

---

---

# Population Dynamics

## *New Approaches and Synthesis*

---

EDITED BY

Naomi Cappuccino

*Department of Zoology*

*University of Texas*

*Austin, Texas*

Peter W. Price

*Department of Biological Sciences*

*Northern Arizona University*

*Flagstaff, Arizona*



ACADEMIC PRESS

San Diego New York Boston London

Sydney Tokyo Toronto

1995

---

## Herbivore–Natural Enemy Interactions in Fragmented and Continuous Forests

Jens Roland and Philip D. Taylor

### I. Introduction

Studies of forest insect population dynamics have generally taken two approaches, using either long-term life-table data from a single forest stand or data from several widely separated sites where each site is treated as a replicate population and a composite picture of the dynamics is inferred from the multiple sites. Examples of the former include studies of the winter moth, *Operophtera brumata*, in Wytham Wood (Varley and Gradwell, 1968) and larch casebearer, *Coleophora laricella* (Ryan, 1990); examples of the latter include studies of the gypsy moth, *Lymantria dispar* (Campbell, 1973), and the spruce budworm, *Choristoneura fumiferana* (Mott, 1963; Royama, 1984).

By considering dynamics at only a single site, or at multiple but distant sites, these studies eliminate potentially critical elements of animal population dynamics: the effect of dynamics at neighboring sites, movement among sites, and how the structure of intervening landscapes differentially influences this movement for the animals in the system (landscape connectivity; Taylor *et al.*, 1993). Fragmentation of forests is one change in landscape structure that has received considerable attention in its effects on animal populations (e.g., Wilcove *et al.*, 1986). Forest fragmentation alters the relative kinds and positions of resources in the landscape and introduces new elements into landscapes that may differentially influence animal movement, and hence population dynamics.

In the case of insect population dynamics, movement of either the herbivore or its natural enemies may be strongly influenced by local habitat structure. Local populations of herbivorous insects whose dynamics are driven by natural enemies will be affected by the dynamics of neighboring populations of herbivores and parasites, depending on the ability of each to move through intervening habitat. The fact that they *are* linked to a greater or lesser extent will therefore influence their regional dynamics. This type of process is evident in the analyses

of spruce budworm dynamics in New Brunswick, Canada, where dispersal of budworm is implicated as an important element in determining local abundance (Royama, 1984). However, the large distances between the studied budworm populations made direct evaluation of the importance of movement impossible.

Empirical evidence exists for the importance of differential herbivore and natural enemy movement from studies done at very fine spatial scales. For example, coccinellid predators are unable to aggregate to local patches of high aphid abundance when habitat (monocultures of the composite *Solidago*) is fragmented into small clumps separated by 1-m clearings (Kareiva, 1987). However, when the habitat is continuous, predators readily move, aggregate, and suppress aphid outbreaks. Maintaining connectivity of the landscape through which the predators forage allows them to respond to and suppress local prey abundance.

There is also evidence that landscape structure at a large spatial scale alters predator-prey interactions. For example, the forest tent caterpillar *Malacosoma disstria* exhibits short outbreaks (2-4 years) in continuous forests and longer outbreaks (3-6 years) in fragmented forests (Fig. 1; Roland, 1993). Suppression of tent caterpillar outbreaks is associated with high mortality by natural enemies, especially by the sarcophagid fly *Sarcophaga* (= *Arachnidomyia*) *aldrichi* (Hodson, 1939), the tachinid flies *Leschenaultia exul* (Bess, 1936; Sippell, 1962) and *Patelloa pachypyga* (Sippell, 1962), and nuclear polyhedrosis virus epizootics (Clarke, 1958; Stairs, 1966; Myers, 1993). Longer outbreaks of tent caterpillar in fragmented boreal forests imply a reduced impact of natural enemies.

We hypothesize that forest fragmentation may reduce the impact of natural enemies on forest tent caterpillar dynamics directly by reducing their efficiency at the forest edge adjacent to clearings. For example, parasitoid behavior may differ near the forest edge, where temperatures and insolation are higher than in the forest interior, and where aggregation of the herbivore (e.g., Bellinger *et al.*, 1989) might "swamp" attacking parasitoids. Viral pathogens may also be deactivated along forest edges because of higher levels of ultraviolet radiation, thereby reducing their effect on tent caterpillar. Alternatively, forest fragmentation may reduce the impact of natural enemies through a differential effect of clearings on movement of parasites and pathogens relative to that of the tent caterpillar.

