Damage by insect herbivores on white spruce in plantation and natural understory regeneration

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Abstract

Damage by insect herbivores on white spruce in plantation and natural understory regeneration

Allison Pamela Yataco

Few studies focused on non-outbreaking herbivorous insects to understand the patterns of damage they inflict on plants. We compared damage by herbivorous insects on young white spruce (*Picea glauca*) between natural regrowth in the understory of mixed wood forest and small extensively-managed plantations. We observed damage to foliage to quantify damage by different groups of herbivores, including leaf chewers, miners and sap-sucking species. Our hypothesis stated that trees in forest understory environments would have higher diversity of damages caused by insects but that plantation trees would have more damaged tree shoots. Our two sampling methods were branch collection, in which we collected a forty-centimeter branch and recorded foliar damage, and field surveys, where one researcher recorded foliar damage on the saplings for three-minute intervals. We also measured tree growth, canopy openness, soil temperature and humidity. We used these environmental variables in general linear models to test their effects on herbivore damage in the two habitats. The results showed that plantation and understory trees did not differ significantly in the overall amount of insect damage. There was no correlation found with any environmental factor. This pattern indicated that the plantation we sampled maintained insect biodiversity similar to that in mixed wood forests. Thus, small, extensively managed multispecies plantations can be less at risk of insect outbreaks.

Acknowledgements

Table of contents

List of Figures

List of Tables

Introduction

Plantation management aims to increase the growth of trees by creating even-aged stands under optimal conditions. However, these trees may be particularly vulnerable to insect pests, as many insect herbivores perform well on leaves with higher sun exposure (Altieri et al., 1984). In addition, climate warming could increase insect damage in northern forests via northward migration of more southern species (Vallières et al., 2015; Ward & Masters, 2007). In northern Canada, unstable weather linked to global warming also modifies outbreak patterns of native insects, such as the eastern spruce budworm (*Choristoneura fumiferana*) (Dukes et al., 2009). Because of these factors, the plantations of coniferous softwood in Canada are particularly vulnerable to insect damage. Therefore, we studied the composition of insect communities and the damage they cause to young trees in plantations compared to those in the forest understory.

Environmental factors differ between both treatments and affect the development of the trees. Canopy openness in plantations implies increased sun exposure, leading to higher temperatures and drought stress, which can negatively impact the plant's defenses against pathogens and insects (Orwig & Abrams, 1997; Kolb et al., 2016). Conversely, high canopy cover was likely to reduce the growth of understory trees (Craine & Dybzinski, 2013) compared to those in plantations. Another factor to consider is the diversity of the surrounding plant community. Higher levels of plant diversity lead to more stable herbivorous arthropod communities and a lower risk of insect outbreaks (Haddad et al., 2011; Pimentel, 1961).

In general, plantation trees are especially vulnerable to defoliation (Lehmann et al., 2020). The higher temperature increases damage by native insect species (Pedlar &

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McKenney, 2017). Sun exposure leads to higher nutritional value of foliage, increasing arthropod feeding damage (Bongers & Popma, 1990; Dudt & Shure, 1994; Murakami & Wada, 1997). However, leaf toughness is essential to the white spruce defence against herbivorous insects (Fuentealba et al., 2020), and increases with sun exposure (Lirette and Despland, 2021). Drought stress also reduces trees' physical and chemical defences over time (Potts et al. 2014). High sun exposure in plantations could thus have both positive and negative effects on susceptibility to insect damage. Lower canopy cover increases the reproductive output of some herbivorous insects in deciduous trees, notably aphids and sawfly larvae (Mattson & Haack, 1987).

Tree diversity is correlated with insect diversity (Li et al., 2012). We hypothesized that elevated plant diversity creates diverse niches, providing environments for several insect species to secure food, shelter, and optimal space for reproduction (Potts et al., 2014). Furthermore, higher plant diversity reduces insect defoliation and lowers the risk of outbreaks (Stamps & Linit, 1997). Macfadyen's biodiversity stability theory explains these patterns. This theory states that heightened plant and insect diversity make forests a more stable system less susceptible to pest insect damage (Jactel et al. 2005).

Identifying these factors' roles in damage distribution can help us understand their effects on insect distribution. Identifying how plantation characteristics influence insect damage is important in planning for reforestation and in managing plantations sustainably (Potts et al., 2014). Remote sensing does not provide enough resolution to identify damage by many herbivorous insects (Hall et al., 2016). Thus, ground-based monitoring of these herbivores is crucial, since they make up most of the insect community (Johns et al., 2016), and their populations could increase to the point of restricting tree growth. Regular

monitoring may be necessary to analyze the stability of recent reforestation (Lieffers et al., 2020). It is also important to compare this to the damage in diverse naturally regrown forests, which represent a baseline insect community.

White spruce is one of the main trees used in plantations in Canada. The goal of tree plantations is to shorten growth rotation and lower losses due to natural disturbances (Government of Canada, 2015). White spruce is a native Canadian softwood species (Farrar, 1995) found in old-growth forests as pure stands and as saplings in mixed wood boreal forests (Government of Canada, 2015). It naturally grows around floodplains, upland slopes and tree lines (Burns & Service, 1990). Young trees grow in the forest understory, under faster-growing hardwoods that regenerate post-fire (Burns & Service, 1990; Government of Canada, 2015). White spruce grow in the shade of fast-growing trees. Low light availability reduces their growth rate. For this study, we used young plantations under 20 years old grown from local seeds. The managers did not thin, use fertilizer, or spray with pesticides.

Choristoneura fumiferana, the eastern spruce budworm and *Pikonema alaskensis,* the yellow-headed sawfly, are amongst the best-known white spruce herbivores (Katovich, 1995; Stocks, 1987). Spruce budworms are one of the major pest species that threatens the production of young white spruce, having caused the death of 15–40% of saplings during the 1972–1996 outbreak (Bouchard & Pothier, 2010). The yellow-headed sawfly is also a primary cause of mortality in saplings. There are other feeding guilds on white spruce saplings: leaf mining, leaf-chewing, sap-sucking and bud feeding insects (Rose & Lindquist, 1994). Many of these common defoliators are non-outbreaking species, but

they still cause low levels of defoliation (Wulder & Franklin, 2006), between 10-15 % of cumulative leaf damage in broad-leave species (Schowalter et al.1986).

In this study, we created a comparative analysis of the arthropod defoliation that occurs in naturally regrown understory white spruce and those in small, extensively managed plantations in a research station (see Figure 1.1). The damage categories encompassed leaf chewers, miners and sap-sucking species. This study involved discerning damage patterns attributable to different arthropod groups or species. Two research questions guided our research: 1) How did the damage inflicted by various herbivorous arthropods in plantations differ from that of natural stands? 2) Was there a correlation between environmental variables (canopy openness, soil humidity and temperature) and the extent of specific damage types?

