PROCESS MODELS, EQUILIBRIUM STRUCTURES, AND POPULATION DYNAMICS: ON THE FORMULATION AND TESTING OF REALISTIC THEORY IN ECOLOGY

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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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Process Models, Equilibrium Structures, and Population Dynamics: On the Formulation and Testing of Realistic Theory in Ecology

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Summary

This paper addresses problems in the formulation and testing of theory to relate structure and dynamic behaviour in complex natural ecosystems. Detailed studies of spruce budworm-coniferous forest interactions in eastern Canada provide a background for the analysis. We argue that the mixed spatial and temporal scales, low density phenomena, and nonlinear interactions characteristic of most ecosystems severely limit traditional statistical approaches to theory building, while rendering most kinds of observational data irrelevant to theory evaluation and testing. We describe an alternative tradition:

1. Cast the theory as a set of «dynamic life tables», bound together by basic ecological process modules; apply available data and field experience to the parameterization of these modules.
2. Compute the consequences of the resulting theory under a wide range of conditions: quantitatively through numerical simulation and qualitatively through the use of topological manifolds.
3. Employ the manifolds to identify key structure- (as opposed to parameter-) dependent predictions of the theory. Compare these with observation, emphasizing behaviour of the system and its theory in extreme natural or experimental situations.

I. A meteorological prologue

In 1803 LUKE HOWARD published an ambitious and elegant paper entitled *Modifications of Clouds*. In it, he set out to describe and classify the consistent forms underlying the flux of the skies. Surely, he argued, in these changing but persistent patterns are to be found the expression and essence of natural law. Some of the most sensitive minds of that most romantic age were drawn to the effort, and the massive portfolios of cloud studies compiled by TURNER, CONSTABLE, RUSKIN, and their followers are a naturalist's joy today, just as they were a century and a half ago. But as a predictive science, Romantic Meteorology was a bust. And, one by one, its real artists died off or turned aside to seek Law, if not Beauty, elsewhere. It remained for geniuses of another sort, in another century, to transmute the infinite variety of clouds into the infinite summations of calculus, and to turn CONSTABLE's *Studies* into the morning forecasts.

In 1966 CHARLES ELTON published an ambitious and elegant book entitled *The Pattern of Animal Communities*. In it he set out to describe and classify the consistent forms underlying the flux of terrestrial ecosystems. Surely, he argued, in these changing distributions of animals within their pattern of habitats is the expression and essence of ecological law. ELTON's text is one of the most beautiful in the ecological literature. Along with the

writings of Darwin, D'Arcy Thompson, Marston Bates, and all too few others it manages to both renew our appreciation and sharpen our perception of ecological pattern in its own right.

Its esthetic appeal notwithstanding, however, the analysis of pattern *per se* has proved an insufficient foundation for development of predictive ecological theory, just as it failed to fulfill the hopes of the 19th century cloud painters. Joel Cohen (1971) had a point when he called «physics-envy . . . the curse of biology». He might have added that a dogged romanticism seems to be its cross.

In this paper, we present an example of the development and evaluation of one ecological theory concerning how one particular kind of ecosystem operates. The spruce budworm-balsam fir system of eastern North America provides the illustration. It is chosen not for its experimental tractability – as a colleague has remarked, where else could you find an animal which occurs, usually at very low densities, ten meters up a tree and is periodically blown half way across the continent? – but because it is still one of the best researched, most intensively and extensively sampled, and most analytically tractable systems known to ecology. By trying to show which of the vast quantity of data available for budworm can, and which cannot, be put to what sorts of predictive purposes, we hope to touch obliquely on the problems of cloud study raised at the outset. More importantly, we wish to illustrate an alternative method of study in sufficient detail to encourage its consideration and criticism by other workers with other beasts to analyze. The approach to be discussed may be outlined as follows:

1. Cast the theory as a «dynamic life table» (Gilbert et al., 1976) bound together by general ecological process modules; apply available data, field experience, and experimental evidence to the parameterization of these modules.
2. Compute the consequences of the resulting theory – quantitatively through analysis and numerical simulation, and qualitatively through the use of topological manifolds.
3. Compare these predictions with observations, emphasizing behaviour of the system at its extremes, and revise the theory accordingly.

In general, this procedure is not distinct from the «scientific method» as it is described in most empirical sciences. The nuances, such as they are, emerge in the details of application. The work reported here is drawn from a larger study of ecological policy design, described at length in Clark et al. (1978, in press) and Holling et al. (1978). Our principal collaborators in that study – the late Dixon Jones of our own Institutes, Gordon Baskerville of the University of New Brunswick, and Charles Miller of the Canadian Forest Service – were instrumental in developing the analysis upon which this discussion is based. The budworm study itself rests upon the monumental researches of Morris (1963) and his coworkers, while the «theory» presented here is essentially Morris and Watt (1964), fifteen years later, in systems-analytic disguise.

II. The spruce budworm-balsam fir system

The spruce budworm *(Choristoneura fumiferana)* is the most widely spread defoliating insect of the North American boreal forest. It ranges from Virginia to Labrador and west across Canada into the Northwest Territories. Throughout most of its range it is usually rare but undergoes periodic outbreaks inflicting extensive mortality on its preferred host trees, the balsam fir *(Abies balsamea)* and white spruce *(Picea glauca)* (Davidson and Prentice, 1967). Detailed studies on the system have been carried out since the late 1940s, especially in eastern Canada.

The data on temporal and spatial behaviour of the budworm-forest system are unusually complete. Tree-ring studies, backed by contemporary records, allow documentation of
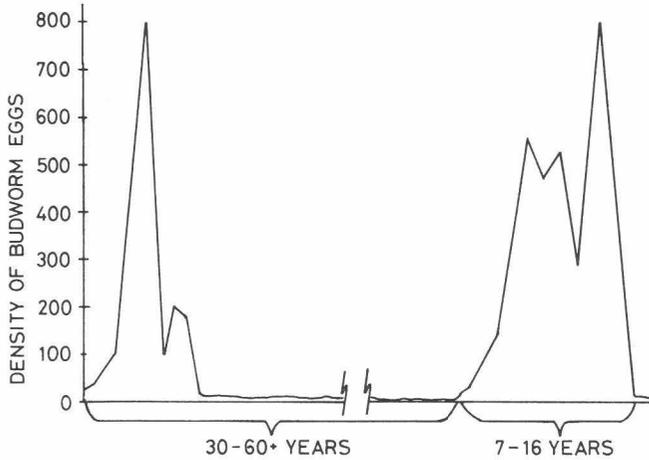
Fig. 1: The pattern in time. Representative historical pattern of spruce budworm outbreaks, synthesized from the work of BLAIS (1968). There have been four major outbreaks since 1770. The density measure of budworm is per typical balsam fir branch (one square meter of branch area).

outbreaks back to 1704 (BLAIS, 1968). The general pattern is one of irregular outbreaks recurring at 30–70 year intervals and lasting from 7–16 years in any given area (Figure 1). Synoptic maps of outbreak development east of the Great Lakes since the early part of this century have been compiled from various sources (DE GRYSE, 1947; BROWN, 1970 ; FIDS, 1938–1978). These show a periodic wavelike spread of infestations, superimposed on a somewhat higher frequency cycle in the prime forests of the Canadian Maritimes. Figure (2) shows the outbreak sequence of 1938–1948, the last full pattern to develop in the absence of insecticide applications. The Canadian province of New Brunswick has
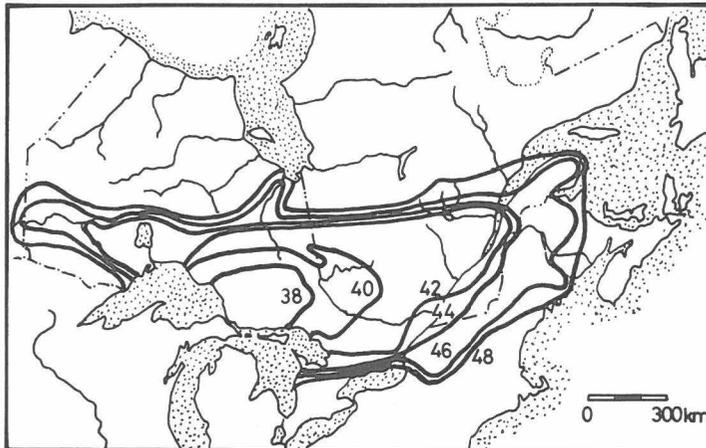

Fig. 2: The pattern in space. Maximal extent of budworm infestations in eastern North America for 1938–1948, the last outbreak sequence before extensive insecticide spraying was introduced. Redrawn from BROWN (1970).

experienced some of the worst outbreaks, undergone the most intensive management, and compiled the most detailed data. Since extensive management began in the 1950s, yearly estimates of insect density have been taken at nearly a thousand locations distributed over a seven million hectare area. These data are summarized in Figure 3 (see also WEBB et al., 1961) and represent one of the most detailed descriptions of time-space population dynamics in the ecological literature. (The departure from the natural outbreak frequency is due to management activities; see the discussion below, CLARK et al., in press; BASKERVILLE, 1976; BLAIS, 1974). They have proved about as useful for the development of our budworm theory as CONSTABLE's *Cloud Studies* were for the formulation of the turbulent flow equations.

