Patterns of biodiversity
Rates and causes of loss of diversity

Measuring Biodiversity

Estimate of diversity depends on ***scale*** of measurement:

Within a species or population, there can be substantial variation in the ***genetic diversity*** among individuals (polymorphism, mean heterozygosity: will return to this later, but quick overview).

[Ohead: Frankham et al p. 50 & p 49]

Two measures of genetic diversity within a population:

1. Polymorphism

   P = # polymorphic loci/# loci examined

   Measures how many loci show genetic variation.

2. Allelic diversity = Mean number of alleles/locus (African lion data from Frankham p 49. for example of calculation)

3. Heterozygosity

   H = # heterozygotes at given locus/ # individuals genotyped for that locus

   Measures the proportion of individuals that are heterozygous at a given locus. Can then average H across loci.

Lion populations (Gir = small, isolated pop, Serengeti = large, connected pop) show major differences in amount of genetic variation they hold.

Differences in the amount of genetic variation contained by a population, species, or higher taxonomic unit are widespread. E.g. birds are not as genetically variable as most other vertebrates, for reasons that are debated.

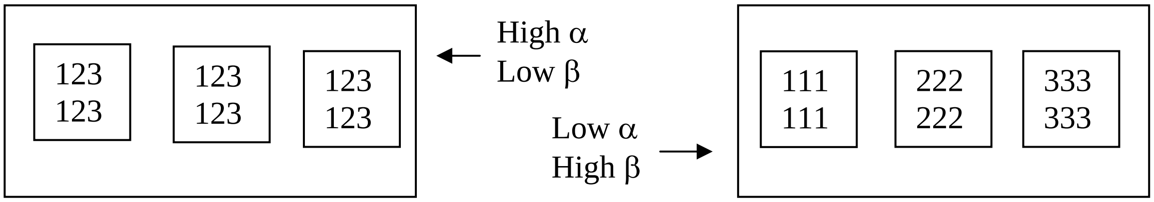
[ohead: Frankham et al. Table 3.3 p 62, Avise Fig. 1.2 & 1.3 – amounts of genetic variation shown in three ways]

Species diversity is commonly measured at three scales:

Alpha diversity: # species within a habitat
Beta diversity: Change in # species present among habitats (beta = gamma/alpha)
Gamma diversity: # species present at landscape scale

[Overhead:Primack Fig 1.4]

Diversity at one level can *reinforce* **or** *offset* diversity at other levels:
Offsetting: low α and high β can be similar to high α and low β



Examples: Low α/High β: interspecific territoriality & competitive exclusion:, eg salamander altitudinal gradients.
High α/Low β: interspecific aggregation at spatiotemporally clumped resource, eg grazing ungulates.

Reinforcing: low α and low β (simple communities) vs high α and high β (complex communities).

Species turnover curves are a good way to compare α and β diversity of different areas.
Height of curve is a measure of α diversity
Slope of the curve is a measure of β diversity
α and β diversity are often correlated.

[Ohead: Meffe & Carroll Fig 4.8]
[Ohead: Cody Fig 5]
[Ohead: Meffe & Carroll 4.7]

Cody (1986) in M. Soule (ed.) Conservation Biology - argued that 'natural rarity' (and conservation concern) is often associated with high diversity.

[Ohead: Cody Table 1.]

Basic Patterns of Diversity:

1. Diversity is the product of species ***richness*** and ***even-ness***.
   Richness = number of species present
   Evenness = distribution of individuals among species

   Several ***diversity indices*** incorporates both richness and evenness into a single measure

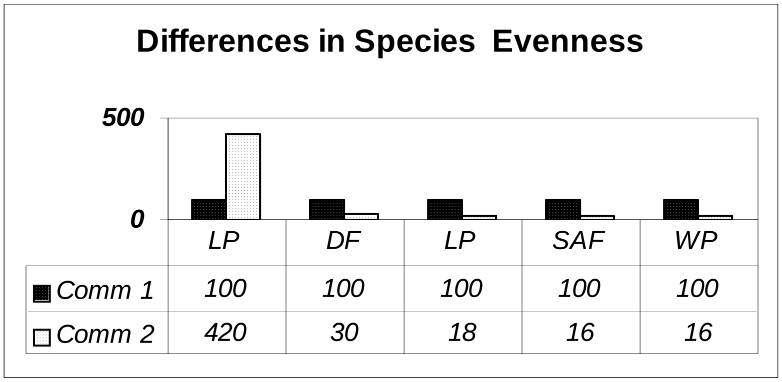
   Shannon-Weiner index

$$H' = -\sum p_i \ln(p_i)$$

Simpson index

$$D = \frac{1}{\sum p_i^2}$$

Details differ but all diversity indices have the property that index ↑ as # species ↑ or evenness ↑



	LP	DF	LP	SAF	WP
■ Comm 1	100	100	100	100	100
□ Comm 2	420	30	18	16	16

	Shannon	Simpson
Community 1	1.61	5
Community 2	0.65	1.40

Using Shannon, Comm1 is 2.5X as diverse as Comm2
Using Simpson, Comm1 is 3.6X as diverse as Comm2

Simpson Index has intuitive interpretation: equal to the number of species (richness) when the distribution of individuals is perfectly even, and declines as even-ness declines

Empirical Distributions of Individuals among Species

In real communities, the same distribution of individuals among species is often observed: a ***lognormal*** distribution.

