

# FOREST STRUCTURE AND THE SPATIAL PATTERN OF PARASITOID ATTACK

7

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## 7.1 INTRODUCTION

The study of forest insect population dynamics has taken three general approaches: (1) long-term intensive study of population processes at a single site, such as that of the winter moth (Varley and Gradwell, 1960); (2) shorter-term study of several widely scattered sites, such as those of the gypsy moth (Campbell and Sloan, 1977); and (3) the monitoring of population response to experimental manipulation of abundance – for example, that of the gypsy moth (Gould *et al.*, 1990).

In the first approach, the impact of population processes such as fecundity, parasitism and predation are estimated over time as population densities rise and fall. The result is detailed knowledge of processes at that particular site, but generalization to other populations is difficult as it is not known how representative the results are of dynamics at a larger spatial scale. In addition, because only a single site is studied, the impact of processes such as dispersal can only be inferred from changes in density not explained by fecundity and mortality (e.g. Royama, 1984).

In the second approach, general population patterns are inferred from a composite of the dynamics at multiple sites. For example, Liebhold (1992) demonstrated double-equilibrium dynamics for gypsy moth populations on patterns of population change pooled from 83 widely separated populations. The assumption of this type of analysis is that populations at all sites pass through similar tra-

jectories of density, fecundity and mortality. Although such studies are able to account for some of the variation in dynamics seen among sites, they obscure fine-scale processes acting at any one of them. This is perhaps not surprising as local dynamics will differ depending on site characteristics and the status of neighbouring populations. If multiple study sites are spaced widely enough for density estimates to be independent, there is no opportunity to estimate one of the most important processes influencing population dynamics – that of movement. Being able to estimate movement between two adjacent sites (a desirable goal in any population study) means by definition that the two are not independent of each other.

The third approach uses experimental manipulation of abundance and it measures the response to this manipulation by processes such as attack by natural enemies (e.g. Gould *et al.*, 1990; Ferguson *et al.*, 1994). These studies are powerful in evaluating the impact of population processes locally but, as their authors point out, their drawback is the limited spatial scale (typically < 1 ha) at which the manipulations are logistically feasible. For example, if host increase normally occurs over a large spatial scale rather than in small foci (eg. Liebhold and McManus 1991), then parasitoids would not aggregate in response to variation in host abundance (because there is very little variation at the scale over which a parasitoid would search); the experimental creation of a 'hot spot' of host abun-

dance might give a false indication of the strength of the parasitoid response.

An understanding of forest insect dynamics at a large scale, and which takes into account habitat variability, habitat configuration and movement of both herbivores and natural enemies, might best be done using a landscape approach.

## 7.2 A LANDSCAPE APPROACH

In addition to the methods described above, a landscape approach to population dynamics examines the way in which fine-scale processes such as parasitism, predation and disease transmission are affected by landscape structure at the local scale (the scale at which individual insects move over their lifetime) and at the regional scale (the scale of populations rather than of individuals). This is different from traditional studies of habitat use which are done at the stand level without concern for factors such as stand adjacency and the configuration of the mosaic of stands. Analytical tools such as spatial statistics and geographical information systems (GIS) make a landscape approach more feasible. Rather than analysing processes at each site independently, analyses can include effects of each variable at different spatial scales (Heads and Lawton, 1983), the effect of stand adjacency, dynamics of nearby populations (Liebhold and Elkinton, 1989), and of habitat connectivity (Taylor *et al.*, 1993). By studying populations that are close to each other (within the movement range of the host and its natural enemies) there is the added potential for insights into the importance of movement between subpopulations. Discovery of plants by herbivores (Solbreck, 1995), discovery of hosts and aggregation by parasitoids and predators (Heads and Lawton, 1983; Kareiva, 1987) and transmission of disease through host populations (Dwyer, 1992) all depend on movement of organisms.

Spatial patterns of mortality have been studied for many insects, but with very few exceptions (e.g. Liebhold and Elkinton, 1989) such analyses are done in a purely statistical manner. For example, the response of parasitoids to host density is assessed by the use of regression analysis (Walde

and Murdoch, 1988; Stiling, 1988; Dempster, 1983), but no consideration is given to the spatial pattern over which host abundance varies. When gypsy moth populations were sampled intensively over a grid of census points with 25–50 m resolution (Liebhold and Elkinton, 1989), densities were found to be highly variable both among sites and between the different life stages. Unfortunately the patterns of mortality and movement which might have caused these changes in densities were not recorded. A spatially process-oriented view of predation and parasitism is useful because the ability of natural enemies to respond to host abundance is governed in part by their ability to move through a mosaic of different habitats in both agricultural (Kareiva, 1987; Kruess and Tschamtkke, 1994) and forested (Rogers and Williams, 1993) landscapes. Such fine-scale effects of habitat on natural enemy movement have been argued as one reason for the obscuring of density-dependent patterns of mortality when averaged over a larger area (Hassell, 1985; Liebhold and Elkinton, 1989), and for the preponderance of density-vague regulation of populations (Strong, 1986).

