

Lecture 26: Diversity and Stability

Methods to describe communities

Measures of community diversity

Measures of community stability

What relationship between diversity and stability?

Elton - MacArthur

May's model

Modifications of May's model – McNaughton's Serengeti & Yellowstone studies

Tilman - Stability of species vs stability of community processes.

Community: An interacting association of populations (members of a single species), found in the same place at the same time. In practice, subsets of a true community are sometimes studied (for example tropical tree communities, discussed below).

Some of the biggest issues in community ecology concern **diversity** and **stability**:

- What communities are most important in terms of conserving biodiversity?
- What properties cause a community to persist or recover in the face of disturbance?
- In particular, are more diverse communities more stable?

“..high rates of extinction [and invasion] put ecosystems under stress, making it critical that we understand how the loss or addition of a species affects the stability and function of the ecosystems we rely on.” McCann (2000) The diversity-stability debate. *Nature* 405:228-233

Communities have properties that are more complex than those of the populations comprising the community. **Methods of describing** communities include:

1. **Trophic structure** (a *species*-based description). Species fall into four classes: producers, herbivores, carnivores and detritivores (decomposers). Listing species in each trophic class is a simple community description.
2. **Food Web** (a *species*-based description). If the interactions among species are known *qualitatively*, the trophic structure is described more completely by a food web. Complete food webs are rarely described except for simple communities.

(Overhead: Fig 22.14 Begon et al. - food web for Bear Island, Arctic Ocean)

(Overhead: Fig 7.9 MacArthur 1972 - food webs with proportions of diet)

3. **Energy or nutrient flow** (a *process*-based description). If the interactions among species are known in *quantitative* detail, can describe community by the flow of energy and/or nutrients.

For a full description of energy flow, need to measure:

- Primary productivity
- Energy intake
- Respiratory heat loss
- Fecal energy loss
- Energy assimilated
- Measure these at each trophic level (or for each species)

4. **Community interaction matrix** (an *interaction*-based description). One entry for every pair of species in community.

		Species i			
		1	2	3	
Species j	1	β_{11}	β_{21}	β_{31}	β_{ij} = effect on species i's growth rate of the density of species j
	2	β_{12}	β_{22}	β_{32}	
	3	β_{13}	β_{23}	β_{33}	

β_{ij} & $\beta_{ji} = 0$ for pair with no interaction

β_{ij} & $\beta_{ji} \rightarrow$ both negative for pair of competitors

β_{ij} & $\beta_{ji} \rightarrow$ one negative and one positive for prey/predator pair

We will use these interaction coefficients to understand models of the way that community diversity affects stability.

Community Diversity.

Diversity has two main components: **richness and evenness**. Both can be measured in several ways.

Species richness: measures the number of species in the community.

Measures of richness:

1. S = number of species counted in a sample. Simple, but depends on sample size, so cannot compare communities that were sampled with different effort.

2. **Margalef Index** $R1 = S - 1/\ln(n)$

S = # species censused
 n = # individuals censused

3. **Menhinick Index** $R2 = S/\sqrt{n}$

Both indices correct for sampling effort, but rely on different assumptions about the relationship between S and n .
 $R1$ assumes $S = k \cdot \ln(n) + 1$
 $R2$ assumes $S = k \cdot \sqrt{n}$.

4. **Rarefaction.** One way to avoid making assumptions about relationship between S and n is to take samples of equal size from all communities to be compared. Rarely possible, because data collected in different studies, then gleaned from journals.

Rarefaction calculates the expected number of species $E(S_n)$ for sample of n individuals, drawn from a set of N individuals distributed among S species.

In other words, begin with a sample of S species tallied in a census of N individuals. Then calculate how many species would be expected from some smaller sample size (n). Can pick a value of n equal to sample size for least-intensively sampled community, and compare expected S values with this n , for all communities.

$$E(S_n) = \sum_{i=1}^s \left\{ 1 - \left[\frac{\binom{N - n_i}{n}}{\binom{N}{n}} \right] \right\}$$