III. Process modules

Ecology is often described as the study of «relationships among animals, plants, and their physical environment». But as GILBERT et al. (1976) have correctly noted, practice has usually put the animals as such first and the relationships a distant second.

The relatively few attempts to study the fundamental relationships of ecology *per se*, however, have been comparatively productive: a fact not usually appreciated by those
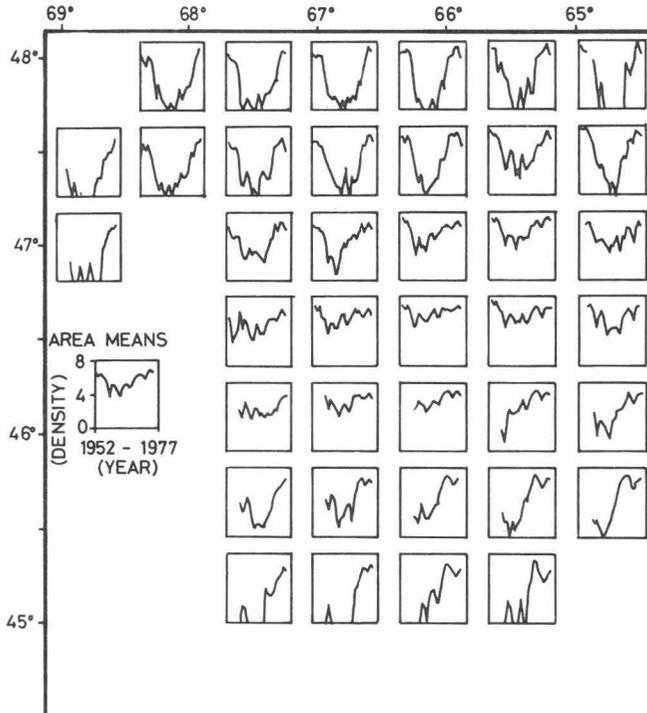

Fig. 3: Budworm densities in New Brunswick under historical management conditions. Each grid represents a 50 × 50 km square located by latitude and longitude. Mean egg densities (n ≈ 20/grid/year) are shown on the ordinate as the natural logarithm of (one plus egg density per square meter of branch area). Time is given on the abscissa for years 1952 to 1977. Mean densities for all areas combined are given in the isolated grid. See Figure 7 for location of New Brunswick.

coming into ecology from other fields or, for that matter, by ecologists themselves. As a result of this work, we can begin to speak of substantive theories for predation and parasitism (e.g., HOLLING, 1965; MURDOCH, this volume; HASSELL, this volume), of development (e.g., SHARPE and DEMICHEL, 1977), of reproduction (e.g., WATT, 1968), of movement (e.g. R. JONES, 1977a, b, in press), of natural selection (FISHER, 1930), and so on, just as a meteorologist would refer to ones for advection, convection, evaporation, and the like. The analogy is worth pursuing, for the meteorologist seeking to explain or predict a given pattern of weather does not start each study *de novo*. Rather, he makes extensive use of the discipline's stock of well-tested process theories, parameterizing and combining them in modular fashion as each specific situation demands. The individual modules provide an *a priori* structure for interpretation of the available data, can often be individually validated, and inevitably highlight the weak or missing aspects of the analysis.

It is no good to argue that such procedures are premature in ecology, for they are already common practice. Our problem is not that we have failed to employ process modules, but that we have spent the vast majority of our research effort exploring formulations selected for their mathematical tractability rather than biological relevance. Neither theories so simple that they are simplistic, nor ones so complex that they are impenetrable have much to offer in science. A variety of approaches seeking the desired intermediate ground are
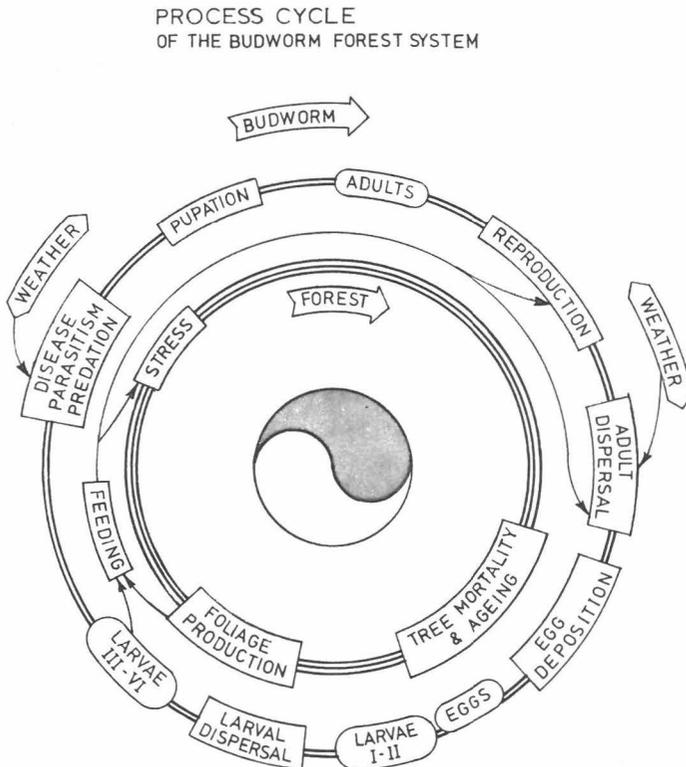

Fig. 4: The process cycle for the budworm-forest system. The inner ring represents the forest cycle, the outer ring the budworm cycle. Ellipses indicate insect life stages; arrows show causal relationships among processes and insect life stage densities. After D. JONES (1977).

surely appropriate – a point stressed by MAY from a somewhat different perspective elsewhere in this volume. Twenty years ago there was little practical alternative to ecological theory based on (for instance) Lotka-Volterra interactions, Gaussian development distributions, and Fickian diffusion. Today, with empirical process studies such as those cited above to provide more realistic equations, and with computers available to solve them, complementary alternatives do exist and merit increasing attention in their own right.

The ecological relationships ultimately represented in the budworm theory are indicated in Figure 4. Each of these was decomposed into its component parts (making use of existing process modules where possible), parameterized through analysis of existing data and field experience, and eventually incorporated in a corresponding simulation model (D. JONES, 1977; YORQUE et al., forthcoming). The procedure can best be illustrated by specific example.

One of the processes affecting survival of large larvae is predation by vertebrate predators (birds and squirrels). It has long been suspected (MORRIS, 1963) that vertebrate predators could play an important role in the dynamics of spruce budworm and other insects when the latter's populations are low. For the very reason that it is so impractical to sample low populations with any reasonable precision and accuracy, however, standard regression modeling approaches have been wholly inadequate to capture the effects of this predation.

The predation process, however, has been analyzed sufficiently so that its variety of forms can be identified and classified (HOLLING, 1965; but see MURDOCH, this volume). Predation is comprised of four necessary and sufficient processes – the functional response to prey density (an instantaneous rate of attack), the competition response, the development response, and the numerical response. Each of these four responses has been shown to have a small number of qualitatively distinctive forms (HOLLING and BUCKINGHAM, 1976). The functional response to prey density, for example, can assume four and only four qualitatively different shapes. Moreover, a simple general equation has been developed whose four limiting conditions generate all these types. Equally important, the sufficient biological conditions can be precisely defined so that the most general of information is enough to classify any specific situation.

We have analyzed existing data on vertebrate predation of budworm in some detail. For such predators, the functional response to prey density (i.e., the instantaneous number of prey eaten per predator per unit time) is known to rise in an S-shaped manner to a plateau. The appropriate form of the general predation equation is therefore established, and it remains only to mobilize the existing data so that feasible parameter ranges can be determined. For the present purpose, only two parameters need be defined – one that determines the plateau of maximum attack rate and one that determines the rate of search.

