Species Interactions.

• **Pairwise Interactions.**
  1. **Competition** (-/-).
     1. Each species reduces growth rate of the other.
     2. Can be **exploitative** or via **interference**.
  2. **Predator-Prey** (+/-)
     a. One species benefits; the other suffers.
     b. **Includes** parasite-host interactions.
  3. **Mutualism** (+/+)
     a. Can be obligate – e.g., Yucca-Yucca moth.
     b. Or not.
  4. **Commensalism** (+/0)
     a. One species benefits from, but does not affect the other.
     b. Cattle egrets / buffalo; redwood epiphytes / redwood trees.

Examples of predator-prey, mutualistic and commensal interactions.
4. Amensalism (-/0).
   a. One species **harmed** by, but does **not affect**, the other.

   b. Short trees can be shaded out by but do not affect taller trees.

   c. **However**, many understory species do not tolerate strong sunlight or at least **do better in the shade**,

   d. Likewise understory trees can compete with canopy species for water and soil nutrients.

**Above.** Competition for space by two species of barnacles. **Next page.** Ant-acacia mutualism.
6. Interactions can **change** with circumstance.

a. Example: Saguaro-nurse plant interaction:

b. Baby saguaro **protected** by nurse plant – minimizes herbivory, desiccation and frost (+/0).

c. Older saguaro unaffected by, but can **interfere with**, nurse plant (0/-).

d. Or the two plants compete for water (-/-).

7. Two-way interactions often **mediated** by third species.

a. *E.g.*, Salvia-grass.

b. *Salvia* (sage) shelters rabbits that eat grass that would otherwise outcompete it.

c. Rabbits don’t eat the sage.

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Rabbits exclude grasses from the periphery of sage. Rabbit removal resulted in the grasses invading the bare areas.
• Pairwise interactions **embedded** in larger networks.

1. Sometimes one can understand system behavior in terms of a **limited number of key interactions**.

2. *Example*: Lynx-hare interaction a part of boreal forest food web.
   a. Arrows indicate flow of energy.
   b. Some surprising connections – e.g. squirrels eat baby hares.
   c. A lot can be understood in terms of three variables: lynx, hare and “vegetation.”
Ecological Niche.

- A way of characterizing a species’ role in nature.

- In terms of tolerances and distribution.

1. **Fundamental niche** – circumstances in which a species can live.

2. **Realized niche** – circumstances in which it does live.

3. $R \subseteq F$. Consequence of
   a. History – where species happen to live.
   b. Exclusion by other species.

- In terms of resource utilization.

- Overlapping niches promote niche divergence (character displacement) – Darwin’s “Principle of Divergence”.

Fundamental and Realized Niches in Barnacles.

- Larval distributions **overlap**; Adult distributions **segregate**.
- The larger *Balanus* overtops *Chthamalus* & smoothers it.
- *Balanus* **excludes** *Chthamalus* from much, **but not all**, of its fundamental niche.

Competition between two species of barnacles. *Balanus* overgrows *Chthamalus* save near high tide where it is kept in check by desiccation, *i.e.*, *Balanus* more sensitive to desiccation than *Chthamalus*.

- Exclusion can be **prevented** by physical or biotic disturbance.
Types of Competition.

- For space: Usually leads to exclusion of one species by the other, e.g. barnacles above.

- For self-renewing resources.
  1. Can lead to coexistence if resources utilized in different ways / proportions.
  2. Famous example - MacArthur’s warblers.
     a. Identical save for plumage differences.
     b. Differences in foraging behavior permit coexistence.

- Alternative distinction is interference vs. exploitation.

- Interference competition
  a. Can result in existence of alternative stable equilibria.
  b. Can result from
     i. Interspecific aggression – e.g. mockingbirds.
     ii. Mutual poisoning.

- Exploitative competition: Most efficient species wins.
In general, two-way competitive interactions equilibrial – one species wins or the two coexist at stable densities.

MacArthur’s warblers (*Dendroica spp.*) coexist by foraging for insects in different parts of spruce trees.
Predator-Prey Interactions can Oscillate.

- Potential for oscillations **inherent**.
  Predators $\uparrow \Rightarrow$ Prey $\downarrow$; Prey $\downarrow \Rightarrow$ Predators $\downarrow$
  Predators $\downarrow \Rightarrow$ Prey $\uparrow$; Prey $\uparrow \Rightarrow$ Predators $\uparrow$

- Oscillations **may or may not** be stable.

