

Are the “seeds” of spatial variation in cyclic dynamics apparent in spatially-replicated short time-series? An example from the forest tent caterpillar

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Variation in the pattern of dynamics of the forest tent caterpillar was assessed over a 13-year interval of population collapse and increase among 68 sites within a 420 km² region. Patterns of population change were compared with the level of forest fragmentation among sites, and interpreted in light of previous studies on the effect of forest fragmentation on the impact of natural enemies of forest tent caterpillar. Outbreaks peaked earlier in contiguous forests than in fragmented forests, and collapsed more rapidly. Parameters of population change for populations in contiguous forests were more characteristic of strongly cyclic dynamics than were those in more fragmented forests, reflecting a significant effect of forest structure on the lagged density-dependent component of tent caterpillar dynamics. Despite the relative shortness of these time series the patterns identified are consistent with a reduction in efficacy of natural enemies in more fragmented forest habitats.

Introduction

In 1993, I published a paper on the effects of large-scale fragmentation of boreal aspen-dominated forests on some components of the dynamics of the forest tent caterpillar, *Malacosoma disstria*, Hübner, based on the spatial extent of defoliation as a surrogate for population density (Roland 1993). The main result of that study was that in areas where forests had been fragmented by up to 50 percent forest loss, outbreaks of the defoliator lasted several years longer compared to outbreaks in areas where forests were continuous. Although the pattern was based on forest structure averaged over entire townships (about 100 km² each), subsequent mechanistic studies

on the effect of landscape on processes driving dynamics (parasitism, viral disease), were done at relatively small spatial scales using landscapes of, at most, 3 km² in area (Roland & Taylor 1997), and often much smaller than that (Roland & Kaupp 1995, Rothman & Roland 1998, Roland 2000). Results from these fine-scale mechanistic studies were in general agreement with the pattern of longer outbreaks in fragmented forests; parasitism was generally lower in fragmented stands (Roland & Taylor 1995, 1997, Rothman & Roland 1998) as was the incidence (Rothman & Roland 1998) and transmission of (Roland & Kaupp 1995) viral disease.

Although a longer outbreak phase of these insects has dramatic practical implications for

fibre production for forestry through the loss of tree growth increment in years of defoliation, from the perspective of population dynamics it is of greater interest to determine how cyclic dynamics generally are affected by habitat structure, thus providing better prediction of outbreaks. Identifying these more general patterns was the initial goal of our studies on forest tent caterpillars.

One of the ecological phenomena which has captured the imagination of population ecologists most is that of dynamics of so-called cyclic species (Kendall *et al.* 1999); be they of vertebrate populations such as snowshoe hares (Ranta *et al.* 1997) and voles (Bjørnstad *et al.* 1996) or of insects such as the larch budmoth (Johnson *et al.* 2004) and pine looper (Kendall *et al.* 2005). The putative cause of cyclic dynamics has been variously ascribed to either the effect of tightly-linked endogenous factors such as delayed induced effects of herbivory on host plants (Haukioja 2005), tightly linked predator-prey (Ranta *et al.* 1997) or parasitoid-host (Turchin 1990, Berryman 1996) interaction, disease dynamics (Myers 1988), or the effect of exogenous factors which themselves exhibit cyclic patterns, such as weather (Hunter & Price 1998) or potentially from autocorrelated patterns of change of such factors as generalist predators (Williams & Liebhold 1995). The recent flourishing of spatial ecology has meant an attendant interest in the way in which eruptive dynamics also vary spatially (Ranta *et al.* 1997, Bjørnstad *et al.* 1999, Grenfell *et al.* 2001). By describing the spatial variation in dynamics, some insight may be gained in understanding what drives the cyclic dynamics by asking three questions: (1) which of the possible mechanistic processes are themselves also varying spatially, (2) to what environmental covariates are the processes most closely related, and (3) at what spatial scales do the covariates have their greatest effect on these processes? For example, if dynamics vary spatially, and if components of those dynamics such as disease transmission rates also vary spatially, and at a scale similar to that of the dynamics, then a strong case can be made for the importance of disease in driving dynamics in that system. Improved prediction of dynamics could be subsequently gained by identifying environ-

mental covariates of transmission rates, which themselves also vary spatially.