Laboratory studies (Huffaker, 1958) and very fine-scale field studies (Kareiva, 1987; Kruess and Tschamtkke, 1994) have examined the effect of habitat structure on dynamics. The importance of habitat structure in each of these fine-scale studies is through its effect in altering movement of the host or predator. Despite several fine-scale examples of altered predator–prey dynamics, Taylor (1991) has pointed out that there are virtually no examples of large-scale effect of habitat structure on predator–prey systems.

## 7.3 HOW CAN LANDSCAPE AFFECT FOREST INSECT POPULATIONS?

### 7.3.1 FECUNDITY

Fecundity of forest insects can be affected by landscape either directly, by distribution of hosts plants, or by the effect of landscape on plant quality. Examples include the effect of the incidence of flower cones on jackpine budworm

(*Choristoneura pinus pinus* Freeman), which tends to be much higher along forest margins than in forest interior (Vince Nealis, Canadian Forest Service, Sault Ste Marie, Ontario, personal communication) and which strongly affects larval growth and survival. The result of this pattern is that margins of jackpine stands adjacent to clearings often have higher density of *C. pinus* and more severe defoliation.

### 7.3.2 MORTALITY

Parasitism is spatially variable and (for species attacking forest defoliators) can be affected by physical structure of the forest. For example, *Compsilura concinnata* (Mg.) parasitizes hosts at a lower rate on isolated trees than on trees in large clumps (Schwenke, 1958). The egg parasitoid *Ooencyrtus kuwanai* (Howard) attacks host egg masses at a higher rate in stand interiors than near or in clearings. Parasitism of forest tent caterpillar cocoons by *Arachnidomyia aldrichi* is lower at the forest edge along lake margins than in the forest interior (Batzler, 1955). The opposite pattern is seen for the chalcid wasp *Brachymeria intermedia* (Nees), which attacks gypsy moth at a greater rate in open sunny areas than in shaded areas (Leonard, 1971). Part of the explanation for these spatial patterns result from microclimatic preferences of the attacking parasitoids, particularly with respect to humidity and insolation (Weseloh, 1976). These two variables exhibit strong gradients along forest edges to a distance of up to 100 m into the forest. Such fine-scale behavioural patterns of natural enemies, when combined with regional patterns of forest structure, could have dramatic effects on regional herbivore dynamics. For example, egg masses of the gypsy moth tend to be more abundant along forest edges compared with the forest interior (Bellinger *et al.*, 1989), as are the eggs of some butterfly species (Courtney and Courtney, 1982). The effect of such an increase in spatial variation in abundance might affect the ability of natural enemies to discover hosts because they are more patchily distributed; or local high abundance could swamp natural enemies, thereby reducing rates of attack per individual.

### 7.3.3 MOVEMENT

Rates of movement of herbivores (Turchin, 1991; Crist and Wiens, 1995; Chapter 18, this volume), predators (Taylor and Merriam, 1995), parasites (Rogers and Williams, 1993; Sheppard, 1994) and other insect natural enemies (Landis and Haas, 1992) can all be limited (or enhanced) by the spatial configuration of habitat mosaic. Some population models have shown that differential dispersal of host and parasitoid create very different dynamics (Reeve, 1988; Hassell *et al.*, 1991). For example, enhanced dispersal of the host can permit 'escape' from its natural enemies even if the latter are effective in suppressing the host locally once it is discovered. Fine-scale empirical studies, both in the laboratory (Huffaker, 1958) and in the field (Kareiva, 1987; Kruess and Tscharntke, 1994) clearly show that habitat structure can affect the movement of herbivores relative to that of their natural enemies and as a result affect dynamics of both.

## 7.4 FOREST FRAGMENTATION AND THE DYNAMICS OF FOREST TENT CATERPILLAR

The forest tent caterpillar, *Malacosoma disstria* Hbnr., is one of the dominant forest defoliators in the boreal forests of North America. Populations exhibit periodic outbreaks over large areas of boreal forest with a frequency of 9–14 years (Sippell, 1962; Daniel, 1990; Myers, 1993). Forest tent caterpillars are subject to parasitism by a suite of parasitoid species. The same parasitoid species are dominant in Ontario (Sippell, 1957), Minnesota (Witter and Kulman, 1972, 1979) and Alberta (Parry, 1995). The two most dominant parasitoids are the tachinid fly *Patelloa pachyppyga* and the sarcophagid fly *Arachnidomyia aldrichi*. *P. pachyppyga* oviposits on caterpillar-damaged trembling aspen foliage, and the eggs are subsequently ingested by the feeding host caterpillar. The fully fed maggot emerges after the host has spun a cocoon in foliage. In contrast to the tachinid, *A. aldrichi* lays eggs directly on the host cocoon. Fully developed *A. aldrichi* maggots emerge well after the host has pupated (Hodson, 1939). Although there are phenological differences in the timing of attack by each of

these species (Sippell, 1957; Parry, 1995), they are both abundant in collections of recently formed pupae. Rates of parasitism by *A. aldrichi* have been recorded as being the same in the canopy and understorey (Sippell, 1957), or higher in the understorey (Parry, 1995). There is no consistent difference in parasitism by *P. pachypyga* in the canopy vs. the understorey (Parry, 1995).

