduce current infestations by manipulating the pest population using remedial tactics) (Sweeney et al. 2023). Regarding cost-benefit analysis, prevention can be much less costly than suppression of an outbreak, such as with the spongy moth in North America (Tobin 2008).

Traditional biological control usually aims for the establishment and longtime pest management of a certain species. On the other hand, conservation biological control is the "modification of the environment or existing practices to protect and enhance specific natural enemies or other organisms to reduce the effect of pests" (Eilenberg, Hajek, and Lomer 2001). This framework is especially interesting in the case of the FTC, as we know that mortality agents are already present in the ecosystem. This can be done in multiple ways, such as protecting or increasing the populations of biological control agents, in our case parasitoid wasps and flies, ants and other predatory insects, by reducing or targeting the use of pesticides (Cadogan, Nealis, and Van Frankenhuyzen 1995) or providing alternate hosts for these natural enemies during endemic stages of the population cycle (Sweeney et al. 2023) as well as decreasing fragmentation (Roland 1993). While my research did not show direct predation by ants on FTC, Despland and Lessard (2022) did in the same system. Therefore, sylvicultural practices promoting the habitat of, especially, predatory or generalist ants would provide further means of "biological control" for FTC outbreaks to stay within bounds that the ecosystem can sustain. FTC often falls below the pest threshold justifying treatments and thus does not necessarily meet the requirements for outright pest management such as the use of Btk or bringing in pest control agents. Therefore, managing the ecosystem in a way that generally promotes biodiversity both at the tree and insect level would be beneficial in controlling FTC populations and those of other insect pests. These practices are also in line with current sylvicultural practices.

Sylviculture refers to the "theory and practice of controlling the establishment and growth of trees to satisfy specific objectives of landowners with forest stands serving as the main unit of intervention" (Achim et al. 2022). By planting a wider variety of trees and supporting the understory ecosystems, these practices can help prevent intense outbreaks and assure the resilience of the forest stands to future outbreaks such as predicted ones for the FTC. Increasing tree species and diversity lowers insect herbivory (Jactel and Brockerhoff 2007). Other maintenance silvicultural strategies can also help maintain stand structure and species composition. While usual silvicultural practices such as thinning do not reduce herbivory from forest defoliators (Muzika and Liebhold 2000), other practices such as reducing the abundance of host species as saplings can be helpful to limit their spread (Vannatta, Hauer, and Schuettpelz 2012).

The importance of NPV in the mortality of FTC, especially at early-instars as found in Chapter 2, is an interesting avenue for sylvicultural practices in the forest. Borrowing from the biocontrol domain, the vulnerability of FTC to this pathogen could keep endemic populations at even lower levels or cap the peak of FTC density during outbreaks by manipulating the spread of NPV. Since it is a virus relatively specific to lepidopterans and with specificity for different species (Rohrmann 1986), it would not negatively impact the rest of the forest ecosystems. NPV, and other baculoviruses, also have the particularity of surviving outside of a host for extended periods (Volkman and Keddie 1990). They can also be cultivated in the lab (Slavicek, Podgwaite, and Lanner-Herrera 1992), which could lead to use as a biocontrol agent.

Additionally, invasive species such as the spongy moth (*Lymantria dispar*) have also been seen to be vulnerable to the pathogen (Woods and Elkinton 1987; Stiles et al. 1983). Spongy moth and FTC share multiple responses to pathogens, including the NPV and bacterium B.t. (*Bacillus thuringiensis*) (Kleiner et al. 1995).

Another factor to consider when managing forests susceptible to FTC outbreaks is the emergence rates. Because of the overwintering nature of the FTC life cycle (Chapter 4), monitoring the hatch rate of forest tent caterpillars throughout its distribution could help predict the course of the coming outbreak. Since temperature can affect overwintering survival rates, development, dispersal, reproduction, and phenology (Hansen and Bentz 2003), models predicting pest impact benefit from adding temperatures throughout the life cycle (Bentz and Powell 2014) and can inform management actions. Emergence rate and a cursory look at some egg masses can help determine the level of mortality and chilling injuries. Since those often correlate to poor maternal health, we could make predictions for the coming season. A phenological mismatch could promote very high morality of early-instar larvae with little to no damage to the trees. However, this prediction relies heavily upon what is observed at the present moment and, as with anything related to climate change, is likely temporary and subject to change in the coming years.

5.4 Future research

One of the limitations of Chapter 2 is the lack of results related to the vertical stratification of FTC survival, especially in maple forests. While not for lack of trying, data was tough to obtain. This was especially since we had to transplant egg masses up to the canopy, an arduous process in which we were limited in the equipment we could bring and the degree of maneuverability. Therefore, some egg masses may have been damaged in the transport. Due to starting the experiments a year after the outbreak, we could only find a few wild FTC colonies in maple forests that were completely unhatched. With another outbreak coming up shortly according to past models of population cycles as well as observations through community science initiative such as iNaturalist, collecting enough egg masses early in the season and putting them up before budburst would allow us to answer questions that we have not been able to answer here. As shown in Fortin and Mauffette (2002), vertical stratification impacts foliage quality, which can affect FTC survival greatly (Lorenzetti, Mauffette, and Bauce 1999). Therefore, having the opportunity to know observed survival in the canopy and quantify the survival of canopy vs understory colonies through their entire life cycle would give us many more answers about the mechanisms of survival of the FTC during and after an outbreak.

Since canopy and habitat openness has been shown to have a large impact on the variation of ant communities (Campbell and Crist 2017; Dalle Laste, Durigan, and Andersen 2019; Solar et al. 2016; Underwood and Fisher 2006; Yusah et al. 2018), future research could use more fine-scale methods of characterizing habitat openness and structure to gain a better understanding of which functional traits of ants are selected for in this case. Such methods could include using Landsat Imagery to describe the habitat more thoroughly (openness, moisture, productivity, phenology) (Oeser et al. 2020), quantifying habitable microclimates in the environment (Seibold et al. 2016) and vegetation surveys. Future research comparing control with managed and disturbed unmanaged sites would allow us to test the difference between natural and artificial disturbance to forest ecosystems.

MacDonald et al. (2022) highlight in their study that multiple mechanisms that are present and structure intraspecific genetic variation. The more populations were geographically separated, the higher the genomic differentiation was. Differences in summer temperatures and length of growing season are also correlated with genetic distance among individuals. Larval growth and survival have been linked many times to spring temperatures (Levesque, Fortin, and Mauffette 2002; Wetzel, Kulman, and Witter 1973; A. C. Hodson 1941; Raske 1975), and these temperature-associated traits can be linked to larval emergence, cold tolerance, female resource allocation, and phenological synchrony (Parry, Goyer, and Lenhard 2001; Uelmen, Lindroth, et al. 2016; Uelmen, Duman, et al. 2016; Lorimer 1979; Mattson Jr and Erickson 1978). Therefore, in future studies, monitoring specific egg masses deposited in the wild could help us gather more data linked to emergence. We also concluded that different populations could have been selected for certain traits that increase their survival in their habitats. However, this has yet to be measured directly. With additional data on phenological synchrony, analysis of the glycerol content and measures of female fitness before and after egg-laying would allow us to decipher the mechanisms better.

Additionally, genomic data could help understand the resilience of different populations to winter temperature variations and potentially test for heredity of cold tolerance between the years. Finally, since genomic differentiation is related to host association, this furthers the hypothesis of the regional adaptation of these populations. Being able to get finer scale genomic data of the populations present within each region (temperate and boreal forest) would allow us to 1) get more evidence on the grouping of each region as a population (which we assumed due to results from Cooke and Lorenzetti (2006) and 2) quantify intra population genetic variation.

5.5 Limitations

The reality of studying cycling populations is that you must catch them at the right time. While I, unfortunately, started the first year after the outbreak, our options were limited, and much of the data collected in the first summer could not be used. Because it is hard to predict exactly when the outbreak will occur, I had to figure out other research questions that I expected at the start of my program.

In Chapter 2, we initially aimed to study parasitism rates as well as the other groups we investigated. However, due to high mortality rates overall, it was difficult to investigate parasitism since caterpillars often died from other causes first. Additionally, unlike species like the spruce budworm, it is near impossible to rear FTC in the lab and thus ensure that there are 1) no contaminants (even with disinfection protocols) and 2) eggs from the egg masses are not already parasitized. We have to source the egg masses from the wild. Synchronizing the hatching period and keeping egg masses from hatching during transport is incredibly tricky.

In Chapter 3, we illuminated some community-level patterns in ants emerging from forest tent caterpillar outbreaks furthering research related to disturbances as drivers of changes in ant communities. However, the mechanisms behind those remains uncertain. Manipulation experiments using resource additions such as the ones used by Lessard et al. (2011) would greatly help figure them out.

The method of automation developed for this project (Chapter 4) gave us more precision in estimating overwintering mortality, bringing us one step closer to understanding the mechanisms behind FTC population dynamics. There are, however, still some flaws to this method. It is hard to identify the timing of mortality events since we only gather egg masses after winter. The environment can weather egg masses or pharate larvae chewing them but subsequently dying before completely emerging.

5.6 Conclusion

With forested ecosystems under mounting pressure, it is more important than ever to understand the pest population dynamics that can further cause deleterious effects on these already endangered ecosystems. Insect disturbances are ecologically important and can tell us a lot about how the ecosystem is structured and how resilient it is.

However, predicting the future scenarios of insect pest disturbances is a herculean task. The use of modelling tools has shown benefits in terms of the efficiency of sampling and control methods in the past (Tobin et al. 2004) and has helped with predicting the distribution of these pests under different climate change scenarios (Carroll et al. 2003; Régnière, Nealis, and Porter 2009). We must know how populations fluctuate to properly manage and mitigate the damage they cause (Cooke and Lorenzetti 2006). Decision-making incorporating the stand and forest-level dynamics and their impacts can help prioritize management areas (Sweeney et al. 2023). With different foci of FTC outbreaks with differing host plants, the forest and stand-level dynamics are fundamental, as a general management approach cannot account for the differing ecosystem dynamics.

The work presented in this thesis provides evidence of trophic interactions impacting the survival of FTC colonies both during and after an outbreak. It contributes evidence related to FTC outbreaks that can be used in these predictive models to manage the forests through a sustainable approach.

References

Aakala, Tuomas, Cécile C. Remy, Dominique Arseneault, Hubert Morin, Martin P. Girardin, Fabio Gennaretti, Lionel Navarro, et al. 2023. "Millennial-Scale Disturbance History of the Boreal Zone." In *Boreal Forests in the Face of Climate Change: Sustainable Management*, edited by Miguel Montoro Girona, Hubert Morin, Sylvie Gauthier, and Yves Bergeron, 53–87. Advances in Global Change Research. Cham: Springer International Publishing. https://doi.org/10.1007/978-3-031-15988-6_2.

Achim, Alexis, Guillaume Moreau, Nicholas C Coops, Jodi N Axelson, Julie Barrette, Steve Bédard, Kenneth E Byrne, et al. 2022. "The Changing Culture of Silviculture." *Forestry: An International Journal of Forest Research* 95 (2): 143–52. https://doi.org/10.1093/forestry/cpab047.

Andersen, Alan N. 2019. "Responses of Ant Communities to Disturbance: Five Principles for Understanding the Disturbance Dynamics of a Globally Dominant Faunal Group." Edited by Mariano Rodriguez-Cabal. *Journal of Animal Ecology* 88 (3): 350–62. https://doi.org/10.1111/1365-2656.12907.

Andersen, Alan N., Penman, Debas, and Houadria. 2009. "Ant Community Responses to Experimental Fire and Logging in a Eucalypt Forest of South-Eastern Australia." *Forest Ecology and Management* 258 (2): 188–97.

Anderson, Kirk E., Jacob A. Russell, Corrie S. Moreau, Stefanie Kautz, Karen E. Sullam, Y. I. Hu, Ursula Basinger, Brendon M. Mott, Norman Buck, and Diana E. Wheeler. 2012. "Highly Similar Microbial Communities Are Shared among Related and Trophically Similar Ant Species." *Molecular Ecology* 21 (9): 2282–96.

Andow, David A. 1991. "Vegetational Diversity and Arthropod Population Response." *Annual Review of Entomology* 36 (1): 561–86.

Arnan, Xavier, Anselm Rodrigo, and Javier Retana. 2007. "Uncoupling the Effects of Shade and Food Resources of Vegetation on Mediterranean Ants: An Experimental Approach at the Community Level." *Ecography* 30 (2): 161–72. https://doi.org/10.1111/j.0906-7590.2007.04796.x.

Asch, Margriet van, and Marcel E. Visser. 2007. "Phenology of Forest Caterpillars and Their Host Trees: The Importance of Synchrony." *Annual Review of Entomology* 52 (1): 37–55. https://doi.org/10.1146/annurev.ento.52.110405.091418.

Bale, J. S., and S. A. L. Hayward. 2010. "Insect Overwintering in a Changing Climate." *Journal of Experimental Biology* 213 (6): 980–94.

Bale, J. S., M. R. Worland, and W. Block. 2001. "Effects of Summer Frost Exposures on the Cold Tolerance Strategy of a Sub-Antarctic Beetle." *Journal of Insect Physiology* 47 (10): 1161–67.