Here I describe recent studies on the cyclic defoliating forest insect, the forest tent caterpillar in Canada, and the effects that forest fragmentation has on the patterns of cyclic behaviour, and on the mechanisms which may be driving those dynamics. In addition, I assess how parameters for population growth models fitted to data from individual subpopulations vary spatially, whereas in a forthcoming paper (J. Roland, B. H. van Hezewijk & S. Lele unpubl. data) we fit a single model that incorporates both covariance in the data among subpopulations and an estimate of the relationship between environmental covariates (specifically forest fragmentation) and the parameters of population change.

Mechanistic studies

Our studies of forest tent caterpillar populations since 1992 have identified a number of ways in which forest fragmentation alters the impact of natural enemies attacking tent caterpillar. Virus is less prevalent in populations in more fragmented sites (Rothman & Roland 1998) and transmission of virus among caterpillars is much less effective in open sites such as at forest edges (Roland & Kaupp 1995). Parasitoids inflict lower rates of parasitism on hosts in fragmented forest stands (even when adjusted for the effects of host density), especially those parasitoid species associated with outbreaking and collapsing tent caterpillar populations (Roland & Taylor 1997). Fragmented forests support fewer and less diverse alternative hosts for tent caterpillar parasitoids (Schmidt 2001), making these sites relatively enemy-free as compared with continuous forest stands. Mortality of parasitoids, especially pupating tachinid parasitoids in the soil, is greater in fragmented sites as a result of higher predation by generalist soil predators (Mitchell 2001), again making these sites relatively enemy-free.

Are there patterns in the dynamics of populations consistent with the results of the fine-scale mechanistic studies described above, and can relatively short time-series begin to identify any such patterns? To answer this question, monitor-

ing of FTC populations in a variety of forested landscapes was begun in 1993.

Estimation of meaningful population growth parameters requires a minimum of 1 cycle, and ideally several cycles (Turchin 1990, Royama 1992). As an alternative, however, spatial replication of shorter time-series including an estimate of the spatial covariance among sites (e.g. Lele *et al.* 1998) can improve parameter estimates based on shorter time-series. Some characteristics of relatively short time-series can be contrasted among spatially replicated sites with a potential of providing insight into possible longer-term dynamics, including timing (year) of peak abundance, peak abundance attained among all years, variation in abundance, and the duration of either the outbreak or the endemic phase of the cycle. How these characteristics vary spatially, and how they vary in response to forest fragmentation, may provide insights into how cyclic dynamics generally are affected by the landscape.

Material and methods

Forest tent caterpillar abundance

Two methods were used to estimate tent caterpillar abundance over the period 1993 through 2004 at all monitoring sites. From 1993 through 1996, we recorded the time taken to find and collect 50 cocoons, in a maximum of 15 minutes. For sites where 50 cocoons were collected in less than 15 minutes, we calculated the number that would have been collected if counting had continued for the full 15 minutes. In 1996, and in all subsequent years, we used pheromone trapping (Schmidt & Roland 2003, Schmidt *et al.* 2003) of males to estimate moth abundance. Data collected in 1996, using both methods, were used to adjust estimates of healthy unparasitized cocoons in 1993 through 1996 to counts of males from pheromone trap counts, thus providing comparable estimates of adult male abundance for all years (Fig. 1). Data for the two methods in 1996 were quite variable but were significantly related to each other (male moths = $0.071 \times$ number of healthy cocoons; $P = 0.04$, $N = 25$, generalized linear model with Poisson errors, proportion of

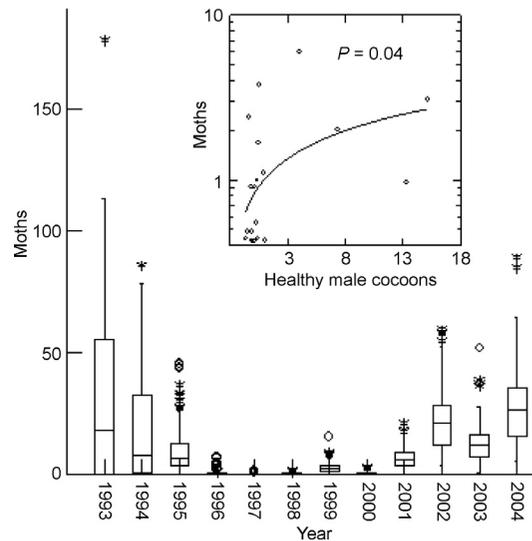


Fig. 1. Estimated density of male moths in each year and from all sites based on pheromone trapping (1997–2004) and based on cocoon collections scaled to density of healthy male moths (1993–1996). Boxplots indicate median (line), interquartile range (box) and range over which there are data points within 1.5 times the inter-quartile range (whiskers). — Inset: relationship between healthy male cocoon counts and male counts in pheromone traps in 1996 (generalized linear model, Poisson errors with log-link, and no constant in the model).

deviance explained = 11%). In addition, defoliation was estimated at each site each year by visual estimation of the percent reduction in leaf area attributable to forest tent caterpillar feeding.