In at least parts of its range, the forest tent caterpillar exhibits longer outbreaks in forests that have been fragmented because of clearing, compared with outbreaks in continuous forests (Roland, 1993). Among individual townships (100 km<sup>2</sup> each), for each additional kilometre of forest edge per km<sup>2</sup> (as a measure of fragmentation) outbreaks last about a year longer (Roland, 1993). Because viral epizootics (Stairs, 1966; Clark, 1958; Myers, 1993) and parasitism (Sippell, 1957; Witter and Kulman, 1979; Parry, 1995) are strongly implicated in causing population collapse, the altered dynamics seen in fragmented forests may result from the interaction between one or both of these sources of mortality and habitat structure (Roland, 1993; Roland and Kaupp, 1995; Roland and Taylor, 1995, 1997).

We have studied both variation in tent caterpillar abundance and variation in the processes that affect abundance in a current outbreak of forest tent caterpillar near Edmonton, Alberta, Canada. This work is done at two spatial scales. The first is a fine-scale grid of 107 population sample points (Figure 7.1) with 50 m spacing between adjacent sites over an area of 32 ha. This grid is characterized by mixed trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) averaging about 13 m in height. The grid has a large clearing along the south edge, and three smaller clearings around water bodies within the grid. A larger grid (420 km<sup>2</sup>) of 127 sample points with 1.8 km spacing between adjacent points was also sampled (see map in Roland and Taylor, 1995) but is not discussed here. In this chapter we present preliminary results on the fine-scale effect of forest structure on the spatial pattern of parasitism of this forest defoliator.

#### 7.4.1 METHODS AND MATERIALS

Abundance of tent caterpillar and parasitism by *P. pachypyga* and *A. aldrichi* were estimated from

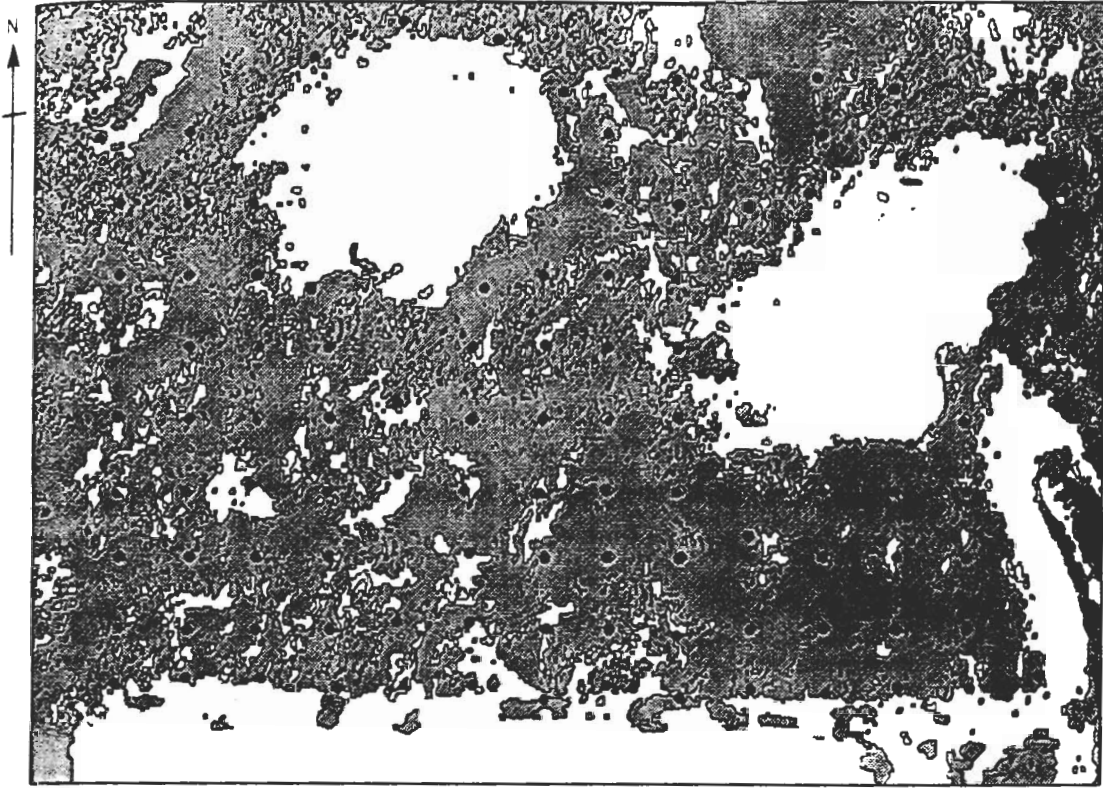
cocoons collected between June 28 and July 4, 1995, at each of the 107 sampling sites. Abundance was estimated from timed collections of cocoons from the understorey; the time taken to collect 50 cocoons, to a maximum of 15 minutes, was recorded. If 50 cocoons were collected in less than 15 minutes then the number which would have been collected in 15 minutes was estimated. Additional cocoons were collected at each site to improve the estimates of parasitism. The number of *P. pachypyga* and *A. aldrichi* produced from each collection was counted and the rate of parasitism was estimated for each of the 107 sites. For each parasite species, the effect of host density (log-transformed) and two landscape features were used as explanatory variables in a multiple regression of parasitism (arc-sine square-root transformed). The two landscape features were: (1) the amount of forest within 100 m of each site and (2) the amount of forest edge per unit forest (expressed as km/km<sup>2</sup>) within 100 m of each site. Landscape features were estimated from a classified air-photo mosaic made from 1:20 000 scale false-colour infra-red photography of the 420 km<sup>2</sup> study. The digitally scanned version of this mosaic had a resolution of 5 m per pixel. Landscape features around each population sample point were estimated using SPANS geographical information system software (Intera Tydac Technologies, 1993).

