

Insect parasitoid species respond to forest structure at different spatial scales

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There is now a solid body of theoretical work^{1–4} demonstrating that the spatial structure of the habitat combined with animal movement strongly influence host–parasitoid dynamics. The spatial pattern over which parasitoid search takes place can be affected by the distribution of the hosts⁵, by the spatial arrangement of the host's habitat⁶ and by the spatial scale at which the parasitoid perceives variation in host abundance^{7,8}. Empirical work, however, has been largely restricted to small-scale field studies of less than one hectare^{6,9} with very few larger^{10,11}. Here we report initial results of a many-year, large-scale study that is among the first to examine the interaction between a population-level process (parasitism) and anthropogenic forest fragmentation at large and at multiple spatial scales. We demonstrate that parasitism by four species of parasitoids attacking the forest tent caterpillar, *Malacosoma disstria*, is significantly reduced or enhanced depending on the proportion of forested to unforested land. Each of the parasitoid species responds to this mosaic at four different spatial scales that correspond to their relative body sizes. Our data give empirical support to the argument that changes in landscape structure can alter the normal functioning of ecological processes such as parasitism, with large-scale population consequences^{3,4}.

We determined the effect of forest structure (mosaic of cleared and forested land) on the rates of parasitism caused by four species of parasitic fly attacking an outbreak population of the forest tent caterpillar (*Malacosoma disstria*) in aspen forests near Edmonton, Alberta, Canada. Studies were done on a large-scale grid 420 km² in area (127 sample points) and a small-scale grid of 0.32 km² area (109 sample points) nested within the larger grid. At each sample point we estimated host population density, rates of parasitism caused by each species, and forest structure. Forest structure around each point was estimated at seven scales, from 53 m around each point up to 3,400 m.

Univoltine fly parasitoids dominate the parasitoid community that attacks forest tent caterpillar^{12–14}. The four species we studied ranged in size from 34 mg for *Carcelia malacosomae* (Tachinidae) which attack host larvae directly, 41 mg for *Patelloa pachygyga* and 68 mg for *Leschenaultia exul* (Tachinidae) which lay eggs on foliage that are subsequently ingested by feeding host caterpillars, and 58 mg for *Arachnidomyia* (= *Sarcophaga*) *aldrichi* (Sarcophagidae) which larviposits on host cocoons. The three largest of these species are considered important in suppressing tent caterpillar outbreaks^{12–14}. Because larvae of all of these flies develop in the late larval and pupal stage of the host there is some competition among them. *A. aldrichi* attacks host pupae and is the last of the four to attack during the host's life cycle. Therefore, it competes with *C. malacosomae* and especially with *P. pachygyga* which remain within the host into the host's pupal stage^{12–14}. Larvae of *L. exul* exit before host pupation and are therefore affected little by competition with *A. aldrichi*¹⁴.

Parasitism by all species varied markedly across the study area (Fig. 1) in response to both forest structure and the abundance of hosts (Table 1). Parasitism by the three largest fly species was

greatest on hosts collected in contiguous forests, and was lower in those from fragmented forests (Table 1; positive coefficients reflect greater parasitism in contiguous forest). However, the spatial scale at which forest structure had its greatest effect differs among the parasite species. Parasitism by the largest species, *L. exul*, was most strongly correlated with forest structure measured at a scale of 850 m around each site. Parasitism by medium-sized flies *A. aldrichi* and *P. pachygyga* was most strongly related to forest structure within 425 m and 212 m, respectively. They caused less parasitism in the areas of greatest forest fragmentation (Fig. 1) and along large forest edges (Fig. 2). In contrast, the smallest fly, *C. malacosomae*, caused higher rates of parasitism in the fragmented forests (Fig. 1) and at forest edges (Fig. 2), and was affected by forest structure at the finest spatial scale (53 m). Parameter estimates for the effects of forest structure were not significantly different when estimated from data

