Quantitative Population Ecology: Elegant Models or Simplistic Biology?

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EARLY this century mathematicians[1] derived simple population dynamics models under the assumptions that population growth rate depends upon current population size,

$$\frac{dN}{dt} = f(N), \tag{1}$$

and that all $N>0$ converge on K, the globally stable equilibrium. The growth rate of continuously reproducing populations was modelled by the Verhulst–Pearl logistic equation

$$\frac{dN}{dt} = rN\frac{(K-N)}{K}, \tag{2}$$

where r is the so called intrinsic rate of natural increase, and is composed of instantaneous birth and death rates. This model gives a good fit to population growth of simple organisms in pure culture under laboratory conditions, and is a reasonable approximation to natural population performance of introduced species into environments with few competitors.[2] It suffers from the unrealistic assumptions of constant r and K, a lack of individual variation and instantaneous density dependence.

Time lags (T) were introduced by Hutchinson[3] in the 1940's and the model refined as

$$\frac{dN_t}{dt} = rN_t\frac{(K-N_{(t-T)})}{K}. \tag{3}$$

At first, it was generally believed that this form led to damped oscillations toward K, as opposed to the monotonic approach to equilibrium of the simple logistic equation (Fig. 1). Recent investigations by Robert May into this and related differential delay equations of population growth have revealed a complex suite of behaviours.[4, 5] The performance of these systems depends upon the magnitude of the time lag (T) relative to the system's response time ($T_R = F(r)$) and to the nature of density dependence.

In particular, May has shown for equation (3), if $0<T/T_K<e^{-1}$ the system monotonically approaches a stable equilibrium; if $e^{-1}<T/T_R<\frac{1}{2}\pi$ it overcompensates with damped oscillations toward the same equilibrium, but when $T/T_R>\frac{1}{2}\pi$, the system bifurcates into stable two-point limit cycles of period = $4T$. Slightly more realistic differential delay equations incorporating a constant *per capita* death rate, but making allowances for nonlinear density dependent recruitment, exhibit even more complicated dynamics. In these more elaborate, but still deterministic models, adjustments in T/T_R and in density dependent recruitment produce outcomes ranging from monotonic convergence on K, damped oscillations, two-point and multipoint stable limit cycles, and even apparently chaotic fluctuations.

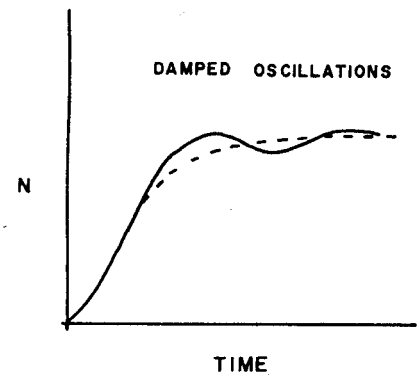

Fig. 1. The simple logistic model approaches equilibrium density monotonically (dashed line) whereas time lags lead to damped oscillations (solid line), and to other complex population responses (see text)

The dynamics of populations exhibiting discrete intervals of growth are characteristically modelled by difference equations under the analogous assumption of the continuous growth models that

$$N_{t+1} = f(N_t). \tag{4}$$

Several alternative forms for $f(N_t)$ have been proposed. In the context of this paper it is sufficient to note that these difference equations, with their built-in time lags, display similar complexities of behaviour to the differential delay equations.

These two classes of simple deterministic growth equations can be used to "explain" the dynamics of any single-species population. Even the simplest forms appear to give a reasonably good fit to empirical laboratory and field data.[5] The message to biologists is clear: population dynamics can be efficiently modelled by simple deterministic expressions. Complex dynamics of natural populations does not appear to require complex modelling.

Even so, these kinds of models have been correctly criticised as biologically simplistic. Ecological theorists have responded by successively eliminating inherent assumptions of the logistic growth model.