In addition to the grid studies described above, earlier studies at Kakabeka Falls, Ontario, in 1992 estimated percentage parasitism along transects from forest edge to forest interior. Collections of late larvae (for tachinid parasites) and cocoons (for *A. aldrichi*) were made at intervals from the forest edge (0 m) to 130 m into the forest along four separate transects. Rates of parasitism were estimated. Proportions were arc-sine square-root transformed and analysed using analysis of covariance with transect as a main factor and distance into the forest as a covariate.

#### 7.4.2 RESULTS

##### (a) *Patelloa pachypyga*

Parasitism by *P. pachypyga* varied from 0 to 89% across the grid. Parasitism increased with host



**Figure 7.1** Grid of population sample points in aspen forests near Cooking Lake, Alberta. Stippled areas, aspen forest; white areas, clearings. Sample points are separated by approximately 50 m.

abundance, but was more strongly influenced by the amount of forest at each collection site (Table 7.1). Tent caterpillars at sites surrounded by large forest stands exhibited higher rates of parasitism by *P. pachygyga* compared with sites with more fragmented forests. Across the grid, *P. pachygyga* caused greater rates of parasitism in the central large section of forest and reduced rates along the large forest edge at the south end of the study area and around the three large clearings at the ponds (Figures 7.1 and 7.2a). This pattern of reduced parasitism with increased forest edge is consistent with fine-scale transect studies of parasitism by tachinids in Ontario boreal forest (Figure 7.3), and in Alberta forests (Parry, 1994) where rates of parasitism were lower within 50 m of the forest edge compared with that in the forest interior. Similarly, large-scale patterns of parasitism by *Patelloa* in

Alberta in 1994 (Roland and Taylor, 1995) showed reduced tent caterpillar parasitism by *P. pachygyga* in fragmented forests compared with that in continuous forests.

#### **(b) *Arachnidomyia aldrichi***

Parasitism by the sarcophagid fly *A. aldrichi* varied across the grid from 0 to 73%. As with *P. pachygyga*, parasitism by *A. aldrichi* increased with increase in host density. Unlike the tachinid, however, there was no effect of forest structure across the grid on rates of parasitism by *A. aldrichi* (Table 7.2); parasitism was similar (Figure 7.2b) regardless of the amount of forest around each point, and regardless of the amount of forest edge. There was no significant reduction in parasitism along the large forest edge at the south end of the study area

**Table 7.1** Multiple regression analysis for rate of parasitism (arc-sine square-root transformed) by the tachinid fly *Patelloa pachypyga* as a function of host density (log-transformed), amount of forest (km<sup>2</sup>) within 100 m, and km of forest edge per km<sup>2</sup> within 100 m of each of 107 sample points in the grid ( $r^2 = 0.17$ )

Variable	Coefficient	t-Value	P
Host density (log)	0.138	2.469	0.015
Forest	0.429	2.199	0.030
Edge/km <sup>2</sup> of forest	-0.001	-0.145	0.885

nor along the edges of the forest adjacent to ponds (Figures 7.1 and 7.2b). Transects from the forest interior to the forest edge (at sites in Ontario) showed no reduction in *A. aldrichi* parasitism (Figure 7.4), unlike the reduction seen for *P. pachypyga*. These patterns are consistent with larger-scale patterns of parasitism by *A. aldrichi* (Roland and Taylor, 1995) which were unrelated to the degree of forest fragmentation.