Forest structure

Proportion of area forested around each of the population monitoring sites was estimated based on a classified photo-mosaic (1:20 000 scale) of the 420 km² study area (Fig. 2). A square area around each population sampling point was delineated into 5×5 grid cells. The number of cells out of 25 which were classified as forest were counted and expressed as a proportion. Because there was no *a priori* expectation of the scale at which forest structure might have the strongest impact on populations, 'proportion forested' was estimated at six spatial scales: squares 53 m on a side, 126 m, 212 m, 425 m, 850 m and 1700 m. These scales correspond to landscapes

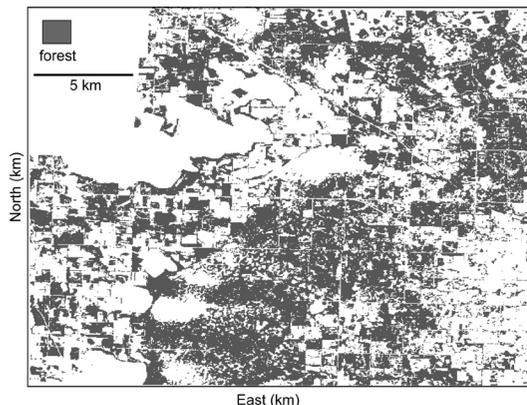


Fig. 2. Map of forest (dark) and non-forest (white) in the 420 km² Ministick Hills study area near Edmonton, Alberta, Canada.

of 0.25 ha, 1.6 ha, 4.5 ha, 18 ha, 72 ha and 290 ha, respectively, and measured for each population monitoring point.

Time-series analysis

If the landscape alters the impact of ecological processes driving dynamics, then it would be expected that estimated parameters of population change would similarly vary with the landscape, and presumably at the same or similar spatial scale. The first step was to identify several general features of population change for each site, including: (a) year of peak abundance, (b) maximum density attained in any year, (c) coefficient of variation (CV) of the time-series, and (d) duration (years) of density above an arbitrary density of 20 moths based on the fact that this number of moths was, on average, associated with a level of stand defoliation of 50 percent (Fig. 3). Each of these features of population change was regressed against the proportion of the 18 ha landscape around each population monitoring site that was forested. Only sites with a continuous uninterrupted series of data from 1994 through 2004 (68 sites) were used in these analyses.

Time-series of moth count data for each population were subsequently fit to a Gompertz population growth model which includes a lagged density dependence term given the puta-

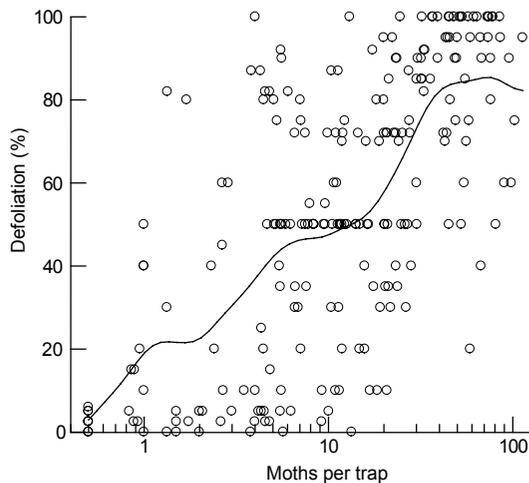


Fig. 3. Relationship between estimated moth density and the level of defoliation at each site. The line is a distance weighted least squares smoother.

tive importance of tightly-linked natural enemies in forest tent caterpillar dynamics:

$$R_t = a_0 + a_1 \log(N_t + 0.5) + a_2 \log(N_{t-1} + 0.5), \quad (1)$$

where R_t is the log of the ratio of population change from one year to the next, N_t and N_{t-1} are the estimated abundance of moths each year, and a_1 and a_2 are the parameters describing the direct and the lagged effects of density, respectively. As such, a_1 and a_2 are estimated simultaneously and are partial coefficients. The tent caterpillar data conform well (Fig. 4) to the assumption of a linear relationship between R_t and log abundance (Saitoh *et al.* 1999). Parameters estimated from this model could then be mapped to determine how they vary spatially (similar to that of Peltonen *et al.* 2002: fig. 3a), and were also regressed against the degree of forest fragmentation to determine if the effects of the landscape on dynamics were consistent with the effects of the landscape on population processes. The combinations of a_1 and a_2 for each site were plotted against each other to help identify the expected types of dynamics (Royama 1992: fig. 2.5, Saitoh *et al.* 1999: fig. 4). This was done not so much to determine their absolute location within this classification, but, rather the relative location given their differences in forest structure.

