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Spruce budworm impact, abundance and parasitism rate in a patchy landscape

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Abstract The hypothesis that vegetational diversity may lessen the impact of forest insect pests by favoring natural enemies is appealing to those who seek ecologically sound solutions to pest problems. We investigated the effect of forest diversity on the impact of the spruce budworm *Choristoneura fumiferana* following the last outbreak, as well as the budworm's current abundance and parasitism rate, in the boreal forest of northwestern Québec. Mortality of balsam fir caused by the budworm was greater in extensive conifer stands than either in "habitat islands" of fir surrounded by deciduous forest or on true islands in the middle of a lake. Adult spruce budworm abundance, assessed by pheromone traps, did not differ significantly between the three types of sites. Larval and pupal parasitism rates were examined by transferring cohorts of laboratory-reared larvae and pupae to trees in the three site types and later collecting and rearing them. The tachinid *Actia interrupta*, a parasitoid of fifth and sixth instar larvae, as well as the ichneumonid pupal parasitoids *Itoplectes conquisitor*, *Ephialtes ontario* and *Phaeogenes maculicornis*, caused higher mortality in the habitat islands than on true islands or in extensive stands. *Exochus nigripalpis tectulum*, an ichneumonid that attacks the larvae and emerges from the pupae, caused greater mortality in the extensive stands of conifers.

Key words *Abies balsamea* · Boreal forest · *Choristoneura fumiferana* · Enemies hypothesis · Landscape diversity

Introduction

The hypothesis that diverse ecosystems should have fewer or less severe insect outbreaks than simple ones has had an important influence on ecologists working in both agricultural systems (Goodman 1975; Andow 1991) and forests (Miller and Rusnock 1993). The idea that pest problems may be remedied or at least mitigated by planting crops or trees in more diverse stands is especially appealing to those who seek more ecologically sound means of pest management. Although numerous tests of the influence of vegetational diversity on the abundance of herbivores and their natural enemies have been conducted in agroecosystems, evidence suggesting that a "silvicultural remedy" may someday protect forests from outbreaks of pest insects remains largely anecdotal.

Diverse vegetation may alter the ability of the herbivore to find or remain in patches of the host plant; alternatively, it may harbor a greater abundance and diversity of the herbivore's natural enemies (Root 1973). The latter scenario, known as the "enemies hypothesis", has received much support from agricultural systems (reviewed by Sheehan 1986; Russell 1989; Andow 1991). Predation and parasitism rates are generally higher in polycultures than in monocultures. The manipulation of habitat diversity to favor indigenous natural enemies is an approach that is attracting increasing attention as the danger of both pesticides and exotic control agents becomes apparent (Kareiva 1996; Settle et al. 1996).

Vegetational diversity can be measured at a range of spatial scales. Most studies in agricultural systems have involved diversity at scales smaller than that of individual fields (Kareiva 1983). In a notable exception, Marino and Landis (1996) found that armyworm para-

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sitism rates were higher in a diverse landscape, although within-field diversity appeared unimportant. Settle et al. (1996) suggest that diversity on a scale of thousands of hectares greatly influences the efficacy of generalist predators in rice fields. The various natural enemies of a pest insect may each respond to habitat heterogeneity at a characteristic spatial scale, as Roland and Taylor (1997) so elegantly demonstrated for the parasitoids of the forest tent caterpillar, *Malacosoma disstria*.

Vegetational diversity appears to be an important factor explaining the variability in the intensity of outbreaks of the spruce budworm *Choristoneura fumiferana* (Clem.), one of the most destructive forest pests in North America (Blum and MacLean 1985). The spruce budworm's main host is balsam fir *Abies balsamea* (L.). Secondary hosts include white spruce *Picea glauca* (Moench) Voss. and red spruce *P. rubens* Sarg. Although spruce budworm populations oscillate synchronously over a large area, the budworm's impact on the forest tends to be more severe in large, pure stands of balsam fir (MacLean 1980). Stands of balsam fir mixed with hardwoods tend to suffer lower mortality following an outbreak (MacLean 1980; Bergeron et al. 1995). Diversity at the landscape scale also influences budworm impact; small "habitat islands" of balsam fir embedded in a matrix of deciduous forest suffered lower mortality following the last budworm outbreak (Bergeron et al. 1995).