Banschbach, Valerie S., and Joan M. Herbers. 1999. "Nest Movements and Population Spatial Structure of the Forest Ant Myrmica Punctiventris (Hymenoptera: Formicidae)." *Annals of the Entomological Society of America* 92 (3): 414–23. https://doi.org/10.1093/aesa/92.3.414.

Bar Dolev, Maya, Ido Braslavsky, and Peter L. Davies. 2016. "Ice-Binding Proteins and Their Function." *Annual Review of Biochemistry* 85: 515–42.

Bardgett, Richard D., William D. Bowman, Ruediger Kaufmann, and Steve K. Schmidt. 2005. "A Temporal Approach to Linking Aboveground and Belowground Ecology." *Trends in Ecology & Evolution* 20 (11): 634–41.

Bardgett, Richard D., and Tancredi Caruso. 2020. "Soil Microbial Community Responses to Climate Extremes: Resistance, Resilience and Transitions to Alternative States." *Philosophical Transactions of the Royal Society B* 375 (1794): 20190112.

Bardgett, Richard D., and Wim H. Van Der Putten. 2014. "Belowground Biodiversity and Ecosystem Functioning." *Nature* 515 (7528): 505–11.

Barnes, Andrew D., Malte Jochum, Jonathan S. Lefcheck, Nico Eisenhauer, Christoph Scherber, Mary I. O'Connor, Peter de Ruiter, and Ulrich Brose. 2018. "Energy Flux: The Link between Multitrophic Biodiversity and Ecosystem Functioning." *Trends in Ecology & Evolution* 33 (3): 186–97.

Bellone, Davide, Christer Björkman, and Maartje J. Klapwijk. 2019. "Top-down Pressure by Generalist and Specialist Natural Enemies in Relation to Habitat Heterogeneity and Resource Availability." *Basic and Applied Ecology*, November, S1439179119302907. https://doi.org/10.1016/j.baae.2019.10.005.

Bentz, Barbara J., and James A. Powell. 2014. “Mountain Pine Beetle Seasonal Timing and Constraints to Bivoltinism: (A Comment on Mitton and Ferrenberg,‘Mountain Pine Beetle Develops an Unprecedented Summer Generation in Response to Climate Warming’).” *The American Naturalist* 184 (6): 787–96.

Bergeron, Yves. 2000. “Species and Stand Dynamics in the Mixed Woods of Quebec’s Southern Boreal Forest.” *Ecology* 81 (6): 1500–1516.

Berryman, Alan A. 1996. “What Causes Population Cycles of Forest Lepidoptera?” *Trends in Ecology & Evolution* 11 (1): 28–32. https://doi.org/10.1016/0169-5347(96)81066-4.

Bestelmeyer, Brandon T., Donat Agosti, Leeanne E. Alonso, C. R. F. Brandão, W. L. Brown, Jaques HC Delabie, and Rogerio Silvestre. 2000. “Field Techniques for the Study of Ground-Dwelling Ant: An Overview, Description, and Evaluation.” In *Ants: Standard Methods for Measuring and Monitoring Biodiversity*.

Birch, Joseph D., James A. Lutz, Suzanne W. Simard, Rick Pelletier, George H. LaRoi, and Justine Karst. 2019. “Density-Dependent Processes Fluctuate over 50 Years in an Ecotone Forest.” *Oecologia* 191 (4): 909–18.

Bird, F. T. 1969. “Infection and Mortality of Spruce Budworm, Choristoneura Fumiferana, and Forest Tent Caterpillar, Malacosoma Disstria, Caused by Nuclear and Cytoplasmic Polyhedrosis Viruses.” *The Canadian Entomologist* 101 (12): 1269–85. https://doi.org/10.4039/Ent1011269-12.

Boggs, Carol L. 2016. “The Fingerprints of Global Climate Change on Insect Populations.” *Current Opinion in Insect Science* 17: 69–73. https://doi.org/10.1016/j.cois.2016.07.004.

Bouchard, Mathieu, Véronique Martel, Jacques Régnière, Pierre Therrien, and David Laginha Pinto Correia. 2018. “Do Natural Enemies Explain Fluctuations in Low-Density Spruce Budworm Populations?” *Ecology* 99 (9): 2047–57. https://doi.org/10.1002/ecy.2417.

Brais, Suzanne, Brian D. Harvey, Yves Bergeron, Christian Messier, David Greene, Annie Belleau, and David Paré. 2004. “Testing Forest Ecosystem Management in Boreal Mixedwoods of Northwestern Quebec: Initial Response of Aspen Stands to Different Levels of Harvesting.” *Canadian Journal of Forest Research* 34 (2): 431–46.

Brockerhoff, Eckehard G., Luc Barbaro, Bastien Castagneyrol, David I. Forrester, Barry Gardiner, José Ramón González-Olabarria, Phil O’B Lyver, Nicolas Meurisse, Anne Oxbrough, and Hisatomo Taki. 2017. “Forest Biodiversity, Ecosystem Functioning and the Provision of Ecosystem Services.” *Biodiversity and Conservation*. Springer.

Broza, Meir, and Ido Izhaki. 1997. “Post-Fire Arthropod Assemblages in Mediterranean Forest Soils in Israel.” *International Journal of Wildland Fire* 7 (4): 317–25.

Cadogan, Beresford L., Vincent G. Nealis, and Kees Van Frankenhuyzen. 1995. “Control of Spruce Budworm (Lepidoptera: Tortricidae) with Bacillus Thuringiensis Applications Timed to Conserve a Larval Parasitoid.” *Crop Protection* 14 (1): 31–36.

Çakır, Meriç. 2019. “The Negative Effect of Wood Ants (Formica Rufa) on Microarthropod Density and Soil Biological Quality in a Semi-Arid Pine Forest.” *Pedobiologia* 77: 150593.

Calderón-Sanou, Irene, Tamara Münkemüller, Lucie Zinger, Heidy Schimann, Nigel Gilles Yoccoz, Ludovic Gielly, Arnaud Foulquier, et al. 2021. “Cascading Effects of Moth Outbreaks on Subarctic Soil Food Webs.” *Scientific Reports* 11 (1): 15054. https://doi.org/10.1038/s41598-021-94227-z.

Calizza, Edoardo, Loreto Rossi, Giulio Careddu, Simona Sporta Caputi, and Maria Letizia Costantini. 2019. “Species Richness and Vulnerability to Disturbance Propagation in Real Food Webs.” *Scientific Reports* 9 (1): 19331. https://doi.org/10.1038/s41598-019-55960-8.

Campbell, Kaitlin U., and Thomas O. Crist. 2017. “Ant Species Assembly in Constructed Grasslands Is Structured at Patch and Landscape Levels.” *Insect Conservation and Diversity* 10 (2): 180–91.

Canada, Agriculture and Agri-Food. 2013. “The Canadian System of Soil Classification (Second Edition).” December 13, 2013. https://sis.agr.gc.ca/cansis/publications/manuals/1987-cssc-ed2/index.html.

Caron, Anne-Sophie, Joshua Joseph Jarry, and Emma Despland. 2022. “Early Instar Mortality of a Forest Pest Caterpillar: Which Mortality Sources Increase during an Outbreak Crash?” *Entomologia Experimentalis et Applicata* 170 (3): 268–76. https://doi.org/10.1111/eea.13131.

Carroll, Allan L, Steve W Taylor, Jacques Regniere, and Les Safranyik. 2003. “Effect of Climate Change on Range Expansion by the Mountain Pine Beetle in British Columbia.” In .

Carvalho, Karine S., and Heraldo L. Vasconcelos. 1999. “Forest Fragmentation in Central Amazonia and Its Effects on Litter-Dwelling Ants.” *Biological Conservation* 91 (2–3): 151–57.

Cerdá, Xim, and Alain Dejean. 2011. “3. Predation by Ants on Arthropods and Other Animals.” In *Predation in the Hymenoptera: An Evolutionary Perspective.* Transworld Research Network. USA: National Academy of Sciences.

Chapman, Samantha K., Stephen C. Hart, Neil S. Cobb, Thomas G. Whitham, and George W. Koch. 2003. “Insect Herbivory Increases Litter Quality and Decomposition: An Extension of the Acceleration Hypothesis.” *Ecology* 84 (11): 2867–76.

Chen, Benrong, and David H. Wise. 1999. “BOTTOM-UP LIMITATION OF PREDACEOUS ARTHROPODS IN A DETRITUS-BASED TERRESTRIAL FOOD WEB.” *Ecology* 80 (3): 761–72. https://doi.org/10.1890/0012-9658(1999)080[0761:BULOPA]2.0.CO;2.

Chen, Cheng-Ping, and Virginia K. Walker. 1994. “Cold-Shock and Chilling Tolerance in Drosophila.” *Journal of Insect Physiology* 40 (8): 661–69.

Chen, Han YH, and Roman V. Popadiouk. 2002. “Dynamics of North American Boreal Mixedwoods.” *Environmental Reviews* 10 (3): 137–66.

Christiansen, Ken, and Peter F Bellinger. 1980. “The Collembola of North America North of the Rio Grande. A Taxonomic Analysis. Part 1. Introduction. General. Families Poduridae and Hypogastruridae. Part 2. Families Onychiuridae and Isotomidae. Part 3. Family Entomobrydae. Part 4. Families Neelidae and Sminthuridae. Glossary. Bibliography. Index.” *The Collembola of North America North of the Rio Grande. A Taxonomic Analysis. Part 1. Introduction. General. Families Poduridae and Hypogastruridae. Part 2. Families Onychiuridae and Isotomidae. Part 3. Family Entomobrydae. Part 4. Families Neelidae and Sminthuridae. Glossary. Bibliography. Index.* https://www.cabdirect.org/cabdirect/abstract/19821972759.

Clark, Robert E., Timothy E. Farkas, Isaac Lichter-Marck, Emily R. Johnson, and Michael S. Singer. 2016. “Multiple Interaction Types Determine the Impact of Ant Predation of Caterpillars in a Forest Community.” *Ecology* 97 (12): 3379–88. https://doi.org/10.1002/ecy.1571.

Cobbold, Christina A., Mark A Lewis, Frithjof Lutscher, and Jens Roland. 2005. “How Parasitism Affects Critical Patch-Size in a Host–Parasitoid Model: Application to the Forest Tent Caterpillar.” *Theoretical Population Biology* 67 (2): 109–25. https://doi.org/10.1016/j.tpb.2004.09.004.

Cohen, Judah L., Jason C. Furtado, Mathew A. Barlow, Vladimir A. Alexeev, and Jessica E. Cherry. 2012. “Arctic Warming, Increasing Snow Cover and Widespread Boreal Winter Cooling.” *Environmental Research Letters* 7 (1): 014007.

Colasurdo, Nadia, Audrey Dussutour, and Emma Despland. 2007. “Do Food Protein and Carbohydrate Content Influence the Pattern of Feeding and the Tendency to Explore of Forest Tent Caterpillars?” *Journal of Insect Physiology* 53 (11): 1160–68. https://doi.org/10.1016/j.jinsphys.2007.06.004.

Colasurdo, Nadia, Yves Gélinas, and Emma Despland. 2009. “Larval Nutrition Affects Life History Traits in a Capital Breeding Moth.” *Journal of Experimental Biology* 212 (12): 1794–1800.

Cooke, Barry J., and François Lorenzetti. 2006. “The Dynamics of Forest Tent Caterpillar Outbreaks across East-Central Canada.” *Forest Ecology and Management* 226: 110–21. https://doi.org/10.1111/j.1600-0587.2011.07083.x.

Cooke, Barry J., and Jens Roland. 2003. “The Effect of Winter Temperature on Forest Tent Caterpillar (Lepidoptera: Lasiocampidae) Egg Survival and Population Dynamics in Northern Climates.” *Environmental Entomology* 32 (2): 299–311.

Cooke, Barry J., Brian R. Sturtevant, and Louis-Etienne Robert. 2022. “The Forest Tent Caterpillar in Minnesota: Detectability, Impact, and Cycling Dynamics.” *Forests* 13 (4): 601. https://doi.org/10.3390/f13040601.

Correa, Michele M., Paulo SD Silva, Rainer Wirth, Marcelo Tabarelli, and Inara R. Leal. 2016. “Foraging Activity of Leaf-Cutting Ants Changes Light Availability and Plant Assemblage in A Tlantic Forest.” *Ecological Entomology* 41 (4): 442–50.

Dalle Laste, Keila Caroline, Giselda Durigan, and Alan N. Andersen. 2019. “Biodiversity Responses to Land-Use and Restoration in a Global Biodiversity Hotspot: Ant Communities in Brazilian Cerrado.” *Austral Ecology* 44 (2): 313–26.

Dansereau-Macias, Éléonore, Emma Despland, and Ira Tanya Handa. 2023. “Decreased Soil Microbial Biomass and Changed Microbial Community Composition Following a Defoliation Event by the Forest Tent Caterpillar.” *Forests* 14 (4): 792. https://doi.org/10.3390/f14040792.

De Caceres, Miquel, and Florian Jansen. 2016. “Package ‘Indicspecies.’” *Indicators* 8 (1).

De Grandpré, Louis, Maryse Marchand, Daniel D. Kneeshaw, David Paré, Dominique Boucher, Stéphane Bourassa, David Gervais, Martin Simard, Jacob M. Griffin, and Deepa S. Pureswaran. 2022. “Defoliation-Induced Changes in Foliage Quality May Trigger Broad-Scale Insect Outbreaks.” *Communications Biology* 5 (1): 463. https://doi.org/10.1038/s42003-022-03407-8.