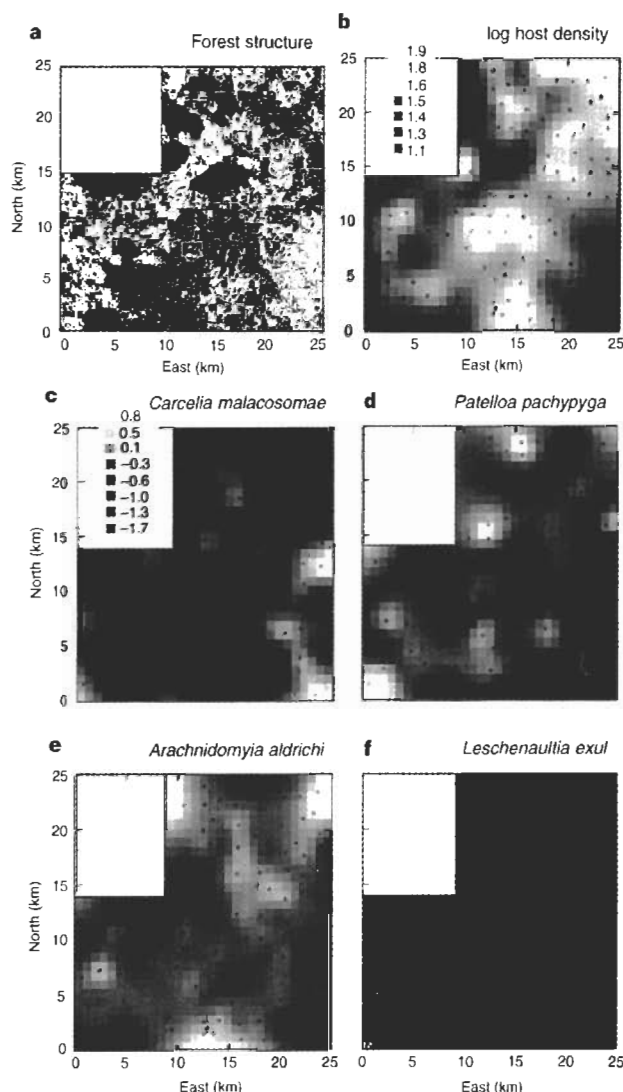


Figure 1 a, Forest structure, b, log host density in 1995 (N_t) and c–f, parasitism by four fly parasitoid species attacking forest tent caterpillar at Ministik Hills, Alberta, Canada. Maps of parasitism are distance-weighted least-squares surface plots²² for each of four parasitoid species attacking tent caterpillar across the coarse-resolution grid: c, *C. malacosomae*; d, *P. pachygyga*; e, *A. aldrichi*; and f, *L. exul*. Colours indicate log host density (b) and log odds-ratios of number parasitized by each species against number not parasitized (c–f). Dots are the 127 population sample sites. The red rectangle (in a) indicates the location of the fine-resolution grid (Fig. 2).

from the coarse-resolution and fine-resolution grids. The similarity of parameter estimates from the grids with different resolution suggests that there are no additional effects of landscape across the large-scale grid beyond those that can be estimated at a given sample point.

Rates of parasitism across the fine-resolution grid were spatially autocorrelated. Again, the distance to which they were autocorrelated differed among the four species. Parasitism by the two smallest species, *C. malacosomae* and *P. pachypyga*, were autocorrelated to

distances of only 44 and 53 m, respectively, reflecting fine-grained variation in parasitism. Parasitism by the two larger fly species, *A. aldrichi* and *L. exul*, was autocorrelated to distances of 421 and 420 m, respectively, reflecting coarser-grained variation in parasitism. These patterns suggest greater movement by the larger fly species, reflected in the larger spatial scale at which they respond to forest structure.

In general, parasitism was higher in areas of high host density, a pattern most evident for *P. pachypyga* and *A. aldrichi*. Interestingly,

Table 1 Coefficients for data from the coarse-resolution grid

Parasitoid species	Pupal mass (mg)	53 m	106 m	212 m	425 m	850 m	1,700 m	3,400 m	N_{t-1}	N_t
<i>Carcelia malacosomae</i>	34	-0.77						0.10	-0.17	-0.26
<i>Patelloa pachypyga</i>	41		2.0					0.17		0.80
<i>Arachnidomyia aldrichi</i>	58			2.23					-0.12	0.52
<i>Leschenaultia exul</i>	68					1.85			-0.24	0.28

Coefficients from logistic regression models estimating the effects of forest structure (Fig. 1a) and host density (Fig. 1b) on the odds of being parasitized by each of four parasitoid species across the large, coarse-resolution grid. We show only the coefficients for the effects of forest structure at the spatial scale at which its effect was strongest, and for the effect of host density. Full models are contained in supplementary information.

