The Use of Mathematics to Describe Biological Systems: The Puzzle of "Distal" Biology

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The Puzzle

- How can large-scale simplicity emerge from small-scale complexity?
- Consider a population of hares.
- The number of hares depends on: individual hare fertility, the weather, health of individual predators, availability of resources, motor vehicle traffic, colour of individual hares, location of individual hares, contingent matters about an individual hare's genetic and behavioural constitution, etc.
- Given all this, it's amazing that we can say *anything* about hare abundance.
- But not only can we say *something*, we can write down a remarkably simple and fairly accurate equation describing the hare abundance.

The Logistic Equation

$$\frac{dN}{dt} = rN(1 - \frac{N}{K})$$

Where r, is the population growth rate; t is time; N is the population abundance; and K is the carrying capacity.

This is a model of a single population's growth—exponential at first and then flattening out as it approaches carrying capacity.

Lotka-Volterra Equations

This model describes the population of the predator and the prey via two coupled first-order differential equations:

$$\frac{dV}{dt} = rV - \alpha VP$$
$$\frac{dP}{dt} = \beta VP - qP$$

Where V is the population of the prey and P is the population of the predator,
r is the intrinsic rate of increase in prey population,
q is the per capita death rate of the predator population,
α is a measure of capture efficiency,
and β is a measure of conversion efficiency.

Some Comments on the Models

- Individual predator and prey behaviour is missing.
- We only have population-level information such as growth rates r, carrying capacity K, capture efficiency α, and conversion efficiency β.
- These "constants" are statistical summaries of the many and various local factors.
- So at least one part of our task is to understand how r, K, α, and β can stand proxy for all the local-level factors that determine the population abundance.

The General Problem

- Ecology is not the only place this happens (e.g., weather and El Niños, gases in equilibrium, students' grades), but it provides a striking and instructive example.
- The general problem is to understand how seemingly complex and unpredictable micro-behaviour results in simple and predictable macro-behaviour?
- Or to focus on one important aspect of the problem: how can we get by with statistical summaries of micro-behaviour when seeking macro-level descriptions?

A Sketch of Enion Probability Analysis I

- *Enions* are the basic units of the system under study. In population ecology the enions are the individual organisms.
- *Macrovariables* are variables concerning only macrostates.
- The macrolevel abstracts away from individual enions and involves only enion statistics
- *Macrovariables* are variables concerning only macrostates. Population abundance and gas pressure, for example, are macrovariables in population ecology and thermodynamics respectively.

A Sketch of Enion Probability Analysis II

- Enion probability analysis is a method for understanding how to get from micro-complexity to macro-simplicity.
- It involves three steps:
  1. (i) The behaviour of the system's enions is specified probabilistically—the probability of a given hare dying, say. These are the *enion probabilities*.
  2. (ii) These probabilities are aggregated, giving a probability distribution describing the behaviour of macrovariables in terms of only macrovariables.
  3. (iii) A macrolevel law is derived from the macrolevel probability distribution.
- Typically, these laws are remarkable in that despite the huge number of microvariables, the laws themselves are very simple, in the sense that they contain very few macrovariables.

A Sketch of Enion Probability Analysis III

- It looks as though the crucial move in all this is step two: the aggregation process. This is where microlevel information drops out of the picture.
- But the techniques employed in this aggregation process rely on the enion probabilities having certain features, so step one is really the crucial step.
- More specifically, the enion probabilities must satisfy *the probabilistic supercondition*: The enion probabilities are not affected by conditioning on microlevel information.
- E.g., if this condition is satisfied for a hare population, the probability of a particular hare dying in a given time period is stochastically independent of the probability of any other hare's death.

Microconstancy

- A system is said to be *microconstant* if the macrovariable probabilities do not depend on the initial conditions of the system (e.g. a roulette wheel).
- Bold Claim: *Many complex systems, including various ecological systems, exhibit microconstancy*.
- This is what explains the satisfaction of the probabilistic supercondition, and ultimately explains the simplicity of macrolevel laws.

Three Views about the Law of Large Numbers

1. Statistical regularities expressed in statistical laws are explained by the law of large numbers; here, probability theory plays the starring role. (Defended by Poisson, Maxwell and Boltzmann.)
2. Statistical regularities are due to some non-probabilistic causes. (Defended by Quetelet and Buckle.) On this view, probability theory plays only a supporting role; the law of large numbers is invoked to argue that short-term probabilistic disorder will, in the long run, cancel out, leaving non-probabilistic order.
3. Frequentism, according to which probabilities are identified with relative frequencies. On this view the law of large numbers plays no explanatory role at all—it's a trivial consequence of the definition of 'probability'. Probabilities cannot explain statistical regularities because probabilities just *are* those regularities.

Mathematical Explanation

- Enion probablity analysis shares a great deal with the first view—the view that probability plays the primary explanatory role in statistical laws.
- Though enion probability analysis does emphasise the explanatory significance of the physical properties that underwrite the legitimacy of the application of the law of large numbers (namely, stochastic independence).
- There are also other questions about, for example, the stability of the system under certain sets of initial conditions; such questions demand mathematical explanation.
- It seems that the full explanation of the macro-level phenomenon requires both micro-level causal stories (proximal biology) *and* probabilistic explanation. Neither will suffice on its own.

Idealisations

- Consider an idealisation such as that a single constant *r* can summarise the growth rate for the whole population.
- Enion probability analysis gives a very interesting justification of such idealisations in terms of the microconstancy of the system in question.
- So while the assumption of a constant growth rate for every individual in the population is false, it can still be true that a single constant *r* can be used in the population-level description.
- Indeed, it might be argued that, properly understood, such moves are not idealisations at all (except in so far as the assumption of the system exhibiting microconstancy is an idealisation).

Conclusion

- There is a puzzle about "distal" biology: How can large-scale simplicity emerge from small-scale complexity?
- Enion probability analysis goes some way to resolving the puzzle.
- Demonstrating that the probabilistic supercondition holds in the various cases of interest is no easy matter, but is crucial to the account.
- If the probabilistic supercondition does hold, then there seems to be a more substantial role for mathematics and statistics in explaining macro-level phenomena.
- An interesting account of a special class of idealisations also emerges: the idealisations in question are justified by the fact that the system in question exhibits microconstancy.

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