Figure 1.1

Plantation and forest treatment images

a)

b)

c)

d)
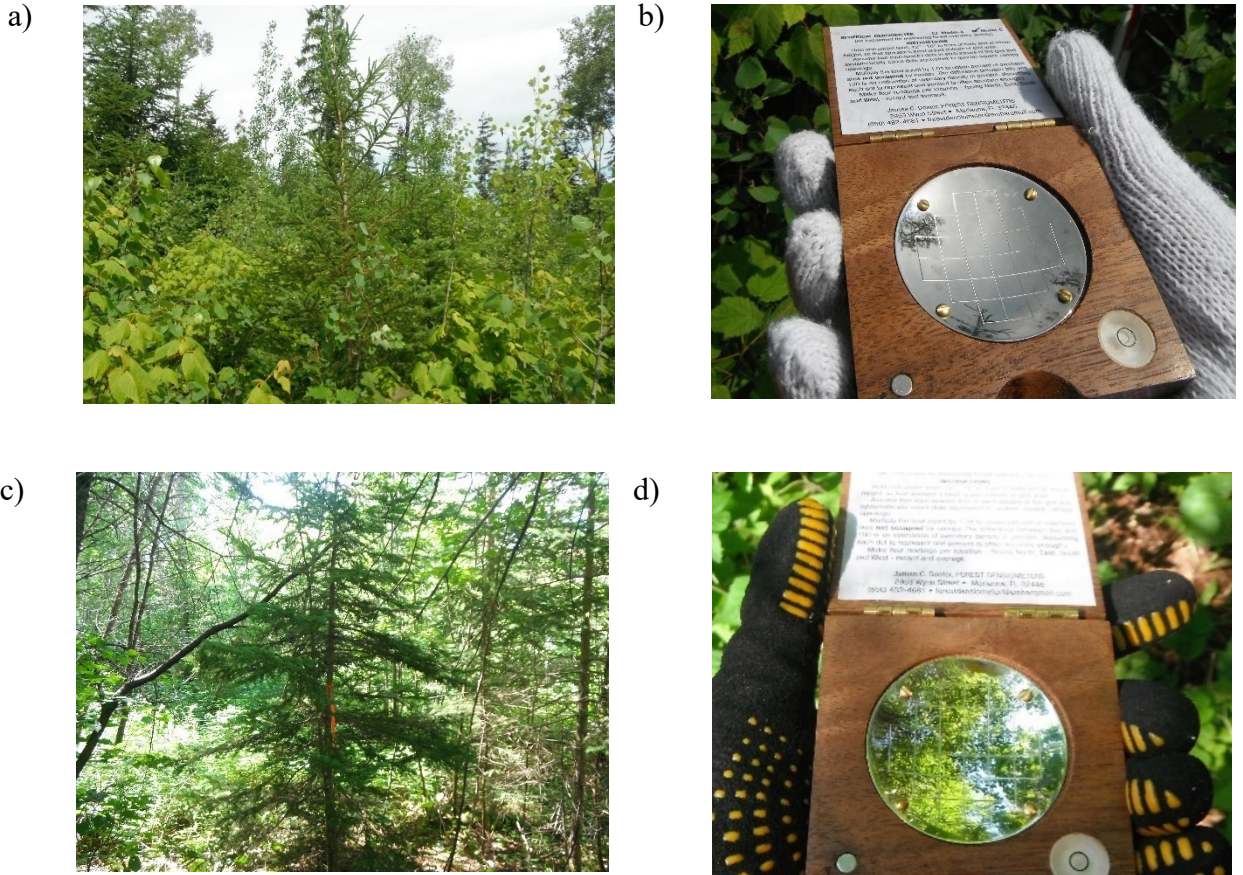
Note: The (a) image shows one of the sampled plantation trees, (b) is an image of the densiometer in a plantation from 2020 that shows the lack of canopy cover around the sampled tree. The image (c) is the photo of a forest tree sampled, and (d) is an image of the densiometer showing the tree cover in the forest site in 2020.

Methods

2.1.1 Location

Sampling took place at the FERLD research station in the region of Abitibi in the province of Quebec, Canada (N 48.513275, W -79.368423). The two environments we compared were plantations and natural regeneration in the understory of a mixed boreal forest. We selected a total of 19 sites with a clinometer measure between 0-8 % from both treatments using GIS maps (Végétation potentielle de la carte écoforestière from Forêts Ouvertes; Ministère des Ressources Naturelles et des Forêts, 2023). We sampled ten trees selected at least 3 meter apart at each site: all trees were between two and 3 meters in height to make sampling feasible with a ladder. We did the sampling in three sessions, 2020 and 2021: late summer (July to August) of 2020, early summer (June) 2021 and late summer of 2021. We decided to sample in early and late summer as different insect larvae feed at different times throughout the season. Most larvae emerged in early summer, with a few species emerging in later summer (Wagner, 2005).

Plantations consisted of small, 100-square-metre white spruce plots planted between 2008 and 2013 in a matrix of stands of different conifers and broad-leaved trees. These plantations did not use fertilizers or pesticides, unlike standard practices used for white spruce production. Brush cutting to remove the overgrown wild plants that could compete with the planted saplings was only done once every seven years after planting. The genetic sources for white spruce in the FERLD were from local tree stands collected in Abitibi.

 Mature trembling aspen (*Populus tremuloides)* and balsam fir (*Abies balsamea)* that had regenerated after a large fire in the 1920s dominated forest sites. Trees of the same height

were likely to be older in forests than in the plantations (Martin, 2005). When possible, we sampled the same trees in 2020 and 2021; however, we could not find some individuals as they had died or had their tags removed. Thus, we selected other trees to sample. We sampled a total of 187 individual trees. Two forest sites had fewer than ten trees. One of these forest sites sampled in 2020 (number 2) became inaccessible in 2021 due to the installation of bear traps.

2.1.2 Environmental variables

We measured the canopy aperture for each tree using a densiometer (Forestry Suppliers Spherical Crown Densiometer Concave Model C) in all sampling sessions. To measure the canopy openness with the densiometer, we stood two meters from the tree and held the densitometer at chest height and levelled the apparatus. Then, we counted the squares not covered by trees on the gridded curved mirror, giving us a percentage of the uncovered area. We did this three times per tree and then averaged the values to obtain the final data point. The measurements were considered an indirect light availability measure (Jennings et al., 1999).

We measured soil temperature and relative humidity using a thermometer and a Time Domain reflectometer humidity sensor (Sharma et al., 2018). We took three measurements for each tree. We took the measurements with the humidity probe 50 cm from the base of the spruce trunk. We used this method because white spruce has shallow roots and thus is affected directly by topsoil humidity (Eis, 1970). We averaged the three measurements for each tree sampled.

