

**SPATIAL STRUCTURE RELATIONSHIP IN A FOREST
INSECT SYSTEM: SIMULATION MODELS AND ANALYSIS**

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FOREWORD

In the early years following IIASA's founding in 1972, its Ecology and Environment Project undertook a number of studies to explore the interface between the natural and policy sciences and to develop approaches to solving problems at this interface. This work focused on specific policy-design problems that nonetheless had broader implications for areas as diverse as fisheries management, Alpine development, regional energy issues, and pest control. Augmented by other work at IIASA and within a network sponsored by the United Nations Environment Programme, these studies yielded a set of concepts, methods, and procedures for environmental policy design.

The first comprehensive account of the findings of this work appeared in C.S. Holling (editor), *Adaptive Environmental Assessment and Management* (Wiley, Chichester, United Kingdom, 1978), volume 3 in IIASA's International Series on Applied Systems Analysis; *Expect the Unexpected: An Adaptive Approach to Environmental Management*, a brief account for the general reader, appeared in 1979 as an IIASA Executive Report.

Detailed accounts of the individual case studies and their scientific and technical foundations are now beginning to appear. The energy work, for example, is described in W. Foell (editor), *Management of Energy/Environment Systems: Methods and Case Studies* (Wiley, Chichester, 1979), volume 5 in the International Series; its extensions will appear soon in the same Series in a volume with the same editor. The pest-management work will be described in some detail in another forthcoming volume in the International Series: William C. Clark *et al.*, *Ecological Policy Design*. The present paper reviews some of the more important scientific results emerging from this pest-management work.

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Spatial structure relationship in a forest insect system: simulation models and analysis¹

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This paper analyses relationships among dispersal, spatial heterogeneity, and local ecological processes in the spruce budworm (*Choristoneura fumiferana* CLEM.) - boreal forest system of eastern North America. A range of simulation and topological models are developed to reflect various hypotheses concerning those relationships. Model predictions are treated as guides to effective experimental design and efficient allocation of research priorities, rather than as ends in themselves. The analysis demonstrates the shortcomings of studies treating either dispersal or local processes alone, and argues instead for an integrated approach to spatial structure research in population ecology.

If we had held this conference a quarter century ago, our discussions of population dynamics would have been largely local in character. New projects on spruce budworm, pine looper, and larch budmoth - to name only those whose wizened descendents are with us today - were then focusing on regulatory interactions among organisms and their immediate environments. Questions of animal movement and environmental heterogeneity were not seriously addressed, except by a few unconventional souls laboring in the wilds of Australia (ANDRE-WARTHA & BIRCH, 1954) and Africa (RAINEY, 1951).

A decade or so later, the situation would have changed. Seminal works of DEN BOER (1968), HUFFAKER (1958), and others had begun to have wide impact, and spatial heterogeneity, habitat patchiness, and the like would have been topics of the day. The relevance of dispersal behavior to population dynamics was also becoming more and more evident. And JOHNHON's (1969) monograph would soon usher in the 1970's as a period of heightened interest and progress in this most difficult area ecological research.

Each of these historical developments introduced new perspectives on classical questions of population dynamics and regulation. But it is only in the last several years that we have begun to interpret changing patterns of animal abundance as a collective and simultaneous function of all three areas of concern. Local interactions, habitat heterogeneity, and animal movement - in short, the spatial structure of ecosystems - have now become the joint foci of population dynamic studies on a range of theoretical (LEVIN, 1978), marine (STEELE, 1978), microtine (KREBS & MYERS, 1974), large mammal (SINCLAIR & NORTON-GRIFFITHS, 1979) and, of course, insect systems.

Professor Delucchi opened this conference by noting that even the best of our long-term studies of local population dynamics did not make sense in the

¹Paper presented at the Conference on «Dispersal of forest insects: evaluation, theory, and management implications», sponsored by the Intern. Union of Forestry Research Organizations (IUFRO), Entomology Dept. of the Swiss Federal Institute of Technology, Zürich and Zuoz, Switzerland, 4-9 September, 1978.

absence of attention to insect dispersal. I argue in this paper that the symmetric argument is equally true. We cannot understand the significance of dispersal and habitat pattern without appreciating the «stage» of local interactions on which they are carried out. Continuing attempts to study dispersal or spatial heterogeneity as such will be interesting and intricate, just as were the isolated local interaction studies of earlier decades. But ten years hence I suspect we will be looking back on integrated spatial structure studies as the source of some of the most exciting practical and theoretical insights of the day.

DATA, MODELS AND QUESTIONS

The conduct of integrated spatial structure studies is certain to be a difficult undertaking, requiring coordination of the best in field study approaches, technical gadgetry, and analytic technique. No single approach is likely to monopolize advances when they do occur, but one thing seems virtually certain. The critical shortage at this point is one of data, not theory or instrumentation. To remedy this we need not just more data but rather an understanding of which data are critical for defining and differentiating alternative spatial structure hypotheses. I shall explore in this paper the role which formal modeling approaches can play in helping to meet these needs. My emphasis will be on the use of models as an explicit framework for the synthesis of existing data and hypotheses, and for the

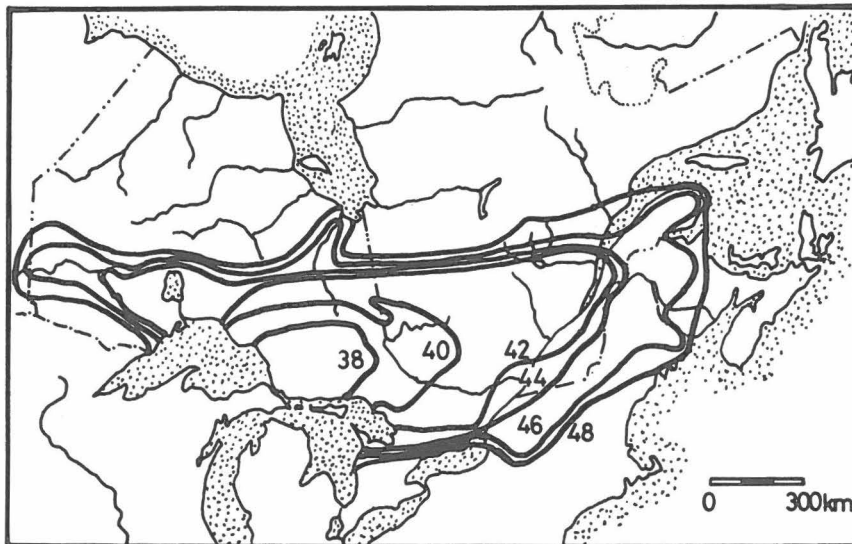


Fig. 1: The spatial outbreak pattern. Maximal extent of heavy budworm defoliation damage in eastern North America for 1938-1948, the last outbreak sequence before extensive insecticide spraying was introduced. Redrawn from BROWN (1970).

analysis of their implications. In this role, models become aids to asking better questions, helping to focus scarce research funds, manpower, and opportunities where they will do the most good.

Relatively few efforts have yet been made to apply modeling approaches to the comprehensive analysis of spatial structure problems in ecology. Some of the

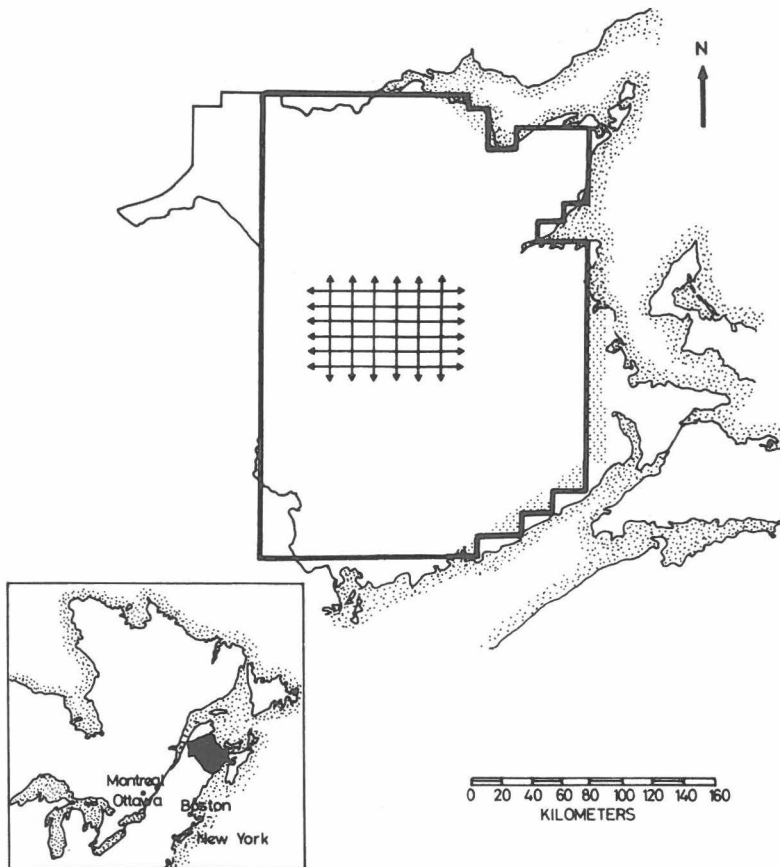


Fig. 2: Location and configuration of the modeled area. Approximately seven million hectares of the Canadian province of New Brunswick are decomposed into 393 grids of dimension 15.43 km (E-W) x 10.92 km (N-S), as shown. Events within grids are treated as spatially homogeneous representations of the model suggested in fig. 3. Grids are linked by insect dispersal.

best work has been done in marine plankton systems (STEELE, 1978; O'BRIEN & WROBLEWSKI, 1976), but pioneering entomological studies have begun to appear as well (MYERS, 1976; R. JONES, 1977 a, b; several papers in this volume). In this paper I shall illustrate some of the problems and potentials of one such approach through a summary of results obtained in studies of the spruce budworm (*Choristoneura fumiferana*) - boreal forest system of eastern North America.