#### 7.4.3 DISCUSSION

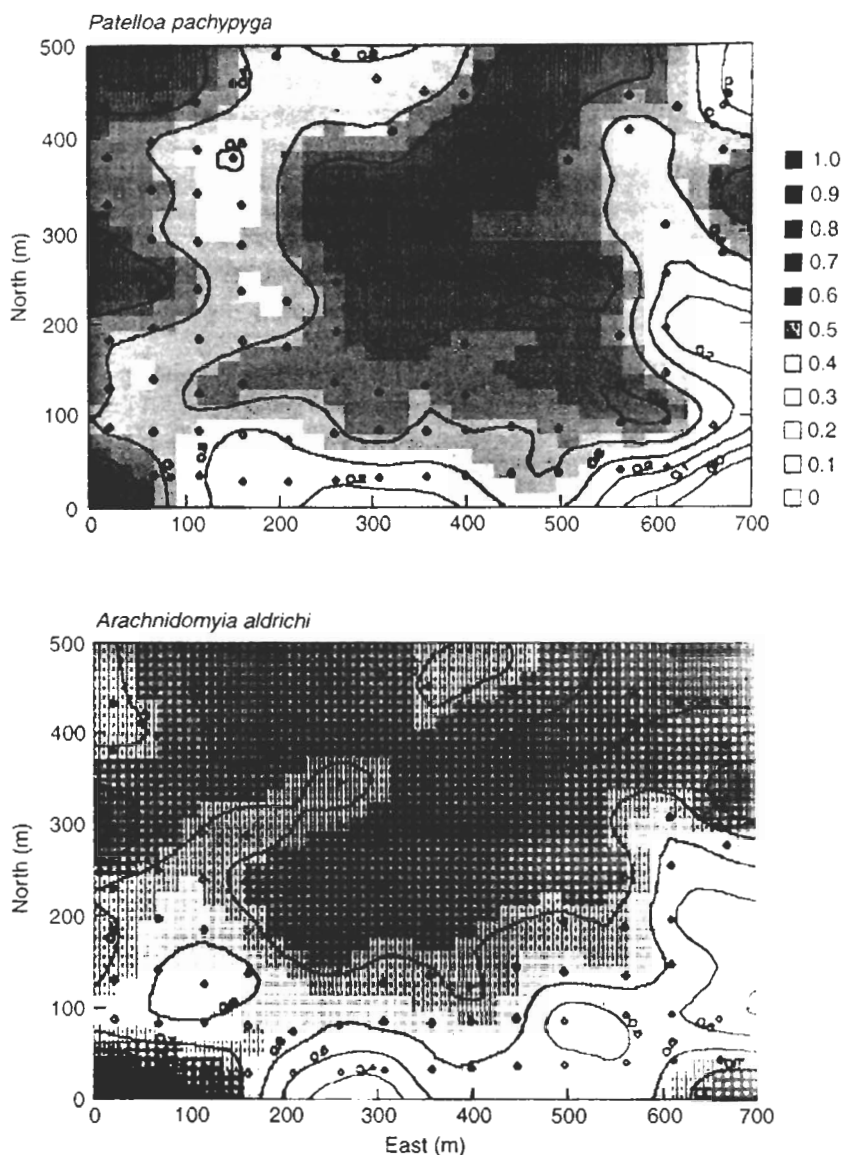
Two dominant parasitoids attacking forest tent caterpillar during population decline are the sarcophagid fly *Arachnidomyia aldrichi* and the tachinid fly *Patelloa pachypyga*. These two species dominate tent caterpillar populations in Ontario (Sippell, 1957), Minnesota (Witter and Kulman, 1979; Hodson, 1939), and in much of Alberta (Parry, 1995). *P. pachypyga* is less efficient in attacking tent caterpillar in forests that are fragmented than in continuous forests. It is not known whether this pattern results from habitat preferences by this fly or from altered search behaviour at the forest edge compared with in the

forest interior. Other tachinids, such as *Compsilura concinnata* (Mg.) attacking the noctuid *Acronycta aceris* L., also exhibit reduced parasitism on individual trees and higher parasitism in clumps of trees (Schwenke, 1958). The egg parasitoid *Ooencyrtus kuwanai* (Howard) caused higher rates of parasitism in forest interiors than in or adjacent to clearings (Weseloh, 1972). Part of the explanation for high parasitism in forest interiors has been attributed to the effect of microclimate preferences of the parasitoids (Weseloh, 1976). Preference by *Ooencyrtus kuwanai* for cool humid conditions result in its abundance in the forest interior and scarcity along forest edges and in open forests (Weseloh, 1976). The opposite pattern – preference for warm dry microclimates – has been documented for other species (Weseloh, 1976), a pattern which is likely to result in higher host parasitism along forest edges than in the forest interior.