De Ruiter, Peter C., Anje-Margriet Neutel, and John C. Moore. 1995. “Energetics, Patterns of Interaction Strengths, and Stability in Real Ecosystems.” *Science* 269 (5228): 1257–60.

Debaly, Zinsou Max, Philippe Marchand, and Miguel Montoro Girona. 2022. “Autoregressive Models for Time Series of Random Sums of Positive Variables: Application to Tree Growth as a Function of Climate and Insect Outbreak.” *Ecological Modelling* 471: 110053.

Del Toro, Israel, Relena R. Ribbons, and Shannon L. Pelini. 2012. “The Little Things That Run the World Revisited: A Review of Ant-Mediated Ecosystem Services and Disservices (Hymenoptera: Formicidae).” *Myrmecological News* 17 (0): 133–46.

Delisle, Johanne, Michèle Bernier-Cardou, and Alain Labrecque. 2022. “Cold Tolerance and Winter Survival of Seasonally-Acclimatised Second-Instar Larvae of the Spruce Budworm, Choristoneura Fumiferana.” *Ecological Entomology* 47 (4): 553–65. https://doi.org/10.1111/een.13140.

Denny, Mark. 2017. “The Fallacy of the Average: On the Ubiquity, Utility and Continuing Novelty of Jensen’s Inequality.” *Journal of Experimental Biology* 220 (2): 139–46.

Despland, Emma. 2013. “Plasticity of Collective Behavior in a Nomadic Early Spring Folivore.” *Frontiers in Physiology* 4. https://doi.org/10.3389/fphys.2013.00054.

———. 2017. “Effects of Phenological Synchronization on Caterpillar Early-Instar Survival under a Changing Climate.” *Canadian Journal of Forest Research* 07 (July 2016): 1–8. https://doi.org/10.1139/cjfr-2016-0537.

Despland, Emma, and Jean-Philippe Lessard. 2022. “Social Predation by Ants as a Mortality Source for an Arboreal Gregarious Forest Pest.” *Basic and Applied Ecology*.

Domisch, Timo, Leena Finér, Seppo Neuvonen, Pekka NiemelÄ, Anita C. Risch, Jouni Kilpeläinen, Mizue Ohashi, and Martin F. Jurgensen. 2009. “Foraging Activity and Dietary Spectrum of Wood Ants (Formica Rufa Group) and Their Role in Nutrient Fluxes in Boreal Forests.” *Ecological Entomology* 34 (3): 369–77. https://doi.org/10.1111/j.1365-2311.2009.01086.x.

Domisch, Timo, Leena Finér, Seppo Neuvonen, Pekka Niemelä, Anita C. Risch, Jouni Kilpeläinen, Mizue Ohashi, and Martin F. Jurgensen. 2009. “Foraging Activity and Dietary Spectrum of Wood Ants (*Formica Rufa* Group) and Their Role in Nutrient Fluxes in Boreal Forests.” *Ecological Entomology* 34 (3): 369–77. https://doi.org/10.1111/j.1365-2311.2009.01086.x.

Doucet, D., V. K. Walker, and W. Qin. 2009. “The Bugs That Came in from the Cold: Molecular Adaptations to Low Temperatures in Insects.” *Cellular and Molecular Life Sciences* 66: 1404–18.

Dubuc, Jean-François. 1996. “La performance biologique et le comportement alimentaire de trois espèces de lépidoptères après défoliation du bouleau blanc (betula papyrifera marsh.).” Université du Québec à Montréal.

Dufrêne, Marc, and Pierre Legendre. 1997. “Species Assemblages and Indicator Species: The Need for a Flexible Asymmetrical Approach.” *Ecological Monographs* 67 (3): 345–66.

Dukes, Jeffrey S., Jennifer Pontius, David Orwig, Jeffrey R. Garnas, Vikki L. Rodgers, Nicholas Brazee, Barry Cooke, et al. 2009. “Responses of Insect Pests, Pathogens, and Invasive Plant Species to Climate Change in the Forests of Northeastern North America: What Can We Predict?” *Canadian Journal of Forest Research* 39 (2): 231–48. https://doi.org/10.1139/X08-171.

Duman, John G. 2015. “Animal Ice-Binding (Antifreeze) Proteins and Glycolipids: An Overview with

Emphasis on Physiological Function.” *The Journal of Experimental Biology* 218 (12): 1846–55.

Dwyer, Greg, Jonathan Dushoff, and Susan Harrell Yee. 2004. “The Combined Effects of Pathogens and Predators on Insect Outbreaks.” *Nature* 430 (6997): 341–45. https://doi.org/10.1038/nature02569.

Easterling, David R., Gerald A. Meehl, Camille Parmesan, Stanley A. Changnon, Thomas R. Karl, and Linda O. Mearns. 2000. “Climate Extremes: Observations, Modeling, and Impacts.” *Science* 289 (5487): 2068–74.

Eilenberg, Jørgen A, Ann Hajek, and C. Lomer. 2001. “Suggestions for Unifying the Terminology in Biological Control.” *BioControl* 46: 387–400.

Ellison, Aaron M., ed. 2012. *A Field Guide to the Ants of New England*. New Haven [Conn.]: Yale University Press.

Ellison, Aaron M, Elizabeth J Farnsworth, and Nicholas J Gotelli. 2002. “Ant Diversity in Pitcher-Plant Bogs of Massachusetts.” *Northeastern Naturalist* 9 (3): 267–84.

Ellison, Aaron M., Nicholas J. Gotelli, Elizabeth J. Farnsworth, and Gary D. Alpert. 2012. *A Field Guide to the Ants of New England*. Yale University Press.

Emlen, John M. 1984. “Natural Selection and Population Density-Feedback II. The Evolution of Functional Response Curves.” *Theoretical Population Biology* 25 (1): 62–77.

Environment and Climate Change Canada. 2023. “Hourly Data - Climate - Environment and Climate Change Canada.” https://climate.weather.gc.ca/climate_data/hourly_data_e.html.

Environment Canada. 2017. “National Climate Data and Information Archive.” Ottawa, On-tario, Canada: Environment Canada. https://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html?stnID=5612&autofwd=1.

Estes, James A., John Terborgh, Justin S. Brashares, Mary E. Power, Joel Berger, William J. Bond, Stephen R. Carpenter, Timothy E. Essington, Robert D. Holt, and Jeremy BC Jackson. 2011. “Trophic Downgrading of Planet Earth.” *Science* 333 (6040): 301–6.

Evans, EW. 1982. “Influence of Weather on Predator/Prey Relations: Stinkbugs and Tent Caterpillars.” *Journal of the New York Entomological Society*, 241–46.

Eveleigh, Eldon S., Kevin S. McCann, Peter C. McCarthy, Steven J. Pollock, Christopher J. Lucarotti, Benoit Morin, George A. McDougall, et al. 2007. “Fluctuations in Density of an Outbreak Species Drive Diversity Cascades in Food Webs.” *Proceedings of the National Academy of Sciences* 104 (43): 16976–81. https://doi.org/10.1073/pnas.0704301104.

Ewers, Robert M., Michael JW Boyle, Rosalind A. Gleave, Nichola S. Plowman, Suzan Benedick, Henry Bernard, Tom R. Bishop, Effendi Y. Bakhtiar, Vun Khen Chey, and Arthur YC Chung. 2015. “Logging Cuts the Functional Importance of Invertebrates in Tropical Rainforest.” *Nature Communications* 6 (1): 1–7.

Fairweather, Aaron D., Jake H. Lewis, Laura Hunt, Donald F. McAlpine, and M. Alex Smith. 2020. “Ants (Hymenoptera: Formicidae) of Rockwood Park, New Brunswick: An Assessment of Species Richness and Habitat.” *Northeastern Naturalist* 27 (3): 576. https://doi.org/10.1656/045.027.0316.

Farji-Brener, Alejandro. 2001. “Why Are Leaf-Cutting Ants More Common in Early Secondary Forests than in Old-Growth Tropical Forests? An Evaluation of the Palatable Forage Hypothesis.” *Oikos* 92 (January): 169–77. https://doi.org/10.1034/j.1600-0706.2001.920120.x.

Ferguson, Kenneth I., and Peter Stiling. 1996. “Non-Additive Effects of Multiple Natural Enemies on Aphid Populations.” *Oecologia* 108 (2): 375–79. https://doi.org/10.1007/BF00334664.

Finér, Leena, Martin F. Jurgensen, Timo Domisch, Jouni Kilpeläinen, Seppo Neuvonen, Pekka Punttila, Anita C. Risch, Mizue Ohashi, and Pekka Niemelä. 2013. “The Role of Wood Ants (Formica Rufa Group) in Carbon and Nutrient Dynamics of a Boreal Norway Spruce Forest Ecosystem.” *Ecosystems* 16 (2): 196–208. https://doi.org/10.1007/s10021-012-9608-1.

Fitzgerald, Terrence D. 1995. *The Tent Caterpillars*. Cornell University Press. https://books.google.ca/books?hl=fr&lr=&id=gO-puH2YCrkC&oi=fnd&pg=PR11&dq=Fitzgerald,+T.+D.+(1995).+The+Tent+Caterpillars.+Cornell+University+Press.&ots=6mpqvMqeWL&sig=40BLvw7uV5pnKBPmeV_3wPPnpco.

Fitzgerald, Terrence D, and James T Costa. 1999. “Collective Behavior in Social Caterpillars.” In

Information Processing in Social Insects, 379–400. Birkhäuser, Basel. https://link.springer.com/chapter/10.1007/978-3-0348-8739-7_20.

Fjellberg, Arne. 1998. *The Collembola of Fennoscandia and Denmark. Part 1: Poduromorpha Fauna*.

———. 2007. *The Collembola of Fennoscandia and Denmark, Part II: Entomobryomorpha and Symphypleona*. Brill.

Folgarait, Patricia J. 1998. "Ant Biodiversity and Its Relationship to Ecosystem Functioning: A Review." *Biodiversity & Conservation* 7 (9): 1221–44.

Fortin, Michel, and Y Mauffette. 2002. "The Suitability of Leaves from Different Canopy Layers for a Generalist Herbivore (Lepidoptera : Lasiocampidae) Foraging on Sugar Maple." *Canadian Journal of Forest Research* 32 (2): 379–89.

Fotso Kuate, Apollin, Rachid Hanna, Maurice Tindo, Samuel Nanga, and Peter Nagel. 2015. "Ant Diversity in Dominant Vegetation Types of Southern Cameroon." *Biotropica* 47 (1): 94–100. https://doi.org/10.1111/btp.12182.

Fowler, Charles W. 1981. "Density Dependence as Related to Life History Strategy." *Ecology* 62 (3): 602–10.

Francis, Jennifer A., and Stephen J. Vavrus. 2012. "Evidence Linking Arctic Amplification to Extreme Weather in Mid-Latitudes." *Geophysical Research Letters* 39 (6).

Francoeur, A. 1973. "Revision Taxonomique Des Especes Nearctiques Du Groupe/Usca, Genre Formica (Formicidae, Hymenoptera). Mem. Soc. Ent. Queb. 3. 316 Pp.. 1979. Formicoidea." *Canada and Its Insect Fauna. Mem. Ent. Soc. Can* 108: 502–3.

Francoeur, André. 1983. "The Ant Fauna near the Tree-Line in Northern Québec (Formicidae, Hymenoptera)." *Nordicana* 47: 177–80.

———. 1986. "Deux Nouvelles Fourmis Néarctiques: Leptothorax Retractus et L. Sphagnicolus (Formicidae, Hymenoptera)." *The Canadian Entomologist* 118 (11): 1151–64.

———. 1997. "Ants (Hymenoptera: Formicidae) of the Yukon."

Francœur, André. 2001. "Les fourmis de la forêt boréale du Québec (Formicidae, Hymenoptera)." *Le Naturaliste Canadien* 125 (3): 8.

Francoeur, André. 2011. "Extension de l'aire Connue de La Fourmi Myrmica Quebecensis (Formicidae, Hymenoptera)."

Frizzo, Tiago LM, Ricardo I. Campos, and Heraldo L. Vasconcelos. 2012. "Contrasting Effects of Fire on Arboreal and Ground-Dwelling Ant Communities of a Neotropical Savanna." *Biotropica* 44 (2): 254–61.

Gagnon Koudji, Essivi, Emma Despland, Anne-Sophie Caron, and I. Tanya Handa. 2023. "Soil Springtail Communities Are Resilient to Forest Tent Caterpillar Defoliation in Quebec Mixed Hardwood Forests." *Forests* 14 (7): 1302. https://doi.org/10.3390/f14071302.

Gardner, Sarah M., Marcelo R. Cabido, Graciela R. Valladares, and Sandra Diaz. 1995. "The Influence of Habitat Structure on Arthropod Diversity in Argentine Semi-Arid Chaco Forest." *Journal of Vegetation Science* 6 (3): 349–56.

Gautreau, E. J. 1964. "Unhatched Forest Tent Caterpillar Egg Bands in Northern Alberta Associated with Late Spring Frost." *Forest Entomology and Pathology Branch, Canadian Department of Forestry, Bimonthly Progress Rep* 20 (3).