[Oheads: 3 figs from Dobson Ch 1]

On linear scale → negative exponential. *A few common species and many rare species*.
On Linear/Log scale → normal.
With less than perfect sampling, left tail is truncated. This can be used to estimate how many species went unsampled:

$$\text{Total species} = \left[\frac{\text{total area under curve}}{\text{sampled area under curve}}\right] \times \text{ number of species sampled}$$

Undersampling correction is important because complete sampling is rarely accomplished

1. We are still discovering new species even in large bodied, well-studied groups such as mammals
2. For small and less well-studied taxa, most species have not been described.

Differences in ecological function or importance among species: We'll see more about this in lectures on diversity/stability, but for now, understand that the approach above is very broad – every species (or individual) has equal weight. IN reality, some species have strong ecological function even when not common.

1. Keystone species
2. High trophic levels (if top-down regulation is strong)

[ohead: Primack Fig 1.7]

Explanations for patterns of rarity and abundance

So there is a general rule that in any location, there will be a few common species and many rare ones. Any rules underlying this pattern?

1. ***There is more than one way to be rare:*** Rabinowitz et al. 1986 Seven forms of rarity. In Soule *Conservation Biology*.

   Survey of flowering plants in British Isles

Max Local Population Density	**Wide Geographic Distribution**		**Narrow Geographic Distribution**	
	Habitat Generalist	*Habitat Specialist*	*Habitat Generalist*	*Habitat Specialist*
High	58	71	6	14
Low	2	6	0	3

3 axes of rarity: Endemism (narrow geographic distribution) E.g. dasyurids
Habitat specialization, e.g panda
Sparseness (low maximum density), e.g African wild dog

A. General Point: the 3 axes of rarity have different causes and consequences for conservation action: E.g. different conservation actions needed:

   habitat specialist endemic with high local density - location based protection

   [oheads: Gentry fig 1, table 1 in Soule 86 p. 154] low density generalist with broad distribution - actions to improve demography/dynamics

[ohead: AWD distribution and comparison of density w/others in guild]

B. Endemics (flowers:23) are less common than those with wide distributions (flowers:137)

Many narrow endemics are already gone.
[ohead: Table 5.1 Case et al. in Fiedler & Jain 1992]

C. More species are specialist (flowers:94) than generalist (flowers:66) in habitat specificity (an effect of interspecific competition and selection to reduce niche overlap, or character displacement).
D. Most species (flowers:149 of 170) can attain high densities under some conditions (many of those that can't already gone)

E. For extinction risk, specialization is not apparently as big a factor as endemism and sparseness. Sparseness is may be a stronger problem than endemism.

1. Small population size is the kiss of death, both demographically and genetically - as we will see in detail.
2. Endemism has easy solution -protect a location. Small population size can arise for many different reasons. Diagnosing and reversing decline can be very difficult. Caughley 1994.

F. One combination doesn't make ecological sense: 0 species.

Similar results for Neotropical migrant birds (Reed 1992), except that specialists are less common than generalists in this case. Data shown are for winter ranges.

Max Local Population Density	**Wide Geographic Distribution**		**Narrow Geographic Distribution**	
	Habitat Generalist	*Habitat Specialist*	*Habitat Generalist*	*Habitat Specialist*
High	66%	10%	7%	2%
Low	5%	5%	0	5%

2. ***Body size.*** Large individuals require more resources, therefore more territory. Thus large-bodied species tend to attain lower local densities. Thus more prone to local extinction.

The pattern that large species are less common is very clear across broad taxonomic groups.

species proportional to $1/(\text{body length})^2$

[ohead p 23 Dobson]

Pattern that larger species attain lower densities also clear across taxonomic groups. True also for narrower taxonomic groups, but weaker relationship.

[ohead: Nee et al. 1991 bird data]

3. Trophic level. Very robust pattern. About 10% of energy at one level makes it to next trophic level. Thus species at tops of food webs are less abundant (they also tend to be larger bodied, see point 2). Finally, species at top of food web require the entire community below them to remain ecologically intact, while species low in web may persist despite loss of species at higher levels.

4. Species- Area Curves

Larger areas hold more species.
The relationship is usually log linear.

$$S = cA^z$$

$$\log(S) = c + (z)\log(A)$$

Empirically, slope (z) usually between 0.2 and 0.35 - we don't know why.
As you will later, estimates of this slope affect estimates of the number of species in the world (which is not known with much accuracy at this point).

(Fig. 4.6 Meffe & Carroll)

Small areas are less diverse in habitats, and small areas support smaller populations. Thus, more local extinctions in small areas. Many data sets from islands (Basis for island biogeography discussed later).

[ohead: Fig 5.2 Case et al in Fiedler & Jain 1992]

5. Geographic Patterns (structural complexity, stability)

Species richness is greater in the tropics and declines toward the poles, for many taxonomic groups.

