INFLUENCE OF BALSAM FIR STAND CONDITION ON THE ABUNDANCE AND DIVERSITY OF EASTERN HEMLOCK LOOPER, *Lambdina fiscellaria fiscellaria* (GUEN.) (LEPIDOPTERA: GEOMETRIDAE) NATURAL ENEMIES

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Influence of balsam fir stand condition on the abundance and diversity of eastern hemlock looper, *Lambdina fiscellaria fiscellaria* (Guen.) (Lepidoptera: Geometridae) natural enemies.

by

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Abstract:

To assess the impact of natural enemies on the distribution of eastern hemlock looper various balsam fir stands were examined at Black Pond, in central Newfoundland. In 1995, 1996 and 1997 insects were collected using Malaise traps suspended into the balsam fir canopy. First, natural enemy abundance was assessed based on balsam fir stand vigour. A non-continuous vigour gradient was established using three silvicultural methods (root pruning, thinning, and fertilizing) and control treatments. Natural enemy abundance, in general and known eastern hemlock looper natural enemy abundance and diversity was higher in balsam fir stands that were more vigourous. These more vigorous stands provided natural enemies with more alternate hosts or prey. Second, natural enemy abundance was estimated based on the time since thinning and vegetation diversity of balsam fir stands. Natural enemy presence in stands that were unthinned, thinned one year prior to the study and thinned 16 years prior to the study were examined. Natural enemy abundance, in general and known eastern hemlock looper natural enemy abundance and diversity was higher in balsam fir stands that had had vigour increased by thinning 16 years prior to the study. The diversity of vegetation in these stands was higher due to the length of time since thinning. This increased vegetation diversity resulted in more resources available to natural enemies: more alternative feeding sites for adults, more shelter and overwintering sites. Balsam fir stands that have low vigour and have little or no understory vegetation seem to provide looper with enemy free space.

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Table of Contents:

List of Tables:

List of Figures:

List of Appendices:

1.0 Introduction

1.1 BACKGROUND

Terrestrial ecosystems with plants as their foundation are comprised of at least three trophic levels: plants, herbivores and the natural enemies of the herbivores (Price *et al.* 1980; Vet and Dicke 1992). Late successional temperate systems, such as the boreal forest of North America, consist of plants that are long-lived and tend to grow in stands of low diversity. In terms of insect herbivores these stands are "predictable" and "apparent". Consequently, the herbivores feeding within these stands should also appear "predictable" and "apparent" to their natural enemies (Price *et al.* 1980).

Natural enemies of insects include arthropods, nematodes, microbial organisms, snails and vertebrates (Ridgeway and Vinson 1976). Based on their foraging ecology they are commonly grouped as predators, parasitoids/parasites or pathogens. Predators comprise a broad spectrum of taxa. They are usually defined as individuals that consume many prey individuals within their lifetime (Godfray 1994; Strand and Obrycki 1996). Parasitoids are much like parasites in that they feed upon their host while the host is still living, however parasitoids kill their host once they have completed their development (Vinson 1976; Godfray 1994; Strand and Obrycki 1996). Parasitoids are primarily members of the Orders Hymenoptera [wasps] and Diptera [flies] (Wharton 1993; Godfray 1994; Strand and Obrycki 1996). Pathogens are typically fungi, bacteria or viruses. These organisms replicate within various cells, tissues and organs of their hosts, generally resulting in a weakening of the infected individual, which occasionally culminates in death.

Within different habitats there may be variability in the quantity and quality of insect herbivores, but ultimately all insects within a habitat can be considered a potential prey item or host. Various theoretical models have been developed to describe how natural enemies forage for insect herbivores (Strand and Obrycki 1996). Optimal foraging theory is the predominant model found in literature today. It assumes that natural selection works to maximize fitness through the optimization of the rate of energy intake and expenditure, growth, and ultimately the number of surviving offspring that an individual produces (van Alphen and Vet 1986; Godfray 1994; Strand and Obrycki 1996).

Information from both the plant and herbivore form the basis for foraging decisions made by natural enemies (Vinson 1976; Baehrecke *et al.* 1990; Vet and Dicke 1992; Godfray 1994; Strand and Obrycki 1996). The process of locating and accepting prey or hosts is called host/ prey selection [termed host selection here after] (Vinson 1976; Strand and Obrycki 1996). Host selection has been broken down into a series of proximate factors (Strand and Obrycki 1996). These proximate factors can be arranged into a hierarchy, starting with host habitat selection, host location, host acceptance and host suitability (Vinson 1976; Baehrecke *et al.* 1990; Vet and Dicke 1992; Godfray, 1994; Strand and Obrycki, 1996). Several studies have suggested that these factors blend together (Vet and Groenewold 1990; Vet and Dicke 1992; Tumlinson *et al.* 1993; Godfray 1994; Strand and Obrycki 1996).

This study focused on host habitat selection by insect predators and parasitoids. Many herbivores are able to escape attack from parasitoids and predators by reducing the probability of being found and contacted (Price *et al.* 1980; Gross 1993). The literature on host selection is mainly comprised of research into the foraging behaviors of parasitoids at various spatial scales and their use of infochemicals as cues in host habitat location. Few studies have dealt with larger spatial scales such as grasslands, marshlands and forests (Nordlund 1994). Of the studies that have considered the ability of natural enemies to forage on large spatial scales, most have noted the difficulties that natural enemies have in controlling herbivore populations (Roland 1993).

Few hosts are randomly distributed in natural environments and they often occur in discrete patches (Roland 1993; Godfray 1994). Parasitoids have several behaviors associated with their search for hosts occurring within these patches. Parasitoids will often restrict their search to a specific area. If their host has a clumped distribution, the parasitoid will search until it finds a suitable host. Once a host is located and parasitized, the parasitoid continues searching for other hosts in that same area. Conversely, if hosts are not clumped but isolated, dispersal after oviposition would be more advantageous strategy (Godfray 1994).

Herbivores can obtain varying degrees of enemy free space by occupying habitats that are seldom or never searched, inaccessible to enemies, or located on a portion of a plant that inhibits enemy searching patterns (Price *et al.* 1980; Gross 1993). Many small predators and parasitoids have specialized searching patterns that often restrict them to a certain plant species or to particular parts of a single plant. With variations in the size and complexity of these plant parts, natural enemies may encounter variation in the accessibility to the herbivores using them (Price *et al.* 1980). For example, *Itoplectis* *conquisitor* (Say.) (Hymenoptera: Ichneumonidae), a parasitoid of many polyphagous insect herbivores, has been found to selectively search the lower two thirds of trees (Cronin and Gill 1989). Knowledge of the foraging behavior of natural enemies at various spatial scales is important in understanding the dynamics of their interactions with prey/host because of the direct link between successful searching and successful attack (Völkl 1994). Most of the recent literature on natural enemy foraging behavior has focused on small spatial scales such as individual plants, branches or leaves (Völkl 1994). There have been few studies that focus on the properties of plant populations (i.e. stands of coniferous trees) that affect a herbivore's natural enemy compliment (Price *et al.* 1980).

Most natural enemies strongly rely on their various senses to locate their hosts (Norlund, 1994). Visual orientation has been recorded in several parasitoid species (Herrebout 1969; van Alphen and Vet 1986; Drost and Cardé 1992). Most of the extensive research into the use of sensory cues used by parasitoids indicates olfaction to be the principal mechanism of host location (van Alphen and Vet 1986).

There is considerable evidence that in the absence of the host itself, odors from the host's microhabitat, or the substrate in which the host develops can attract parasitoids (Ding *et al.* 1989; Godfray 1994). The ability of *Leptopilina heteromoma* (Thomson) (Hymenoptera: Eucoilidae) to locate

hosts by the odor of the microhabitat in which the host is found has been noted by several authors (Papaj and Vet 1990; Vet *et al.* 1990). These wasps are able to orient toward the scent of apple-yeast, beet, mushroom and other substrates in which their hosts develop. When there is increasing experience of successful oviposition in association with these odors there is an increased preference for the odor (Papaj and Vet 1990; Vet *et al.* 1990).

Additional studies indirectly indicate the importance of the host plant for parasitoid searching. Insect hosts that are taxonomically unrelated but which feed on the same food plant frequently share the same parasitoids, and the amount of parasitism suffered by a polyphagous host insect is often related to the food plant that it is attacking (Ding *et al.* 1989; Godfray 1994). Strong evidence for the importance of host plant odors have been obtained from behavioral studies using y-tube olfactometers and wind tunnels with various plant volatiles. These studies have indicated that wasps detect unique volatile compounds released from plants and they utilize these compounds to orient towards their host (Tumlinson *et al.* 1993). For example, Ramachandran and Norris (1991) found that the parasitoid *Microplitis demolitor* Wilkinson (Hymenoptera: Braconidae) was more sensitive to the volatiles of its host's food plant, than those of its host.

The dynamics of insect predator-prey systems and the severity of insect herbivore outbreaks may be strongly affected by the spatial heterogeneity of natural environments (Roland 1993). Within forest landscapes dominated by a single tree species, such as the forests of the boreal zone, a significant portion of spatial heterogeneity arises from variations in tree density. Pockets of dense trees may limit the dispersal of natural enemies. These areas may support high herbivore densities with little or no threat of mortality from natural enemies. Moreover these pockets may act as local sources of dispersing herbivores that can sustain a population in a continuous forest while in a decline, or allow for a rapid increase initially in an outbreak situation (Roland 1993).

In patches where tree density is low, light is able to penetrate the canopy and reach the forest floor. This light allows additional plant species to grow beneath the forest canopy (Page 1974). These patches are more diverse providing necessary resources for natural enemies such as alternate feeding sites (nectar, pollen and honeydew), alternate hosts or prey, or over-wintering sites, thus enhancing natural enemy abundance in the surrounding environment (Price *et al.* 1980; Murphy *et al.* 1996). The nutrients acquired by natural enemies from these additional sources often increase their longevity and fecundity (Simmons *et al.* 1975; Price *et al.* 1980). Therefore, patches with low tree diversity and high vegetation diversity may provide natural enemies with a broader spectrum of resources.

The odors of associated plants may affect the foraging activities of predators and parasitoids. For example, in agricultural situations where weeds are present in the monoculture, natural enemies may be attracted to the odors of the weeds or adjacent crop species and will often forage on the herbivores found on the associated crop plants (Read *et al*, 1970; Smith, 1969). Conversely, associated plants may reduce the attractiveness of the plant to both the herbivore and its natural enemies (Price *et al*, 1980). The volatiles released by associated plants may mask the odor of the herbivores' food plant impairing the specific search mechanisms of natural enemies (Price *et al*, 1980; Godfray, 1994), or they may actually have repellent properties to the herbivore, natural enemy or both (Price *et al*, 1980).

1.2 EASTERN HEMLOCK LOOPER (EHL), *LAMBDINA FISCELLARIA FISCELLARIA* (GUEN.)

1.2.1 Eastern Hemlock Looper in Newfoundland

Despite their uniform appearance, the balsam fir (*Abies balsamea* (L.) Mill.) forests of Newfoundland vary in both the density of trees and the associated understory plants. Currently the predominant insect herbivore of these forests is the eastern hemlock looper, *Lambdina fiscellaria fiscellaria* (Guen.). Eastern hemlock looper (EHL) populations are typically distributed in a fragmented or patchy manner across the landscape; concentrated primarily within dense, slow-growing stands (Otvos *et al*, 1979). Presumably these stands offer the hemlock looper fitness advantages over other stand types, either by 1) having high foliage quality, providing the looper with the required nutrients for growth and reproduction or; 2) having a reduced probability of mortality due to natural enemies.