Gibb, Heloise, and Dieter F. Hochuli. 2003. "Colonisation by a Dominant Ant Facilitated by Anthropogenic Disturbance: Effects on Ant Assemblage Composition, Biomass and Resource Use." *Oikos* 103 (3): 469–78.

Ginzburg, Lev R., and Dale E. Taneyhill. 1994. "Population Cycles of Forest Lepidoptera: A Maternal Effect Hypothesis." *Journal of Animal Ecology* 63 (1): 79–92. https://doi.org/10.2307/5585.

Girona, Miguel Montoro, Tuomas Aakala, Núria Aquilué, Annie-Claude Bélisle, Emeline Chaste, Victor Danneyrolles, Olalla Díaz-Yáñez, Loïc D'Orangeville, Guillaume Grosbois, and Alison Hester. 2023. "Challenges for the Sustainable Management of the Boreal Forest under Climate Change." In *Boreal Forests in the Face of Climate Change: Sustainable Management*, 773–837. Springer.

Glasgow, Margaret A. 2006. "The Effects of Forest Fragmentation on Generalist Predation on Forest Tent

Caterpillars (Malacosoma Disstria)."

Glasier, James RN, Scott E. Nielsen, John Acorn, and Jaime Pinzon. 2019. "Boreal Sand Hills Are Areas of High Diversity for Boreal Ants (Hymenoptera: Formicidae)." *Diversity* 11 (2): 22.

Gloning, Philipp, Nicole Estrella, and Annette Menzel. 2013. "The Impacts of Climate Change on the Winter Hardiness Zones of Woody Plants in Europe." *Theoretical and Applied Climatology* 113: 683–95.

Gösswald, Karl. 1990. "Die Waldameise. Band 2. Die Waldameise in Okosystem Wald, Ihr Nutzen Und Ihre Hege." *Wiesbaden: Aula-Verlag.* 510 S. https://scholar.google.com/scholar?hl=fr&as_sdt=0%2C5&q=Go%C2%BB+sswald+K+%281990%29+Die+Waldameise%2C+band+2.+Die+Waldameise+im+O%C2%BB+kosystem+Wald%2C+ihr+Nutzen+und+ihre+Hege.+Aula%2C+Wiesbaden&btnG=.

Gotelli, Nicholas J., and Aaron M. Ellison. 2002. "Biogeography at a Regional Scale: Determinants of Ant Species Density in New England Bogs and Forests." *Ecology* 83 (6): 1604–9.

Gould, Juli R., Joseph S. Elkinton, and W. E. Wallner. 1990. "Density-Dependent Suppression of Experimentally Created Gypsy Moth, Lymantria Dispar (Lepidoptera: Lymantriidae), Populations by Natural Enemies." *The Journal of Animal Ecology*, 213–33.

Gravel, Dominique, Camille Albouy, and Wilfried Thuiller. 2016. "The Meaning of Functional Trait Composition of Food Webs for Ecosystem Functioning." *Philosophical Transactions of the Royal Society B: Biological Sciences* 371 (1694): 20150268.

Green, GW, and CR Sullivan. 1950. "Ants Attacking Larvae of the Forest Tent Caterpillar, Malacosoma Disstria Hbn. (Lepidoptera: Lasiocampidae)." *The Canadian Entomologist* 82 (9): 94–195.

Greene, D. F., D. D. Kneeshaw, C. Messier, V. Lieffers, D. Cormier, R. Doucet, K. D. Coates, A. Groot, G. Grover, and C. Calogeropoulos. 2002. "Modelling Silvicultural Alternatives for Conifer Regeneration in Boreal Mixedwood Stands (Aspen/White Spruce/Balsam Fir)." *The Forestry Chronicle* 78 (2): 281–95.

Grevé, Michael E., Jörg Hager, Wolfgang W. Weisser, Peter Schall, Martin M. Gossner, and Heike Feldhaar. 2018. "Effect of Forest Management on Temperate Ant Communities." *Ecosphere* 9 (6): e02303. https://doi.org/10.1002/ecs2.2303.

Grisdale, D. G. 1968. "A Method for Reducing Incidence of Virus Infection in Insect Rearings." *Journal of Invertebrate Pathology* 10 (2): 425.

———. 1985. "Malacosoma Disstria." In *Handbook of Insect Rearing*, 2:369–79. New York: Elsevier Science Publishers.

Hahn, Daniel A., and David L. Denlinger. 2007. "Meeting the Energetic Demands of Insect Diapause: Nutrient Storage and Utilization." *Journal of Insect Physiology* 53 (8): 760–73.

———. 2011. "Energetics of Insect Diapause." *Annual Review of Entomology* 56: 103–21.

Halaj, Juraj, and David H. Wise. 2002. "IMPACT OF A DETRITAL SUBSIDY ON TROPHIC CASCADES IN A TERRESTRIAL GRAZING FOOD WEB." *Ecology* 83 (11): 3141–51. https://doi.org/10.1890/0012-9658(2002)083[3141:IOADSO]2.0.CO;2.

Han, Er-Ning, and Eric Bauce. 1995. "Glycerol Synthesis by Diapausing Larvae in Response to the Timing of Low Temperature Exposure, and Implications for Overwintering Survival of the Spruce Budworm, Choristoneura Fumiferana." *Journal of Insect Physiology* 41 (11): 981–85.

Hanec, W. M. 1966. "Cold-Hardiness in the Forest Tent Caterpillar, Malacosoma Disstria Hübner (Lasiocampidae, Lepidoptera)." *Journal of Insect Physiology* 12 (11): 1443–49.

Hansen, E. Matthew, and Barbara J. Bentz. 2003. "Comparison of Reproductive Capacity among Univoltine, Semivoltine, and Re-Emerged Parent Spruce Beetles (Coleoptera: Scolytidae)." *The Canadian Entomologist* 135 (5): 697–712. https://doi.org/10.4039/n02-109.

Hawkins, Bradford A., Howard V. Cornell, and Michael E. Hochberg. 1997. "Predators, Parasitoids, and Pathogens as Mortality Agents in Phytophagous Insect Populations." *Ecology* 78 (7): 2145–52. https://doi.org/10.1890/0012-9658(1997)078[2145:PPAPAM]2.0.CO;2.

Hedlund, Katarina, Bryan Griffiths, Søeren Christensen, Stefan Scheu, Heikki Setälä, Teja Tscharntke, and Herman Verhoef. 2004. "Trophic Interactions in Changing Landscapes: Responses of Soil Food Webs."

Basic and Applied Ecology 5 (6): 495–503.

Hill, Steven B., Azim U. Mallik, and Han YH Chen. 2005. “Canopy Gap Disturbance and Succession in Trembling Aspen Dominated Boreal Forests in Northeastern Ontario.” *Canadian Journal of Forest Research* 35 (8): 1942–51.

Hochuli, Dieter F. 2001. “Insect Herbivory and Ontogeny: How Do Growth and Development Influence Feeding Behaviour, Morphology and Host Use?: ONTOGENETIC CONSTRAINTS ON INSECT HERBIVORY.” *Austral Ecology* 26 (5): 563–70. https://doi.org/10.1046/j.1442-9993.2001.01135.x.

Hodson, AC. 1977. “Some Aspects of Forest Tent Caterpillar Population Dynamics.” http://agris.fao.org/agris-search/search.do?recordID=US201301275468.

Hodson, Alexander Carlton. 1941. “An Ecological Study of the Forest Tent Caterpillar, Malacosoma Disstria Hbn., in Northern Minnesota.”

Hoffmann, Benjamin D., and Alan N. Andersen. 2003. “Responses of Ants to Disturbance in Australia, with Particular Reference to Functional Groups.” *Austral Ecology* 28 (4): 444–64. https://doi.org/10.1046/j.1442-9993.2003.01301.x.

Hölldobler, Bert, and Edward O. Wilson. 1990. *The Ants*. Harvard University Press.

Hopkin, Steve P. 2007. *A Key to the Collembola (Springtails) of Britain and Ireland.* FSC publications.

Hunter, AF, and JS Elkinton. 2000. “Effects of Synchrony with Host Plant on Populations of a Spring-feeding Lepidopteran.” *Ecology* 81 (5): 1248–61.

Hunter, Mark D. 2001. “Insect Population Dynamics Meets Ecosystem Ecology: Effects of Herbivory on Soil Nutrient Dynamics.” *Agricultural and Forest Entomology* 3 (2): 77–84. https://doi.org/10.1046/j.1461-9563.2001.00100.x.

Ibarra-Isassi, Javier, Ira Tanya Handa, and Jean-Philippe Lessard. 2023. “Community-Wide Trait Adaptation, but Not Plasticity, Explains Ant Community Structure in Extreme Environments.” *Functional Ecology* 37 (1): 139–49.

iNaturalist. 2023. “Malacosoma disstria.” iNaturalist. 2023. https://www.inaturalist.org/observations.

Ives, WGH. 1971. *The Forest Tent Caterpillar in Alberta*. Natural Resources Canada. http://www.cfs.nrcan.gc.ca/publications/publications?id=11812.

Jaccard, Paul. 1901. “Étude Comparative de La Distribution Florale Dans Une Portion Des Alpes et Des Jura.” *Bull Soc Vaudoise Sci Nat* 37: 547–79.

Jactel, Hervé, Eckehard Brockerhoff, and Peter Duelli. 2005. “A Test of the Biodiversity-Stability Theory: Meta-Analysis of Tree Species Diversity Effects on Insect Pest Infestations, and Re-Examination of Responsible Factors.” In *Forest Diversity and Function*, 235–62. Springer.

Jactel, Hervé, and Eckehard G. Brockerhoff. 2007. “Tree Diversity Reduces Herbivory by Forest Insects.” *Ecology Letters* 10 (9): 835–48.

Jactel, Hervé, Julia Koricheva, and Bastien Castagneyrol. 2019. “Responses of Forest Insect Pests to Climate Change: Not so Simple.” *Current Opinion in Insect Science* 35: 103–8.

Jepsen, Jane U., Snorre B. Hagen, Rolf A. Ims, and Nigel G. Yoccoz. 2008. “Climate Change and Outbreaks of the Geometrids Operophtera Brumata and Epirrita Autumnata in Subarctic Birch Forest: Evidence of a Recent Outbreak Range Expansion.” *Journal of Animal Ecology* 77 (2): 257–64. https://doi.org/10.1111/j.1365-2656.2007.01339.x.

Johns, Robert C., Joseph J. Bowden, Drew R. Carleton, Barry J. Cooke, Sara Edwards, Erik J. S. Emilson, Patrick M. A. James, et al. 2019. “A Conceptual Framework for the Spruce Budworm Early Intervention Strategy: Can Outbreaks Be Stopped?” *Forests* 10 (10): 910. https://doi.org/10.3390/f10100910.

Jurgensen, M. F., Leena Finér, Timo Domisch, Jouni Kilpeläinen, Pekka Punttila, M. Ohashi, Pekka Niemelä, Liselotte Sundström, S. Neuvonen, and A. C. Risch. 2008. “Organic Mound-Building Ants: Their Impact on Soil Properties in Temperate and Boreal Forests.” *Journal of Applied Entomology* 132 (4): 266–75.

Karban, Richard. 1982. “Increased Reproductive Success at High Densities and Predator Satiation for Periodical Cicadas.” *Ecology* 63 (2): 321–28.

Karhu, Kari J., and Seppo Neuvonen. 1998. “Wood Ants and a Geometrid Defoliator of Birch: Predation

Outweighs Beneficial Effects through the Host Plant." *Oecologia* 113 (4): 509–16.

Kaspari, Michael. 1996. "Testing Resource-Based Models of Patchiness in Four Neotropical Litter Ant Assemblages." *Oikos* 76 (3): 443. https://doi.org/10.2307/3546338.

Kaukonen, Maarit, Anna Liisa Ruotsalainen, Piippa R Wäli, Minna K Männistö, H Setälä, Karita Saravesi, Karoliina Huusko, and Annamari Markkola. 2013. "Moth Herbivory Enhances Resource Turnover in Subarctic Mountain Birch Forests?" *Ecology* 94 (2): 267–72. https://doi.org/10.1890/10-1922.1.

Kilpeläinen, J., L. Finér, P. Niemelä, T. Domisch, S. Neuvonen, M. Ohashi, A. C. Risch, and L. Sundström. 2007. "Carbon, Nitrogen and Phosphorus Dynamics of Ant Mounds (Formica Rufa Group) in Managed Boreal Forests of Different Successional Stages." *Applied Soil Ecology* 36 (2): 156–63. https://doi.org/10.1016/j.apsoil.2007.01.005.

Kilpeläinen, Jouni, Leena Finér, Seppo Neuvonen, Pekka Niemelä, Timo Domisch, Anita C. Risch, Martin F. Jurgensen, Mizue Ohashi, and Liselotte Sundström. 2009. "Does the Mutualism between Wood Ants (Formica Rufa Group) and Cinara Aphids Affect Norway Spruce Growth?" *Forest Ecology and Management* 257 (1): 238–43.

Kleiner, Karl W., David D. Ellis, Brent H. Mccown, and Kenneth F. Raffa. 1995. "Field Evaluation of Transgenic Poplar Expressing a Bacillus Thuringiensis cry1A (∞) d -Endotoxin Gene Against Forest Tent Caterpillar (Lepidoptera: Lasiocampidae) and Gypsy Moth (Lepidoptera: Lymantriidae) Following Winter Dormancy." *Environmental Entomology* 24 (5): 1358–64. https://doi.org/10.1093/ee/24.5.1358.

