SERG Final report: **Ecosystemic impacts of forest tent caterpillar outbreaks**

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Abstract

The forest tent caterpillar (*Malacosoma disstria*) is a significant defoliator of hardwoods throughout Canada. Historically, infestations usually collapsed after one or two years of defoliation, but longer and more severe outbreaks have been observed in recent years, leading to mortality of both sugar maple and trembling aspen, and making the forest tent caterpillar another pest whose impacts are increasing under a changing climate.

This project examines how forest tent caterpillar outbreaks influence soil ecosystems, in both temperate deciduous and mixed boreal forests. We will assess inputs to soil ecosystems associated with forest tent caterpillar outbreaks and determine impacts on soil arthropod communities and tree regeneration. We also examine the different sources of mortality of the forest tent caterpillar colonies during and after the outbreak. It will thus provide empirical data to assess effects of forest tent caterpillar outbreaks on forest ecosystems and successional processes as well as population dynamics throughout the outbreaking cycle. Results suggest that defoliation favours the growth of non-host saplings. They also suggest that sources of mortality change during the different parts of the outbreak. Results will also contribute to the development of novel silvicultural approaches taking into account the effects of forest tent caterpillar outbreaks on forest regeneration and the need to keep process promoting regulation of forest tent caterpillar populations.

Résumé

La livrée des forêts (*Malacosoma disstria*) est un défoliateur important des forêts feuillues du Canada. Dans le passé, les épidémies s'effondraient généralement après une ou deux années de défoliation sans causer de dommages significatifs à la forêt, mais l'observation récente d'épidémies plus longues et plus sévères, suivies de mortalité des tiges de peuplier faux-tremble et d'érable à sucre, suggèrent que les impacts de la livrée des forêts, comme de plusieurs autres insectes ravageurs, augmentent en raison des changements climatiques.

Ce projet examine les effets d'une épidémie de livrée des forêts sur l'écosystème du sol dans deux écosystèmes forestiers: la forêt feuillue et la forêt boréale mixte. Nous examinerons les apports en nutriments au sol associés aux épidémies de livrée et évaluerons les effets sur la communauté d'arthropodes du sol et sur la régénération des arbres. Nous avons aussi examiné les sources de mortalité des colonies de livrée des forêts durant et après l'épidémie. Les résultats fourniront des données empiriques pour évaluer les impacts des épidémies de livrée sur les écosystèmes forestiers et les processus de succession écologiques ainsi que les dynamiques de populations à travers les cycles épidémiques. Les résultats suggèrent que la défoliation peut bénéficier la croissance des jeunes arbres non-hôtes. Ils suggèrent aussi que les sources de mortalité diffèrent lors des différentes parties du cycles épidémiques. Les résultats contribueront aussi au développement d'approches sylvicoles qui prennent en considération le rôle de la livrée dans la régénération des forêts.

Background

Insect outbreaks shape forest stands and landscapes. They not only cause loss of productivity, stand decline and tree mortality, but can also influence soil processes and forest regeneration. Under a changing climate, these outbreaks are becoming more unpredictable in terms of frequency, severity, duration and spatial scale, and hence their effects on forest ecosystems require further study. We investigate whether forest tent caterpillar outbreaks can initiate a trophic cascade.

Trophic cascades occur when top-down pressure from predators spread downward through food webs influencing an entire community beyond the prey species. In this case, forest tent caterpillar outbreaks could influence forest ecosystems beyond the simple negative effect on defoliated trees, by increasing nutrient inputs to soil ecosystems and thus promoting activity of soil microbial and invertebrate communities and stimulating tree growth. As insects eat foliage, nutrients contained in leaves fall to the soil as insect frass, exuviae and carcasses, as well as greenfall and leachate. This organic matter pulse can stimulate decomposition, increasing nutrient availability for plants. Herbivory thus provides an influx of nitrogen-based resources; and since, nitrogen is the main limiting nutrient in forest ecosystems, even a short-term pulse can have significant long-term effects. Indeed, in both deciduous and mixedwood forests, experimental manipulations of frass and greenfall have been shown to increase soil respiration and soil nutrient cycling (Hunter 2001). Soil arthropods play a role in accelerating nutrient cycling, and also benefit from higher nutrient availability, often via an increase in community abundance and diversity. Nutrient pulses are likely to increase abundance and species richness of ants, spiders, beetles, and microarthropods (Yang 2006). In addition, nutrient, particularly nitrogen, influxes in soil clearly benefit plants in general, but can also influence the outcome of competition between species and thus affect stand composition.

The forest tent caterpillar (*Malacosoma disstria*) is a significant defoliator of hardwood stands throughout Canada. In Quebec, there are two foci in which outbreaks appear to cycle independently: one in the south on sugar maple *(Acer saccharum*) and one in the northwest on trembling aspen (*Populus tremuloides*) (Cooke and Lorenzetti 2006). Severe outbreaks occur at approximately 10-year intervals, last for 2-5 years causing complete defoliation of host trees, then collapse dramatically. Outbreak collapses seem to be due to to parasitoids and diseases, but the mortality sources responsible for keeping endemic populations low ae less well understood and generalist predators could be involved (Nixon & Roland) (Berryman 1996).. Historically, infestations usually collapsed after one or two years of defoliation with relatively little damage to forest stands, but longer and more severe outbreaks have been observed in more recent years (Man and Rice 2010), leading to stem mortality in both trembling aspen (Cooke et al 2009; Perrette et al 2014) and sugar maple (Hartmann & Messier 2008; Wood et al 2009).

Indeed, forest tent caterpillar outbreaks negatively impact growth, nutrient and energy translocation of host trees, which has negative implications for the tree's resilience in the face of other disturbances (Hartmann & Messier 2008; Wood et al 2009; Perrette et al. 2014). They have also been suggested to increase canopy opening and to accelerate succession from deciduous trees to conifers in mixed boreal forest (Moulinier et al. 2013). The implications of forest tent caterpillar outbreaks for soil processes are predicted to differ between the boreal mixedwood and temperate forests of Quebec. The main host plant attacked by the forest tent caterpillar is trembling aspen in the boreal mixedwood, and sugar maple in the temperate deciduous forest. In the aspen stands of the boreal mixedwood forest, the overstory canopy decline due to intense outbreaks is expected to release understory conifers and accelerate forest succession from hardwood to conifer dominance (Moulinier 2013). It is harder to make predictions for the temperate deciduous forest, but one might expect increased growth of understory saplings (Rozendaal & Kobe 2016), an acceleration of the current climate-related sugar maple decline (Bishop et al 2015) and a transition to mixed stands with American beech (Nolet et al. 2008).