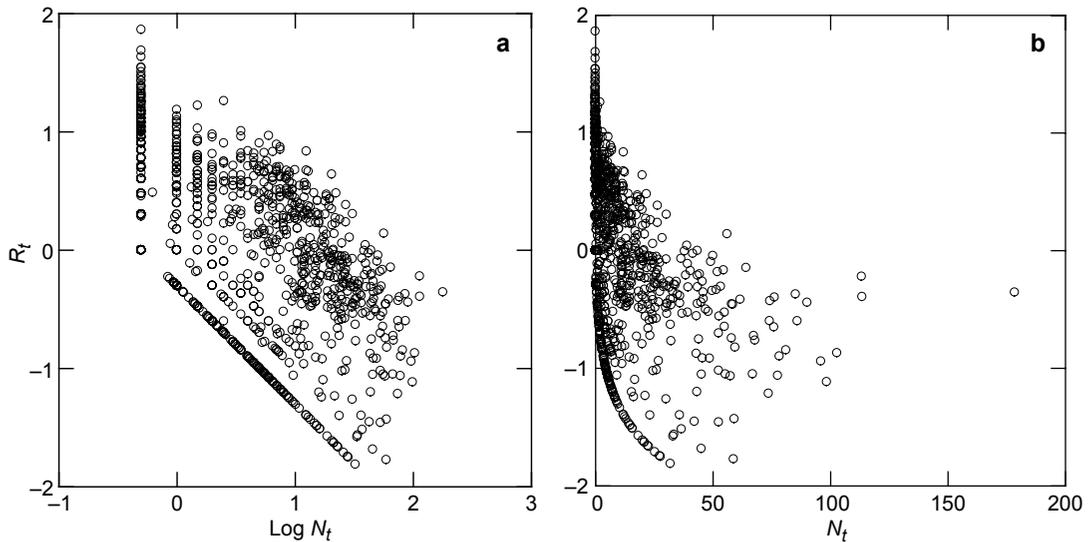


Fig. 4. Relationship between forest tent caterpillar population growth rate R_t (defined as $\log N_{t+1} - \log N_t$) and (a) log abundance, $\log(N_t + 0.5)$ and (b) abundance, N_t .

Results

Population patterns

The general pattern of dynamics from 1993 through 2004 was for densities to peak early in the interval (1993–1995), collapse through 1996–1998, remain at low endemic density for several years before increasing over several years to higher, but as yet non-defoliating, densities in 2004. Despite this general pattern, there was variation among the sites across the 20 × 20 km study area, some of which was related to forest fragmentation.

For almost all characteristics of populations, forest structure had its greatest effect, based on significance levels and variance explained, when measured at the 18-ha (425 m × 425 m) scale around each population monitoring site. Interestingly, this scale is intermediate among the spatial scales (53 m to 850 m) at which dominant parasitoid species attacking forest tent caterpillar respond to forest structure (Roland & Taylor 1997).

Tent caterpillar outbreaks peaked on average 1.5 years earlier in contiguous forest landscapes than in more fragmented sites (Fig. 5a). Not only did populations in continuous sites peak earlier, but they also reached higher peak density,

particularly at sites above a threshold of 40% forest cover (Fig. 5b), and then collapsed rapidly. Although populations in fragmented forests never reached as high density (Fig. 5b), they were actually more variable (Fig. 5c) suggesting that fragments are characterized by more erratic but lower-density dynamics. These patterns are consistent with populations reaching higher density where resources are more concentrated, and where mean dispersal is more likely to be contained within stands. The more rapid collapse in larger stands likely results from more efficacious natural enemies. Similarly, populations in more fragmented stands do not increase as rapidly nor to as high density, presumably because of the effect of more diffuse resources and the effect of more forest ‘edge’ per unit area for small stands, thus promoting dispersal out of the stands. The weaker impact by natural enemies in fragmented stands (Roland & Taylor 1997) would presumably result in slower host population decline.