2.1.3 White spruce growth measurements

We measured the total tree size with a five-meter-long telescopic levelling rod (Allenuild Thenths 10th) in late summer 2020 and 2021. We used the bud scarring visible on the branches to measure the total growth of the tree in past years (Kozlowski & Clausen, 1966). The scars were visible on the bark and faded after four years of growth. In this thesis, we only considered the previous two years (2019 and 2020) as these scars faded after four years, and we did not want to cause uncertainty in the results.

We measured needle toughness in the late summer of 2020 with a manual penetrometer (Fuentealba et al., 2020). This machine uses a hypodermic needle (25-G insulin BD Luer Lock) to obtain the force required to pierce the cuticle of the spruce leaf. The needle was replaced after four uses to prevent its tip from dulling and causing inaccurate measurements (Fuentealba et al., 2020). In 2021, we used an electronic penetrometer designed by Juan Albaroz and Janice Cooke at the University of Alberta that contains the same type of hypodermic needle and provides more precise measurements. We selected four trees at random to measure toughness. We collected three shoots from each tree. We used ten needles from those shoots to obtain piercing force measurements. We averaged these measures to obtain each tree's final needle toughness value. The models that used toughness in the analysis included the four trees per site where toughness was measured.

2.1.4 Herbivory damage measurement

We classified different damage types using a guide from the Quebec Ministry of Forests Fauna and Parks (MFFP) (Rose & Lindquist, 1994). We used two methods to assess the damage to foliage: field surveys in early and late summer 2021 and branch sampling in

late summer 2020 and 2021. The survey method examined the current-year growth around the tree at eye level for three minutes. We put the three minutes in place to standardize the visual survey time. We only noted the buds that were at eye level around the tree. We counted the total number of buds with a clicker. The branch sampling method took place in the late summer of both years. We sampled a 40 cm branch from each tree to analyze the extent of damage done by burrowing larvae that were not visible with the visual survey. We cut them, placed them in bags, and brought them to the lab to count the damage types. We used the Fettes method to record overall defoliation by estimating the proportion of leaves removed on the current year shoot. There were twelve levels of defoliation, ranging from 1, no defoliation, to 11, complete defoliation, and 12, missing the stem (Kanoti, 2018). We estimated Fettes defoliation on twelve shoots per branch and averaged these to obtain one value per branch. We counted the number of healthy and damaged buds and those that did not develop. We classified the damages into the following groups:

- Galls were considered one damage type and consisted of two species: *Adelges abietis* and *Adelges cooleyi*. They were only differentiated when doing the branch analysis. During surveys, it was difficult to distinguish between these two species. *Adelges abietis*, spruce gall adelgid colonies, form galls from new white spruce shoots called "pineapple galls". These are vegetative cell growths at the bottom of the needles that form a pineapple-like structure. The insects form colonies in these shoots. *Adelges cooleyi* are similar but their galls are much longer and have a red

tint. Dried galls from previous years were not counted in the experiment. We estimated damages by the number of shoots affected by this insect.

- *Cytospora kunzei,* a fungal pathogen, was identified by the reddening of needles and the drooping of shoots at the end of the stem (Bergdahl & Hill, 2016). We considered each damaged spruce shoot as one damage.

- We identified spruce budworm (*Choristoneura fumiferana)* damage by the presence of silk and frass on dead or damaged shoots. Other identifiers are the presence of larvae and nests formed from needles. These structures are formed by two or more shoots tied together by silk, curving into each other with needles eaten at the centre. This structure would then count as two buds damaged.

- Shoots with hollow orange needles identified Spruce needle miner (*Endothenia* spp.) damage. We only counted the damage when there were five or more damaged needles.

- We estimated damage caused by spruce web-spinning sawfly (*Cephalcia fascipenni*s) by counting the number of buds with webbed nests. The silk of this species was brown, and they formed tubular-shaped cocoons. The larvae cannot survive without this nest, lacking the prolegs to cling and move on the tree's shoots.

- We estimated the defoliation by all other sawflies (*Pikonema alaskensis, Pikonema dimmockii, Pikonema lena, Gilpinia hercynia*e) by counting the number of shoots with the typical sawfly feeding pattern with all needles removed from one side of the shoot.

- The spruce bud midge is a cecidomyiid fly *(Rhabdophaga swainei)* that infects the bud early in its development. We identified it by stunted bud growth and the swollen cone-like shape of the bud. We dissected the buds to confirm the presence of midge damage, such as pupae shell, egg, dead fly or parasitoid wasp.

- A group of tiny larvae called microlepidoptera caused damage resulting in buds destroyed before they opened and expanded into shoots. We counted the presence of unidentifiable larvae dug into dried buds and small curved shoots. This group included *Archips strian* and *Griselda radicana* species that feed on young buds.

2.1.5 Statistical analysis

We analyzed survey (early and late summer of 2021) and branch (late summer 2021 and 2022) data sets using the Generalized Linear Mixed-Effects Model (GLMER) from the 'Lme4' (Bates et al., 2015) package in the R statistical computing software (R Core team, 2020). The data had a hierarchical structure, as the trees were samples in different sites within two treatments. Therefore, we included the site sampled as a random variable in the model.

We used a GLMER to test the difference in Shannon diversity between the two treatments. We also used this analysis to compare the treatments' tree growth and environmental differences. We used GLMER.NB (Generalized Linear Mixed-Effects

Model with Negative Binomial Distribution) to analyze the damage types because the data was left skewed and over-dispersed.

Shannon diversity

We calculated the Shannon diversity index by independently taking all survey and branch data damages. We used the R vegan package (Oksanen et al., 2022). This method was developed to compare habitat damage diversity (Pelini et al., 2009). Below is the GLMER model used:

Shannon diversity ~ Treatment + Canopy + Soil Temperature + Soil Humidity + (1|site)

We measured the following environmental variables: canopy openness, soil temperature and humidity. We added these measurements as fixed variables to the mixed model to evaluate their effect on diversity patterns (Brezzi et al., 2017).

Damage types: survey data

We compared the total damage between the two environments using the survey data sets. We added the same fixed factors to the GLMER as those used in the Shannon diversity models. Individual trees were not independent from one another, as many of them belonged to the same site. This data stratification indicated that they were pseudo-replicates (Hurlbert, 1984); thus, we considered the site as a random factor in the model (Bates et al., 2015). We use the following models:

Damage type ~ Treatment + Soil humidity + Soil temperature + Canopy + (1 | Sampling site)

Testing for heterogeneity with residuals was only done after selecting a model (Zuur et al., 2009b).

Damage types: branch data

The branch dataset was not normally distributed. We used the GLMER.NSB to compare between sites using the following model:

Damage type ~ Treatment + Soil humidity + Soil temperature + Canopy + (1 | Sampling site)

We compared the Fettes defoliation between both treatments (Bates et al., 2015; Kanoti, 2018; Marschner & Donoghoe, 2018). We used a GLMER model to analyze the difference between the treatments. The fixed and random variables were the same as in the previous models.