Spatial heterogeneity within the balsam fir forests may influence the natural enemies of the EHL. Dense stands may limit the mobility of natural enemies, causing an increase in foraging times and reducing foraging efficiency. As balsam fir stands mature there is a decrease in tree density. This decreasesd stand density allows pockets of light to reach the forest floor, often resulting in an increase in the density and diversity of understory vegetation (Page 1974). These stands may provide natural enemies with more shelter, more prey/host and alternative feeding sites (nectar and pollen) for adults. The differential success of natural enemies foraging in dense stands versus less-dense stands may ultimately result in the patchy distribution of hemlock looper populations.

To date, no studies have been undertaken to relate the spatial dynamics of hemlock looper to the abundance and distribution of natural enemies. Previous work with natural enemies has consisted of taxonomic surveys, parasitoid introductions and studies of parasitism rates. The degree to which predaceous invertebrates affect hemlock looper populations is unknown.

There has been no survey of the predaceous invertebrate species that prey upon the hemlock looper, given the difficulty of observing invertebrates feeding in the field (Otvos, 1973). By contrast, there have been extensive surveys of the parasitoids of hemlock looper. The most commonly collected parasitoids are *Winthemia occidentis* Rnd. (Diptera: Tachinidae), *Itoplectis conquisitor* and *Ephialtes ontario* (Cress) (Hymenoptera: Ichneumonidae). Other organisms that have been recorded as natural enemies of the hemlock looper in Newfoundland include a variety of bird species, and several pathogens (Otvos, 1973).

1.2.2 Eastern Hemlock Looper Lifecycle

Carroll (1956) described the life history of the hemlock looper in detail. Briefly, eggs hatch in early June to the middle of July, coinciding with the initiation of balsam fir bud burst. Larvae develop for approximately 50 days. Looper found in Newfoundland have four larval instars, whereas on the mainland larvae complete 5 instars. Pupation begins in late July and lasts about 21 days. Adult moths begin to eclose around the end of August. The duration of moth flight lasts until late fall with moths reaching peak numbers during September. Mated females deposit eggs singly on a variety of substrates within the forest. The eggs then over winter until the larvae emerge the next spring.

1.3 STUDY OBJECTIVES

The primary objective of the investigation was to assess the effect of balsam fir stand conditions on the distribution of EHL natural enemies. This question was addressed by evaluating two hypotheses. The first was that natural enemies forage in thinned stands due to the reduced stand density and the ease of mobility within and through the stands. The second hypothesis was that natural enemies forage in stands where balsam fir was thinned while the trees were young. These stands have more alternative feeding sites and shelter available to natural enemies because of an increase in the structural and vegetative complexity associated with thinning early in the stands' regeneration. This investigation is part of a larger study on EHL spatial dynamics by Dr. Allan Carroll of the Canadian Forest Service.

2.0 Methods and Materials

2.1 STUDY SITE

The study site was located in central Newfoundland (Fig. 1), 20 km southwest of Millertown adjacent to Black Pond (48°47' N, 56°36'W). This area is in the Red Indian sub-region of the Central Newfoundland ecoregion (Damman 1983). The topography of the sub-region is rolling or undulating. The study site was comprised of an even-aged balsam fir stand that regenerated following clear cutting in the 1940's and has been described in detail by Carroll (1999). The study site is classified as a *Hylocomium*-balsam fir forest (Meades and Moores 1994). This forest type is usually found on moist mid-slopes that have gleyed podzol soils ranging from sandy loam to loam, with medium soil fertility (Meades and Moores 1994).

During the collection seasons, EHL populations in the study area were present but infrequently encountered in the plots and the surrounding area (A. Carroll, pers. comm.). However there have been seven waves of EHL epidemics in Newfoundland since 1910 (six listed in, Otvos *et al.* 1979). The last two occurred from 1966-1972 and 1982-1988. During the last epidemic there was heavy balsam fir defoliation in areas near the study site. Since 1990, Newfoundland EHL populations have remained patchy and localized (Hudak *et al.* 1996).

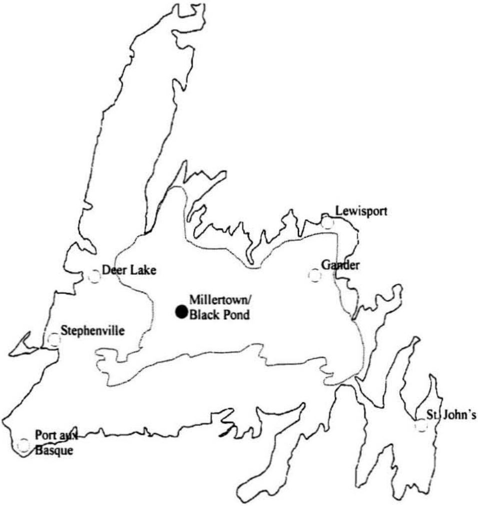

Figure 1: Map of insular Newfoundland illustrating the location of the study site in relation to other municipalities. Dotted line represents the boundaries to the Central Newfoundland region (Damman 1983).

2.2 EXPERIMENTAL DESIGN

2.2.1 Balsam fir stand vigour *versus* natural enemy abundance

A randomized block design with two replicate blocks, each containing four treatment plots, was established to assess the influence of balsam fir stand treatment on the presence of EHL natural enemies. During the summer and fall of 1994, two 30x30 m blocks, approximately 100 m apart, oriented north-south, each sub-divided into four 15x15 m treatment plots were established by A Carroll. Treatments were chosen to establish a vigour gradient. In order of increasing vigour treatments were; root pruned (RP), control (C), thinned (T), and thinned and fertilized (TF) (Fig 2). T and TF plots were thinned to a density of approximately 2500-3800 stems ha^{-1}, approximately 2 m between trees (Table 1). Root pruning was achieved by cutting trenches 30 cm deep within 50 cm of the root collar along the west and east side of each tree in the plot. The plot was initially pruned in the fall of 1994 and then re-pruned in June of 1996. In early 1995, thinned and fertilized plots were fertilized with an equal ratio of elemental N, P, and K at a rate of 150 kg ha^{-1} (Luther and Carroll, 1999). Flying insects were collected in 1996-1997 in each of these four treatments. The natural enemies that were caught during these collections were counted to allow a comparison between the natural enemy compliment and stand treatment.

2.2.2 Time since balsam fir thinning *versus* natural enemy abundance

In 1980 Abitibi Consolidated and the Newfoundland Forest Service pre-commercially thinned large areas of balsam fir forest in the Millertown area. Pre-commercial thinning is a silvicultural practice where stands are thinned to a

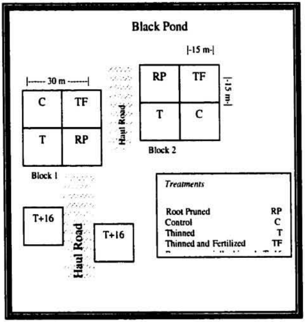

Figure 2: Experimental layout for both the randomized blocks of the balsam fir stand vigour *versus* natural enemy abundance experiment and the treatment plots for the time since balsam fir thinning *versus* natural enemy abundance investigation.

Table 1: Stand densities (stems ha^{-1}) for each treatment plot (root pruned (RP), control (C), thinned (T), thinned and fertilized (TF) and pre-commercially thinned (T+16)) in the Black Pond study site. Stem densities were estimated from the number of live trees in a 5x5-m subplot. Stand densities of T, TF and T+16 were determined from the number of trees remaining in the plot post treatment (A. Carroll, unpublished).

	RP	**C**	**T**	**TF**	**T+16**
Block 1	10400	7200	3244	2533	2222
Block 2	16000	11200	3867	3822	2489

predetermined stem density before stems achieve a commercial value. This practice usually decreases the time for trees to reach commercial value by decreasing competition between trees. These balsam fir stands were thinned to a density of approximately 2500 stems ha^{-1}. One such area lay adjacent to the two study blocks. In July 1996 two 15x15m plots were delineated in this thinned stand. These treatment plots were oriented on the same north-south coordinates as the vigour treatments (Fig. 2). To assess the potential for changes in stand condition related to the time since thinning on the natural enemy assemblage, EHL natural enemy numbers from these pre-commercially thinned plots (T+16) were compared to the numbers caught in both thinned (T) and control (C) treatments.

2.3 INSECT SAMPLING

A single Malaise trap was suspended within the center of each plot to collect potential natural enemies. The trap was placed in the upper crown of the stand. This was the optimum position for the trap since EHL larvae typically feed in the upper crown of a fir tree and any natural enemies foraging for, or potentially feeding on, them should be found in that general area. Each trap was 2.1 meters high and 1.2 meters wide, made of white tricot polyester netting with reinforced seams of nylon carpet tape. The collecting head was the "dry-type" with a 20-cm high x 10-cm diameter cylindrical chamber made of clear acrylic with an inverted truncated funnel at the bottom. A chamber for a solid killing agent (Vapona ®) was built into the cap. The collecting head was attached to the trap using a bungie cord. A pulley system was used to raise and lower the trap for emptying (Fig. 3). The side panels of the tent were kept open using ropes tied to surrounding trees.

In 1996 and 1997 trapping in the vigour treatments began about the time of EHL egg hatch, early to mid June, and ended after moth flight in late October. Dates were determined from historical records (Carroll, 1956; Canadian Forest Service, Forest Insect and Disease Service (CFS FIDS), unpublished). During the EHL larval period, Malaise trap samples were taken twice weekly to monitor temporal changes in the natural enemy fauna. During the pupal and the adult stage samples were collected once per week. An additional collection was made in 1995, (A. Carroll, unpublished). This collection was made weekly, however it was not started until early August (corresponding to the presence of late-larval instars of EHL) and was added to this study to supplement the 1996 and 1997 data.

T+16 treatments were not established until July of 1996, therefore the collections for the time since balsam fir thinning *versus* natural enemy abundance started later than the vigour collections. For the comparison, the totals for C and T collections were adjusted (the data set for both C and T started on the same date as the T+16 samples) so that all treatments had equal trap periods. In 1997 trapping periods corresponded to the vigour collections.

Insects that were collected in each trap in each sampling period were emptied into a container and frozen. The specimens were later sorted to taxonomic order and preserved in 70% ethanol. Possible predators and parasitoids, from the orders Hymenoptera and Diptera, were pinned and identified to family. Parasitoids were then

Figure 3: Malaise trap suspended into the upper crown of one of the study plots.

identified to genus and where possible to species. Known EHL parasitoids (Otvos *et al.* 1979) were counted. Several taxonomic keys were used to identify the natural enemies at the various taxonomic levels including Guimaraes 1972, Bradley 1974, Bradley 1978, McAlpine *et al.* 1981, Wood 1987, Borror *et al.* 1989, and Goulet and Huber 1993.

Predators and parasitoids collected during this investigation were generalists (i.e. utilizing a variety of prey/host species) (Otvos *et al.* 1979; Brothers and Finnamore 1993). If present in a stand, generalist natural enemies may exploit prey/host species other than EHL. Using the same malaise trap samples, estimates of the number of alternative lepidopteran herbivore prey/host items present in each plot and block were made. Only moths that were greater than 5 mm in length were considered. Totals were determined for the periods July to October, 1996, and June to October, 1997.