The budworm-forest system is described by several contributors to this volume (see especially the contribution by SANDERS). In the briefest of terms, it consists of a lepidopteran defoliator which, in its periodic epidemic irruptions, is capable of inflicting heavy mortality on several important tree species. (*Abies balsamea*, *Picea glauca*) of the eastern boreal forest. Outbreaks occur irregularly at 20-80 year intervals (BLAIS, 1968), expanding to cover many millions of hectares in a few years (fig. 1).

Budworm-forest relationships have been studied extensively, particularly in the Canadian Province of New Brunswick (fig. 2). The classic population dynamics research reported in MORRIS (1963) provided a solid base on which much subsequent work has been based (see, e.g., PREBBLE, 1975; BELYEA, 1975).

More recently these studies have been extended to include analysis of the managerial and policy design aspects of man-budworm-forest interactions (BASKERVILLE, 1976; CLARK *et al.*, in press). Finally, a growing awareness of the importance of spatial structure considerations to both ecological and managerial understanding of the system led in the early 1970's to a unique multidisciplinary research program on budworm dispersal (GREENBANK *et al.*, unpublished). Modeling studies to synthesize these findings have been reported elsewhere (JONES 1977; CLARK *et al.*, 1978; CLARK, 1979; CLARK & HOLLING, in press), and are summarized below under the headings of local structure, dispersal, and spatial structure (cf. LEVIN, 1976).

LOCAL STRUCTURE

A simulation model of local processes

It is convenient to begin with a discussion of budworm-forest interactions as they would occur over an arbitrarily small spatial area in the absence of adult

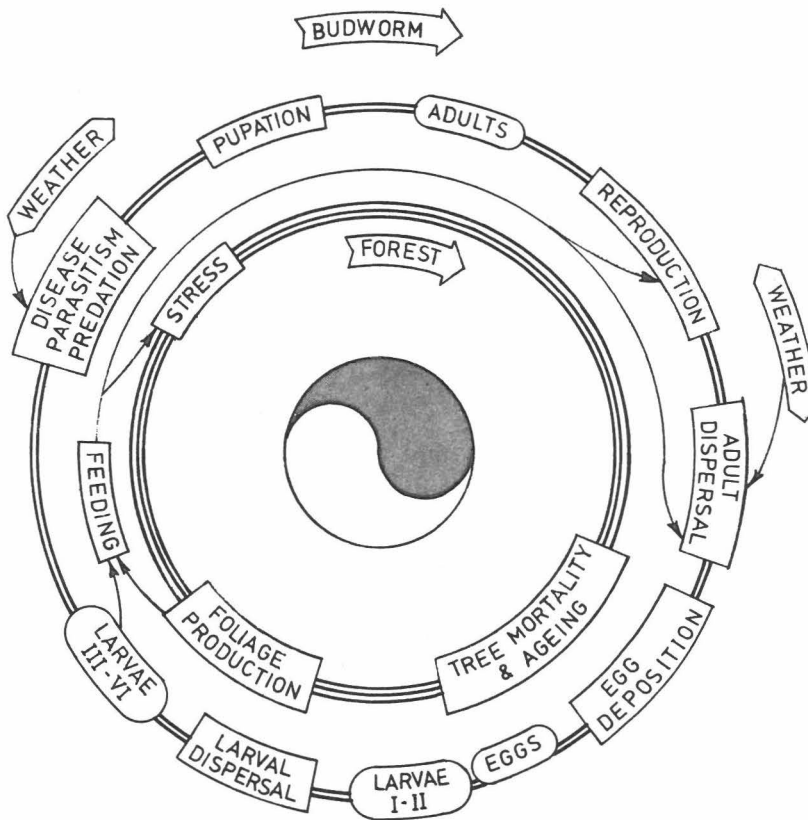


Fig. 3: The process cycle for the budworm-forest system. The inner ring represents the forest cycle, the outer ring the budworm cycle. Ellipses indicate insect life stages; arrows show causal relationships among processes and insect life stage densities. After JONES (1977).

moth dispersal. The relevant relationships at this scale are essentially those studied by MORRIS (1963) and his colleagues: growth, feeding, reproduction, predation, parasitism and the like. Using MORRIS' (1963) and more recent data, these relationships are combined in what GILBERT *et al.* (1976) have called a «dynamic life table» model of the budworm-forest system. The equations and parameter values are given in JONES (1977). Figure 3 summarizes those relationships for the budworm and forest as they apply to a single year's modeled population dynamics.

Because the model is biologically realistic, its equations must be solved by recourse to computer simulation. When such simulations are carried out, they yield predictions of outbreak magnitude and frequency which are not inconsistent with observations made on the real world system (CLARK & HOLLING, in press). But although computer simulation is a necessary tool for exploring complex ecological models it is not a particularly satisfactory approach for gaining understanding of the system's behavior.

Equilibrium manifolds for budworm

My colleagues and I have found it useful to supplement our extensive simulation studies with a form of graphical compression known as «equilibrium manifolds». Introduced into the ecological literature by JONES (1975), similar approaches have since been put to good use in the analysis of a wide range of population dynamic studies (SOUTHWOOD & COMINS, 1976; JONES & WALTERS 1976; MAY, 1977; PETERMAN *et al.*, in press; BERRYMAN, 1979). The development of manifolds for our budworm-forest model is described at length in CLARK & HOLLING (in press). For present purposes a brief summary will suffice.

Figure 4 shows a typical equilibrium manifold calculated from our local model of budworm-forest interactions. The ordinate gives the population densities of budworm (\bar{N}) which have the characteristic that, other things being equal, growth equals mortality and they will not change from one generation to the next. The abscissa shows a measure of forest density (F), roughly equal to mean tree age. For forest densities less than F' there is no nonzero budworm equilibrium. No matter what insect density is present at the beginning of one generation, this will fall towards zero in the next year due to the sparse condition of the forest resource. For $F > F''$ there is a single stable equilibrium (\bar{N}^+), corresponding to the epidemic condition of the insect population. No matter how low the initial insect densities in such mature forests, subsequent populations will rise towards an outbreak at \bar{N}^+ . Between F'' and F''' , three budworm equilibria are present simultaneously. A lower stable surface (\bar{N}^-) corresponds to the endemic situation, while the upper stable surface (\bar{N}^+) represents the epidemic situation as before. An intermediate unstable equilibrium surface (\bar{N}^0) separates these two stable surfaces, forming a «Watershed» between the epidemic and endemic conditions. All initial insect densities less than \bar{N}^0 will be drawn towards \bar{N}^- , and all greater than \bar{N}^0 will move towards \bar{N}^+ . The \bar{N}^0 surface is thus analogous to the «escape» threshold of HOLLING (1959, 1973), MORRIS (1963), TAKAHASHI (1964), and later writers.

Manifolds for systems analysis

It is worth emphasizing that the manifold of fig. 4 is calculated directly from the realistic simulation model of budworm-forest interactions. Its configuration

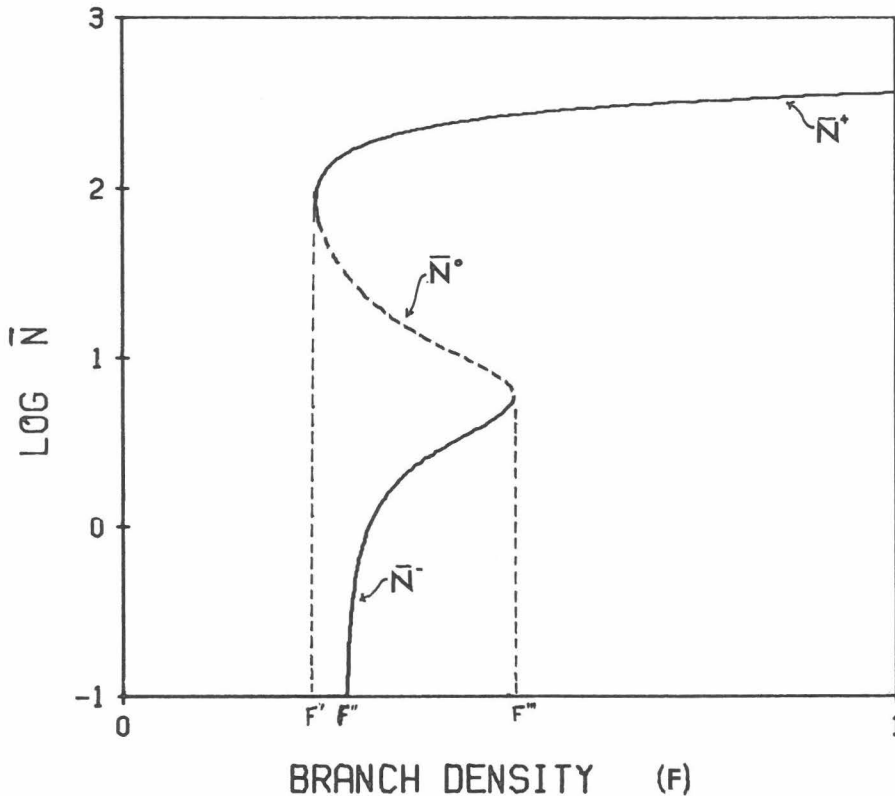


Fig. 4: Equilibrium manifold for the local structure model of budworm-forest interactions, assuming no dispersal. The surface represents larval densities (\bar{N}) which show no tendency to change when branch (forest) density is held constant at its specified value. \bar{N}^+ , \bar{N}^- , and \bar{N}^o are stable epidemic, stable endemic, and unstable «release» equilibria, respectively.

therefore reflects the detailed ecological relationships included in that model. In particular, it can be shown (PETERMAN *et al.*, in press) that the upper equilibrium surface (\bar{N}^+) is largely defined by intraspecific competition for food among high density budworm. The intermediate unstable surface can arise from any number of Allee-type mechanisms which impart an increasing survivorship rate over some range of densities (OKUBO, 1974; SEGEL & LEVIN, 1976). In the present model the «pit-like» configuration formed by this unstable surface (\bar{N}^o) and the lower stable one (i.e. \bar{N}^-) is due to the saturating «Type-III» functional response of the budworms vertebrate predator guild (MORRIS, 1963; HOLLING, 1965; MURDOCH & OATEN, 1975). The general possibility of similar effects from invertebrate predators and parasitoids has been stressed by HASSELL *et al.* (1977). In any event, as predation is decreased from the level found in nature to zero, the «pit» gradually disappears in the manner shown in fig. 5. The significance of such changes in the manifold configuration can be appreciated as follows.