Under each hypothesis, the effect of fragmentation is to uncouple the forest tent caterpillar population from the parasite/pathogen community associated with population collapse. It is likely that fragmentation will influence parasites and pathogens differently from its effect on the herbivore, resulting in potentially quite complex dynamics. For example, clearings may inhibit the movement of some parasitoids or the transmission of virus. Alternatively, or in addition, clearings may enhance the absolute distances that moths disperse by causing a more strongly directional pattern of movement compared to their movement through a continuous forest canopy. Each of these scenarios results in the natural enemies lagging behind the herbivore in fragmented forests, when compared to continuous forests. Such a pattern of decreasing parasitism with increased fragmentation

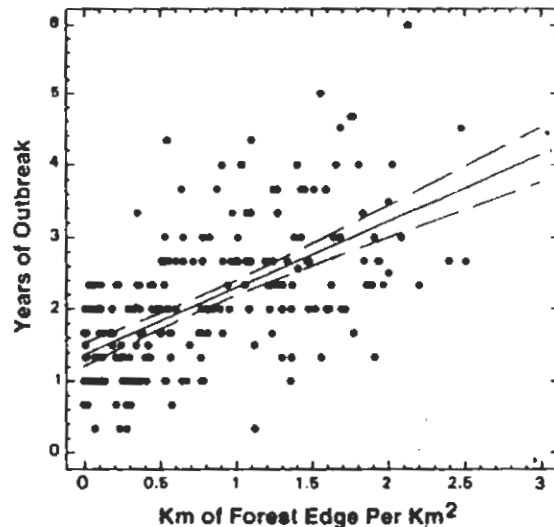


Figure 1. Mean duration (in years) of forest tent caterpillar outbreaks in northern Ontario townships as a function of the amount of forest edge in each township (after Roland, 1993).

has been implicated in fine-scale field studies of insect parasitism in habitat clumps of red clover (Kruess and Tschamtkke, 1994). Consistent effects of landscape structure on fine-scale local movements of herbivores and their parasites and pathogens should produce large-scale changes in the population dynamics of these animals when there is extensive alteration of landscape structure such as forest fragmentation.

We have approached the study of forest tent caterpillar population dynamics by examining patterns of distribution of the herbivores and of the parasites at several spatial scales and simultaneously by examining how individual animals are influenced by different kinds of landscape structure. In this chapter, we present a broad outline of the spatial approach used to study this host and natural enemy system, and give an example of the details with a subset of our larger data set. This analysis shows, at two spatial scales, differential effects of fragmentation on forest tent caterpillar parasitism by two species of parasitic flies, *S. aldrichi* and *P. pachypyga*.

## II. Methods

### A. General Approach

We approach the study of tent caterpillar and its natural enemies at a spatial scale (420 km<sup>2</sup>) that is sufficiently large to detect variation in dynamics among

subpopulations, but we do so with study sites arrayed at a sufficiently fine scale to permit linkage of local dynamics to those in adjacent stands. We feel that the associated problems of lack of independence among study sites is more than outweighed by the benefits of being able to identify the impact of dynamics at adjacent sites and of movement among sites. Spacing of study sites at a scale large enough to ensure independence would in effect obscure one of the most important factors driving the dynamics, that of movement.

### 1. Sampling Sites

Our main study area includes 127 population sample points (megagrid) spread across an area of 420 km<sup>2</sup> in the Cooking Lake and Ministik Hills area of Alberta, Canada (113° 00' W, 53° 22' N, Fig. 2). This area is at the southern edge of boreal forest and is dominated by trembling aspen (*Populus tremuloides*), the preferred host plant of forest tent caterpillar. Other tree species intermixed with aspen and in decreasing importance are balsam poplar (*Populus balsamifera*), paper birch (*Betula papyrifera*), and white spruce (*Picea glauca*). Clearing for agriculture has been variable in intensity throughout the study area, resulting in a broad range of forest fragmentation from highly fragmented to continuous forest (Fig. 2).