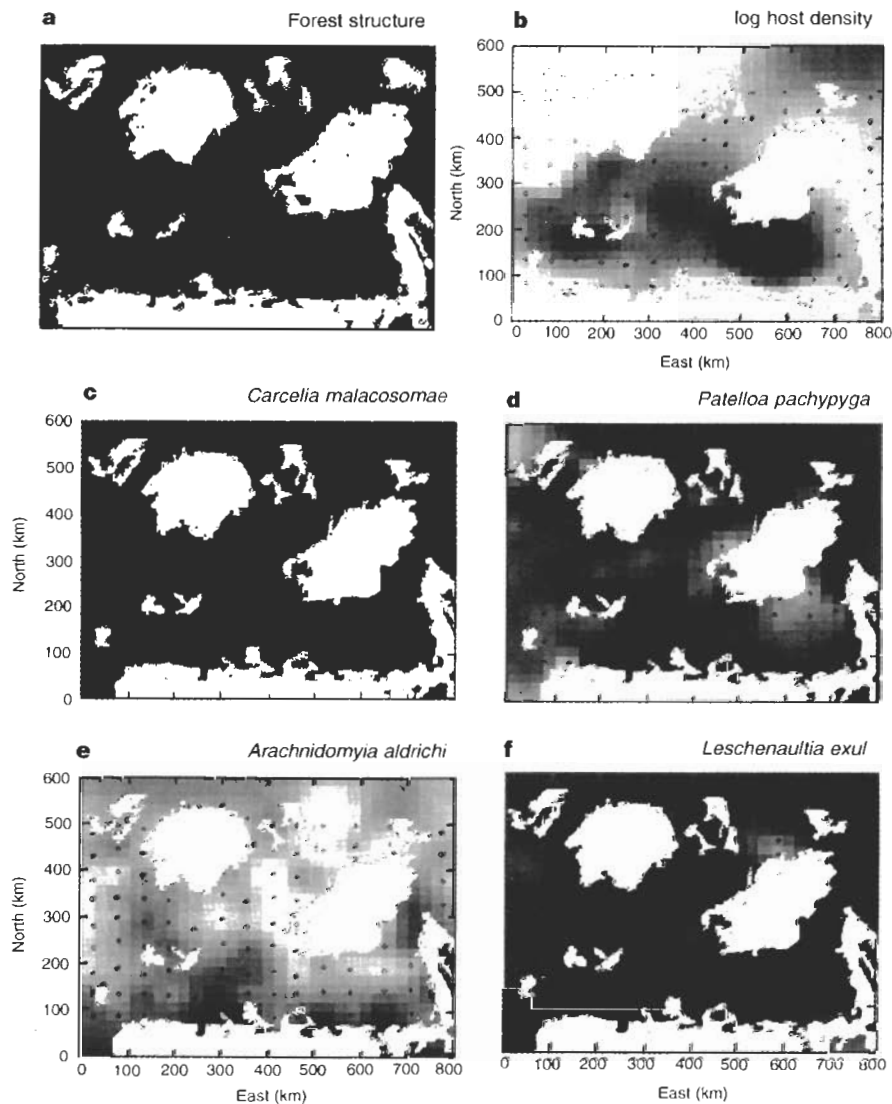


Figure 2 a, Forest structure, b, log host density in 1995 (N_t), and c-f, parasitism across the 0.32, m² fine-resolution grid. Parasitism is estimated for c, *Carcelia*

malacosomae; d, *Patelloa pachypyga*; e, *Arachnidomyia aldrichi*; and f, *Leschenaultia exul*. Methods and symbols as in Fig. 1).

the smallest parasitoid species again showed a pattern opposite to that of the other three species, causing higher rates of parasitism in areas of low host density (Table 1). For the two smallest parasitoid species (*C. malacosomae* and *P. pachypyga*), there was a significant interaction between host density and forest structure on the rates of parasitism they cause. *C. malacosomae* responded positively to host density in partially cleared forests (at 53 m scale) but did not respond to host abundance in continuous forests. These patterns suggest that forest acts as a barrier to movement (aggregation) by *C. malacosomae*, or that their numbers increase little in continuous forest. *Patelloa pachypyga*, in contrast, responded strongly and positively to host abundance in continuous forests, and only weakly so in partially cleared forests, suggesting that clearings may inhibit movement by *P. pachypyga*. Theoretically, such limits on parasitoid redistribution undermine any stabilizing effect of parasitoid aggregation¹⁵. There were no such interactions for the two largest fly species, suggesting that any response to host abundance was consistent regardless of habitat structure.