2.4 VEGETATION DESCRIPTION

The ages of balsam fir stands in the Black Pond study site were assessed in 1994. Ages of T and TF plots were determined by counting the rings of 20 randomly selected stumps following the thinning of the stand. The ages of C and RP treatments were inferred from the immediately adjacent T and TF plots. Trees in the C and RP plots were not assessed directly since the use of an increment borer could potentially affect tree vigour. This also applied to trees in the T+16 plots (Carroll 1999). The age of T+16 trees was determined by coring 10 trees immediately adjacent to the T+16 plots.

To determine if variation in vegetation between treatment plots influenced the presence of natural enemies, percent cover estimates were used to compare plant density and forest floor composition. Ten $1m^2$ quadrats were sampled in 1997, within each of the four treatments (C, RP, T, TF) in each block and the two T+16 plots. The random generation of x and y-coordinates within each plot determined the location of each quadrat. Forest floor plants and debris were classified into twelve categories: bare soil, dead wood, litter, fungi, mosses, grasses, ferns and allies, herbaceous plants, shrubs and trees height (seedlings 0-10 cm, 11-100 cm, 100-300 cm).

2.5 DATA ANALYSES

All statistics were performed using SYSTAT 7.0.1 for Windows™ (1997). Graphics were developed using SigmaPlot 4.0 for Windows™ (1997). To normalize the data prior to analysis a square root transformation was performed on the data after adding 0.5. The data was considered normal if the plot of the residuals versus the fits plots were evenly distributed. Unless stated otherwise, all values are reported as means ± one standard error. For each experiment the mean number of each abundant natural enemy group caught in each treatment was plotted. A timeline of was also plotted of the mean number of each abundant natural enemy group caught in each treatment. The timelines were plotted using a three week running average. Each point represented the average number of the natural enemy group in question caught the week before, the week after and the week of the particular point plotted. The method of using running averages may hide subtle changes that occur from week to week. However, in the current study running averages are used to illustrate trends on a seasonal scale.

2.5.1 Insect Numbers

Insect data were analyzed based on the following groupings: (1.) all insects that are natural enemies of balsam fir folivores, and (2.) known EHL natural enemies. Known

EHL natural enemies were divided into two subgroups, i.) predators, which comprised members of the family Vespidae, and ii.) recorded EHL parasitoids. Natural enemies were defined as any insects that either parasitize or prey upon larval insect herbivores (usually soft-bodied caterpillars) as either larvae or adults. Natural enemies in the collection were members of the order Hymenoptera, sub-order Apocrita families Braconidae, Ichneumonidae and Vesidae and the order Diptera, family Tachinidae. Hymenoptera of the sub-order Apocrita are predominantly carnivorous; several species are predaceous while 75% of them are parasitic (Brothers and Finnamore 1993). Vespids were categorized as predators since most members of this family feed their larvae the larvae of other insects (Brothers and Finnamore 1993). Moreover, vespid wasps have been observed preying upon EHL larvae (A. Carroll pers. comm.). Hymenopterous parasitoids of the families Braconidae and Ichneumonidae have been reared from field-collected EHL larvae (Otvos *et al.* 1979; CFS FIDS, unpublished). Members of the family Tachinidae (Diptera) were included as natural enemies since the larvae of all species are parasitoids of arthropods (Wood 1987). Five tachinid species have been collected from EHL larvae in Newfoundland (Otvos *et al.* 1979; CFS FIDS, unpublished).

The diversity of known EHL natural enemies within the treatments was compared using rarefaction (Krebs 1989). Rarefaction is a statistical method used to estimate the number of species expected in a random sample of individuals taken from a collection. The number of known EHL parasitoids and predators collected in each treatment, for both blocks and each of the three years was totaled. The analysis was performed using

RAREFACT version 3.0 (Krebs 1991). The species number estimates for each of the treatments calculated by the RAREFACT were plotted against the number of individuals per sample.

A three-way analysis of variance (ANOVA) was used to assess the impacts of sample week, block and treatment (RP, C, T or TF) on (i) natural enemy abundance (total number/trap/week) and (ii) the number of potential alternative host/ prey items (total number/trap/week). Since natural variability was expected to occur between blocks, a block x treatment interaction was not considered (Sokal and Rohlf 1995). For natural enemies the analysis was restricted to the more abundant taxa (groups where the numbers in at least one vigour treatment was greater than 10 during one week.

Differences in natural enemy abundance (total number/trap/week) and the number of potential alternative host/ prey (total number/trap/week) at different times after stand thinning were assessed using a two-way ANOVA including sample and treatment (C, T, and T+16) and a sample week x treatment interaction. For the natural enemies, the analysis was also restricted to abundant taxa.

In both experiments a Tukey's post hoc comparisons of means were performed to determine which treatments differed significantly. All p-values were considered significant if they were lower than the adjusted α. ($\alpha' = 0.05/K$, where K=number of comparisons) (Bonferroni method, see p. 240, Sokal and Rohlf 1995).

2.5.2 Vegetation Description

Two separate principle component analyses on the vegetation data were performed, to determine if there were differences in vegetation or structural diversity between treatments, one for the balsam fir stand vigour *versus* natural enemy abundance experiment (PCA1) and the other for the time since balsam fir thinning *versus* natural enemy experiment (PCA2).

3.0 Results

3.1 INSECT COLLECTIONS

Insect natural enemies collected in the Malaise traps included Hymenoptera of the families Ichneumonidae, Braconidae and Vespidae and Diptera of the family Tachinidae. Table 2 compared the parasitoid species collected in the current study to those of previous collections. Out of the 10 parasitoids collected by Otvos *et al.* (1979) there were only 6 species collected in the Black Pond treatments. The current study had 5 of the 17 found in the FIDS (unpublished) reference collections. Two additional microgastrinid species were collected not listed previously, *Cotesia* sp. and *Glyptapanteles* sp. These species were considered to be EHL parasitoids because of the reorganization of the *Apanteles* genus. Many of the specimens that were collected by FIDS were identified before the reorganization and may now be misidentified.

3.1.1 Balsam fir stand vigour *versus* natural enemy abundance

NATURAL ENEMY ASSEMBLAGE

The number of natural enemies differed significantly among the treatments in 1995 and 1996 (Table 3). The number of predators and parasitoids caught in the RP treatments was consistently lower than the numbers in the other three treatments (Fig. 4a.), numbers in C, T, or TF treatments were 2.5 to 3.0 times greater than RP treatments. In both 1995 and 1996 natural enemy numbers in RP treatments were significantly lower than those of all other treatments (Table 4; Fig. 4a.). Natural enemy numbers in T treatments were also significantly lower than numbers in C and TF treatments in 1996.

Table 2: List of parasitoids collected in the current study compared to previous collections. Species introduced against EHL †. Species introduced against spruce budworm ‡.

Parasitoid Species	Otvos *et al.* (1979)	CFS St. John's FIDS collection	Current Study
Egg parasitoid			
Hymenoptera			
Teleomus sp.	*		
Larval and pupal parasitoids			
Diptera: Tachinidae			
Blondelia eufitchiae (Tns.)	*	*	*
Madremyia saundersii (Will.)	*	*	
Phryxe pecosensis (Tns.)	*	*	
Winthemia occidentis Rnd. †	*	*	
Winthemia sp.		*	*
Hymenoptera: Ichneumonidae			
Aoplus velox (Cress.)	*	*	
Ephialtes ontario (Cress.) ‡	*	*	*
Itoplectis conquisitor (Say.)	*	*	*
Phaeogenes gaspesianus Provancher		*	
Phaeogenes hariolus (Cresson)		*	
Mesochorus discitergus (Say.)		*	
Mesochorus vittator (Zetterstedt)		*	
Mesochorus sp.		*	
Casineria sp.		*	
Hymenoptera: Braconidae			
Apanteles sp	*		*
Cotesia sp.			*
Protapanteles paleacritae Riley		*	
Protapanteles sp.		*	*
Glyptapanteles sp.			*
Phobocampe sp	*	*	
Zele sp.	*	*	

Table 3: Three-way ANOVAs comparing the more abundant natural enemy taxa *versus* balsam fir stand vigour (RP, C, T, TF) for each collection year, 1995, (n=104), 1996 (n=152) and 1997 (n=144), Black Pond, Newfoundland. Variables tested were block, treatment, and sample week (SW) with a treatment X SW interaction. Significance at $\alpha'=0.05/K$ (where K= is the number of comparisons for each source) *.

				Natural enemies			Vespidae			*Winthemia* sp.		
Year	Source	α'	df	MS	F-stat	p-value	MS	F-stat	p-value	MS	F-stat	p-value
1995	Block	0.025	1	9.72	6.93	0.011 *	0.62	2.67	0.11	0.15	0.41	0.526
	Treatment	0.013	3	18.60	13.27	<0.0001 *	2.62	11.29	<0.0001 *	1.01	2.76	0.050
	SW	0.0039	12	3.66	2.62	0.009	1.70	7.31	<0.0001 *	2.80	7.64	<0.0001 *
	Treatment X SW	0.0014	36	0.79	0.56	0.963	0.24	1.04	0.443	0.30	0.82	0.730
	Error		51	1.40			0.23			0.37		
1996	Block	0.025	1	0.93	1.11	0.296	2.642	8.78	0.004	0.78	5.02	0.03
	Treatment	0.013	3	31.36	37.26	<0.0001 *	2.73	9.06	<0.0001 *	0.89	5.71	0.001
	SW	0.0027	18	7.13	8.48	<0.0001 *	1.95	6.49	<0.0001 *	6.37	40.90	<0.0001 *
	Treatment X SW	0.0009	54	0.81	0.97	0.548	0.40	1.32	0.131	0.16	1.05	0.423
	Error		75	0.84			0.30			0.16		
1997	Block	0.025	1	96.24	66.74	<0.0001	3.81	10.54	0.002	1.12	12.58	0.001 *
	Treatment	0.013	3	3.49	2.42	0.07	1.21	3.35	0.02	0.05	0.55	0.650
	SW	0.0028	17	8.69	6.03	<0.0001	0.70	1.93	0.03	0.79	8.86	<0.0001 *
	Treatment X SW	0.001	51	0.92	0.64	0.955	0.18	0.50	1.00	0.04	0.40	1.00
	Error		71	1.44			0.36			0.09		

Table 4: Significant differences between individual treatments (RP, C, T, TF) using a Tukey's post hoc analysis for each abundant taxa *versus* balsam fir stand vigour portion for each collection year, 1995 (n=104), 1996 (n=152) and 1997 (n=144), Black Pond, Newfoundland. Significance at $\alpha=0.05$ indicated by *.

1995

Natural enemies

	C	T	TF
RP	*	*	*
C			
T			

Vespidae

	C	T	TF
RP	*	*	*
C			
T			

Winthemia sp.

	C	T	TF
RP			
C			
T			

1996

Natural enemies

	C	T	TF
RP	*		*
C		*	
T			*

Vespidae

	C	T	TF
RP	*		*
C		*	
T			

Winthemia sp.

	C	T	TF
RP	*		*
C			
T			

1997

Natural enemies

	C	T	TF
RP			
C			
T			

Vespidae

	C	T	TF
RP		*	
C			
T			

Winthemia sp.

