Diversity – Stability:
Does biodiversity beget stability?

Historical overview of Diversity-Stability in ecology

1. The early years
2. Bob May and the limits to diversity
3. Diversity and food web structure

Current understanding

Components of stability

Two approaches to understanding stability

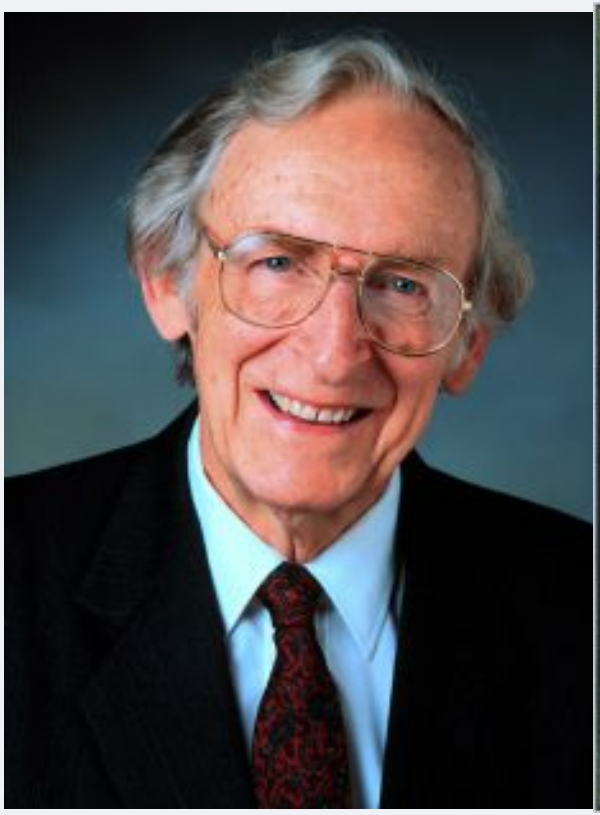
1. General D-S relationships
2. Food web properties and stability

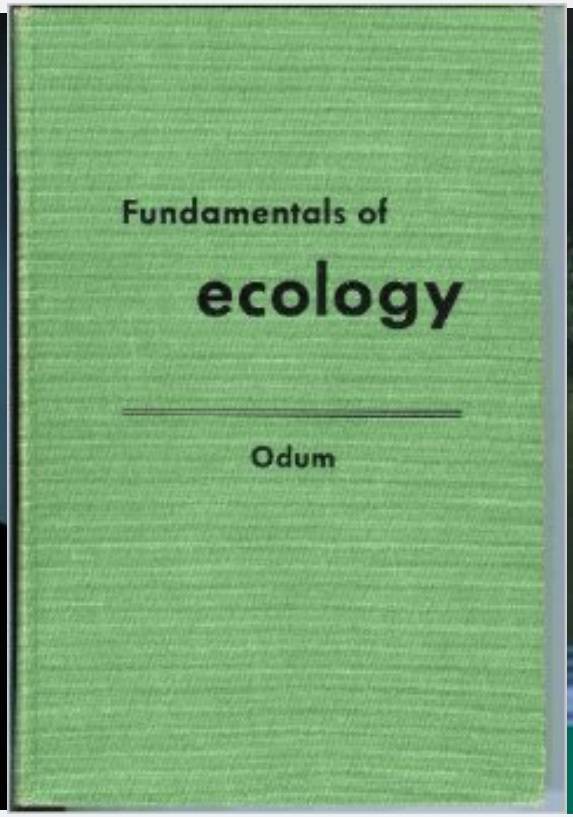
Food web *= a set of species that are connected to one another via trophic interactions (i.e. by fluxes of matter and energy)*