The parameter values are influenced by the size of the predator and its searching habits. This permits the separation of budworm predator species into distinct, parameter-defined groups. The birds attacking budworm are classified into three types – the small arboreal birds (e.g., warblers), the medium sized birds searching nearer the ground (e.g., white-throated sparrows), and the larger birds with a variety of searching modes (e.g., grosbeaks). Existing data on maximum consumption, sizes of predators, and rates of searching establish maximum and minimum feasible values for the search and satiation parameters for each class. Together, these define a feasible range for the percentage of late instar budworm larvae that can be eaten by birds (Figure 5). The biological relevance of this remaining uncertainty can be assessed by computing consequences for the theory as a whole under various feasible extremes of predation. An example of this procedure is given in the following section (see HOLLING et al., forthcoming, for a more detailed analysis). The
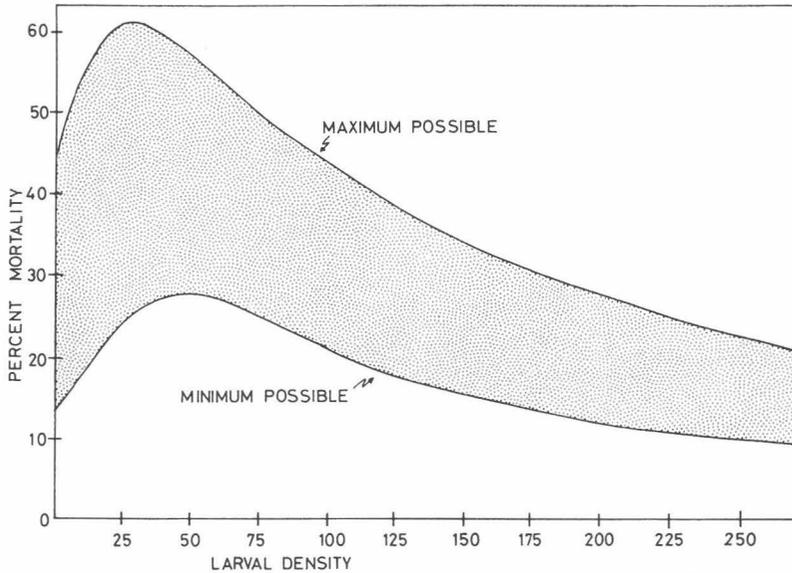
Fig. 5: Effect of vertebrate predators on budworm populations. Ordinate shows percent of sixth instar larval population consumed by all vertebrate predators combined as a function of larval density (units of thousands of larvae per hectare of land). Function shown is maximum, minimum, and range of predation rates consistent with available field data.

same general approach is used to define the other processes of Figure 4, as reported in D. JONES (1977), CLARK et al. (in press), and YORQUE et al. (forthcoming). A number of applications of the process module outlook to other systems are summarized in GILBERT et al. (1976) and PETERMAN et al. (in press).

IV. Computation of consequences

Once the process modules have been described, there remains the problem of linking them all together into a coherent and meaningful whole; i.e., of computing their consequences as an aggregate theory. Because the theory has been constructed according to criteria of ecological relevance rather than mathematical elegance, it usually is necessary to perform these computations via a numerical simulation model.

Simulation solutions of the model summarized in Figure 4 are shown in Figure 6. Starting conditions for this simulation were chosen to reflect those actually occurring in New Brunswick in the spring of 1953. The values of the variables in subsequent years are the numerical solutions of the model derived from those initial conditions. Note that the general pattern implicit in the model reflects the historical one described earlier: outbreaks peaking at about 30 year intervals, lasting about 10 years, and separated by long periods of very low densities.

The numbers presented in Figure 6 are averages over space. The theory itself is explicitly spatial, however, in order to account for the process of insect dispersal. The simulation model of the theory is constructed as a set of 393 grids covering seven million hectares of New Brunswick forest (Figure 7). Within each grid budworm-forest interactions are assumed to be homogeneous and are represented by the local model of Figure 4. Grids are
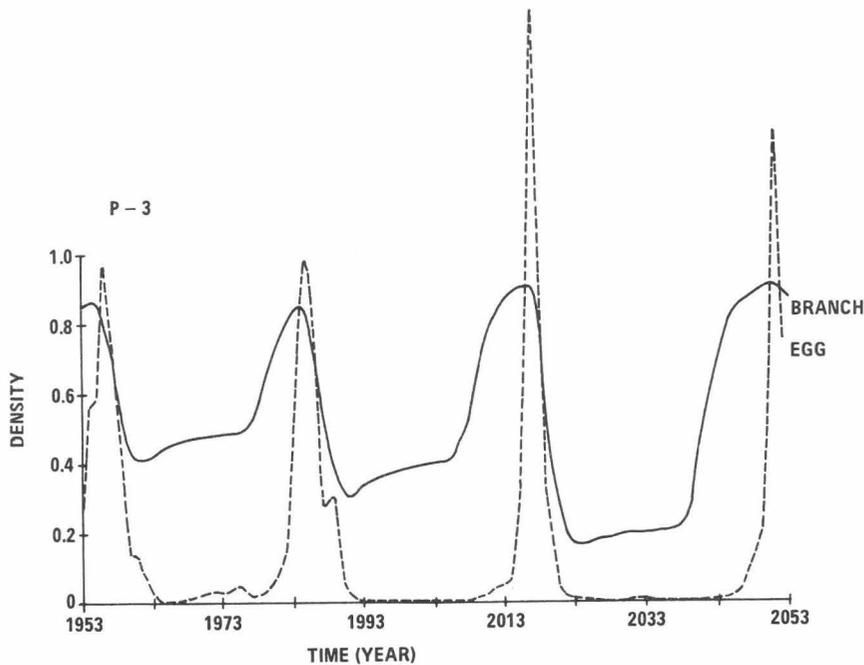
Fig. 6: Typical outbreak pattern generated by the model with no management or harvesting imposed. Ordinate is a scale running from 0 to 1,000 budworm eggs per square meter of branch area; and from 0 to 1 for the Branch Density Index which closely parallels the average forest age and wood volume (see CLARK et al., in press). Initial conditions are those for New Brunswick in 1953. Data are averaged over the 393 grids.

linked via dispersal of insects and management activities. A sample of direct results of the simulation, of which Figure 6 is the spatial average, is shown in Figure 8. These spatial solutions again generally reflect the recorded historical pattern of outbreak spread. We will return to this comparison-with-observation issue in the next section, but it will be worthwile first to explore the consequences of the theory in a bit more detail.

Simulation models are indeed the only tool available for solving realistic ecological models, but they are no more attractive for their inevitability. To compute results of the sort shown above is always expensive, frequently ambiguous, and potentially misleading. We need understanding as well as solutions, and space-time streams of simulation output are notoriously inadequate for this purpose. One intermediate approach we have found productive involves applying numerical simulation techniques to calculate «equilibrium» conditions[1] for the theory under a range of ecological meaningful conditions, plotting these conditions as equilibrium manifolds of the sort found in qualitative analysis and topology and then using the manifolds directly to assess the «how» of the theories' predictions (THOM, 1975; MAY 1977 and this volume; LUDWIG et al., 1978; LEVIN, 1978b). The use of equilibrium manifolds to «compress» a complex simulation model is quite straightforward,

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[1] Here a term used simply to mean the values at which a specified variable will remain constant in time, provided that other factors are held constant.

as can be shown from a few examples of its application to the budworm analysis (for the original development see JONES, 1975; more extensive treatment is provided in HOLLING et al., 1978).

Consider again the theory outlined in Figure 4 and assume for the moment that the number of insects entering a particular spatial area through immigration equals the number leaving through emigration. Any specified combination of forest conditions, weather, and budworm density is then sufficient to determine budworm density for the following year. The simulation can compute this quantity very quickly for a range of interesting conditions, since only a single time step iteration of the model is required. This has been done for average weather and an undefoliated, medium-aged forest, and the results plotted as
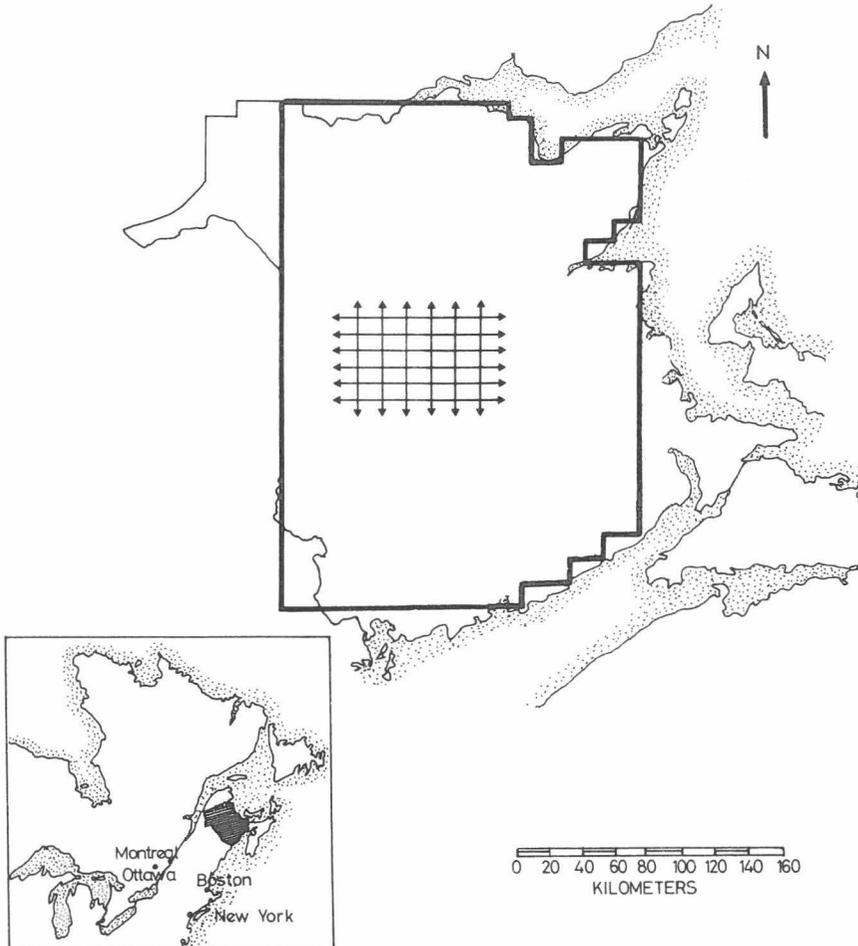