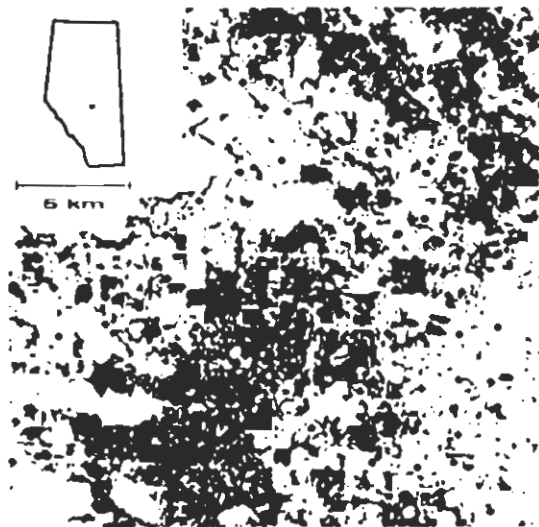


Figure 2. Map of large-scale study area (megagrid). Dark areas are forested, light gray areas are water, and white areas are pasture and cropland. Sample points of the megagrid are shown as black dots.

Each sample point of the megagrid is separated from adjacent points by, on average, 1.8 km. This large scale provides a proximity among sample points that is within the dispersal capabilities of both the forest tent caterpillar and its major parasitoids. Nested within this main study area is a smaller-scale grid (mesogrid) of 109 points with an average separation of 50 m, which permits us to examine the effects of fine-scale landscape structure on population dynamics in the absence of the larger-scale effects. At an even finer scale we sample from 14 small ( $10 \times 10$  m) isolated fragments of aspen forest (isolates) scattered throughout the main study area. These isolated patches allow us to examine the relative ability of individual tent caterpillars and parasitoids to colonize new sites, compared to sites in continuous forest.

## 2. Life Tables

At each sample point in the megagrid and mesogrid we estimate forest tent caterpillar abundance and several discrete mortality factors. These are not complete life tables (Varley and Gradwell, 1968), but sampling does include those stages acted on by the agents considered most important in causing collapse of forest tent caterpillar outbreaks (i.e., virus and late-larval and pupal parasitoids; Sippell, 1957; Hodson, 1939; Myers, 1993). A time-limited search for cocoons is used to estimate abundance; the time taken to find and collect 50 cocoons is recorded up to a maximum of 15 minutes. For samples that required less than 15 minutes, the count of 50 is multiplied by 15 minutes and divided by the actual time taken. In this way, an estimate is made of the number of cocoons that would have been collected if continued for a full 15 minutes. By monitoring the phenology of herbivore pupal development and of parasitism (Sippell, 1957), the two tachinid parasitoids *L. exul* and *P. pachypyga* can be recovered from cocoons, as well as the slightly later sarcophagid *S. aldrichi*. Parasitism is estimated for each by rearing the herbivore pupae until emergence of the parasitoid. Subtle differences in phenology of each parasitoid species (and its effect on absolute level of parasitism) is not considered a major problem because it is the relative rates of parasitism in the two landscapes for each species that is of greatest interest to us here.

Other data collected at each site, but not presented here, are (1) fecundity of tent caterpillar estimated from abdominal width of female pupal cases and the known relationship between abdominal width and egg mass size (J. Roland and R. Bouchier, unpublished) and (2) the presence/absence of nuclear polyhedrosis virus using a DNA probe for tent caterpillar virus (Kaupp and Ebling, 1993) on pupal and larval exuviae and dead bodies from each site.

## 3. Outbreak Spread

Each year we acquire false-color infrared aerial photography of the entire study area. The spatial pattern of defoliation provides a detailed record of cater-

pillar abundance, from which we can measure the spread of increasing populations and the contraction of declining populations. Life-table data at each point can then be related to life-table data at the same point in previous years, life-table data at adjacent points in the same or previous years, and the pattern of population spread or contraction around the site.

#### 4. Individual Movement

We use two methods to assess movement of tent caterpillar and parasitoids, one direct and one indirect. First, mark-release-recapture of parasitoids is used to estimate movement through continuous forest and through fragmented forest. Second, we indirectly assess the difference in the ability of moths and parasitic flies to move across clearings of various sizes by examining their relative rates of "discovery" of isolated patches of the host plant, trembling aspen (*Populus tremuloides*).

### B. Detailed Methods

#### 1. Small-Scale Studies

Fourteen isolated fragments (50 to 450 m from large stands of aspen forest) were surveyed to estimate the relative ability of each insect to "discover" fragments at increasing distance from infested continuous stands. These were contrasted with 14 control sites in continuous forest. Presence of tent caterpillar cocoons and of parasitoids attacking the cocoons was assessed with respect to distance to nearest forest and distance to known defoliation in the previous year (from the false-color infrared aerial photography). Isolated sites were compared to sites within continuous forests with respect to abundance of tent caterpillar and level of parasitism by each fly species. The prediction was that clearings would act as barriers to parasitoid movement, and that parasitism of cocoons in forest isolates should decline as distance from continuous forest increased.