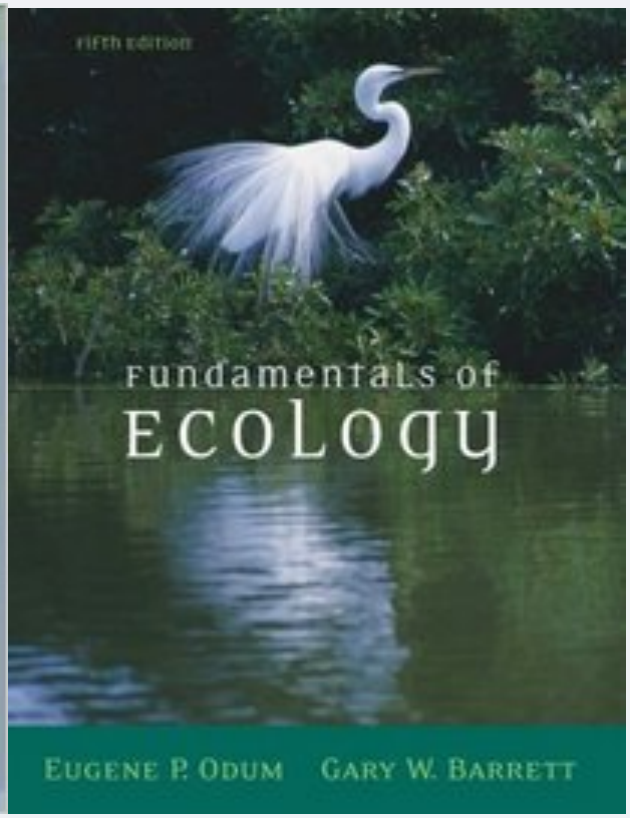
Diversity – Stability:
1. The Early Years (1950s)

Community Stability: 'the amount of choice which the energy has in following the paths up through the food web' – E.P. Odum 1953

-based on intuition that portioning up the 'energetic pie' ought to stabilize the system….The 'precise assumptions behind this intuitive argument remained a mystery' – McCann 2009







http://people.wku.edu/charles.smith/chronob/odum.jpg

Diversity – Stability:
1. The Early Years (1950s)

Robert MacArthur (1955) Fluctuations of animal populations, and a measure of community stability. *Ecology* 36: 533-536.

COMMUNITY STABILITY

In some communities the abundance of species tends to stay quite constant, while in others the abundances vary greatly. We are inclined to call the first stable and the second unstable. This concept can be made more precise, however. Suppose, for some reason, that one species has an abnormal abundance. Then we shall say the community is unstable if the other species change markedly in abundance as a result of the first. The less effect this abnormal abundance has on the other species, the more stable the community.

This stability can arise in two ways. First, it can be due to patterns of interaction between the species forming the community; second, it can be intrinsic to the individual species. While the second is a problem requiring knowledge of the physiology of the particular species, the first can be at least partially understood in the general case. Only this kind of stability will be considered here.

http://potash.marlboro.edu/sites/potash.marlboro.edu/files/2013/summer/Robert%20MacArthur%201_0.jpg

Diversity – Stability:
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- *sketched a series of simplified food webs and discussed the ramifications of energy partitioning for stability using elementary quantitative arguments*

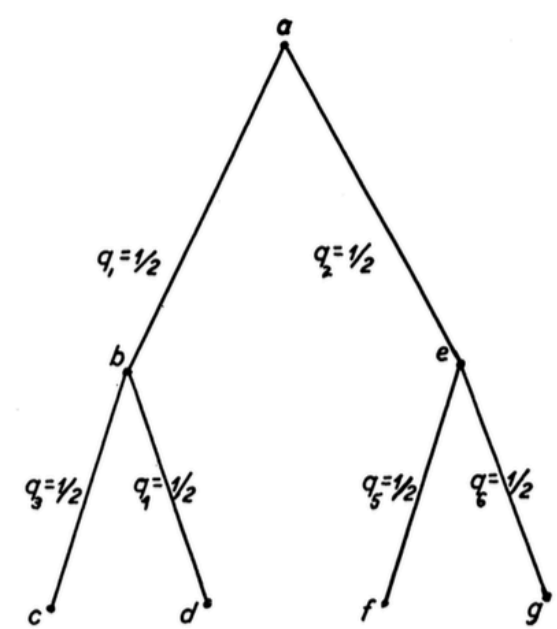

FIG. 3. A food web. *a*, *b*, *c*, *d*, *e*, *f* and *g* are species, and *q* on the line joining predator and prey signifies that fraction of the total number of prey species formed by the prey species in consideration.

Properties of stability (according to MacArthur):

1. *Stability increases as the number of links increases.*
2. *Stability can be achieved either by a large number of species each with a fairly restricted diet, or by a smaller number of species each easting a wide variety of other species.*

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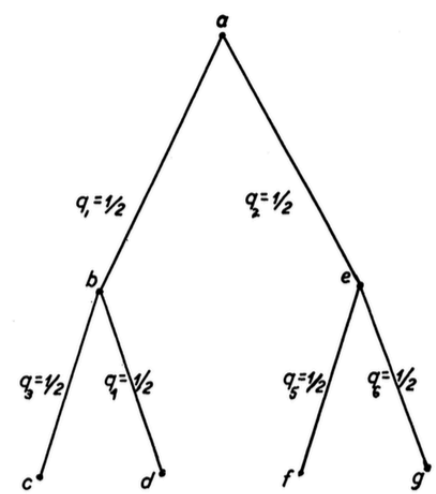