Fig. 7: Location and configuration of the modeled area. Approximately seven million hectares of the Canadian province of New Brunswick are decomposed into 393 grids of dimension 15.43 km (E-W) × 10.92 km (N-S), as shown. Events within grids are treated as spatially homogeneous representations of the model suggested in Figure 4. Grids are linked by insect dispersal and management activities.
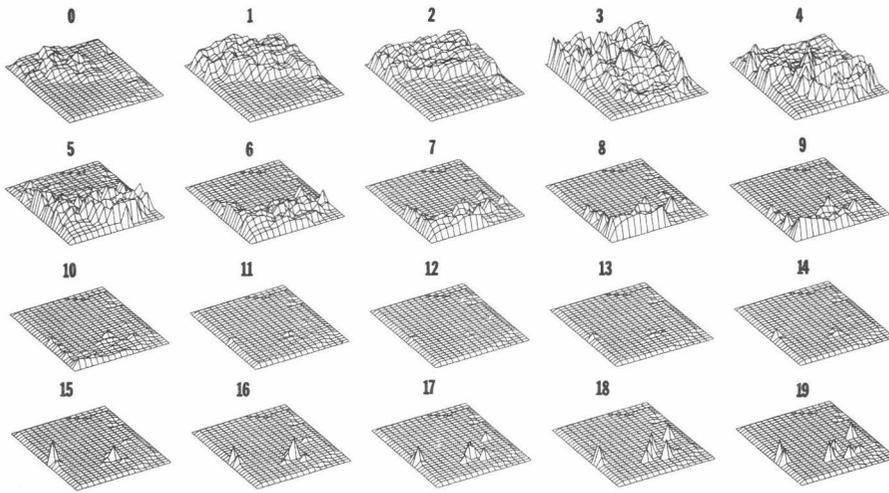
Fig. 8: Twenty-year sequence of spatial patterns predicted by the model when no management or harvesting is imposed. Horizontal (x.y) coordinates define a north-south by east-west spatial grid of 393 individual patches, each representing about 17,000 hectares of New Brunswick forest. Initial conditions are those for corresponding locations in New Brunswick in 1953. The vertical (z) axis depicts relative budworm egg densities on a linear scale.
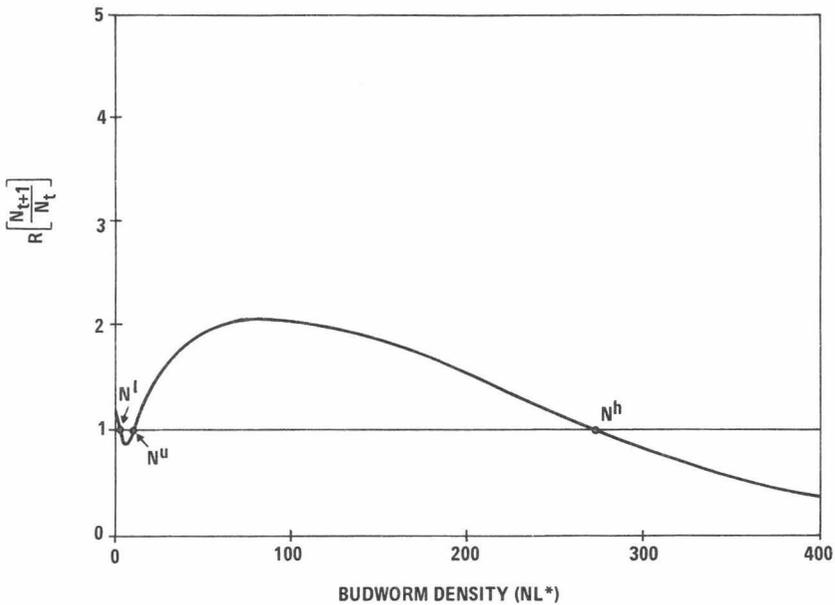

Fig. 9: Recruitment curve for budworm. Forest conditions are those for a medium aged, undefoliated forest. Weather conditions are mean. Abscissa is larvel density per square meter of branch area in year «t». Ordinate is recruitment factor, i.e., $N(t+1)/N(t)$. Three equilibria are represented, one unstable (N^u) and two stable (N^l, N^h).

«recruitment curves» (RICKER, 1954) in Figure 9. It is immediately clear that the theory embodied in the simulation implies three budworm density equilibria, one at each of the densities where the recruitment curve crosses the $(N_{t+1}/N_t) = 1.0$ line. (These would be the roots of the equations of the model in N, if we could solve the equation explicitly.) The middle equilibrium N^u is unstable for budworm, because densities slightly larger lead to continued increase and densities slightly smaller to continued decrease. The high and low density equilibria, N^h and N^l, are stable to changes in budworm density by an analogous argument. It is intuitively plausible, and turns out to be correct, to identify the lower equilibrium with endemic budworm conditions, the upper one with outbreak conditions, and the middle, unstable one with a threshold density of budworm which, once exceeded, allows the system to move to its upper outbreak level (TAKAHASHI, 1964).

The shape of the recruitment curve directly reflects the dominant processes described earlier. It can be shown by selectively adding and deleting processes from the model and recomputing the curves that a basic survival rate, relatively independent of budworm density, is set by weather, a variety of constant factors, and forest density. The reduction of survival at high budworm densities is largely due to competition for food. Very low density survival is reduced by parasitism. The obvious «dip» in the recruitment curve at medium-low densities is in large part attributable to vertebrate predation on the insects (PETERMAN et al., in press).

Consider now a medium-aged forest with budworm densities at their low equilibrium value N^l (curve «A» in Figure 10). As the forest ages it is necessary to compute new recruitment curves. If plotted on the same figure, these successive curves are higher and higher – that is, the recruitment rate at any given density becomes larger and larger. Simultaneously, the lower and middle equilibria grow closer together until they coalesce as
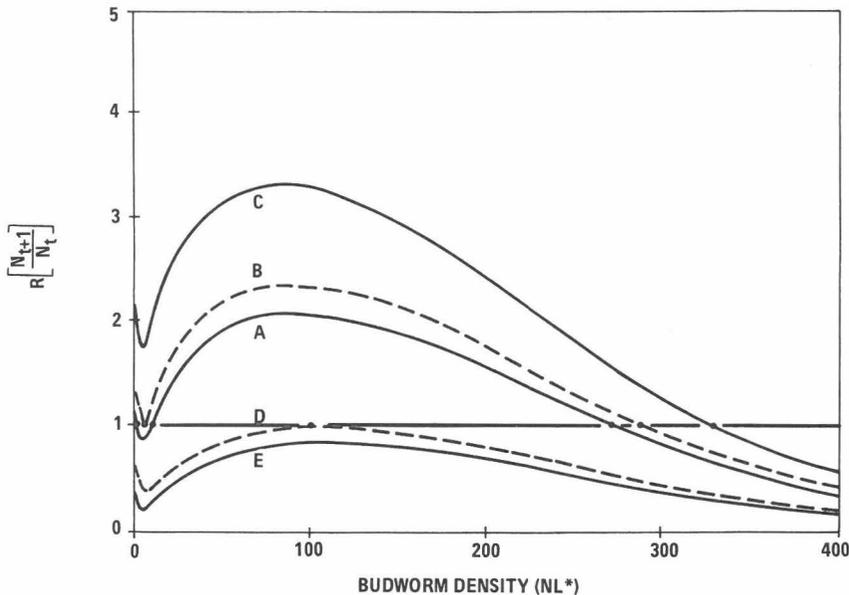

Fig. 10: Recruitment curves for budworm. Forest conditions are undefoliated, weather conditions are mean. Curve «A» is a medium aged forest, curve «C» a mature forest, and curve «E» a very young forest. Note the changing number of equilibria points which are marked for each curve.

in curve «B» of Figure 10. At this point any positive perturbation to the insect population will result in further increase and, indeed, as the forest ages even more («C»), both lower equilibria disappear and an outbreak – i.e., a rise to the upper equilibrium – is inevitable.