#### 2. Large-Scale Studies

At each sample point of the megagrid, percentage defoliation by tent caterpillar was classified on a nonlinear scale from 1 to 9. Using false-color infrared photographs from 1993, we estimated the degree of forest fragmentation around each point by counting the number of quarter-sections ( $800 \times 800$  m) around the point that contained greater than 50% forest cover, giving a crude estimate of fragmentation that ranged from complete (0) to no fragmentation (4). We also measured the distance to the closest area of tent caterpillar defoliation in the previous year (1993). Pupae were sampled at all sites over a 1-week period from late June to early July, 1994. We test for the effects of the estimated abundance of forest tent caterpillar, the distance to areas of high defoliation in the previous year, and the degree of forest fragmentation around the sample point, on the

abundance of fly parasites, *S. aldrichi* and *P. pachypyga*, recovered from the collected pupae.

### 3. Statistical Models

Statistical models were fit using the generalized linear models procedure in Splus (StatSci). The goodness-of-fit of a given model was assessed by (1) plotting fitted and residuals versus predicted values, (2) computing the overall change in model deviance when terms of interest were dropped, and (3) considering the size of the estimated standard errors of parameter estimates (*t*-tests, maximum probabilities of type-I error: 5%).

For the isolate data, we fit logistic models (binomial errors; McCullagh and Nelder, 1989) to the odds of a cocoon being parasitized versus not being parasitized. The proportion of cocoons parasitized was fit to a model that included the main effects of species (*S. aldrichi* versus *P. pachypyga*), distance to defoliation in the previous year (hereafter simply called distance), whether the sample came from an isolate or not, and the two-way interactions among these. We then sequentially dropped terms from the model and tested for a significant change in deviance against a  $\chi^2$  distribution.

For the large-scale data (megagrid), the response variable was the count of the total number of parasites of both species at each point. We fit a model to the counts (Poisson errors) of fly parasites, including the main effects of distance, fragmentation and fly species, and all two-way interactions. We again assessed the importance of each term by sequentially dropping them from the model, and testing for a significant change in deviance against a  $\chi^2$  distribution.

## III. Results

### A. Isolates

Cocoons from isolated patches were less likely to be parasitized than were those from continuous forest (Isolate term, Table 1), and the effect was much stronger for parasitism by *P. pachypyga* than for *S. aldrichi* (Species  $\times$  Isolate interaction). *Patelloa pachypyga* caused a lower rate of parasitism in isolates than did *S. aldrichi* ( $4.4 \pm 0.76\%$  versus  $19.7 \pm 1.3\%$ , respectively); both caused similar rates of parasitism in continuous forest ( $15.7 \pm 1.4\%$  versus  $18.5 \pm 1.6\%$ , respectively). Cocoons in both the isolates and continuous forest were more likely to be parasitized when closer to an area of high defoliation in the previous year (Table 1; Main effect of distance). The distances of the isolates in which *S. aldrichi* parasitized tent caterpillar cocoons ranged up to 400 m from the nearest continuous forest; the only cocoons that *P. pachypyga* parasitized were in isolates within 125 m of nearby forest.



**TABLE 1**  
**Analysis of Deviance Table for Logistic Models**  
**Assessing the Odds Ratio of a Cocoon Being Parasitized**  
**as a Function of Fly Species (*Sarcophaga aldrichi* versus**  
***Patelloa pachygya*), Distance from the Previous Year's**  
**Defoliation, and Forest Isolates versus Continuous Forest**

Term	df	D <sup>a</sup>	p( $\chi^2$ )
Species	1	7.20	0.01
Distance	1	26.00	<0.001
Isolate	1	6.40	0.01
Species × Isolate	1	10.70	0.0011
Residuals	43	91.31	

<sup>a</sup>The change in deviance (D) when the term is dropped from the full model is shown.

### B. Megagrid

The dominance of each parasitoid species depended on both the degree of forest fragmentation and distance from the previous year's outbreak (Table 2; Species × Distance; Species × Fragmentation interactions). Parasitism by *P. pachygya* declined with increasing fragmentation (Fig. 3), whereas *S. aldrichi* maintained its presence irrespective of the level of fragmentation. Numbers of attacks by both fly species declined as the distance from areas of high defoliation in previous years increased, but *P. pachygya* was more prevalent at points close to previous year's outbreaks than was *S. aldrichi* (Table 2; Species × Distance interaction). The mean count of *P. pachygya* from cocoons at sites within the area of the previous year's outbreak was  $48 \pm 5.5$  versus  $36 \pm 6.2$  for *S. aldrichi*.