Population growth parameters

Direct density-dependence, a_1 , was smallest (most strongly negative) in the fragmented forests (compare Fig. 2 with 6a, and *see* Fig.

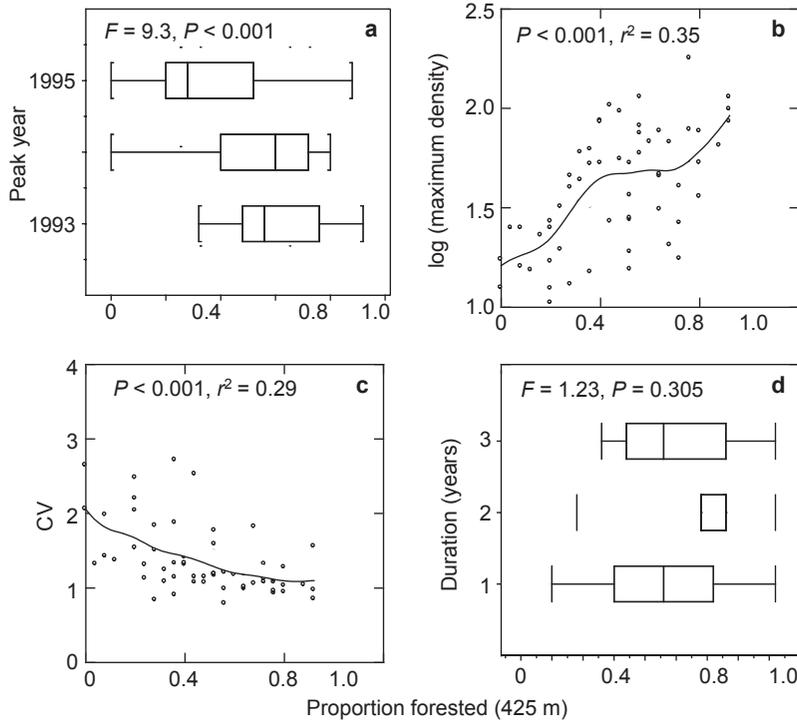


Fig. 5. Characteristics of population dynamics as a function of proportion of the landscape within 18 hectares of each population monitoring site that was forested. — **a**: year in which the peak density among all years was observed, — **b**: maximum density observed among all years, — **c**: coefficient of variation for each time-series, — **d**: number of years duration for which the population was greater than 20 moths. Lines are distance-weighted least-squares smoother; significance and variance explained are from linear least-squares fit. Boxplots indicate median (line), interquartile range (box) and range over which there are data points within 1.5 times the inter-quartile range (whiskers).

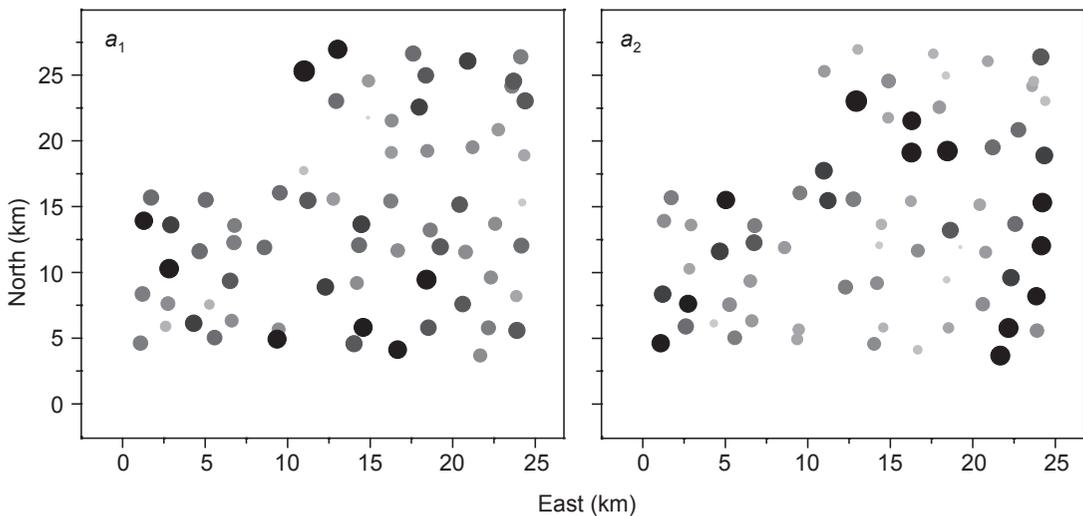


Fig. 6. Map of parameters for direct density dependence (a_1), and lagged density-dependence (a_2) across the 420 km² study area at Ministik Hills, Alberta, Canada. Compare with forest cover in Fig. 2.