If the present diagrams told the whole story, the system would remain at the outbreak «equilibrium» forever. In fact (and in the theory), such high insect densities rapidly kill the forest, reducing its average age to that shown by curve «E» in Figure 10. This time it is the upper equilibrium that coalesces with the lower ones (curve «D») and finally disappears, leaving the system back at a low, endemic budworm density. A recruitment curve for forest – as opposed to budworm – density has been computed and shows this explicitly.

Although information on rates of density change between equilibria is available from the recruitment curves, attention in the above discussion focused on the evolution of the «equilibrium» points on those curves. This realization allows a further graphical compression to be carried out in which only the equilibria are plotted. Thus, Figure 11 reproduces all of the information about equilibria contained in the earlier Figure 10, but more completely and succinctly. Figure 11 is a manifold of equilibria of the sort commonly encountered in the analysis of differential equations. Here we emphasize that its computation from the simulation model simply consists of holding forest age fixed and searching for insect densities which remain constant from one generation to the next. These
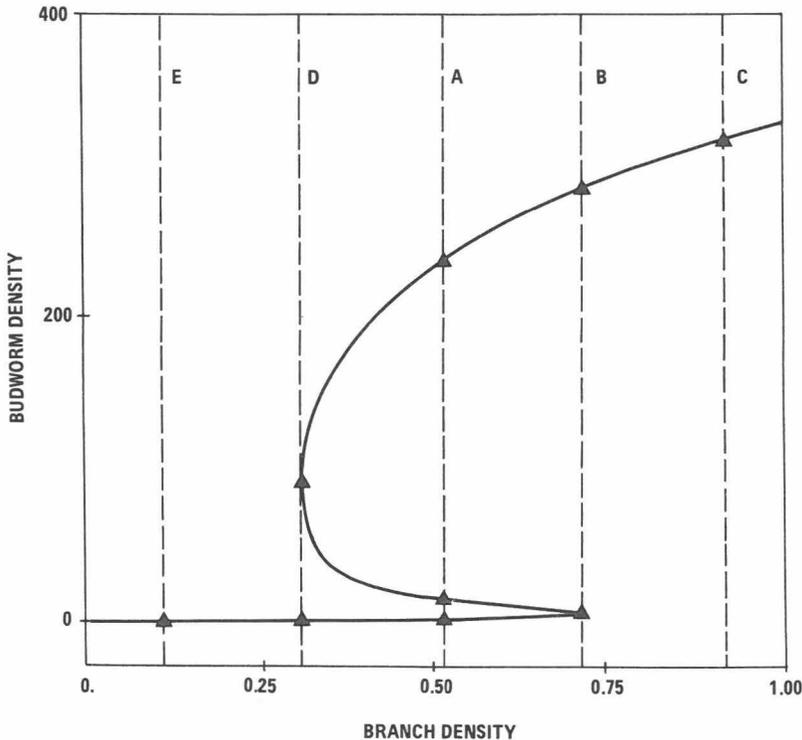

Fig. 11: Equilibrium manifold for budworm. Forest conditions are undefoliated, weather conditions are mean. Manifold is obtained by plotting only the equilibrium budworm densities (larvae/square meter branch area) for a continuous range of branch densities (≈ forest mean age). The dotted lines show the equilibria for each single branch density shown in Figure 10.

equilibrium densities are the points of the manifold surface. The outbreak sequence initially portrayed with the recruitment curves of Figure 10 may be more easily followed on the manifold, particularly when an axis reflecting foliage conditions is added (Figure 12).

The most important use of the manifolds, however, is in the study of relationships between the process modules discussed earlier and the emergent topological structure and consequences of the theory. Returning to the predation example discussed earlier, computations with the simulation model showed that when the amount of predation was reduced much below the «minimum possible» level defined by the process analysis (Figure 5), the qualitative behaviour of the system shifted drastically. Instead of the persistent «boom-and-bust» outbreak cycles of Figure 1, the low-predation theory predicted a trend towards the higher frequency, lower amplitude oscillations shown in Figure 13.

With the appropriate manifolds it is easy to understand this change. In Figure 14, the foliage axis of Figure 11 has been replaced by one on which the quantity of predation is varied. (Again, the manifold surface is computed by fixing forest age and predation parameters, searching for values of insect density which do not change from one year to the next, and repeating the procedure for many combinations of predation intensity and forest age.) The maximum predation level shown is that derived for the original theory, and the associated manifold is therefore identical to that shown earlier. As predation is decreased, the reflexive character of the manifold is lost and with it the potential for persistent low frequency, high amplitude cycling. At minimum predation, there is almost no reflexion left at all. When the system reaches the rather young forest age necessary to release the insects from their lower equilibrium, densities quickly rise to a moderate level and thereafter creep upwards only with further increases in forest age. Even these densities kill some trees however, and analysis shows that these forces tend to balance, moving the system towards a stable equilibrium of moderate forest and insect densities. The high frequency oscillations developing in the later years of Figure 13 arise from the interaction of insects and foliage in a typical prey-predator cycle superimposed on the relatively constant forest density.
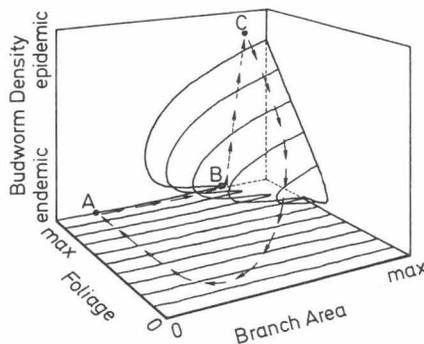

Fig. 12: Equilibrium manifold for budworm as a function of foliage and branch density (units are third instar larvae/square meter of branch area, with foliage and branch density scaled 0 to 1; see text). Weather is mean. Trajectory shows a typical unmanaged outbreak of the sort shown in Figure 6. Segment AB is the long endemic period with budworm at low densities and the forest full of foliage and slowly growing until lower equilibrium disappears at B. Segment BC is the outbreak with budworm densities rapidly rising to upper equilibrium C. At these densities, foliage is rapidly destroyed, leading to destruction of the forest and collapse of the outbreak along CA. The final section sees the rapid recovery of foliage in a young forest, with budworm locked at their low density near A. Note that the manifold for FOLIAGE = 1. is the same as that shown in Figure 11.
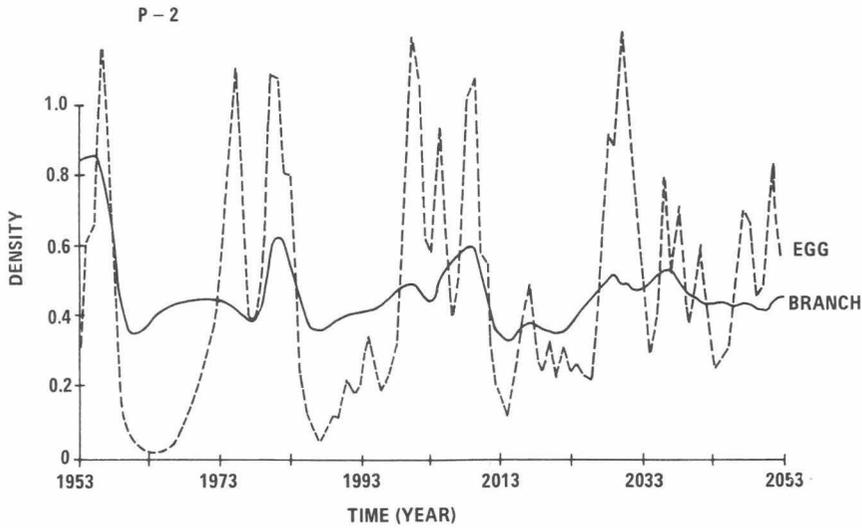
Fig. 13: Typical outbreak pattern generated by the model when predation severely reduced. No management or harvesting. Other conventions as in Figure 6.