Among the many hypotheses that might explain the negative correlation between forest diversity and budworm-caused tree mortality is the possibility that the natural enemies of the budworm are more abundant or more effective in diverse stands or diverse landscapes. Since several parasitoids attacking the spruce budworm also attack lepidopteran larvae on deciduous trees (Maltais et al. 1989; Bradette 1994), mixed stands may have higher parasitoid densities, potentially resulting in greater parasitism rates. Mixed stands also have a greater diversity of understory flowering herbs (De Grandpré et al. 1993), a potentially important source of nectar for parasitoids (Leius 1967; Simmons et al. 1975; Bradette 1994).

In the present study, we examine the influence of landscape-level vegetational diversity on the spruce budworm in the boreal forest of northwestern Québec. We combine data on balsam fir mortality resulting from the last budworm outbreak with data on the current abundance of the spruce budworm, as well as on larval and pupal parasitism rates. Three types of stands were compared: extensive stands of balsam fir and other conifers, "habitat islands" of fir surrounded by deciduous trees, and stands of fir on true islands in the middle of a lake.

Materials and methods

Study area and species

The study took place in the Abitibi region of northwestern Québec in the forest surrounding Lake Duparquet (79°12′W, 48°28′N) and on several of the lake's 150 islands. The most recent outbreak of the spruce budworm in this region occurred between 1970 and 1987 (Morin et al. 1993) and was part of an extensive irruption that covered much of eastern Canada and the northeastern United States (Blais 1983). No attempt to control the outbreak with insecticides was made in the study area. The budworm is currently in the late endemic phase in Abitibi.

In the Abitibi region, second-instar spruce budworms emerge from diapause in late May or early June and begin to feed on the buds of balsam fir or on the previous year's foliage if the buds have not yet opened. The larvae feed singly from shelters made of foliage loosely webbed together with silk. They complete their development by early July and pupate on the foliage. Adults appear in mid-July. Females lay masses of approximately 20 eggs on the needles of fir or spruce. Hatchling larvae do not feed, but instead move to a sheltered site on the branch to spin a hibernaculum, in which they overwinter after molting to second instar.

Vegetational diversity in the Lake Duparquet study area

Lake Duparquet and the surrounding forest are situated in an area of proglacial lacustrine deposits known as the Northern Clay Belt of Québec and Ontario. The rich soils of this region, combined with perturbations from both fire and spruce budworm outbreaks, result in a diverse mosaic of forest types surrounding the lake (Bergeron and Dansereau 1993). Early-successional communities, on sites having burned within the last 40–80 years, support stands of trembling aspen *Populus tremuloides* Michx. and paper birch *Betula papyrifera* Marsh. Older forests (> 200 years old) are comprised mainly of balsam fir *Abies balsamea* (L.), white spruce *Picea glauca* (Moench) Voss and northern white cedar *Thuya occidentalis* L. As the forests age, the diversity of understory flowering herbs decreases dramatically, and increases again only in sites where severe budworm-related tree mortality opens gaps in the coniferous canopy (De Grandpré et al. 1993).

An important component of the vegetational diversity surrounding Lake Duparquet is the presence of patches of older coniferous forest embedded in a matrix of younger deciduous forest. These "habitat islands" are the result of fires that burned unevenly, leaving patches of older stands surrounded by early-successional forest initiated after the fire.