Among the modifications are the classic growth models of two species in competition

$$\frac{dN_1}{dt} = r_1N_1\frac{(K_1-N_1-\alpha_{12}N_2)}{K_1} \tag{5}$$

and

$$\frac{dN_2}{dt} = r_2N_2\frac{(K_2-\alpha_{21}N_1-N_2)}{K_2}, \tag{6}$$

where α_{12} and α_{21} are the *per capita* effects from competition of species 2 on the growth rate of species 1, and

of species 1 on species 2, respectively. For n species these relations generalise to

$$\frac{dN_i}{dt} = r_i N_i \frac{(K_i - N_i - \sum \alpha_{ij} N_j)}{K_i}, \qquad (7)$$

with the added assumption of linearity of the competition coefficients. Similar simultaneous growth equations have been used to model predator–prey interactions, plant–herbivore systems, resource sub-division among coexisting consumers and so on. The single-species logistic has been refined to incorporate stochastic events[6] and innumerable models have been proposed for specific cases.

Successive refinements of the logistic have occupied, and continue to occupy, the interests of large numbers of ecological theorists, and have had a large influence on the orientation of empirical ecology. These improvements have not been without cost.

First, successive refinement toward ever more realistic and precise models is outstripping the ability of empirical ecologists to test them.[7] Instead, the intrinsic variability of ecological systems seems to demand general and perhaps qualitative models. Second, successive refinement of the logistic has determined in large part the kinds of questions addressed by ecologists. All of these models explicitly or implicitly assume that populations are the important entity of ecological systems. Individual variation, when considered, is modelled as "noise" around population averages. This may be more or less valid for resource management problems, yet even here, the genetic make-up of the population and the expressed phenotypic composition should be considered. If populations are not the essential element of ecological systems, population centred theory is an inefficient framework.

If we consider instead that individual variation is "the stuff" of evolutionary ecology, then the key question would no longer be "what are the equilibrial states of populations?" but would become "what are the equilibrial strategies of phenotypes comprising populations?" Structuring theory to answer this second question would mean that population dynamics would be a necessary outcome of individual strategies. Population dynamics, after all, is simply the weighted products of individual survival and fecundity probabilities.

To some degree, this goal is attained by matrix analogues to the logistic. Age-structured models have been used in ecology since the 1940's, but are clearly inappropriate for organisms where age classifications do not reflect demographic states. So called stage-classified models offer great promise, but are still subject to the assumptions of earlier population projection models.[8] These matrix models are limited because they are also oriented toward population processes as opposed to individual level phenomena. Population level transition probabilities specify the form of the age or stage distribution, but are inadequate to evaluate phenotypic variability.

The next step would seem to be the simultaneous solution of several phenotype-specific transition models. When solved, we would have not only the form of the age or stage distribution, but also the relative densities of alternative phenotypes. Under the usual demographic constraints of constant transition probabilities, the solution would give stable age or stage distributions, as well as the equilibrium proportions of the different phenotypes. Then we could ask the crucial questions: "what demographic traits must a new phenotype possess in order to become established in the population?" and "how do the equilibrial proportions of phenotypes respond to environmental variability as reflected by changes in the transition matrices?"

But if refinements of relatively simple population models pose problems for empirical ecologists, then surely those difficulties in testing models against data would be compounded by the more elaborate models I propose here. Perhaps not. Many of the problems confronting empirical ecologists in testing current models are based on unavoidable imprecision in estimating natural populations.[7] Initial tests of phenotype models would not require population estimates because these tests would address questions related to the characteristics of individual phenotypes. Sampling from the infinite array of possible phenotypes could prove to be a formidable problem, but there are no strong *a priori* reasons to suppose that tests of phenotype structured theory should be more demanding than the tests of current theory.

Lomnicki[9] has offered another alternative. His model evaluates phenotypic variability in resource intake. The assumption is that foraging efficiency is in some way related to genetic fitness. The Lomnicki model may work reasonably well for small animals with high metabolic rates, but because it is at least one step removed from genetic fitness, more general life history models hold more promise.

Reductionists might ask "why stop at life history models? Why not extend the concept of phenotypic variability into the realm of population genetics? Why not develop an integrated theory of population biology based on genetic models?"

