Biodiversity

• Evolutionary Development
• “Paradox of the Plankton”
• Definition
  – Margalef, Shannon-Wiener
  – Diversity-index
• Oceanic Diversity
• Intermediate Disturbance Hypothesis
• How do we actually measure it?
"If today is a typical day on planet Earth, we will lose 116 square miles of rainforest, or about an acre a second. We will lose another 72 square miles to encroaching deserts, as a result of human mismanagement and overpopulation. We will lose 40 to 100 species, and no one knows whether the number is 40 or 100. Today the human population will increase by 250,000. And today we will add 2,700 tons of chlorofluorocarbons to the atmosphere and 15 million tons of carbon. Tonight the Earth will be a little hotter, its waters more acidic, and the fabric of life more threadbare."

Defining Biodiversity

• 1992, International Convention on Biodiversity signed Agenda 21
  – Can refer to habitats; local or global species counts; or genetic variability within a species
  – Diversity is *always* the product of evolution, but we also must take into account extinction (also a product of evolution)
Determining Diversity

• Numerous ecological models (based on math), but **none** of these is based on a theoretical rationale!

• Ramon Margalef (1951):
  – \( R = \frac{(S -1)}{\log N} \)
    • \( R=\) Richness
    • \( S=\) # of Species
    • \( N=\) # of individuals(of all species)
Determining Diversity

- Shannon-Wiener Index (H’) (1949)
  - \( S = \# \text{ of species} \)
  - \( N = \text{total} \# \text{ of individuals} \)
  - \( p_i = \text{proportion of individuals of } S(i) \text{ compared to } N \)
  - \( H’ = \sum_{i=1}^{S} (p_i \cdot \ln(p_i)) - [(S-1)/2N] \)

- More complicated than Margalef’s index, but does essentially the same thing….
Diversity Index (D*):

Margalef and H’ simply scale the number of species to calculate diversity, and do NOT take into account how closely related the species are… the Diversity Index includes how similar the species are, and decreases the weighting of closely related species….
What Causes Diversity?

• The Time Hypothesis
• The Environmental Stability Hypothesis
• The Spatial Heterogeneity Hypothesis
• The Productivity Hypothesis
• The Competition Hypothesis
• The Predation Hypothesis

**Intermediate Disturbance Hypothesis:** too much variability is bad, but so is too much stability—maximize diversity at an intermediate level of disturbance
**Evolutionary Trends**

- In general, species richness increases with time
- In general, extinctions are constant
- Theory of Punctuated Equilibrium (Eldridge and Gould 1972)

*Figure 15.1* Diversity of marine families through the geological record since metazoan organisms first appeared. Note the steady increase until the end of the Ordovician (O in the lower scale), when the first of the mass extinctions occurred. Then the numbers of families remained roughly constant until the mass extinctions of the Triassic (T) and the beginning of the fragmentation of the supercontinent Pangea (see Figure 15.4). Compare the steady increase in numbers of families since the Triassic with the patterns of continental drift shown in *Figure 15.4*. The one interruption was the mass extinction at the end of the Cretaceous (Cr), which more-or-less coincided with the split developing between Australasia and Antarctica, and resulted in the start of circumpolar circulation in the Southern Ocean (redrawn from Sepkowski). (V = Vendian; C = Cambrian; O = Ordovician; S = Silurian; D = Devonian; Ca = Carboniferous; P = Permian; T = Triassic; J = Jurassic; Cr = Cretaceous; Cz = Cenozoic.)
Mass Extinctions Past—and Present?

**TIMELINE OF EXTINCTION** marks the five most widespread die-offs in the fossil history of life on Earth.

**END ORDOVICIAN**
- **Duration:** 10 million years (my)
- **Marine Genera Observed Extinguished:** 60%
- **Calculated Marine Species Extinct:** 85%
- **Suspected Cause:** Dramatic fluctuations in sea level

**LATE DEVONIAN**
- **Duration:** <3 my
- **Marine Genera Observed Extinguished:** 57%
- **Calculated Marine Species Extinct:** 83%
- **Suspected Causes:** Impact; global cooling; loss of oxygen in oceans

**RUGOSE CORAL**

**Placoderm**

**END PERMIAN**
- **Duration:** Unknown
- **Marine Genera Observed Extinguished:** 82%
- **Calculated Marine Species Extinct:** 95%
- **Suspected Causes:** Dramatic fluctuations in climate or sea level; asteroid or comet impacts; severe volcanic activity