Longer outbreaks of forest tent caterpillar in fragmented forests may in part be the result of reduced abundance or reduced efficiency of at least part of the parasitoid community. In addition to parasitism, population processes such as virus

**Table 7.2** Multiple regression analysis for rate of parasitism (arc-sine square-root transformed) by the sarcophagid fly *Arachnidomyia aldrichi* as a function of host density (log-transformed), amount of forest (km<sup>2</sup>) within 100m, and km of forest edge per km<sup>2</sup> within 100 m of each of 107 sample points in the grid ( $r^2 = 0.22$ )

Variable	Coefficient	t-Value	P
Host density (log)	0.252	5.195	0.000
Forest	0.166	0.992	0.323
Edge/km <sup>2</sup> of forest	0.001	0.795	0.428

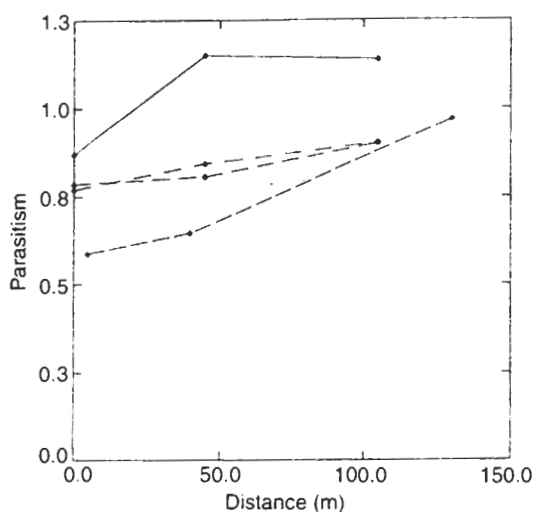


**Figure 7.2** Spatial pattern of parasitism by (a) tachinid fly *Patelloa pachypyga* and (b) sarcophagid fly *Arachnidomyia aldrichi* across 32 ha grid. Smoothed estimates are distance-weighted least squares. (Wilkinson *et al.*, 1992.)

transmission, may be reduced along forest edges (Roland and Kaupp, 1995).

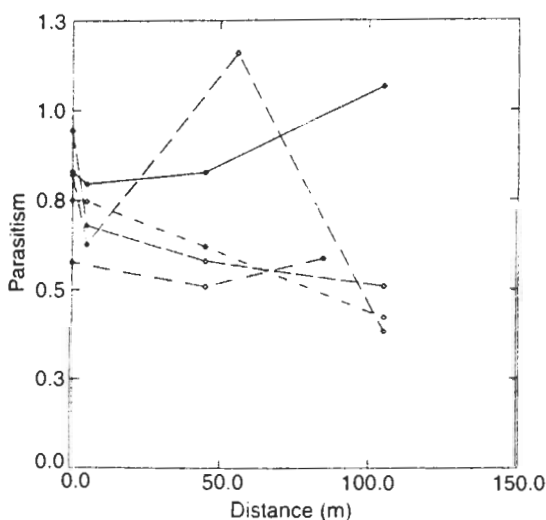
Other forest insect species appear to exhibit landscape-dependent dynamics. Mott (1963) noted that population outbreaks of spruce budworm were

more severe in large forests than in those which were fragmented. Similarly, the western spruce budworm, *Choristoneura occidentalis* Freeman, shows more severe, longer-lasting and more synchronous outbreaks in the southwestern United



**Figure 7.3** Parasitism by tachinids along four transects from forest edge to forest interior (in metres from edge) at Kakabeka Falls, Ontario, 1992 ( $N = 25$  larvae per point). Parasitism is reduced near forest edge ( $F = 19.63$ ,  $P = 0.003$ ).

States, over the same period that forests have become more contiguous (a result of favourable



**Figure 7.4** Parasitism by *Arachnidomyia aldrichi* along four transects from forest edge to forest interior (in metres from edge) at Kakabeka Falls, Ontario, 1992 ( $N = 100$  cocoons per point). There is no effect of distance on parasitism ( $F = 1.57$ ,  $P = 0.232$ ).

climate and fire suppression) (Swetnam and Lynch 1993). The two budworm species show a pattern opposite to that for forest tent caterpillar, suggesting that although landscape may be an important component of forest insect dynamics, the patterns of interaction between population process and landscape are likely to be species dependent.

The data presented here were collected in a single year of widespread host abundance. The real impact of reduced parasitism in fragmented forests will not be evident until the current outbreak begins to collapse. As the outbreak declines it is predicted that pockets of outbreak should linger in the more fragmented parts of the 420 km<sup>2</sup> study area, and should decline more rapidly in the contiguous forests. Lingering pockets of tent caterpillar in fragmented forests would be predicted to be parasitized at a lower rate than in comparable pockets in continuous forests. Preliminary results here suggest that this may be most strongly manifested through parasitism by tachinids. We feel that large-scale spatial studies of population processes, interacting with habitat, carried out over the course of population rise and collapse will provide valuable insight into the role of natural enemies on host dynamics.