In late May 1994, we located four clusters of habitat-islands, each containing two to four coniferous patches ranging in size from roughly 0.25 to 2.0 ha. Three of the four clusters were located on the southern shore of Lake Duparquet; the fourth was located along a logging road 10 km west of the lake (Fig. 1). Tree-ring analysis indicated that the habitat islands south of the lake were once part of a large stand of mature coniferous forest initiated in 1717. The surrounding deciduous forest originated following a fire in 1944. The habitat islands along the logging road were part of a once extensive stand originating in 1760, which still covers a large area on the western shore of the lake (Fig. 1). The deciduous forest surrounding these habitat islands originated following a fire in 1923. The understory of the 1944 deciduous stand supports a greater diversity of flowering herbs than that of the 1970 coniferous stand (De Grandpré et al. 1993).

In each habitat island we established a sampling station, which consisted of a 16 × 16 m quadrat for estimating balsam fir mortality, five mature trees for sampling larval density, and saplings 1–3 m tall for assessing larval and pupal mortality. Four clusters of sampling stations were also established in the large tract of coniferous forest originating from the 1760 fire (Fig. 1). Finally, one station was established on each of ten islands, five in the northwestern bay of the lake and five in the center (Fig. 1).

The placement of sampling stations represents a compromise between the availability and accessibility of particular stand types and our desire to achieve adequate replication. Clusters of stations were generally separated from each other by over 1 km, although two of the habitat-island clusters in the 1944 stand are only approximately 0.5 km apart (Fig. 1). We realize that this introduces a potential problem with spatial correlation. We might have been able to include additional, more distant habitat islands; however

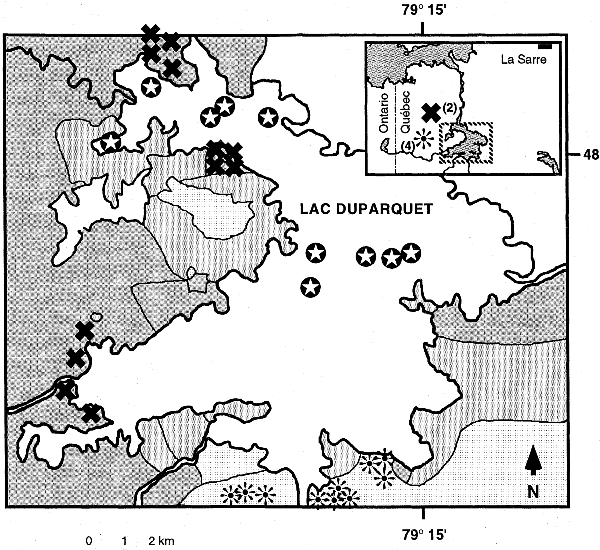

Fig. 1 Map of Lake Duparquet and the surrounding forest. *Shaded areas* indicate forest stands of different ages. The *darkest shading* represents coniferous stands >200 years old, *light shading* represents early-successional, deciduous forest, and *moderate shading* represents mixed stands. Each *cross* indicates a sampling station in the old forest, each *asterisk* represents a sampling station in one coniferous habitat island embedded within deciduous forest, and each star denotes a sampling station on an island. *Inset* shows two groups of sampling stations located to the west of the lake (number of stations in parentheses)

our choice of sites was constrained by the importance of being able to introduce or harvest larvae at all sites in 2 days. Thus, sites that could not be reached easily were not considered.

Mortality of balsam fir

At each sampling station, all living and dead balsam fir greater than 5 cm DBH were counted in the 16 × 16 m quadrats. Great care was taken to identify all dead stems. Sampling was done during the summer of 1994, 9–10 years after the maximum mortality caused by the last budworm outbreak (Morin et al. 1993). Balsam fir killed during the outbreak were easily identified because they were either still standing or present on the forest floor with bark and branches still intact. Since annual natural mortality due to factors other than the budworm is low (MacLean and Ostaff 1989) and since balsam fir wood decomposes relatively rapidly (Lambert et al. 1980), by considering only trees with bark and branches intact, we are confident that we have not overestimated mortality by including trees that died before the outbreak. Furthermore, by considering only those trees with a diameter at breast height (DBH) greater than 5 cm, we reduced the chance of including trees killed by intense suppression.

