

Mathematical Models in Ecology

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Fundamental Questions in the Philosophy of Science:

- What is a scientific theory?
- How are scientific theories tested?
- What is a scientific explanation?

My talk:

- What is an ecological *model*?
- Can ecologists build *successful* models?
- How should ecological models be *evaluated*?
- How can ecological models be *explanatory*?

What are Models in Ecology?

Greg Cooper writes,

Perhaps the first question should be, “What is a model?”
This is one of those large philosophical questions that I
am determined to avoid; still, something must be said.
(2003, 255)

Yes, something must be said... A mathematical model is
characterized by sets of assumptions about:

- Variables (the things which change),
- Parameters (the things which do not change), and
- functional forms (the relationship between the two)

Example: The Lotka-Volterra Predator-Prey Model

- ✓ Growth of prey population is exponential in absence of predators
- ✓ Predator declines exponentially in absence of prey
- ✓ Individual predators can consume an infinite number of prey
- ✓ Predator and prey encounter one another randomly in a homogenous environment

So, \times is LVPP just in case \times satisfies the following laws of succession:

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

However, these assumptions are false!

Models in ecology are characterized by *idealized assumptions*—they all contain false assumptions. Thus, a hypothesis:

A representation is a model only if it is idealized—its characterization contains at least one false assumption.

However, this is *necessary* but not *sufficient*. Why? *Every* false theory would then be a model! My account of models:

Models are representations that are characterized by sets of assumptions at least one which is idealized and where an *idealization* is a false assumption that is useful.

Example: Natural selection and random genetic drift—assume N is infinite; however this ensures that actual and expected reproductive success is the same.

A Deflationary Semantic View of Models (Not Theories)

- Theoretical definition—a relational structure, $\langle \text{objects}, \text{relations} \rangle$
- Theoretical hypothesis—a claim that there is mapping or relation of fit between model and world

A Suppes' Set-theoretic Predicate

x is a Lotka-Volterra predator-prey system if and only if

1. $x = \langle T, V, P, \alpha, \beta, r, q \rangle$
2. T is an interval of real numbers—a time interval,
3. V and P are state variables whose domains are the set of non-negative real numbers—the prey and predator abundances,
4. α , β , r , and q are parameters which are real numbers—the capture efficiency, conversion efficiency, intrinsic rate of increase of the predator, and intrinsic mortality rate of the predator respectively, and
5. For $t \in T$, $dV/dt = rV - \alpha VP$ and $dP/dt = \beta VP - qP$.

Caution! Models \neq Theories

- Mathematical models are relational structures.
- There can no mathematical relations between models and world per se – degree of fit, isomorphism, homomorphism, etc. are relations between mathematical structures.
- Theories have epistemic properties – they can be the objects of propositional attitudes; mathematical structures cannot be.
- Theories have semantic properties that mathematical structures cannot – truth-values for example.

Thus,

- For a model to fit or bear some mapping to the world, the empirical system must be construed as a relational structure, *a model of the data*.
- It is *theoretical hypotheses* which are believed, confirmed, accepted, etc.
- Theories are thus *hybrid entities* – structures *and* propositions.
- When we say that model *predicts* some feature of system, we are claiming that the model *fits* the systems in some respect to some degree.
- When we say that a model *explains* some feature of a system, we are claiming that the model *fits* the system in some respect and to some degree such that it *preserves* the causal relation of interest.

Can Ecologists Build Successful Models?

In *Geographical Ecology*, Robert MacArthur writes,

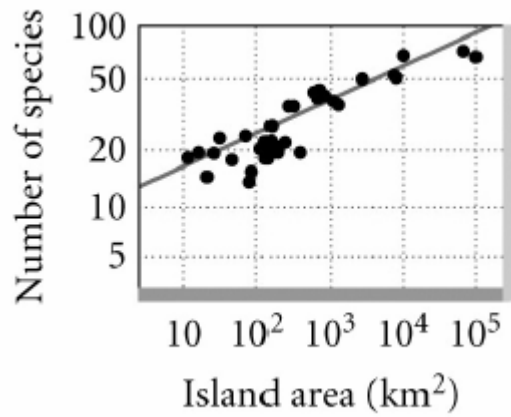
To do science is to search for general patterns. Not all naturalists want to do science; many take refuge in nature's complexity in a justification to oppose any search for patterns. This book is addressed to those who do wish to do science. (1972, 1)

However, if MacArthur's program is to succeed the ecological world must cooperate.

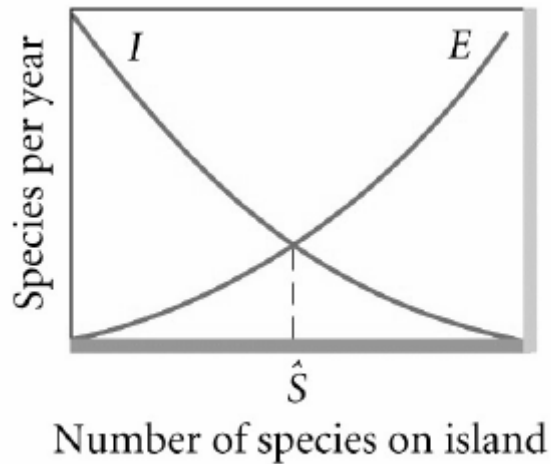
MacArthur's Bet: If ecological modeling is to be successful, then there must be discoverable general ecological patterns.