## REFERENCES

- Batzer, H.O. (1955) Some effects of defoliation of aspen, *Populus tremuloides* Michx., stands in northern Minnesota by the forest tent caterpillar, *Malacosoma disstria* Hbn., with notes on parasitism of cocoons by *Sarcophaga aldrichi* Park, and cocooning habits of the host. MSc Thesis, University of Minnesota, St Paul, 66 pp.
- Bellinger, R.G., Ravlin, F.W. and McManus, M.L. (1980) Forest edge effects and their influence on gypsy moth (Lepidoptera: Lymantriidae) egg mass distributions. *Environmental Entomology* **18**, 840–843.
- Campbell, R.W. and Sloan, R.J. (1977) Natural regulation of innocuous gypsy moth populations. *Environmental Entomology* **6**, 315–322.
- Clark, E.C. (1958) Ecology of the polyhedrosis of tent caterpillars. *Ecology* **39**, 132–139.
- Courtney, S.P. and Courtney, S. (1982) The 'edge-effect' in butterfly oviposition: causality in *Anthocharis cardamines* and related species. *Ecological Entomology* **7**, 131–137.



- Crist, T.O. and Wiens, J.A. (1995) Individual movements and estimation of population size in darkling beetles (Coleoptera: Tenebrionidae). *Journal of Animal Ecology* **64**, 733–746.
- Daniel, C.J. (1990) Climate and outbreaks of the forest tent caterpillar in Ontario. MSc Thesis, University of British Columbia, Vancouver.
- Dempster, J.P. (1983) The natural control of butterflies and moths. *Biological Reviews* **58**, 461–481.
- Dwyer, G. (1992) On the spatial spread of insect pathogens: theory and experiment. *Ecology* **73**, 479–494.
- Ferguson, C.S., Elkinton, J.S., Gould, J.R. and Wallner, W.E. (1994) Population regulation of gypsy moth (Lepidoptera: Lymantriidae) by parasitoids: does spatial density dependence lead to temporal density dependence? *Environmental Entomology* **23**, 1155–1164.
- Gould, J.R., Elkinton, J.S. and Wallner, W.E. (1990) Density dependent suppression of experimentally created gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), populations by natural enemies. *Journal of Animal Ecology* **59**, 213–234.
- Hassell, M.P. (1985) Insect natural enemies as regulating factors. *Journal of Animal Ecology* **54**, 323–334.
- Hassell, M.P., Comins, H.N. and May, R.M. (1991) Spatial structure and chaos in insect population dynamics. *Nature* **353**, 255–258.
- Heads, P.A. and Lawton, J.H. (1983) Studies on the natural enemy complex of the holly leaf-miner: the effects of scale on the detection of aggregative responses and the implications for biological control. *Oikos* **40**, 267–276.
- Hodson, A.C. (1939) *Sarcophaga aldrichi* Parker as a parasite of *Malacosoma disstria* Hbn. *Journal of Economic Entomology* **32**, 396–401.
- Huffaker, C.B. (1958) Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* **27**, 343–383.
- Intera Tydac Technologies (1993) *SP4.VS GIS Reference Manual*, Intera Tydac Technologies, Nepean, Ontario.
- Kareiva, P. (1987) Habitat fragmentation and the stability of predator-prey interactions. *Nature* **326**, 388–390.
- Kruess, A. and Tschamtkke, 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. *Environmental Entomology* **21**, 409–416.
- Leonard, D.E. (1971) *Brachymeria intermedia* (Hymenoptera: Chalcidae) parasitizing gypsy moth in Maine. *Canadian Entomologist* **103**, 654–656.
- Liebholt, A.M. (1992) Are North American populations of gypsy moth (Lepidoptera: Lymantriidae) bimodal? *Environmental Entomology* **21**, 221–229.
- Liebholt, A.M. and McManus, M.L. (1991) Does larval dispersal cause the expansion of gypsy moth outbreaks? *Northern Journal of Applied Forestry* **8**, 95–98.
- Liebholt, A.M. and Elkinton, J.S. (1989) Use of multi-dimensional life tables for studying insect population dynamics. In *Estimating Insect Populations* (eds L. McDonald, B. Manly, J. Lockwood and J. Logan) pp. 360–369. Springer-Verlag, Berlin.
- Mott, D.G. (1963) The forest and the spruce budworm. In *The Dynamics of Epidemic Spruce Budworm Populations* (ed. R.F. Morris) *Memoirs of the Entomological Society of Canada* **31**, 189–202.
- Myers, J.H. (1993) Population outbreaks in forest Lepidoptera. *American Scientist* **81**, 240–251.
- Parry, D. (1994) The impact of predators and parasitoids on natural and experimentally created populations of forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae). MSc Thesis, University of Alberta, 91 pp.
- Parry, D. (1995) Larval and pupal parasitism of the forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), in Alberta, Canada. *Canadian Entomologist* **127**, 877–893.
- Reeve, J. (1988) Environmental variability, migration, and persistence in host-parasitoid systems. *American Naturalist* **132**, 810–835.
- Rogers, D.J. and Williams, B.G. (1993) Monitoring trypanosomiasis in space and time. *Parasitology* **106**, S77–S92.
- Roland, J. (1993) Large-scale forest fragmentation increases the duration of tent caterpillar outbreaks. *Oecologia* **93**, 25–30.
- Roland, J. and Kaupp, W.J. (1995) Reduced transmission of forest tent caterpillar NPV at the forest edge. *Environmental Entomology* **24**, 1175–1178.
- Roland, J. and Taylor, P.D. (1995) Herbivore-natural enemy interactions in fragmented and continuous forests. In *Population Dynamics: New Approaches and Synthesis* (eds N. Cappuccino and P.W. Price), pp. 195–208. Academic Press, San Diego.
- Roland, J. and P.D. Taylor (1997) Insect parasitoid species respond to forest structure at different spatial scales. *Nature* **386**, 710–713.
- Royama, T. (1984) Population dynamics of the spruce budworm *Choristoneura fumiferana*. *Ecological Monographs* **54**, 429–462.
- Schwenke, W. (1958) Local dependence of parasitic insects and its importance for biological control. *Proceedings of the Tenth International Congress of Entomology* **4**, 851–854.