**TABLE 2**  
**Analysis of Deviance Table for Poisson (Count) Models**  
**of the Abundance of *Sarcophaga aldrichi* and *Patelloa***  
***pachygya* as a Proportion of All Fly Parasitism at Sample**  
**Points in the Large-Scale Survey (Megagrid)**

Term	df	D	p( $\chi^2$ )
Distance <sup>a</sup>	1	6.43	0.0011
Species × Distance	1	12.26	0.0005
Species × Fragmentation	1	7.13	0.0007
Residuals	242	829.40	

<sup>a</sup>Distance is the distance from the site to the nearest defoliated forest in the previous years, and the degree of fragmentation is fit as an ordinal factor.

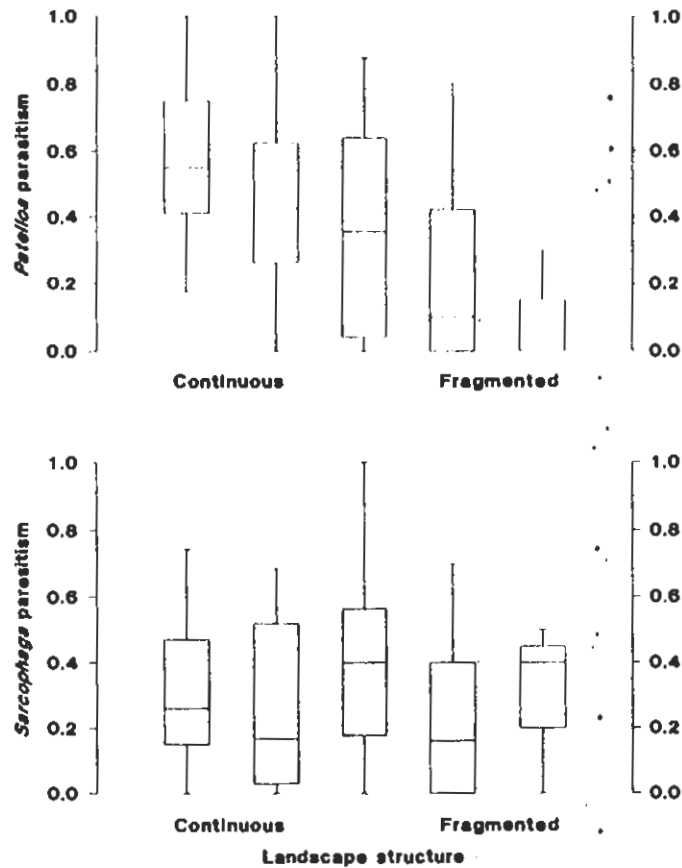


Figure 3. Boxplots showing mean (middle bar), interquartile range (inner bars), and range (outer bars) of parasitism rates for the two parasitoid species *Patelloa pachypyga* and *Sarcophaga aldrichi* across five levels of forest fragmentation.

#### IV. Discussion

##### A. Medium-Scale Dynamics of Tent Caterpillar

Two of the parasitic flies that attack forest tent caterpillar, *Sarcophaga aldrichi* and *Patelloa pachypyga*, are affected in different ways by forest fragmentation. Our results from both the isolate and megagrid studies show uniform parasitism by *Sarcophaga* at all sites, supporting the idea that clearings do not act as barriers to their movement. By contrast, the reduction in parasitism by *Patelloa* in forest

isolates suggests there is limited movement of this fly across clearings. In preliminary mark-recapture studies, we have observed movement by *Sarcophaga* across clearings more than 300 m wide, over a period of several days. We have not yet done mark-recapture studies of *Patelloa* and so cannot unequivocally say that reduction in *Patelloa* efficacy in fragments is due to reduced movement. Results are consistent with a differential effect of landscape structure on movement by the two fly species, although other effects of fragmentation could explain the observed pattern. Parasitoid efficiency is reduced at forest edges (J. Roland and P. Taylor, unpublished), but that effect would not be expected to be related to distance from continuous forest unless movement was involved.