Klemola, Netta, Tommi Andersson, Kai Ruohomäki, and Tero Klemola. 2010. "Experimental Test of Parasitism Hypothesis for Population Cycles of a Forest Lepidopteran." *Ecology* 91 (9): 2506–13. https://doi.org/10.1890/09-2076.1.

Klemola, Tero, Miia Tanhuanpaa, Erkki Korpimaki, and Kai Ruohomaki. 2002. "Specialist and Generalist Natural Enemies as an Explanation for Geographical Gradients in Population Cycles of Northern Herbivores." *Oikos* 99 (1): 83–94. https://doi.org/10.1034/j.1600-0706.2002.990109.x.

Klironomos, JN, P Widden, and I Deslandes. 1992. "Feeding Preferences of the Collembolan Folsomia Candida in Relation to Microfungal Successions on Decaying Litter." *Soil Biology and Biochemistry* 24 (7): 685–92.

Knight, G A, R J Lavigne, and M G Pogue. 1991. "The Parasitoid Complex of Forest Tent Caterpillar, Malacosoma Disstria (Lepidoptera: Lasiocampidae), in Eastern Wyoming Shelterbelts" 24 (4): 8.

Knight, J. D. 1986. "Insect Cold Hardiness: Supercooling and Prefreeze Mortality." *Cryo-Letters* 7: 194–203.

Kristensen, Jeppe A., Daniel B. Metcalfe, and Johannes Rousk. 2018. "The Biogeochemical Consequences of Litter Transformation by Insect Herbivory in the Subarctic: A Microcosm Simulation Experiment." *Biogeochemistry* 138 (3): 323–36.

Kristensen, Jeppe Å., Johannes Rousk, and Daniel B. Metcalfe. 2020. "Below-ground Responses to Insect Herbivory in Ecosystems with Woody Plant Canopies: A Meta-analysis." Edited by Paul Kardol. *Journal of Ecology* 108 (3): 917–30. https://doi.org/10.1111/1365-2745.13319.

Kukan, Barbara, and Judith H. Myers. 1997. "Prevalence and Persistence of Nuclear Polyhedrosis Virus in Fluctuating Populations of Forest Tent Caterpillars (Lepidoptera: Lasiocampidae) in the Area of Prince George, British Columbia." *Environmental Entomology* 26 (4): 882–87. https://doi.org/10.1093/ee/26.4.882.

Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safranyik. 2008. "Mountain Pine Beetle and Forest Carbon Feedback to Climate Change." *Nature* 452 (7190): 987–90. https://doi.org/10.1038/nature06777.

Lach, Lori, Catherine Parr, and Kirsti Abbott. 2010. *Ant Ecology*. Oxford university press.

Laine, Kari J., and Pekka Niemelä. 1980. "The Influence of Ants on the Survival of Mountain Birches during an Oporinia Autumnata (Lep., Geometridae) Outbreak." *Oecologia* 47 (1): 39–42.

Lait, Linda A., and Paul DN Hebert. 2018. "Phylogeographic Structure in Three North American Tent Caterpillar Species (Lepidoptera: Lasiocampidae): Malacosoma Americana, M. Californica, and M. Disstria." *PeerJ* 6: e4479.

Lajoie, Paul G. 1967. "Étude Pédologique Des Comtés de Hull, Labelle et Papineau." *Québec)(Ottawa:*

Ministère I'agriculture).

Lavoie, Janie, Miguel Montoro Girona, Guillaume Grosbois, and Hubert Morin. 2021. "Does the Type of Silvicultural Practice Influence Spruce Budworm Defoliation of Seedlings?" *Ecosphere* 12 (4): e03506.

Leal, Inara R., Bruno K. C. Filgueiras, Juliana P. Gomes, Luciana Iannuzzi, and Alan N. Andersen. 2012. "Effects of Habitat Fragmentation on Ant Richness and Functional Composition in Brazilian Atlantic Forest." *Biodiversity and Conservation* 21 (7): 1687–1701. https://doi.org/10.1007/s10531-012-0271-9.

Lee, Richard E. 2010. "A Primer on Insect Cold-Tolerance." *Low Temperature Biology of Insects*, 3–34.

Lehmann, Philipp, Tea Ammunét, Madeleine Barton, Andrea Battisti, Sanford D. Eigenbrode, Jane Uhd Jepsen, Gregor Kalinkat, Seppo Neuvonen, Pekka Niemelä, and John S. Terblanche. 2020. "Complex Responses of Global Insect Pests to Climate Warming." *Frontiers in Ecology and the Environment* 18 (3): 141–50.

Lessard, Jean-Philippe, Tara E. Sackett, William N. Reynolds, David A. Fowler, and Nathan J. Sanders. 2011. "Determinants of the Detrital Arthropod Community Structure: The Effects of Temperature and Resources along an Environmental Gradient." *Oikos* 120 (3): 333–43. https://doi.org/10.1111/j.1600-0706.2010.18772.x.

Lessard, J.-P., R. R. Dunn, and N. J. Sanders. 2009. "Temperature-Mediated Coexistence in Temperate Forest Ant Communities." *Insectes Sociaux* 56 (2): 149–56. https://doi.org/10.1007/s00040-009-0006-4.

Levesque, K. R., M. Fortin, and Y. Mauffette. 2002. "Temperature and Food Quality Effects on Growth, Consumption and Post-Ingestive Utilization Ef. Ciencies of the Forest Tent Caterpillar Malacosoma Disstria (Lepidoptera: Lasiocampidae)." *Bulletin of Entomological Research* 92 (2): 127–36.

Lewis, Gregory P., and Gene E. Likens. 2007. "Changes in Stream Chemistry Associated with Insect Defoliation in a Pennsylvania Hemlock-Hardwoods Forest." *Forest Ecology and Management* 238 (1–3): 199–211.

Lorenzetti, Francois, Yves Mauffette, and Eric Bauce. 1999. "Relationship between Foliar Chemistry and Insect Performance: The Forest Tent Caterpillar." In *In: Horsley, Stephen B.; Long, Robert P., Eds. Sugar Maple Ecology and Health: Proceedings of an International Symposium; 1998 June 2-4; Warren, PA. Gen. Tech. Rep. NE-261. Radnor, PA: US Department of Agriculture, Forest Service, Northeastern Research Station: 93-97.* Vol. 261.

Lorimer, N. 1979. "Differential Hatching Times in the Forest Tent Caterpillar (Lepidoptera: Lasiocampidae)." *Great Lakes Entomologist* 12 (4): 199.

Lovett, Gary M., Lynn M. Christenson, Peter M. Groffman, Clive G. Jones, Julie E. Hart, and Myron J. Mitchell. 2002. "Insect Defoliation and Nitrogen Cycling in Forests." *BioScience* 52 (4): 335. https://doi.org/10.1641/0006-3568(2002)052[0335:IDANCI]2.0.CO;2.

Lovett, Gary M., and Adriana E. Ruesink. 1995. "Carbon and Nitrogen Mineralization from Decomposing Gypsy Moth Frass." *Oecologia* 104 (2): 133–38.

MacDonald, Zachary G., Kyle L. Snape, Amanda D. Roe, and Felix A. H. Sperling. 2022. "Host Association, Environment, and Geography Underlie Genomic Differentiation in a Major Forest Pest." *Evolutionary Applications* 15 (11): 1749–65. https://doi.org/10.1111/eva.13466.

MacKay, William P, and Emma Mackay. 2002. *The Ants of New Mexico (Hymenoptera: Formicidae)*. Edwin Mellen Press Lewiston, NY.

Maeto, K., and S. Sato. 2004. "Impacts of Forestry on Ant Species Richness and Composition in Warm-Temperate Forests of Japan." *Forest Ecology and Management* 187 (2–3): 213–23.

Mahon, Michael B., Kaitlin U. Campbell, and Thomas O. Crist. 2017. "Effectiveness of Winkler Litter Extraction and Pitfall Traps in Sampling Ant Communities and Functional Groups in a Temperate Forest." *Environmental Entomology* 46 (3): 470–79. https://doi.org/10.1093/ee/nvx061.

Man, Rongzhou, Gordon J. Kayahara, James A. Rice, and G. Blake MacDonald. 2008. "Response of Trembling Aspen to Partial Cutting and Subsequent Forest Tent Caterpillar Defoliation in a Boreal Mixedwood Stand in Northeastern Ontario, Canada." *Canadian Journal of Forest Research* 38 (6): 1349–56.

Man, Rongzhou, and James A. Rice. 2010. "Response of Aspen Stands to Forest Tent Caterpillar

Defoliation and Subsequent Overstory Mortality in Northeastern Ontario, Canada." *Forest Ecology and Management* 260 (10): 1853–60. https://doi.org/10.1016/j.foreco.2010.08.032.

Maňák, Vítězslav, Niklas Björklund, Lisette Lenoir, and Göran Nordlander. 2015. "The Effect of Red Wood Ant Abundance on Feeding Damage by the Pine Weevil Hylobius Abietis." *Agricultural and Forest Entomology* 17 (1): 57–63.

Maravalhas, Jonas, and Heraldo L. Vasconcelos. 2014. "Revisiting the Pyrodiversity–Biodiversity Hypothesis: Long-Term Fire Regimes and the Structure of Ant Communities in a N Eotropical Savanna Hotspot." *Journal of Applied Ecology* 51 (6): 1661–68.

Marshall, Katie E., and Brent J. Sinclair. 2010. "Repeated Stress Exposure Results in a Survival–Reproduction Trade-off in Drosophila Melanogaster." *Proceedings of the Royal Society B: Biological Sciences* 277 (1683): 963–69.

———. 2012. "The Impacts of Repeated Cold Exposure on Insects." *Journal of Experimental Biology* 215 (10): 1607–13. https://doi.org/10.1242/jeb.059956.

———. 2015. "The Relative Importance of Number, Duration and Intensity of Cold Stress Events in Determining Survival and Energetics of an Overwintering Insect." *Functional Ecology* 29 (3): 357–66. https://doi.org/10.1111/1365-2435.12328.

Martineau, René. 1985. *Insectes Nuisibles Des Forêts de l'est Du Canada*. Inistère des approvisionnements et services du Canada. Ottawa, Ontario: M. Broquet. https://omni.laurentian.ca/discovery/fulldisplay/alma991006709189705165/01OCUL_LU:OMNI.

Mason, Charles J., and Kenneth F. Raffa. 2014. "Acquisition and Structuring of Midgut Bacterial Communities in Gypsy Moth (Lepidoptera: Erebidae) Larvae." *Environmental Entomology* 43 (3): 595–604. https://doi.org/10.1603/EN14031.

Mattson Jr, William J., and Glen W. Erickson. 1978. "Degree-Day Summation and Hatching of the Forest Tent Caterpillar, Malacosoma Disstria (Lepidoptera: Lasiocampidae)." *The Great Lakes Entomologist* 11 (1): 7.

McClure, Melanie, and Emma Despland. 2010. "Collective Foraging Patterns of Field Colonies of Malacosoma Disstria Caterpillars." *The Canadian Entomologist* 142 (5): 473–80. https://doi.org/10.4039/n10-001.

McCoy, Earl D., and Susan S. Bell. 1991. "Habitat Structure: The Evolution and Diversification of a Complex Topic." In *Habitat Structure*, 3–27. Springer.

McGlynn, Terrence P. 2006. "Ants on the Move: Resource Limitation of a Litter-Nesting Ant Community in Costa Rica1: Limitation of Litter-Nesting Ants." *Biotropica* 38 (3): 419–27. https://doi.org/10.1111/j.1744-7429.2006.00153.x.

Mestre, L., J. Piñol, J. A. Barrientos, and X. Espadaler. 2013. "Ant Exclusion in Citrus over an 8-Year Period Reveals a Pervasive yet Changing Effect of Ants on a Mediterranean Spider Assemblage." *Oecologia* 173: 239–48.

Metcalfe, Daniel B., Gregory P. Asner, Roberta E. Martin, Javier E. Silva Espejo, Walter Huaraca Huasco, Felix F. Farfán Amézquita, Loreli Carranza-Jimenez, et al. 2014. "Herbivory Makes Major Contributions to Ecosystem Carbon and Nutrient Cycling in Tropical Forests." Edited by Wim van der Putten. *Ecology Letters* 17 (3): 324–32. https://doi.org/10.1111/ele.12233.

Metcalfe, Daniel B., Gregory M. Crutsinger, Bright B. Kumordzi, and David A. Wardle. 2016. "Nutrient Fluxes from Insect Herbivory Increase during Ecosystem Retrogression in Boreal Forest." *Ecology* 97 (1): 124–32.

MFFP. 2015. "Aires infestées par la livrée des forêts au Québec en 2015." Version 1.0. Québec: Gouvernement du Québec, Direction de la protection des forêts. https://mffp.gouv.qc.ca/documents/forets/fimaq/Liv_2015_P.pdf.

———. 2016. "Aires infestées par la livrée des forêts au Québec en 2016." Version 1.0,. Québec: Gouvernement du Québec, Direction de la protection des forêts. https://mffp.gouv.qc.ca/publications/forets/fimaq/insectes/livree/Liv_2016_P.pdf.