Objectives

We measured the effects of a forest tent caterpillar outbreak that occurred in 2016-2017 on 1) soil nutrient availability, 2) soil arthropod communities with specific focus on ants, and 3) tree seedling growth. We monitored these processes in two Quebec forest biomes: the temperate broadleaf and boreal mixedwood forests. We also measured 4) the sources responsible for forest tent caterpillar mortality in both outbreak-affected and control stands.

Methods

Study sites

Studies are conducted in parallel at Kenauk Nature Reserve (broadleaf forest, Outaouais region) and FERLD (boreal mixedwood, Abitibi). Both these sites had been heavily defoliated by a forest tent caterpillar outbreak in 2016 and 2017, but no significant defoliation was recorded in 2018. Our project thus investigates ecosystem processes following the outbreak, comparing defoliated and non-defoliated (control) plots at each site. Sampling was conducted in the in 2018 and 2019 field seasons.

The Lake Duparquet Research and Teaching Forest (FERLD) is a forested area dedicated to forest ecology research created in 1996 and located in the boreal mixedwood forest within the balsam fir-white birch bioclimatic domain (48°30' N, 79°22' O). Soils are luvisoils on glaciolacustrine clay deposits and are rich in basic cations but have poor drainage. The sites used in this study are 95-year-old aspen stands originating from a 1923 fire (UQAT, 2019); defoliated plots (N=14) experienced complete defoliation by the forest tent caterpillar in 2015-2017 but none in 2018. No defoliation was observed in control plots (N=13). The dominant tree is trembling aspen, and the recruitment layer includes trembling aspen, striped maple and balsam fir saplings.

Kenauk Nature Reserve is a private reserve located in Southwest Quebec, in the sugar maple-basswood bioclimatic domain with very few conifers (45°71' N, 74°89' O). Podzols rich in nutrients are the dominant soil types, developed in the glacial till left from the most recent Ice Age (Robitaille et Saucier, 1998). The forest in Kenauk has not experienced significant natural disturbances apart from insect outbreaks. Therefore, most stands are in a late successional stage, showing a strong dominance by sugar maple with sugar maple, American beech and black cherry in the shaded understory. The defoliated plots (N = 12) experienced severe forest tent caterpillar defoliation in 2016 and 2017 but none in 2018, and no caterpillar activity was observed in the control plots (N=12).

Soil chemistry and sapling regeneration

In each plot, three 40 m^2 subplots were installed during the 2018 field season. Within each plot, we tallied saplings (stems < 5 cm DBH) of the host plant (sugar maple in the temperate forest, trembling aspen in the boreal) and of the main understory competitor (American beech in the temperate and balsam fir in the boreal forest). Terminal height increment over the past three years (2016-2018) was measured on all saplings: this corresponds to two years during high defoliation and one year following the outbreak. We also collected soil samples for chemical analyses (pH, C, N, P, Ca, Mg, and cation exchange capacity). Soil samples were collected in the three sub-plots in July 2018 and 2019, in order to follow a time course of soil processes over 2 years following the outbreak.

Arthropod communities:
Sampling was done in 2018 and 2019 to get a picture of the soil arthropod community and of the forest tent caterpillar natural enemies. Arthropod sampling involved placing three pitfall traps per site at ground-level, and three sugar-baited falcon tubes in the canopy of a dominant tree. To identify larval parasitoids, individual forest tent caterpillars were collected from each site at the late larval stages and reared to pupation. The individuals were checked regularly to see if parasitoids had emerged and, if so, the parasitoids were collected and stored in ethanol for identification.

Included in the natural enemy counts were the following groups, previously shown to feed on forest tent caterpillars:

- Stink bugs (Hemiptera)
- Beetles, especially from the genus *Calosoma*
- Spiders
- Parasitoids (both Hymenopteran and Dipteran)
- Ants

Each group will be counted, but identification to genus or species will only be done for ants and parasitoids, while the other groups will be grouped at higher taxonomic level. The sampling was done twice in each field season: during the first two weeks of June and the last two weeks of July, to get a snapshot of the community while keeping the number of specimens manageable. For the ants, abundance was calculated in terms of presence/absence in traps since, because of eusocial life history, high abundance of individual ants does not mean higher abundance of ant colonies surrounding the focal tree.

Larval mortality:
The data are presented only for FERLD since the sampling size was insufficient to do meaningful analysis at Kenauk. At each site, a triad of experimental devices were set up in aspen saplings, each categories of device in a different sapling (between 1 and 3 m tall) to quantify sources of larval mortality in 2017, 2018 and 2019. These egg masses were placed in aspen samplings in late May (a little before hatching) and left until late June (when forest tent caterpillar reach 4th instar) in one of three set-ups. Each triad contained these three different set-ups referred to from now on as enclosure treatments:

- Free: an egg mass is attached to a branch, making the emerging colony vulnerable to both flying and crawling natural enemies.
- Tanglefoot: The base of the branch on which the egg mass is placed is coated with Tanglefoot (the Tanglefoot Company), a physical barrier made from a sticky non-drying resin. This barrier prevents crawling arthropods, but not flying predators/parasitoids, from reaching the sentinel caterpillar colony.
- Caged: A fine mesh cage encloses the branch on which the egg mass is placed, excluding all predators and parasitoids.

Egg masses were collected in early spring in the outbreaking stand and stored in a refrigerator at 4°C until they were installed in the trees shortly before budburst (i.e. 23-05-2017, 28-05-2018, 06-06-2019). Before being placed in the trees, the egg masses were sterilized with bleach (Grisdale 1968). This method prevents the spread of pathogens that could be present on the twig to which the egg mass is attached.

In 2017 and 2018, we placed one egg mass on each of 84 trees across 28 sites (14 per defoliation level).