The spatial distribution of the herbivore and parasites across the megagrid is consistent with the results from the forest isolates; tent caterpillar readily colonize isolated and fragmented stands, *Sarcophaga* readily discover and parasitize tent caterpillar at all sites within 400 m of continuous forests, and *Patelloa* is unable to effectively attack tent caterpillar in fragmented forests where the fragments are more than 125 m from continuous stands. This pattern suggests that forest structure differentially affects the rates of movement of the three insects (herbivore and two parasitoids). Moths appear to move more readily than do flies, since sites that are far from the previous year's outbreak had moths but no flies (Fig. 4). Our sampling of herbivore cocoons to detect presence of parasitoids requires that the moths do colonize fragments first, a fact that biases the detection of greater movement by the tent caterpillar. The high abundance of cocoons at some of the distant sites (Fig. 4), however, suggests that tent caterpillar have been there for more than one year (although not presently at outbreak levels) and remain undiscovered by flies. Similar patterns of reduced parasitism with distance from main population sources for other insect species (Landis and Haas, 1992; Kruess and Tschardtke, 1994) have been attributed, in part, to reduced movement of parasitoids across clearings.

## B. Large-Scale Dynamics of Tent Caterpillar

The large-scale pattern of prolonged outbreaks of tent caterpillar in fragmented boreal forests in Ontario (Roland, 1993) could result from a variety of mechanisms, including the reduced efficiency of parasitoids and a reduction in parasitoid movement in response to herbivore abundance in fragmented forests. *Patelloa pachypyga* is limited in fragmented forests because of either its limited movement across clearings or its reduced efficiency in fragments. Data presented here suggest that one parasitoid species, *S. aldrichi*, is affected little by forest fragmentation. Many other parasitoid species attack tent caterpillar (Witter and Kulman, 1979), several of which will likely to be hindered by forest fragmentation. Reduction in efficiency of those species dominant during tent caterpillar decline (*P. pachypyga* is among these) would result in prolonged outbreak. Reduction in

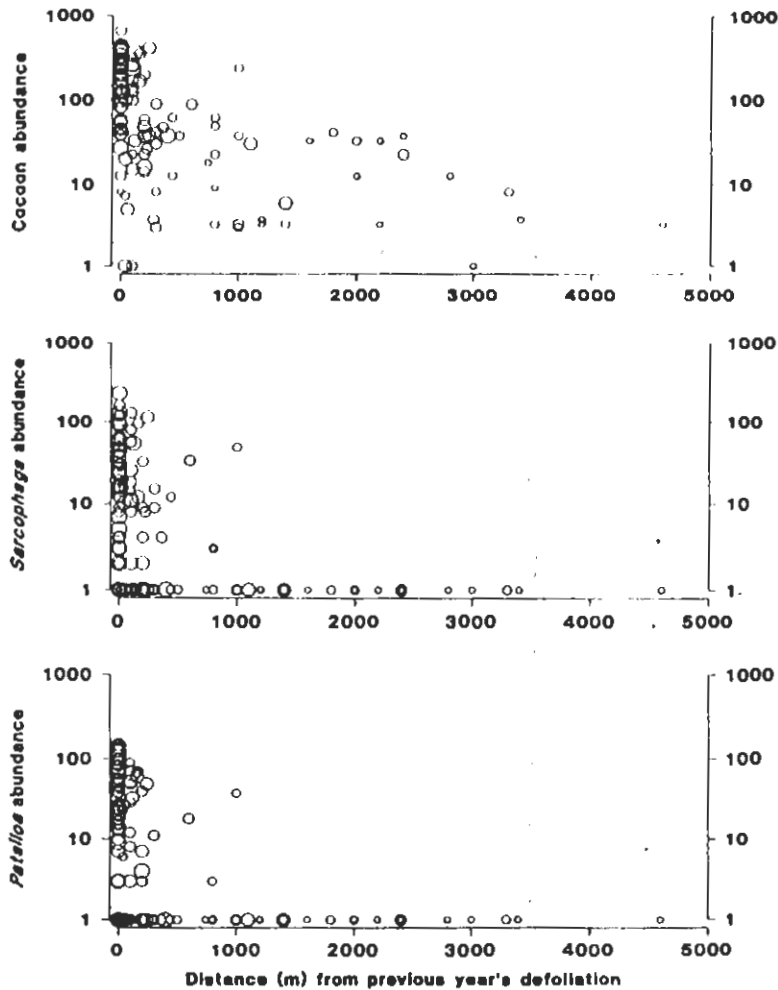


Figure 4. Estimated abundance of forest tent caterpillar cocoons, *Sarcophaga aldrichi*, and *Patelloa puchyryga* as a function of distance from areas of high defoliation in the previous year. Level of fragmentation is indicated for each site by the size of the circle: large circles = continuous forest, small circles = highly fragmented forest.

efficiency of those parasites that are thought to maintain low tent caterpillar densities (e.g., the braconid wasp *Aleiodes malacosomatus*; Sippell, 1962) would shorten the interval between outbreaks. Regulation of tent caterpillar at low density, however, is not known.