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- *'His idea, although intriguing, still reads like an intuitive appeal masqueraded in mathematics' – McCann 2009*
- *Ignored population and community dynamics – thus essentially allowing a definition of stability identical to Odum (i.e. multiple pathways in a food web might stabilize the system). Little mechanistic insight*

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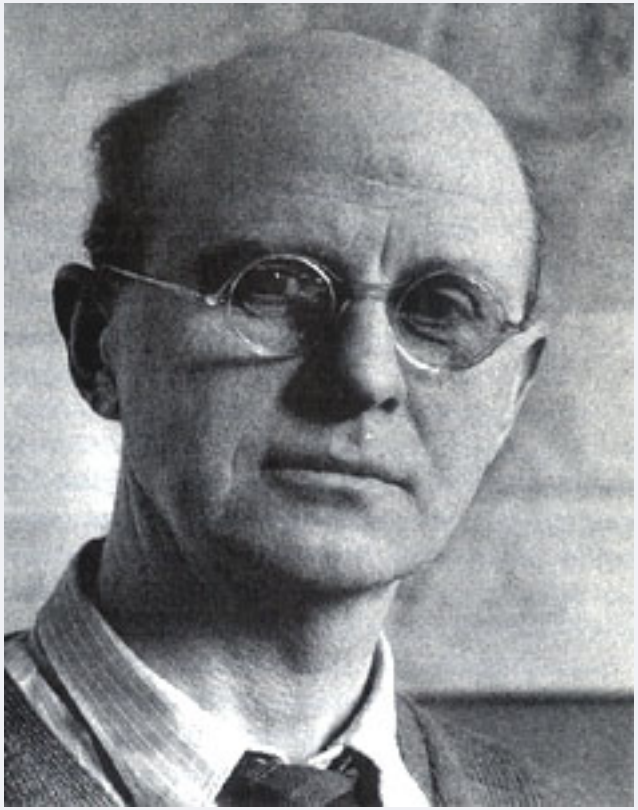


Charles Elton (1958) The Ecology of Animal and Plant Invasions

- *1) because simple model systems were subject to extraordinary instabilities, increased stability would likely accompany increased model complexity and diversity*
- *2) simplified F.W. more vulnerable to invaders*
- *3) island F.W. often impacted by invasive species (logic being that island food webs are less diverse than mainland areas)*

Diversity seemed to be related to each of these arguments thus implying diversity positively related to stability

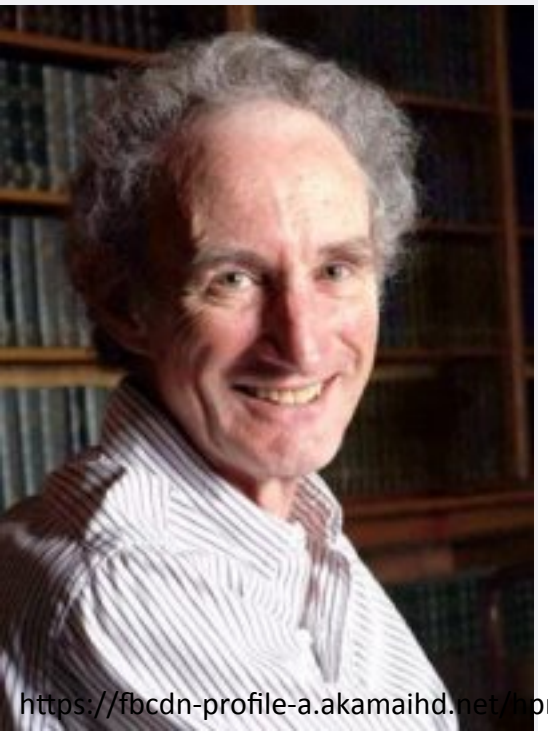
BUT…still no clear mechanism

Diversity – Stability:
2. 1970s: Bob May and the Limits to Diversity

-May's Mathematical Model: generated diversity and connectance using a random statistical universe (i.e. no other assumptions about diversity).

-Criticized as overly simplified constructs <u>but</u> was a clear test of early intuitive ideas about D & S, namely that diversity and increased connectance, in and of themselves lead to stability

-Models showed in no uncertain terms that complexity and diversity readily and rapidly drive enormous INSTABILTIY. That is: DIVERSITY BEGETS INSTABILITY!