MacArthur's Bet

Example: General pattern—Species-area relationship



Equilibrium model of island biogeography



But really, are there general patterns??? The problems of contingency and complexity!!

Contingency

One can argue that there simply are no general patterns about which ecologists can theorize.

As Kim Sterelny writes:

The worry posed by extreme versions of the contingency hypothesis is that there are no patterns at all. The thought here is that membership and abundance within a community is sensitive to so many causal factors that we cannot project from one community to another (2001, 158–159).

Ecological systems can be sensitively dependent on their prior states.

Sensitive-dependence: if the system's state at time t had been otherwise, then the system at $t + \Delta t$ would be significantly different.

Example: In 1883, several volcanic explosions removed the island of Krakatoa of all biota. The reassembled island was the product of

- Area
- Distance from mainland
- Species pool

However, *the order of arrival* of species is an important factor in determining who survives; and if things had been different, so would species identity, richness, and evenness.

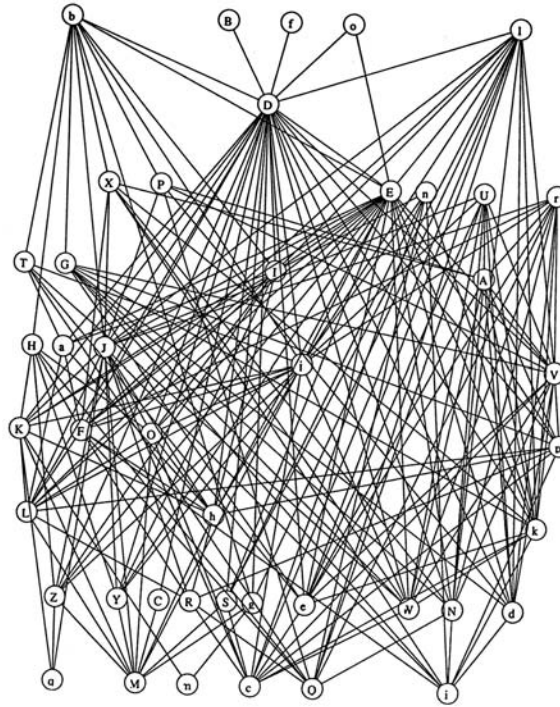
Complexity

Ecological systems are multivariate systems – there are *lots* of variables that are weakly interacting and thus are difficult to experimentally control.

- The number of variables to measure is so large and the time frame for ecological fieldwork and experiments so short that the systems are *unmeasurable*.
- The number of parameters and variables are so large that the equations are in such complex functional forms that they are *uninterpretable*.
- The equations cannot be solved in closed form and hence are analytically *insoluble*.

Food Tangles?

Example: Joah Roughgarden constructed this food web of 44 species from St. Martin in the Caribbean.



This would give us a 44×44 community matrix—1936 independent parameters.

$$\begin{bmatrix} \alpha_{1,1} & \alpha_{1,2} & \cdots & \alpha_{1,44} \\ \alpha_{2,1} & \alpha_{2,2} & \cdots & \alpha_{2,10} \\ \vdots & \vdots & \ddots & \vdots \\ \alpha_{44,1} & \alpha_{10,2} & \cdots & \alpha_{44,44} \end{bmatrix}$$

However, if the interactions between pairs of species are affected by other species—there are higher-order effects α_{ijk} —then matters are only made worse.

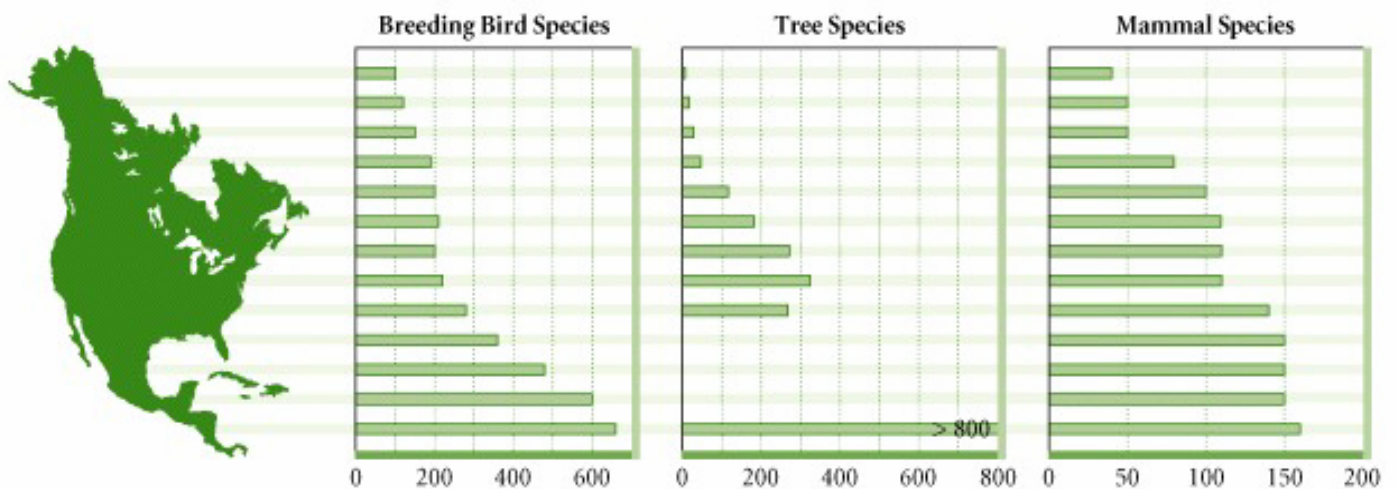
Contingency—A Response

Not everything is *equally contingent!* MacArthur writes concerning spatiotemporal patterns of species,

Ecological patterns, about which we construct theories, are only interesting if they are repeated. They may be repeated in space or time, and they may be repeated from species to species. A pattern which has all of these kinds of repetition is of special interest because of its generality, and yet these very general events are only seen by ecologists with rather blurred vision. The very sharp-sighted always find discrepancies and are able to say that there is no generality, only a spectrum of special cases.