Colony monitoring

Colonies were monitored from hatching to the fourth larval stage when the colonies were taken down from the trees, before the free colonies began to disperse in the tree. All colonies were collected at the end of the experiment, and surviving larvae were counted. Egg masses were recovered and cleaned. Each egg was visually scored as either hatched, unhatched or unknown (either destroyed or with holes not concordant with forest tent caterpillar emergence) using NIS-Elements Br 3.0 imaging software (Nikon, Tokyo, Japan) and FIJI imaging software (Schindelin et al. 2012).

Larval survival rates were calculated as the number of observed live larvae divided by the number of hatched eggs.: *Sc* = survival rate of caged colonies, *St* = survival rate of tanglefoot colonies, *Sf*= survival rate of free colonies.

Results

Soil chemistry:

Soil nutrient results for 2018 are shown in Fig. 1. No increase in available nitrogen was observed in either temperate or boreal forest, but samples from both forests showed a minor increase in cation exchange capacity, linked to increase in Ca. Because of this lack of differences, the samples collected in 2019 were not analysed since the cost was too steep given the likeliness of obtaining similar results.

Sapling regeneration:

In the temperate forest, density of beech saplings did not differ between control and defoliated sites, but density of sugar maple saplings was higher on defoliated sites (Fig 2). Growth rate of sugar maple saplings was lower than that of beech saplings, but growth rates did not differ significantly between control and defoliated sites.

In the boreal mixedwood, aspen dominated the regeneration strata on both control and defoliated sites, but growth rate of fir increased considerably on defoliated sites, to exceed that of aspen (Fig. 3).

Total arthropod abundance:

The 2018 data shows that, in both types of forest (Fig. 4 and 5), slightly lower numbers of arthropods were observed in previously defoliated than in control sites. In both regions, flies were the most abundant group. No parasitoids were collected from the reared pupae.

Ant activity

The 2018 data shows that in the temperate forest, previously defoliated sites show lower presence of ants in the pitfall traps (35%) than in the control sites (45%), but, in the boreal forest, all traps contained ants (Fig.6). Ants from the temperate forest site have been identified to the genus level, allowing for comparison of community composition between control and defoliated sites; however, no significant difference was observed (Fig. 7).

Larval mortality:

As expected, larval survivorship was highest in the caged colonies, followed by the Tanglefoot colonies and then the free colonies, and the results show a significant effect of enclosure treatment ($p < 0.001$) (Fig 8). The enclosure treatments were all significantly different from one another with the Tukey post-hoc test showing $p \leq 0.001$ for all of the combinations. The free colonies show consistently lower survival than either caged and Tanglefoot colonies, in both control and defoliated stands and across all three years of the study. The results also show an effect of year (GLM, χ, $p < 0.0001$), but defoliation did not have quite a significant effect (GLM, χ, $p=0.007$) in terms of overall survivorship. Survival was higher during the last year of the outbreak (2017) than in the following year (Tukey HSD, $p < 0.001$) and control and outbreak sites were significantly different (Tukey HSD, $p = 0.001$).

Discussion

One year following the outbreak, no significant differences in soil nitrogen were observed between control and defoliated sites in either forest type, suggesting that any additional nitrogen released was rapidly taken up by soil organisms (Rozendaal & Kobe 2016). These results suggest rapid nutrient cycling, and research is underway to measure soil respiration as an index of the rate of uptake and cycling of nutrients. These results also do not inform as to whether additional nutrients liberated by defoliation had been taken up by plant roots or had fed an expanding food web; these questions were addressed by examining the density and growth of saplings and characterising arthropod communities.

In the temperate forest, defoliation appears to have increased density of sugar maple, but not of American beech saplings. Similar increases in sugar maple sapling density have been previously observed following opening of small canopy gaps, leading to the suggestion that slight increases in gaps could favour sugar maple over American beech (Nolet et al 2008). However, in our study, growth rate of beech saplings during and immediately following the outbreak was higher than that of maple, suggesting that beech could still outcompete maple (Bishop 2015). Previous work shows that growth and vigour of mature sugar maple trees were negatively affected by forest tent caterpillar defoliation, inciting stress and predisposing these trees to death later (Hartmann & Messier 2008; Wood et al 2009). Sugar maple is in decline over much of its range, including southern Quebec (Bishop 2015); forest tent caterpillar outbreaks are thought to contribute to the decline of mature sugar maple trees (Hartmann & Messier 2008; Wood et al 2009), but their impact on the understory, and hence on succession, is less clear (Cooke & Lorenzetti 2006; Rozendaal & Kobe 2016).

In the boreal mixedwood, although aspen saplings were more abundant than balsam fir on both control and defoliated sites, the growth rate of fir increased dramatically on defoliated sites, such that it surpasses that of aspen. This suggests that conditions linked to forest tent caterpillar outbreaks favour fir over aspen seedlings, leading to the increase in conifer cover observed after severe defoliation in longer term studies (Moulinier 2013). Factors responsible for this effect could include increased soil nutrients and increased light availability in canopy gaps. In addition, if the aspen saplings observed are root suckers of the adult trees, they could be further disadvantaged by the loss of carbohydrate reserves in roots linked to defoliation of the main stem (Man & Rice 2010). It also thought that aspens do not trigger suckering after defoliation because the apical dominance of mature trees remain intact, and therefore the auxin hormones remain in the aboveground area of the tree and cannot descend into the roots where the buds lay dormant (Bergeron et al. 2014). In addition, similar to what is observed in sugar maple, mortality of mature aspen trees tends to increase sharply several years after a forest tent caterpillar outbreak; and the extent of mortality increases with the number of years of defoliation (Cook et al 2009). The increased growth rate we observed in understory fir saplings could explain how, in this circumstance, forest tent caterpillar defoliation accelerates transition from aspen to conifer dominated stands (Man et Rice, 2010; Bergeron et al 2014).

Forest tent caterpillar defoliation thus appears to nudge forest composition away from host species, and our results suggest that, in the boreal forest, this is linked to increased growth rate of non-host fir saplings in the understory. A role of insect outbreaks in decreasing host density in forest stands implies a closed feedback loop between the effect of forest structure on insect dynamics, and the reciprocal impact of insects on the forest; indeed, a similar loop has also been shown for two other major Canadian defoliators, the jack pine budworm and the spruce budworm (Cooke et al 2009).