Oscillatory dynamics in two species predator-prey models. 

- **a.** Pd gut capacity (PGC) = $K_v = \infty$; 
- **b.** PGC = $\infty$; $K_v$ finite; 
- **c.** PGC, $K_py$ finite; 
- **d.** PGC, $K_py$ finite plus “predator Allee effect can produce an “ecological neuron” – i.e., stimulate, “fire”, return to resting state.
Lynx-Hare Cycle.

- Ten-year” cycle has persisted since late 1700’s.

- Lynx eat hare (principally); hares eat vegetation.

- Long-standing dispute as to whether oscillation is predator-prey or plant-herbivore.

- Field experiments suggest both important.

- Three treatments:

  1. Hares given supplemental food.

  2. Terrestrial (but not avian) predators excluded with fences through which hares can pass.

  3. Both.
• Results:

1. Supplemental food
   a. Increases hare densities, but
   b. Doesn’t delay the population crash.

2. Predator exclusion\(^1\) has negligible effect.

3. Combined treatment
   b. Increases hare densities and postpones crash

4. All treatment responses can be replicated by a three variable (predator, hare, vegetation) model.

5. Suggestive, but still trunk wiggling due to parameter uncertainty.

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\(^1\) The exclosures had no roofs, i.e., hares still at risk to avian predation.
Keystone Predators.

1. **Increase** prey species diversity by preventing competition from going to completion.

2. **Starfish Pisaster** a classic example. Results of removal experiment below.

3. **Physical** disturbance has same effect with maximum diversity occurring at intermediate disturbance levels.
Inducible Prey Defenses.

- Exposure of prey to predators or a chemical signal indicating their presence can induce **changes** in prey growth and development that inhibit predation.

- Such changes called **predator-induced polyphenisms**.

- Examples include

  1. Larger helmets in *Daphnia*.
  2. Increased shell thickness in mussels.

- Often the stimulus is a chemical signal called a **kairomone** – see exp. next page.

- In some cases, the trait can be **passed to the offspring**.

- “Transgenerational effects” nothing less than the **inheritance of acquired characteristics**.

Colored scanning electron micrographs of the water flea *Daphnia cucullata*. **Left.** Standard shape. **Right.** Predator-induced morph with enlarged helmet (green) and tail (blue). Photo from Sciencephoto.com.
Predator-induced Polyphenism in Mussels.

- Differences observed in nature.

(a) Prey and predator

Blue mussels  Crabs

(b) Correlation between predation rate and prey defense
- Are the differences at least partly inducible?
1. **But.** Induced difference less\(^2\) than that observed between different populations.

2. Suggests something else is going on. Can you think of some possibilities?

3. Can you think of experiments to sort things out?

\(^2\) Note the difference in scale between this and the figure on page 16.
Communities.

- A **community** may be defined as

  1. **All the species** that live together in a particular area.

  2. A **subset of the same** united by **common role** in the economy of nature – *e.g.*, seed-eating rodents of the southwestern deserts.

- In some cases, ecologically equivalent species replace each in comparable habitats other as one goes from one geographic region to another.

Seed eating rodents of three southwestern deserts. These animals store seeds in **external** cheek pouches, which are analogous, but unrelated, to the **internal** pouches of old world gerbils.
• **Plant communities** are neither random assemblages of species nor tightly structured “superorganisms”.

• Along environmental gradients, species come and go neither in concert nor independently.

• Often we define plant communities by presence of one or a few prominent species or growth forms.

• For example, a drive up Mt. Lemmon takes you through

  1. **Cactus desert.**
  2. **Oak woodland.**
  3. **Pine forest.**
  4. **Spruce-fir forest.**

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**Top.** Species distributions along a moisture gradient. **Bottom.** Distribution of plant communities with respect to temperature and moisture. **Arrow** approximates a drive up Mt. Lemmon. Can you think of additional factors that determine which plants you encounter along the way?
1. Changes in species composition over time.

2. **Primary succession** begins with colonization of previously barren rock – e.g., by lichens.

Primary succession on glacial moraines (deposits left by retreating glaciers) in Alaska. As the soil accumulates, so also does soil nitrogen, the product of nitrogen fixing bacteria. The term “mineral soil” refers to the soil layer below the superficial litter.
3. **Secondary succession** follows disturbance of a previously occupied site – *e.g.*, an old field following its abandonment.