Since older trees generally suffer greater mortality following a budworm outbreak (MacLean 1980; Bergeron et al. 1995), in comparing balsam fir mortality in the three habitat types it was important to ascertain whether there were differences in the ages of the trees. We cored four to seven randomly chosen living trees in each quadrat. The ages of dead trees could not be determined.

Spruce budworm abundance

From 11 to 15 June 1994 we conducted samples to determine the density of spruce budworm larvae. At each station, two branches of approximately 50 cm in length were cut from each of five mature balsam fir at a height of 14 m with a pole pruner. These branches were placed in feed sacks and brought indoors, where they were meticulously searched for budworm larvae.

Because this method proved to be excessively time-consuming (approximately 250 person-hours to find ten larvae), in 1995 we opted for sampling adults as a means of comparing densities among stand types. From 3 July through 5 August, three pheromone traps (Multi-pher, les Services Bio-contrôle, Ste-Foy, Québec) baited with eastern spruce budworm pheromone (Biolure, Consep, Inc., Corvallis, Oregon) were deployed at each station. The traps were hung from the branches of fir trees at a height of approximately 6 m. Each trap contained a 4 × 6 cm bar of insecticide (dichlorvos 19.2%; Vapona, la Société Majeco, Rimouski, Québec) to kill the incoming male spruce budworm adults, which were counted at the end of the flight season.

Assays for parasitism rates

Parasitism rates in the different stand types were compared by introducing laboratory-reared spruce budworm larvae (Canadian Forest Service, Sault-Ste-Marie, Ontario) to each sampling station. The larvae arrive as diapausing second instars in rolls of parafilm-backed gauze. To transfer the larvae to the trees we cut small rectangles of gauze containing 10–30 larvae and pinned them to the branchlets with a common pin. On 15 May 1995, approximately 1 week before budburst, larvae were introduced to four branches of each of eight saplings per sampling station. Roughly one-third of the larvae were harvested on each of three dates: 6, 19, and 25 June, when most of the larvae had reached third, fourth-fifth, and fifth-sixth instar, respectively. Larvae were reared indoors on artificial diet in individual vials inverted into a bed of sand.

In 1994, to obtain pupae for transfer to the field, larvae were reared in plastic food-storage boxes. Fresh balsam fir foliage was provided every other day. Just before pupation, five larvae were transferred to each of 88 2-l freezer bags containing a branch of balsam fir approximately 30 cm long. The larvae pupated attached to the foliage as they do in the field. One branch was then attached with twist ties to each of two trees per station. The pupae were harvested 5 days following introduction and reared for parasitoids.

Analysis

Analysis of variance was used to assess differences among habitat type, except one case with heterogeneous variances, which was analysed by a Kruskal-Wallis test. Tree mortality and budworm parasitism rates were arcsin transformed before analysis. Nested ANOVAs were performed, with clusters of stations nested within forest stand type (coniferous forest, habitat island or true island). Only in the heteroscedastic case mentioned above was a significant amount of variability explained by clusters within stand type; thus only the main effects of habitat type are reported in the results.

Results

Density, age and mortality of balsam fir

The density of balsam fir differed significantly among habitat types, in particular, density was significantly higher on the islands than in the coniferous forest (Fig. 2A, ANOVA: stand type $F_{[2,28]} = 5.54$, $P = 0.012$). The mean age of living trees did not differ significantly among the three habitat types (ANOVA: $F_{[2,\ 22]} = 1.25$, $P = 0.307$; sample size is lower since some plots did not have any live balsam fir).