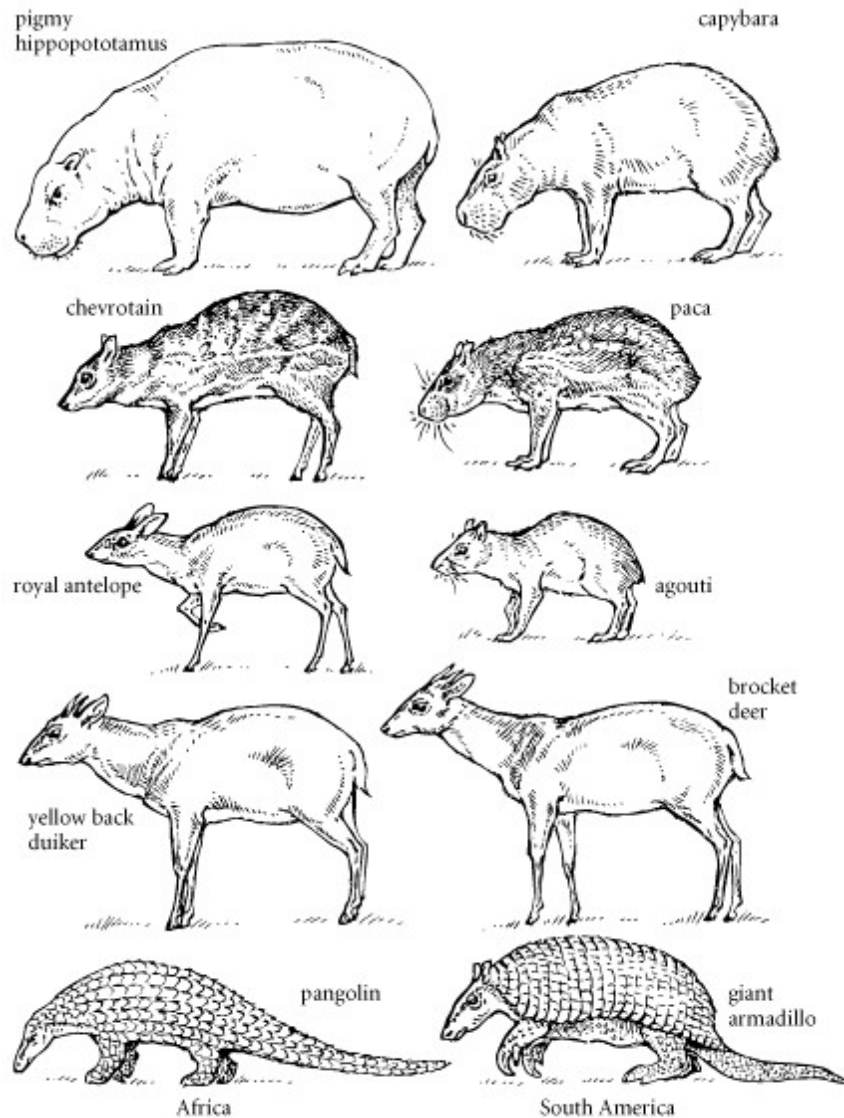
Latitudinal Gradients of Diversity

The number of species in most groups of organisms increases along a gradient from the temperate zone to the tropics.



