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Effect of forest structure on dynamics of forest tent caterpillar populations

by

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ABSTRACT

We studied the population dynamics of the principal defoliator of aspen forests as it relates to spatial structure of forests. Life-table and experimental studies were used to identify the effects of forest fragmentation on the process driving population collapse, and on the rate of collapse itself. Outbreaks last longer forests which have been fragmented to some degree. The efficacy of two main sources of tent caterpillar mortality, insect parasitoids and viral disease, is reduced in fragmented forests. This pattern is associated with the longer outbreaks. The variation in dynamics due to forest structure is also assessed relative the larger-scale effects of such things as long-term climate patterns across Alberta. Recommendations are made for methods of managing forests which reduces the duration of outbreaks of this defoliator, and hence reduces the loss of annual growth increment and tree mortality.

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INTRODUCTION

Forest tent caterpillar are one of two principal defoliating insects of the boreal mixedwood forest; the other being spruce budworm. Tent caterpillar undergo dramatic increase and collapse of populations, with a period of approximately 10 to 11 years. During the outbreak phase of their cycle, tent caterpillar are probably the most abundant animal (in terms of biomass) in aspen-dominated boreal forest, causing complete defoliation of trembling aspen trees. Their defoliation not only reduces the incremental growth of aspen trees to almost zero (ref.), but repeated defoliation of aspen trees, also increases the risk of tree mortality (Hildahl and Reeks, 1960). In Ontario, increased fragmentation of boreal mixedwood forests through forestry and agriculture, is associated with longer duration of tent caterpillar outbreaks by several years (Roland 1993).

This study examines how forest structure interacts with population process which drive tent caterpillar dynamics, and identifies not only the forest structure needed for these processes to operate normally, but also identifies the spatial scale at which that structure needs to be maintained. Although the dynamics of tent caterpillar can be divided into the increase phase and decline phase, the bulk of this project examines with the effects of forest structure on processes acting on peak and declining populations. In practical terms, therefore, although forest structure affects both the 'risk of outbreak' and the 'rate of population collapse', here we focus on the latter.

This research was undertaken for two main reasons: 1. to identify how aspen-dominated forests might be physically structured to minimize the impact of this defoliator (the corollary being how not to structure aspen forests, promoting outbreak), and 2. to understand how altered forest structure affects the dynamics of a predator-prey system generally.

SUMMARY OF DATA ANALYSIS

Projects:

1. Observational study of effect of forest structure on parasitism (Jens Roland, Phil Taylor, Helena Bylund [Wennergren Foundation PDF].

This study examines the effects of forest structure on several species of parasitoid which are associated collapse of tent caterpillar populations - as part of the explanation for longer-lasting insect outbreaks in fragmented forests. Two components of this project are identifying these effects (are parasitism rates higher or lower in more fragmented forests) and the spatial scale at which that fragmentation has its greatest effect (is it the fragmentation at the local scale that determines rates of parasitism, or at some spatial larger scale).

Tent caterpillar populations were sampled at 127 sites covering an area of 400 km2 near Ministik Hills, Alberta. The forest structure around each of these sites was characterized at 6 spatial scales (53m, 106m, 212m, 425m, 850m, 1700m), based on a 1:20:000 photo mosaic (5.3m pixel size) of the study area, classified by forest and non-forest habitat. By measuring forest structure at several spatial scales, the level of parasitism for each of a number of parasitoid species could be related for the degree of forest fragmentation estimated at each spatial scale. The assumption in this analysis is that the scale of measurement which provides the strongest relationship between landscape and parasitism, is the scale at which that species of parasitoids responds to habitat structure (Roland and Taylor, 1997); presumably via it's search behaviour. Parasitism by four species of parasitoid was analyzed in this way: *Carcelia malacosomae*, *Patelloa pachypyga*, *Leschenaultia exul*, and *Arachnidomyia aldrichi*. Of these, the latter three are consistently associated with collapse of tent caterpillar populations, be they in Ontario (Sippell, 1962), Minnesota (Witter and Kulman, 1979), or in Alberta (Parry, 1995).