Refer to fig. 6, which shows the same basic local structure manifold developed earlier in fig. 4. As the forest grows following fire, logging, or previous bud-

worm attacks, the forest density (F) rises. At $F > F'$, nonzero budworm equilibria become possible. The budworm population tracks along the \bar{N}^- surface, and any random fluctuations are drawn down to that surface. As the forest matures past F'' , the lower endemic equilibrium surface (\bar{N}^-) disappears, and all budworm densities are drawn to the epidemic equilibrium at \bar{N}^+ . Note, however, that although this upper surface is stable for the budworm, it is not so for the forest. High insect populations inflict mortality on the forest, reducing F , lowering budworm, and finally cycling the system back to its original endemic condition. It is evident that changes to local system structure (such as decreases in predation) which reduce the «depth» of the low density «pit» should permit this natural outbreak cycle to initiate at lower forest densities (F'''). This is born out by simulation experiments which confirm the additional expectation that smaller «pits» tend to yield higher frequency outbreak cycles.

Immigration and local structure

Before turning to an explicit consideration of the dispersal process, it is useful to consider the several effects of exogenously generated budworm immigrants on local system structure. In the previously developed outbreak scenario of

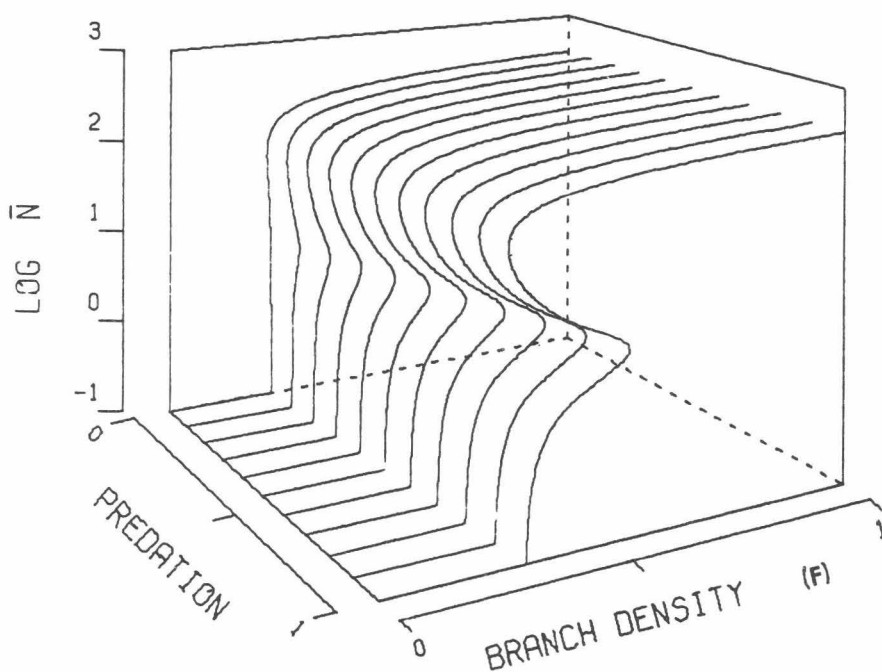


Fig. 5: Equilibrium manifold for budworm as a function of predation intensity and branch density. Predation scaled from 0 (no predation) to 1 (natural level of predation as included in model); other conventions as in fig. 4. Note that the manifold for PREDATION = 1 is the same as that shown in fig. 4.

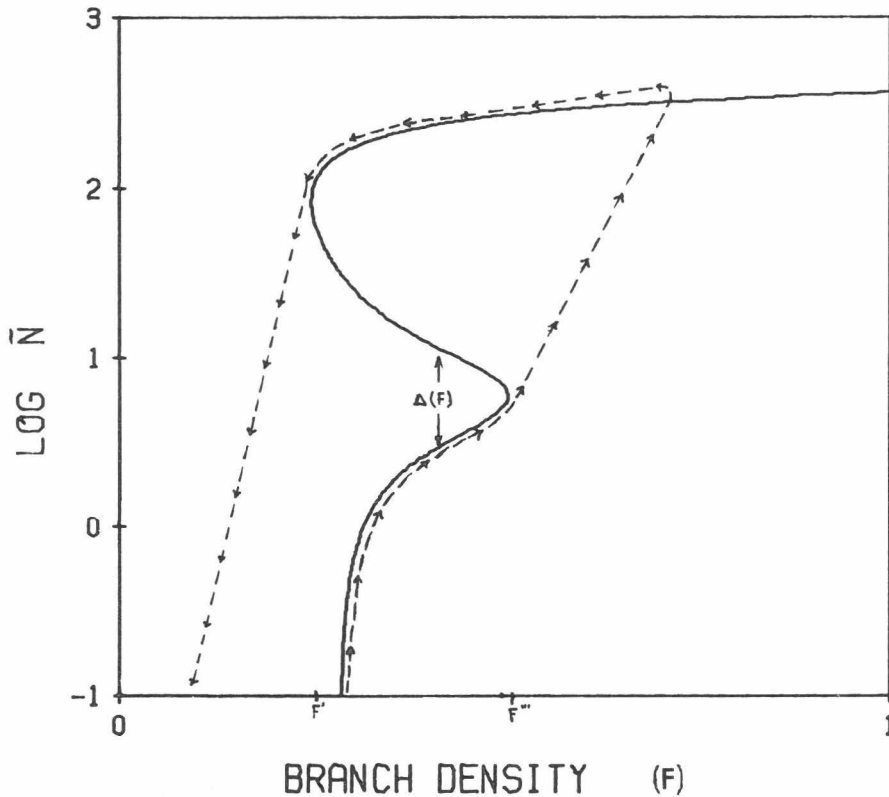


Fig. 6: Equilibrium manifold for the local structure budworm model showing a typical outbreak trajectory. $\Delta(F)$ is the quantity of random fluctuation or immigration necessary to boost the system from its endemic to its epidemic attractor surface.

fig. 6, budworm populations remain locked on the lower stable equilibrium surface (\bar{N}) provided that forest densities are less than F'' . But for $F' \leq F \leq F''$, random fluctuation in budworm density or immigration of a quantity of budworm greater than $\Delta(F)$ (see fig. 6) is sufficient to boost the system across the unstable equilibrium \bar{N}^0 and into a «premature» outbreak. The necessary level of perturbation $\Delta(F)$ decreases as F increases until, above F'' , the outbreak occurs spontaneously. Viewing the same relationship another way, an increase in the net level of immigration causes a decrease in the range of forest conditions over which the three distinct budworm equilibria exist. This is shown graphically in fig. 7, where I have recomputed manifolds for the local structure model under an arbitrary range of constant immigration rates.

The resemblance between these immigration manifolds and those computed for decreased predation levels (fig. 5) is striking and significant. In both cases, the alteration of a biological rate or process results in a major alteration of the system's low density equilibrium structures. The range of forest conditions under

which triple equilibria occur is reduced, the minimum forest density for spontaneous outbreak decreases, and the system's natural oscillation frequency rises. In short, the effects of decreased predation and increased immigration are so similar that most observations of system behavior will be unable to distinguish them. Furthermore, experimental analyses of either process alone clearly risk being confounded by unmeasured variation in the other. The strategic implications for experimental design are clear, though related tactical issues require further detailed investigation.

Finally, it is evident from fig. 7 that the quantity of immigrants actually arriving at a local site can have a major qualitative impact on system dynamics there. The remainder of this paper focuses on the interaction of local structure with insect dispersal processes and environmental heterogeneity to determine that quantity.