	C	T	TF
RP			
C			
T			

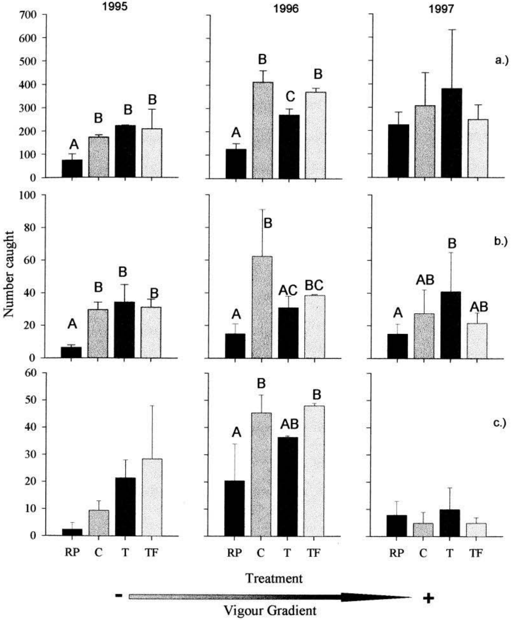

Figure 4: The mean (±SE) of each abundant natural enemy group caught in each vigour treatment a.) All natural enemies, b.) Vespidae and c) *Winthemia* sp. The 1995 collection were started in August, both 1996 and 1997 collections were started mid-June, Black Pond Newfoundland. Different capital letters indicate significant differences between treatments for the seam taxonomic group that year.

The relationship between treatment and the presence of natural enemies was consistent throughout the season (no treatment x sample week interaction; Table 3).

Spatial and temporal differences were evident in the abundance of natural enemies within each treatment. In both 1995 and 1997, the block in which treatment was replicated significantly influenced the number of natural enemies collected (Table 3). In 1995 and 1996, parasitoid and predator presence in each stand varied significantly depending on sample week (Table 3). There were no distinct patterns in natural enemy abundance throughout the season, with fewer natural enemies were usually captured in RP stands (Fig. 5), except 1997.

KNOWN EHL NATURAL ENEMIES

The only known EHL predators collected were vespids. However, nine genera of known eastern hemlock looper parasitoids were collected, namely, *Ephialtes ontario*, *Itoplectis* sp., and *Pimpla* sp. (Hymenoptera: Ichneumonidae); *Protapanteles* sp., *Glyptapanteles* sp., *Cotesia* sp., and *Apanteles* sp. (Hymenoptera: Braconidae: Microgastrinae); and *Winthemia* sp., and *Blondelia eufitchiae* (Diptera: Tachinidae) (Appendix I).

Abundant Taxa

Predators: Vespidae

In the 1995 and 1996 collection years, the number of vespids varied significantly among the different stand treatments (Table 3). Depending on the year, the number of vespids caught in C, T, or TF treatments were 0.5 to 5 times higher than the RP treatments. Vespid numbers were significantly lower in RP treatments compared to all

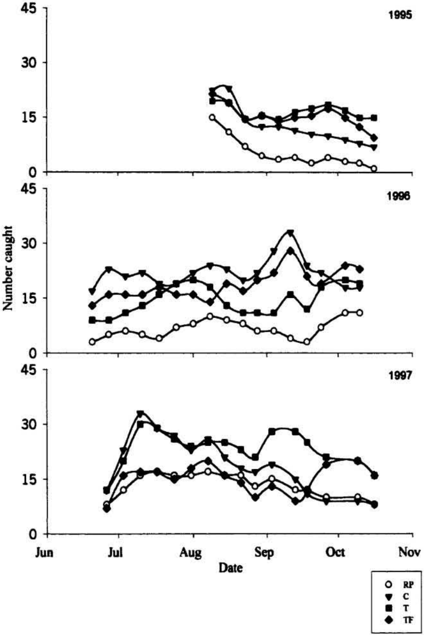

Figure 5: Mean (±SE) number of natural enemies caught per week in 1995, 1996, and 1997 for each vigour treatment using a running average based on three-week intervals, Black Pond, Newfoundland.

other treatments in 1995, C and TF treatments in 1996, and T treatments in 1997 (Table 4; Fig. 4b). In 1996 vespid numbers were also significantly higher in C treatments than T treatments.

The abundance of vespids varied spatially and temporally. In both 1996 and 1997 there were significant differences in the number of vespids collected between blocks (Table 3). Vespids were most abundant in the August and September collections in 1995, however in 1996 and 1997 numbers were higher in the late-August through October collections (Fig. 6). However, the presence of vespids varied significantly, depending on the sample week only in the first two study years (Table 3).

Parasitoids: Tachinidae: *Winthemia sp.*

In 1995 and 1996 fewer *Winthemia* sp. were found in RP treatments compared to C, T, or TF treatments (Fig. 4c.) However, only in 1996 were differences between individual treatment pairs detected (RP differed from C and TF). No obvious trends were evident in the 1997 *Winthemia* sp. counts.

Spatial variation in *Winthemia* sp. numbers was evident in 1997. The block which contained treatment replicates significantly affected the number collected (Table 3; Fig. 4c.). Temporal differences in *Winthemia* sp. numbers existed both between years and within a season. The half collection from 1995 had 2.2 times more *Winthemia* sp. than 1997 and the complete collection from the 1996 season had 5.3 times more than 1997. The prevalence of *Winthemia* sp. in each treatment varied significantly throughout the season in all three collection years (Table 3). The timelines for *Winthemia* sp. in each plot illustrated a peak in the number caught around the beginning of August (Fig. 7).

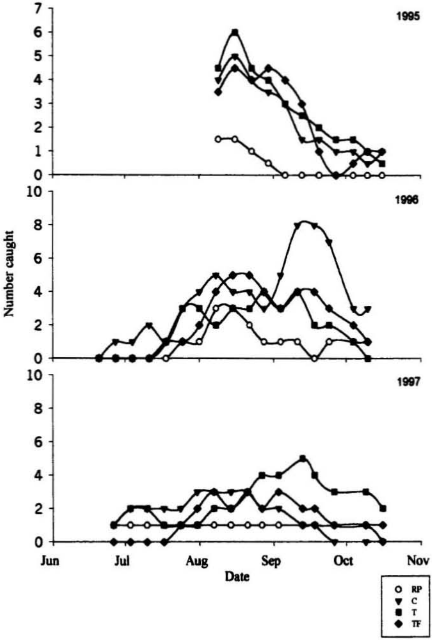

Figure 6: Mean (±SE) number of vespids caught per week in 1995, 1996, and 1997 for each vigour treatment using a running average based on three-week intervals, Black Pond, Newfoundland.

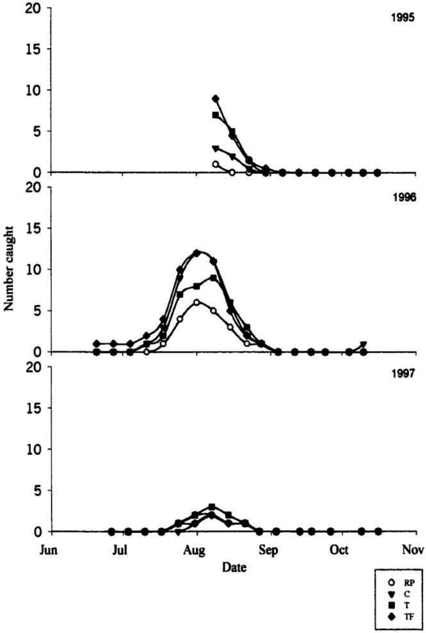

Figure 7: Mean (±SE) number of ***Winthemia*** sp. caught per week in 1995, 1996, and 1997 for each vigour treatment using a running average based on three week intervals, Black Pond, Newfoundland.

This time period corresponded to the 3rd and 4th larval instars of EHL. These are the stages that this and most other parasitoids predominantly attack (Otvos *et al.* 1979). This peak in *Winthemia* sp. numbers in early August resulted in significant differences in the number caught from sample week to week (Table 3).

Rare Taxa

Parasitoids: Ichneumonidae

Three of the Ichneumonid parasitoids collected belonged to the sub–family Pimplinae (Appendix I). *Ephialtes ontario* was the most abundant pimplinid species. In 1995 and 1996, there were 19 and 23 individuals caught respectively. In both years this parasitoid was collected in all 4 treatments. In 1997 there were only 2 *E. ontario*, one each in C and TF. Two other pimpline species were caught; *Itoplectis* sp. and *Pimpla* sp. However, only a single representative of each was encountered during the 3 years of the study (Appendix I).

Braconidae: Microgastrinae

There were four microgastrinid species collected; *Protapanteles* sp., *Glyptapanteles* sp., *Cotesia* sp. and *Apanteles* sp. During 1995, microgastrinids were caught in each treatment with only slight differences between treatments (Appendix I). However, microgastrinid numbers increased in 1996 (26 specimens) and were only collected in the C, T, and TF. In 1997, slightly fewer (20) specimens were collected and they were distributed among all four treatments. In all years the microgastrinids appeared sporadically throughout the season.

Tachinidae: *Blondelia eufitchiae*

Several specimens of the tachinid parasitoid, *Blondelia eufitchiae*, were collected. However this species was only collected in 1995 (Appendix I).

DIVERSITY OF KNOWN EHL NATURAL ENEMIES

The rarefaction curves (Fig. 8) for the treatments illustrated that the species richness of known predator and parasitoids of EHL increased from RP, C, T, to TF. The graph also illustrates that RP treatments had lower known natural enemy numbers with few species. C, T and TF treatments had slightly higher counts and larger known EHL natural enemy diversity (8 versus 6 in RP).

ALTERNATIVE HOSTS/PREY PRESENCE

In the last two collection years, the number of potential alternative hosts/prey caught in the Malise traps significantly differed among the treatments (Table 5). In both years C treatments had higher counts than other treatments (Table 6; Fig. 9) and RP treatments had the lowest counts, however these differences were not significant.

3.1.2 Time since balsam fir thinning *versus* natural enemy abundance.

NATURAL ENEMY ASSEMBLAGE

In each of the two years of this experiment, the number of natural enemies collected differed significantly among treatments (Table 7). In both years T+16 treatments had on average more natural enemies than T treatments (Table 8; Fig. 10a).

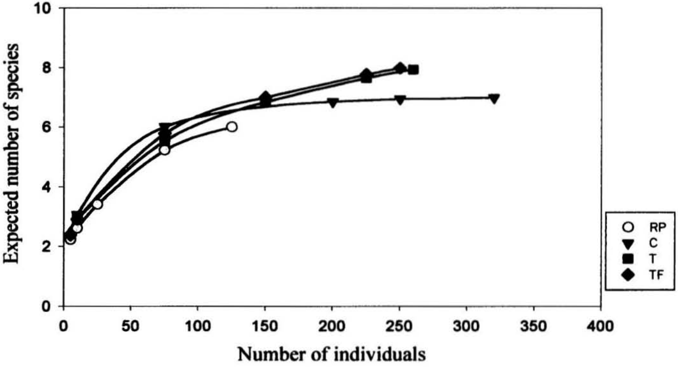

Figure 8: The number of known EHL natural enemy species expected to be collected in each of the vigour treatments (n=2) as the number of individuals per sample increased, Black Pond, Newfoundland. Values provided by RAREFACT version 3.0 (Krebs 1991).

Table 5: Significant variables from the analyses of variance which compared the alternative host/ prey abundance *versus* balsam fir stand vigour, Black Pond, Newfoundland. Variables tested for were block, treatment and sample week (SW) with a treatment X SW interaction, in 1996 (n=112) and 1997 (n=144). Significance at α'=0.05/K (where K= is the number of comparisons for each source) *.