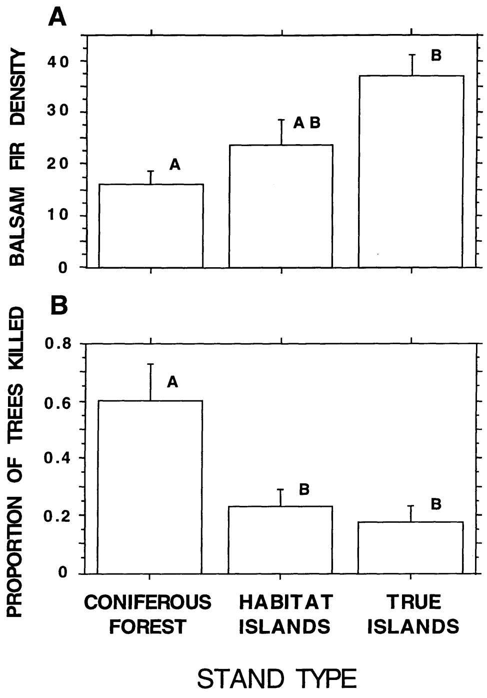

Fig. 2 **A** Density and **B** mortality of balsam fir following the last spruce budworm outbreak in three stand types. *Bars* show means and standard errors (mortality data are back-transformed following analysis on arcsin square root-transformed data). Means with the same *letter* are not significantly different at $\alpha = 0.05$ according to Fisher's PLSD test

Mortality following the last spruce budworm outbreak was significantly lower for balsam fir growing in the habitat islands surrounded by deciduous forest than for those growing in contiguous coniferous forest (Fig. 2B, ANOVA: stand type $F_{[2,28]} = 5.72$, $P = 0.009$). Mortality on true islands was also significantly lower than that in the coniferous mainland forest but did not differ significantly from that in the habitat islands (Fig. 2B).

Spruce budworm abundance

Because the spruce budworm population in the Abitibi region is currently at endemic levels, the 1994 larval census proved to be an inefficient means of comparing densities between the different stand types. Only ten larvae were found on 430 branches: eight on islands, two in habitat islands and none in the large coniferous stands.

Pheromone trapping was a much more efficient means of comparing current budworm densities between sites, yielding a mean of 59.7 individuals per site (±4.7 SE). The number of adult males captured in the traps in 1995 did not differ significantly between forest types (ANOVA, $F_{[2,28]} = 1.18$, $P = 0.323$).

Larval and pupal parasitism

Mortality of larvae introduced as second instars and then harvested as third instars was mainly imposed by the braconid wasps *Apanteles morrisi* Mason, *Microgaster canadensis* Muesebeck and *Dolichogenidea absona* Muesebeck (Table 1). Per capita mortality from these species combined ranged from 0.023 to 0.048 and did not differ significantly between forest types (ANOVA, $F_{[2,28]} = 0.618$, $P = 0.546$).

Larvae harvested as fourth, fifth and sixth instars were parasitized by the tachinid fly *Actia interrupta* Curr., as well as by several species of hymenopterans, including the ichneumonids *Tranosema rostrale* (Brischke) and *Phytodiatus fumeriferanae* Rowher (Table 1). These species all emerged before the larvae pupated. Another ichneumonid, *Exochus nigripalpis tectulum* (Townes) was also present in these larvae but did not emerge until after the larvae had pupated.

Because of the similarity of the parasitoid assemblage emerging from older larvae, only the analysis of the data for the last harvest is presented here. Data from the second harvest revealed the same patterns although overall levels of parasitism were lower. Of the two parasitoid species that were abundant enough to warrant separate analysis, *A. interrupta* attacked a significantly higher proportion of larvae in the habitat islands (Fig. 3A; ANOVA, $F_{[2,28]} = 9.126$, $P < 0.0009$) while *E. nigripalpis tectulum* attacked a significantly higher proportion of larvae in the extensive coniferous stands (Fig. 3B; Kruskal-Wallis test $H = 7.75$, $P = 0.021$). Parasitism by the ichneumonids *T. rostrale*, *P. fumiferanae* and others, was significantly lower on the true islands (Fig. 3C; ANOVA, $F_{[2,28]} = 3.763$, $P = 0.036$) than in the coniferous forest; however, even in coniferous forest parasitism by these species affected <1% of the larvae. The total parasitism rate by all parasitoids combined was lower on the true islands than in either the habitat islands or the coniferous forest (Fig. 3D, ANOVA, $F_{[2,28]} = 5.44$, $P = 0.01$).