Moths move readily across clearings and easily colonize fragmented, iso-

lated sites (sites indicated by small circles in Fig. 4). Fragmentation does not appear to inhibit moth movement and may actually enhance movement. Forest fragments could act as "stepping stones" for more rapid and more strongly directional dispersal compared to that through a continuous forest canopy. Both fly species parasitize tent caterpillar at up to 1000 m from the previous year's outbreak (Fig. 4), but if the intervening forest is fragmented, *Patelloa* drops out (Fig. 3). On the basis of the isolate data, we suspect that *Sarcophaga* moves readily through fragmented forest, and that *Patelloa* may move readily through continuous forest; the two forest types are approximately equally represented across our megagrid sites (Fig. 2). Similar overall distances moved by both fly species for the entire study area (Fig. 4) are therefore not surprising; it is the differential movement in each of the two landscapes that is of most interest here.

Parasitism rates across the megagrid do show a differential effect of forest fragmentation on the two fly species. *Sarcophaga* contributes about 35% of the total fly parasitism at all sites in the megagrid, regardless of level of fragmentation (Fig. 3). This pattern suggests that *Sarcophaga*, as a component of the parasitoid community, is able to keep up with changing spatial patterns of herbivore abundance. *Patelloa*, on the other hand, contributes 60% of the fly-caused parasitism in continuous-forest sites and contributes virtually nothing to parasitism at the most fragmented sites (Fig. 3). If the reduced parasitism in fragments is due to reduced discovery, it implies that *Patelloa* is less able to keep up with the spread of tent caterpillar populations in fragmented forest. Data from the forest isolates support the idea that differential movement of the two flies is important; *Sarcophaga* successfully parasitize tent caterpillar in forest isolates that are much farther from nearby forest (400 m) compared to the maximum distance at which *Patelloa* is able to parasitize (125 m).

In this chapter, we have shown that intervening habitat structure can affect the impact of parasitoids that are dominant during suppression of one of the most important defoliators of boreal forest. We have also shown that the impact of landscape structure differs between parasitoid species. If both flies had been negatively affected by forest fragmentation, then the pattern may simply have arisen from an effect of fragmentation on the herbivore (e.g., higher herbivore density in fragments resulting in "swamping" of all parasitoids), and not because of an effect of fragmentation on the flies themselves. The fact that one fly species was negatively affected by forest fragmentation and one species was not confirms that fly distribution is not simply a consequence of effects of forest structure on the tent caterpillar.

The interaction of landscape structure and population dynamics likely occurs for other insects, but the effect may not be the same as seen for tent caterpillar. For example, outbreaks of eastern spruce budworm tend to be more severe and longer lasting in continuous forests than in fragmented forests (Mott, 1963), a pattern opposite to that seen for tent caterpillar. The mechanism causing the dif-

ference in pattern of budworm outbreak in the two landscape types is not known. Dispersal of spruce budworm is on the order of tens or hundreds of kilometers (Royama, 1984) and many of its parasitoids are generalists with more than one generation per year, requiring alternate hosts later in the summer. Therefore, budworm are more loosely coupled with its parasitoid fauna than is forest tent caterpillar. Because of the looser linkage between budworm and its parasites, fragmentation may have little effect on further decoupling the interaction. In this situation, large continuous areas of host plants of the budworm (white spruce, black spruce, and balsam fir) may in fact promote longer outbreaks compared to those in small stands of these trees. Tight linkage between forest tent caterpillar and its parasites combined with shorter dispersal distances by the moths would make the effects of forest structure on natural enemies much more apparent.

In the study of population dynamics and conservation ecology it is becoming increasingly clear that ecological processes are affected by landscape structure at many spatial scales (Edwards *et al.*, 1993). It is also clear that new insights into the functioning of the systems emerge when data are collected at several spatial scales. To us this means that ultimately population dynamics studies will need to be placed within the landscape framework for dynamics to be fully understood.