	1996					1997				
Source	α'	df	MS	F-stat	p-value	α'	df	MS	F-stat	p-value
Block	0.0025	1	0.04	0.13	0.725	0.0025	1	3.03	7.85	0.007
Treatment	0.013	3	3.53	12.41	<0.0001*	0.013	3	1.57	4.08	0.010*
SW	0.0037	13	4.65	16.37	<0.0001*	0.0028	17	4.54	11.75	<0.0001*
Treatment X SW	0.0013	39	0.41	1.43	0.111	0.0010	51	0.32	0.82	0.768
Error		55	0.28				71	0.39		

Table 6: Significant differences between individual treatments (RP, C, T, TF) using a Tukey's post hoc analysis for the alternative host/ prey *versus* balsam fir stand vigour, for each collection year, in 1996 (n=112) and 1997 (n=144) Black Pond, Newfoundland. Significance at α=0.05 indicated by *.

1996

	C	T	TF
RP	*		
C		*	*
T			

1996

	C	T	TF
RP	*		
C			
T			

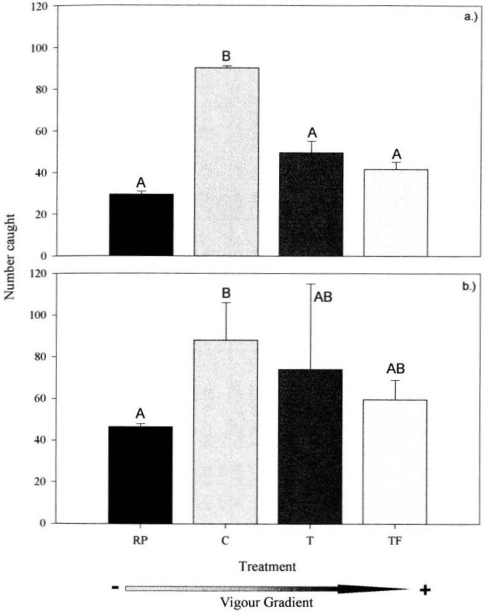

Figure 9: Mean (±SE) of lepidopteran (>5mm) herbivores caught in each vigour treatment (RP, C, T, TF) in a.) 1996 (July-October) and b.) 1997 (June-October) Black Pond Newfoundland. Different capital letters indicate significant differences between treatments for the seam taxonomic group that year.

Table 7: Two-way ANOVAs comparing the more abundant natural enemy groups *versus* long-term balsam fir stand vigour (C, T, T+16) for the two collection years, 1996 (n=84) and 1997 (n=108), Black Pond, Newfoundland. Variables tested were vigour, and sample week (SW) with a treatment X SW interaction. Significance at α'=0.05/K (where K= is the number of comparisons for each source) *.

				Natural enemies				Vespidae				*Winthemia* sp.			
Year	Source	α'	df	MS	F-stat	p-value		MS	F-stat	p-value		MS	F-stat	p-value	
	Treatment	0.017	2	4.95	4.73	0.014	*	1.34	2.83	0.070		1.69	7.90	0.001	*
1996	SW	0.0037	13	8.07	7.72	<0.0001	*	1.50	3.18	0.002	*	8.58	40.19	<0.0001	*
	Treatment X SW	0.0019	26	0.96	0.91	0.590		0.66	1.39	0.17		0.26	1.22	0.277	
	Error		42	1.04				0.47				0.21			
	Treatment	0.017	2	44.48	13.47	<0.0001	*	0.59	1.36	0.27		0.69	6.41	0.003	*
1997	SW	0.0028	17	13.07	9.96	<0.0001	*	0.64	1.48	0.14		1.14	10.62	<0.0001	*
	Treatment X SW	0.0015	34	1.08	0.33	1.000		0.19	0.49	0.99		0.13	1.18	0.290	
	Error		54	3.30				0.43				0.11			

Table 8: Significant differences between individual treatments (C, T, T+16) using a Tukey's post hoc analysis for each abundant taxa *versus* time since balsam fir thinning for each collection year, 1996 (n=84) and 1997 (n=108), Black Pond, Newfoundland. Significance at $\alpha=0.05$ indicated by *.

1996

Natural enemies

	C	T
T	*	
T+16		*

Vespidae

	C	T
T	*	
T+16		

Winthemia sp.

	C	T
T		
T+16	*	*

1997

Natural enemies

	C	T
T		
T+16	*	*

Vespidae

	C	T
T		
T+16		

Winthemia sp.

	C	T
T		
T+16	*	*

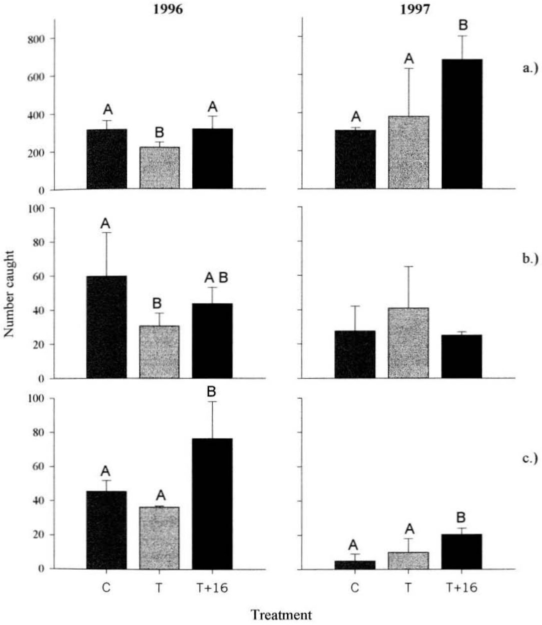

Figure 10: The mean (±SE) of each abundant natural enemy group caught in the thinned treatments a.) All natural enemies, b.) Vespidae and c) *Winthemia* sp. The 1996 samples were started in July and 1997 samples were started in June, Black Pond, Newfoundland. Different capital letters indicate significant differences between treatments for the seam taxonomic group that year.

However, in 1996 no differences were evident between T+16 and C treatments (Table 8; Fig. 10a). In 1997, natural enemy counts were clearly higher in T+16 and significantly different than natural enemy counts in each of the other treatments. In both years natural enemy numbers also varied between sample weeks (Table 7). Furthermore, the number of predators and parasitoids collected in the T+16 was consistently higher throughout the 1997 season (Fig. 11a).

KNOWN EHL NATURAL ENEMIES

Like the balsam fir vigour treatments the only known EHL predators collected were vespids. Eight genera of known EHL parasitoids were collected: *Ephialtes ontario*, and *Pimpla* sp. (Hymenoptera: Ichneumonidae); *Protapanteles* sp., *Glyptapanteles* sp., *Cotesia* sp. and *Apanteles* sp. (Hymenoptera: Braconidae: Microgastrinae); and *Winthemia* sp., *Blondelia eufitchiae* (Diptera: Tachinidae) (Appendix II).

Abundant Taxa

Predators: Vespidae

Vespid abundance among the time since balsam fir thinning treatments showed no clear pattern (Fig. 10b). Significant differences between treatments in 1996 were evident, with C having significantly more than T (Tables 7 and 8). In 1997 vespids were equally likely to be found in either treatment (C, T or T+16) (Tables 7 and 8).

The abundance of vespids throughout the season varied in 1996 (Table 7), with numbers peaking in C and T+16 treatments late August through September (Fig. 11b.). However in 1997 the number of vespids caught did not vary throughout the season (Table

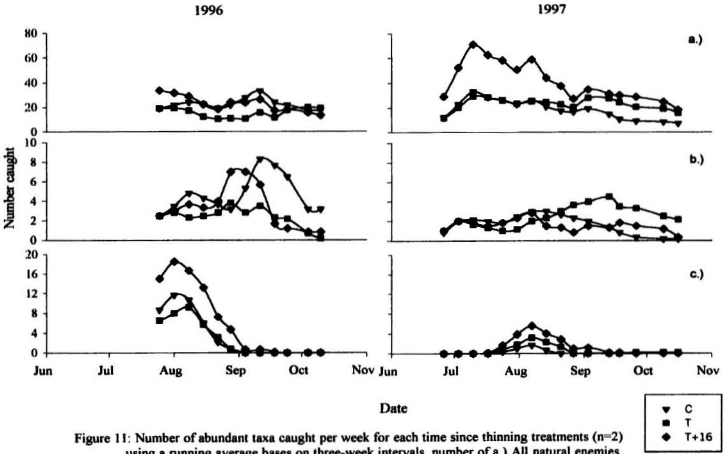

Figure 11: Number of abundant taxa caught per week for each time since thinning treatments (n=2) using a running average bases on three-week intervals, number of a.) All natural enemies, b.) Vespidae and c.) *Winthemia* sp. caught, Black Pond, Newfoundland.

7).

Parasitoids: Tachinidae: *Winthemia* sp.

During both years of the study the abundance of *Winthemia* sp. was significantly different between the time since thinning treatments (Tables 7 and 8). There was a notable decline in *Winthemia* sp. numbers in 1997. In spite of the decline, *Winthemia* sp. was present more frequently in T+16 treatments than either T or C (Fig. 10c.).

The number of *Winthemia* sp. within the treatments varied throughout the season in both 1996 and 1997 (Table 7, Fig. 11c.). Similar to balsam fir vigour treatments, numbers peaked from the end of July through to the end of August corresponding to 3rd and 4th larval instars of EHL.

Rare Taxa

Parasitoids: Ichneumonidae

Two species of the sub-family Pimplinae, *Ephialtes ontario* and *Pimpla* sp. were collected in the time since thinning treatments. Few specimens of each species were collected (Appendix II). In 1996 both species were only collected in thinned treatments (T and T+16) (Appendix II). In 1997, *E. ontario* was collected in all three treatments. *Pimpla* sp. was not present in the 1997 samples.

Braconidae: Microgastrinae

Protapanteles sp., *Glyptapanteles* sp., *Cotesia* sp. and *Apanteles* sp. were the four microgastrinids present in the time since thinning treatments. Depending on the treatment, microgastrinid numbers increased in 1997 from 3-25 times the number caught in 1996 (Appendix II).

Tachinidae: *Blondelia eufitchiae*

Blondelia eufitchiae was collected only in T+16 treatments in both 1996 (n=6) and 1997 (n=7) (Appendix II). All individuals were caught in late July through early August, this time period corresponds to 3rd and 4th larval instars of EHL, the stages that the parasitoids are known to attack.

DIVERSITY OF KNOWN EHL NATURAL ENEMIES

Time since thinning rarefaction curves (Fig. 12) illustrated that the number of species expected was highest in T+16 treatments that were thinned 16 to 17 years earlier. The thinning of T treatments 2-years prior may not have resulted in a more abundant natural enemy assemblage (Fig 10a.) or increased numbers of known natural enemies (Fig. 12) however the number of expected species was one more than C with smaller numbers of individuals collected.

ALTERNATIVE HOST/ PREY PRESENCE

The availability of alternative host and/or prey species in the time since thinning treatments varied depending on treatment only in 1996 (Table 9 and 10). Herbivores were found, on average, more frequently in C treatments (Table 10; Fig. 13a.). In 1997, variability among treatment replicates (Fig. 13b.) resulted in no detectable differences between treatments (Table 9). In both years fewer herbivore were found in T treatments (Figure 13 a and b).