**PHYTAUS TEETH**

**END TRIASSIC**
- **Duration:** 3 to 4 my
- **Marine Genera Observed Extinguished:** 53%
- **Calculated Marine Species Extinct:** 80%
- **Suspected Causes:** Severe volcanism; global warming

**END CRETACEOUS**
- **Duration:** <1 my
- **Marine Genera Observed Extinguished:** 47%
- **Calculated Marine Species Extinct:** 76%
- **Suspected Causes:** Impact; severe volcanism

**Mosasaur**

**SPECIES [Scientific name]** | **LAST SEEN, LOCATION** | **EXTINCTION CAUSES**
--- | --- | ---
Deepwater ciscoe (*Coregonus johanni*) | 1952, Lakes Huron and Michigan | Overfishing, hybridization
Pupfish (*Cyprinodon variegatus*) | 1988, Ojo de Agua La Presa, Mexico | Loss of food supply
Dobson’s fruit bat (*Dobsonia chapmani*) | 1970s, Cebu Islands, Philippines | Forest destruction, overhunting
Caribbean monk seal (*Monachus tropicalis*) | 1950s, Caribbean Sea | Overhunting, harassment
Guam flycatcher (*Myiagra freycinetii*) | 1983, Guam | Predation by introduced brown tree snakes
Kaua’i ’O’o (*Moho braccatus*) | 1987, Island of Kaua’i, Hawaii | Disease, rat predation
Xerces Blue Butterfly (*Glaucopsyche xerces*) | 1941, San Francisco Peninsula | Land conversion, predation
Tobias’ Caddis Fly (*Hydropsyche tabini*) | 1950s, Rhine River, Germany | Industrial and urban pollution

**Sources:** Committee on Recently Extinct Organisms; BirdLife International; Xerces Society; World Wildlife Fund.
The 6th Extinction Event?

Figure 2 | Extinction magnitudes of IUCN-assessed taxa in comparison to the 75% mass-extinction benchmark. Numbers next to each icon indicate percentage of species. White icons indicate species ‘extinct’ and ‘extinct in the wild’ over the past 500 years. Black icons add currently ‘threatened’ species to those already ‘extinct’ or ‘extinct in the wild’; the amphibian percentage may be as
Figure 3 | Extinction rate versus extinction magnitude. Vertical lines on the right illustrate the range of mass extinction rates (E/MSY) that would produce the Big Five extinction magnitudes, as bracketed by the best available data from the geological record. The correspondingly coloured dots indicate what the extinction rate would have been if the extinctions had happened (hypothetically) over only 500 years. On the left, dots connected by lines
Terrestrial vs. Marine

- 11 Terrestrial vs. 28 Marine phyla
- 1900 copepod species vs. 1000x more beetles
- ~5000 phytoplankton species, but approximately 250,000 green plants
He has an inordinate fondness for beetles... J.B.S. Haldane

PYRAMID OF DIVERSITY

TO A FIRST APPROXIMATION, all multicellular species are insects. Biologists know the least about the true diversity and ecological importance of the very groups that are most common.

INSECTS
TOTAL SPECIES (BEST ESTIMATE): 8,750,000
NAMED SPECIES: 1,065,000

Fungi
1,500,000
72,000

BACTERIA AND ARCHAEA
1,000,000
4,000

ALGAE
400,000
40,000

NEMATODES AND WORMS
400,000
25,000

VIRUSES
400,000
1,550

PLANTS
320,000
270,000

OTHER LIFE
250,000
110,000

MOLLUSKS
200,000
70,000

PROTOZOA
200,000
40,000

CRUSTACEANS
150,000
43,000

FISH
35,000
26,959

BIRDS
9,881
9,700

REPTILES
7,628
7,150

MAMMALS
4,809
4,650

AMPHIBIANS
4,780
4,780

“Everything is everywhere, but environment selects”

First proposed by Baas-Becking, 1934. Concept is that for small (<1 µm) organisms, they can be dispersed universally but only measurable where conditions promote their growth. Forms the basis for the idea that microbes can’t go extinct…
R versus k strategies

Based on the concept of ‘maximizing’ reproductive efficiency by balancing offspring versus parenting