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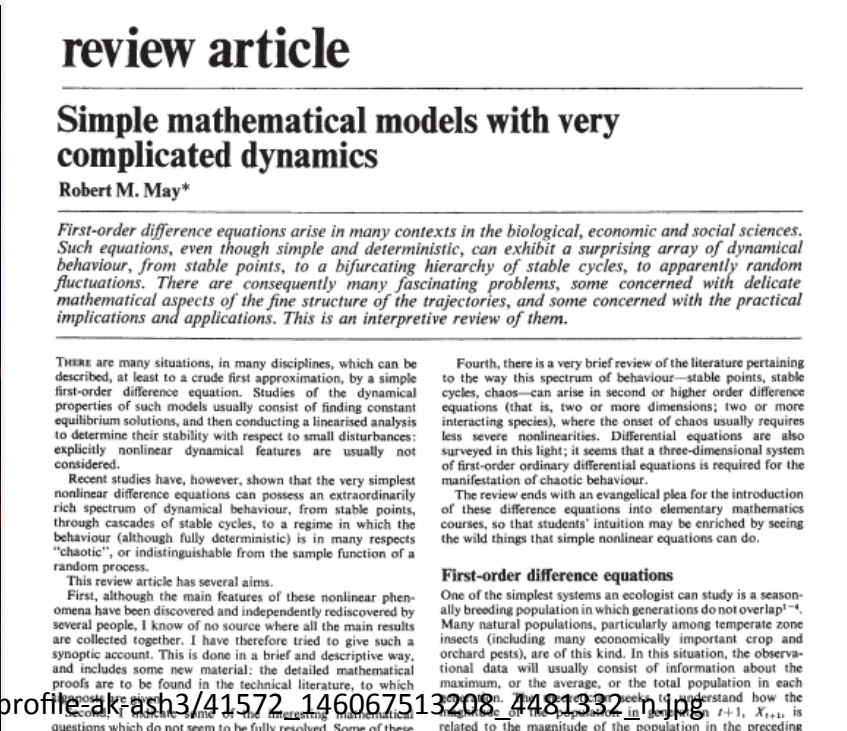


review article

Simple mathematical models with very complicated dynamics

Robert M. May*

First-order difference equations arise in many contexts in the biological, economic and social sciences. Such equations, even though simple and deterministic, can exhibit a surprising array of dynamical behaviour, from stable points, to a bifurcating hierarchy of stable cycles, to apparently random fluctuations. There are consequently many fascinating problems, some concerned with delicate mathematical aspects of the fine structure of the trajectories, and some concerned with the practical implications and applications. This is an interpretive review of them.

THERE are many situations, in many disciplines, which can be described, at least to a crude first approximation, by a simple first-order difference equation. Studies of the dynamical properties of such models usually consist of finding constant equilibrium solutions, and then conducting a linearised analysis to determine their stability with respect to small disturbances: explicitly nonlinear dynamical features are usually not considered.

Recent studies have, however, shown that the very simplest nonlinear difference equations can possess an extraordinarily rich spectrum of dynamical behaviour, from stable points, through cascades of stable cycles, to a regime in which the behaviour (although fully deterministic) is in many respects "chaotic", or indistinguishable from the sample function of a random process.

This review article has several aims.

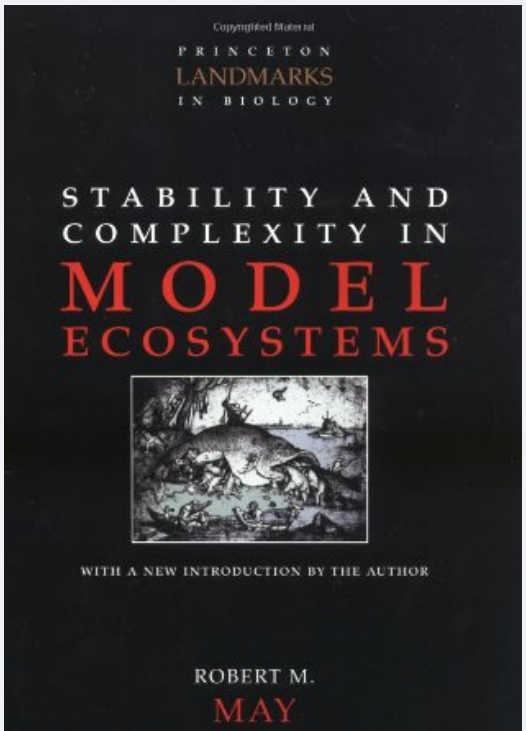
First, although the main features of these nonlinear phenomena have been discovered and independently rediscovered by several people, I know of no source where all the main results are collected together. I have therefore tried to give such a synoptic account. This is done in a brief and descriptive way, and includes some new material: the detailed mathematical proofs are to be found in the technical literature, to which [illegible] questions which do not seem to be fully resolved. Some of these