DISPERSAL

The dispersal process

Insect dispersal is now widely recognized as a distinct behavioral process through which organisms interact with spatial variation in their environments. As

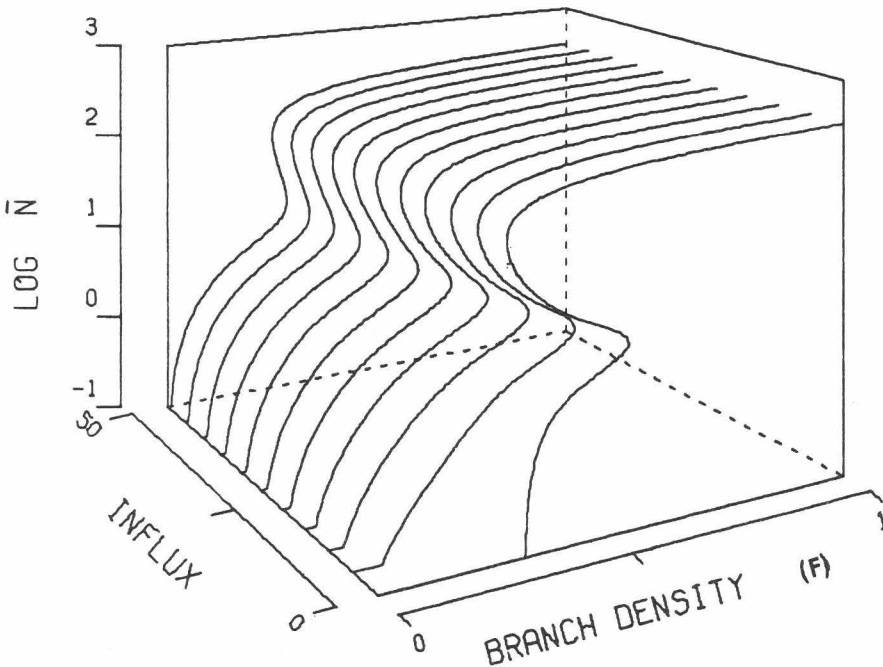


Fig. 7: Equilibrium manifold for budworm as a function of externally generated budworm immigration rate and branch density. Immigration scale from 0 (no immigration) to 1 (an arbitrary but feasible rate; see CLARK *et al.* 1978). Other conventions as in fig. 4; compare with fig. 5.

with other ecological behaviors, it can be analyzed via a functional components approach of the sort developed for predation studies by HOLLING (1966). Reviews by KENNEDY (1975, 1961), SOUTHWOOD (1962), DINGLE (1974, 1972), JOHNSON (1969, 1966), SCHNEIDER (1962), and WILLIAMS (1957) identify three basic components of flight dispersal, although terminology varies: the *exodus response* determines who leaves the local habitat, and under what conditions they do so; the *displacement response* determines the distance and direction moved following exodus; the *settling response* determines the «trivial» or «appetitive» search flight undertaken on termination of displacement activities and locates the animal in its new habitat.

I analyze budworm moth dispersal with respect to each of these components in the following Sections. Data are drawn from the largely unpublished studies of DAVID GREENBANK (Canadian Forest Service), R.C. RAINEY (Center for Overseas Pest Research) and GLEN SCHAEFER (Cranfield Institute of Technology). A jointly authored article by these authors is in preparation, while some preliminary results are reported in GREENBANK (1973), RAINEY (1976), and SCHAEFER (1976). I review these data at length elsewhere (CLARK, 1979), and summarize some of the more interesting results below.

The exodus response

In his review of insect dispersal strategies, SOUTHWOOD (1962; see also 1977) concludes that «irruptive» species in general should exhibit facultative, habitat-sensitive exodus behavior. The same conclusion is reached in theoretical studies of GADGIL (1971), and has been discussed in the general context of multiple equilibrium systems by CLARK *et al.* (1978).

Two «variable exodus» hypotheses have received most attention in recent budworm dispersal studies. The first (called «Type C» for historical reasons), is based on early observations of WELLINGTON & HENSON (1947) and BLAIS (1953). It is an essentially ontogenetic argument which supposes a minimum basal exodus rate such that at least 35% of locally produced eggs are exported. This fraction increases substantially when stressful conditions lead to the production of small, light weight, low fecundity moths. A more recent hypothesis, first raised by GREENBANK (1973), postulates a direct density dependence in which no exodus flight occurs at low moth densities (less than, say, 1 moth/m² of branch area). Above this «threshold» density the exodus rate rises rapidly to a maximum of 50% or so of total fecundity.

This essay is not the place to argue the relative merits of these two hypotheses or their obvious variants. What is useful, however, is to show how we can explore their relative effects on the local structure analysis. Recall that the equilibrium manifolds of figs. 4–7 were computed on the assumption of zero exodus and, except for fig. 7, of zero immigration. Maintaining the zero immigration assumption but introducing the two exodus hypotheses described above allows calculation of the more realistic manifolds shown in fig. 8. Several interesting conclusions can be drawn immediately from inspection of these manifolds, whereas an exploration of the alternative hypotheses by direct simulation is time consuming and confusing in the extreme.

Focusing first on the «Type C» (ontogenetic) manifold, it is clear that the basal exodus rate (here, 35%) will have a major effect on system dynamics. The

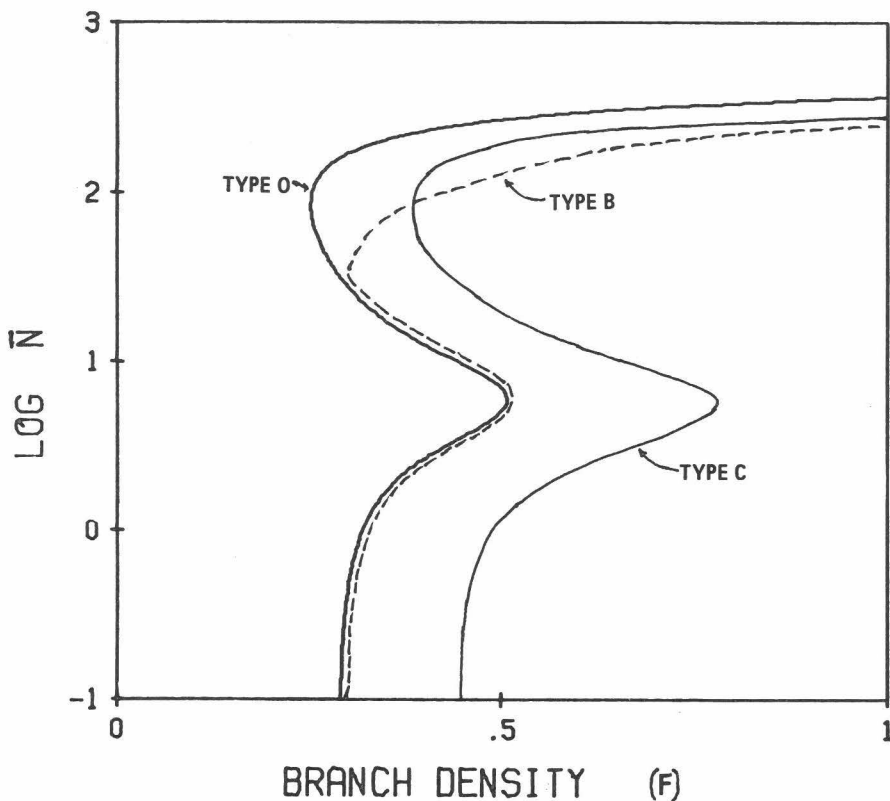


Fig. 8: Equilibrium manifolds for the budworm model under three exodus hypotheses and no immigration (see text). The Type O manifold is identical to that of fig. 4.

minimum forest densities necessary to permit and to trigger outbreaks are all much higher, and natural outbreak frequencies will be correspondingly lower than in the zero exodus (Type O) case. Similarly, for any given forest density (F), the necessary $\Delta(F)$ to flip the system from its edemic to its epidemic attractor is much larger under Type C exodus. One additional point of interest is not evident in fig. 8. This Type C manifold, reflecting the Wellington/Blais fecundity-mediated variable exodus rate, is essentially indistinguishable from a manifold computed under the assumption of a constant basal rate of exodus. Further analysis of this observation (CLARK, 1979) shows that the postulated fecundity effect occurs only at such high insect densities as to rarely affect local dynamics, and thus merits a low priority rating in future research efforts.

Compare now the manifold for the moth density-mediated Type B exodus. Here, the refusal of moths to exodus at all below a certain threshold density causes the Type B and Type O (zero migration) manifolds to overlap at low densities. Significantly, the actual threshold values hypothesized turn out to be largely above the «pit» formed by the unstable (\bar{N}^0) and endemic (\bar{N}^-) equilibrium surfaces (see fig. 8). It follows that predictions of system behavior under endemic and

outbreak release situations will be essentially identical under Type O and Type B exodus hypotheses, while these will differ radically from those under Type C exodus. Finally, fig. 8 shows that the strong exodus response of the Type B hypothesis above the threshold density level will result in substantially lower epidemic equilibria (\bar{N}^+) than either the zero migration (Type O) or ontogenetic (Type C) hypotheses. This can have profound implications for system dynamics by affecting the level of tree stress and mortality induced under epidemic conditions (see section «Exploring alternative dispersal hypotheses»).

Analyses of the sort summarized here cannot determine which, if any, of the competing exodus hypotheses are correct. What they have done is to identify certain priority research areas (Is there in fact a low density exodus threshold?), deemphasize others (What is the fecundity or size vs. exodus relationship?), and suggest critical tests to differentiate alternative theories.

The displacement response

As the budworm moth leaves its breeding place in exodus flight, it rises above the boundary layer (TAYLOR, 1958) and is displaced via the wind system prevailing at the time and altitude of flight. Where the insect lands is a complex function of its own behavior, environmental conditions, and wind field heterogeneities of the sort discussed by RAINEY (1979). But though it would be very difficult to assess the fate of a given insect on a given flight, some useful things can be said about the mean seasonal displacement distribution of the total population of moths emigrating from a source location through the course of a full dispersal season.

Several early estimates of this displacement distribution were made using a variety of techniques (GREENBANK, 1973), but it is only with the advent of radar techniques (SCHAEFER, 1976) that quantitative estimates of moth flight duration have become available. Combined with data on wind velocity at flight altitudes and moth air speed, these yield the displacement distance distributions of fig. 9.