Three species of generalist ichneumonid wasps, *Itoplectis conquisitor* (Say), *Ephialtes ontario* (Cress.) and *Phaeogenes maculicornis hariolus* (Cress.), attacked and emerged from the introduced pupae (Table 1). The overall pupal parasitism rate was significantly higher in the habitat islands (Fig. 4; ANOVA, $F_{[2, 28]} = 6.95$, $P = 0.003$).

Discussion

After several years of severe defoliation by the spruce budworm *Choristoneura fumiferana*, balsam fir stands in the Abitibi region of Québec suffered levels of mortality attaining 100% in many sites. However, the budworm's impact on the forest was not uniform in space. Bergeron et al. (1995) found that coniferous stands embedded in a matrix dominated by deciduous stands were less vulnerable than large expanses of coniferous forest. In the present study, conducted at nearby, but independent, sampling sites, balsam fir mortality was likewise more severe in large conifer stands that in either "habitat islands" of conifers surrounded by deciduous trees or in

Table 1 Parasitoids reared from spruce budworm larvae and pupae

		Larval instar at harvest			
		3[a]	4–5	5–6	pupa
Diptera					
Tachinidae	*Actia interrupta* Curr.		X	X	
Hymenoptera					
Braconidae	*Apanteles morrisi* Mason	X			
	Dolichogenidea absona Muesebeck	X			
	Microgaster canadensis Muesebeck	X			
Ichneumonidae	*Tranosema rostrale* (Brischke)		X	X	
	Phytodietus fumiferanae Rowher		X		
	Exochus nigripalpis tectulum (Townes)		X	X	
	Mesochorus sp.		X		
	possibly *Coccygominus* sp.		X		
	Itoplectis conquisitor (Say)				X
	Ephialtes ontario (Cress.)				X
	Phaogenes maculicornis hariolus (Cress.)				X

[a] Since only obviously live larvae were harvested, *Elachertus cacoeciae* (Hymenoptera:Pteromalidae), which paralyzes the larvae, was not recovered by our sampling methods. However, *E. cacoeciae* has been reared from moribund larvae in a separate study conducted at the same sites

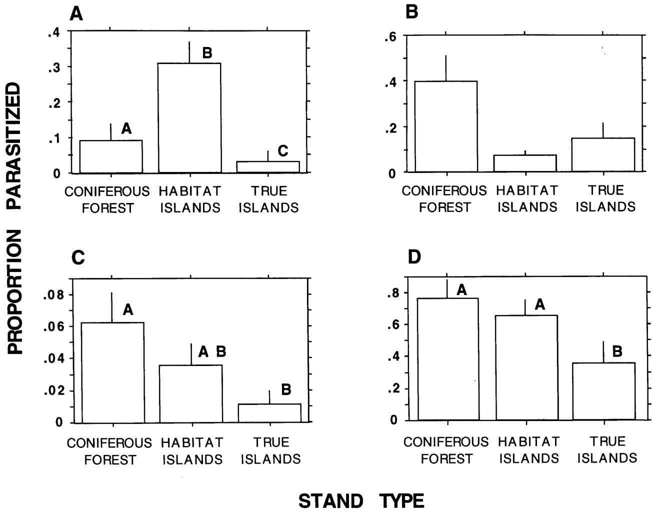

Fig. 3A–D Per capita parasitism of larvae harvested as fifth and sixth instars. **A** parasitism of larvae by the tachinid *Actia interrupta*, **B** parasitism of larvae by the ichneumonid *Exochus nigripalpis tectulum*, **C** parasitism of larvae by miscellaneous ichneumonids, including *Tranosema rostrale* and *Phytodiatus fumeriferanae* and **D** parasitism by all larval parasitoids combined. *Bars* show means and standard errors (back-transformed following analysis on arcsin square root-transformed data). Means with the same *letter* are not significantly different at α = 0.05 according to Fisher's PLSD test. Fisher's PLSD not shown for **B**, which was analyzed by Kruskal-Wallis test instead of ANOVA because it did not meet the assumption of homoscedasticity