Fourth, there is a very brief review of the literature pertaining to the way this spectrum of behaviour—stable points, stable cycles, chaos—can arise in second or higher order difference equations (that is, two or more dimensions; two or more interacting species), where the onset of chaos usually requires less severe nonlinearities. Differential equations are also surveyed in this light; it seems that a three-dimensional system of first-order ordinary differential equations is required for the manifestation of chaotic behaviour.

The review ends with an evangelical plea for the introduction of these difference equations into elementary mathematics courses, so that students' intuition may be enriched by seeing the wild things that simple nonlinear equations can do.

First-order difference equations

One of the simplest systems an ecologist can study is a seasonally breeding population in which generations do not overlap[1-4]. Many natural populations, particularly among temperate zone insects (including many economically important crop and orchard pests), are of this kind. In this situation, the observational data will usually consist of information about the maximum, or the average, or the total population in each [illegible] seeks to understand how the [illegible] $t+1$, X_{t+1}, is related to the magnitude of the population in the preceding



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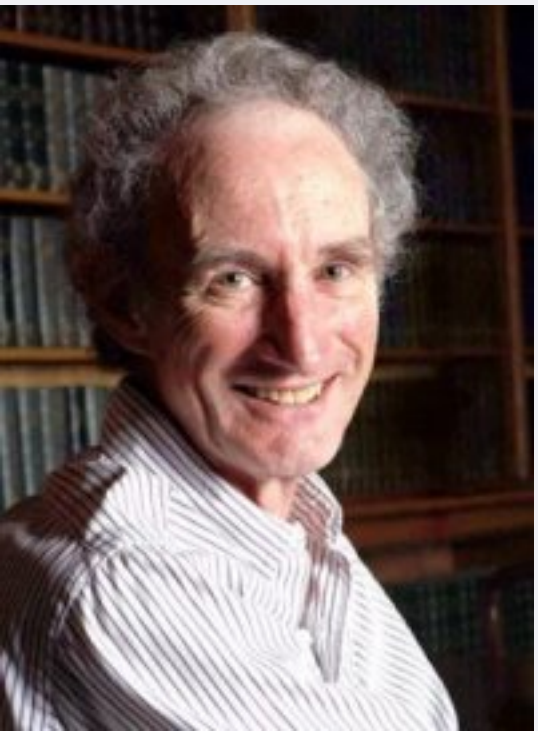


"A variety of explicit counterexamples have demonstrated that a count of food web links is no guide to stability.

This straightforward fact contradicts the intuitive verbal argument often invoked, to the effect that the greater the number of links, and alternative pathways in the web, the greater the chance of absorbing environmental shocks, thus damping down incipient oscillations.

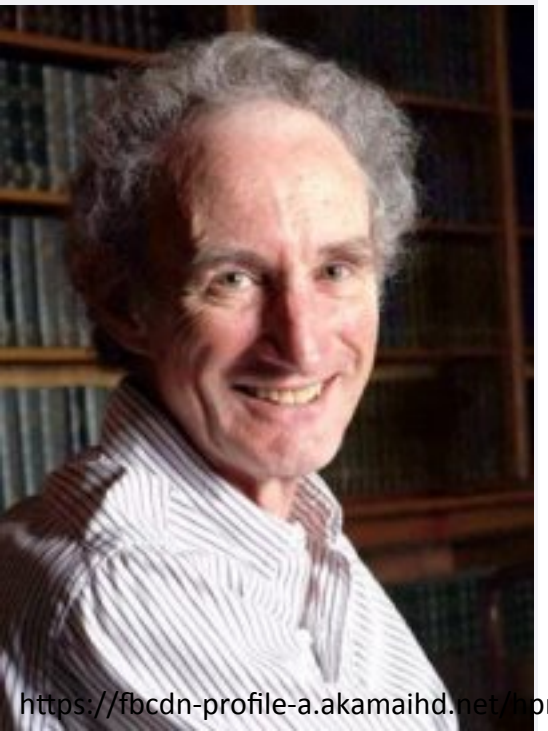
The fallacy in this intuitive argument is that the greater the size and connectance of the web, the larger the number of characteristic modes of oscillation it possesses: since in general each mode is as likely to be unstable as stable…the addition of more and more modes simply increases the chance for the total web to unstable" – May 1973