## Acknowledgments

Field studies were assisted by Kirsty Ward, Norine Ambrose, and Stacey Rasmussen. Helpful comments on the manuscript were provided by MaryCarol Rossiter and Naomi Cappuccino. This project is funded by the Natural Sciences and Engineering Research Council (J.R.), Green Plan Canada through the Canadian Forest Service (J.R.), Canadian Circumpolar Institute (P.D.T.), and the Central Research Fund, University of Alberta (P.D.T.).

## References

- Bellinger, R. G., Ravlin, F. W., and McManus, M. L. (1989). Forest edge effects and their influence on gypsy moth (Lepidoptera: Lymantriidae) egg mass distributions. *Environ. Entomol.* **18**, 840-843.
- Bess, H. A. (1936). The biology of *Leschenaultia exul* Townsend, a tachinid parasite of *Malacosoma americana* Fabricius and *Malacosoma disstria* Hübner. *Ann. Entomol. Soc. Am.* **29**, 593-613.
- Campbell, R. W. (1973). Numerical behavior of a gypsy moth population system. *For. Sci.* **19**, 162-167.
- Clarke, E. C. (1958). Ecology of the polyhedrosis of tent caterpillars. *Ecology* **39**, 132-139.
- Edwards, P. J., May, R. M., and Webb, N. R. (1993). "Large-Scale Ecology and Conservation Biology." Blackwell, Oxford.

- Hodson, A. C. (1939). *Sarcophaga aldrichi* Parker as a parasite of *Malacosoma disstria* Hbn. *J. Econ. Entomol.* **32**, 396–401.
- Kareiva, P. (1987). Habitat fragmentation and the stability of predator–prey interactions. *Nature (London)* **326**, 388–390.
- Kaupp, W. J., and Ebling, P. M. (1993). Horseradish peroxidase-labelled probes and enhanced chemiluminescence to detect baculoviruses in gypsy moth and eastern spruce budworm larvae. *J. Virol. Methods* **44**, 89–98.
- Kruess, A., and Tscharntke, T. (1994). Habitat fragmentation, species loss, and biological control. *Science* **264**, 1581–1584.
- Landis, D. A., and Haas, M. J. (1992). Influence of landscape structure on abundance and within-field distribution of European corn borer (Lepidoptera: Pyralidae) larval parasitoids in Michigan. *Environ. Entomol.* **21**, 409–416.
- McCullagh, P., and Nelder, G. A. (1989). "Generalized Linear Models." Chapman & Hall, London.
- Mott, D. G. (1963). The forest and the spruce budworm. *Mem. Entomol. Soc. Can.* **31**, 189–202.
- Myers, J. H. (1993). Population outbreaks in forest Lepidoptera. *Am. Sci.* **81**, 240–251.
- Roland, J. (1993). Large-scale forest fragmentation increases the duration of forest tent caterpillar outbreak. *Oecologia* **93**, 25–30.
- Royama, T. (1984). Population dynamics of the spruce budworm *Choristoneura fumiferana*. *Ecol. Monogr.* **54**, 429–462.
- Ryan, R. B. (1990). Evaluation of biological control: Introduced parasites of larch casebearer (Lepidoptera: Coleophoridae) in Oregon. *Environ. Entomol.* **19**, 1873–1881.
- Sippell, W. L. (1957). A study of the forest tent caterpillar *Malacosoma disstria* Hbn., and its parasite complex on Ontario. Ph.D. Thesis, University of Michigan, Ann Arbor.
- Sippell, W. L. (1962). Outbreaks of the forest tent caterpillar, *Malacosoma disstria* Hbn., a periodic defoliator of broad-leaved trees in Ontario. *Can. Entomol.* **94**, 408–416.
- Stairs, G. R. (1966). Transmission of virus in tent caterpillar populations. *Can. Entomol.* **98**, 1100–1104.
- Taylor, P. D., Fahrig, L., Hencin, K., and Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos* **68**, 571–573.
- Varley, G. G., and Gradwell, G. R. (1968). Populations models for the winter moth. In "Insect Abundance" (T. R. E. Southwood, ed.), pp. 132–142. Blackwell, Oxford.
- Wilcove, D. S., McLellan, C. H., and Dobson, A. P. (1986). Habitat fragmentation in the temperate zone. In (M. E. Soulé, ed.) "Conservation Biology: The Science of Scarcity and Diversity" Sinauer Assoc., Sunderland, MA.
- Witter, J. A., and Kulman, H. M. (1979). The parasite complex of the forest tent caterpillar in northern Minnesota. *Environ. Entomol.* **8**, 723–731.