R < ---------------------------------------------------------------> k

Rapid Growth  Slow growth
Multiple offspring  Fewer offspring
Short Life  Long Life
Small body size  Large body size
Invasive/Transient  Established
Generalists  Specialist
Ramon Margalef (1978) updated the idea of R-k strategies for the ocean...said that you can define species succession based on a “phase space” defined by energy (turbulence) and nutrients.
Horizontal (East-West) Gradients

Onshore-Offshore variability in species is dominated by the shelf-break, and then by the diversity of the shoreline habitat.
Figure 15.15 Total numbers of species of four pelagic taxa caught at six stations along along 20°W in the northeast Atlantic; at each station 14 day and 14 night samples were collected systematically from the top 2000 m of water column.
Sampling Bias?

For well studied organisms like corals and gastropods, it’s less clear that there is a strong latitudinal gradient....
But evidence from phytoplankton models supports the theory.

Fig. 1. (A) Diversity of modeled phytoplankton types in the uppermost 260 m, averaged annually across 10 ensemble members. Diversity is defined as the number of phytoplankton types comprising greater than 0.1% of the total biomass. (B) Zonal mean diversity, as well as the Shannon Index (10), for the map shown in (A). (C) Annual mean $R^*$ (small black dots) of all phytoplankton types with a concentration above $10^{-12}$ mmol N m$^{-3}$ along a meridional transect through the Atlantic Ocean at 20°W in an idealized global model with a single limiting nutrient (12). The large red dots show the $R^*$ for only the most abundant type in each latitude.
There is a maximum in diversity at the shelf-break depth, declining inshore and in deeper waters.

**Figure 15.17** Depth profiles of the expected numbers of species found in a sample of S specimens, randomly selected from dredge and sledge samples down-slope in the northwestern Atlantic, of (a) proto-branch molluscs, (b) polychaetes, (c) cumaceans (crustaceans), and (d) gastropod molluscs (redrawn from Rex^{14}).
Intermediate Disturbance Hypothesis

• Proposed by Connell in 1978
• Basic concept is that too stable ecosystems have low diversity (highly specialized organisms survive), while highly unstable ecosystems also have very low diversity (only generalist “weed” species are present)

• Maximum diversity should occur at “intermediate disturbance”... this can be spatial, such as the continental shelf break, or temporal, such as the upwelling-relaxation cycle in the coastal ocean
Intermediate Disturbance Hypothesis

Diversity

High

Less disturbance

Grossly stressed community
e.g. beneath site of cage cultivation of fish

Increasing disturbance

Climax community
e.g. deep water coral reef

Low

Frequent disturbance

Immediately post-disturbance

Intense disturbance

Infrequent disturbance

Long after a disturbance

Minimal disturbance
Diversity

Disturbance

Li, Nature 419: 154-158, 2002
Figure 1 Oscillations on three resources. 

**a.** Time course of the abundances of three species competing for three resources. 
**b.** The corresponding limit cycle. 
**c.** Small-amplitude oscillations of six species on three resources. 
**d.** Large-amplitude oscillations of nine species on three resources.

Figure 4 Competitive chaos and the coexistence of 12 species on five resources. 

**a.** The abundances of species 1–6; 
**b.** the abundances of species 7–12.
Competing Ecological Theories:

- IDH and Competitive Exclusion Hypothesis suggest that you should have maximum diversity with some level of disturbance--Paradox of the Plankton can be explained by invoking chaotic oscillations in “stable” environments and the rest of the ocean is controlled by classic IDH principles.

- Time-Stability hypothesis suggests that you can have evolution of neutral coexistence in nutrient-limited environments (“gleaners”), with low diversity in seasonally unstable environments (“opportunists”) and biodiversity hotspots where physical mixing is faster than competitive exclusion.
Why Do We care About Diversity?

Fig. 2. Some proposed mechanisms linking biodiversity to ecosystem functioning. (A) Stability: in a hypothetical system, temporal variation in aggregate trophic level biomass is reduced relative to variability of individual species (see Stachowicz et al. 2002 for a real example). (B) Productivity: mean biomass production is greater in hypothetical assemblages with higher diversity, because species interact to enhance aggregate productivity (complementarity) and/or because highly productive species are more likely to be present in a diverse assemblage (sampling effect) (see Duffy et al. 2003 for a real example). ■ means for individual species or combinations; ○ mean (with estimate of variance) of all combinations at that level of diversity; ———: trend of mean productivity with species richness; ————: bounds of the range of productivity. Note that variance in productivity is higher in diverse mixtures than at low diversity (e.g. for single species) as in (A)

Duffy and Stachowicz,
Marine Ecology Progress
Series 311: 179-189, 2006
Why Do We care About Diversity?