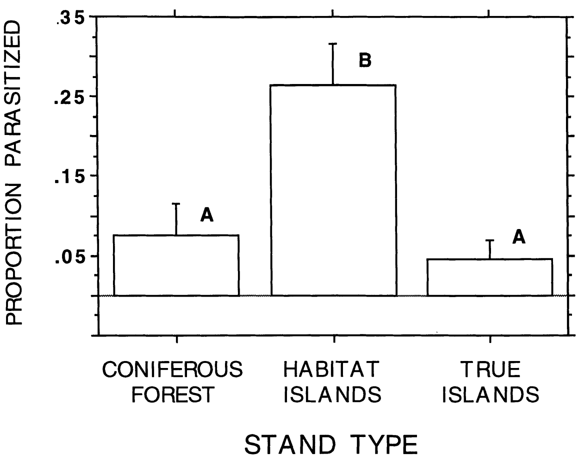

Fig. 4 Parasitism of pupae by the ichneumonids, *Itoplectis conquisitor*, *Ephialtes ontario* and *Phaeogenes maculicornis hariolus*. *Bars* show means and standard errors (back-transformed following analysis on arcsin square root-transformed data). Means with the same *letter* are not significantly different at α = 0.05 according to Fisher's PLSD test

stands on true islands. The age of a stand generally plays an important role in determining budworm-caused mortality, since older, larger trees are often more vulnerable than younger, smaller ones (Archambault et al. 1990). However, the average age of surviving balsam fir did not differ significantly among the three stand types. Most fir stands in the area of our study sites are approximately 60 years old (Plourde 1994), since the majority of individuals recruited following the early-1930s budworm outbreak (Morin et al. 1993).

Several hypotheses can be proposed to explain the lower mortality of balsam fir in the habitat islands and on the true islands. Lower mortality might simply result from a greater tolerance of the trees to a given level of herbivore damage. In the study of Bergeron et al. (1995), however, edaphic factors that might make trees more or less tolerant of damage – drainage, soil type and slope – did not explain a significant amount of the variance in tree mortality. Although stand density was higher on the islands, previous studies have not shown stand density to be a significant predictor of stand mortality (Craighead 1925, reviewed by MacLean 1980).

It is also possible that trees in habitat islands or on true islands had lower mortality because they received less herbivore damage during the last outbreak. No data were taken on budworm larval densities during the 1970s and 1980s. At the present time, the budworm population in Abitibi is at such a low level that quantifying larval density is impractical. Adult densities, however, did not differ significantly between the three stand types, indicating that trees in habitat islands and on true islands are at least accessible to male moths, although the link between this and female abundance and oviposition during the last outbreak is, of course, tenuous.

Trees in the habitat islands may have been spared the brunt of the outbreak because pressure by natural enemies on the budworm was greater there. Again, although we do not have information on larval mortality rates during the outbreak, in the present study, parasitism rates by the tachinid fly *Actia interrupta*, as well as by ichneumonid pupal parasitoids, were higher in the habitat islands. On the other hand, *Exochus nigripalpis tectulum*, an ichneumonid that attacked the larvae but did not emerge until after pupation, caused significantly higher mortality in the large tracts of coniferous forest. Because this parasitoid allows the larvae to complete their development, it affords less "protection" to the foliage than *A. interrupta*, which kills the larvae before they complete their development.