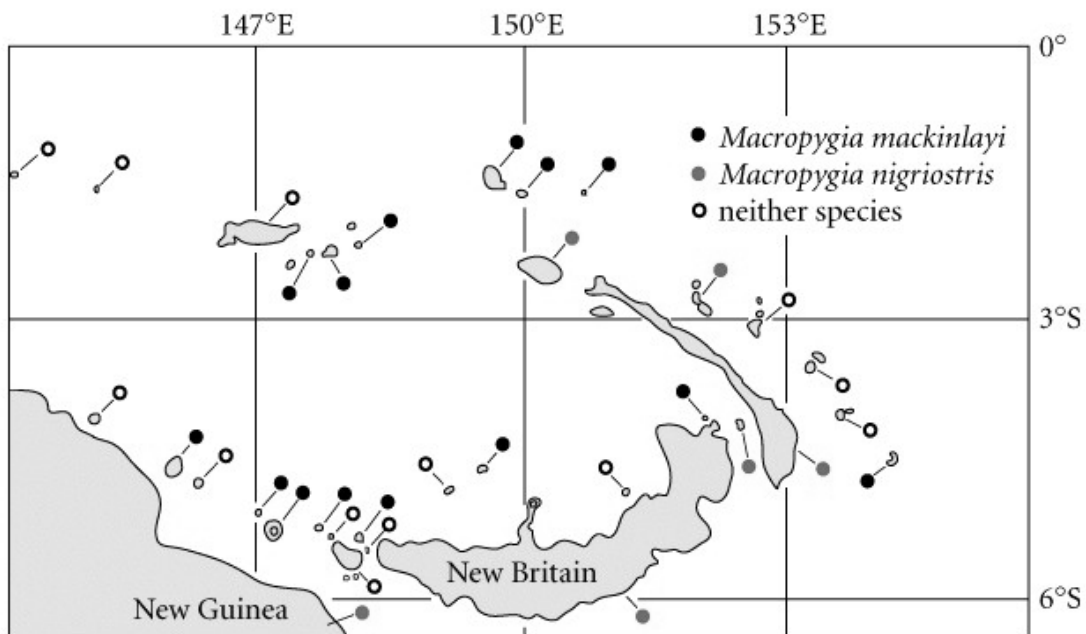
Evolutionary Convergence

Morphological convergence among unrelated African (*left*) and Neotropic (*right*) rain forest mammals. Species occupying similar niches or functional roles due to interspecific competition?



Checkerboard Distributions

Two species of cuckoo-dove, *Macropygia nigriostris* and *M. mackinlayi*, occur on six and fourteen islands in the Bismark Archipelago respectively. However, they never co-occur on any island.

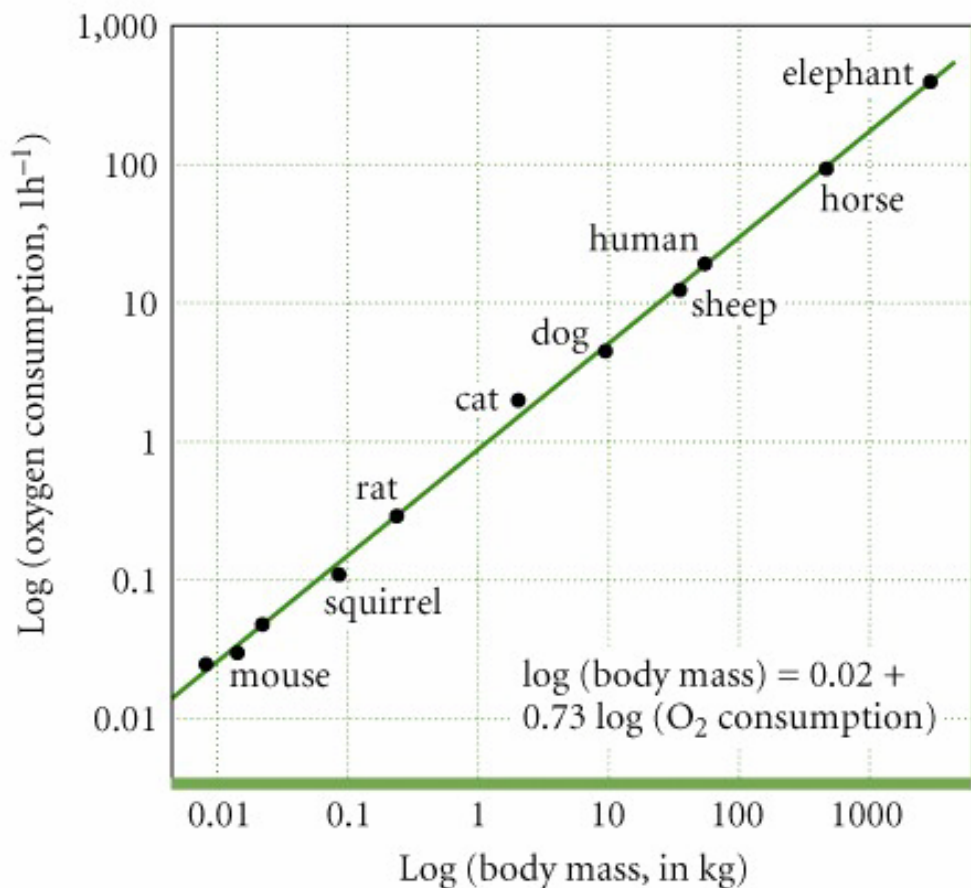


Jared Diamond claimed that this “checkerboard pattern” or complementary distribution resulted from interspecific competition was at work through niche differentiation and provided the basis of *community assembly rules*.

Allometries

The allometric relationship between resting metabolic rate (RMR), measured by the amount of oxygen consumer per hour, and body mass in a variety of mammals can be described by:

$$\text{resting metabolic rate} = (\text{body mass})^{3/4}$$



Complexity—A Response

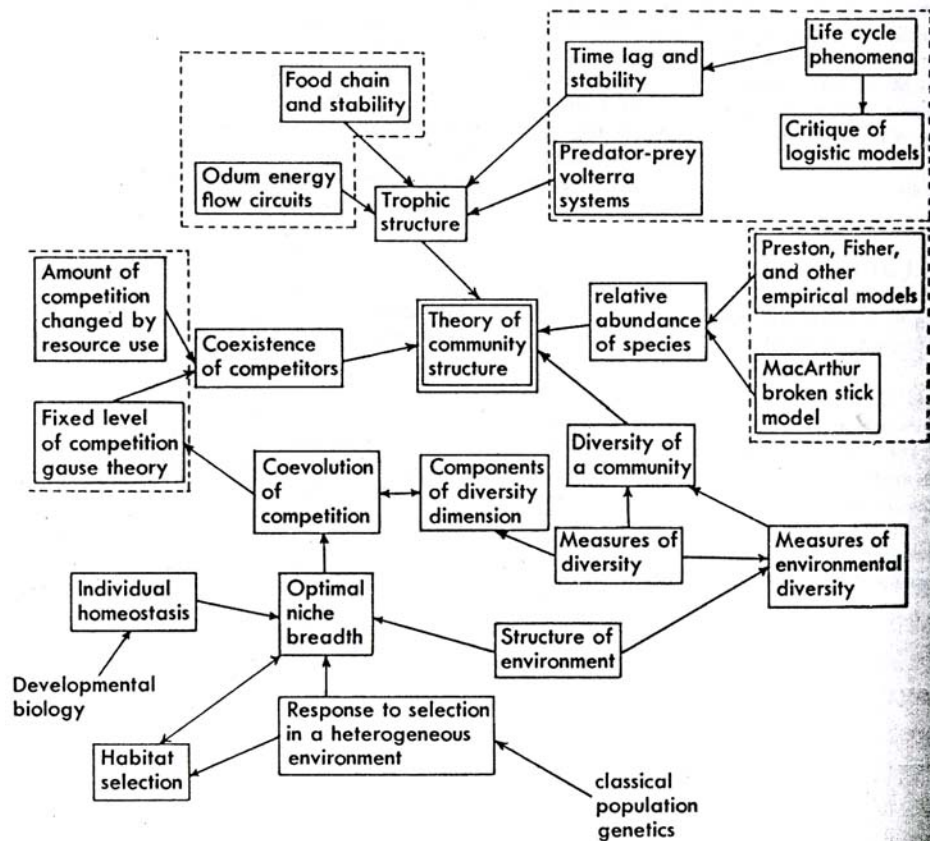
If the systems are too complex, change your models! Theories are *clusters* of such models and their *robust* consequences.

Richard Levins' trade-offs:

Type I Models: Generality is sacrificed for precision and realism.

Type II Models: Realism is sacrificed for generality and precision.

Type III Models: Precision is sacrificed for generality and realism.



How Should Ecologists Evaluate Their Theories and Models?

The Critics' Argument—Ecology as Numerology

Ecologist Daniel Simberloff (1981) writes,

Ecology is awash in all manner of untested (and often untestable) models, most claiming to be heuristic, many simple elaborations of earlier untested models. Entire journals are devoted to such work, and are as remote from biological reality as are faith-healers.

Ecologist R. H. Peters (1991) writes,

If scientific theories are characterized by predictive ability, the branches of science are distinguished by the objects of prediction. Ecology seeks to predict the abundances, distributions and other characteristics of organisms in nature.... This book contends that much of contemporary ecology predicts neither the characteristics of organisms nor much of anything else. Therefore it represents neither ecological nor more general scientific knowledge.

A model is predictively inaccurate if: (a) They do not make predictions; (b) those predictions are untestable; or (c) the testable predictions are dramatically false

1. Ecological models are predictively inaccurate.
2. A model is successful only if it is predictively accurate
3. Therefore, ecological models are not successful.

Problems with the argument—Premise 1 is overstated

Many ecological models are predictively accurate in *some* respects, to *certain* degrees, concerning *particular* systems.

Nicholson-Bailey Host-Parasitoid Model:

$$H(t+1) = bH(t) \left[e^{-aP(t)} \right] \quad P(t+1) = cH(t) \left[1 - e^{-aP(t)} \right]$$

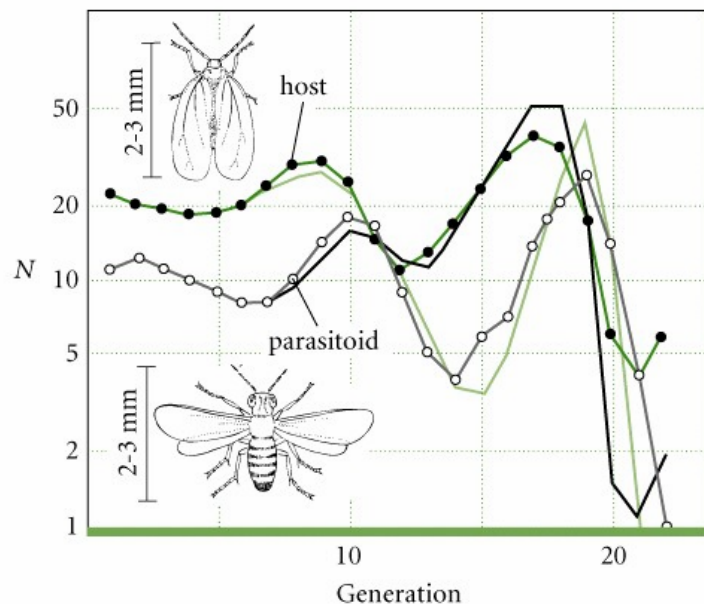
$H(t+1)$ = the number of hosts in $(t+1)$

$P(t+1)$ = the number of parasitoids in $(t+1)$

a = search efficiency of the parasitoid

c = number of parasitoid offspring resulting in from attach of a host

b = per capita birth rate of hosts



Population trajectories of the whitefly *Trialeurodes vaporariorum* (•) and its chalcid wasp parasitoid *Encarsia Formosa* (◦). The values of $a = 0.068$, $b = 2$ (experimentally imposed), and $c = 1$ gave a reasonable fit to the data.