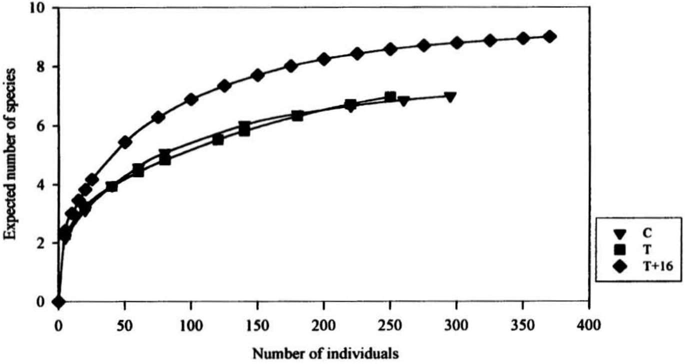

Figure 12: The number of known EHL natural enemy species expected to be collected in each of the thinning treatments (n=2) as the number of individuals per sample increased, Black Pond, Newfoundland. Values provided by RAREFACT version 3.0 (Krebs 1991).

Table 9: Significant variables from the analyses of variance which compared the alternative host/ prey abundance *versus* time since balsam fir thinning, Black Pond, Newfoundland. Variables tested for were treatment and sample week (SW) with a treatment X SW interaction, in 1996 (n=84) and 1997 (n=108). Significance at α'=0.05/K (where K= is the number of comparisons for each source) *.

	1996					1997				
Source	α'	df	MS	F-stat	p-value	α'	df	MS	F-stat	p-value
Treatment	0.017	2	4.54	12.39	<0.0001*	0.017	2	1.22	2.22	0.118
SW	0.0037	13	1.88	5.14	0.010	0.0028	17	4.44	8.07	<0.0001*
Treatment X SW	0.0019	26	0.39	1.08	0.406	0.0015	34	0.36	0.65	0.908
Error		42	0.36				54	0.55		

Table 10: Significant differences between individual treatments (C, T, T+16) using a Tukey's post hoc analysis for the number of alternative host/ prey *versus* time since balsam fir thinning portion for each collection year, in 1996 n=84 and 1997 n=108, Black Pond, Newfoundland. Significance at α=0.05 indicated by *.

1996

	C	T
T	*	
T+16		

1997

	C	T
T		
T+16		

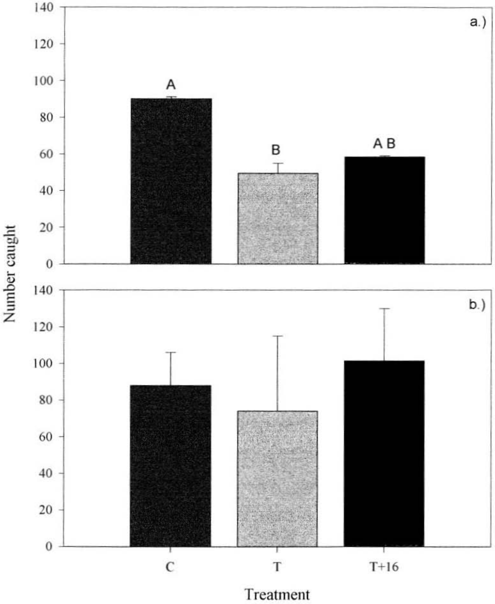

Figure 13: The mean (±SE) of lepidopteran (>5mm) herbivores caught in each time since thinning treatment (C, T, T+16) in a.) 1996 (July-October) and b.) 1997 (June-October) Black Pond Newfoundland. Different capital letters indicate significant differences between treatments for the same taxonomic group that year.

3.2 BALSAM FIR TREATMENT *VERSUS* VEGETATIONAL/ STRUCTURAL DIVERSITY

3.2.1 Balsam fir stand vigour *versus* natural enemy abundance

A principle component analysis of the vegetation data from RP, C, T and TF treatments showed that there were few differences in the vegetation characteristics among the treatments (Fig. 14 a.). Most of the variation occurred among individual quadrats within a treatment. The quadrats from all treatments were scattered across factor 1 and, since they intermingled it is hard to attribute any of the specific vegetation categories to a specific treatment. Quadrats that were plotted on the negative end of factor 1 had more moss, grasses, ferns and allies, herbs and trees (height=101-300 cm) (Table 11). Quadrats on the positive end of factor 1 had more litter and tree seedlings (Table 11). The mean and standard error for each vegetation category is presented in Table 12.

3.2.2 Time since balsam fir thinning *versus* natural enemy abundance

The principle component analysis of the thinned and C plots illustrated that the three treatments compared did have some vegetative and structural differences (Fig. 14 b.), with mean and standard error for each vegetation category presented in Table 12. The quadrats from the individual treatments used in this analysis were much more similar to each other than (Fig. 14 a.). Quadrats from C treatments were mostly found on the positive end of factor 1 indicating more litter, lichens and tree seedlings (Tables 11 and 12). Quadrats examined from the T treatments were scattered along the axis (factor 1), half in the positive and half in the negative. The T+16 treatments were predominantly on

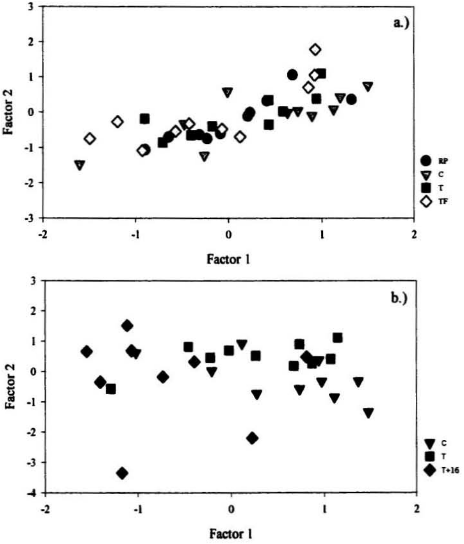

Figure 14: Scatterplot of the first two principle component factor scores from a PCA performed on the vegetation data collected from 10 2-m2 quadrats in each treatment a.) PCA of the vegetation data from the four vigour treatments and b.) PCA of the vegetation data from the time since thinning treatments, Black Pond, Newfoundland.

Table 11: Eigenvectors (loading scores) for understory vegetation categories from PCA1 (Balsam fir stand vigour, RP, C, T *versus* TF) and PCA2 (Time since balsam fir thinning, C, T *versus* T+16) for factors 1 and 2 (with the percent of variation explained by to each axis). Bold value indicates that this category is influencing the distribution of quadrats along the axis (Fig. 14) associated with the factor.

	PCA 1		**PCA 2**	
Vegetation Category	**Factor 1 (28%)**	**Factor 2 (14%)**	**Factor 1 (35%)**	**Factor 2 (13%)**
Dead wood	0.431	0.096	0.378	-0.476
Bare soil	0.226	0.405	0.428	0.261
Litter	**0.686**	0.110	**0.750**	-0.274
Fungi	0.363	0.371	0.367	0.038
Lichen	0.364	-0.346	**0.832**	-0.031
Moss	**-0.582**	-0.419	**-0.627**	0.477
Grasses	**-0.607**	**0.708**	**-0.536**	-0.487
Ferns	**-0.715**	-0.088	**-0.769**	0.036
Herbs (0-10 cm)	**-0.617**	-0.337	**-0.706**	0.265
Shrubs (0-50 cm)	0.218	0.223	0.224	0.231
Tree (seedling 0-10 cm)	**0.629**	0.131	**0.671**	0.300
Tree (11-100 cm)	-0.452	0.004	**-0.654**	-0.126
Tree (101-300 cm)	**-0.607**	**0.708**	-0.270	**-0.752**

Table 12: Various vegetation measures from all five Black Pond, Newfoundland treatments (RP, C, T, TF, T+16); mean percent cover (standard error) (n=20) for the understory vegetation present in the 10 2-m^2 quadrats; mean and standard error for balsam fir DBH (cm) and balsam fir height (m); balsam fir age (mean±SD).

Vegetation Category	RP		C		T		TF		T+16	
Dead Wood % cover	21.0	(3.85)	26.3	(3.64)	16.0	(3.69)	17.5	(2.98)	27.4	(5.27)
Bare Soil % cover	22.3	(4.55)	11.6	(5.03)	17.3	(3.60)	20.4	(5.92)	5.5	(1.35)
Litter % cover	26.8	(5.08)	42.8	(5.94)	20.5	(3.22)	18.8	(3.20)	16.0	(4.52)
Fungi % cover	1.1	(0.78)	0.7	(0.34)	1.2	(0.45)	1.7	(0.81)	0.7	(0.25)
Lichens % cover	10.8	(2.21)	8.4	(1.13)	6.8	(1.29)	8.1	(2.11)	3.4	(0.94)
Moss % cover	69.5	(4.34)	63.3	(6.67)	76.0	(3.75)	69.5	(6.56)	82.0	(3.00)
Grass % cover	0.0	(0.00)	0.0	(0.00)	0.5	(0.50)	0.0	(0.00)	4.3	(2.59)
Ferns % cover	1.6	(1.26)	1.7	(1.02)	1.5	(1.09)	3.0	(1.28)	6.0	(2.16)
Herbs (0-10 cm) % cover	3.6	(1.45)	2.1	(1.27)	2.8	(1.47)	5.1	(2.04)	16.4	(5.10)
Shrubs (0-50 cm) % cover	0.0	(0.00)	0.0	(0.00)	0.3	(0.25)	1.1	(0.46)	0.0	(0.00)
Tree (seedling 0-10 cm) % cover	6.9	(1.19)	8.8	(2.21)	8.3	(1.78)	5.7	(1.04)	6.0	(2.50)
Tree (11-100 cm) % cover	1.1	(0.58)	0.8	(0.75)	0.6	(0.34)	1.6	(0.89)	7.4	(2.57)
Tree (101-300 cm) % cover	0.0	(0.00)	0.0	(0.00)	0.3	(0.25)	0.0	(0.00)	1.3	(1.02)
Balsam fir DBH (cm)	7.3	(0.28)	8.6	(0.50)	10.4	(0.21)	11.0	(0.29)	12.5	(0.21)
Balsam fir Height (m)	8.3	(0.22)	9.1	(0.34)	10.1	(0.13)	10.2	(0.17)	10.3	(0.21)
Age (mean±SD)					53.1 (n=20)	(5.45)	50.6 (n=20)	(4.32)	41.4 (n=10)	(4.32)

the negative end of factor 1, this indicated that there were more moss, grass, ferns and allies, herbs and trees (11-100 cm) (Tables 11 and 12).

4.0 Discussion

4.1 BALSAM FIR STAND VIGOUR VERSUS NATURAL ENEMY ABUNDANCE

Several environmental factors such as stand composition, height of the canopy, climate and light are known to influence natural enemy flight activity (Hebert *et al.* 1990). The variation of natural enemy abundance and diversity may be explained by these environmental factors, more specifically differences in stand density or vegetational diversity between treatments. In addition to environmental factors influencing natural enemy abundance the abundance of alternate hosts/ prey within the treatments would also influence natural enemy numbers.