This criticism has been eloquently addressed by Lewontin[10] and Stearns.[11] As Fig. 2 shows, population genetics and population ecology are separated by little known to "unknowable" transformation rules. The genetic transformations are probably better understood than the ontogenetical, ecological and behavioural ones, yet even these appear infinitely complex. We know, for example, that ecological traits (and certainly those related to survival and fecundity) are subject to polygenic

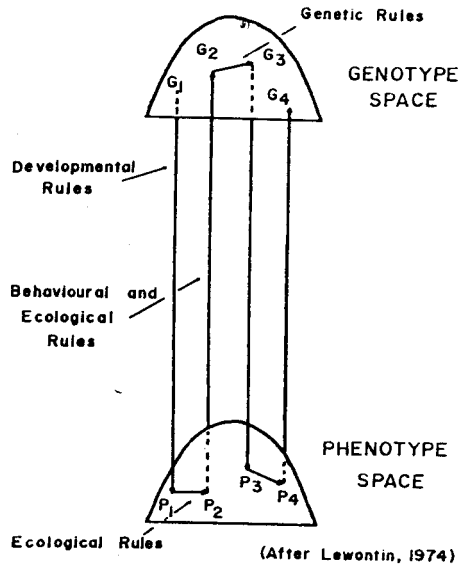

Fig. 2. The transformation rules of evolutionary biology (after Lewontin[10])

inheritance. Interactions among loci are likely to be nonlinear and frequency dependent. Furthermore, the importance of chromosomal rearrangements, and of so called regulatory genes which control transcription of linked segments of structural genes, may overpower that of the structural genes themselves.[11]

Given this high degree of imperfection, a complete synthesis of population genetics and population ecology may be impossible.

Evolutionary ecology seems to need a theory based on individual strategies. Some direction to the new theory can be found in studies on the evolution of optimal life history traits. The goal of these life history theories is to predict features such as the optimal amount of effort to expend in any given reproduction and the optimal timing and frequency of reproduction. The over-all objective is to determine the optimal age or stage-specific strategy which maximises reproductive fitness. The difficulty lies in estimating fitness. A good guess would be a collective term expressing survival and fecundity simultaneously. Ronald Fisher[12] proposed the term "reproductive value" as an estimate of age-specific fitness, viz.,

$$V_x = \int_x^{\infty} b_t \frac{(l_t)}{l_x} e^{-r(t-x)}\, dt, \qquad (8)$$

where V_x is reproductive value at age x, b_t is fecundity at time t, l_t/l_x is the probability of survival from x to t and $e^{-r(t-x)}$ is a correction term for growing or declining populations. Caswell[8] has recently shown how to calculate reproductive value for stage-structured populations.

The models implicitly assume that most of the ecologically important variability in fitness is age or stage related. Age and stage specific models evaluate the optimal reproductive strategy by assuming finite resources for maintenance, growth and reproduction. Increasing reproduction at time t will, on average, decrease the supply of resources for maintenance and growth, and so decrease survival to time $t+1$, or decrease reproduction at time $t+1$. When the general shape of the trade-off is known, it is relatively easy to predict the optimal strategy, except in the case of multiple optima.[13]

James Smith's[14] work on song sparrow life histories demonstrates the limitations of this approach. Contrary to the predictions of the trade-off models, Smith showed that both breeding success and future survival increased with clutch size. Most bewildering of all, heritability of clutch size was near zero. In Smith's song sparrows, clutch size and survival are complex phenotypic traits. Given our ignorance of ontogenetical, ecological and behavioural transformation rules (Fig. 2), it may be impossible or unreasonable to predict optimal reproductive strategies.

Perhaps our interpretation of evolution by natural selection needs reappraisal. New insights into natural selection are unlikely to come from comparative studies of adaptation, but will be fostered instead by examining the mechanisms of evolutionary change. At the biochemical level, different structural configurations of enzymes may only slightly reduce enzyme efficiency. If regulatory genes are common throughout the genome, slight inefficiencies are easily compensated with little cost by increasing the quantity of gene product.