Fig. 3. Global loss of species from LMEs. (A) Trajectories of collapsed fish and invertebrate taxa over the past 50 years (diamonds, collapses by year; triangles, cumulative collapses). Data are shown for all (black), species-poor (<500 species, blue), and species-rich (>500 species, red) LMEs. Regression lines are best-fit power models corrected for temporal autocorrelation. (B) Map of all 64 LMEs, color-coded according to their total fish species richness. (C) Proportion of collapsed fish and invertebrate taxa, (D) average productivity of noncollapsed taxa (in percent of maximum catch), and (E) average recovery of catches (in percent of maximum catch) 15 years after a collapse in relation to LME total fish species richness. (F) Number of fished taxa as a function of total species richness. (G) Coefficient of variation in total catch and (H) total catch per year as a function of the number of fished taxa per LME.

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Why Do We care About Diversity?

On giant filter feeders, Lionel Cavin, Science 327: 968-969, 2010
Why Do We care About Diversity?

Climate, Critters, and Cetaceans: Cenozoic Drivers of the Evolution of Modern Whales, Marx and Uhen, Science 327:993-996, 2010
Summary

• The oceans have not always had the same organisms—groups come and go depending on large-scale forcing and evolutionary pressure

• We DON’ T KNOW what the natural rate of extinction is, but we do know that there are, occasionally, mass extinctions that allow for rapid diversification afterwards

• In the modern ocean, there is some predictability of what organisms will be found where/when based on fairly simple principles (e.g. Margalef’s Mandala—each type of phytoplankton are adapted to a particular environment)

• Generally, there is more diversity under low-biomass conditions, and less diversity under high-biomass conditions
Summary (cont.)

• This suggests that in regions impacted by humans (e.g. eutrophication) we will drive down diversity, even as we drive up biomass....

• Why do we care? Higher diversity supports a more stable and more productive ecosystem

• Genetic diversity is complicating our simple (simplistic?) view of marine diversity....

Figure 22.3 Characteristics of the benthic communities across the Garroch Head sewage sludge dump site: A, abundances of animals per cm²; B, biomass in 100 g wet weight per m²; S, numbers of species per 0.1 m². The arrow indicates the centre of the dump site (redrawn from Pearson').
DNA Barcoding

“DNA barcoding has the potential to be a practical method for identification of the estimated 10 million species of eukaryotic life on earth.”

mitochondrial cytochrome c oxidase subunit I (COI) [in animals]
rbcL (RUBISCO) and matK (chloroplast genes) [in plants]
16S rDNA (for bacteria)
Figure 5. ARMS are biocubes of artificial habitat that sample recruiting individuals and standardize the sources of potential sampling bias across sites. ARMS were tested by the Smithsonian under MBP. A. ARMS in situ, B. photo-documentation of one plate for landscape analyses, C. 2 mm -500 um fraction, D. 500-1000 um, E. Scraped fraction, F. Preliminary 454 results from mtCOI analyses of 3 Moorea ARMS, newly developed primers capture broad spectrum of taxa (incl. 20+ phyla). Note consistency of replicate 10g homogenates from same scraped fraction (blue), and diversity of 500-100 (red) fraction is consistently greater than 500-200 fraction (green). Microbial profiles will be generated from same bulk extractions.
Figure 2. Preliminary data on a biocube of coral reef on Moorea: a. Photo of a sampled biocube, and the enormous richness of biodiversity found at this small spatial scale [1]. In total, over 1000 individuals >1mm were identified through live sorting; 600 of these were DNA bar-coded as part of the MBP database. b. A community phylogeny (CO1 neighbor-joining tree) showing the evolutionary relationships between most species in the biocube. c. Size-scaled image of a crustacean morphospecies lot. Such images will be automatically analyzed by software to estimate functional traits of all individuals. d. Body size and chelae size distribution for decapods shown in a. f. A food web (N=363) of species in the biocube, based on 18,199 separate pair-wise links determined using expert knowledge and literature. (Photo courtesy of David Liittschwager.)
Harder than you think!