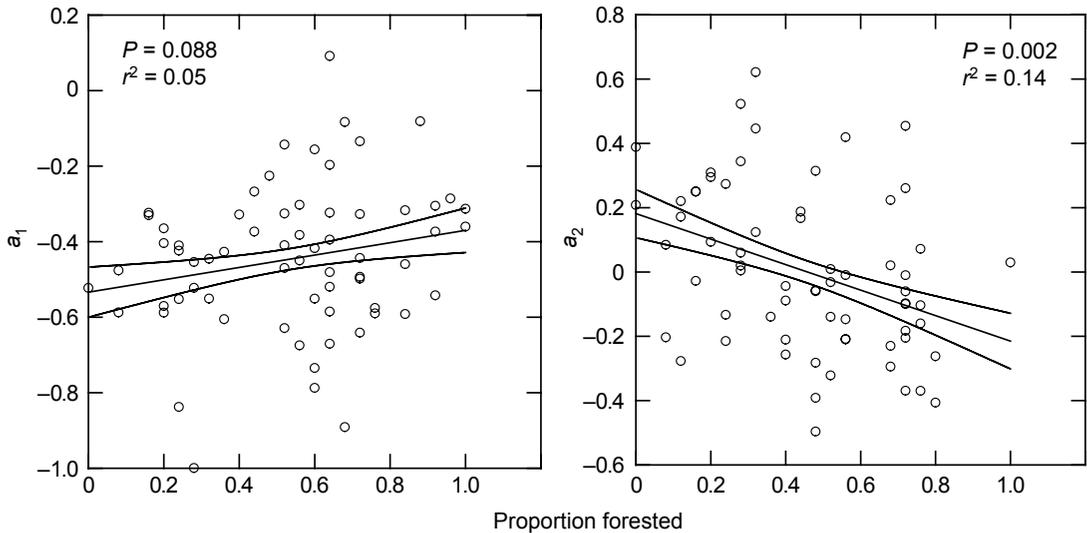


Fig. 7. Effect of proportion forested on the magnitude of parameters a_1 and a_2 . The strength of the effect of forest cover on parameter size depends on the scale at which forest is measured. The respective scales giving the strongest response, and which are used in the plots, are 4.5 ha, and 72.3 ha. Lines are least-squares fit to the data with 95% confidence interval around each.

7a), but the trend was weak. In contrast, that for lagged density-dependence, a_2 , was smallest (most strongly negative) in the larger, more contiguous forests (compare Fig. 2 with 6b, and see Fig. 7b). There is great variation in each of these patterns (Fig. 7), but they imply two things. Firstly, that fragmentation of aspen forests renders direct density-dependent processes such as rapidly induced defense, intra-specific competition, or dispersal more strongly so. It is difficult to imagine why plant defences would be more strongly induced in a forest fragment, given the same population size, as compared with those in contiguous forests, and similarly why density-dependent competition would be stronger in fragments as compared with that in contiguous forest with the same herbivore densities. On the other hand, density-dependent dispersal could be manifest more strongly in fragments given that there is a greater proportion of forest edge to forest area and hence density-dependent emigration would be enhanced. Secondly, that greater delayed density-dependence in continuous forests results either from delayed induced defences or from tightly linked natural enemies that are more efficacious in continuous forests. Indeed we have repeatedly demonstrated that natural

enemies of forest tent caterpillar are more effective in continuous forests (see Introduction).

Parameter space

Parameters for the forest tent caterpillar populations (a_1 and a_2) range over two regions of Royama's parameter space: region I characterized by monotonic dampening to an equilibrium, and region IV characterized by multi-year cyclic dynamics (Royama 1992: figs. 2.5 and 2.6). Although none of the forest tent caterpillar populations had gone through a full cycle, the sites with parameter combinations that would generate cyclic dynamics (region IV) are those sites characterized by larger, more contiguous forests (Fig. 8). Those sites with parameters that would generate non-cyclic dynamics (region I) tend to be those with less forest cover (Fig. 8). Because these patterns are based on short time-series, it is important, however, to consider the relative values among sites rather than the absolute values, since the latter will surely change once a full cycle (or several cycles) has occurred. In fact, very few of the individual estimates of a_1 and a_2 are significant. The important point here,