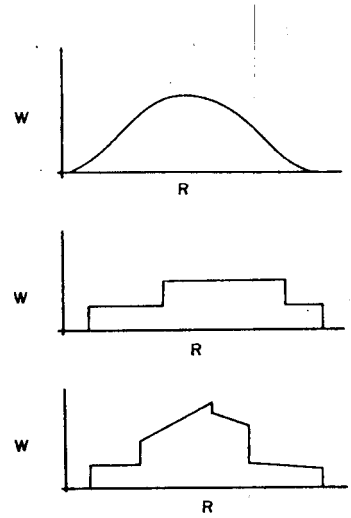

Fig. 3. Alternative representations of the importance of different classes of genes on genetic and ecological systems. Each curve can be thought of as a representation of the frequency of genes, genotypes or phenotypes. The top curve is the classical view of continuous variation in structural genes. The middle curve is the hypothetical case where all genetic information other than that due to regulatory genes is masked. The lower curve is one of an infinite number of synthetic views where both regulatory genes and structural genes confer selective advantage

This is in sharp contrast to the classical view of the over-riding importance of structural genes, yet it is this idea of continuous genetic variation which is embodied in our theories of population biology. General acceptance of regulatory genes may profoundly modify population theory. I show this influence schematically in Fig. 3. The top curve represents continuous variation in structural genes. This leads to a smooth unimodal frequency distribution of genes in biochemical space, a similar distribution of genotypes in genotype space and continuous variation in phenotypes with one optimum, in phenotype space. The middle curve represents the discrete distribution resulting from the overpowering importance of regulatory genes. At the biochemical level, steps represent changes in regulatory genes (or major genetic rearrangements). In this view, structural gene differences are masked by the compensatory abilities of the regulators. This gives rise to a similar step function in genotype space where the heritable equivalence of genotypes is forced by the regulatory genes. In phenotype space, each step represents a platykurtic optimum where strategies by different phenotypes convey equal fitness. In this scenario, regulatory genes have a major effect on fitness and are subject to strong selection.

Genetic reorganisation resulting from changes in regulatory genes would be more likely to occur between than within populations. Comparative studies between populations would indicate different selective optima, whereas studies within populations would reveal multiple optima. The lower curve represents one example of an infinite array of more realistic curves where both regulatory genes and continuous variation in structural genes are important. Regulatory genes still result in step functions in genotype and phenotype space, but the cumulative effects of structural genes may confer some secondary selective advantage. Single optima may or may not exist within populations, but between populations we should still be able to detect important phenotypic differences.

All of these possibilities assume a one-to-one correspondence of functional genotypes and phenotypes. Phenotypic plasticity responding to environmental and

social variation could have equally profound effects. In the absence of experimental control, this leads to the frightening possibility of all life histories being possible with similar rewards. Current theory is incapable of dealing with this complexity.

Similar difficulties face ecologists in data analysis. Multivariate habitat analyses will serve to illustrate some of these shortcomings.

Ecologists using computer-generated multivariate statistics require specific rules for multivariate data manipulations. Factor analytical procedures, for example, are commonly used by ecologists to "reduce" the dimensionality of multivariate data. Interpretations of the underlying factors seldom give rise to new field measurements. The goal of reduced dimensionality is only partially realised because most or all of the measurements must be repeated in subsequent studies. Ecologists must accept much of the blame for this problem; however, their task would be greatly simplified by the development of consistent stepwise factoring routines with explicit statistical rules for variable deletion.

A more serious dilemma is posed by the difficulty ecologists face in dealing with sources of variation in ecological systems. For example, a study of habitat differences between two co-occurring rodent species (*Microtus pennsylvanicus* and *Peromyscus leucopus*) in Southern Ontario indicated that the two species were separated on the basis of microhabitat.[15] The habitats frequented by each species were significantly different in so called foliage height diversity (FHD, an index of the structural complexity of vegetation). But the analysis was across different habitat types (Fig. 4) and was not as much an analysis of differences in microhabitat between species, as much as a reflection of structural differences among alternative habitats.

Variation in habitat can logically be decomposed into microhabitat and macrohabitat effects (Fig. 5). Macrohabitats represent more or less homogeneous probability density "ridges" of microhabitat variation. Analysis of microhabitat differences must then be constrained to a particular homogeneous process (macrohabitat).