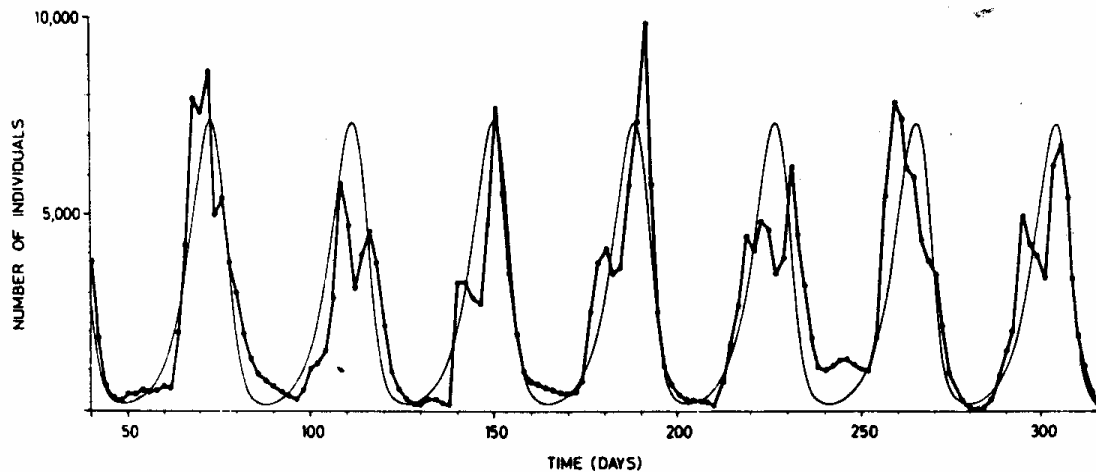
Delay Logistic Model

$$\frac{dN(t)}{dt} = rN(t) \left[1 - \frac{N(t-\tau)}{K} \right]$$

$N(t)$ = population size at t

K = carrying capacity of population

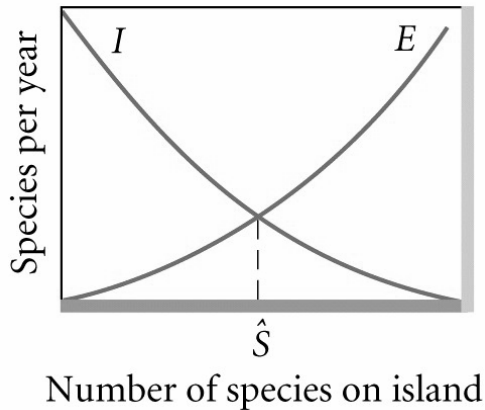
τ = time lag



The fit between the delayed logistic and the phenomena of Nicholson's Blowflies graphically represented. From the one-parameter family of limit cycles generated by the time-delayed logistic equation, we display that which best fits the oscillations in Nicholson's blowfly populations. The experimental data are from Nicholson (1954); the theoretical curve, with $r\tau = 2.1$, is in good agreement considering the crudity of the model.

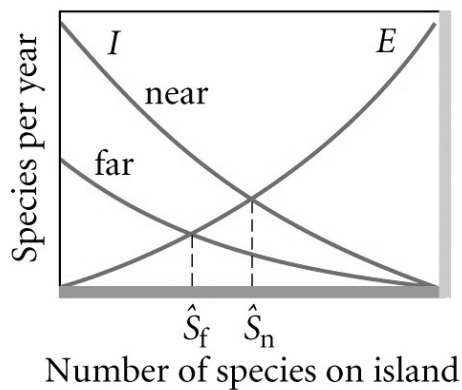
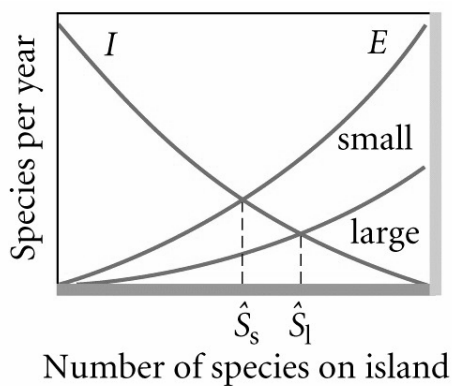
Island Biogeography

MacArthur and Wilson reasoned that:



I should decrease as more and more species arrive on the island. E should increase as the number of species on the island increases – there are more species to go extinct! Thus, \hat{S} – the species equilibrium – is a “balance” of those two rates.

However, they also reasoned that a smaller island will have a higher extinction rate than a larger island (resources are more scarce). Likewise, the farther an island was from the mainland the smaller its immigration rate will be compared to a closer island.



Thus, they argued that close, large islands will have greater \hat{S} than far, small islands.

So, Wilson and a student of his Daniel Simberloff decided that they would experimentally test their model. In the Florida Keys, there are thousands of small mangrove islands with 20 – 50 species per island. So, they hired some fumigators and applied methyl bromide to 6 islands killing the insects.