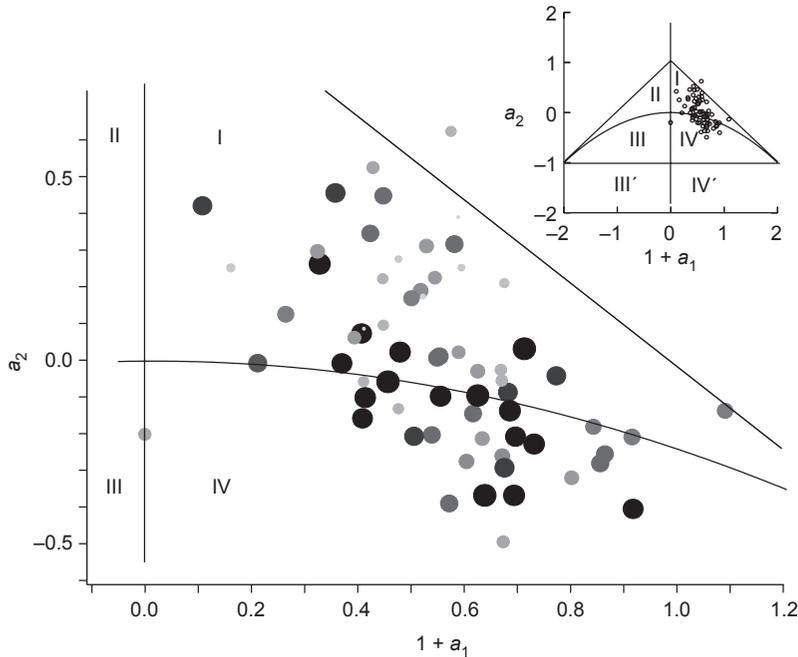


Fig. 8. Parameter space (after Royama 1992) for direct density-dependence ($1 + a_1$, x-axis) and for lagged density-dependence (a_2 , y-axis). — Inset: large scale plot of the same data. Symbol size and shading are a function of proportion forested within 18 ha of the population monitoring sites; large dark circles are heavily forested landscapes and small light circles are patchily forested landscapes. Regions identified with roman numerals as in Royama (1992).

however, is that the more strongly cyclic populations are those in more contiguous forests.

Discussion

Despite the relatively short time-series of tent caterpillar population data in this analysis, the pattern of dynamics are consistent with results from studies on the effects of forest fragmentation on population processes, and consistent with longer time series (35 years) of defoliation data (Roland 1993). Although individual short time-series from each site produce poor parameter estimates, the fact that the resulting parameters correlate with environmental variables known to affect population processes (parasitism and viral infection) is encouraging. Results here provide the prediction of more strongly regulated dynamics in larger stands — a prediction which longer time-series will either confirm or refute. Similarly, statistical analysis of spatially replicated time-series that incorporates estimates of covariance among sites (e.g. Lele *et al.* 1998) will likely improve the estimates.

Of necessity, many studies of spatial dynamics of forest defoliators rely on data on the spatial extent of defoliation as a surrogate for

insect abundance (Roland 1993, Daniel & Myers 1995, Roland *et al.* 1998, Cooke & Roland 2000, Peltonen *et al.* 2002, Johnson *et al.* 2004). Defoliation is easier to estimate over sufficiently large areas and with sufficient resolution compared to sampling of any particular insect life-stage. There is, however, valid concern that ‘area defoliated’ may not accurately reflect change in abundance for two reasons. Firstly, ‘area defoliated’ and insect abundance will likely be well correlated at only one spatial scale; it is easy to imagine that density at an outbreaking site could remain the same over several years as the spatial extent of defoliation either expands or contracts around it. If defoliation is used as a surrogate of density, then ensuring that the area over which the proportion of forest defoliated is made becomes critical. Secondly, mechanisms of population change assumed by models to which data are fit assume that processes such as dispersal and parasitism are affected by insect density, an assumption for which there is much empirical evidence. In contrast, there is virtually nothing known regarding the effect of ‘area defoliated’ or ‘area of outbreak’ on these processes. For these reasons, it is encouraging that the analysis based on short series of direct measures of abundance produce patterns supportive of analyses based

on long time-series of defoliation data (Roland 1993) and *vice versa*.