Succession of plant species on abandoned fields in North Carolina. Annual plants (pioneer species) are followed by communities of perennials and grasses, shrubs, softwood trees (pines) and finally hardwood trees (dicots). The entire process, from **pioneer** (annuals) to **climax** (hardwood trees) species, takes about 120 years.
4. **Freshwater succession.**
   a. Oligotrophic (nutrient poor) lake →
   b. Eutrophic (nutrient rich) lake →
   c. Marsh → Bog → Forest.

Vegetation in and adjacent to a freshwater lake. With the passage of time, litter and soil fall into the lake, and the marginal vegetation moves toward the center. Eventually, the lake fills in and becomes part of the forest. Eutrophication of oligotrophic streams and lakes can be accelerated by runoff containing fertilizers and detergents containing N and P. The latter chemicals accelerate plant growth.
Productivity.

- Plants capture ~ 5% of energy in solar radiation.
  1. Facilitates carbohydrate production (Lecture III.1)
  2. Remainder (95%) re-radiated as heat (infrared) or consumed by evaporation.

- **Gross Primary Production** (GPP)
  1. The *rate* at which plants capture energy.
  2. Measured in g/m\(^2\)/y, where “g” refers to grams of carbon.

- **Net Primary Production** (NPP): what’s left over after plant metabolism.
  1. NPP = GPP – respiration;
  2. Also measured in units of g/m\(^2\)/y.
  3. **Open ocean** and **tropical rainforests** principal contributors to total world productivity.
  4. Consequence of **extensiveness** (ocean) and **per area NPP** (rain forest).
Above and to the right. Ecosystems characterized by

a. Per cent of earth’s surface area; b. Average NPP; c. Per cent of earth’s total NPP. Open ocean and tropical rainforest are the premier contributors to earth’s total NPP, the former because there is so much of it, the latter, because tropical forests are so productive.
Energy flow through an ecosystem. Note the inverted food pyramid (blue): Herbivores → Primary Carnivores → Secondary Carnivores. Here one sees the 2nd Law of Thermodynamics (aka ecological inefficiency) in action on a grand scale. Omitted is non-photosynthetic autotrophy. See Lecture III.1 for review of oxygenic photosynthesis and cellular respiration.
Food Chains / Trophic Levels (TLs).

- 1\textsuperscript{st} TL: **Producers** – green plants – energy from the sun.
- 2\textsuperscript{nd} TL: **Herbivores** – animals that eat green plants
- 3\textsuperscript{rd} TL: **Primary Carnivores** – animals that eat herbivores.
- 4\textsuperscript{th} TL. **Secondary carnivores** – animals that eat primary carnivores.
- **Detritivores** – subsist on the remains / waste products of all the above.
Energy flow from one TL to the next ≤ 10%.

Energy and biomass pyramids. In the open ocean, producers are unicellular algae. Extremely rapid turnover (faster than grass or trees) allows small producer biomass to support greater herbivore biomass than on land.
Food Webs.

- Food chains an idealization.
- Real world patterns of tropic interaction more complex.

1. In the boreal forest food web on page 6, squirrels and other small rodents (2\textsuperscript{nd} TL) eat baby snowshoe hares (also 2\textsuperscript{nd} trophic level).

2. Especially in the ocean, predators progress to higher TLs as they grow.
Biogeochemical Cycles

- Movement of materials among “compartments”.

1. *E.g.*, Atmosphere and oceans; rocks and soil; Biosphere

2. Nitrogen and Carbon cycles important examples.
Nitrogen and Carbon Cycles are linked.

Photosynthesis consumes CO$_2$ and requires N, thereby linking the carbon and nitrogen cycles. **Red arrow** indicates anthropogenic inputs of CO$_2$. The positive effect of increased CO$_2$ in plant growth and CO$_2$ removal from the atmosphere is widely believed to be of minimal importance due to N limitation.
Photosynthetic Response to CO$_2$ Fertilization.

- Growth chamber experiments: Photosynthesis increases with $[CO_2]_{atm}$ until other factors, i.e., nutrients, become limiting.

- Expectation: Long-term response to enhanced $[CO_2]_{atm}$ will be suppressed by lack of available P and N.