Parasitism by *P. pachypyga*, *L. exul* and *A. aldrichi* were positively rated to the amount of forest cover; they caused the highest rate of parasitism in contiguous blocks of forest (positive coefficients in Figs. 1b, c, d); as fragmentation increases these fly species cause lower rates of parasitism. The scale at which forest fragmentation has it's greatest effect differs among the three species. The smallest of the three species, *P. pachypyga*, responds most strongly to structure at a scale of 212m (Fig 1b); *A. aldrichi* responds most strongly to forest structure at a scale of 425m (Fig. 1c); parasitism by the largest of the three species, *L. exul* is affected most strongly by the level of fragmentation at a scale of 850m (Fig. 1d). One fly species, *C. malacosomae*, actually causes lower rates of parasitism in contiguous forests, and responds most strongly to fine-scale local forest structure (53m).

The over-all pattern for the parasitoids important during collapse is for a reduced efficacy. The magnitude of this effect is equivalent to a reduction in parasitism by half, for forests fragmented to one-half coverage compared to an intact forest. In order for all of these parasitoids to function normally, forest stands should remain intact at scales of at least 850m on a side and probably a bit larger (72 - 100 ha) , but not as large as 1700m on a side (290 ha). Although outbreaks would still occur in these stands, the implication from these results is that they would collapse within a few years and not be prolonged. This pattern is important in light of the relative importance of number of years of tree defoliation vs severity of defoliation; the number of years of defoliation not only determines the amount of lost tree increment, but also the risk of canker and tree mortality.

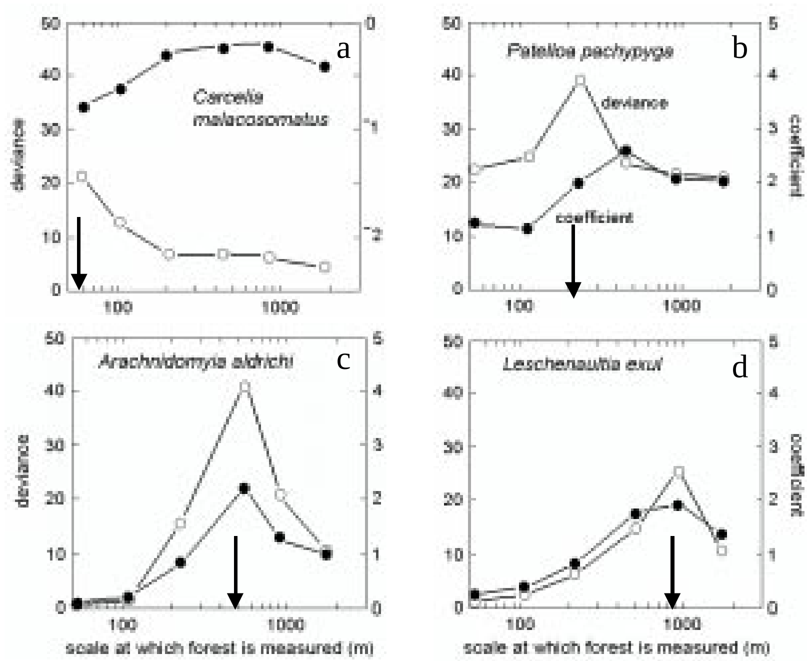

Figure 1. Regression statistics for the effects of forest structure measured at 6 different scales on the coefficient (●) and deviance accounted for (○) on parasitism by four species of parasitoid attacking forest tent caterpillar. Arrow for each species indicates the spatial scale at which forest structure has its greatest effect on parasitism (See Roland and Taylor, 1997 for details). Note that coefficients for *Carcelia malacosomae* are negative indicating greater parasitism in areas with less forest.

2. Experimental and observational study of mortality from virus (Lorne Rothman, [NSERC PDF], Jens Roland).

These studies were conducted, like those described above for parasitism, to estimate the effects of forest fragmentation on virus mortality of tent caterpillar. Detailed life-table studies of caterpillar colonies permitted the estimation of these effects relative to the effects on mortality from other sources (Rothman and Roland, 1997).

Colonies of first-instar larvae were prepared by combining subsets of individuals hatching from different egg masses collected at sites off of the study grid. These colonies were monitored every second day until pupation, and the fate of each individual was determined. Survival was assessed in relation to the degree of forest fragmentation at each site, measured at two spatial scales: 53m and 106m.