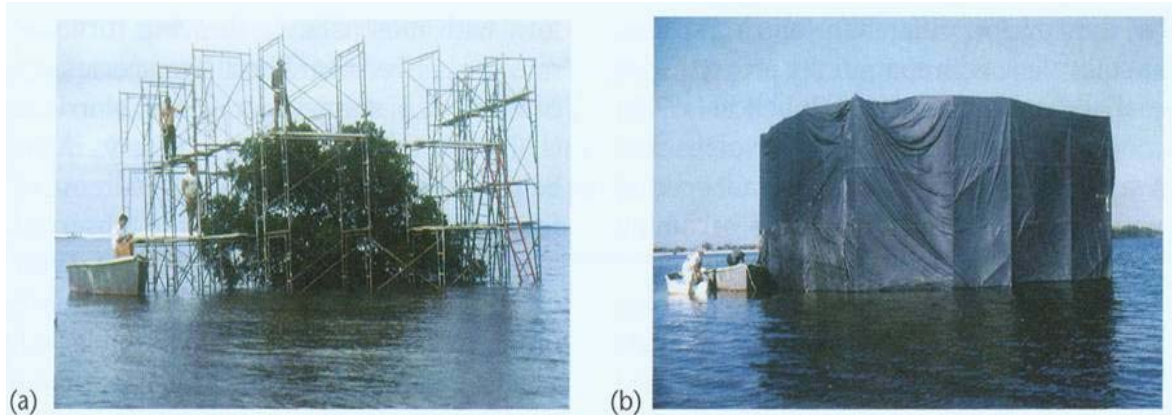


Figure 19.16 Experimental defaunation of a mangrove islet in the Florida Keys. (a) Construction of a scaffold frame. (b) Installation of a large tent into which insecticide was introduced, killing all arthropods. Commercial pest control operators from Miami were hired to perform the fumigation. The tent and scaffold were removed after defaunation, and recolonization was monitored. (Photos by Daniel Simberloff, Florida State University.)

Over the next year, they repeatedly censused the islands and the basic predictions of the model were confirmed:

- Abundance returned to their previous number;
- S was a function of island size and distance; and
- There was substantial species turnover.

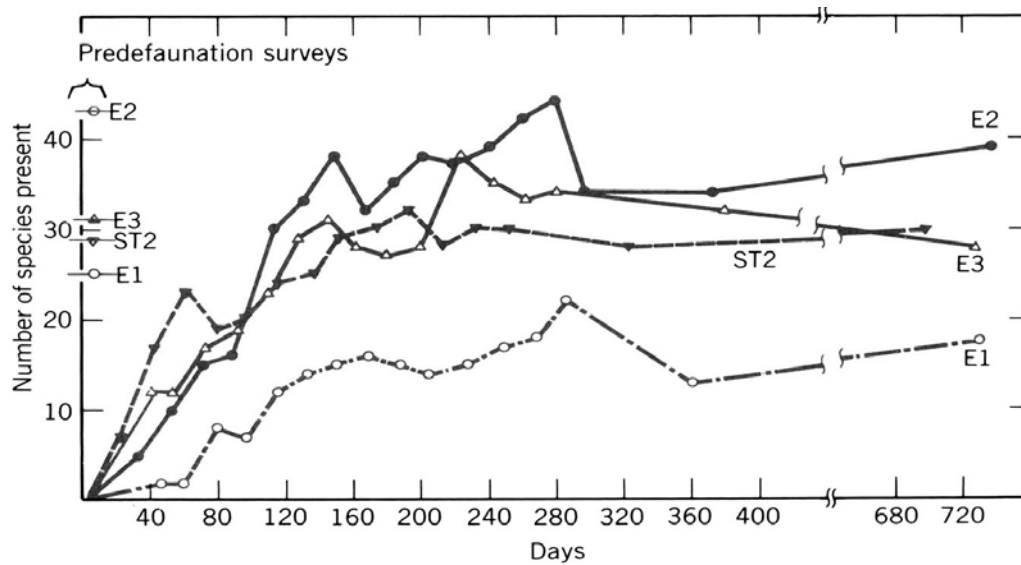


FIGURE 21.5

Recolonization of defaunated mangrove islets.

The species numbers before defaunation for each islet are shown at the left. E1 is the nearest island, E2 the farthest, and the other two are intermediate. (From Simberloff and Wilson, 1970.)

However, species turnover \hat{T} was a different deal. Originally, they estimated that there was a turnover rate of 0.67 per day.

In 1976, Simberloff reanalyzed the data eliminating transient individuals who did not stay on the island and reproduce (“false” extinctions).

Thus, his corrected estimate was that the turnover rates was only 1.5 extinctions per year!

Problems with Argument—Premise 2 is false

Models can be successful even when predictively inaccurate. They are used for at least three basic purposes in theoretical ecology (ignoring explanation and prediction):

- 1) Models are used to *explore possibilities*.
- 2) Models serve as *simple baselines*
- 3) Models provide scientists with *conceptual frameworks*.

The Possibility of Chaos

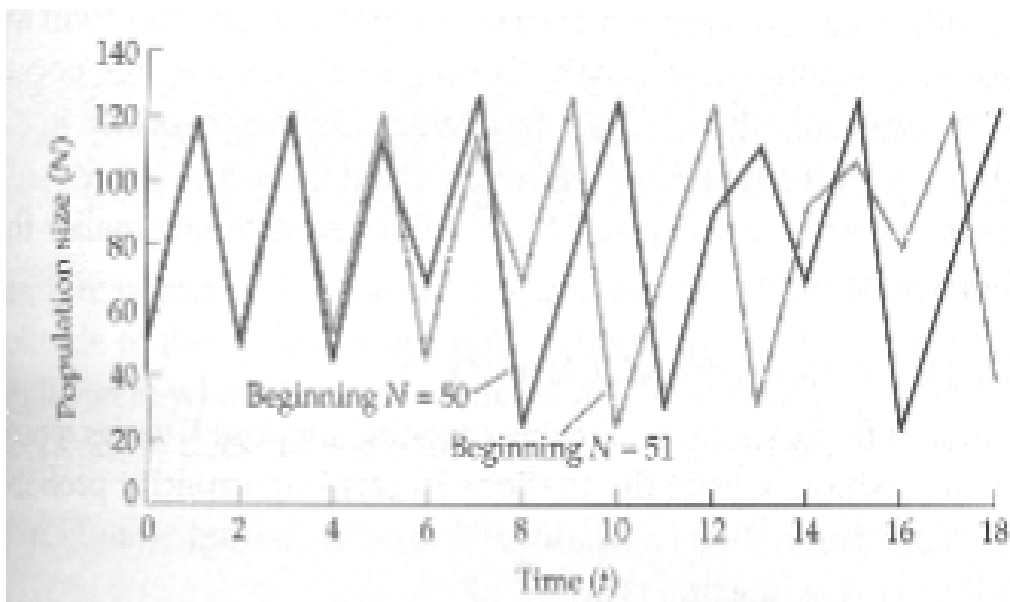
Robert May demonstrated that simple discrete difference equations like could exhibit chaos.