We did not observe the expected increase in soil arthropod abundance on defoliated sites. In fact, the defoliated sites had slightly lower arthropod abundance, even though the relationship was not significant. Analysis of 2019 samples is ongoing, and these additional data will elucidate trends of arthropod community response to the outbreak.

Several generalist predatory arthropods are known to prey on the forest tent caterpillars, especially in the early larval instars, including spiders, Hemipteran stink bugs, and predatious beetles (especially of the genus *Calosoma*). Flies and wasps, on the other hand, can include both generalist and specialist parasitoids. Although we observed rather low numbers of stink bugs and wasps, abundances of spiders, beetles and flies were high, especially in the temperate forest. This could imply increased opportunities for predation on forest tent caterpillars, but this has not been tested directly in our study. Further analysis, particularly species-level identification, will ascertain whether the individuals collected are functionally relevant to forest tent caterpillar predation.

Many of the observed arthropods are generalist predators and increased abundance could generate a feedback loop hat contributes to the decline of forest tent caterpllar outbreaks. However, generalist predators are adapted to persist at low-density host populations (Gould, Elkinton, and Wallner 1990), which could explain why they show no response to increase in one prey item, and thus do not differ between control and outbreak sites. Indeed, these generalist invertebrate predators are not generally thought to play an important role in the collapse of forest tent caterpillar outbeaks (Berryman, Nixon). Their high abundance in non-defoliated sites does support a role for controlling endemic forest tent caterpillar populations and preventing the onset of outbreaks.

Ants are particularly important in northern ecosystems. Moreover, forest tent caterpillars have been reported as a food source for some species of ants, especially species from the *Camponotus* carpenter ant genus (Parry, Spence, and Volney 1998; Green and Sullivan 1950). In the community analysis presented here, ants were only identified to genus. This is likely not a high enough taxonomic resolution to differentiate between communities and species-level identification is underway.

Ants are more likely candidates for density dependent predation on forest tent caterpillars than the other predatory arthropods examined here. The conditions created by the outbreak would promote the establishment of ant colonies, which could then feed on forest tent caterpillar at higher densities and contribute to suppressing the outbreak. Indeed, the creation of gaps and increase of nutrient flow during outbreaks could support the establishment of ant colonies. In the temperate forest, both control and outbreak sites show ants being present in less than half of the traps, showing that ants are not an intense pressure in these sites. In the boreal forest, we cannot make any inferences on the variation between the control and outbreak sites since all traps in these sites contained ants. This, however, can imply that ants could act as a bigger pressure in boreal than temperate forests.

Larval survivorship decreased from 2017 to 2018 regardless of caging treatment and was lower in outbreak sites. Lower survivorship in recently defoliated sites leads some credence to a lagged density dependence effect of mortality which could help keep populations down after the crash of the outbreak. However, the picture is more complicated than this.

We observed high numbers of predatory arthropods in both control and defoliated sites, and this is consistent with them contributing to keeping endemic populations low. The increase in caged mortality with defolation can be due to disease. Therefore, even though our egg masses were thoroughly cleaned before installation, the lack of control from other sources of exposure to NPV and the intrinsic resistance or lack thereof may have played a bigger part than what we initially thought. In the boreal forest sites, we observed higher mortality in 2017 than 2018 and, in terms of the enclosure treatments, mortality was higher in tanglefoot than caged and higher in free than in both tanglefoot and caged. Therefore, this suggests the impact of some flighted enemies (flies and wasps) as well as walking predators (ants, beetles, spiders and stink bugs). This difference in mortality was consistent with some of the arthropod results, owever see a higher impact of spiders in the outbreak sites, fitting with our hypothesis that previously defoliated sites would harbor generalist arthropods that could be feeding on forest tent caterpillars (Nixon and Roland 2012). The lack of differences in the outbreak groups might results from the fact that generalists will generally follow changes in prey densities rather rapidly (Haukioja et al. 1998). Therefore, even one year after the peak of the outbreak, the numbers of these predators might not reflect their propensity to use FTC as prey.

The difference in mortality we saw between years and defoliation history at FERLD could result from better overall growing conditions in the outbreak sites, which would explain why the outbreak was intense in these sites and that it was not present in the others, even with relatively close proximity. Good growing conditions could mean higher nutritional value in the leaves and, therefore, these sites would become more favorable for FTC colonies (Lorenzetti, Mauffette, and Bauce 1999). The outbreak sites were also more vegetatively diverse than the control sites, therefore being able to support a greater diversity or abundance of natural enemies (Root, 1973; Russell, 1989).

In Canada, natural disturbance-based forest management has traditionally been inspired by the effects of fire on forest ecosystems. However, insect outbreaks are also key elements of forest ecosystem dynamics and may have lasting effects on forest structure and composition through their effects on soil processes and tree regeneration (Hunter 2001). They can even contribute to shifting Canadian forests from carbon sinks to carbon sources (Cooke et al., 2009). The relationship of these outbreaks with the natural enemies, however, remains nebulous. There is a need to provide a better picture of the predator-parasitoid-prey complex which would lead a better understanding of the trophic interactions governing the outbreak. In this context, a better understanding of the effects of forest tent caterpillar outbreaks on soil arthropods and understory saplings is key to, both in broadleaf and boreal mixedwood forests, future monitoring of the effects of insect outbreaks on stand composition and structure, but there remains a piece of the puzzle missing.