4.1.1 Habitat variability

The stand manipulations performed in each treatment (RP, C, T, TF) were chosen to establish a vigour gradient. Ferretti (1997) defined vigour as the growth of a tree in relation to a hypothetical optimum. The term vigour is often used both subjective and qualitatively to describe the relative physiological condition of a tree or stand (McCullough and Wagner, 1987). Both the amount of needles in the upper part of the canopy (Strand 1995) and combinations of biochemical constituents have been used as indices of vigour. In the case of the Black Pond treatments vigour was assessed based on combination of the concentrations of nitrogen, protein, several secondary chemicals, water and sugar (Luther and Carroll 1999; Carroll pers. comm.).

Luther and Carroll (1999) determined chemically that a linear vigour gradient was established between RP, C, T, and TF treatments. Nitrogen and protein concentrations in the balsam fir foliage increased from RP to C, T and TF (Luther and Carroll 1999) and secondary chemicals such as phenols, monoterpenes and tannins decrease from RP to C, T and TF. Therefore RP treatments could be considered low-vigour and TF high-vigour with C and T lieing inbetween.

Stand density was higher in the RP and C treatments compared to the T and TF treatments. A principle component analysis performed on the understory vegetation showed that there was little variation in the understory vegetation between treatments. Since climatic conditions are known to vary among habitats (Lewis and Martin 1990) the differences in stand density would likely cause variation in temperature and humidity. Open forest canopies, like those of the thinned treatments, often result in climatic extremes within the stand (Hunter 1990). Thinning is also known to increase soil temperature (Bauce 1996) and undoubtedly there would be changes in temperature and air currents throughout the thinned stands.

With several stand characteristics known to influence natural enemy flight activity (Hebert *et al.* 1990), it was expected that natural enemy numbers in the Black Pond study would also differ between the treatments based on stand density. However, stand density did not influence the abundance of natural enemies. C, T and TF treatments had higher natural enemy counts, regardless of the taxa considered, than RP treatments. RP stands were just as dense as C stands, yet in the first two study years RP stands had significantly lower natural enemy counts than C treatments. If natural enemies were simply using thinned stands as corridors for moving from one area to another there would be higher numbers in both T and TF treatments compared to C. This was not the case, in some years more natural enemies were caught in C treatments than T treatments and/ or TF treatments. The differences in natural enemy numbers cannot be linked to differences in understory vegetation since there were no differences in understory vegetation detected between the treatments. It appears that there is some aspect other than density and understory vegetation of the RP treatments that caused natural enemies to avoid the treatment and be caught more frequently in higher vigour stands.

The availability of alternative hosts and prey items within the stands may also play a role in the presence of natural enemies within a stand. The natural enemies considered in this study were generalists, they do not forage solely for EHL. Since populations of EHL in these stands were known to be minimal, at endemic levels, there would have to be alternative food sources in these stands for the natural enemies to feed upon.

Brodmann *et al.* (1997) stated that predator densities respond numerically to prey densities so that predators become more concentrated where prey are most abundant. This was the case in the Black Pond collections where natural enemy presence in the vigour treatments closely followed the presence of herbivores or alternative hosts/ prey in the treatments. There were fewer natural enemies in RP treatments because there were fewer alternative hosts or prey.

4.1.2 Diversity of known EHL natural enemies

The results of the rarefaction analysis of the known EHL natural enemy numbers from the balsam fir vigour treatments showed an increase in the diversity of known EHL natural enemies along the vigour gradient. As stated previously, the abundance of known natural enemy species was low in RP treatments, as was the diversity. This may be due to the low abundance of alternative hosts/ prey which would not support an abundant or diverse natural enemy fauna. C had the most abundant natural enemy fauna and a higher number of known EHL natural enemy species compared to the low-vigour (RP) stands. The larger alternative host/ prey populations in this treatment could explain the higher number of natural enemy species. T and TF treatments both had the highest number of known EHL predator and parasitoid species present, but they did not have the overall abundance of C. The higher number of species in these stands cannot be related to the presence of alternative hosts/ prey in the stands since their numbers were lower than alternate host/ prey in C. There appears to be some other aspect of the T and TF treatments that make them attractive to known EHL parasitoid and predator species but do not attract natural enemies in the numbers that C treatments do.

4.2 TIME SINCE BALSAM FIR THINNING *VERSUS* NATURAL ENEMY ABUNDANCE

The first portion of the experiment did not determined to what degree understory vegetation influenced natural enemy abundance and diversity. The second portion of this investigation more closely examined understory vegetation in treatments where thinning was performed at different times in the regeneration of the stand.

4.2.1 Habitat variability

Differences in the understory vegetation between the three treatments used in the time since balsam fir thinning investigation were evident. A principle component analysis on the understory vegetation showed that there was more variability in the plants found in the individual quadrats studied in the T+16 treatments compared to T and C quadrats. Higher mean percent cover of mosses, ferns, herbs and grasses in the T+16 treatments show that there was a larger vegetation component to the understory in these treatments. There were also noticeable differences in the coarse woody debris (dead wood) in the treatments, with on average more in T+16 treatments. Once the canopy closes in a balsam fir stand the vegetational complexity decreases. As the stand ages tree density decreases leaving breaks in the canopy that permit more light to penetrate to the forest floor. The additional light results in increased growth and diversity of the understory vegetation (Page 1974). The vegetational differences in T+16 treatments compared to C and T, as well as the other vigour treatments, were the results of increased light due to the opening of the canopy 16 years previously.

Several studies have shown that habitat diversification can provide essential resources for natural enemies, namely feeding sites for adults that provide pollen and nectar (Murphy *et al.* 1996). The degree of vegetation diversification in an environment can profoundly affect how insect herbivore and natural enemy populations interact. In agroecosystems diversification provides over-wintering sites, which enhance colonization and establishment of natural enemies. Cappuccino *et al.* (1998) identified a link between vegetation diversity and parasitism rates in spruce budworm larvae. Diverse systems increase specialist natural enemy colonization relative to simple systems (Murphy *et al.* 1998). In the Black Pond study it was evident that the T+16 had both a higher abundance of natural enemies and a higher abundance and diversity of known EHL predators and parasitoids.

Habitats that have more abundant and diverse vegetation like the T+16 treatments have more niches available to herbivorous insect species (Andow and Risch 1987).

Therefore, it would be expected that the T+16 treatments would have had higher numbers of alternative host/ prey present. However, this was not the case. Significant differences in herbivore numbers between time since thinning treatments were detected only in 1996, where C stands had on average higher herbivore numbers. Contrary to natural enemy abundance, herbivore numbers in the Black Pond study do not appear to be influenced by the time since balsam fir thinning or the vegetational diversity of the stand's understory. Therefore natural enemy abundance cannot be related to alternative host/ prey number due to the lack of a clear pattern in herbivore number between the treatments.

4.2.2 Diversity of known EHL natural enemies

The abundance of natural enemies in a system increases with an increase in vegetational diversity (Andow and Risch, 1987; Murphy *et al.* 1996; Cappuccino *et al.* 1998). It is expected then that with this increase in natural enemy abundance there would be a corresponding increase in natural enemy species diversity. The results of the current study clearly illustrate this. In the two study years there were approximately 30% more species known to be predators and parasitoids of EHL caught in T+16 treatments compared to C and T treatments. The natural enemy fauna in T+16 treatments was more abundant and more diverse. The additional diversity of the forest floor in these stands would provide additional resources to the adult predators and parasitoids (food and shelter) to sustain more EHL natural enemy species and more individuals within each species.

4.3 SPATIAL AND TEMPORAL VARIABILITY

Microclimatic and macroclimatic conditions vary within and among habitats (Lewis and Martin 1990) and with Black Pond being a natural system it was expected that there would be some natural variation in insect numbers between individual blocks. In both 1995 and 1997 there were significant differences in the number of natural enemies caught among the blocks of the balsam fir vigour experiment. The position of the block in relation to the pond, the forest structure around the block, varation in density between the blocks (Block 2 had a higher overall stem density than Block 1) individual air currents through the blocks and a variety of other characters of each block would naturally be different, and may have affected the abundance of natural enemies.

Spatial variation in the presence of vespids in both 1996 and 1997 could be linked to their colonial lifestyle. Social insects such as yellow jackets generally have a central location where members of the colony radiate from during foraging. This may explain the variability of vespids between the blocks because if a colony was established on or near the edge of a block there would be more individuals of that group collected in that block.

Temporal variability and fluctuations could be explained primarily in terms of the lifecycles of insects and climatic variability within and between seasons. Depending on the lifecycle of an insect and its ecological niche its presence in the Malaise trap will vary throughout the season. For example, parasitoids as *Winthemia* sp., which attack a specific developmental stage of their host, appear at the times that correspond to these stages. This was evident in the Black Pond collections where *Winthemia* sp. was present predominately mid-July, through August, into September when it attacks EHL in its late instars.

There was a noticeable decrease in *Winthemia* sp. numbers from year to year. This decrease can be explained by the collapse of an EHL outbreak that began in the area in 1994 (Hudak *et al.* 1996). The increases and decreases in the natural enemy populations are known to slightly lag behind the population fluctuations of their prey or hosts (Price 1975). The reduction of *Winthemia* sp. numbers from 1996 to 1997 may actually be explained by the decline of EHL populations in the area.

4.4 STUDY LIMITATIONS

Throughout the project the study was limited by several factors. The major limitation of the study was that the study site and experimental design was established before the project was initiated. This project was therefore confined to the location and size of the study plots, as well as the procedures that were used to establish the treatments. The size of the treatment plots limited the number of Malaise traps that could be set up. This resulted in a small sample size and the inability to sample at different levels in the canopy. The pre-treatment density of the blocks was different. To reduce some of the variablity between blocks, for the purpose of this study, it would have been preferred to thin both blocks to a predetermined density and then perform the stand manipulations. Logistics was also a problem it took a great deal of time to set up the Malaise traps, do the sampling, as well as sort throught all the insects collected in the two Blocks. There was a third Block present in the study site but there was a problem getting the additional equiptment and assistance in order to sample that block. With the limited resources available there was not enough time to collect from that stand and analyze the data collected.

There were several attempts made to collect EHL larva in the treatments. This would have provided information on the density of EHL in the stands and rearing would have confirmed that the population was indeed being parasitized by the parasitoids collected in the Malaise traps. There were no larva collected during any of the attempts made. Branch sampling, manual collecting from branchs, found no EHL larva in the stands or in the areas surrounding the stands. This limited the ability of the current study to make any conclusions about which parasitoids were actually attacking larvae within the treatments examined. The differences in the number of species collected in the current study compared to previous collections made in Newfoundland (Otvos *et al.* 1979; FIDS CFS St. John's collections) may be explained by fact that none of the records in this came from branch rearings whereas the previous studies all relied on branch sampling and pheromone traps (active trapping rather than the passive trapping associated with the Malaise trap). The samples in this collection were compared to previous collections and those insects previously identified as EHL natural enemies were counted. If any of the other EHL parasitoids that were not collected in this study it may be likely that they were in the stands however the location of the trap may not have been within the area that they normally search for hosts.

The examination of the presence of alternative hosts/prey in stands was initiated after the field collections were complete. This limited the estimations of alternative hosts/prey to the samples that were collected in the Malaise traps. Additonal active collection methods, i.e. sweep sampling the understory, would have provided a more complete assessment of the alternative host/prey present in the stands.