[Oheads: Fig 4.4 & 4.5 Meffe & Carroll]

These patterns thought to arise because of:

A. Habitat ***structural complexity*** in tropics - allows for more niche differentiation and adaptive radiation

[ohead: Figs 1-3 MacArthur & MacArthur 1961, bird data]

B. ***Primary productivity*** higher in tropics, supporting more complex food webs.

C. ***Environmental stability*** in tropics:

Diversity can increase through evolutionary time in stable conditions, in response to A & B above.

Fewer 'resets' of diversity through catastrophic changes.

D. Huston (1994) ***Productivity-Disturbance Balance*** hypothesis: diversity is maximized when the rate of environmental disturbance is matched to the rate of population growth and competitive exclusion.

For a given rate of population growth (productivity):

- too little disturbance reduces diversity by allowing competitive exclusion.
- too much disturbance reduces diversity by failure of some species to rebound from crashes.

[Ohead: 4.13 Meffe & Carroll]

Global Biodiversity

How many species are there on earth? We don't know (!)

1. About 1.5 million species have been described.
2. We know that undescribed species exist for all taxa, even large mammals. The level of knowledge varies greatly among taxa.

Vertebrates: 40,000 (80%) of estimated 50,000 species are described.
Nematodes: 20,000 (2%) of estimated 1,000,000 species are described.

[Ohead: tree kangaroo]

3. Can use the ratios of known to unknown species in samples to estimate how many species remain undescribed. Terry Erwin did this for tropical forest beetles.

[Ohead: beetles]

4. Ratios of known:unknown species give estimates of 7 to 15 million species total, vast majority of which are invert animals. Some authors estimate more like 20-50 million species. Substantial uncertainty.

Vertebrates: 40,000 species or less than 1% of total
Plants: 300,000 species or less than 5% of the total
Bacteria, protozoans, viruses: ca. 10% of the total
Beetles alone - 2.3 million species, or 25% to 33% of the total

[Ohead: numbers of species by taxon]

5. Haldane's beetle story.

6. As mentioned in previous lecture, much of this biodiversity is in the tropics. Tropical rainforests - 2.3% of the earth's surface, >50% of all species.

How fast are we losing diversity? Is this rate unusual?

Fossil record allows estimation of pre-human extinction rate.

For every million fossil species, loss of 1 to 10 species per decade.

So, if there are now 10 million species, expected background extinction rate of 1-10 spp/yr.

Current loss rate is estimated at 100 to 10,000 species per year. Note the uncertainty – this is a wide range.

But the range is from 10x to 10,000x above the background extinction rate.

[Ohead Fig 16 PAI]

However, note that mass extinctions, with big jumps above the background rate of extinction, are known to have occurred in prehuman history.

Major extinction events at Devonian, Permian/Triassic, Cretaceous/Tertiary

[Fig 14.6 Maynard Smith]

Each of these apparently allowed adaptive radiation of lineages that survived the extinction event

[Fig 14.5 Maynard Smith -replace w/fig 4 p 350 Futuyma]

If all IUCN listed T&E species were lost in next 100 years, this would represent a further10x increase above current rate.

Martha Groom has summarized several estimates of extinction rate due to tropical deforestation, which range from 10%-40% of species lost in 20-40 years.

[Table A, p 138 Meffe & Carroll]

***Causes of Extinction*:**

1. Human population growth.

[Ohead Figs 1 & 6 PAI 2000]
[Fig 1 Soule 1993]
[Fig 8 PAI 2000]

1a. Note that human population growth rates are highest where diversity is still highest: wealth and demographic transitions slow the human growth rate.

[Dobson p 213]
[Fig 5.3 Meffe & Carroll]

2. Habitat loss and fragmentation.

[Fig 4 PAI 2000]
[Table 5.1 Meffe & Carroll]
[Fig B p 129 Meffe & Carroll]

3. Introduced species.

[Fig 19 PAI]
[Fig 5.1 Meffe & Carroll]

4. Overharvest. Whale example.

[Dobson p 116]
[Dobson p 123 - fisheries]

5. Pollution, global environmental changes.

Vitousek 1994 Ecology 75: 1861-1876: Half of all nitrogen produced by humans in history has come since 1982.

[Fig 20 PAI - river nitrogen]
[Dobson p 219 - sparrowhawks and orgo cmpds]
[Dobson p222, p224 - CO2, temperature, range changes]

6. Soule 1993 argues that force of these problems varies:

   a. Between developed and undeveloped nations
   b. Across levels from genes to ecosystems

[Soule 1993 Fig 2]

Habitat loss, fragmentation, introduced species - problems everywhere
Pollution - developed countries
Overharvest - undeveloped countries

Ok in general but I think the harvest conclusion is too simple, because better resources often mean higher offtake. Consider whaling and fisheries - technologies coming from developed nations can increase harvest everywhere.

7. All of these factors cause population sizes to become small. Once a population is small, extinction risk becomes high even if systematic causes of decline are removed.