———. 2017. "Aires infestées par la livrée des forêts au Québec en 2017." Version 1.0,. Québec: Gouvernement du Québec, Direction de la protection des forêts.

https://mffp.gouv.qc.ca/publications/forets/fimaq/insectes/livree/Liv_2017_P.pdf.

———. 2019. “Aires infestées par la livrée des forêts au Québec en 2018.” Version 1.1,. Québec: Gouvernement du Québec, Direction de la protection des forêts.

Mikola, Juha, Gregor W. Yeates, Gary M. Barker, David A. Wardle, and Karen I. Bonner. 2001. “Effects of Defoliation Intensity on Soil Food-Web Properties in an Experimental Grassland Community.” *Oikos* 92 (2): 333–43.

Milford, Elizabeth Remington. 1999. “Ant Communities in Flooded and Unflooded Riparian Forest of the Middle Rio Grande.” *The Southwestern Naturalist*, 278–86.

Mokadam, Chloe. 2021. “Native and Non-Native Ant Impacts on Native Fungi.” Master of Science, Buffalo State College.

Montllor, Clytia B., and Elizabeth A. Bernays. 1993. “Invertebrate Predators and Caterpillar Foraging.”

Montoro Girona, Miguel, Lionel Navarro, and Hubert Morin. 2018. “A Secret Hidden in the Sediments: Lepidoptera Scales.” *Frontiers in Ecology and Evolution* 6 (January): 2. https://doi.org/10.3389/fevo.2018.00002.

Moreira, Xoaquín, Kailen A. Mooney, Rafael Zas, and Luis Sampedro. 2012. “Bottom-up Effects of Host-Plant Species Diversity and Top-down Effects of Ants Interactively Increase Plant Performance.” *Proceedings of the Royal Society B: Biological Sciences* 279 (1746): 4464–72.

Morin, Hubert, Danielle Laprise, and Yves Bergeron. 1993. “Chronology of Spruce Budworm Outbreaks near Lake Duparquet, Abitibi Region, Quebec.” *Canadian Journal of Forest Research* 23 (August): 1497–1506. https://doi.org/10.1139/x93-189.

Moulinier, J. 2013. “Impacts de La Défoliation Par La Livrée Des Forêts Sur La Mortalité Du Peuplier Faux-Tremble et La Dynamique Forestière Post-Épidémie En Forêt Boréale.” http://depositum.uqat.ca/id/eprint/588.

Moya-Laraño, Jordi, and David H. Wise. 2007. “Direct and Indirect Effects of Ants on a Forest-Floor Food Web.” *Ecology* 88 (6): 1454–65. https://doi.org/10.1890/05-1474.

Müller, C. B., and H. Charles J. Godfray. 1999. “Indirect Interactions in Aphid–Parasitoid Communities.” *Researches on Population Ecology* 41 (1): 93–106. https://doi.org/10.1007/PL00011986.

Muzika, R. M., and A. M. Liebhold. 2000. “A Critique of Silvicultural Approaches to Managing Defoliating Insects in North America.” *Agricultural and Forest Entomology* 2 (2): 97–105.

Myers, Judith H. 1990. “Population Cycles of Western Tent Caterpillars: Experimental Introductions and Synchrony of Fluctuations.” *Ecology* 71 (3): 986–95. https://doi.org/10.2307/1937367.

———. 1993. “Population Outbreaks in Forest Lepidoptera.” *American Scientist* 81 (3): 240–51.

Myers, Judith H., and Jenny S. Cory. 2013. “Population Cycles in Forest Lepidoptera Revisited.” *Annual Review of Ecology, Evolution, and Systematics* 44 (1): 565–92. https://doi.org/10.1146/annurev-ecolsys-110512-135858.

Myers, Judith H., and Barbara Kuken. 1995. “Changes in the Fecundity of Tent Caterpillars: A Correlated Character of Disease Resistance or Sublethal Effect of Disease?” *Oecologia* 103 (4): 475–80. https://doi.org/10.1007/BF00328686.

Navarro, Lionel, Hubert Morin, Yves Bergeron, and Miguel Montoro Girona. 2018. “Changes in Spatiotemporal Patterns of 20th Century Spruce Budworm Outbreaks in Eastern Canadian Boreal Forests.” *Frontiers in Plant Science* 9: 1905.

Nedvěd, O., D. Lavy, and H. A. Verhoef. 1998. “Modelling the Time–Temperature Relationship in Cold Injury and Effect of High-Temperature Interruptions on Survival in a Chill-Sensitive Collembolan.” *Functional Ecology* 12 (5): 816–24.

Niemela, Jari, Yrjo Haila, Eero Halme, Timo Pajunen, and Pekka Punttila. 1992. “Small-Scale Heterogeneity in the Spatial Distribution of Carabid Beetles in the Southern Finnish Taiga.” *Journal of Biogeography* 19 (2): 173. https://doi.org/10.2307/2845503.

Nixon, Amy E., and Jens Roland. 2012. “Generalist Predation on Forest Tent Caterpillar Varies with Forest Stand Composition: An Experimental Study across Multiple Life Stages.” *Ecological Entomology* 37 (1): 13–23. https://doi.org/10.1111/j.1365-2311.2011.01330.x.

Oberg, EW, I Del Toro, and SL Pelini. 2012. “Characterization of the Thermal Tolerances of Forest Ants of New England." *Insectes Sociaux* 59 (2): 167–74.

Odum, Eugene P. 1970. "The Strategy of Ecosystem Development." *Ekistics* 29 (173): 234–38.

Oeser, Julian, Marco Heurich, Cornelius Senf, Dirk Pflugmacher, Elisa Belotti, and Tobias Kuemmerle. 2020. "Habitat Metrics Based on Multi-Temporal Landsat Imagery for Mapping Large Mammal Habitat." *Remote Sensing in Ecology and Conservation* 6 (1): 52–69. https://doi.org/10.1002/rse2.122.

Overland, James E., and Muyin Wang. 2015. "Increased Variability in the Early Winter Subarctic North American Atmospheric Circulation." *Journal of Climate* 28 (18): 7297–7305.

Palladini, Jennifer D., Maureen G. Jones, Nathan J. Sanders, and Erik S. Jules. 2007. "The Recovery of Ant Communities in Regenerating Temperate Conifer Forests." *Forest Ecology and Management* 242 (2–3): 619–24.

Parker, Ingrid M., Daniel Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, BMPB Von Holle, P. B. Moyle, and J. E. Byers. 1999. "Impact: Toward a Framework for Understanding the Ecological Effects of Invaders." *Biological Invasions* 1: 3–19.

Parmentier, T., W. Dekoninck, and T. Wenseleers. 2014. "A Highly Diverse Microcosm in a Hostile World: A Review on the Associates of Red Wood Ants (Formica Rufa Group)." *Insectes Sociaux* 61 (3): 229–37. https://doi.org/10.1007/s00040-014-0357-3.

Parmesan, Camille. 2006. "Ecological and Evolutionary Responses to Recent Climate Change." *Annual Review of Ecology, Evolution, and Systematics* 37 (1): 637–69. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100.

Parr, Catherine L., Hamish G. Robertson, Harry C. Biggs, and Steven L. Chown. 2004. "Response of African Savanna Ants to Long-Term Fire Regimes." *Journal of Applied Ecology*, 630–42.

Parry, D. 1995. "Larval and Pupal Parasitism of the Forest Tent Caterpillar, Malacosoma Disstria Hübner (Lepidoptera: Lasiocampidae), in Alberta, Canada." *The Canadian Entomologist* 127 (6): 877–93.

Parry, Dylan. 1994. "The Impact of Predators and Parasitoids on Natural and Experimentally Created Populations of Forest Tent Caterpillar, Malacosoma Disstria Hübner (Lepidoptera: Lasiocampidae)." Master of Science, Edmonton, Alberta: University of Alberta.

Parry, Dylan, Richard A. Goyer, and Gerald J. Lenhard. 2001. "Macrogeographic Clines in Fecundity, Reproductive Allocation, and Offspring Size of the Forest Tent Caterpillar Malacosoma Disstria." *Ecological Entomology* 26 (3): 281–91. https://doi.org/10.1046/j.1365-2311.2001.00319.x.

Parry, Dylan, John R. Spence, and W. Jan A. Volney. 1998. "Budbreak Phenology and Natural Enemies Mediate Survival of First-Instar Forest Tent Caterpillar (Lepidoptera: Lasiocampidae)." *Environmental Entomology* 27 (6): 1368–74. https://doi.org/10.1093/ee/27.6.1368.

Parry, Dylan, John Spence, and W. Volney. 1997. "Responses of Natural Enemies to Experimentally Increased Populations of the Forest Tent Caterpillar, *Malacosoma Disstria*." *Ecological Entomology* 22 (1): 97–108. https://doi.org/10.1046/j.1365-2311.1997.00022.x.

Petal, Joanna. 1978. "Role of Ants in Ecosystems." *International Biological Programme*.

Piñol, Josep, Xavier Espadaler, Núria Cañellas, JORDI MARTÍNEZ-VILALTA, José A. Barrientos, and Daniel Sol. 2010. "Ant versus Bird Exclusion Effects on the Arthropod Assemblage of an Organic Citrus Grove." *Ecological Entomology* 35 (3): 367–76.

Pitman, R. M., E. I. Vanguelova, and S. E. Benham. 2010. "The Effects of Phytophagous Insects on Water and Soil Nutrient Concentrations and Fluxes through Forest Stands of the Level II Monitoring Network in the UK." *Science of the Total Environment* 409 (1): 169–81.

Polis, Gary A., Wendy B. Anderson, and Robert D. Holt. 1997. "TOWARD AN INTEGRATION OF LANDSCAPE AND FOOD WEB ECOLOGY:The Dynamics of Spatially Subsidized Food Webs." *Annual Review of Ecology and Systematics* 28 (1): 289–316. https://doi.org/10.1146/annurev.ecolsys.28.1.289.

Prentice, R. M. 1954. "Decline of Populations of the Forest Tent Caterpillar in Central Saskatchewan." *Can. Dep. Agric., For. Biol. Div., Bi-Monthly Prog. Rep* 10 (5).

Punttila, Pekka, Yrjö Haila, Jari Niemelä, and Timo Pajunen. 1994. "Ant Communities in Fragments of Old-Growth Taiga and Managed Surroundings." In *Annales Zoologici Fennici*, 131–44. JSTOR.

Punttila, Pekka, Yrjö Haila, Timo Pajunen, and Harri Tukia. 1991. "Colonisation of Clearcut Forests by

Ants in the Southern Finnish Taiga: A Quantitative Survey." *Oikos*, 250–62.

Punttila, Pekka, Pekka Niemelä, and Kari Karhu. 2004. "The Impact of Wood Ants (Hymenoptera: Formicidae) on the Structure of Invertebrate Community on Mountain Birch (Betula Pubescens Ssp. Czerepanovii)." In *Annales Zoologici Fennici*, 429–46. JSTOR.

R Development Core, Team. 2017. *A Language and Environment for Statistical Computing*. The R Foundation for Statistical Computing, Department of Agronomy, Faculty ….

Raske, A. G. 1975. "Cold-Hardiness of First Instar Larvae of the Forest Tent Caterpillar, Malacosoma Disstria (Lepidoptera: Lasiocampidae)." *The Canadian Entomologist* 107 (1): 75–80.

Redmon, Joseph, Santosh Divvala, Ross Girshick, and Ali Farhadi. 2016. "You Only Look Once: Unified, Real-Time Object Detection." arXiv. http://arxiv.org/abs/1506.02640.

Régnière, Jacques, and Barbara Bentz. 2007. "Modeling Cold Tolerance in the Mountain Pine Beetle, Dendroctonus Ponderosae." *Journal of Insect Physiology* 53 (6): 559–72.

Régnière, Jacques, Vince Nealis, and Kevin Porter. 2009. "Climate Suitability and Management of the Gypsy Moth Invasion into Canada." *Ecological Impacts of Non-Native Invertebrates and Fungi on Terrestrial Ecosystems*, 135–48.

Reynolds, Barbara C., Mark D. Hunter, and D. A. Crossley Jr. 2000. "Effects of Canopy Herbivory on Nutrient Cycling in a Northern Hardwood Forest in Western North Carolina." *Selbyana*, 74–78.

Reynolds, B.C., and M.D. Hunter. 2001. "Responses of Soil Respiration, Soil Nutrients, and Litter Decomposition to Inputs from Canopy Herbivores." *Soil Biology and Biochemistry* 33 (12–13): 1641–52. https://doi.org/10.1016/S0038-0717(01)00085-2.

Ricciardi, Anthony, Martha F. Hoopes, Michael P. Marchetti, and Julie L. Lockwood. 2013. "Progress toward Understanding the Ecological Impacts of Nonnative Species." *Ecological Monographs* 83 (3): 263–82.

Riihimäki, Janne, Pekka Kaitaniemi, Julia Koricheva, and Harri Vehviläinen. 2005. "Testing the Enemies Hypothesis in Forest Stands: The Important Role of Tree Species Composition." *Oecologia* 142 (1): 90–97. https://doi.org/10.1007/s00442-004-1696-y.