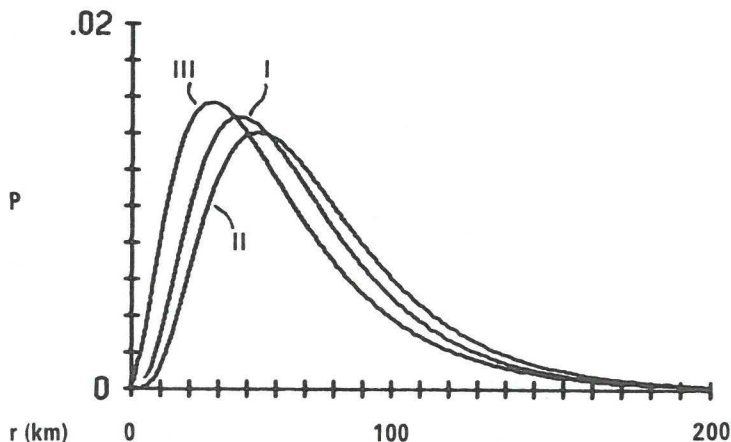


Fig. 9: Probability distribution for single flight displacement of dispersing budworm moths under three interpretations of radar observation data. P is normalized for 1 km increments from 0-200 km.

The three plotted functions result from three alternative interpretations of the available flight duration data, and are sufficiently similar to justify a deemphasis of concern regarding those alternatives. For all curves, the shape of the empirical distribution is qualitatively that of the Gaussian plume models discussed by CAMERON & McMANUS (1979). Few moths land within 10 km of their exodus site, about 25% fly less than 30 km, and 25% of the moths fly 75 km or more. Such dispersal scales are consistent with analyses of the rate of outbreak expansion (FIDS, 1938-1975; CLARK, 1979). Furthermore, simulation experiments of the sort discussed in section on spatial structure show that large scale patterns of population dynamics are relatively insensitive to changes on the order of $\pm 50\%$ to the displacement distributions of fig. 9, again suggesting that this phase of the dispersal studies on budworm may now be satisfactorily developed.

The settling response

A third component of insect dispersal behavior is referred to as «settling» (JOHNSON, 1966), «stopping» (R. JONES, 1977a), «immigration/deposition» (GREENBANK, 1973), or «a return of appetitive response» (KENNEDY, 1975). Whatever their terminology, most authors agree that the phenomenon encompasses termination of long-range movement and installation of the disperser in its new habitat. For many insects this installation constitutes an active, sensory search for appropriate vegetative stimuli (SOUTHWOOD, 1962; DINGLE, 1972). But beyond such broad generalizations, the settling response is little understood or studied: in his massive monograph on insect flight dispersal, JOHNSON (1969) declares the problem to constitute a subject in itself, and leaves it to others - still not in evidence - for review.

Research on settling response in budworm is almost nonexistent, and relevant evidence is both largely anecdotal and wholly descriptive. In such cases, an approach of last resort is to pose various extreme but physically feasible hypotheses, assess the sensitivity of emergent population dynamics to those extremes, and focus subsequent field research accordingly.

For the budworm studies reported here, the physical model suggested by fig. 10 has been employed. To settle successfully, moths must descend on land containing host species of trees (on average, about 40% of New Brunswick). Those which do so must also reach trees of an age class which will support larval development (ages > 20 years are classed as «susceptible»). Finally, moths landing on susceptible host trees must locate live foliage on which to oviposit (a potentially difficult task under outbreak conditions).

In the most pessimistic case for budworm, success at each stage of the settling process will be proportional to the relative target areas. Total success will be a product of those individual rates. Under circumstances commonly encountered early in an outbreak, total settling success under this assumption will average less than 30%. Not too far towards the opposite extreme, a physical model based on the assumption of multiple, but still passive, targeting attempts at each stage can easily yield total settling successes in the neighborhood of 80% (CLARK, 1979). The implied difference of 50% in settling survival rates would be expected to have major consequences for population dynamics, especially when it is recognized that it operates directly on reproductive females. Simulation experiments confirm this expectation (see section on exploring alternative dispersal hypotheses), pointing to

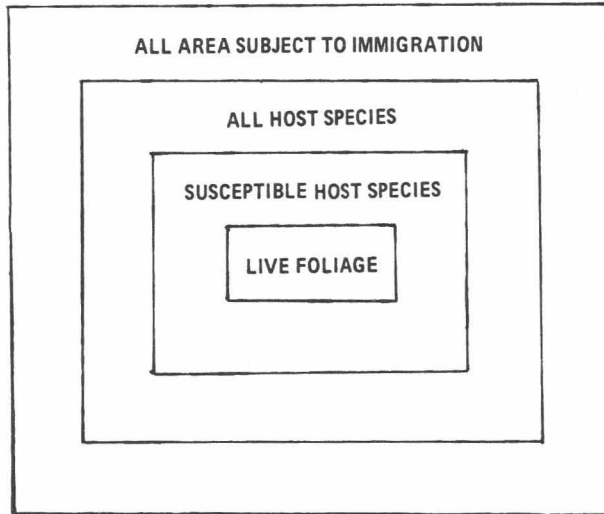


Fig. 10: Settling response model for budworm moth dispersal. Successful dispersers must sequentially target on the portion of the environment containing host tree species, susceptible age classes of those species, and live foliage.

the collection of meaningful settling response data as perhaps the highest priority item for future research on the budworms' (and perhaps other insects') dispersal behavior.

SPATIAL STRUCTURE

A simulation model of spatial interactions

Analysis of local structure and dispersal movements along the lines discussed in previous sections can provide the basic components for spatial theories of population dynamics. But to assess the long term, large scale interactions of those components, and to incorporate the effects of environmental heterogeneity in the analysis, it is necessary to develop an explicitly spatial model of the budworm-forest system. In the present study, this is done by subdividing the 7 million hectares of New Brunswick into 393 local «patches» (fig. 2).

Population dynamics in each patch are governed independently by the local structure equations and manifolds, and patches are linked via the dispersal processes, as discussed in the two previous sections. It is necessary realistically to specify the proportion of each patch covered by the budworm's preferred host species, the age-class structure of those species, and the «initial» budworm densities at each location. These data were gathered from historical forest inventory and insect survey records for the year 1953, and used as starting conditions for model runs and validation tests (CLARK & HOLLING, in press).

The typical simulation model run begins with the historical conditions of 1953 and invokes the previously discussed ecological process relationships to generate the next year's conditions for each of the 393 local patches of the system. The results are most directly viewed as a temporal map sequence of predicted

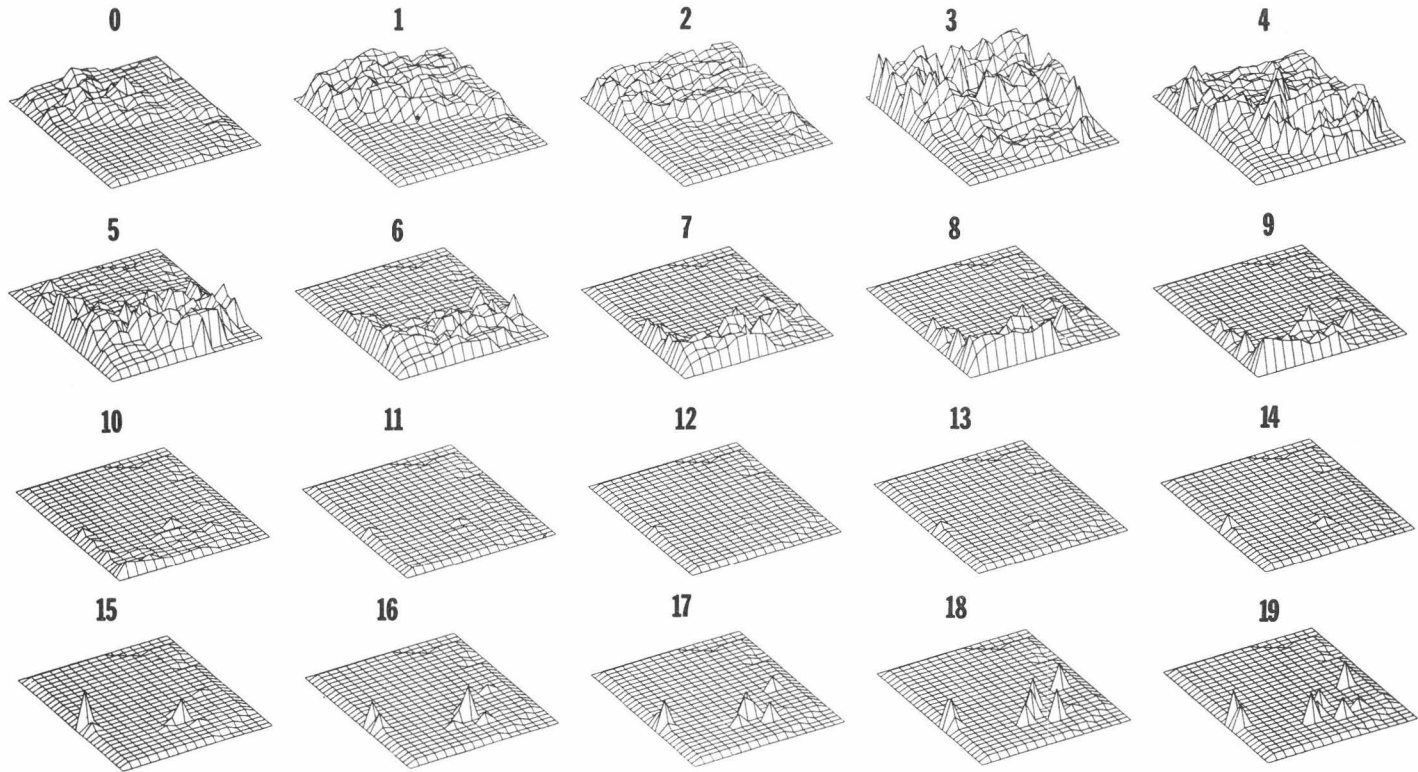


Fig. 11: Twenty-year sequence of spatial patterns predicted by the model. Horizontal (x,y) coordinates define a north-south by east-west spatial grid of 393 individual patches, each representing about 17,000 hectares of New Brunswick forest. Initial conditions are those for corresponding locations in New Brunswick in 1953. The vertical (z) axis depicts relative budworm egg densities on a linear scale.