Chaos \approx extreme sensitivity to initial conditions and behavior is unstable and aperiodic

$$N_{t+1} = N_t + RN_t \left(1 - \frac{N_t}{K} \right)$$

If $R \leq 2.57$, then stable equilibrium and stable cycles

If $R > 2.57$, then chaos



Population regulation...

Nicholson vs. Andrewartha!

Density-dependence \Rightarrow Stable population numbers

Density-independence \Rightarrow Wildly fluctuating numbers

May on population regulation,

These studies of the Logistic Map revolutionized ecologists' understanding of the fluctuations of animal populations... With the insights of the Logistic Map, it was clear that the Nicholson-Birch controversy was misconceived. Both parties missed the point: population-density effects can, if sufficiently strong..., look identical to the effect of external disturbances. It's not a question of either/or. (May 2002, 39-40)

Even if we can never confirm or disconfirm the existence of chaos in natural populations we have May challenged a fundamental assumption of the debate through mathematical models.

Can Ecological Models Be Explanatory?

The *truth assumption* (Hempel 1965, Salmon 1984):

If a model or theory explains some event or regularity, then the model's characterization or theory must be true.

However, ecologists claim that their idealized models are explain events and regularities. How can they be explanatory?

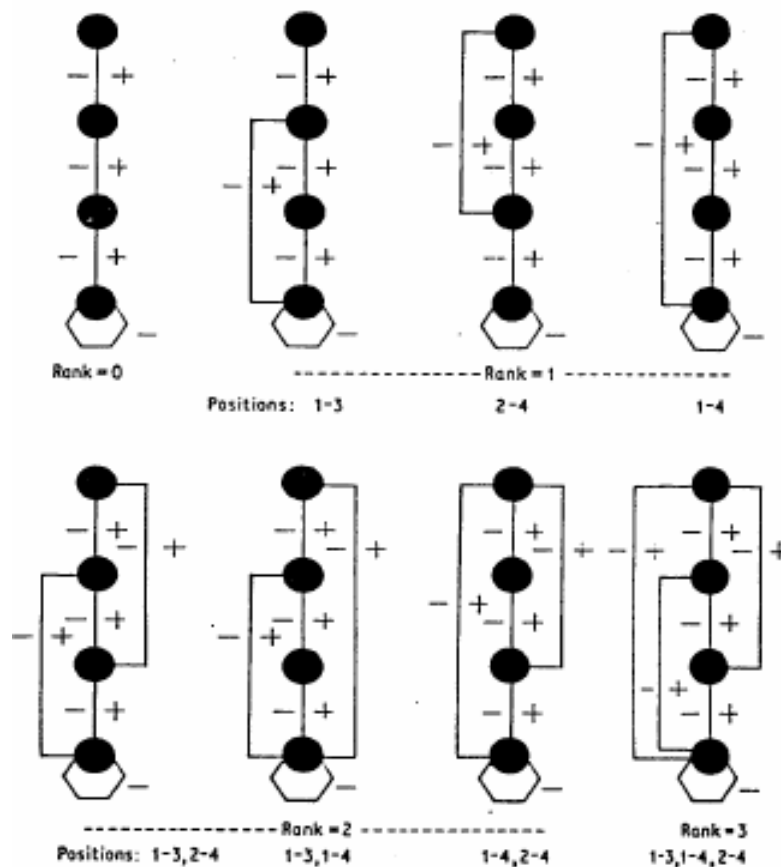
Omnivory and Explanation

Example: “why is omnivory rare in vertebrate food webs rather than common?”

In 1978, Stuart Pimm and John Lawton, using Lotka-Volterra community models, argued that this was because food webs with high degrees of omnivory were *dynamically fragile*.

$$\frac{dN_i}{dt} = N_i \left(r_i + \sum_{j=1}^n a_{ij} N_j \right) \quad \text{where } a_{ij} = -\frac{r_i \alpha_{ij}}{K_i}$$

They demonstrated by computer simulations that food webs with omnivores were generally dynamically unstable.



That is, they were locally unstable or their return times were excessively long.

Of 58 food chains, 24 had no omnivores, 23 had rank one omnivory, and 11 had rank two omnivory!

Now the Lotka-Volterra community model is a caricature of empirical food webs.

- ✓ There is no migration
- ✓ No age or genetic structure in the populations
- ✓ Density-dependence is linear.

How can these model be explanatory or provide understanding if they are *literally false*?

Note, that citing examples like the one above is not sufficient to show that the truth assumption is false; one can just claim that it is an “explanation sketch”!