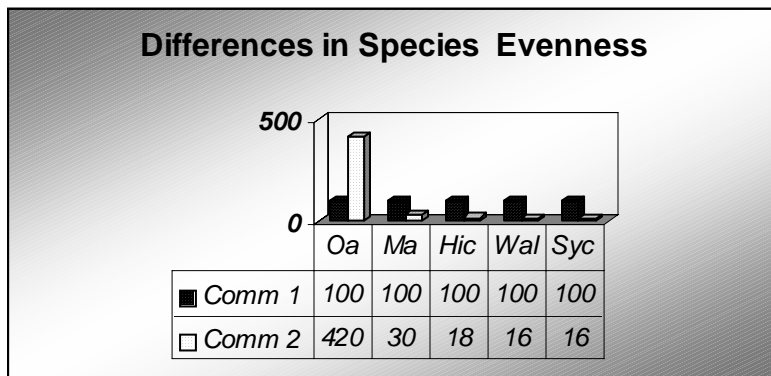
Programs available to do the rarefaction calculations.

(Overhead: Fig 8.1 Ludwig & Reynolds - rarefaction applied to compare avian communities.)

This method assumes that the relationship between S and N does not differ among communities, but doesn't assume a given form to the relationship, so it is the least restrictive measure of richness.

Species Evenness

Two communities might hold the same set of species but still differ a great deal in diversity.



Community 1 - likely to encounter several tree species at any point

Community 2 - likely to see nothing but oak at any point

Evenness in distribution of individuals among species \Rightarrow greater diversity

There are many indices of evenness; the most common is *Pielou's index* of evenness

$$J' = H'/\ln(S)$$

Where H' is Shannon's diversity index (see below)

$$H' = - \sum_{i=1}^s (p_i \ln(p_i))$$

J' expresses a community's actual diversity (H') as a proportion of its theoretical maximum diversity (which occurs when $n = S$, maximum number of species with one individual each).

Diversity combines *Richness* and *Evenness*

Measures of *diversity* combine richness and evenness.

1. Simpson's index

$$D = \sum_{i=1}^s \frac{1}{p_i^2}$$

where p_i = proportion of total individuals that are species i .

$D = S$ when all p_i are equal (perfect even-ness)

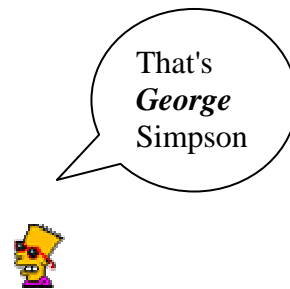
$D < S$ with less than perfect even-ness.

2. Shannon's Index

$$H' = - \sum_{i=1}^s p_i \ln(p_i)$$

H' is the most commonly used index of diversity, and comes from 'information theory'.
 H' measures the degree of uncertainty in predicting the species of a random individual from a community with S species and N individuals.

$H' = 0$ with one species in sample (low diversity), and reaches maximum when all p_i are equal (high diversity).



What ecological processes promote diversity within a community?

Much of the research on this question has tried to explain latitudinal gradients in diversity. For most taxonomic groups, diversity is high in the tropics and low near the poles.

(Overheads Figs 8-8, 8-9 & 8-10 MacArthur 1972: Latitudinal species counts for birds, gastropods, plankton).

This pattern holds true after controlling for species-area relationships:

(Overhead: Fig 8-12 MacArthur 1972: Land bird diversity on equal sized islands, tropical and temperate).

So why are there more species in the tropics? These explanations can also be applied to local differences in community diversity.

1. ***Evolutionary time.*** The temperate zones lost diversity in the last glacial period, and have not had time for speciation to produce as many specialists as are found in the tropics. Greater specialization = greater diversity. Note : this hypothesis basically argues that stability → diversity.
2. ***Climactic stability.*** If climate varies greatly, all species must be generalists to cope with wide range of conditions. If climate is stable, species can specialize.

In particular topics are stable in temperature - the tropics are less stable than temperate zone w.r.t . precipitation.

(Fig. 8-1 MacArthur 1972; climate of Toronto, Canada and Belem, Brazil)

As a result of climate, tropics have more constant productivity (e.g. tropical trees do not have seasonal growth rings). Constancy might allow greater specialization.

3. ***Productivity.*** Because tropics receive greater annual solar energy, they are on average more productive. In productive ecosystem, specialization on a few foods is possible. With low productivity, must generalize more to take all available food.
4. ***Competition.*** If diverse communities hold populations near their carrying capacities (this is not known), then selection will favor competitive ability (K-selection), which produces individuals that specialize on a narrow niche. Narrow niches = more species in given niche-space.
5. ***Intermediate Disturbance.*** This hypothesis directly opposes the previous one. Connell (1978) suggested that diversity is highest with intermediate rates of

disturbance (e.g. severe storm, drought) that depopulate areas within a community (create 'gaps').