4.5 EHL DISTRIBUTION

The stand conditions used in this experiment encompassed the range of balsam fir growing conditions in Newfoundland. As stated previously EHL populations are found primarily in dense, older, slow-growing balsam fir stands. The density of these stands is usually high with the vigour of the stands being low; resembling the RP stands of this investigation. Therefore, it appears that stands where EHL generally reside are not stands that natural enemies frequent in large numbers. Natural enemies were more abundant in less dense stands that are moderate- to high-vigour (C, T, and TF) and are found more frequently in stands that have higher understory plant diversity and abundance (T+16). These stands provide natural enemies with more resources such as alternative feeding sites and a more stable climate with over-wintering protection.

Other research projects from the Black Pond study have illustrated that the vigour of balsam fir stands influences the survival of EHL in a stand. Carroll (1998) found that despite the high quality of foliage of high-vigour stands there was optimal EHL survival in low to moderate-vigour stands due to greater synchrony between egg hatch and balsam fir bud burst. Bud burst-egg hatch synchrony is critical to the survival of the early instars of EHL larvae (Carroll 1999).

Balsam fir stand vigour influences both the survival of EHL and the presence of its associated natural enemies. EHL being predominantly found in the slow-growing balsam fir stands of Newfoundland seem to be sacrificing the benefits of higher quality foliage for a habitat that provides enemy free space. Populations of EHL are maintained at higher numbers in these low quality balsam fir stands due to their lower probability of mortality by natural enemy attack. Numerous studies have shown that animals will sacrifice food intake both qualitatively and quantitatively in order to avoid potential danger from predators (Krebs and Kacelnik 1991). The distribution of EHL may have evolved out of natural enemy pressure in areas where balsam fir stands were more vigourous and diverse. The dense slow growing balsam fir stands that EHL inhabit are found in pockets across the Newfoundland landscape. These pockets may act as sources of dispersing EHL and allow for rapid population increases in outbreak situations.

4.6 STAND BIODIVERSITY

Current and past forestry practices on the island have promoted dense slow-growing balsam fir that are not vegetatively diverse. These conditions exist by allowing clear-cut stands to regenerate maintaining high tree density throughout the growth and maturation of the stands (A. Carroll pers. comm). With low light levels in the understory there is a resulting in low understory plant abundance and diversity (Page 1974). Often small pockets of dense, slow-growing trees are not harvested during clear-cutting because they are not considered economical. These pockets may provide refuge for EHL and the dense slow-growing regenerating stands provide the perfect habitat for EHL. The current study has illustrated that these conditions are not conducive to the presence of a diverse natural enemy fauna that forages on EHL and other herbivores. Furthermore this study illustrated how *Winthemia* sp. a species introduced to the island to control EHL is also found more abundantly in more vigourous balsam fir stands and it is even more abundant in stands that have increased structural and vegetational diversity.

The natural enemy counts from the Black Pond study illustrate that silvicultural practices such as thinning and thinning and fertilization early in the regeneration of a stand help to promote and maintain the biodiversity of balsam fir stands. In the long run the opening of the canopy as the stand matures would increase the complexity of the stand with more diverse and abundant understory vegetation. These habitats provide natural enemies with more niches, higher availability of alternative hosts/ prey, better shelter and more over-wintering protection; overall these stands provide more stable habitat. Such silvicultural practices have also been suggested by other authors to both promote and maintain natural enemy biodiversity and to lessen the impact of other herbivours on balsam fir forests (Cappuccino *et al.* 1998).

5.0 Conclusions

The current study attempted to determine the impact of natural enemies on the spatial distribution of EHL. The presence of natural enemies was assessed in several balsam fir stands, which encompassed the range of balsam fir growing conditions that are available to EHL in Newfoundland.

When natural enemy presence was assessed relative to balsam fir vigour, natural enemies were not abundant in low-vigour stands but were found more frequently in more vigorous stands. Specific known EHL parasitoids and predators were also found to be less abundant in the low-vigour (RP) stands. These low-vigour stands had fewer alternate hosts/prey, available to natural enemies than higher vigour stands, which may explain the low natural enemy numbers in the stands.

Further examination of stands in which balsam fir vigour increased early in their regeneration showed a natural enemy population that was more abundant and diverse. The larger, more species-rich natural enemy fauna in these stands can be linked to the higher understory plant diversity and abundance within these stands. The understory plants would provide natural enemies with alternative feeding sites for pollen and nectar, and shelter for over-wintering.

By examining the current distribution of looper in relation to the forest habitats where natural enemies were more abundant, at least in the Black Pond study, it appears that EHL has a distribution which provides it with a certain degree of enemy free space. EHL predominates in slow-growing balsam fir stands, with a similar vigour to that of the RP treatments. In the current study natural enemies seemed to avoid these stands.

Forestry practices widely in use result in the dense regeneration of balsam fir stands and their slow growing nature. These practices almost encourage the development of EHL outbreaks. If silvicultural practices such as pre-commercial thinning were practiced more frequently there would be an increase in the overall diversity of balsam fir stands this would increase the suitability of habitats for natural enemies thereby limiting enemy-free space to EHL.

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Appendix I: Mean (standard error) for the natural enemies collected in each balsam fir stand vigour treatment (n=2) at Black Pond, Newfoundland in 1995, 1996 and 1997. The 1995 collections started in August 1996 and 1997 collections started in June.

	RP			C			T			TF		
	1995	**1996**	**1997**	**1995**	**1996**	**1997**	**1995**	**1996**	**1997**	**1995**	**1996**	**1997**
Natural Enemies	74.5 (25.50)	125.0 (24.00)	225.0 (54.00)	170.5 (10.50)	412.5 (49.50)	307.0 (142.00)	220.5 (2.50)	272.5 (26.50)	380.0 (252.00)	207.0 (84.00)	370.0 (17.00)	248.0 (62.00)
Hymenoptera												
Vespidae	6.5 (1.50)	15.0 (6.00)	15.0 (6.00)	29.5 (4.50)	62.5 (28.50)	27.5 (14.50)	34.0 (11.00)	31.0 (7.00)	41.0 (24.00)	31.0 (5.00)	38.5 (0.50)	21.5 (6.50)
Ichneumonidae	31.5 (12.50)	51.0 (6.00)	123.0 (49.00)	71.5 (10.50)	149.0 (68.00)	193.0 (39.00)	111.5 (15.50)	120.0 (30.00)	130.0 (48.00)	97.5 (37.50)	193.0 (3.00)	46.5 (1.50)
Ephialtes ontario	3.0 (1.00)	1.0 (0.00)	0.0 (0.00)	2.0 (0.00)	3.5 (3.50)	0.5 (0.50)	1.5 (0.50)	3.0 (1.00)	0.0 (0.00)	3.0 (1.00)	4.0 (3.00)	0.5 (0.50)
Pimpla sp.	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.5 (0.50)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)
Itoplectis sp.	0.0 (0.00)	0.5 (0.50)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)
Braconidae	10.5 (4.50)	12.5 (4.50)	18.0 (1.00)	17.0 (0.00)	38.0 (11.00)	24.5 (4.50)	20.0 (5.00)	16.5 (4.50)	13.0 (9.00)	15.0 (6.00)	35.5 (2.50)	9.0 (6.00)
Microgastrinae	1.5 (0.50)	0.0 (0.00)	1.0 (1.00)	2.0 (1.00)	7.0 (1.00)	5.5 (0.50)	2.0 (2.00)	1.5 (0.50)	1.5 (1.50)	1.0 (1.00)	4.5 (1.50)	2.0 (1.00)
Apanteles sp.	0.0 (0.00)	0.0 (0.00)	1.0 (1.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.5 (0.50)	0.0 (0.00)	1.0 (1.00)	0.0 (0.00)
Cotesia sp.	0.5 (0.50)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.5 (0.50)	0.5 (0.50)	1.5 (1.50)	0.5 (0.50)	1.0 (1.00)	0.5 (0.50)	0.0 (0.00)	0.5 (0.50)
Glyptapanteles sp.	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	2.0 (1.00)	2.0 (1.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.5 (0.50)
Protapanteles sp.	1.0 (1.00)	0.0 (0.00)	0.0 (0.00)	2.0 (1.00)	4.5 (1.50)	3.0 (1.00)	0.5 (0.50)	1.0 (0.00)	0.0 (0.00)	0.5 (0.50)	3.5 (0.50)	1.0 (1.00)
Diptera												
Tachinidae	13.5 (1.50)	27.0 (13.00)	117.0 (8.00)	29.5 (2.50)	103.0 (15.00)	113.0 (60.00)	40.5 (3.50)	58.5 (9.50)	126.5 (83.50)	50.5 (29.50)	57.0 (7.00)	45.5 (7.50)
Winthemia sp.	2.5 (2.50)	20.5 (13.50)	8.0 (5.00)	9.5 (3.50)	45.5 (6.50)	5.0 (4.00)	21.5 (6.50)	36.5 (0.50)	10.0 (8.00)	28.5 (19.50)	48.0 (1.00)	5.0 (2.00)
Blondelia eufitchiae	0.5 (0.50)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	2.0 (1.00)	0.0 (0.00)	0.0 (0.00)	0.5 (0.50)	0.0 (0.00)	0.0 (0.00)

Appendix II: Mean (standard error) for the natural enemies collected in the natural enemy compliment *versus* time since thinning treatments (n=2) in 1996 and 1997. Note 1996 collections were started in July and 1997 collections were started in June.

	C				T+1				T+16			
	1996		1997		1996		1997		1996		1997	
Natural Enemies	311.5	(47.50)	307	(142.00)	217.5	(28.5)	380	(252.00)	314.5	(66.50)	679	(123.00)
Hymenoptera												
Vespidae	59.5	(25.50)	27.5	(14.50)	30.0	(7.00)	41	(24.00)	43.5	(9.50)	25	(2.00)
Ichneumonidae	102.0	(59.00)	193	(39.00)	93.5	(23.50)	130	(48.00)	113	(26.00)	175	(132.00)
Ephialies ontario	0.0	(0.00)	0.5	(0.50)	1.0	(1.00)	0	(0.00)	0.5	(0.50)	1	(1.00)
Pimpla sp.	0.0	(0.00)	0	(0.00)	0.5	(0.50)	0	(0.00)	0.5	(0.50)	0	(0.00)
Braconidae	28.5	(14.50)	24.5	(4.50)	11.5	(2.50)	13	(9.00)	24	(11.00)	23	(13.00)
Microgastrinae	2.0	(1.00)	5.5	(0.50)	0.5	(0.50)	1.5	(1.50)	0.5	(0.50)	12.5	(4.50)
Apanteles sp.	0.0	(0.00)	0	(0.00)	0.0	(0.00)	0.5	(0.50)	0	(0.00)	2	(2.00)
Cotesia sp.	0.5	(0.50)	0.5	(0.50)	0.5	(0.50)	1	(1.00)	0.5	(0.50)	1	(0.00)
Glyptapanteles sp.	1.0	(1.00)	2	(1.00)	0.0	(0.00)	0	(0.00)	0	(0.00)	2	(0.00)
Protapanteles sp.	0.5	(0.50)	3	(1.00)	0.0	(0.00)	0	(0.00)	0	(0.00)	7.5	(2.50)
Diptera												
Tachinidae	79.0	(5.00)	113	(60.00)	39.0	(2.00)	126.5	(83.50)	74.5	(8.50)	153.5	(75.50)
Winthemia sp.	45.5	(6.50)	5.0	(4.00)	36.5	(0.50)	10	(8.00)	76.5	(21.50)	20.5	(3.50)
Blondelia eufitchiae	0.0	(0.00)	0	(0.00)	0.0	(0.00)	0	(0.00)	3	(2.00)	3.5	(1.50)