Ripple, William J., James A. Estes, Oswald J. Schmitz, Vanessa Constant, Matthew J. Kaylor, Adam Lenz, Jennifer L. Motley, Katharine E. Self, David S. Taylor, and Christopher Wolf. 2016. "What Is a Trophic Cascade?" *Trends in Ecology & Evolution* 31 (11): 842–49.

Risch, A. C., and M. F. Jurgensen. 2008. "Ants in the Soil System-a Hydrological, Chemical and Biological Approach." *Journal of Applied Entomology* 132 (4): 265.

Risch, A C, M F Jurgensen, M Schütz, and D S Page-Dumroese. 2005. "The Contribution of Red Wood Ants to Soil C and N Pools and CO2 Emissions in Subalpine Forests." *Ecology* 86 (2): 419–30. http://dx.doi.org/10.1890/04-0159.

Rohrmann, G. F. 1986. "Evolution of Occluded Baculoviruses."

Roland, Jens. 1993. "Large-Scale Forest Fragmentation Increases the Duration of Tent Caterpillar Outbreak." *Oecologia* 93 (1): 25–30. https://doi.org/10.1007/BF00321186.

Roland, Jens, and William J. Kauppp. 1995. "Reduced Transmission of Forest Tent Caterpillar (Lepidoptera: Lasiocampidae) Nuclear Polyhedrosis Virus at the Forest Edge." *Environmental Entomology* 24 (5): 1175–78. https://doi.org/10.1093/ee/24.5.1175.

Roland, Jens, and Philip D. Taylor. 1997. "Insect Parasitoid Species Respond to Forest Structure at Different Spatial Scales." *Nature* 386 (6626): 710–13. https://doi.org/10.1038/386710a0.

Romero, Gustavo Q., Pablo AP Antiqueira, and Julia Koricheva. 2011. "A Meta-Analysis of Predation Risk Effects on Pollinator Behaviour." *PloS One* 6 (6): e20689.

Ronnås, Cecilia, Stig Larsson, Andrea Pitacco, and Andrea Battisti. 2010. "Effects of Colony Size on Larval Performance in a Processionary Moth." *Ecological Entomology* 35 (April): 436–45. https://doi.org/10.1111/j.1365-2311.2010.01199.x.

Root, Richard B. 1973. "Organization of a Plant-Arthropod Association in Simple and Diverse Habitats: The Fauna of Collards (Brassica Oleracea)." *Ecological Monographs* 43 (1): 95–124.

Rosengren, R. 1991. "The Interaction between Red Wood Ants, Cinara Aphids, and Pines. A Ghost of Mutualism Past?" In *Ant-Plant Interactions*, 80–91. https://ci.nii.ac.jp/naid/10004342066/.

Rosengren, Rainer, Wilhelm Fortelius, Kaj Lindström, and Annika Luther. 1987. “Phenology and Causation of Nest Heating and Thermoregulation in Red Wood Ants of the Formica Rufa Group Studied in Coniferous Forest Habitats in Southern Finland.” In *Annales Zoologici Fennici*, 147–55. JSTOR.

Rossiter, M. C. 1991. “Environmentally-Based Maternal Effects: A Hidden Force in Insect Population Dynamics?” *Oecologia* 87 (2): 288–94.

Rosumek, Felix B., Fernando A. O. Silveira, Frederico de S. Neves, Newton P. de U. Barbosa, Livia Diniz, Yumi Oki, Flavia Pezzini, G. Wilson Fernandes, and Tatiana Cornelissen. 2009. “Ants on Plants: A Meta-Analysis of the Role of Ants as Plant Biotic Defenses.” *Oecologia* 160 (3): 537–49. https://doi.org/10.1007/s00442-009-1309-x.

Rothman, Lorne D. 1997. “Immediate and Delayed Effects of a Viral Pathogen and Density on Tent Caterpillar Performance.” *Ecology* 78 (5): 1481–93. https://doi.org/10.1890/0012-9658(1997)078[1481:IADEOA]2.0.CO;2.

Rothman, Lorne D., and Jens Roland. 1998. “Forest Fragmentation and Colony Performance of Forest Tent Caterpillar.” *Ecography* 21 (4): 383–91.

Rothman, Lorne, and Judith Myers. 1996. “Is Fecundity Correlated with Resistance to Viral Disease in the Western Tent Caterpillar?” *Ecological Entomology* 21 (4): 396–98. https://doi.org/10.1046/j.1365-2311.1996.00029.x.

Royama, T. 1984. “Population Dynamics of the Spruce Budworm Choristoneura Fumiferana.” *Ecological Monographs* 54 (4): 429–62. https://doi.org/10.2307/1942595.

Royama, T., and T. Royama. 1992. “Basic Properties and Structure of Population Processes.” *Analytical Population Dynamics*, 3–46.

Royama, Tomo-o. 2001. “Measurement, Analysis, and Interpretation of Mortality Factors in Insect Survivorship Studies, with Reference to the Spruce Budworm, Choristoneura Fumiferana (Clem.) (Lepidoptera: Tortricidae).” *Population Ecology* 43 (2): 157–78. https://doi.org/10.1007/PL00012027.

Russell, Edmund P. 1989. “Enemies Hypothesis: A Review of the Effect of Vegetational Diversity on Predatory Insects and Parasitoids.” *Environmental Entomology* 18 (4): 590–99.

Sabelis, Maurice W. 1992. “Predatory Arthropods.” In *Natural Enemies: The Population Biology of Predators, Parasites and Diseases*. Hoboken, New Jersey, USA: John Wiley & Sons. https://doi.org/10.1002/9781444314076.ch10.

Sandén, Hans, Mathias Mayer, Sari Stark, Taru Sandén, Lars Ola Nilsson, Jane Uhd Jepsen, Piippa Riitta Wäli, and Boris Rewald. 2020. “Moth Outbreaks Reduce Decomposition in Subarctic Forest Soils.” *Ecosystems* 23: 151–63.

Saravesi, Karita, Sami Aikio, Piippa R. Wäli, Anna Liisa Ruotsalainen, Maarit Kaukonen, Karoliina Huusko, Marko Suokas, Shawn P. Brown, Ari Jumpponen, and Juha Tuomi. 2015. “Moth Outbreaks Alter Root-Associated Fungal Communities in Subarctic Mountain Birch Forests.” *Microbial Ecology* 69: 788–97.

Schall, Peter, Martin M. Gossner, Steffi Heinrichs, Markus Fischer, Steffen Boch, Daniel Prati, Kirsten Jung, Vanessa Baumgartner, Stefan Blaser, and Stefan Böhm. 2018. “The Impact of Even-Aged and Uneven-Aged Forest Management on Regional Biodiversity of Multiple Taxa in European Beech Forests.” *Journal of Applied Ecology* 55 (1): 267–78.

Schindelin, Johannes, Ignacio Arganda-Carreras, Erwin Frise, Verena Kaynig, Mark Longair, Tobias Pietzsch, Stephan Preibisch, Curtis Rueden, Stephan Saalfeld, and Benjamin Schmid. 2012. “Fiji: An Open-Source Platform for Biological-Image Analysis.” *Nature Methods* 9 (7): 676–82.

Schlyter, P, I Stjernquist, L Bärring, Am Jönsson, and C Nilsson. 2006. “Assessment of the Impacts of Climate Change and Weather Extremes on Boreal Forests in Northern Europe, Focusing on Norway Spruce.” *Climate Research* 31 (June): 75–84. https://doi.org/10.3354/cr031075.

Schowalter, Timothy D. 2017. “Biology and Management of the Forest Tent Caterpillar (Lepidoptera: Lasiocampidae).” *Journal of Integrated Pest Management* 8 (1). https://doi.org/10.1093/jipm/pmx022.

Seibold, Sebastian, Claus Bässler, Roland Brandl, Boris Büche, Alexander Szallies, Simon Thorn, Michael D. Ulyshen, and Jörg Müller. 2016. “Microclimate and Habitat Heterogeneity as the Major Drivers of

Beetle Diversity in Dead Wood." *Journal of Applied Ecology* 53 (3): 934–43. https://doi.org/10.1111/1365-2664.12607.

Serttaş, Ayhan, Özer Bakar, Uğur Melih Alkan, Arif Yılmaz, Halil Ibrahim Yolcu, and Kahraman Ipekdal. 2020. "Nest Survival and Transplantation Success of Formica Rufa (Hymenoptera: Formicidae) Ants in Southern Turkey: A Predictive Approach." *Forests* 11 (5): 533.

Settle, William H, Hartjahyo Ariawan, Endah Tri Astuti, Widyastama Cahyana, Arief Lukman Hakim, Dadan Hindayana, and Alifah Sri Lestari. 1996. "Managing Tropical Rice Pests through Conservation of Generalist Natural Enemies and Alternative Prey." *Ecology* 77 (7): 1975–88.

Shepperd, Wayne D., Dale L. Bartos, and Stephen A. Mata. 2001. "Above-and below-Ground Effects of Aspen Clonal Regeneration and Succession to Conifers." *Canadian Journal of Forest Research* 31 (5): 739–45.

Silveira, Juliana M., Julio Louzada, Jos Barlow, Rafael Andrade, Luiz Mestre, Ricardo Solar, Sébastien Lacau, and Mark A. Cochrane. 2016. "A Multi-Taxa Assessment of Biodiversity Change after Single and Recurrent Wildfires in a Brazilian Amazon Forest." *Biotropica* 48 (2): 170–80.

Sinclair, Brent J. 2015. "Linking Energetics and Overwintering in Temperate Insects." *Journal of Thermal Biology* 54: 5–11.

Sinclair, Brent J., and Steven L. Chown. 2005. "Deleterious Effects of Repeated Cold Exposure in a Freeze-Tolerant Sub-Antarctic Caterpillar." *Journal of Experimental Biology* 208 (5): 869–79.

Sinclair, Brent J., Laura V. Ferguson, Golnaz Salehipour-Shirazi, and Heath A. MacMillan. 2013. "Cross-Tolerance and Cross-Talk in the Cold: Relating Low Temperatures to Desiccation and Immune Stress in Insects." *Integrative and Comparative Biology* 53 (4): 545–56.

Sinclair, Brent J., and Katie E. Marshall. 2018. "The Many Roles of Fats in Overwintering Insects." Edited by Raul K. Suarez and Hans H. Hoppeler. *Journal of Experimental Biology* 221 (Suppl_1): jeb161836. https://doi.org/10.1242/jeb.161836.

Sippell, WL. 1962. "Outbreaks of the Forest Tent Caterpillar, Malacosoma Disstria Hbn., a Periodic Defoliator of Broad-Leaved Trees in Ontario." *The Canadian Entomologist* 94 (4): 408–16.

Sirois, Luc. 1993. "Impact of Fire on Picea Mariana and Pinus Banksiana Seedlings in Subarctic Lichen Woodlands." *Journal of Vegetation Science* 4 (6): 795–802.

Slavicek, James M., John Podgwaite, and Carita Lanner-Herrera. 1992. "Properties of Two Lymantria Dispar Nuclear Polyhedrosis Virus Isolates Obtained from the Microbial Pesticide Gypchek." *Journal of Invertebrate Pathology* 59 (2): 142–48. https://doi.org/10.1016/0022-2011(92)90024-X.

Solar, Ricardo Ribeiro de Castro, Jos Barlow, Alan N. Andersen, José H. Schoereder, Erika Berenguer, Joice N. Ferreira, and Toby Alan Gardner. 2016. "Biodiversity Consequences of Land-Use Change and Forest Disturbance in the Amazon: A Multi-Scale Assessment Using Ant Communities." *Biological Conservation* 197 (May): 98–107. https://doi.org/10.1016/j.biocon.2016.03.005.

Sorensen, Thorvald A. 1948. "A Method of Establishing Groups of Equal Amplitude in Plant Sociology Based on Similarity of Species Content and Its Application to Analyses of the Vegetation on Danish Commons." *Biol. Skar.* 5: 1–34.

Souza, Roberth Fagundes, Diego V. Anjos, Raquel Carvalho, and Kleber Del-Claro. 2015. "Availability of Food and Nesting-Sites as Regulatory Mechanisms for the Recovery of Ant Diversity after Fire Disturbance." *Sociobiology* 62 (1): 1–9.

Stairs, G. R. 1965. "Quantitative Differences in Susceptibility to Nuclear-Polyhedrosis Virus among Larval Instars of the Forest Tent Caterpillar, Malacosoma Disstria (Hübner)." *Journal of Invertebrate Pathology* 7 (4): 427–29. https://doi.org/10.1016/0022-2011(65)90117-5.

Stelzer, Milton J. 1967. "Control of a Tent Caterpillar, Malacosoma Fragile Incurva, with an Aerial Application of a Nuclear-Polyhedrosis Virus and Bacillus Thuringiensis." *Journal of Economic Entomology* 60 (1): 38–41. https://doi.org/10.1093/jee/60.1.38.

Stiles, Brad, John P. Burand, Marta Meda, and H. A. Wood. 1983. "Characterization of Gypsy Moth (Lymantria Dispar) Nuclear Polyhedrosis Virus." *Applied and Environmental Microbiology* 46 (2): 297–303.

Stockan, Jenni A., Shaila Rao, and Robin Pakeman. 2010. "Nesting Preferences of the Threatened Wood

Ant Formica Exsecta (Hymenoptera: Formicidae); Implications for Conservation in Scotland." *Journal of Insect Conservation* 14 (3): 269–76. https://doi.org/10.1007/s10841-009-9255-9.