Fettes ~ Treatment + Soil humidity + Soil temperature + Canopy + (1 | Sampling site)

We did not measure toughness for every data point; thus, we made a model that only contained the sites where the toughness was measured. We used a subset of the data set to create the model. We included the following fixed factors in the model: soil humidity, temperature and canopy openness. We took the site as a random variable.

Toughness ~ Treatment + Soil humidity + Soil temperature + Canopy + (1 | Sampling site)

Multivariate analysis of branch data

We used non-metric multidimensional scaling (NMDS) (De'ath, 1999) to illustrate the special distributions of the sites based on the similarity of the data, using the vegan package in R (Oksanen et al., 2022). We used the damage data from different insects to create the matrix for the plot, consisting of Bray-Curtis distances for both branch and survey data (Beals, 1984). The NMDS did not have distortions caused by the linear assumption, which occurred when using other methods, such as the RDA. The NMDS also showed the patterns that different environmental variables had on the distribution of insect damage.

Results

We use the GLMER models to compare the differences between treatments in the
environmental factors and developmental data for the saplings. Canopy cover was
significantly higher in forests compared to plantations ($p < 0.001$) see Table 3.1. The soil
temperature was higher in plantations than in naturally regrown spruce ($p < 0.001$).
Growth of the saplings was also much higher in plantations than in forests ($p < 0.001$).
The GLM for the toughness of needles showed that it was significantly higher in
plantations ($P = 0.006$). Table 3.1 summarizes the complete data set for both sampling
methods. We illustrated the distribution of the different damage types in the Figure 3.1
plots. Figure 3.2 shows the histogram of each damage type. The graph indicates many
more zeros than non-zero values in the data.

Table 3.1

Branch sampling and field survey summary table.

| Sampling type	Damages	Plantations		Forest	
		Mean	Std. error	*Mean*	Std. error
Survey	Galls	1.516	0.312	0.141	0.039
	Spruce budworm	0.382	0.059	0.635	0.115
	Sawfly	0.720	0.118	1.071	0.166
	Bud feeding	4.129	0.440	5.082	0.491
Branch	Galls	0.756	0.112	0.131	0.030
	Spruce budworm	0.005	0.005	0.038	0.022
	Sawfly	0.371	0.060	0.574	0.101
	Bud feeding	1.117	0.162	1.437	0.208
	Spruce gall midge	0.010	0.010	0.044	0.022
	Spruce bud midge	0.040	0.019	0.071	0.025
	Environmental				
	Soil temperature	23.706	0.311	21.749	0.261
	Soil humidity	19.481	0.755	13.545	0.627
	Canopy	38.207	1.654	90.402	0.815
	Growth				
	Toughness	57.211	2.263	50.027	1.315
	Lateral 2021	10.382	0.320	5.971	0.189
	Lateral 2020	13.753	0.297	7.471	0.255
	Apical 2021	26.632	1.049	7.009	0.558
	Apical 2021	37.512	0.895	11.157	0.655

Note: We showed the means and standard error for the damage types, environmental variables and growth of trees for each environment.
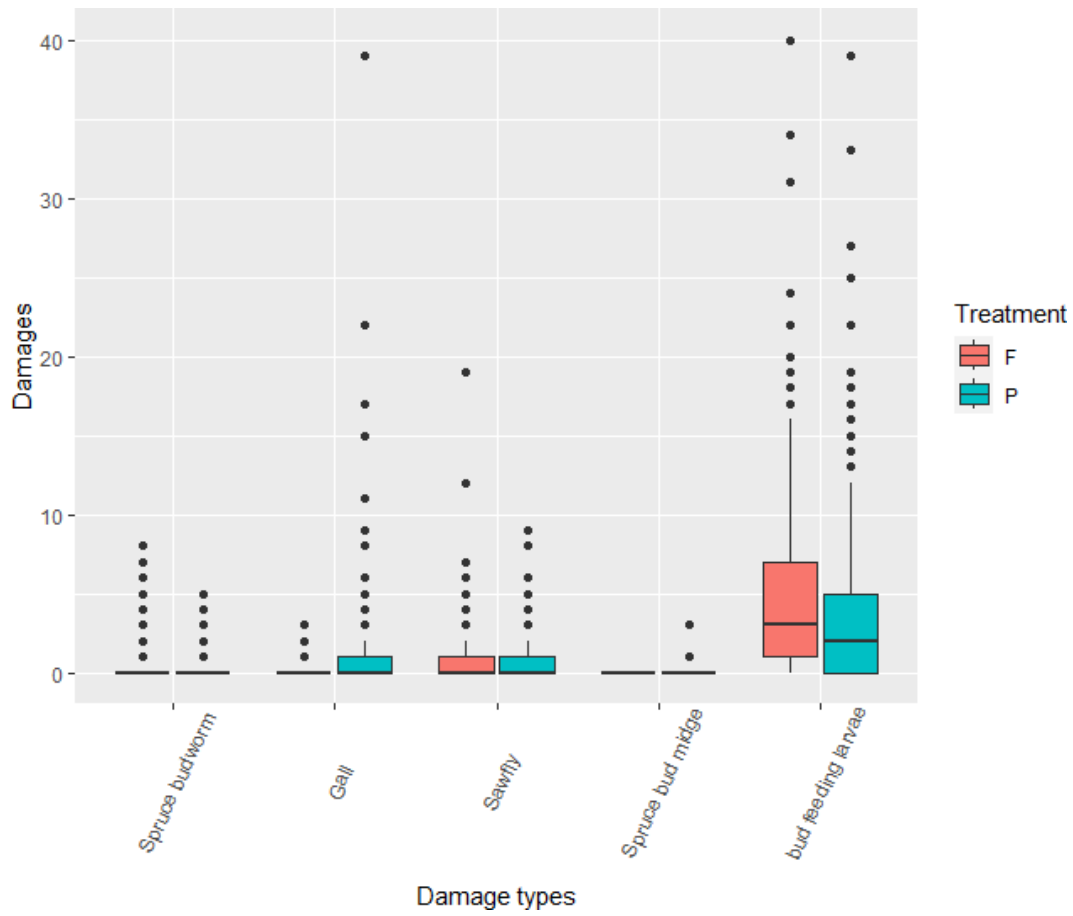
Figure 3.1