High rate of disturbance = few species that are good colonists, allowing them to resettle the disturbed area and persist while competition is not severe (r-selected)

Low rate of disturbance = few species that are good competitors, allowing them to competitively exclude weaker competitors under constant ('climax') conditions

Intermediate rate of disturbance = allows poor colonists time establish population, but prevents competitive exclusion

(Overhead: Fig. 21.10 Begon et al: IDH schematic)

There have been field tests that support this hypothesis

(Overhead: Table 21.2 Begon et al: algae communities on boulders of different size)

(Overhead: Figure 21.11 Begon et al: invertebrates in fast flowing NZ streams)

6. *Circular networks, or nontransitive competitive interactions.*

Transitive competitive relationships: A beats B beats C

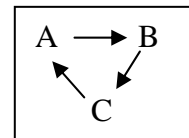
With transitive competition, succession in a given spot will be $C \rightarrow B \rightarrow A$

Leads to landscape dominated by A

Nontransitive competitive relationships A beats B beats C beats A.

(Like the Rock-Scissors-Paper game)

In this case, succession in a given spot will be a cycle, rather than a linear sequence to an endpoint.



Leads to landscape that is mosaic of A, B and C

Measures of Community Stability

(Overhead: Fig. 22.5 Begon et al: resistance and resilience, local and global)

Resistance - measures how strong a disturbance must be before a community's structure changes

Resilience - measures how likely a community is to return to its former state, following a change

Stability, especially resilience, can be **local** - in response to small changes, or **global** - in response to large changes.

When addressing conservation problems, we can focus on resistance or resilience.

E.g. September 1987 — the Exxon Valdez dumps millions of gallons of oil into Prince William Sound. At spill time, many changes in community, demonstrating that it was not *resistant* to a disturbance of this magnitude. After the oil was cleaned up, there were persistent changes in the plankton, filter feeder and fish communities, demonstrating that the community was also not *resilient* in this case.

When *retrospectively* addressing the outcome of a given disturbance, we're usually concerned with *resilience*. When *prospectively* assessing how vulnerable a community is to disturbance, we're concerned with *resistance first and resilience second*.

(One outcome of the Valdez spill was that Exxon spent enough in legal defense to fund the entire National Science Foundation budget for all ecological research for 187 years.)

What relationship is there between diversity and stability?

1. Diversity promotes stability - the conventional view.

Elton (1958) and MacArthur (1955) established the conventional view that communities that are more diverse are more stable. This grew from economic observation that simple economies (producing few products) collapse more often than diversified economies - the problem of Banana Republics.

MacArthur - the more pathways by which energy passes through a community, the less likely it is that a change in one species will strongly affect another species.

Elton - compiled five observations

(Overhead: Table 22.1 Begon et al. - Elton's statements)

- A. Simple models for 2 species are inherently unstable
- B. Lab communities of few species often go extinct
- C. Islands, which usually have few species, are vulnerable to invasion by new species
- D. Tropical communities have many species and are less vulnerable to pest outbreaks.
- E. Cropland, usually a monoculture, is vulnerable to invasions by weeds and outbreaks of pests.

All of these observations have been challenged, though C and E are widely held to be true.

- E.g.
- B. No evidence that lab communities with more species would be more stable. (this challenge has recently been challenged - reading by McGrady-Steed et al).
 - D. tropical locust outbreaks are severe.

2. Diversity reduces stability - a challenge to the conventional view.

A historically important challenge to the idea that diversity → stability came from a model by May (1972).

May used simulations to make 'randomly assembled' food webs. For each simulation, he made a community interaction matrix (see page 2) with:

1. All self-interaction terms ($\beta_{11}, \beta_{22}, \beta_{33} \dots$) = -1 (this models density dependence)
2. A variable number of β_{ij} values set to 0
3. Random values for other entries,

Measured three properties of these food webs:

S = number of species

β = average interaction strength

C = connectedness = fraction of all β values that were not zero

May altered the number of individuals of one species, and looked at changes in number of individuals of other species in the web.