Although our spatial analyses clearly show that the landscape patterning of forests influences the percentage of host attacked by parasites, the real question is whether this effect translates into altered host-parasitoid dynamics. Data from other studies suggest in fact that the effects of forest structure we document in this paper do indeed alter dynamics in a profound way. In particular, the three parasitoid species that are less effective in fragmented forests are those that normally dominate in declining populations of tent caterpillar in several parts of North America¹²⁻¹⁴. Outbreaks of tent caterpillar last longer in fragmented than in continuous forest¹⁶. On the basis of our analysis, a reduction in forest cover from continuous to 50 per cent cover reduces the odds of parasitism by the three dominant parasite species to about half of that in intact forests. These species would be predicted to be most efficacious in only those areas with relatively large blocks of contiguous forests,

212 to 850 metres square in size (Fig. 3). The one parasitoid species that benefits from partial clearing of forests, *C. malacosomae* (Table 1), plays a minor role during tent caterpillar outbreak and collapse^{12,13}. Forest fragmentation, therefore, may exacerbate outbreaks of tent caterpillar by decoupling it from its natural enemies.

We suggest that the mechanism for altered parasitism is through the effects of habitat structure on movement. We have shown elsewhere¹⁷ that the larger species (*A. aldrichi*) can 'colonize' isolated forest stands up to 400 m from contiguous forest compared to only 125 m for the smaller species, *P. pachypyga*. Our analysis here also suggests that the ability of parasitoids to aggregate in response to host density is affected by landscape. It may be argued that forest fragmentation alters microclimate along forest edges, which different species may either favour or avoid¹⁸. However, we have controlled the effect of distance to edge at our large-grid sites by placing each sampling point 20 m into the forest; and we have removed the effect of distance to edge in the analysis of the fine-grid data. Therefore, although there may be an effect of edge, the fragmentation effect detected here is not directly related to the edge. Differences in spatial patterns seen among the fly species may reflect a strong spatial pattern for one species, for example *A. aldrichi*, combined with its ability to out-compete the other species. However, such an effect on another species would be expected to result in a response to forest structure in the opposite direction (higher parasitism in the fragmented stands where *A. aldrichi* does poorly) but at the same spatial scale (425 m). The most likely competitors with *A. aldrichi* either show the same (positive) direction of their response to forest structure (*P. pachypyga*) or respond to forest structure at a much finer scale (*C. malacosomae*).

Changes in landscape structure such as forest fragmentation have been predicted to affect animals differentially depending on their size and the spatial grain of the habitat mosaic¹⁹. Populations of animals that evolved a specific 'ambit' within, for example, a

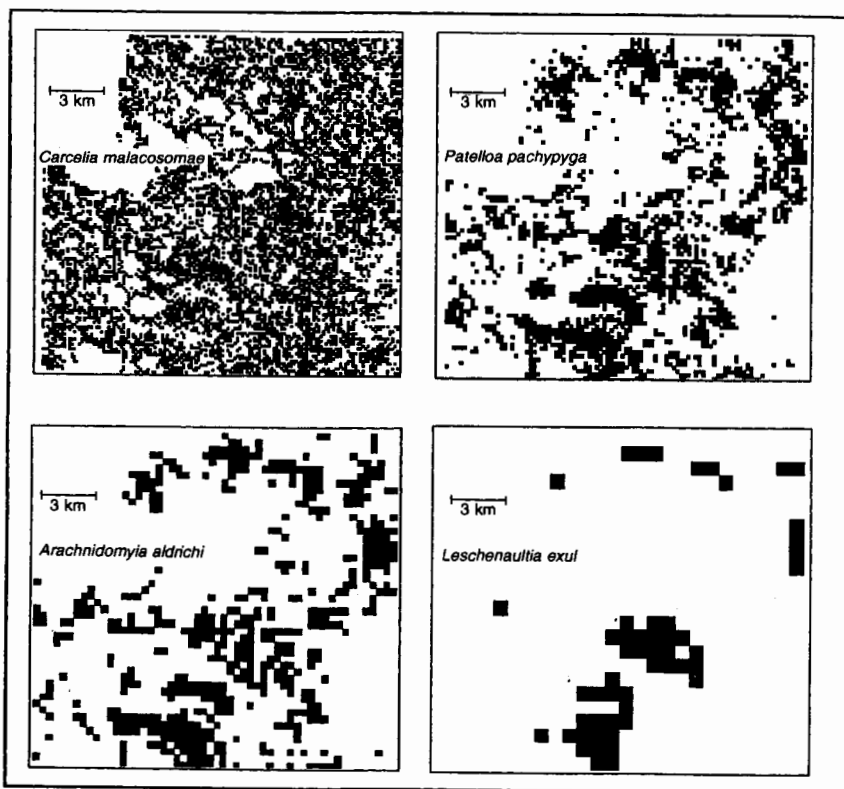


Figure 3 The extent of forested habitat in which each parasitoid species would be most effective, disregarding effects of host density. Patterns are based on the effects of forest structure on parasitism (positive or negative) and the spatial scale

at which each species responds to forest structure most strongly (from Table 1). Forests where the efficacy of each species is reduced from its maximum are deleted. Compare to Fig. 1a for the distribution of all forest.