Boxplot of damages of herbivore groups

a)
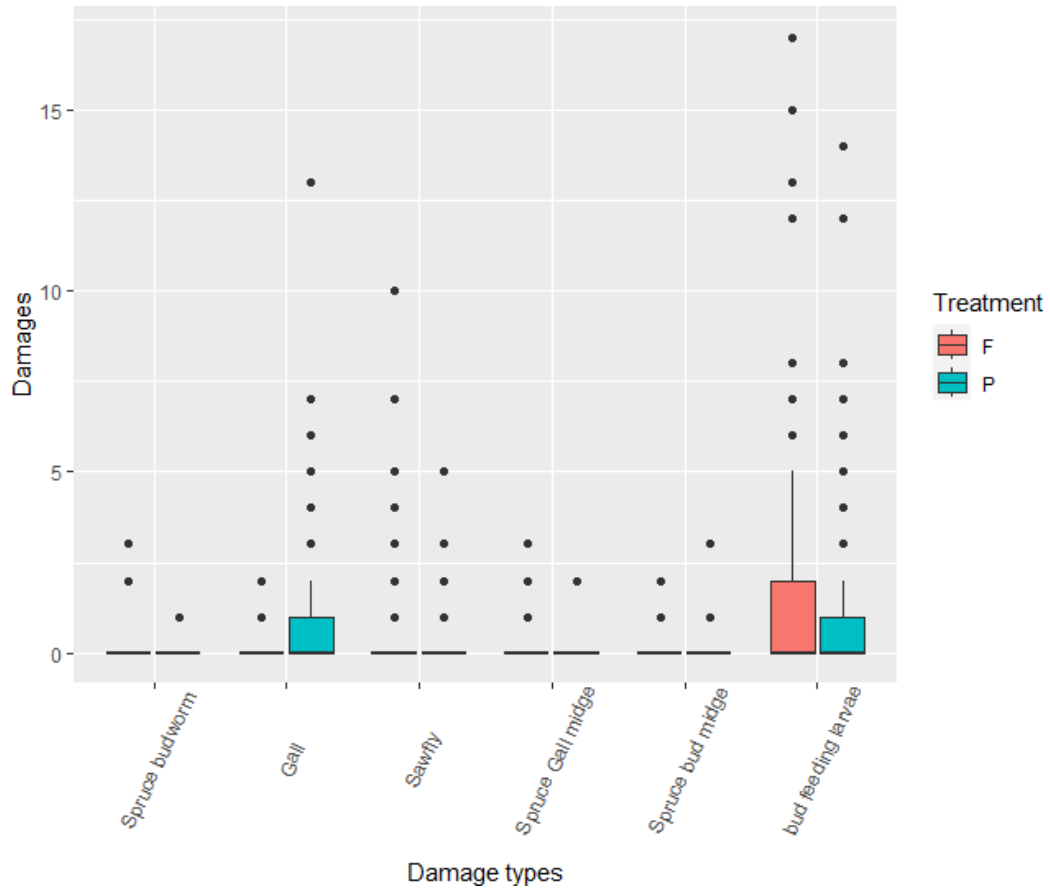
b)

Note: F represents the forest sites, and P represents the plantation sites. (a) branch data for late summer 2020 and 2021 combined and (b) survey data for early and late summer 2021 combined.

Figure 3.2

Histogram of damaged types present in shoots

a)
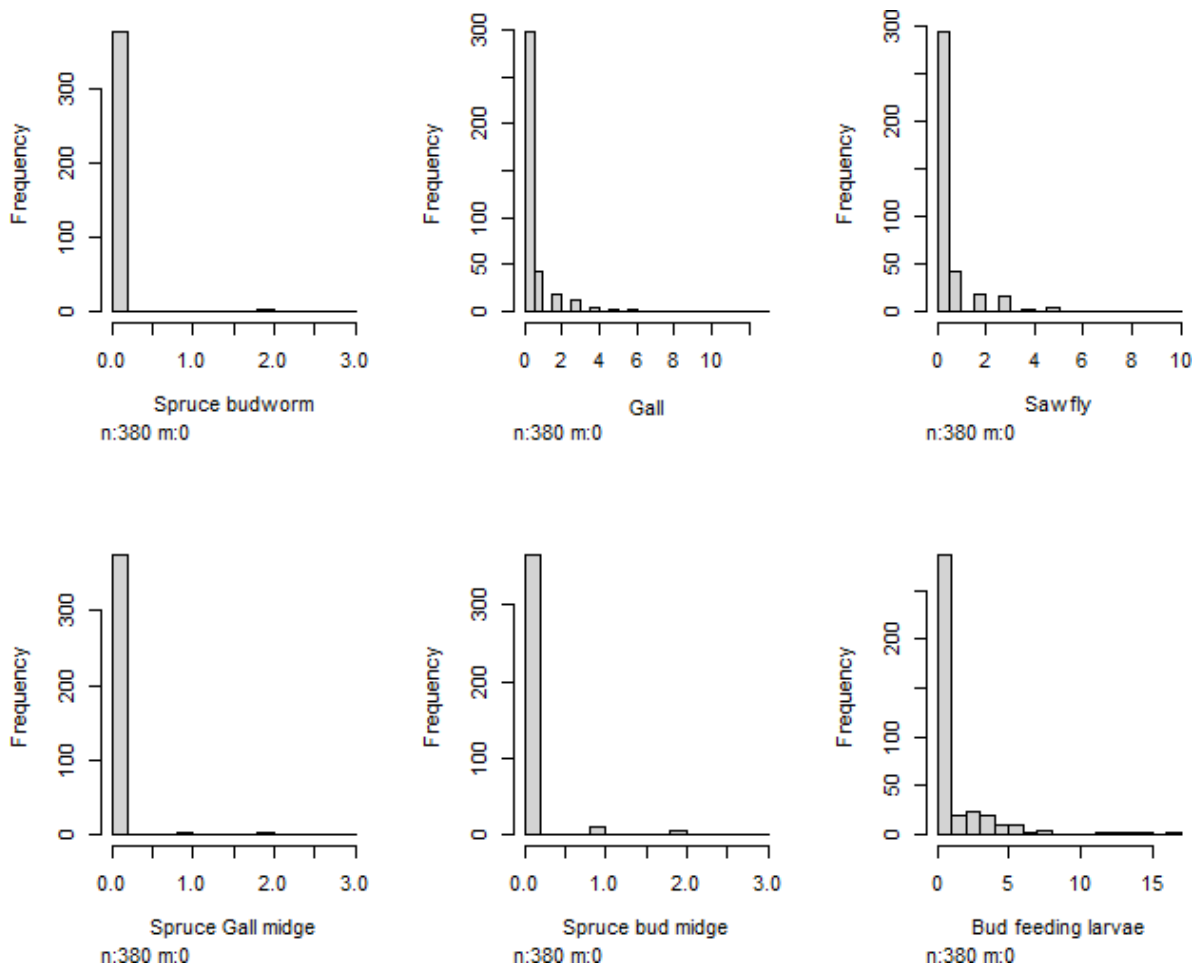
b)

Note: The (a) graphs are the histograms from branch data from late summer 2020 and 2021 combined. The graph from (b) survey data of early and late summer 2021 combined. The "n" value is the total number of data point in the histogram, thus the total number of trees sampled from branch and survey data.