Found that these webs were locally resilient only when:

$$\beta(SC)^{1/2} < 1$$

Stability ↓ as number of species ↑, as connectedness ↑, and as interaction strength ↑, exactly the *opposite* of the Elton/MacArthur conventional wisdom.

(Overhead: Fig.1 Ashby & Gardner 1970)

So who's right?

3. Modifications to May's model - DATA provide a reality check.

Data and more sophisticated models show that the relationship between diversity and stability is likely to depend on the *type of community* studied, the *type of disturbance*, and the *measure of stability* being assessed.

A. Lawlor (1978) highlighted an important problem with May's model. Randomly constructed food webs contain biologically impossible components (predators with no prey) or unrealistic components (loops in which A eats B eats C eats A).

Eliminating these problems, one still finds that stability ↓ as diversity ↑, but the relationship is weaker and there is no sharp threshold as in May's model.

B. MacNaughton (1978) applied May's model to real community: 20 species of plants in Serengeti. Data from 17 grassland sites.

As $S \uparrow$, $\beta \downarrow$
As $S \uparrow$, $C \downarrow$

(Overheads: Figs 1 & 2, MacNaughton 1978).

If β and $C \downarrow$ as $S \uparrow$, then as $S \uparrow$, $\beta(SC)^{1/2} \downarrow$

If this is true in real world, then more species \rightarrow greater stability.

MacNaughton found a similar result for grasses in Yellowstone, where disturbance was drought in 1988. Sites with higher diversity (Shannon's Index), showed less change.

(Overhead: Fig 22.9 Begon et al: YNP study) Broad generality of these results to other types of communities are not known.

C. Donor-controlled communities: If consumers are limited by food supply, but food supply is not depressed by consumers, then increasing diversity increases stability or has no effect. The measure of stability here is species composition.

This is a community limited 'from the bottom up'. *Conclusion:* diversity promotes stability in communities that are regulated mainly from the bottom up. But not necessarily in communities regulated 'from the top down' by predation.

D. Species-deletions: Models that assess the impact of removing one species completely from a web, which is a very specific kind of disturbance.

Pimm removed one species from a web, and measured *species-deletion stability*, defined as proportion of the time that no other species were lost as a result of removing one species.

For predators: Stability \downarrow as connectedness \uparrow
For producers: Stability \uparrow as connectedness \uparrow
Overall: Stability \downarrow as connectedness \uparrow , but weak effect

Conclusion: trophic level that is disturbed affects relationship between diversity (community structure) and stability

(Overhead: Fig 22.6 Begon et al. Species deletion stability)

E. What measure of stability? Species composition stability (resistance) vs return time (resilience): Pimm found that species-deletion stability \downarrow as connectedness \uparrow .

However, for those communities that did return to original structure, the time it took to return ↓ as connectedness ↑.

Conclusion: different measures of stability have different relationship to diversity, even for the same food web.

(Overhead: Fig 22.7 Begon et al.)

F. What measure of disturbance? Species composition vs productivity: Experiment by MacNaughton (1977)

- Serengeti grassland plant community.
- Fenced some plots (control). Heavy grazing by buffalo in neighboring plots (disturbed).
- Some plots had low initial diversity (low S = few species), others had high initial diversity (high S = many species).
- Measured difference between control and disturbed plots, in **productivity** and **species composition**

Effect of disturbance:

	Initially Simple	Initially Diverse
Species Composition	Slight Δ	Large Δ
Productivity	Large ↓	Slight ↓

This experiment highlights some tentative conclusions about diversity-stability relationships.

1. Diverse communities are generally more stable in productivity (Elton).
2. Diverse communities may be less stable in species composition, based on simple models (May), but some data (not all) suggest the opposite (MacNaughton)
3. Other factors complicate the general patterns. These factors include:
 - the trophic level that is disturbed,
 - how community is limited (top-down by predation, bottom-up by resources)

A final hypothesis: Some argue that stability and diversity are positively correlated, but the causation is opposite to that argued by Elton. Stability might lead to diversity, rather than vice-versa. Simple hypothesis, that more species accumulate in communities that occur in stable environments. This is basically the "evolutionary time" explanation for diversity.

Next:

Tilman's experimental plant community plots.

McGrady-Steed's invertebrate community experiments.

Stability of species vs stability of ecological processes.

Averaging effect

Negative covariance effect

Weak interaction effect.