Diversity – Stability:
2. 1970s: Bob May and the Limits to Diversity

-Didn't fit intuition or match empirical results

**Note: May's results do NOT suggest that diversity is uncorrelated to stability but rather his models are a strong argument against diversity (i.e. # of species) as the major driver of stability

-*Ecologists, thus, needed to seek what components of Food Web Structure impart stability…*



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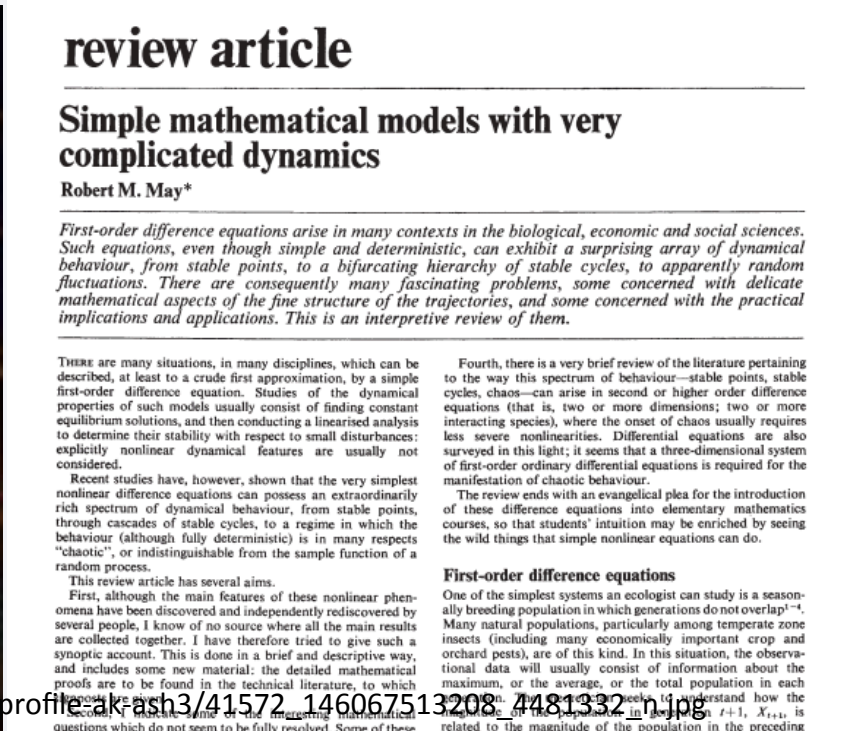

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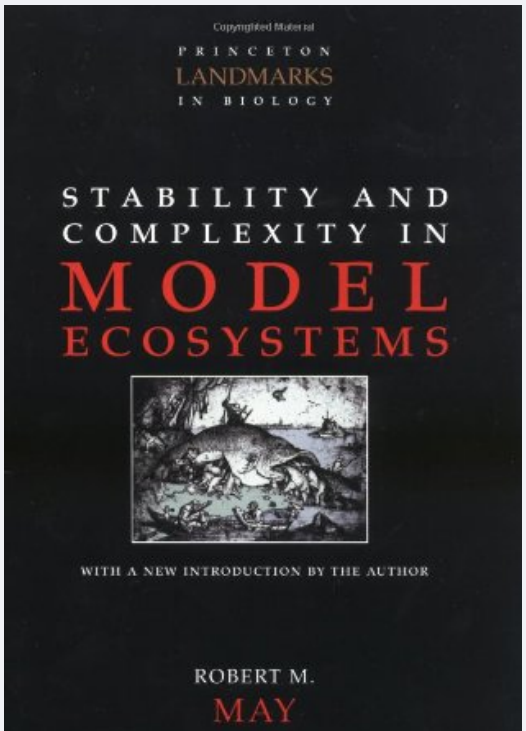
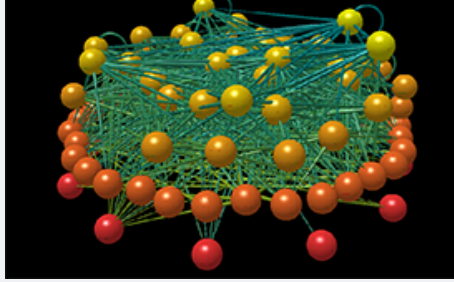