Shannon diversity

The diversity of damage types did not differ between plantation and forest sites (p > 0.05) when analyzing either data sets. No environmental factors affected the Shannon diversity index.
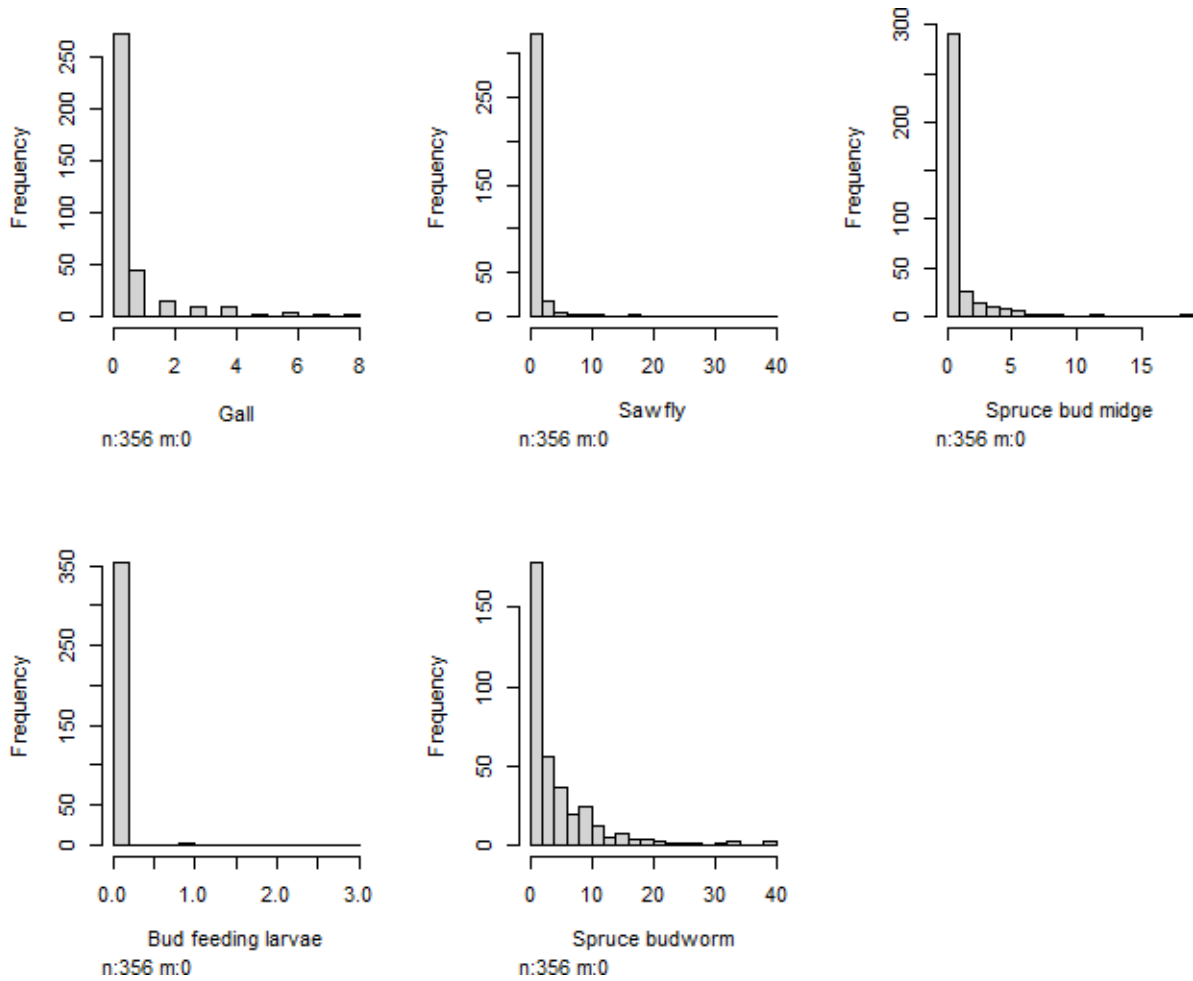
Damage types

Galls were more abundant in plantations than in forests in both the survey and branch analyses (see Table 3.2). However, there were no significant differences between forest and plantation trees in any other damage types with either survey or branch sampling, or in overall Fettes defoliation (p = 0.06). Number of buds was higher in plantations (p = 0.03); however, there was no difference in underdeveloped buds between treatments (p = 0.24).

Table 3.2

Differences between treatments in branch and survey data

Model	Components	Estimate	Std. error	*z* value	*P*-value
Spruce budworm Survey	Intercept*	-0.38	1.19	-2.52	0.01
	Treatment	-0.12	0.98	-0.12	0.90
	Humidity	0.01	0.02	0.40	0.69
	Temperature	0.02	0.02	0.87	0.39
	Canopy	0.00	0.01	-0.10	0.92
Sawfly Survey	Intercept	1.23	1.15	1.07	0.29
	Treatment	-0.71	0.58	-1.23	0.22
	Humidity	0.01	0.01	0.92	0.36
	Temperature	-0.09	0.04	-2.16	0.03
	Canopy	0.00	0.01	-0.06	0.95
Galls survey*	Intercept**	-5.09	1.56	-3.27	0.00
	Treatment*	2.42	1.02	2.38	0.02
	Humidity	0.01	0.02	0.42	0.68
	Temperature	0.01	0.05	0.32	0.75
	Canopy	0.01	0.01	1.14	0.26
Early bud-feeding larvae survey	Intercept	1.03	0.54	1.91	0.06
	Treatment	-0.10	0.39	-0.26	0.79
	Humidity	0.00	0.01	0.50	0.62
	Temperature	-0.01	0.01	-0.44	0.66
	Canopy	0.00	0.00	1.00	0.32
Spruce bud midge survey	Intercept	-44.15	1182.42	-0.04	0.97
	Treatment	34.00	1182.42	0.03	0.98
	Humidity	-0.08	0.12	-0.66	0.51
	Temperature	0.14	0.17	0.81	0.42
	Canopy	0.03	0.03	0.99	0.32
Spruce budworm branch	Intercept	-9.08	5.21	-1.74	0.08
	Treatment	-1.20	2.95	-0.41	0.69
	Humidity	0.04	0.06	0.74	0.46
	Temperature	-0.00	0.22	0.00	1.00
	Canopy	0.01	0.03	0.42	0.68
Sawfly branch	Intercept	-1.15	1.46	-0.79	0.43
	Treatment	0.37	0.57	0.64	0.52