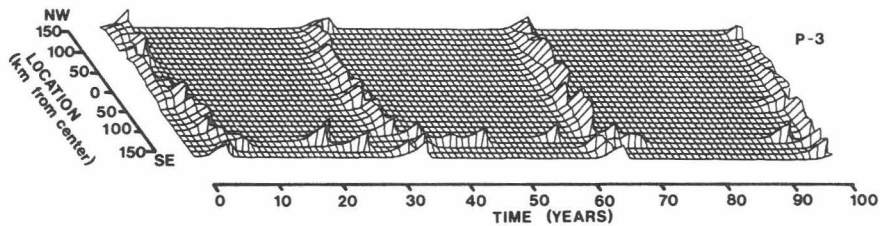


Fig. 12: Space-time plot for the basic model. This figure shows a time series plot of predicted egg densities on a one-dimensional spatial transect of the full map series for the basic model as originally shown in fig. 11. Each transect runs from NW to SE through the center of the modeled region, and shows the relative budworm egg density on the vertical (z) axis. A separate transect sample is taken for each of the 100 simulated years, and arranged sequentially on the time (x) axis. This figure shows clearly the 30-odd year outbreak periodicity characteristic of the province as a whole, as well as the tendency for a few patches (usually near the SE end of the transect) to oscillate out of phase and at a higher rate. Note the evident spread of the initial ($t=0$) outbreak from NE to SW; the origin of the second outbreak sequence ($t\approx 30$) in the center and its spread NW and SE; and the progression of the third outbreak ($t\approx 60$) from SE to NW. Compare with the complete data of fig. 11 'P-3' is an index code for the computer run.

densities for forest and budworm. A sample series is shown in fig. 11. The general asymmetrical wave pattern, the rates of spread, and the out-of-phase «hot spots» are nicely in accord with historical observation, as are responses to managerial perturbation (CLARK *et al.*, 1978).

For many purposes, it is more revealing and concise to compress the full map series predictions by sampling each map along a fixed linear transect, and then plotting the transects as a temporal series. This is done in fig. 12 for the full simulation results of which fig. 11 shows the first 20 years. Again, the rates of spread and «hot spots» are obvious, and now the typical 30 year outbreak interval is clear as well. In the next section I couple this spatial output format with local manifold analyses to illustrate some of the question-asking purposes to which the spatial simulation model can be put.

Exploring alternative dispersal hypotheses

The spatial implications of the alternative dispersal hypotheses developed in the section on dispersal can now be explored through integrated use of the full simulation model and equilibrium manifolds. As a preliminary check, fixing the exodus rate in each of the 393 local sites at zero (Type O exodus) results in a loss of the integrated wave pattern and the emergence of independent outbreak phasing in the individual patches of forest (CLARK *et al.*, 1978; fig. 14a). It follows that the historically observed pattern of spatial coherence in budworm outbreaks requires the homogenizing influence of moth dispersal, and does not follow from forest age class structure or environmental heterogeneities alone. On the other hand, as expected from the manifold analysis, moth dispersal is not a necessary precondition for local outbreak development.

Fig. 13 shows the results of several other representative dispersal experiments. For fig. 13A, the Type C (ontogenetic) exodus used in the simulation of fig. 12 is replaced by the alternative Type B (threshold) exodus hypothesis. The consequences are dramatic, and the periodic outbreak pattern is replaced by a more and more even distribution of budworm in space and time. This result is historically unprecedented, and the temptation is to conclude that the Type B

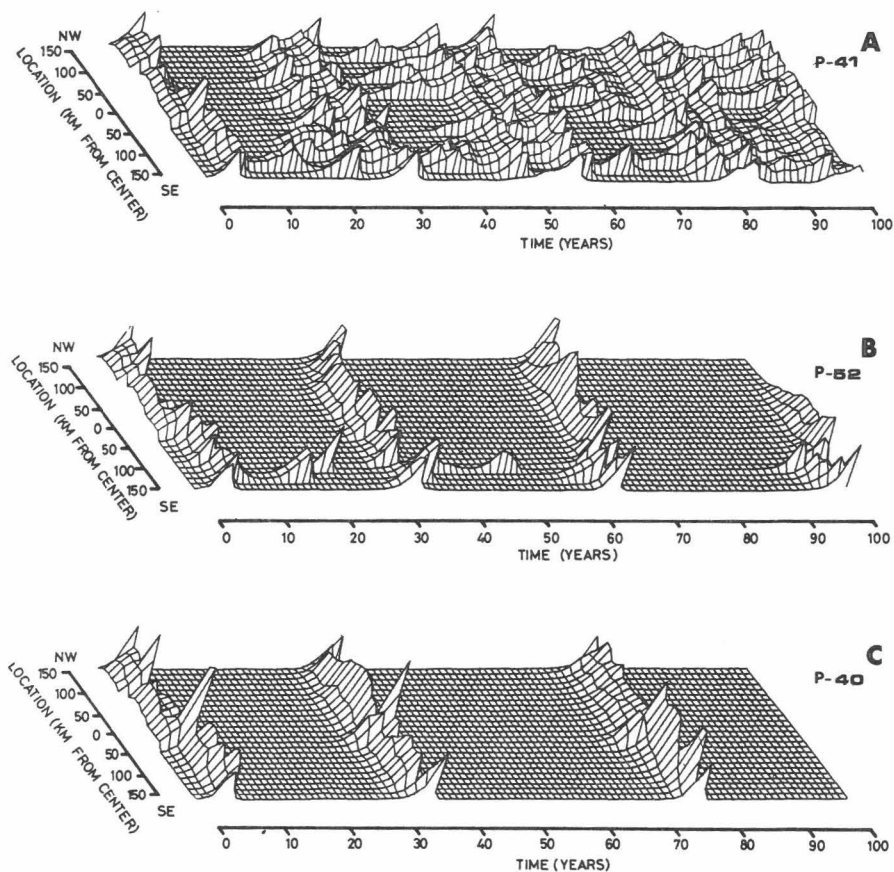


Fig. 13: Space-time plots for alternative dispersal hypotheses. The basic format is the same as that for fig. 12. A (run P-41) shows the results of substituting Type B exodus (fig. 8) for the Type C exodus used to generate fig. 12. B (run P-52) reflects a flight displacement distribution with ordinate values one half of those given in fig. 9 and used for the simulation of fig. 12. C replaces the poor targeting success of fig. 12 with more effective assumptions. See text.

exodus hypothesis is false. This may be the case, but the only valid conclusion at this point is that the total theory represented by the local structure, spatial heterogeneity, Type B exodus, and other dispersal processes of the present model generate predictions at odds with reality. The confusing spatial picture of fig. 13A can, however, be somewhat unravelled by returning to the manifold considerations of the section on the exodus response. Further analysis at this level suggests that the shortcomings of the theory may in fact lie not in the dispersal formulations, but rather in the local structure relationships between budworm feeding and tree mortality. New research efforts are consequently focused on those insect-tree relationships, as well as the exodus process per se. But whatever the eventual findings of this research, it is important to realize that the potential shortcomings of the present local structure theory were revealed only through an explicitly spatial analysis of system dynamics. This is a good specific illustration of STEELE'S (1975)

general contention that such spatial models may often constitute the only practical means of distinguishing among otherwise similar local hypotheses.

For fig. 13B, I again employ the Type C exodus hypothesis, but now introduce a displacement function for which all of the distances on the ordinate of fig. 9 are halved. The resulting patterns of population dynamics are virtually indistinguishable from the standard case of fig. 12, supporting my earlier conclusion regarding the relative unimportance of precise refinements to the existing displacement data.

Finally, fig. 13C shows the result of shifting from the pessimistic, low success settling hypothesis used in generating fig. 12, to the more optimistic «multiple attempt» hypothesis described in the section on the settling response. The higher survival rates thus imposed effectively shift the Type C manifold of fig. 8 towards the Type O form. The result is higher outbreak densities, more dispersers, and a consequently greater degree of spatial homogeneity (including elimination of isolated «hot-spots»). The associated increases in forest mortality drive F further left on the manifolds, leading in turn to a lengthening of the interoutbreak period. Once again, the population dynamic consequences of the alternative hypotheses are substantially different, thus indicating a priority area for future research.

Spatial heterogeneity

It remains to explore consequences of what LEVIN (1976) has called «local uniqueness» – i.e. the fact that various biological «rules of change» may differ among local patches of the total spatial system.

RAINEY (1951; 1976 and references therein) was one of the first to point out that wind field heterogeneities affecting insect dispersal could constitute a «local uniqueness» factor of critical importance to population dynamic studies. His recent work on budworm (RAINEY, 1979) has contributed greatly to our understanding of the atmospheric arena in which that insect executes its dispersal processes. In consultation with RAINEY and others, the spatial structure theory generating the predictions of fig. 12 was formulated so as to include influence on moth displacement of wind convergence and frontal phenomena (see also the comments on «sea breeze fronts» by CAMERON *et al.*, this volume).

Somewhat to our surprise, when these heterogeneous effects are removed – leaving only the spatially homogeneous patterns of mean prevailing winds – the predictions of fig. 14a result. The large-scale, long-term dynamics of the budworm system model seem to be qualitatively similar in the cases with and without wind field heterogeneities, though the quantitative values at given locations certainly are affected.