Diversity – Stability:
3. Diversity and Food Web Structure



- 1970s theoretical work inspired a 'factory-like' production of researchers interested in documenting and revealing patterns in FW topologies;
- *Recurring Structures in Well Documented Food Webs:*

*1) **Omnivory:** Polis showed omnivory not rare (as previously suggested). Instead, common in desert ecosystems*

*2) **Spatial subsidies and multi-channel pathways in food webs:** Polis and Strong (1996) argued ecologists needed to expand their spatial scale and recognize that many of the focal food webs being studied were actually coupled through generalist consumers via both top-down (consumption) and bottom-up (nutrient transfer) mechanism*

Gary Polis (1946-2000) – desert ecologist

Don Strong (Prof. UC Davis)

Diversity – Stability:
Current understanding

Kevin McCann, U. of Guelph

'Diversity CAN be expected, on average, to give rise to ecosystem stability. This does NOT infer that diversity is the driver of this relationship. Instead, diversity can be regarded as the passive recipient of important ecological mechanisms that are inherent in ecosystems.' – McCann 2000 'The diversity-stability debate' Nature

Recently, ecologists have begun to consider 'how specific natural food web structures and variability in space and time govern the stability of ecological systems.

The emerging answer suggest(s) that the ***variability itself may ultimately be responsible for the persistence of*** *these enormously complex entities'-McCann 2009 In: Princeton Guide to Ecology*

KEY: Change in perspective from equilibrium view of ecosystems

http://www.uoguelph.ca/ib/people/faculty/images_faculty/mcann.jpg

Components of Stability

Two categories of definitions:

System's Dynamic Stability:

(1) Variability: the variability in population dynamics of individual species or groups of species. Low variability = high stability;

System's Capacity to Defy Change:

(2) Resistance: the ability to retain structure in the face of a perturbation (e.g., a community is resistant to an invasive species)

(3) Resilience: dynamic response to a temporary perturbation (e.g., equilibrium or nonequilibrium stability; effectively tracks how fast densities return/recoil to their original values).

-based on Pimm 1984, McCann 2000, 2009

The search for a general diversity-stability relationship

TEMPORAL STABILITY:

- the consistency of a quantity (e.g. species abundance or biomass) over time
- for entire community or its constituent species

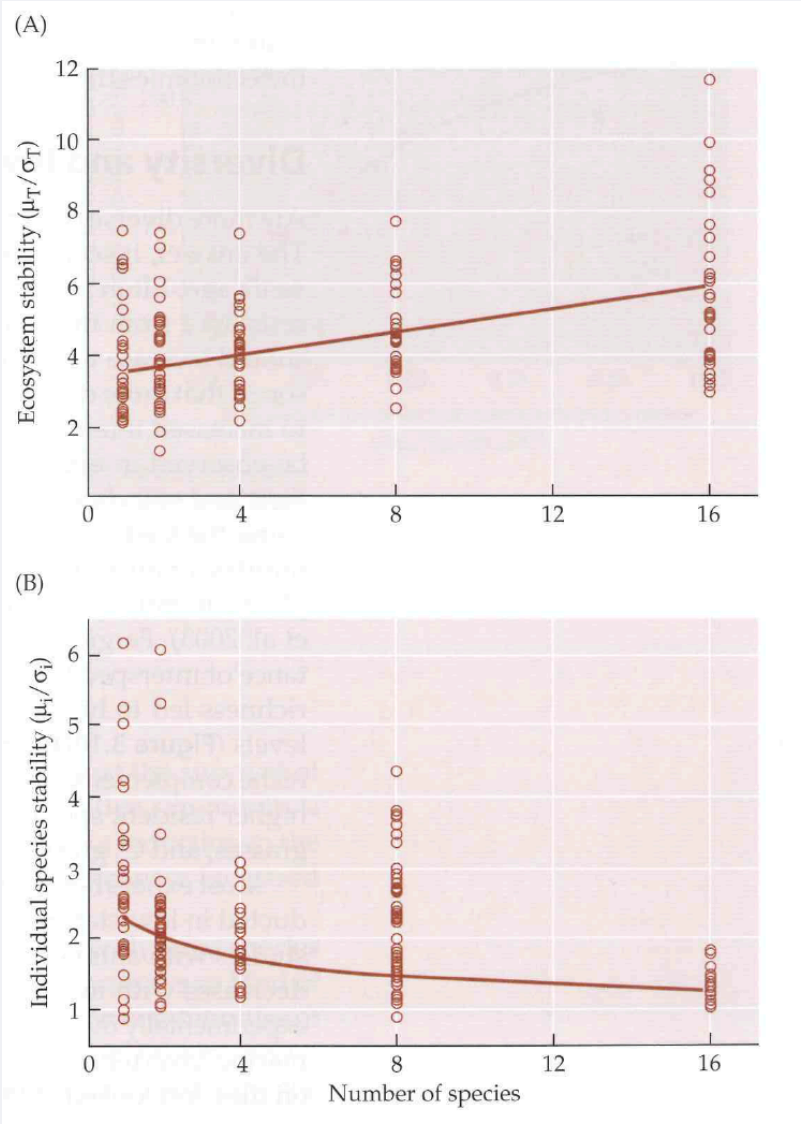
$$S_T = \frac{\mu_T}{\sigma_T} = \frac{\sum \text{Abundance}}{\sqrt{\sum \text{Variance} + \sum \text{Covariance}}}.$$