	Component				
	Humidity	0.00	0.02	0.50	0.62
	Temperature	-0.06	0.05	-1.35	0.18
	Canopy	0.01	0.01	1.67	0.10
Galls branch*	Intercept	-1.75	1.27	-1.38	0.17
	Treatment*	1.50	0.58	2.56	0.01
	Humidity	0.00	0.02	-0.29	0.77
	Temperature	-0.02	0.04	-0.42	0.67
	Canopy	0.00	0.01	-0.62	0.53
Early bud-feeding larvae branch	Intercept	-1.69	0.90	-1.89	0.06
	Treatment	-0.12	0.74	-0.16	0.88
	Humidity	0.01	0.01	0.84	0.40
	Temperature	-0.01	0.03	-0.18	0.86
	Canopy*	0.01	0.00	2.18	0.03
	Intercept	-4.35	2.67	-1.63	0.10
	Treatment	-0.38	1.02	-0.38	0.71
	Humidity	-0.03	0.04	-0.77	0.44
	Temperature	0.06	0.09	0.70	0.49
	Canopy	0.00	0.02	0.16	0.88

Note: The table shows each model's intercept, treatment, humidity, temperature, and canopy components. The presence of one star (*) in front of the component and model indicates that the P-value is significant at the 0.05 level.

Multivariate analysis of branch data

The NMDS showed significant overlap in the composition of damaged communities between the plantation and forest sites. We illustrated the Bray distance NMDS in Figure 3.3. There was no correlation or pattern in the distribution of the data set. Adding a canopy cover to the figure showed no pattern in damage distribution. The plot shows that spruce budworm and spruce bud midge were the farthest in the distribution, being the damages with the least similar distributions compared to the others. However, there was no significant difference in the overall pattern between environments.
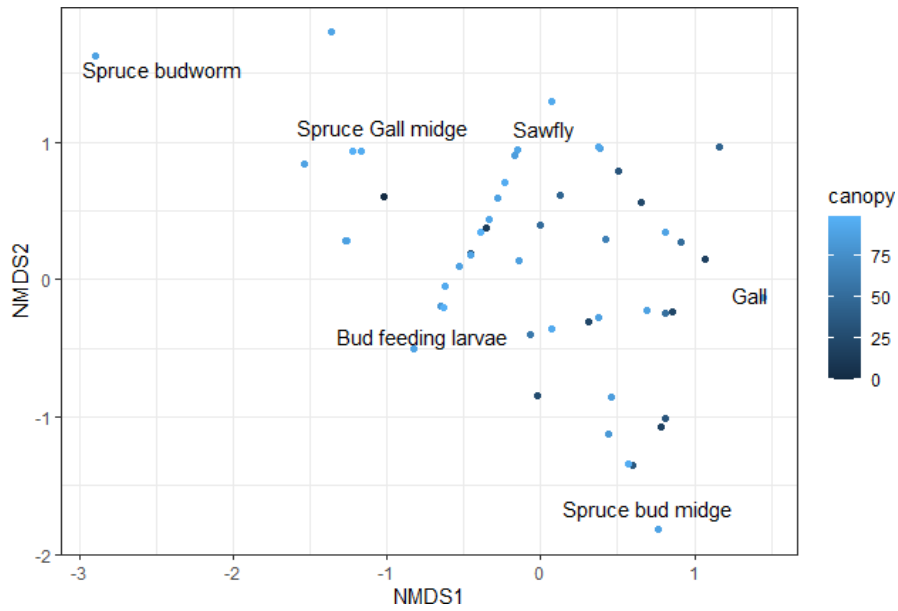
Figure 3.3

NMDS plots for the survey and branch data.
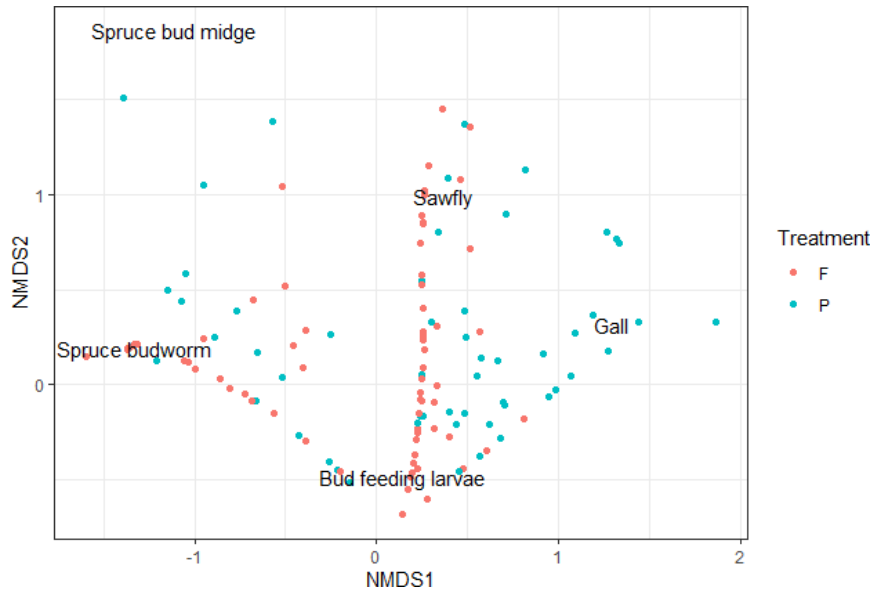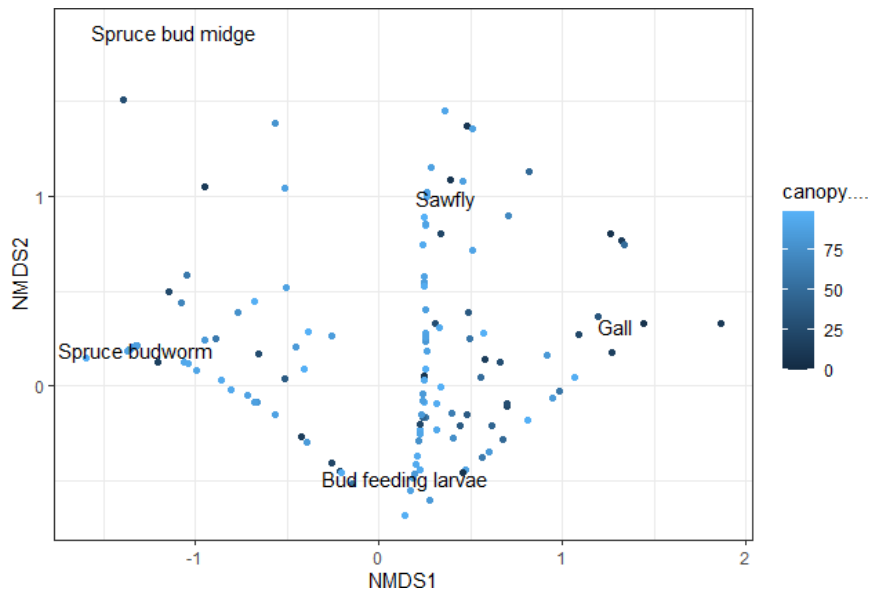
a)
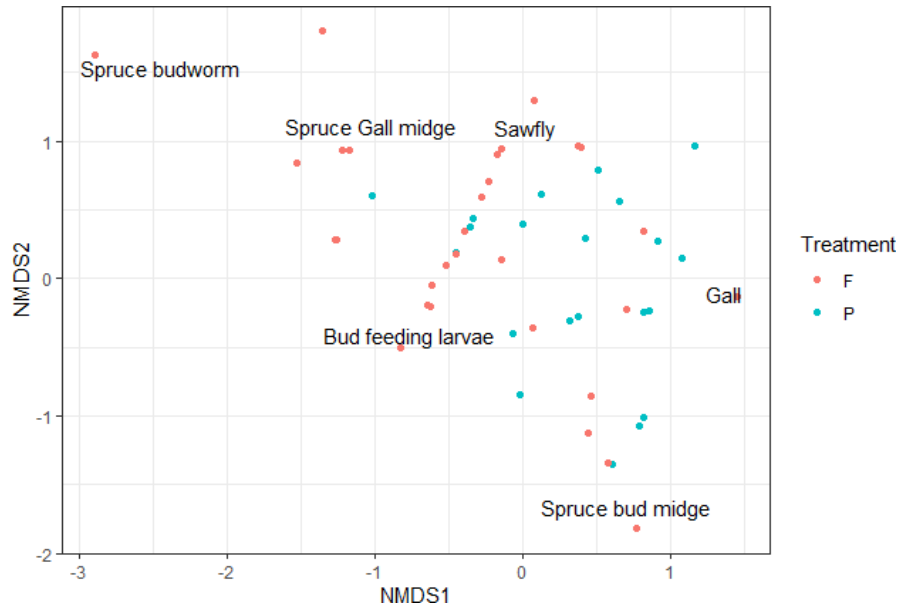
b)