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Figures

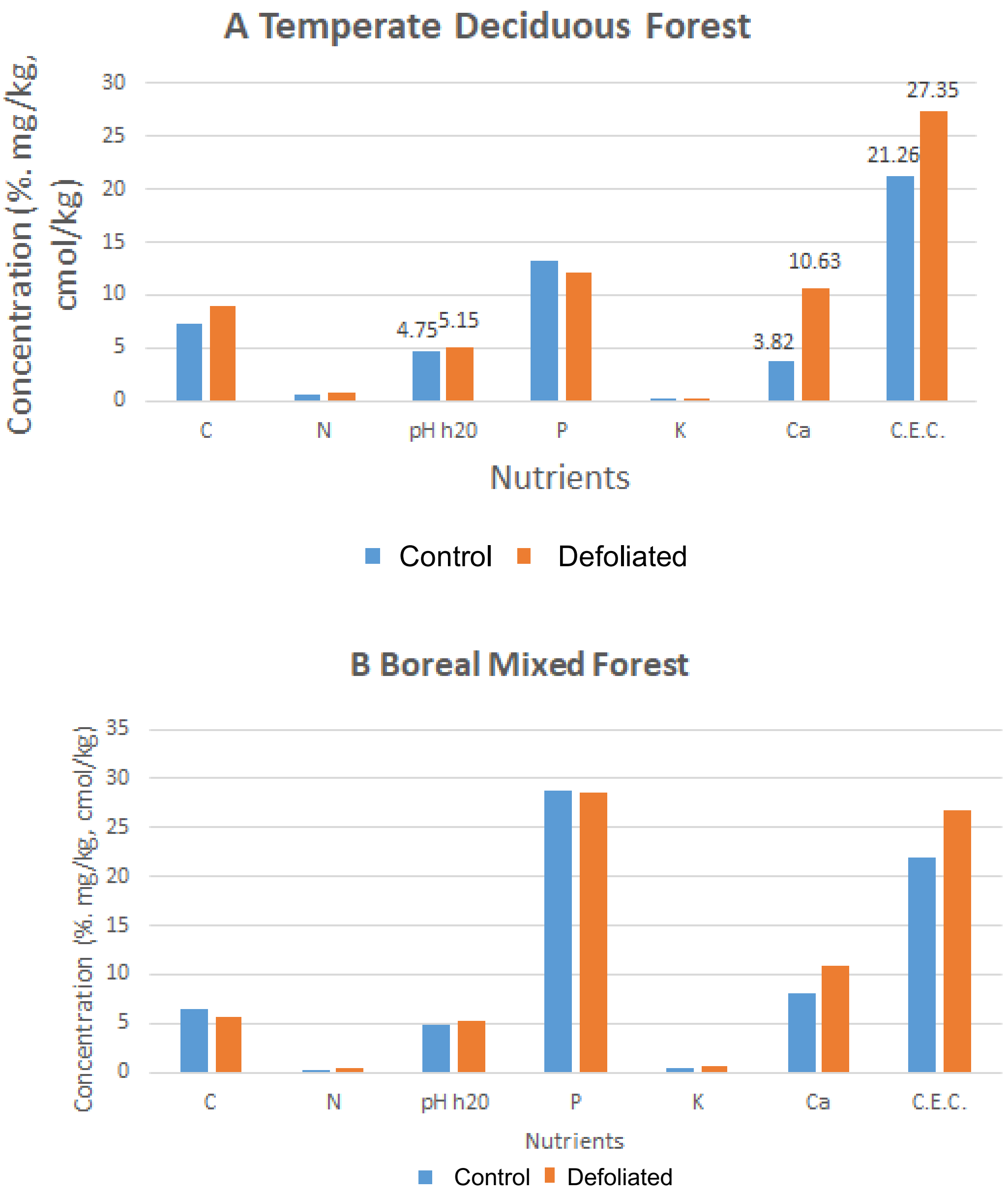

Fig 1: Soil chemical content measured in 2018 in defoliated (orange) and control (blue) plots in A temperate deciduous and B boreal mixedwood forests. Values shown include Carbon (C), Nitrogen (N), soil pH (pH H2O), Phosphorus (P), Potassium (K), Calcium (Ca) and total cation exchange capacity (C.E.C.).