continuous forest system, may behave differently in areas of altered habitat structure. Successful predictions about the behaviour of complex systems and their response to disturbance may be possible using such simple relationships as those between animal size, spatial scale of search and grain of habitat structure. We reiterate the plea by others² that ecological studies be conducted at sufficiently large and multiple spatial scales to successfully extract such generalizations. □

Methods

Estimates of parasitism and host abundance. At each sample point 50 to 100 late-instar caterpillars were collected to estimate parasitism by *C. malacosomae*, *P. pachygyga* and *L. xyl*, and 50 to 100 host cocoons were collected 10 days later to estimate rates of parasitism by *A. aldrichi*. The collection of late-instar hosts to estimate parasitism by *C. malacosomae* and *Patelloa pachygyga*¹²⁻¹⁴ was made before the attack by *A. aldrichi*, which is known to out-compete the other parasites in the host pupa. Hosts from each collection were reared all together and the number of emerging parasitoids of each species were counted. Density was estimated using a time-restricted search; the time taken to collect 50 cocoons (to a maximum of 15 min) was recorded. If less than 15 min were needed to collect 50, we estimated the number which would have been collected in 15.

Estimates of forest structure. Forest structure was estimated at each of the sample points across the 420 m² grid. Landscape structure was estimated at each point from a classified aerial photo-mosaic (1:20,000 scale) scanned at a resolution of 5.3 m per pixel. Using SPANS Geographic Information System software (Intergraph Technologies, Nepean, Ontario, Canada), we calculated the amount of forest in a series of seven squares, geometrically increasing in spatial scale from 53 m on a side to 3,400 m on a side (Table 1) and centred on each sampling point. The amount of forest within each square was scaled from 0 (virtually no forest) to 1 (complete coverage of continuous forest); it is therefore an index of forest continuity.

Model fitting. For each parasitoid species, models included as potential explanatory variables: the log-transformed density of forest tent caterpillar in the previous year (N_{t-1} , 1994), the log-transformed density of forest tent caterpillar in the current year (N_t , 1995), and terms for the location of each sample point on a cartesian grid (east, north, coefficients not shown) and the square of these locations. Location terms were included to account for any unknown historical patterns of spread of the outbreak across the coarse-resolution grid. Model-building proceeded in a stepwise fashion by separately testing the importance of landscape structure measured at each of the seven spatial scales in each of seven separate models (each including density and location terms). We selected the model with the landscape term that caused the maximum reduction in overall deviance of the respective model, and for which the coefficient was most significantly different from zero²⁰. Once the best model was selected, additional terms were added to it to identify any additional effects of forest structure at scales smaller and larger than that which appeared to be most important. This strategy was used to identify the scale at which forest structure had its greatest effect, and then to examine whether additional terms contributed to the overall fit of the model. When testing for the effects of forest in the 3,400 m square surrounding a point, we used a subsample of points spaced by at least 4 km, thereby ensuring independence of forest structure estimates among points. Pupal mass was estimated from samples of 20 individuals of each fly species pooled from several sites. Full models are presented as supplementary information.

A second set of models (not shown) were fitted to data from the fine-resolution grid, but forest structure was only estimated within 53 m and 106 m around each sample point. Forest structure within 106 m of each point was again estimated using a subset of points to ensure independence of estimates. Distance of each sample point to the nearest forest edge was estimated and included in the model. Coefficients for the effect of forest structure (53 m and 106 m) on parasitism estimated from the fine-scale grid were not significantly different from those estimated from the coarse-resolution grid (53 and 106 m samples). All models were fit using S-PLUS software (MathSoft Inc., Seattle). Spatial autocorrelation of parasitism estimates for each species were based on the fit of a spherical model semivariogram with a minimum lag of 50 m, using GS* geostatistics software (Gamma Design Software, Plainwell, Michigan).

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Supplementary Information is on www.nature.com. Paper copies are available from Mary Sheehan at the London editorial office of Nature.

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