c)

d)

Note: Plot (a) and (b) represent branch data and (c) and (d) graphs are plots for the survey data. Graphs (a) and (c) show the relationship between treatment and the statistical distance between the sites. The statistical difference being how different was one data point's composition different from another. F represents the forest sites, and P represents the plantation sites. Graphs (b) and (d) show the relationship between canopy cover and the different data points in the matrix. The position of the points on the graph showed the effect of the herbivorous damage types (spruce budworm, gall, sawfly, spruce bud midge, spruce gall midge, early bud-feeding larvae).

Discussion

The overall findings initially revealed that arthropod herbivore damage diversity did not differ between the two environments. We had predicted higher diversity in forest sites because they were more complex environments and had more niches for various species (Potts et al., 2014). However, contrary to our hypothesis, the data did not support the lower diversity in plantations. Additionally, the amount of damage was only marginally higher in plantations for specific damage types. These results suggested that the types of plantations used in FERLD are not at elevated risk for herbivore damage.

There were several possible explanations for why the plantation damages were higher for some specific insects. One may have been the higher canopy openness and temperature. High temperatures generally accelerate insect development rates (Rouault et al., 2006). However, this can also decrease reproductive rates in some insects (Zhang et al., 2015). Overall, generalist pest insects were expected to thrive in higher temperatures (Pelini et al., 2009). Gall adelgids were sap-sucking insects; they produced two generations per year, which could have enabled them to rapidly take advantage of warmer conditions in plantations to increase population size. *Hylobius abietis* tended to increase in abundance at the crown of *Picea glauca* (Pilichowski et al., 2014), indicating they did well under sun-exposed conditions. Previous work suggested that gall adelgid damage was higher in plantations because of lower parasitism rates and lower pathogen infection of the insects in these environments (Fernandes & Price, 1992).

Spruce budworm damage increased from 2020 to 2021. Budworm outbreaks are infrequent but can last for decades and cause mortality of white spruce and other conifers

over multiple square kilometres (Bouchard et al., 2018). Younger forest trees were also susceptible to small larval populations found at the start of a new outbreak (Lavoie et al., 2021). Navarro et al. (2018) identified an outbreak hotspot in Abitibi, north of Quebec, near the research station where we conducted our study. Budworms were active in early spring, and budworm damage was thus more straightforward to identify in the early season sampling. Identifying budworms was more difficult in the later months as the silk was no longer present due to the rain washing it away.

Our data suggested that plantations could be a suitable habitat for many insect species, as observed damages were comparable to naturally regrown trees. As most herbivorous insects were flighted, they could disperse between the plantations and the surrounding forest (Anderson & Sturtevant, 2011). The proximity between different trees facilitated the movement and exchange of generalist herbivore species. The plantations were within 100 meters of other plantations and naturally regrown forests.

The management approach of FERLD left early succession plants growing around the saplings on the plantation. This method could have contributed to maintaining insect biodiversity. Studies indicated that early successional plants enhance insect diversity (Swanson et al., 2011). Their presence increased overall plant diversity, potentially leading to more niches for insect species in these environments (Poniatowski et al., 2020; Thomas, 2010). In summary, the findings suggested that these plantations support a similar diversity of herbivorous insects to naturally regrown forest environments. Consequently, creating smaller plantations may be advantageous as having more diversity could improve environmental resilience (Jactel et al., 2005) and protect against outbreaking species (Messier et al., 2022).

As of 2020, the world had an estimated 280 million ha of planted forests, which is continuously increasing (Bahar et al., 2020). Of these, 131 million ha were monospecific planted forests under intensive management. Although monospecific planted forests were critical in providing timber, they harbored less biodiversity and were potentially more susceptible to disturbances than natural or diverse planted forests. Diverse stands also sequester more carbon than monocultures (Hulvey et al.,2013). Here, we pointed out the increasing scientific evidence for increased resilience and ecosystem service provision of functionally and species-diverse planted forests (hereafter referred to as diverse planted forests).

Our results suggested that plantation stands in FERLD offer a suitable quality habitat for various insect species, similar to that found in natural forests. The silvicultural hypothesis indicated that stands made of diverse trees decrease the prevalence of pest species (Jactel & Brockerhoff, 2007). This hypothesis also supported the practice of multispecies plantations with minimalist intervention to suppress non-commercial species (Messier et al., 2022).

Conclusion

Our results indicated that the insect damage types do not differ significantly between young white spruce trees in plantation relative to those in naturally regrown forests. Thus, the sampled plantations seem to be a good reservoir for herbivorous insect species. There was no correlation between insect distribution and the environmental variables we measured. However, a spruce budworm outbreak was progressing in the region (Government of Quebec, 2022), and thus, a continued survey of herbivorous insects may be important to identify insect community changes under this increasing spruce budworm population.

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