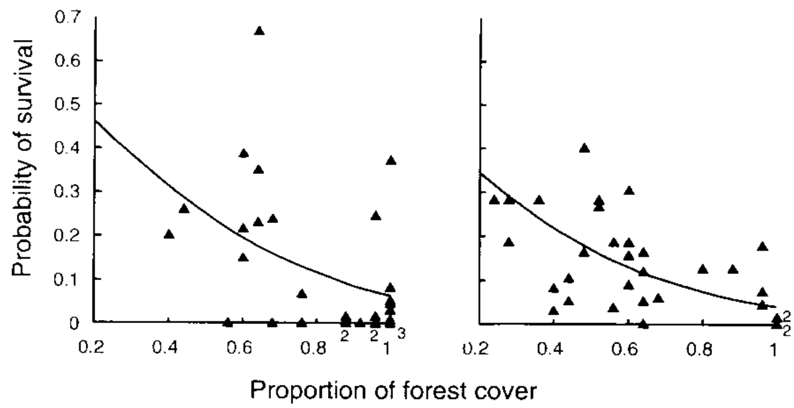

Figure 2. Probability of forest tent caterpillar from egg to pupation as a function of proportion cover by forest (within 53m of each sampling site) across two 32ha grids. The regressions are significant for both grids (from Rothman and Roland 1998).

Survival of tent caterpillars was lower in contiguous forests than in fragmented forests, particularly for the early instar larvae (Fig. 2). Of the larval mortality, that attributable to virus infection was the greatest (Table 1). Survival from virus was much lower in contiguous blocks of forest compared to that in fragmented forests (Fig. 3) within both plots (Rothman and Roland, 1997). In this particular study, forest structure was measured at only two scales: 53m and 106m. The effect of fragmentation on reduction of virus was most evident at the finest scale of measurement, suggesting that the effect is very local. This pattern is consistent with reduced transmission of virus among tent caterpillar at the forest edge (Roland and Kaupp, 1997) due to the inactivation of virus in sunlight, given that edge effects tend to be fine-scale effects.

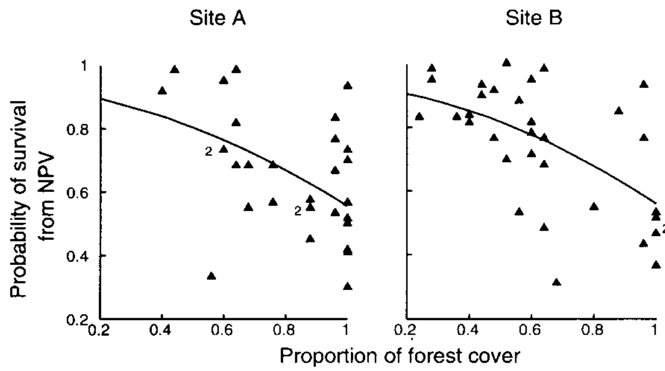

Figure 3. Probability of forest tent caterpillar surviving from NPV virus as a function of amount of forest cover within 53m of each sampling site. The logistic regressions are significant for both grids. (from Rothman and Roland, 1998).

The implication of these results for forest management is that fine-scale fragmentation of forests can provide refuges from viral mortality for forest tent caterpillar. Small stands with large proportions of forest edge to area will be largely free of active tent caterpillar virus, and hence either

3. Dendrochronological study of long-term and large-scale tent caterpillar dynamics (Barry Cooke, Ph.D. candidate, University of Alberta).

These studies are being completed this summer and fall, with defense of the thesis planned for Christmas, 1999. The use of tree-ring increment from mature trembling aspen trees, permits the identification of pattern of tent caterpillar outbreak over very long (> 80 years).

Fine-scale patterns of outbreak dynamics. Sections were cut from the base of 3 trees at each of 127 sites across the 400 km2 Ministik Hills study area. The resolution of this grid is about 2km on average. Disks were sanded and polished, and the width of each year's growth was measured under a dissecting scope. Incremental growth was adjusted to effects of drought (Cooke thesis in prep.), and years with reductions in growth were deemed to be years of high tent caterpillar abundance and tree defoliation. The patterns of outbreak frequency are then related to the surrounding landscape at each sample point.

Large-scale patterns of outbreak dynamics. In order to assess the significance of patterns of outbreak determined from the fine-scale dendrochronological studies described above, a larger-scale series of 9 sites across northern Alberta were analyzed similarly, but with more trees taken per site. Samples were taken at: Peace River, Peerless Lake, Fort McMurray, Whitecourt, Calling Lake, Christina Lake, Drayton Valley, Cooking Lake, and Bonnyville (Fig. 3).