Subedi, Anoj, Philippe Marchand, Yves Bergeron, Hubert Morin, and Miguel Montoro Girona. 2023. "Climatic Conditions Modulate the Effect of Spruce Budworm Outbreaks on Black Spruce Growth." *Agricultural and Forest Meteorology* 339: 109548.

Swank, Wayne T., J. B. Waide, D. A. Crossley, and R. L. Todd. 1981. "Insect Defoliation Enhances Nitrate Export from Forest Ecosystems." *Oecologia* 51 (3): 297–99.

Sweeney, Bernard W, and Robin L Vannote. 1982. "Population Synchrony in Mayflies: A Predator Satiation Hypothesis." *Evolution*, 810–21.

Sweeney, Jon, Kevin J. Dodds, Christopher J. Fettig, and Angus J. Carnegie. 2023. "IPM: The Forest Context." In *Forest Entomology and Pathology: Volume 1: Entomology*, 581–646. Springer.

Symondson, WOC, KD Sunderland, and MH Greenstone. 2002. "Can Generalist Predators Be Effective Biocontrol Agents."

Taylor, Steve W, Allan L Carroll, René I Alfaro, Les Safranyik, and Bill Wilson. 2006. "The Mountain Pine Beetle: A Synthesis of Biology, Management, and Impacts in Lodgepole Pine." Victoria: Canadian Forest Service, Natural Resources Canada. https://scholar.google.com/scholar_lookup?title=The%20Mountain%20Pine%20Beetle%3A%20A%20Synthesis%20of%20Biology%2C%20Management%20and%20Impacts%20in%20Lodgepole%20Pine&pages=67-94&publication_year=2006&author=Taylor%2CSW&author=Carroll%2CAL&author=Alfaro%2CRI&author=Safranyik%2CL.

Thunes, Karl H, Ivar Gjerde, and John Skartveit. 2018. "The Red Wood Ant Formica Aquilonia (Hymenoptera : Formicidae) May Affect Both Local Species Richness and Composition at Multiple Trophic Levels in a Boreal Forest Ecosystem." *Annales Zoologici Fennici* 55: 159–72. https://doi.org/10.5735/086.055.0603.

Tilman, David. 1978. "Cherries, Ants and Tent Caterpillars: Timing of Nectar Production in Relation to Susceptibility of Caterpillars to Ant Predation." *Ecology* 59 (4): 686–92. https://doi.org/10.2307/1938771.

Tobin, Patrick C. 2008. *Cost Analysis and Biological Ramifications for Implementing the Gypsy Moth Slow the Spread Program*. Vol. 37. US Department of Agriculture, Forest Service, Northern Research Station.

Tobin, Patrick C., Alexei A. Sharov, Andrew A. Liebhold, Donna S. Leonard, Anderson E. Roberts, and Matthew R. Learn. 2004. "Management of the Gypsy Moth through a Decision Algorithm under the STS Project." *American Entomologist* 50 (4): 200–209.

Trudeau, M., Y. Mauffette, S. Rochefort, E. Han, and E. Bauce. 2010. "Impact of Host Tree on Forest Tent Caterpillar Performance and Offspring Overwintering Mortality." *Environmental Entomology* 39 (2): 498–504. https://doi.org/10.1603/EN09139.

Turchin, P., AD Taylor, and JD Reeves. 1999. "Dynamical Role of Predators in Population Cycles of a Forest Insect: An Experimental Test." *Science* 285 (5430): 1068–71. https://doi.org/10.1126/science.285.5430.1068.

Turchin, Peter, Simon N. Wood, Stephen P. Ellner, Bruce E. Kendall, William W. Murdoch, Andreas Fischlin, Jerome Casas, Edward McCauley, and Cheryl J. Briggs. 2003. "Dynamical Effects of Plant Quality and Parasitism on Larch Budmoth." *Ecology* 84 (5): 1207–14. https://doi.org/10.1890/0012-9658(2003)084[1207:DEOPQA]2.0.CO;2.

Uelmen, Johnny A., John G. Duman, Richard L. Lindroth, Ezra G. Schwartzberg, and Kenneth F. Raffa. 2016. "Supercooling Points of Diapausing Forest Tent Caterpillar (Lepidoptera: Lasiocampidae) Eggs." *The Canadian Entomologist* 148 (5): 512–19. https://doi.org/10.4039/tce.2015.88.

Uelmen, Johnny A., Richard L. Lindroth, Patrick C. Tobin, Peter B. Reich, Ezra G. Schwartzberg, and Kenneth F. Raffa. 2016. "Effects of Winter Temperatures, Spring Degree-Day Accumulation, and Insect Population Source on Phenological Synchrony between Forest Tent Caterpillar and Host Trees." *Forest Ecology and Management* 362 (February): 241–50. https://doi.org/10.1016/j.foreco.2015.11.045.

Underwood, Emma C., and Brian L. Fisher. 2006. “The Role of Ants in Conservation Monitoring: If, When, and How.” *Biological Conservation* 132 (2): 166–82.

University of California Davis. 2015. “Definition of Integrated Pest Management.” 2015. https://www2.ipm.ucanr.edu/What-is-IPM/.

Vannatta, A. R., R. H. Hauer, and N. M. Schuettpelz. 2012. “Economic Analysis of Emerald Ash Borer (Coleoptera: Buprestidae) Management Options.” *Journal of Economic Entomology* 105 (1): 196–206.

Vasconcelos, Heraldo L., Jonas B. Maravalhas, and Tatiana Cornelissen. 2017. “Effects of Fire Disturbance on Ant Abundance and Diversity: A Global Meta-Analysis.” *Biodiversity and Conservation* 26 (1): 177–88.

Véle, Adam, Jaroslav Holuša, and Jakub Horák. 2016. “Ant Abundance Increases with Clearing Size.” *Journal of Forest Research* 21 (2): 110–14.

Vellend, Mark, Lander Baeten, Isla H Myers-Smith, Sarah C Elmendorf, Robin Beauséjour, Carissa D Brown, Pieter De Frenne, Kris Verheyen, and Sonja Wipf. 2013. “Global Meta-Analysis Reveals No Net Change in Local-Scale Plant Biodiversity over Time.” *Proceedings of the National Academy of Sciences of the United States of America* 110 (48): 19456–59. https://doi.org/10.1073/pnas.1312779110.

Vincent, Jean-Serge, and Léon Hardy. 1977. “L’évolution et l’extension Des Lacs Glaciaires Barlow et Ojibway En Territoire Québécois.” *Géographie Physique et Quaternaire* 31 (3–4): 357–72.

Vindstad, Ole Petter Laksforsmo, Sabrina Schultze, Jane Uhd Jepsen, Erik Martin Biuw, Lauri Teemu Kapari, Anne Sverdrup-Thygeson, and Rolf Anker Ims. 2014. “Numerical Responses of Saproxylic Beetles to Rapid Increases in Dead Wood Availability Following Geometrid Moth Outbreaks in Sub-Arctic Mountain Birch Forest.”

Volkman, Loy, and Basil Keddie. 1990. “Nuclear Polyhedrosis Virus Pathogenesis.” *Semin. Virol.* 1 (January): 249–56.

Volney, W.Jan A, and Richard A Fleming. 2000. “Climate Change and Impacts of Boreal Forest Insects.” *Agriculture, Ecosystems & Environment* 82 (1–3): 283–94. https://doi.org/10.1016/S0167-8809(00)00232-2.

Wardle, David A., Fujio Hyodo, Richard D. Bardgett, Gregor W. Yeates, and Marie-Charlotte Nilsson. 2011. “Long-Term Aboveground and Belowground Consequences of Red Wood Ant Exclusion in Boreal Forest.” *Ecology* 92 (3): 645–56. https://doi.org/10.1890/10-1223.1.

Watt, Kenneth EF. 1960. “The Effect of Population Density on Fecundity in Insects.” *The Canadian Entomologist* 92 (9): 674–95.

Way, M J, and K C Khoo. 1992. “Role of Ants in Pest Management,” 27.

Wellington, W. G. 1957. “Individual Differences as a Factor in Population Dynamics: The Development of a Problem.” *Canadian Journal of Zoology* 35 (3): 293–323.

———. 1960. “Qualitative Changes in Natural Populations during Changes in Abundance.” *Canadian Journal of Zoology* 38 (2): 289–314.

Wellington, W. G., P. J. Cameron, W. A. Thompson, I. B. Vertinsky, and A. S. Landsberg. 1975. “A Stochastic Model for Assessing the Effects of External and Internal Heterogeneity on an Insect Population.” *Population Ecology* 17 (1): 1–28.

Weseloh, R. M. 1989. “Simulation of Predation by Ants Based on Direct Observations of Attacks on Gypsy Moth Larvae.” https://doi.org/10.4039/ENT1211069-12.

Wetzel, B. W., H. M. Kulman, and J. A. Witter. 1973. “Effects of Cold Temperatures on Hatching of the Forest Tent Caterpillar , Malacosoma Disstria (Lepidoptera, Lasiocampidae).” *The Canadian Entomologist* 105: 1145–49.

Wheeler, George Carlos, Jeanette Wheeler, and others. 1963. *The Ants of North Dakota*. University of North Dakota Grand Forks.

Williams, Caroline M., Hugh AL Henry, and Brent J. Sinclair. 2015. “Cold Truths: How Winter Drives Responses of Terrestrial Organisms to Climate Change.” *Biological Reviews* 90 (1): 214–35.

Williams, Caroline M., Katie E. Marshall, Heath A. MacMillan, Jason DK Dzurisin, Jessica J. Hellmann, and Brent J. Sinclair. 2012. “Thermal Variability Increases the Impact of Autumnal Warming and Drives Metabolic Depression in an Overwintering Butterfly.” *PLoS One* 7 (3): e34470.

Williams, D J M, D Parry, and D.W. Langor. 1996. “Sampling and Identification of Forest Tent Caterpillar Parasitoids in the Prairie Provinces.” 1. Canadian Forest Service Northern Forestry Centre Information.

Williams, Kathy S, Kimberly G Smith, and Frederick M Stephen. 1993. “Emergence of 13-Yr Periodical Cicadas (Cicadidae: Magicicada): Phenology, Mortality, and Predators Satiation.” *Ecology* 74 (4): 1143–52.

Witter, J. A. 1979. “The Forest Tent Caterpillar (Lepidoptera: Lasiocampidae) in Minnesota: A Case History Review.” *Great Lakes Entomologist* 12 (4): 191–97.

Witter, J A, and H M Kulman. 2017. “Estimating the Number of Eggs per Egg Mass of the Forest Tent Caterpillar, Malacosoma Disstria (Lepidoptera: Lasiocampidae)” 2 (2): 10.

Witter, JA, WJ Mattson, and HM Kulman. 1975. “Numerical Analysis of a Forest Tent Caterpillar (Lepidoptera: Lasiocampidae) Outbreak in Northern Minnesota.” *The Canadian Entomologist* 107 (8): 837–54.

Woods, S. A., and J. S. Elkinton. 1987. “Biomodal Patterns of Mortality from Nuclear Polyhedrosis Virus in Gypsy Moth (Lymantria Dispar) Populations.” *Journal of Invertebrate Pathology* 50 (2): 151–57.

Work, Timothy T, David P Shorthouse, John R Spence, W Jan A Volney, and David Langor. 2004. “Stand Composition and Structure of the Boreal Mixedwood and Epigaeic Arthropods of the Ecosystem Management Emulating Natural Disturbance (EMEND) Landbase in Northwestern Alberta.” *Canadian Journal of Forest Research* 34 (2): 417–30. https://doi.org/10.1139/x03-238.

Yamamoto, Shin-Ichi. 2000. “Forest Gap Dynamics and Tree Regeneration.” *Journal of Forest Research* 5 (4): 223–29.

Yang, L. H. 2006. “Interactions between a Detrital Resource Pulse and a Detritivore Community.” *Oecologia* 147 (3): 522–32. https://doi.org/10.1007/s00442-005-0276-0.

Yang, Louie H. 2006. “Interactions between a Detrital Resource Pulse and a Detritivore Community.” *Oecologia* 147 (3): 522–32. https://doi.org/10.1007/s00442-005-0276-0.

Yang, Louie H., Kyle F. Edwards, Jarrett E. Byrnes, Justin L. Bastow, Amber N. Wright, and Kenneth O. Spence. 2010. “A Meta-Analysis of Resource Pulse–Consumer Interactions.” *Ecological Monographs* 80 (1): 125–51. https://doi.org/10.1890/08-1996.1.

York, Alan. 2000. “Long-Term Effects of Frequent Low-Intensity Burning on Ant Communities in Coastal Blackbutt Forests of Southeastern Australia.” *Austral Ecology* 25 (1): 83–98.

Yusah, Kalsum M., William A. Foster, Glen Reynolds, and Tom M. Fayle. 2018. “Ant Mosaics in Bornean Primary Rain Forest High Canopy Depend on Spatial Scale, Time of Day, and Sampling Method.” *PeerJ* 6: e4231.

Zalucki, Myron P., Anthony R. Clarke, and Stephen B. Malcolm. 2002. “Ecology and Behavior of First Instar Larval Lepidoptera.” *Annual Review of Entomology* 47 (1): 361–93. https://doi.org/10.1146/annurev.ento.47.091201.145220.