In retrospect, the reasons for this similarity are again implicit in the local structure manifold of fig. 6. Wind field heterogeneities concentrate airborne moths, thus yielding sufficient influx $\Delta(F)$ to trigger outbreaks at a lower forest density and with a lower total quantity of moths than would otherwise be possible. But once a sizable outbreak is initiated, there are far more than the necessary $\Delta(F)$ moths available for colonization of even a hundred kilometers from the outbreak center (CLARK, 1979). Wind field heterogeneities are therefore superfluous to rapid outbreak spread. Furthermore, in the present theory such sizable outbreaks inevitably develop, independent of disperser concentrations, since forest growth eventually carries forest density beyond the F''' threshold.

The implication of this analysis is that we need not be overly concerned with complex wind field patterns in our future work on the «macro» spatial dynamics of spruce budworm. This conclusion holds precisely to the extent that we credit the basic budworm theory modeled here. To conclude otherwise requires another equally plausible theory of budworm-forest interactions in which there is no equivalent to the forcing-function role of forest density, or a much lower level of overall dispersal [Note, however, that nothing said in the foregoing argument discounts the potential importance of wind field heterogeneities for short-term, local dynamics and management in the budworm-forest system].

Spatial heterogeneities

A second and more commonly considered sort of heterogeneity includes all those geographic, edaphic, and other factors which make the «stages» of real

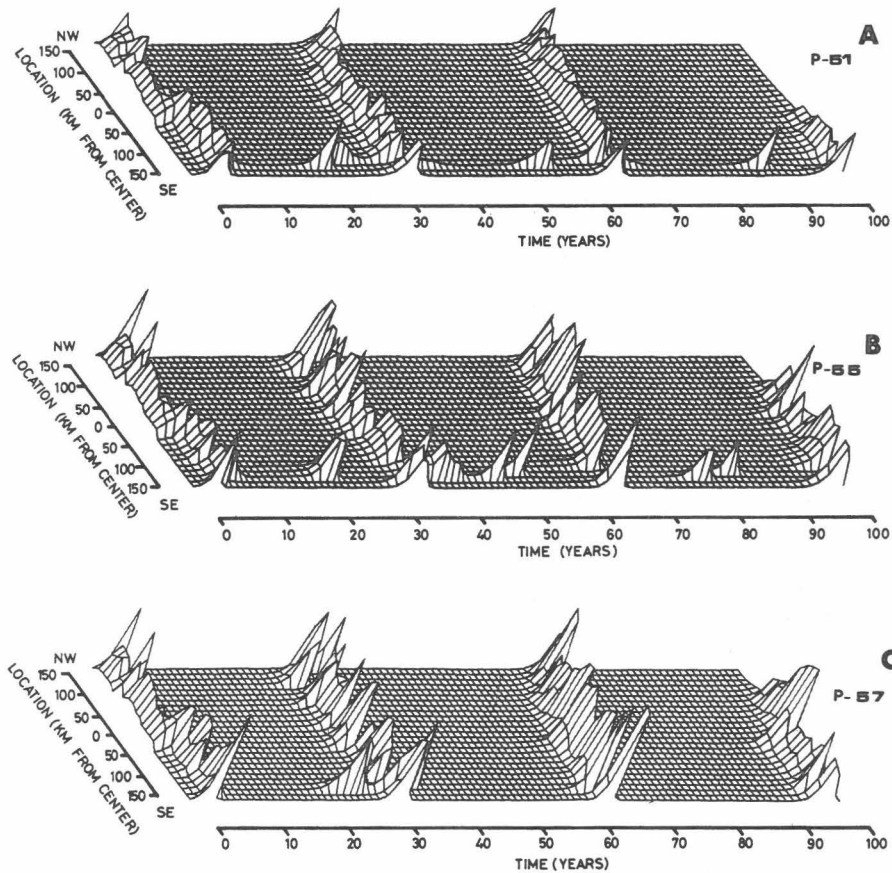


Fig. 14: Space-time plots for alternative spatial heterogeneity hypotheses. A (run P-51) shows the results of removing all wind field heterogeneities used in the basic theory of fig. 12. B (run P-55) imposes a reduced tendency for exodus in the high, cold (generally NW) region of the study area. C (run P-57) supplements the heterogeneities of P-55 with an additional phenological influence on larval survival.

world spatial structure different from place to place. The question here is not whether such heterogeneity exists – which of course it does – but rather which aspects of the heterogeneity make a substantial difference to overall patterns of population dynamics.

The basic spatial structure theory underlying fig. 12 is constructed on the simple assumption that no spatial heterogeneities are necessary to account for qualitative patterns of population dynamics in the New Brunswick budworm system. A variety of more complex alternative hypotheses are available in the literature. In fact, the patterns predicted of figs. 11 and 12 appear to be rather more homogeneous than those encountered in nature (CLARK *et al.*, 1978). A statistical effort to screen alternative hypotheses by correlating observed spatial variance in population dynamic patterns with a range of geographically distributed variables suggested two potentially important heterogeneities for detailed investigation (CLARK, 1979). Sample results are shown in figs. 14B and 14C.

Several workers (e.g. GREENBANK, 1973) have suggested that rapid radiation cooling in the evening might well prevent moth emigration from highland areas of New Brunswick, while still allowing immigration to those areas from lowland sources. Imposing this hypothesis on the model yields predictions of the sort shown in fig. 14B. Population densities do become more heterogeneous, with a clear concentration of insects in the highland (NW) area of the map transect. Outbreak spread rates and frequencies, as well as the «hot-spot» phenomena of the basic model, remain largely unchanged.

A second potential source of heterogeneity is implied by the hypothesis that budworm larvae survive better in areas that are phenologically advanced (tree development early in season) than in those which are phenologically retarded (see MORRIS, 1963). Incorporating this effect with the previously described altitude-temperature-flight inhibition relationship produces a spatial structure theory with the predictions shown in fig. 14C. Again, a comparatively high degree of population heterogeneity is induced, while outbreak frequency remains unchanged. On the other hand, the typical «hot-spot» heterogeneities of earlier evaluations are largely eliminated. Further manifold analysis shows that this is due to increased budworm survival in the phenologically advanced «hot-spot» area, which in turn leads to increased tree mortality, which finally removes the food supply upon which hot-spots had formally fed.

Many other environmental heterogeneities could be introduced. It seems likely that a number of these will have the general effect seen above, creating spatial heterogeneities in population densities and maintaining them in the face of substantial homogenizing dispersal. How much effort we should expend in this endeavour depends on how necessary or desirable we view an ability to realistically predict small scale spatial pattern in our theories of population dynamics. This, however, is as much a question of aesthetics as science, and therefore offers a convenient point at which to close the present discussion.

SUMMARY

In this essay, I have attempted to sketch some approaches to spatial structure analysis developed in the course of studies on population dynamics of the spruce budworm system. The basic framework for the analysis has been an array of formal theories or models hypothesizing various relationships among local

structure, insect dispersal, and spatial heterogeneity in the budworm-forest ecosystem. Such theories are perpetually incomplete, and are better viewed as aids to critical question asking, rather than as predictors of future population dynamics. The analysis of these budworm models emphasizes the fundamental role of local system structure as a stage from which dispersal processes are carried out, and on which they attain their broader adaptive significance. Furthermore, it promotes an integrated perspective of what we don't yet know, as well as what we do, thereby allowing a more productive allocation of overall resources for continuing research.

The study of spatial structure-population dynamics relationships is of critical importance, both to our general understanding of ecosystem behavior, and to our ability to manage such systems effectively. The time is ripe for progress, but this is as unlikely to come from mathematicians and modelers as it is from population and behavioral ecologists, so long as both groups continue to work in isolation from each other. The examples of RAINEY, BALTENSWEILER, and FISCHLIN (this volume) provide an encouraging sign that times are changing in this regard. The next ten years should be truly exciting ones.

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BIBLIOGRAPHY

- ANDREWARTHA, H.G. & BIRCH, L.C. 1954. *The distribution and abundance of animals*. University of Chicago Press, Chicago.
- BALTENSWEILER, W. & FISCHLIN, A. 1979. *The role of migration for the population dynamics of the larch bud moth, Zeiraphera diniana Gn. (Lep. Tortricidae)*. Mitt. Schweiz. Ent. Ges. 52: 259-271.
- BASKERVILLE, G. (ed.) 1976. *Report of the task force for evaluation of budworm control alternatives*. Dept. of Natural Resources, Fredericton, New Brunswick, Canada.
- BELYEA, R. et al. 1975. *The spruce budworm*. Forestry Chronicle 51: 135-160.
- BERRYMAN, A. 1979. *Effects of dispersal on the dynamics of an elementary bark beetle population model*. Mitt. Schweiz. Ent. Ges. 52: 227-234.
- BLAIS, J.R. 1953. *Effects of the destruction of the current years foliage of balsam fir on the fecundity and habits of flight of the spruce budworm*. Can. Entomol. 85: 446-448.
- BLAIS, J.R. 1968. *Regional variation in susceptibility of eastern North American forests to budworm attack based on history of outbreaks*. For. Chron. 44: 17-23.
- BROWN, C.E. 1970. *A cartographic representation of spruce budworm infestation in eastern Canada 1909-1966*. Can. For. Serv. Publ. No. 1263.
- CAMERON, E.A. & McMANUS, M.L. 1979. *Dispersal and its impact on the population dynamics of the gypsy moth in the USA*. Mitt. Schweiz. Ent. Ges. 52: 169-179.
- CLARK, W.C. 1979. *Spatial structure and population dynamics in an insect epidemic ecosystem*. Unpublished Ph. D. thesis; Department of Zoology, University of British Columbia; Vancouver, Canada.
- CLARK, W.C. & HOLLING, C.S. 1979. *Process models, equilibrium structures, and population dynamics: on the formulation and testing of realistic theory in ecology*. In: HALBACH, U. & JACOBS, J. (eds.) *Population ecology*. Fortschritte der Zoologie, G. Fischer Verlag, Stuttgart (in press).
- CLARK, W.C.; JONES, D.D. & HOLLING, C.S. 1978. *Patches, movements, and population dynamics in ecological systems: a terrestrial perspective*. In: STEELE, J.S. (ed.) *Spatial pattern in plankton communities*. Plenum Press, N.Y.: 385-432.
- CLARK, W.C., JONES, D.D. & HOLLING C.S. 1979. *Lessons for ecological policy design: a case study of forest ecosystem management*. Ecological Modelling (in press)
- DEN BOER, P.J. 1968. *Spreading of risk and stabilization of animal numbers*. Acta Biotheor. Leiden. 18: 165-194.