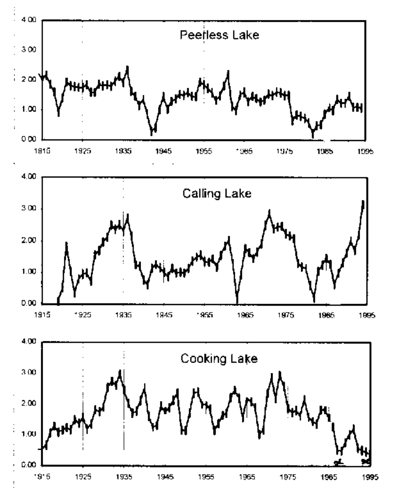

Figure 4. Incremental growth of trembling aspen trees from 1915 through 1998 at three of nine sites across northern Alberta (details in Cooke thesis in prep.).

Although detailed analysis is currently being done with respect to effects of climate and forest structure on outbreak dynamics (Cooke thesis, in prep), generally there are more frequent outbreaks in the more southerly sites such as Cooking Lake and Bonnyville, compared to more northerly sites like Peerless Lake and Fort McMurray. These patterns will be considered in light of similar analyses for long-term spruce budworm outbreak in spruce and fir forests in (Hubert Morin, UQ Chicoutimi).

The implications from this study will be to assess the relative importance of variation in outbreak which is due to local effects of forest structure, in light of over-all variation at much larger scales due to processes such as climate. If large-scale effects dominate, then the local effects of forest structure may be irrelevant and forest management could largely ignore managing structure; if local effects such as forest structure dominate, then there is great potential for using forest management to reduce either the severity or duration of defoliator outbreak.

4. Large-scale monitoring (Jens Roland and Chris Schmidt, U of A).

In addition to the monitoring of collapsing populations at Ministik Hills (point 1 above), we have we have been monitoring low-density populations across the Alberta Pacific Forest Industries FMA in northeastern Alberta since 1995. Pheromone trapping technology was used to estimate density of adult males at each of 175 sites each year. Sites are approximately 5km apart, and run from Athabasca, to Lac la Biche and north past Ft. McMurray, and northwest to Wabasca. Density at each site and the change in density between years are to be related to local forest structure. Forest data are yet to be estimated from the forest cover maps (Alpac and Pearson Timberline, Edmonton). The general pattern for the interval 1995 through 1998, is for an increase in the number of sites with tent caterpillar, and that the density is increasing at sites where tent caterpillar are present (Table 2). These data are still to be analyzed in light of landscape structure around each sampling point.

Table 2. Proportion of sites across Alpac FMA with forest tent caterpillar moths and mean density in 1997-98. Data are based on catches in two pheromone traps per site.

year	N sites	proportion of sites with moths	mean number of moths per site (*SE*)
1997	119	0.45	0.66 (0.08)
1998	134	0.48	1.37 (0.26)

Improved trapping protocol is being developed in collaboration with PheroTech (Delta B.C.), and funded by an NSERC CRD grant. These studies will ensure that population estimates based on pheromone catch will be as accurate as possible. This work combines studies on: 1. optimal blend of the pheromone based on improvements to previously published pheromone blends (Chisholm *et al.* 1980; Palansiwamy *et al.* 1983), and on improved release technology using ‘Flexlure’ (PheroTech) which gives a flat release of pheromone over time rather than a negative exponential release as seen for rubber septa. These improved techniques will ensure that counts are as consistent as accurate as possible and therefore make density estimates among years readily comparable.

MANAGEMENT APPLICATIONS

The principal implications of the results to date relate most strongly to the amount of forest in “leave” areas, and the scale at which these amounts are assessed.

1. Greater fragmentation of boreal forests is associated with outbreaks of forest tent caterpillar that last 1 to 3 years longer than in contiguous forests.
2. Increase in the number of years of defoliation results in reduced annual increment of aspen and reduced tree survival.
3. Because the aspen canopy is virtually totally removed in an outbreak year, there is an associated increase penetration of sunlight to the forest floor, and increase in nutrient to the forest floor as the canopy is converted into insect ‘frass’.
4. Physical structure of forests can be manipulated to minimize the duration of caterpillar outbreak.
5. Leave areas must be at least 850m on a side in order that parasitoids are as efficacious as possible during caterpillar population collapse.
6. Small forest blocks, adjacent to large ones, should be removed to eliminate possible refuges from mortality due to parasitoids and/or virus.
7. Edge-to-area ratios of “leave” areas should be as small as possible to minimize the size of refuges from mortality due to parasitism and virus infection.