Although higher parasitism rates on herbivores in more diverse vegetation have been previously documented in several agricultural systems (Russell 1989) and orchards (Altieri and Schmidt 1986), the mechanisms behind this pattern remain largely unexplored (Kareiva 1984; Russell 1989). Diverse vegetation may furnish food resources and alternative host species that are absent from homogeneous vegetation. The understory of deciduous or mixed stands in the boreal forest is considerably more diverse in flowering plants (DeGrandpré et al. 1993), which could possibly provide nectar for foraging parasitoids (Simmons et al. 1975; Bradette 1994). The pupal parasitoid *Itoplectis conquisitor*, important in the habitat islands in the present study, was shown by Leius (1967) to cause higher mortality in apple orchards having more understory wildflowers. *I. conquisitor*, *A. interrupta* and other parasitoids have been shown to cause less budworm mortality in dense, heavily shaded stands than in open fir stands with richer understories (Simmons et al. 1975), an observation that may explain the lower parasitism rates in the dense island stands. The hypothesis that understory nectar is important to foraging parasitoids is substantiated by studies demonstrating that artificial nectar increases the longevity and fecundity of parasitoids in the laboratory (Syme 1975). Furthermore, artificial honeydew has been shown to increase the abundance of a variety of natural enemies in field experiments (Evans and Swallow 1993).

For some species of parasitoids, the presence of alternative or alternate host species may be even more critical than the presence of flowering plants. For example, the braconid parasitoid *Meteorus trachynotus* does not overwinter in spruce budworm larvae, and thus cannot persist in budworm populations in the absence of an alternate host within which to overwinter. An important overwintering host for *M. trachynotus* is the oblique-banded leafroller *Choristoneura rosaceana* (Maltais et al. 1989), a generalist lepidopteran that feeds on deciduous foliage. Although *M. trachynotus* was not found in the present study, it is often an important parasitoid during the decline phase of an outbreak (Dowden and Carolin 1950). If it is indeed more abundant when deciduous foliage is available, as one might expect from its dependence on deciduous-feeding alternate hosts, the decline of an outbreak in diverse forests may be hastened with respect to that in large coniferous stands, thus lessening tree mortality. Like *M. trachynotus*, *A. interrupta*, the tachinid that was more abundant in the habitat islands in the present study, is bivoltine (J. Régnière, personal observation) and may also depend on alternate hosts in which to overwinter. The pupal parasitoids, *I. conquisitor*, *E. ontario* and *P. maculicornis*, which were also found to be important mortality agents in the habitat islands, attack lepidopterans on a wide variety of host plants. In the forests of Lake Duparquet, *I. conquisitor* has also been found in populations of the birch tube-maker *Acrobasis betulella* (Cappuccino and Martin 1997), again implying the potential for interactions between the spruce budworm and deciduous-plant feeding Lepidoptera via natural enemies.

Although the present study identifies a potentially important link between vegetational diversity and parasitism rates, parasitism of the larvae and pupae is but one small piece of the dynamical puzzle explaining budworm abundance and consequent damage to the foliage. Mortality during other stages of the life cycle, adult immigration and emigration, as well as female fecundity and oviposition preferences, may all differ between homogeneous and heterogeneous stands. During outbreaks, losses related to larval dispersal are important. Dispersal-related mortality can be higher in mixed stands, where there is a greater probability that wandering larvae will become stranded on non-host trees (Kemp and Simmons 1979). Larvae on the true islands of Lake Duparquet, although perhaps suffering lower pressure from parasitoids during the outbreak, may have been subject to high dispersal-related losses as ballooning larvae wafted over the water.

The impression that severe outbreaks have been associated with a decline in the diversity of the boreal forest has led many authors to suggest silvicultural remedies to lessen the impact of the spruce budworm (reviewed by Miller and Rusnock 1993). It is unreasonable to believe that altering the diversity of the forest could completely stop outbreaks from occurring. The population peaks and troughs of insects with complex dynamics have proven to be remarkably resistant to perturbation (Myers and Rothman 1995). Although it may not be possible to break the cycle of the spruce budworm, it may be possible to mitigate outbreak severity, by managing forests to increase vegetational diversity. In the present study, we have considered only diversity on the scale of a few hectares. Since each natural enemy species will respond to habitat heterogeneity at a characteristic spatial scale (Roland and Taylor 1997), we must study the effect of stand diversity on parasitism at scales ranging from a few square meters to several square kilometers. Such multi-scale studies are the key to developing sound forest management strategies.

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