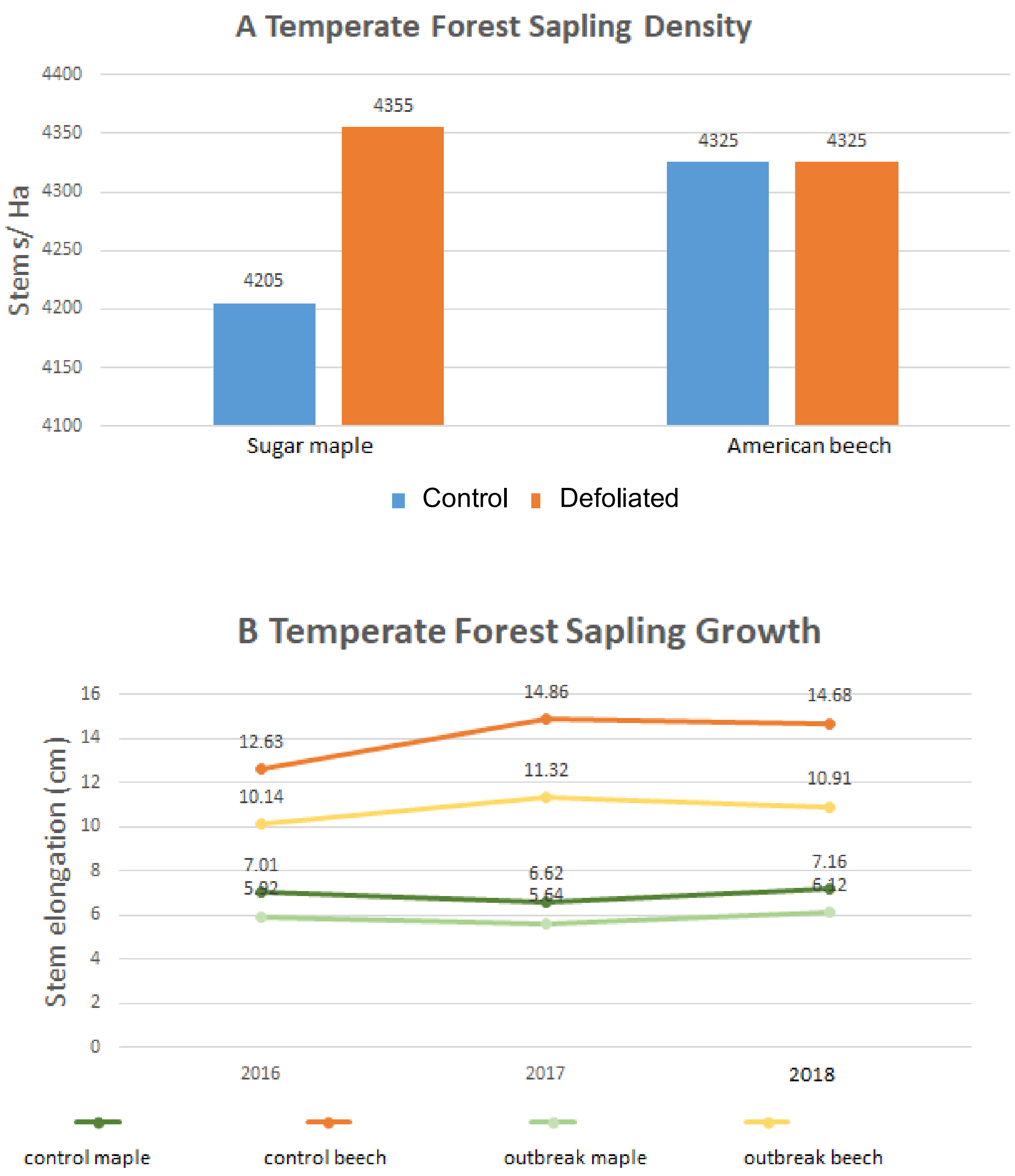

Fig 2: A Density and B growth of sugar maple and American beech saplings in the control and defoliated temperate forest sites

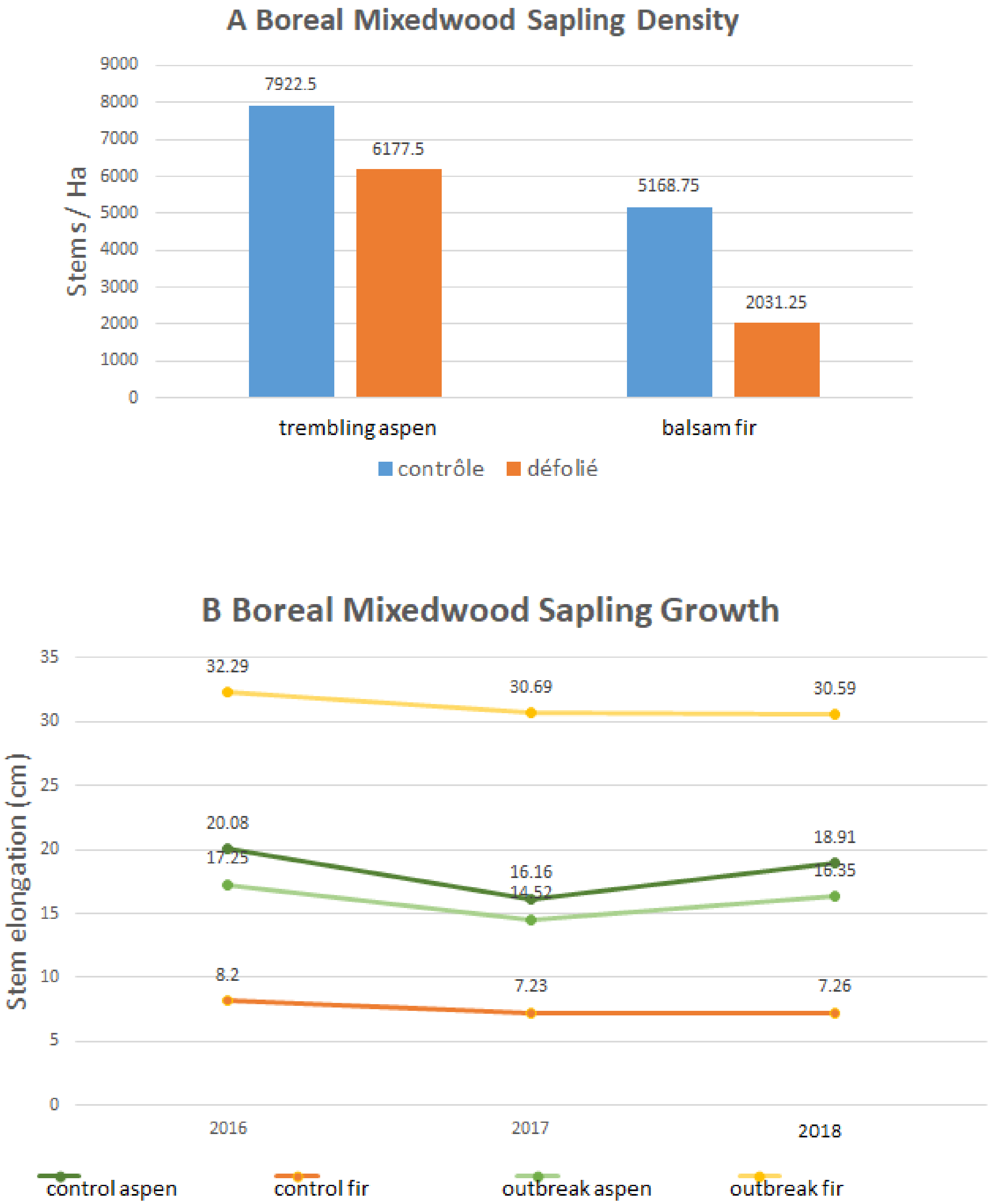

Fig 3: A Density and B growth trembling aspen and balsam fir saplings in the control and defoliated boreal mixed forest sites