A parallel argument can demonstrate the role of dispersal in our theory of the budworm system. Recall that although the full theory and its simulation model dealt explicitly with intersite dispersal, a losses-equals-gains assumption was invoked to simplify the initial development of recruitment curves and manifolds. This assumption can be relaxed by calculating actual losses-to-gains ratios from observational data or the simulation, and then evaluating the effect of a range of such ratios on the manifold structure.

Figure 15 is the now familiar basic manifold with the third axis replaced by an index of net dispersal gains. The resemblance to the predation manifolds is striking, a fact that leads directly to an appreciation of the symmetric relationship between these two apparently unrelated processes. Recall that vertebrate predation is the major factor in depressing low density survival, leading to the «pit» of the recruitment curves (Figure 9) and the reflexive character of the manifolds (Figure 11). Decreasing the amount of predation increases survivorship at these densities, so that less and less forest «fuel» is necessary to trigger an
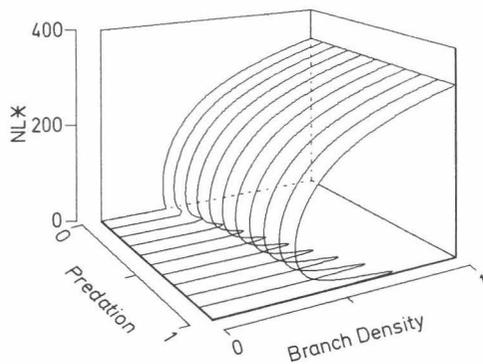

Fig. 14: Equilibrium manifold for budworm as a function of predation intensity and branch density. Predation scaled from 0 (no predation) to 1 (natural level of predation as included in model); other conventions as in Figure 12; foliage is fixed at 1. Note that the manifold for PREDATION = 1. is the same as that shown in Figure 11.

oubreak (Figure 14). Increased immigration similarly increased effective survivorship, and a given *number* of immigrants will have a greater effect on the survivorship *rate* at low densities than at high, also leading to a loss of the recruitment «pit» and manifold reflexion. In effect, immigration serves to satiate the local predators, allowing the resulting local insect population to escape predation; changes in the immigration rate can be compensated for by changes in the predation rate and vice versa. A fuller analysis of dispersal effects on manifold structure, including a treatment of the «critical patch size» problem of KIERSTEAD and SLOBODKIN (1953), is given in CLARK et al., 1978. Parenthetically, if obviously, only the joint effects of immigration/predation interaction – i.e., the shape of the emergent manifold – can be deduced from observations of the resulting budworm density dynamics.

An analogous use of equilibrium manifolds to compress and analyze a complex simulation model of Pacific salmon *(Oncorhynchus)* is given in PETERMAN et al. (in press). A qualitative analysis approach to budworm manifold development is discussed by LUDWIG et al. (1978). Other general applications are reviewed by MAY (1977, this volume). Further exploration of the topological manifolds as a tool in the context of management, «optimization», and policy design is discussed at length by CLARK et al. (in press), HOLLING et al. (1978), and JONES and WALTERS (1976). Their use in experimental design and hypothesis testing for complex theories is touched on in the next section.

V. Comparison with observation

So far we have dealt with the *formulation* of theories, emphasizing the advantages of giving them process modular structure, and with the subsequent *computation* of the theories' implications, emphasizing the use of qualitative analysis for understanding. It remains to discuss the *comparison* of the theory with the facts. But just any facts – in fact, most facts – won't do. The central problem is not to assemble a large volume of quantitative data accurately reflecting historical behaviour of the system, and then to compare it with computed consequences of the model. Rather, we must first use our understanding of the relationship between the theory's structure and its consequences to define the small (usually very small) subset of feasible observations which will strongly reflect on the credibility of the theory and serve to identify its relative strengths and weaknesses. Then we must go out and find in nature or create by experiment those observations.

Even when good historical data are available, a meta-problem of samples-and-populations remains: how representative of *all possible* behaviours of the system is the *single* history which did in fact occur? In what sense *should* computed consequences of the theory «conform» to the observations of history? Figure 16 shows the computed consequences of the theory when realistic state-dependent rules of historical management are included (for details see BASKERVILLE, 1976; CLARK et al., in press). Again, the initial conditions are those of 1953 in New Brunswick and the results of the simulation should therefore correspond to the actual historical data originally presented in Figure 3. Do they? It requires no formal statistical test to show that they do not.

Correspondence of the spatial averages over time is not, in fact, too bad. In both the theory's predictions and the historical data the typical «boom-and-bust» outbreaks of the unmanaged world are transformed into a seething infestation of low amplitude, high frequency oscillations. But considering the statistical noise in the historical record and the degrees of freedom remaining in even modularly structured realistic theories of population dynamics, qualitative comparisons between observation and prediction may constitute rather weak discriminators of alternative theories. STEELE (1975) has emphasized this problem in the context of marine ecosystem models. He concludes that the explicit
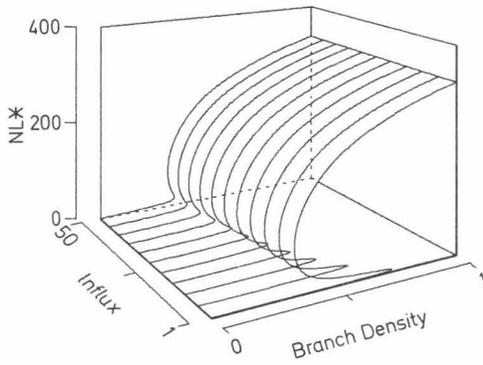
Fig. 15: Equilibrium manifold for budworm as a function of externally generated budworm immigration rate and branch density. Immigration scale from 0 (no immigration) to 1 (an arbitrary but feasible rate; see CLARK et al. 1978). Other conventions as in Figure 12; compare with Figure 14.

inclusion of spatial considerations in data collection and theory building is one means, perhaps the most practical one, of increasing our ability to discriminate between superficially and substantively adequate understanding in population dynamics. More study is needed on both the necessity and sufficiency of accurate spatial prediction as a validation criterion for ecological models. In our own work, however, it is precisely through analysis of its spatial properties that the weaknesses of our present budworm theory are most clearly identified.

In particular, a comparison of Figures 3 and 16 shows that while the historical outbreak «stalled» in central New Brunswick and passed into the northern part of the Province only in the late 1960s, the theory predicts a rapid and sustained spread throughout the modelled region. In principle, this discrepancy could be due to a basic error in formulation of the
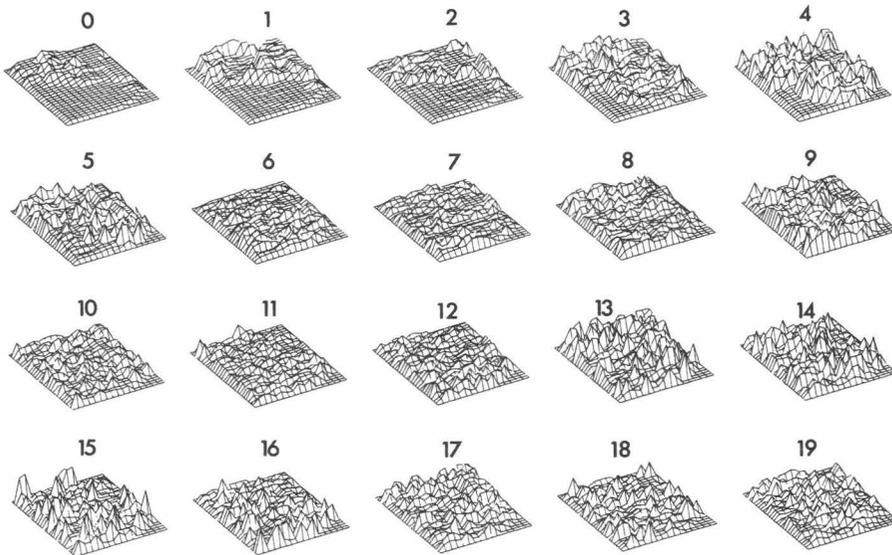