- Sheppard, D.C. (1994) Dispersal of wild-captured, marked horn flies (Diptera: Muscidae). *Environmental Entomology* **23**, 29–34.
- Sippell, W.L. (1957) A study of the forest tent caterpillar *Malacosoma disstria* Hbn., and its parasite complex in Ontario. PhD Thesis, University of Michigan, Ann Arbor. 147 pp.
- Sippell, W.L. (1962) Outbreaks of the forest tent caterpillar, *Malacosoma disstria* Hbn., a periodic defoliator of broad-leaved trees in Ontario. *Canadian Entomologist* **94**, 408–416.
- Solbreck, C. (1995) Long-term population dynamics of a seed-feeding insect in a landscape perspective. In *Population Dynamics: New Approaches and Synthesis* (eds N. Cappuccino and P.W. Price), pp. 279–301. Academic Press, San Diego.
- Stairs, G.R. (1966) Transmission of virus in tent caterpillar populations. *Canadian Entomologist* **98**, 1100–1104.
- Stiling, P. (1988) Density-dependent processes and key factors in insect populations. *Journal of Animal Ecology* **57**, 581–593.
- Strong, D.R. (1986) Density-vague population change. *Trends in Ecology and Evolution* **1**, 39–42.
- Swetnam, T.W. and Lynch, A.M. (1993) Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs* **63**, 399–424.
- Taylor, A. (1991) Studying metapopulation effects in predator-prey systems. In *Metapopulation Dynamics: Empirical and Theoretical Investigations*, pp. 305–323. Academic Press, London.
- Taylor, P.D. and Merriam, G. (1995) Wing morphology of a forest damselfly is related to landscape structure. *Oikos* **73**, 43–48.
- Taylor, P.D., Fahrig, L., Henein, K. and Merriam, G. (1993) Connectivity is a vital element of landscape structure. *Oikos* **68**, 571–573.
- Turchin, P. (1991) Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* **72**, 1253–1266.
- Varley, G.C. and Gradwell, G.R. (1960) Key factors in population studies. *Journal of Animal Ecology* **45**, 313–325.
- Walde, S.J. and Murdoch, W.W. (1988) Spatial density dependence in parasitoids. *Annual Review of Entomology* **33**, 441–466.
- Weseloh, R.M. (1972) Spatial distribution of gypsy moth (Lepidoptera: Lymantriidae) and some of its parasitoids within a forest environment. *Entomophaga* **17**, 339–351.
- Weseloh, R.M. (1976) Behavior of forest insect parasitoids. In *Perspectives in Forest Entomology* (eds J.F. Anderson and H.K. Kaya), pp. 99–110. Academic Press, New York.
- Wilkinson, L., Hill, M., Miceli, S. *et al.* (1992) *SYSTAT for Windows: Graphics, Version 5 Edition*. Evanston, Illinois. 636 pp.
- Witter, J.A. and Kulman, H.M. (1972) A review of the parasites and predators of tent caterpillars (*Malacosoma* spp.) in North America. *Minnesota Agriculture Experimental Station, Technical Bulletin* **289**, 48 pp.
- Witter, J.A. and Kulman, H.M. (1979) The parasite complex of the forest tent caterpillar in northern Minnesota. *Environmental Entomology* **8**, 723–731.