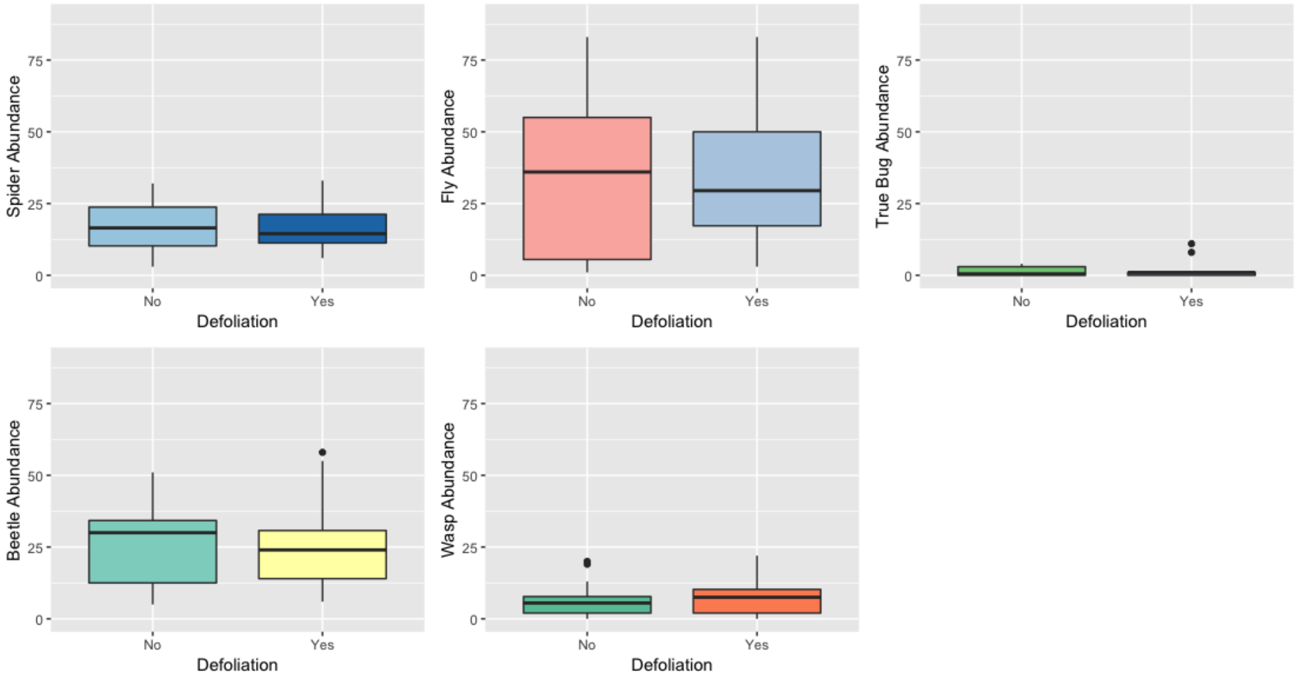

Fig. 4 Abundance of different arthropod groups of interest (Spiders, Flies, True Bugs, Beetles and Wasps) in the temperate forest sites. Each of the graphs show the abundance in sites that were defoliated during the last outbreak ("Yes") and those that were not ("No").

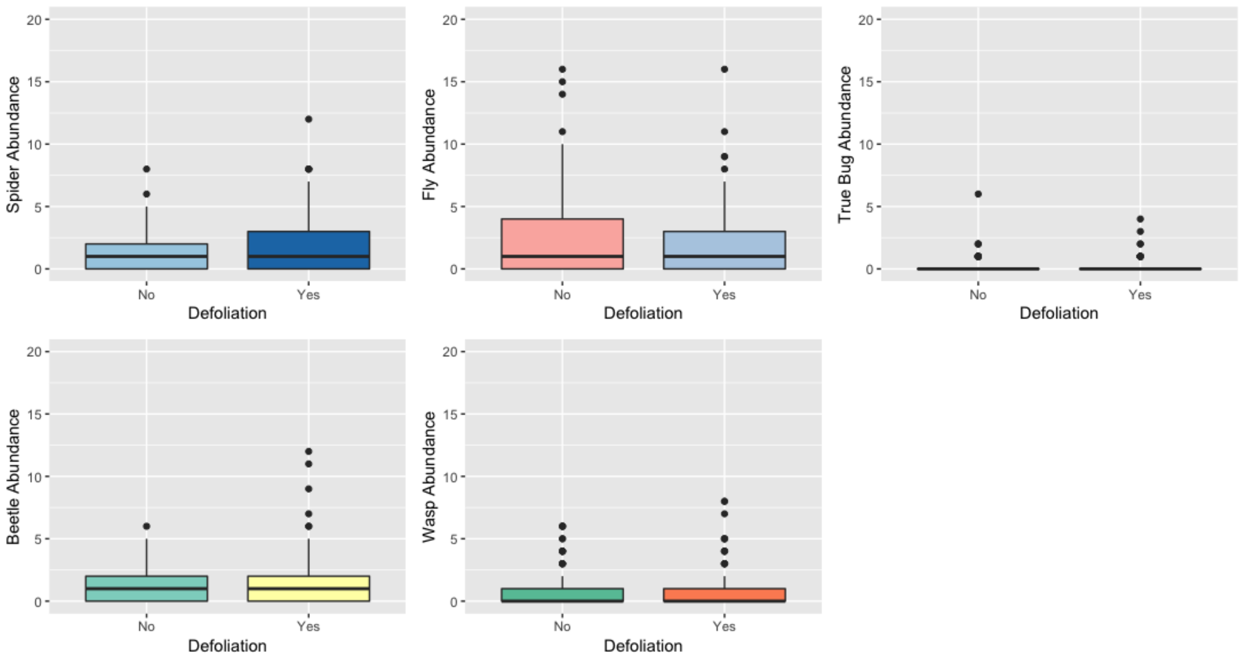

Fig. 5 Abundance of different arthropod groups of interest (Spiders, Flies, True Bugs, Beetles and Wasps) in the boreal forest sites. Each of the graphs show the abundance in sites that were defoliated during the last outbreak ("Yes") and those that were not i.e. control sites ("No"). Individual traps at the different sites were not pooled for this analysis.