In addition, the patterns of forest tent caterpillar dynamics indicated here are similar to results of recent analysis of long time-series of defoliation data for other forest defoliators, in particular that of the larch budmoth (*Zeiraphera diniana* Hübner), in the European Alps (Johnson *et al.* 2004). For budmoth, there exist long, multi-cycle time-series data to which forest fragmentation is correlated, but for which little is known of the effect of fragmentation on population processes. In contrast, time series data for forest tent caterpillar abundance are relatively short, but there is much information on landscape effects on population processes. Dynamics of both insects show similar patterns: (1) in order for outbreaks to occur there must be areas of sufficiently large forest, and outbreaks tend to originate there, (2) outbreaks spread from these areas, and (3) outbreaks of both insects collapse sooner in the contiguous forests, due presumably to the greater efficacy of natural enemies in these stands.

Why are some of the effects of fragmentation seen at large scales (100 km², Roland 1993) at odds with some of the results seen at fine scales (less than a km²), in particular the effects of fragmentation on the duration of outbreaks? At the larger scale of entire townships, outbreaks last longer if forests are fragmented by up to 50 percent. At the scale of landscapes of 18 ha, however, there is no difference in duration of outbreaks (Fig. 5d) even though they are initiated later and peak later than those in continuous forests (Fig. 5a). The answer may simply be because measures of population response are made at very different scales (cf. Hanski & Meyke 2005). Population abundance measured at the larger scale is of course the summation of dynamics in many stands across the 100 km² area, including continuous forest stands where populations can reach high density quickly (upper sites of Fig. 5b), and fragmented stands where natural enemies are not very effective. Each township would have a greater or lesser amount of each stand type. Those townships with only continuous forests will tend to have severe but short outbreak, townships with both continuous forests and fragmented forests (presumably linked by dispersal) would have longer-lasting outbreaks.

The resultant dynamics would therefore be the sum of the fine-scale dynamics in fragmented and continuous stands linked through dispersal; a certain amount of forest is needed for defoliating outbreaks to occur, but a certain amount of fragmentation allows for regions of inefficiency of natural enemies. In the historical analysis of Ontario tent caterpillar populations (Roland 1993), townships with greater fragmentation had longer outbreaks, but even the most fragmented among these still had more than 50% forest cover. As a result, townships were either totally forested or had a large component of forest with some fragmentation. If there had been townships with only highly fragmented forests, they might be expected to have FTC populations that rarely reach outbreaks and whose dynamics are dominated by dispersal (from larger forests?) rather than by interaction with natural enemies; in effect 'forced' by dispersal from cyclic populations in relatively continuous forests. In regions with highly fragmented aspen forests, such as aspen parkland and open prairies, forest stands may simply not be large enough to sustain outbreak populations, no matter how ineffective natural enemies might be. Indeed, there are few records of forest tent caterpillar outbreak in these regions of Canada, and if they do occur, they usually disappear within one generation (Brown 1965, Hildahl & Campbell 1975). Large-scale, multi-year outbreaks of forest tent caterpillar most commonly occur in Canada along the interface between aspen dominated boreal forest and areas cleared for agriculture in both Ontario (Roland 1993) and in Alberta (Hildahl & Campbell 1975), in particular those outbreaks that persist for many years (Roland 1993).

There is little doubt that important processes affecting tent caterpillar also operate at scales much larger than that examined here. Forest tent caterpillar populations tend to be synchronized at distances of up to 200 km in both Alberta (Cooke 2001) and British Columbia (Peltonen *et al.* 2002). Large-scale dispersal, or large-scale perturbation, may swamp local landscape effects on population process. Given the relatively small scale of data used in this study (relative to the scale of synchrony), such large scale effects are largely controlled for when looking for effects of the landscape.

This paper demonstrates that the spatial variation in dynamics of the forest tent caterpillar are reflected in parameters of population change consistent with the effects of the landscape on population processes, especially those on natural enemies. Estimated parameters for individual sub-populations are related to forest fragmentation, with those in more contiguous forests exhibiting patterns associated with more strongly cyclic dynamics. Clearly, longer time-series would be needed to confirm this. As a next step (J. Roland, B. H. van Hezewijk & S. Lele unpubl. data), a single model combining time-series data from all sites, and making use of the covariance among them (Lele *et al.* 1998) can be assessed, in particular if the landscape was also included as a covariate scaling the magnitude of each parameter (a_0 , a_1 and a_2) among sites.

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