Fig. 16: Twenty-year sequence of spatial patterns predicted by the model under historical rules for insecticide spraying and tree harvest. Conventions and initial conditions as in Figure (8). Note the loss of spatial cohesion and temporal pattern relative to Figure (8).
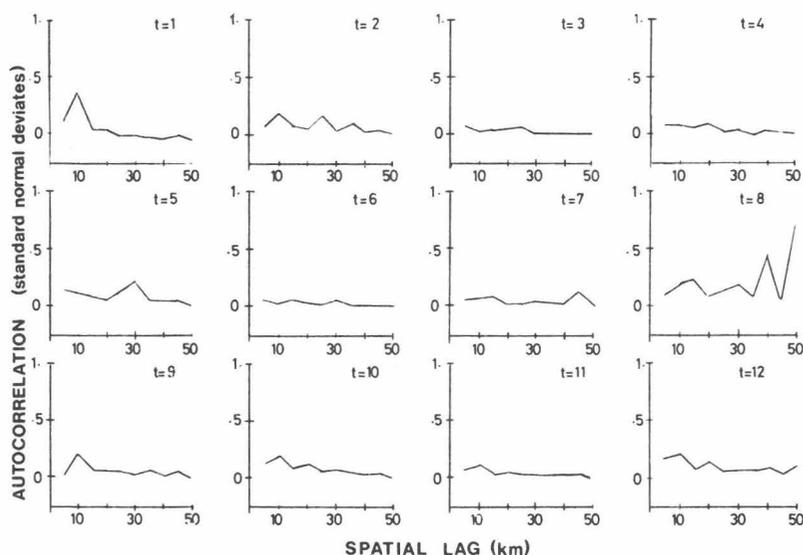
Fig. 17: Spatial autocorrelation function for the real world, managed pattern of insect densities of Figure 3. Ordinate is scaled in standard normal deviates of CLIFF and ORD's (1973; CLIFF et al., 1975) crossproduct statistic, evaluated under their randomization assumption. Abscissa represents lag in kilometers, summed over all directions. Sequence covers data for 1962 (t = 1) to 1973 (t = 12). Note that there is no significant linear spatial structure at scales of less than 50 km.

«local» laws governing budworm growth and dispersal, to large scale spatial heterogeneities not represented in our theory, to «phasing» or initial condition errors, or to interactions among these factors (LEVIN, 1978a). In fact, multivariate statistical studies of the historical pattern fail to reveal any large scale heterogeneities in population recruitment rates, while spectral and autocorrelation analyses (Figure 17) show no significant small scale (< 50 km) structure in either the historical or predicted patterns (CLARK et al., 1978; YORQUE et al., forthcoming). Once again, the historical population survey data have proved to be of limited utility, even for purposes of theory validation. We could argue for provisional acceptance or total rejection of the theory on the basis of such comparisons, but in either case the discussion would be largely sterile. Two points may help put this problem in context.

It is important to realize that for many complex dynamic systems (and some very simple ones[2]), two otherwise identical systems which are made to differ by arbitrarily small amounts in parameter or state values at one time can in consequence evolve large differences in the state values at some later time. This is true whether the initial «small differences» are due to actual perturbation of the system or to observational errors in the description of system state. To continue our meteorological comparisons, it is clear that numerical correspondence between the mesoscale predictions of theory and the actual weather is *in principle* impossible over periods of more than a couple of weeks due to the inevitability of finite observational errors in initializing the computational models (WIENER, 1948; MONIN, 1972; CHARNEY, 1975). The same problem has been raised with

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[2] Consider, for instance, the «strange attractors» and «chaos» behaviours discussed in this volume by MAY, OSTER, and others; also GRUEMM (1975); MAY and OSTER (1976) and references therein.

respect to modeling studies of plankton patchiness (PLATT et al., 1977). For budworm, our preliminary analysis has suggested that the choice of any finitely large grid size for initialization and numerical computation of the theory's spatial consequences may, through the averaging of local densities, lead to such divergence of model and reality over time periods represented by the historical data set though probably not in the longer run. Further work on this issue is continuing.

Even when exact numerical correspondence between the theory's consequences and observed reality are not expected, it is often held reasonable to demand that theory and observation yield variables with «the same long run statistical properties». Without worrying too much about what such a statement really means, two related difficulties may be noted. First, since there seem to be no firm grounds for *a priori* definition of how long is long, the statement as given still provides no criterion for rejecting a theoretical expectation which remains «nonconforming» after some given period of time. Second, there is no *a priori* reason to believe that even the very long term statistics of ecological systems are unique; i.e., that different sets of such statistics will not emerge in association with the same small perturbations discussed earlier. This is implicit in the existence of multiple equilibrium ecosystems of the sort documented by, among others, HOLLING (1973), SUTHERLAND (1974), SOUTHWOOD and COMINS (1976), MAY (1977), and GILPIN (this volume). And, again, the possibility of such «intransitivity» has been raised in meteorology (LORENZ, 1968) and demonstrated with physical models of the atmosphere (e.g. FULTZ et al., 1959). Since the important question for ecology is whether such statistics are unique within time periods feasible for measurement rather than ones infinitely long, the likelihood of what LORENZ has called «almost-intransitivity» seems particularly strong, and the prospect for any sort of direct strong inference utilizing general population survey data particularly weak. An exactly analogous argument has been made regarding economic modeling by HAYEK (1975). MURDOCH's (this volume) concept of «stochastic boundedness» may provide one means for addressing this difficulty, but practical evaluations of the concept are still necessary.

A supplementary approach to the comparison-with-observation issue, and one with good historical precedent outside of ecology, continues the theme of process-oriented, qualitative analysis which we have stressed throughout. For although most of the behaviour predicted by a theory may be ambiguous, it often turns out that predictions «at the edges» are qualitatively distinct and sufficiently unlikely to put the theory at risk (for discussion of practical considerations in model «validation» see WAIDE and WEBSTER, 1976; OVERTON, 1977; HOLLING et al., 1978). When such predictions can be identified and the corresponding real world observations either sifted from the historical record or manufactured from experiment, then substantial progress in evaluation of even very complex theories can be made. Again, the potential can best be illustrated by a few examples.

As suggested in Figure 4, the budworm theory treats weather as an aggregate stochastic input variable affecting large larval survival. Consequences of the theory presented so far were calculated using a probability distribution of weather conditions characteristic of New Brunswick. An analysis of the appropriate manifolds and recruitment curves suggested that it would be useful to compute the consequences of weather conditions much better, and much worse, than those of New Brunswick, and to compare these predictions with the actual behaviour of the budworm in other geographic areas.

Figure 18b shows simulation results from a spatially uniform model of the budworm theory, using weather distributions representative of the comparatively good (i.e., warm, dry) conditions encountered in northwestern Ontario. Comparing this with similar spatially uniform simulation results using typical New Brunswick weather conditions

A) STANDARD NEW BRUNSWICK SCENARIO
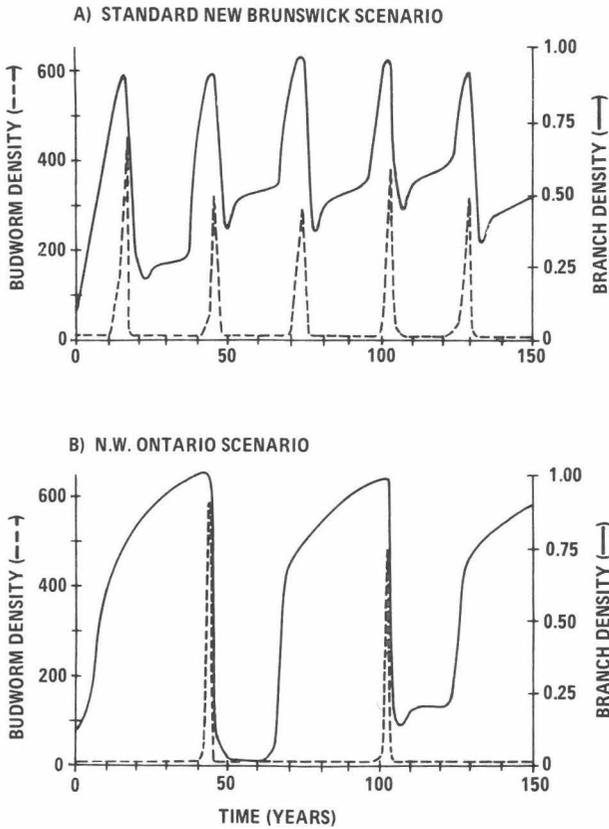

B) N.W. ONTARIO SCENARIO

Fig. 18: Diagnostic runs of the single grid, spatially homogeneous model. All emigrant moths are «reflected» back into the grid as immigrants. No management or harvesting. Abscissa is time in years. Ordinates are third instar larval density per square meter of branch area, and relative branch density index. (a) Standard run for New Brunswick weather and forest type. (b) Same model as (a) but with conditions for NW Ontario: a lower proportion of the forest is susceptible tree species; weather is better for budworm.
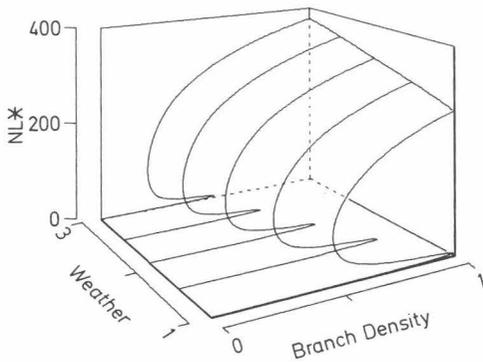

Fig 19: Equilibrium manifold for budworm as a function of a weather index and branch density. Weather scaled from 1 (poor for budworm) to 3 (good for budworm); other conventions as in Figure 12; foliage is fixed at 1. Note that the manifold for WEATHER = 2 (mean for New Brunswick) is the same as that shown in Figure 11.