If foliage height diversity is an important cue to *Microtus–Peromyscus* separation, a within-habitat multivariate analysis should be capable of classifying *Peromyscus* and *Microtus* habitat on the basis of FHD. Stepwise multiple discriminant function analysis of *Microtus–Peromyscus* habitat separation in two mutually occupied macrohabitats resulted in significant microhabitat separation, but FHD was not among the discriminating variables (Table I).[16]

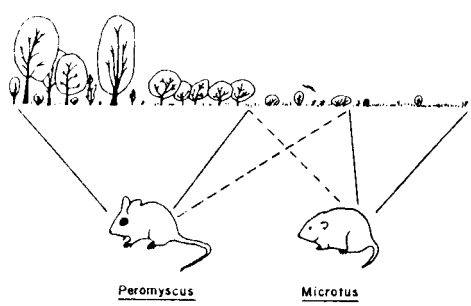

Fig. 4. Habitat affinities of two rodent species (*Microtus pennsylvanicus*—short tail; *Peromyscus leucopus*—long tail) in Point Pelee National Park Canada. *Peromyscus* alone are permanent residents in the forest and sumac habitats whereas both species co-occur in the old field and grassland. An analysis of species separation across habitats will contain both habitat and species effects

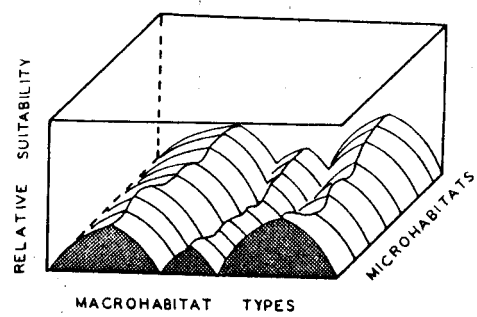

Fig. 5. One interpretation of variability in habitat. Macrohabitats are represented as homogeneous but amorphous probability density ridges composed of microhabitat variability. A time-specific transect of microhabitat measures across habitats would result in coordinate probability density functions displayed in the x, y plane at the front of the figure. Summation of all possible transects gives rise to the three-dimensional "ridge"

Table I

***Microtus–Peromyscus* Microhabitat Separation by Stepwise Multiple Discriminant Function Analysis of 14 Habitat Variables in Two Habitat Types in Point Pelee National Park**

Habitat	Year	*F*-Ratio	Discriminating variables
Grassland	1978	28·03**	LMAT, SUMQ
Grassland	1979	10·42**	AP2, SUMQ, SBDEN
Old Field	1978	6·44*	Q1, AP2
Old Field	1979	24·64**	Q1, BUSHN, STDEN

* $0{\cdot}01 > p > 0{\cdot}001$; ** $p < 0{\cdot}001$.
AP2—arcsin proportion of vegetation in the 0·25 to 1 m vegetation layer; BUSHN—square root of shrub numbers within 3 m of the census station; LMAT—logarithm of depth of ground litter; Q1—amount of vegetation from 0 to 0·25 m above the ground; SBDEN—square root of the distance to the nearest shrub; STDEN—square root of the distance to the nearest tree >10 cm DBH; SUMQ—total vegetation recorded below 1·75 m.

One recent approach to the analysis of heterogeneous habitat data deserves special mention. Some ecologists routinely subject pooled microhabitat data from several macrohabitats to some form of factor or ordination analysis to reduce dimensionality, then follow that with a between technique like discriminant function analysis. The assumption is that microhabitat is continuously distributed and independent of habitat type. This is the opposite of my interpretation where macrohabitats represent homogeneous units.

It is unlikely that biological organisms recognise either macro- or microhabitat as distinct entities. Macro- and microhabitat are artificial constraints imposed on ecologists by available statistical models. Contemporary statistics may not represent informative models of many complex biological systems. Again, the underlying mathematical theory greatly influences the kinds of questions asked by ecologists.

But the only rule governing distribution and abundance of biological organisms is the opportunity for reproduction and replacement. Let us assume evolution by natural selection as the working paradigm, and construct our mathematical and statistical models around that paradigm. This may mean that we need explicit biological models rather than using those of physics, engineering and statistics. Is self replication a

unique phenomenon requiring its own sets of rules and logic?

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