Diversity-Stability

One rationale for maintaining biodiversity is a presumed relationship between the number of species in a community and the stability of the community.

This diversity-stability relationship is not without controversy...

1. Origin – MacArthur (1957) and Elton (1958)
   Each proposed that more complex ecological systems were more stable

Elton's 6 reasons

1. simple models fluctuate more than complex models
2. the more pathways available for energy to reach a consumer, the less severe the consequences of losing one pathway (redundancy)
3. agricultural monocultures more prone to pest outbreaks than mixed communities
4. pest outbreaks rare in tropical ecosystems (more diverse than temperate)
5. population cycles occur primarily in species-poor ecosystems (arctic regions)
6. invasion by new species is easiest in oceanic islands that are species-poor

Definitions have long been a part of the controversy

Stability – A system is stable if and only if the variables all return to initial equilibrium state after a perturbation (Pimm 1986) {a mathematical definition of stability}

  4 components:
  - Resilience – speed of return to equilibrium
  - Persistence – the time a variable lasts before changing to a new value
  - Resistance – how large a disturbance is needed to perturb system
  - Variability – the normal range of values at equilibrium

Other ways to define stability:

Constancy – resistance to changes in composition (few ecological communities can be called "constant")

Resiliency – ability to return to a pre-disturbance state after perturbation
  (sounds like Pimm's defintion)
  (hard to define the equilibrium point in ecological systems)

Dynamic stability – future states are largely determined by current state of system (i.e., they have more influence on future state than the perturbation. This implies that stability reduces variability.

A Little history......

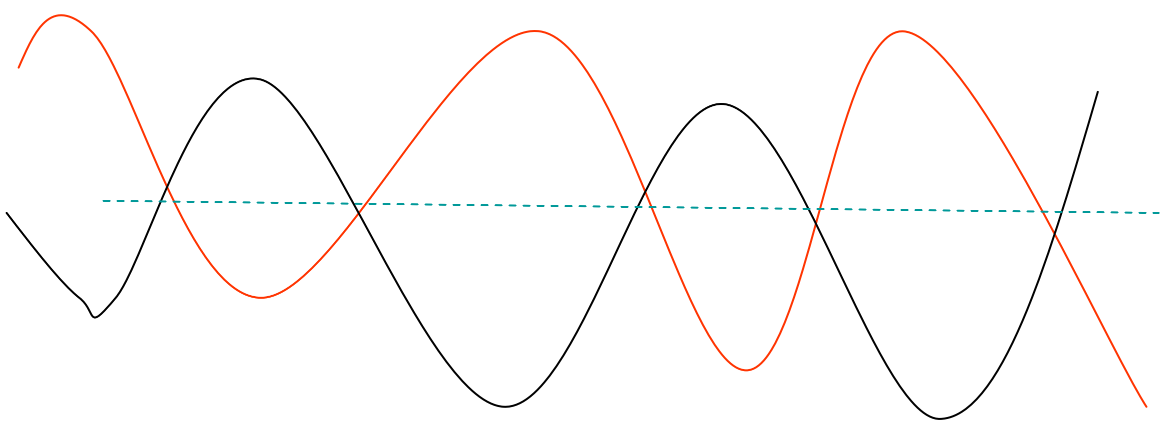
Elton (1958) – more complex systems more stable

May (1973) – mathematical models of interacting populations showed that population dynamics of individual species were less stable (higher variance) as number of species increased.

McNaughton (1977) Serengeti plant community productivity – increased diversity led to increased stability of biomass (lower variance) in response to disturbance by herbivores

Tilman (1994, 1996, and others) Increased grassland diversity experimentally shown to reduce the variability of community biomass (i.e., more stable community by this one measure)

Doak et al (1998) Diversity correlated with stability of biomass simply due to emergent statistical properties. The relationship would arise even in the absence of any ecological relationships due to the probablistic outcomes of "averaging" the independent biomass fluctuations of numerous species (see below, 2 fluctuating biomass measures and average value)



The Current Thinking –

Controversy is not over, but most lean toward this:

-Diversity gives rise to stability (dynamic) BUT diversity is not the driving force of the relationship

-The cause is the increased ability of more diverse communities to exhibit differential responses to change

-communities are structured by weak interactions, which prevents large fluctuations in the face of perturbation. As # spp decreases, the average interaction strength increases, and the probability of de-stabilization increases...

So what? What lessons are there for conservation biology?

1. To keep ecosystem functions intact, keep species assemblage intact (shades of Aldo Leopold " the first rule of intelligent tinkering is to keep all of the parts")

2. Species loss OR addition will change interaction strengths and cause major community/ecosystem changes

Notes on Tilman (1996):

Design:

207 plots of grassland community
11 years of data collection
9 treatments (control and 8 levels of nutrient addition)
biomass destructively sampled annually on subplots

Stability measures – estimated stability by examining variability in measures of productivity (biomass)

A. community measures
- 1- RGR
- 2- $CV_{84\text{-}94}$ *CV=100* (SD/mean), standardizes variation relative to mean
- 3- CV_{ND}

B. species measures
- 1-$CV_{sp\text{-}all}$
- 2- $CV_{sp\text{-}ND}$

Results:

[ohead – Tilman fig. 1]

Severe drought in 1988 – reflected in patterns of biomass

[ohead] – Tilman fig. 2]

Nitrogen fertilization increased community BIOMASS ($p<0.01$) (2A)
Nitrogen fertilization altered species proportional composition of grassland (2B)
Nitrogen fertilization REDUCED RICHNESS (2C)

[ohead – Tilman fig. 4]

increased richness caused decreased time for biomass to recover from drought

[ohead – Tlman fig. 5]

species richness predicts proportion of pre-drought biomass that was attained by communities during the drought
species richness also predicts RGR ($p<0.001$)

[ohead – Tilman table 1]

multiple regression controlling for other factors such as field identity, and various species biomasses retains species richness as a significant predictor of RGR

[ohead – Tilman table 2]

$CV_{84\text{-}94}$ significantly NEGATIVELY correlated with species richness ($p<0.001$) and also dependent on field - so less variability in productivity in richer (more diverse) communities. Same pattern for non-drought years ($p<0.001$)

[ohead – Tilman fig. 6]

average richness significantly correlated (NEGATIVELY) with CV for 3 of 4 fields

[ohead – Tilman fig.8]

Individual species – many showed increased biomass beyond average change in biomass through drought

[ohead – Tilman fig. 9]

Individual species – CV INCREASES with increased species richness

Conclusions:

1. Diversity enhances community stability and decreases stability of populations of individual species (supports May's (1973) model results).

2. Diversity had stronger effect on RESISTANCE than on RESILIENCE

3. Why the diversity-stability relationship?
   - a) species vary in their resistance to perturbation
   - b) species compete for resources – when one declines due to perturbation another compensates by increasing (competitive release)
   - {size of increase in biomass of increasing spp was correlated with size of decrease of declining spp during drought $p<0.01$}