- DINGLE, H. 1972. *Migration strategies of insects*. Science 175: 1327-1335.
- DINGLE, H. 1974. *The experimental analysis of migration and life history strategies in insects*. In: BROWNE, L.B. (ed.) *Experimental analysis of insect behavior*, 329-342. Springer Verlag, N.Y.
- FIDS 1938-1978: *Forest insect and disease survey annual reports*. Ottawa: Canadian Forest Service.
- FISCHLIN, A. & BALTENSWEILER, W. 1979. *Systems analysis of the larch bud moth system*. Mitt. Schweiz. Ent. Ges. 52: 273-289.
- GADGIL, M. 1971. *Dispersal: population consequences and evolution*. Ecol. 52: 253-261.
- GILBERT, N., GUTIERREZ, A.P., FRAZER, B.D., & JONES, R.E. 1976. *Ecological relationships*. Freeman, San Francisco.
- GREENBANK, D.O. 1973. *The dispersal process of spruce budworm moths*. Can. For. Serv., Maritimes For. Res. Cen. Info. Rpt. M-X-39.
- GREENBANK, D.O., SCHAEFER, G., & RAINEY, R.C. (unpublished). *Spruce budworm moth flight and dispersal: new understanding from canopy observations, radar, and aircraft*.
- HASSELL, M.P., LAWTON, J.H., & BEDDINGTON, J.R. 1977. *Sigmoid functional responses by invertebrate predators and parasitoids*. J. Anim. Ecol. 46: 249-262.
- HOLLING, C.S. 1959. *The components of predation as revealed by a study of small mammal predation of the European pine sawfly*. Can. Entomol. 91: 293-320.
- HOLLING, C.S. 1965. *The functional response of predators to prey density and its role in mimicry and population regulation*. Mem. Entomol. Soc. Can. 45: 1-60.
- HOLLING, C.S. 1966. *The functional response of invertebrate predators to prey density*. Mem. Ent. Soc. Can. 48: 1-86.
- HOLLING, C.S. 1973. *Resilience and stability of ecological systems*. Ann. Rev. Ecol. Syst. 4: 1-23.
- HUFFAKER, C.B. 1958. *Experimental studies on predation: dispersion factors and predator-prey oscillations*. Hilgardia 27: 343-383.
- JOHNSON, C.G. 1966. *A functional system of adaptive dispersal in flight*. Ann. Rev. Ent. 11: 233-260.
- JOHNSTON, C.G. 1969. *Migration and dispersal of insects by flight*. Methuen, London.
- JONES, D.D. 1975. *The application of catastrophe theory to ecological systems*. In: INNIS, G.S. (ed.), *New directions in the analysis of ecological systems*, Pt. II: Simulation Councils Proc. 5(2): 133-148, Reprinted in *Simulation*, 29: 1-15, 1977.
- JONES, D.D. 1977. *The budworm site model*. In: NORTON, G.A. & HOLLING C.S. (eds.), *Proc. Conf. Pest Management*, October, 1976. IIASA CP-77-6: 91-155.
- JONES, D.D., & WALTERS, C.J. 1976. *Catastrophe theory and fisheries regulation*. J. Fish. Res. Bd. Can. 33: 2829-2833.
- JONES, R.E. 1977a. *Movement patterns and egg distribution in cabbage butterflies*. J. Anim. Ecol. 46: 195-212.
- JONES, R.E. 1977b. *Search behavior: a study of three caterpillar species*. Behavior. 60: 237-259.
- KENNEDY, J.S. 1961. *A turning point in the study of insect migration*. Nature. 189: 785-791.
- KENNEDY, J.S. 1975. *Insect dispersal*. In: PIMENTEL, D. (ed.), *Insects, science, and society*, 103-119, Academic Press, New York.
- KREBS, C.J., & MYERS, J.H. 1974. *Population cycles in small mammals*. Adv. Ecol. Res. 267-399.
- LEVIN, S.A. 1976. *Population dynamic models in heterogeneous environments*. Ann. Rev. Ecol. Syst. 7: 287-310.
- LEVIN, S.A. 1978. *Population models and community structure in heterogeneous environments*. In: LEVIN, S.A. (ed.), *Populations and communities*, 2, pp. 439-476, Math. Assoc. Amer. Studies in Mathematical Biology.
- MAY, R.M. 1977. *Thresholds and breakpoints in ecosystems with a multiplicity of stable states*. Nature. 269: 471-477.
- MORRIS, R.F. (ed.). 1963. *The dynamics of epidemic spruce budworm populations*. Mem. Ent. Soc. Can. 31: 1-332.
- MURDOCH, W.W. & OATEN, A. 1975. *Predation and population stability*. Adv. Ecol. Res. 9: 1-125.
- MYERS, J.H. 1976. *Distribution and dispersal in population capable of resource depletion: a simulation model*. Oecol. 23: 255-269.
- O'BRIEN, J.J. & WROBLEWSKI, J.S. 1976. *A simulation of the mesoscale diffusion of the lower marine trophic levels off West Florida*. In: PATTEN, B.C. (ed.) *Systems analysis and simulation in ecology*, Vol. 4, 63-110, Academic Press, N.Y.
- OKUBO, A. 1974. *Diffusion-induced instability in model ecosystems: another possible explanation of patchiness*. Tech. Rpt. 86, Chesapeake Bay Inst., Johns Hopkins Univ.
- PETERMAN, R.M., CLARK, W.C., & HOLLING, C.S. in press. *The dynamics of resilience: shifting stability domains in fish and insect systems*. In: ANDERSON, R.M. & TURNER, B.D. (eds.), *Population dynamics*. Proc. Symp. Brit. Ecol. Soc., April 1978. Blackwells, Oxford.
- PREBBLE, M.L. (ed.) 1975. *Aerial control of forest insects in Canada*. Dept. of Environment, Ottawa, 330 pp.

- RAINEY, R.C. 1951. *Weather and movements of locust swarms: a new hypothesis*. Nature, Lond. 168: 1057-1060.
- RAINEY, R.C. 1976. *Flight behavior and features of the atmospheric environment*. In: RAINEY, R.C. (ed.) *Insect flight*, Symp. Roy. Ent. Soc., Lond. 7: 75-112; Blackwell, London.
- RAINEY, R.C. 1979. *Dispersal and redistribution of lepidoptera and orthoptera by flight*. Mitt. Schweiz. Ent. Ges. 52: 125-132.
- SANDERS, C.T. 1979. *The role of sex pheromones in the dispersal of the spruce budworm*. Mitt. Schweiz. Ent. Ges. 52: 223-226.
- SCHAEFER, G. 1976. *Radar observations of insect flight*. In: RAINEY, R. (ed.), *Insect flight*, Symp. Roy. Ent. Soc., Lond. 7, 157-197, Blackwells, Oxford.
- SCHNEIDER, F. 1962. *Dispersal and migration*. Ann. Rev. Ent. 7: 223-242.
- SEGEL, L.A. & LEVIN, S.A. 1976. *Application of nonlinear stability theory to the study of the effects of diffusion on predator-prey interactions*. In: PICCIRELLI, R.A. (ed.), *Topics in statistical mechanics and biophysics: a memorial to J.L. Jackson*, Proc. AIP. Conf. 27: 123-152.
- SINCLAIR, A.R.E. & NORTON-GRIFFITHS, M. (eds.) 1979. *Serengeti: dynamics of an ecosystem*. Univ. Chicago Press, Chicago.
- SOUTHWOOD, T.R.E. 1962. *Migration of terrestrial arthropods in relation to habitat*. Biol. Rev. 37: 171-214.
- SOUTHWOOD, T.R.E. 1977. *Habitat, the templet for ecological strategies?* J. Anim. Ecol. 46: 337-366.
- SOUTHWOOD, T.R.E. & COMINS, H.N. 1976. *A synoptic population model*. J. Anim. Ecol. 45: 949-965.
- STEELE, J.H. 1975. *Biological modeling II*. In: NIHOUL, J.C.J. (ed.) *Modeling of marine systems*, 207-216, Elsevier, Amsterdam.
- STEELE, J. (ed.) 1978. *Spatial pattern in plankton communities*. Plenum Press, N.Y.
- STEELE, J.H., & HENDERSON, E.W. 1977. *Plankton patches in the northern North Sea*. In: STEELE, J.H. (ed.), *Fisheries mathematics*, 1-19, Academic Press, London.
- TAKAHASHI, R. 1964. *Reproduction curve with two equilibrium points: a consideration on the fluctuation of insect population*. Res. Popul. Ecol. 6: 28-36.
- TAYLOR, L.R. 1958. *Aphid dispersal and diurnal periodicity*. Proc. Linn. Soc. Lond. 169: 67-73.
- WELLINGTON, W.G., & HENSON, W.R. 1947. *Notes on the effects of physical factors on the spruce budworm, Choristoneura fumiferana (Clem.)*. Can. Entomol. 79: 168-70.
- WILLIAMS, C.B. 1957. *Insect migration*. Ann. Rev. Ent. 2: 163-179.