(Figure 18a), it can be seen that the budworm cycle frequency has been halved and the amplitude increased by a third in the Ontario case. The forest mortality has increased accordingly. Although many other changes could doubtless be included to make the comparison more realistic, these predictions are all in line with field observations that record northwestern Ontario outbreaks as being less frequent (BLAIS, 1968) and more severe (ELLIOTT, 1960) than those of New Brunswick.

Exploring the opposite extreme of weather effects yields even more illuminating results. A weather manifold for the budworm theory is shown in Figure 19. The expected value of the weather index for New Brunswick is 2.0, yielding the familiar manifold of earlier figures. It is clear from this figure that if weather is sufficiently poor (e.g., an index of 1.0 or less), then no forest density is sufficient to trigger an outbreak. Further, incipient outbreaks initiated under better weather conditions can be, as it were, spontaneously aborted by subsequent years of bad weather. A simulation evaluation including a comparatively poor weather distribution typical for Newfoundland is shown in Figure 20a. This time, frequency and amplitude of budworm outbreaks are reduced to insignificance. The remaining
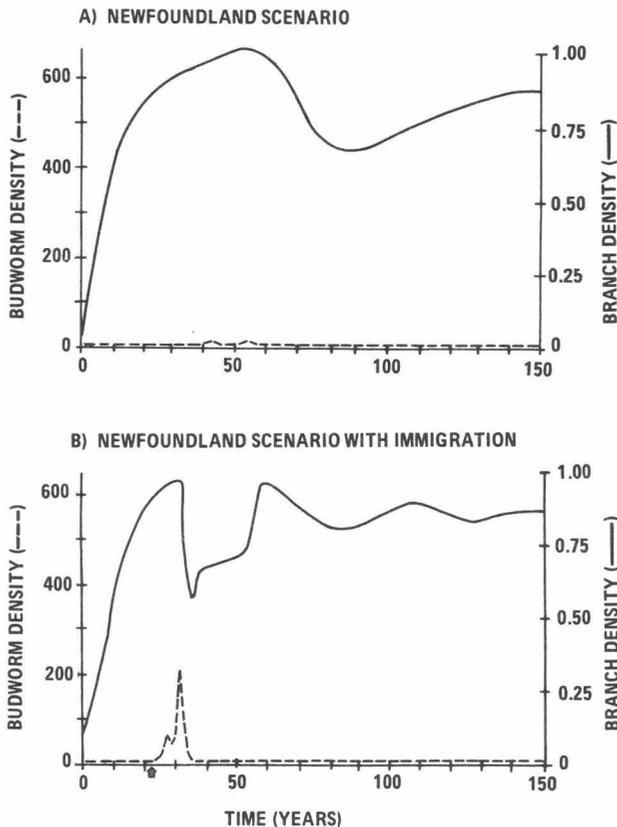

Fig. 20: Diagnostic runs of the single grid, spatially homogeneous model. Conventions as Figure 18. (a) Conditions for Newfoundland: a higher proportion of the forest is susceptible tree species, weather is worse for budworm. (b) Identical conditions for Newfoundland but with moth immigration from mainland in years 25 and 26.

forest «cycle» simply reflects the initial age class distribution of trees. The theoretical predictions are indistinguishable from the irregular, short-lived, very low-density «outbreaks» that constituted budworm's history in Newfoundland until the 1970s (FIDS, 1938–1970).

Note, however, that the weather manifold of Figure 19 indicates that outbreaks are not impossible even under the poorest weather conditions. If budworm densities were to somehow be increased into the region above the unstable undersurface of the manifold (i.e., a larval density of about 25), then the theory predicts that they would continue to rise to the (comparatively low) outbreak densities of the upper surface. Now immigration of dispersers is the most likely mechanism to accomplish such an increase, and immigration is something that the island of Newfoundland usually has very little of. But by the late 1960s, management efforts on the adjoining mainland had created an historically unprecedented situation: the persistent, seething outbreak which has already been described in Figures 3 and 16. Due to the moderate defoliation accompanying this mainland outbreak, an extraordinary number of females dispersed and were recorded as immigrants in Newfoundland light-trap surveys. A moderately serious outbreak followed in the early 1970s which has by now spread across much of the island and is causing some forest mortality (FIDS 1965–1978). To evaluate the theory with respect to this observation, we performed the same simulation computations as for Figure 20a but imposed an external invasion of dispersers in years 25 and 26 (Figure 20b). As observed in the field, a moderate outbreak was precipitated by the immigrants and resulted in some destruction of forest. As expected from the manifold analysis, this single outbreak failed to repeat itself in the absence of further immigrant invasions. Though inconclusive as always, such results are hardly discouraging.

One general point should be noted before leaving the Newfoundland example. There are other areas in the budworm system that also exhibit the relatively poor weather conditions of Newfoundland. Most of these, however, adjoin areas of better weather that exhibit regular budworm outbreaks. It is immediately clear from the preceding discussion and inspection of the weather manifold that such areas can provide at best ambiguous points of comparison for the theory. For, even if the theory is correct, outbreaks in such poor weather areas may be expected to occur sporadically as a function of largely unmeasurable immigration from surrounding areas. It is the unique *combination* of circumstances embodied in the Newfoundland situation that makes it a valuable point for comparison.

Other work with the manifolds and recruitment curves suggests that when forest mortality is retarded or prevented (i.e., location on the branch density axis is held fixed at high levels), the budworm is likely to begin a qualitatively distinct high frequency, relatively low amplitude oscillation with foliage. The insecticide spraying program initiated in New Brunswick in the early 1950s was designed to protect foliage and thereby the forest. It did so admirably, and also precipitated the «seething outbreak» pattern of Figure 3. As was noted earlier, when the basic budworm theory is coupled to a realistic management module (see BASKERVILLE, 1976; CLARK et al., in press) and the consequences are computed, the result is indeed the qualitatively distinct high frequency «foliage cycle» (Figure 16).

As a final example, recall the predation manifold presented earlier in Figure 14, and consider the effects of suddenly reducing predation in an endemic budworm situation with a forest density on the order of 0.6. If the theory and its manyfold are correct, this should eliminate the lower equilibrium and precipitate an outbreak as densities rise to the single equlibrium surface which exists under low predation, moderate forest conditions. Simulations show that this is in fact the dynamic model prediction (Figure 13). It is exactly this sort of unambiguous, qualitatively distinct response that we are searching for in our efforts

to evaluate the theory, but we could find no natural experiment (such as Newfoundland provided for the dispersal questions) to provide the necessary observations. Ecology is an experimental science, however, and in this instance the theory and its equilibrium manifolds can be employed to define a critical experiment. Field studies can identify a set of forest stands of moderate density with endemic budworm populations and totally removed from external dispersal influences. The predators can then be removed from a sample of these sites in the spring and kept out during the period of budworm activity. Such predator removal experiments have been carried out for other forest defoliators (Dowden et al., 1953; Campbell and Sloan, 1977) and are planned for budworm. If predation is indeed responsible for the lower equilibrium, such experimental areas should show qualitatively distinct signs of outbreak in three generations at most. If outbreaks can't be produced, we'll need a new theory.

VI. Conclusion

In conclusion, we carry the following biases from our theory-building work on budworm:

1. Population survey data, however well collected, are unlikely to help much in the analysis or prediction of population dynamics. Factors responsible include the nonlinear nature of ecological relationships, particularly at low density; the physical scale and coupling problems introduced by animal movement; and the long time scales characteristic of many ecological systems.

2. More empirical work on the structure of individual ecological relationships is a high priority need. The few existing studies in this area have been unusually productive, and the augurs of analogy to other sciences are good.

3. The consequences of ecological theory must be understood, not just enumerated, before the theory can be critically evaluated. Understanding is most effectively focused on qualitative structural questions rather than quantitative behavioral ones. Equilibrium manifolds provide one tool for the task at hand.

4. Most natural system behaviour and most experiments have at best marginal bearing on the evaluation of theory. But an understanding of the theory's qualitative structure and implications can often be used to predefine special limiting conditions in which observation will be particularly illuminating. A wide-ranging search for natural experiments presenting such conditions is rewarding in a surprising number of cases and prescriptions for experimental interventions follow naturally.

Whether these biases can really help to improve the ecologist's version of the morning forecast remains to be seen.

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