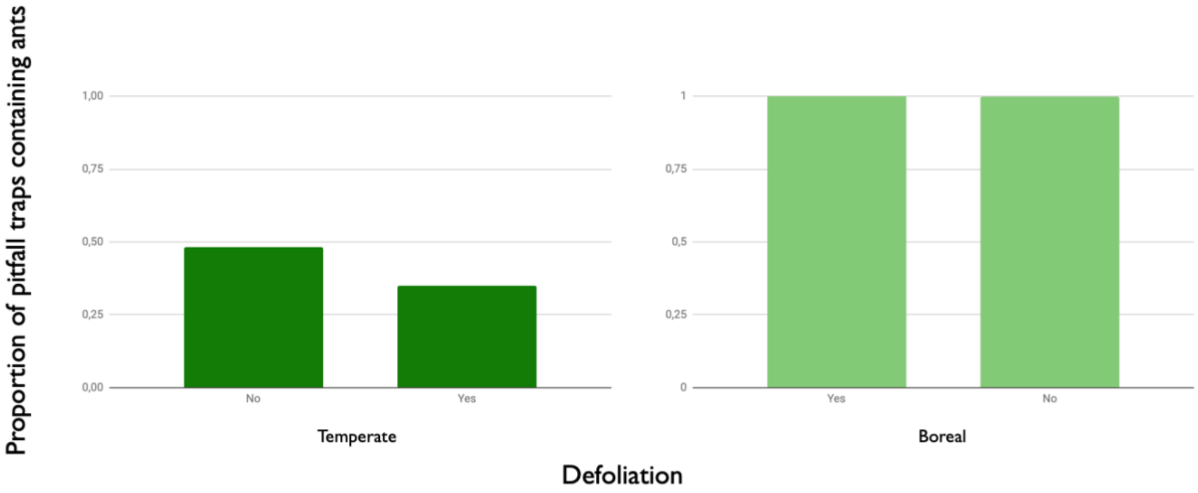

Fig. 6 Proportion of pitfall traps containing ants in temperate (dark green) and boreal (light green) forests. Each of the graphs show the proportion for sites that were defoliated during the last outbreak ("Yes") and those that were not, i.e. control sites ("No").

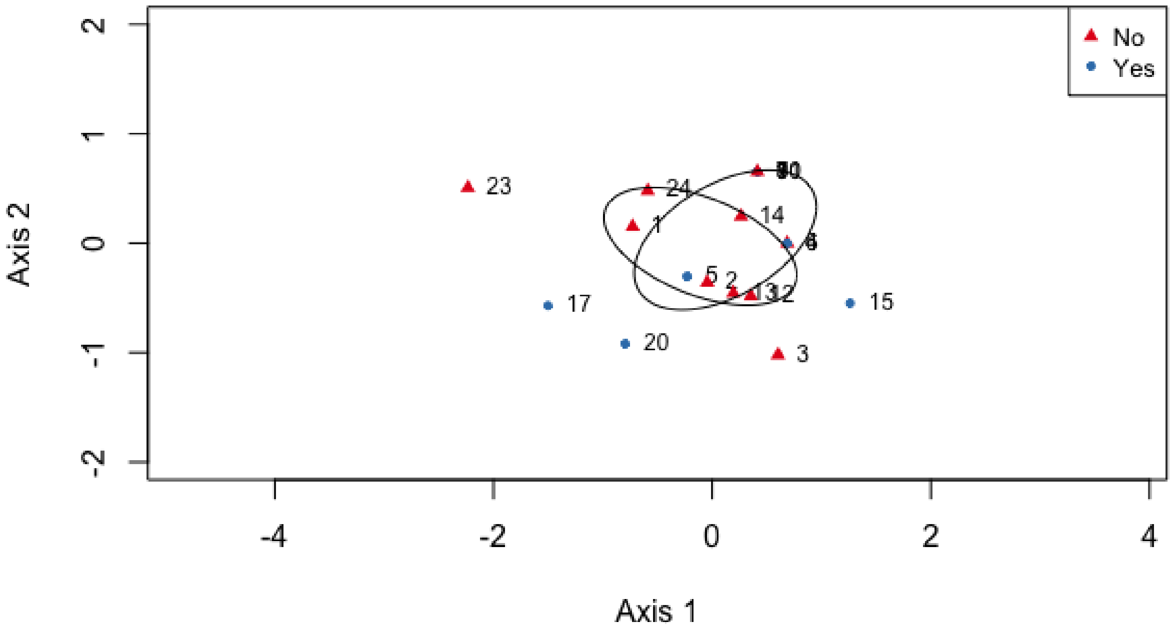

Fig. 7 NMDS ordination of Kenauk ant community between control and outbreak sites. Each point indicates the location of a site points in control and outbreak stands and corresponding colour are shown in the legend. Points which are located more closely together show communities that are more similar than points located further away from one another. Values for all environmental variables tested are shown on in the NMDS space as well. The location of each habitat centroid along with the 68% confidence areas is shown.

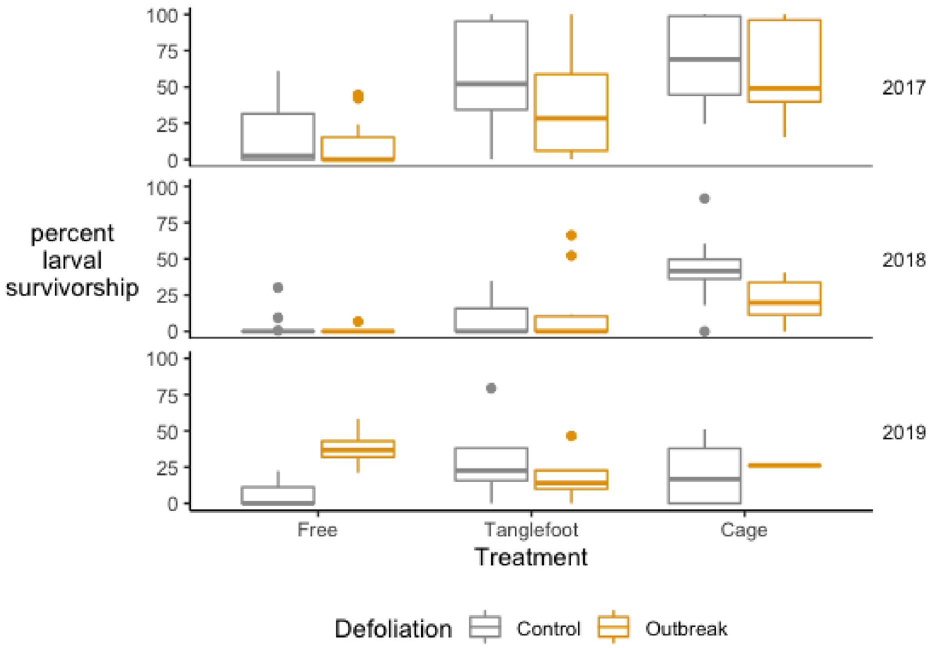

Figure 8 Survivorship of forest tent caterpillar (Malcosoma disstria) colonies completely from predators (cage), protected partially (tanglefoot) and in an unprotected control (free). Colonies were established in stands that had been previous defoliated (outbreak) or not (control) over three years (2017-2019)