CONCLUSIONS

Based on the studies to date, forest fragmentation appears to reduce the efficacy of natural enemies of forest tent caterpillar, and is associated with prolonged outbreak of this aspen defoliator. As a result, the structure of forests could be managed to ensure the normal functioning of the predator-prey interaction between caterpillar, parasitoids and viral disease, in an effort to minimize the effects of outbreak.

REFERENCES

Chisholm, M.D., E.W. Underhill, W. Steck, K,N. Slessor, and G.G. Grant 1980. (*Z*)-5,(*E*)-7-dodecadienal and (*Z*)-5,(*E*)-7-dodecadien-1-ol, sex pheromone components of the forest tent caterpillar, *Malacosoma disstria*. Environmental Entomology, 9: 278-282.

Hildahl, V. & W.A. Reeks 1960. Outbreaks of the forest tent caterpillar, *Malacosoma disstria* Hübner, and their effects on stands of trembling aspen in Manitoba and Saskatchewan. Canadian Entomologist, 92: 199-209.

Mondor, E. B. & J. Roland 1997. Host location behaviour of *Leschenaultia exul* and *Patelloa pachypyga*: Two tachinid parasitoids of the forest tent caterpillar *Malacosoma disstria*. Entomologia Experimentalis et Applicata 85: 161-168.

Mondor, E. B. & J. Roland 1998. Host searching and oviposition by *Leschenaultia exul*, a tachinid parasitoid of the forest tent caterpillar, *Malacosoma disstria*. Journal of Insect Behavior 11: 583-592.

Palaniswamy, P., M.D. Chisholm, E.W. Underhill, D.S. Reed, and S.G. Peesker. 1983. Disruption of forest tent caterpillar (Lepidoptera: Lasiocampidae) orientation to baited traps in aspen groves by air permeation with (5*Z*,7*E*)-5,7-dodecadienal. Journal of Economic Entomology, 76: 1159-1163.

Parry, 1995. Larval and pupal parasitism of the forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), in Alberta. The Canadian Entomologist, 127: 877-893.

Roland J. 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreaks. Oecologia 93: 25-30.

Roland, J. 2000. Landscape ecology of parasitism. In: Parasitoid Population Biology (M.E. Hochberg and A.R. Ives, eds.) Princeton University Press (*in press*)

Roland J. & W.J. Kaupp. 1995. Reduced transmission of forest tent caterpillar NPV at the forest edge. Environmental Entomology, 24: 1175-1178.

Roland J. Mackey B & B. Cooke. 1998. Effects of climate and forest structure on duration of forest tent caterpillar outbreaks across central Ontario, Canada. Canadian Entomologist. 130: 1-12.

Roland J. & P.D. Taylor. 1995. Herbivore-natural enemy interactions in fragmented and continuous forests. In: Population Dynamics: New Approaches and Synthesis (N. Cappuccino and P.W. Price eds.) Academic Press, San Diego (pp. 195-208).

Roland, J., P.D. Taylor & B. Cooke. 1997. Forest structure and the spatial pattern of parasitoid attack. *In* Forests and Insects. (Watt, A.D., N.E. Stork & M.D. Hunter eds.) Chapman & Hall, pp. 97-106.

Roland J. & P.D. Taylor. 1997. Insect parasitoid species respond to forest structure at different spatial scales. Nature 386, 710-713.

Rothman L. & J. Roland 1998. Relationships between forest fragmentation and colony performance in the forest tent caterpillar, *Malacosoma disstria*. Ecography 21: 383-391.

Sippel, W.L. 1962. Outbreaks of the forest tent caterpillar *Malacosoma disstria* Hbn., a periodic defoliator of broad leafed trees in Ontario. The Canadian Entomologist, 94: 408-416.

Witter, J.A. & H.M. Kulman 1979. The parasite complex of the forest tent caterpillar in northern Minnesota. Environmental Entomology, 8: 723-731.