The search for a general diversity-stability relationship

Tilman's Cedar Creek experiments (1982-.; 200 plots):

A) Temporal stability of total community biomass increases with species richness.

B) Temporal stability of individual plant species declined with species richness



Tilman et al. 2006

The search for a general diversity-stability relationship

Why might this positive relationship occur?

1) AVERAGING EFFECT(Doak et al. 1998): Statistical averaging of the fluctuations in species' abundances -> PORTFOLIO EFFECT (Tilman et al. 1998)
2) NEGATIVE COVARIANCE EFFECT (Tilman et al. 1998) –

Either way, idea = species richness increases stability at the community level b/c diverse plant communities respond differentially to variable environment. The differential responses sum, through time, to give STABLE COMMUNITY DYNAMICS

Loreau (2010) – Asynchrony of species responses to environmental fluctuations

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The Statistical Inevitability of Stability-Diversity Relationships in Community Ecology

D. F. Doak,* D. Bigger, E. K. Harding, M. A. Marvier, R. E. O'Malley, and D. Thomson†

ABSTRACT: In this article, we explain an often overlooked process that may significantly contribute to positive correlations between measures of species diversity and community stability. Empirical studies showing positive stability-diversity relationships have, for the most part, used a single class of stability (or, more accurately, instability) measures: the temporal variation in aggregate community properties such as biomass or productivity. We show that for these measures, stability will essentially always rise with species diversity because of the statistical averaging of the fluctuations in species' abundances. This simple probabilistic process will operate in the absence of any strong species interactions, although its strength is driven by the relative abundances of species, as well as by the existence of positive or negative correlations in the fluctuations of species. To explore the possible importance of this effect in real communities, we fit a simple simulation model to Tilman's grassland community. Our results indicate that statistical averaging might play a substantial role in explaining stability-diversity correlations for this and other systems. Models of statistical averaging can serve as a useful baseline for predictions of community stability, to which the influences of both negative and positive species interactions may then be added and tested.

Keywords: stability, diversity, null model, random sums, community ecology, averaging.

Food web structure and stability

Interaction Strength (IS): the dynamic influence of one species on another; often measured by energy or biomass flux .e.g IS of predator on prey is equivalent to the amount of biomass consumed by the predator

-Peter Yodzis (1981) showed FWs with real IS more stable than randomly constructed ones, but reason unknown

-Increasing diversity can increase stability under one condition: distribution of consumer-resource ISs must be skewed towards weak ISs =

-Weakly interacting species stabilize community dynamics by dampening strong, potentially destabilizing consumer-resource interactions.

Weak trophic interactions and the balance of nature

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Department of Environmental Sciences and Policy, University of California, Davis, California 95616, USA

Ecological models show that complexity usually destabilizes food webs[1,2], predicting that food webs should not amass the large numbers of interacting species that are in fact found in nature[3–5]. Here, using nonlinear models, we study the influence of interaction strength (likelihood of consumption of one species by another) on food-web dynamics away from equilibrium. Consistent with previous suggestions[1,6], our results show that weak to intermediate strength links are important in promoting community persistence and stability. Weak links act to dampen oscillations between consumers and resources. This tends to maintain population densities further away from zero, decreasing the statistical chance that a population will become extinct (lower population densities are more prone to such chances). Data on interaction strengths in natural food webs[7–11] indicate that food-web interaction strengths are indeed characterized by many weak interactions and a few strong interactions.

For tomorrow's discussion, write a short paragraph addressing the following:
Does diversity beget stability?
If not, what does?

Please either email me your paragraph before class, or hand it in to me in class.