- Results of twelve year Duke Forest experiment:
  1. Increased carbon fixation sustained by increased root growth and fungal/microbial activity.
  2. Negative effects of increased ozone concentrations likewise compensated for as ozone-tolerant individuals / species took up the slack.

NPP in the final years of a 12 year study. Shaded and un-shaded bars compare trees exposed to elevated CO$_2$ (top) and O$_3$ (bottom) with controls. From Zak et al. (2011. Ecology Letters).
Such unexpected results

1. Due to web-like complexity of biological (in this case ecological) interactions;

2. That produce “slow variable” feedback.

3. A ubiquitous property of biological systems.

Doesn’t exclude possibility that next twelve years won’t witness the expected suppression.

More recently (Houlten et al., 2018), it has been suggested that plants can obtain N from rocks in significant amounts.
Bedrock Holds Unexpected Source of Global Nitrogen

4 April 2018 Michelle Hampson

For centuries, the prevailing science has indicated that all of the nitrogen on Earth available to plants comes from the atmosphere. But a study from the University of California, Davis, indicates that more than a quarter comes from Earth’s bedrock.

The study, to be published April 6 in the journal Science, found that up to 26 percent of the nitrogen in natural ecosystems is sourced from rocks, with the remaining fraction from the atmosphere.

Before this study, the input of this nitrogen to the global land system was unknown. The discovery could greatly improve climate change projections, which rely on understanding the carbon cycle. This newly identified source of nitrogen could also feed the carbon cycle on land, allowing ecosystems to pull more emissions out of the atmosphere, the authors said.

“Our study shows that nitrogen weathering is a globally significant source of nutrition to soils and ecosystems worldwide,” said co-lead author Ben Houlten, a professor in the UC Davis Department of Land, Air and Water Resources and director of the UC Davis Muir Institute. “This runs counter the centuries-long paradigm that has laid the foundation for the environmental sciences. We think that this nitrogen may allow forests and grasslands to sequester more fossil fuel CO2 emissions than

UC Davis press release. Possible climate change implications of Houlten et al. highlighted.
A Startling New Discovery Could Destroy All Those Global Warming Doomsday Forecasts

Climate Change: Scientists just discovered a massive, heretofore unknown, source of nitrogen. Why does this matter? Because it could dramatically change those dire global warming forecasts that everybody claims are based on “settled science.”

The researchers, whose findings were published in the prestigious *Journal Science*, say they’ve determined that the idea that the only source of nitrogen for plant life came from the air is wrong. There are vast storehouses in the planet’s bedrock that plants also feed on.

This is potentially huge news, since what it means is that there is a vastly larger supply of nitrogen than previously believed.

Massive source of ‘missing’ nitrogen could revolutionise climate change projections

'This runs counter the centuries-long paradigm that has laid the foundation for the environmental sciences,’ say researchers behind study

Josh Gabbatiss Science Correspondent | @josh_gabbatiss | Thursday 5 April 2018 20:05 BST | 140 comments

The press (*Investor’s Business Daily* and *The Independent*) weighs in: Armageddon postponed!
Believer Pushback. *Climate Feedback* goes after *IBD*. Rebuttal includes “clarification” by Houlton. Shades of Buffon and the Sorbonne Faculty of Theology in 1751. See, for example, [Quodlibeta. 21 January, 2009](#). Likewise, the saga (Secord, 2000) of physiologist William Lawrence in Regency England). See my Lecture V, pp. 52-54, ECOL 249.
• From the paper:

“Lastly, the availability of N singly and in combination with P profoundly limits terrestrial C storage, with nontrivial effects on global climate change (4, 46). Our previous work demonstrated a doubling of ecosystem C storage among temperate conifer forests residing on N-rich bedrock (7). Our model indicates that rock N inputs could make up >29% of total N inputs to boreal forests, which could help to explain the high C uptake capacity observed for this biome and partially mitigate the mismatch of C and N budgets in Earth system models” [Houlten et al., 2018, 62]

• And in retrospect:

“Our nitrogen study does not detract from the urgency of the climate problem, nor the unequivocal evidence of the role of carbon pollution in causing global climate change. The climate threat is clear and present and we must solve it rapidly by reducing emissions and capturing existing CO$_2$ from the atmosphere. [Houlton (2018) quoted at https://climatefeedback.org/evaluation/investors-business-daily-editorial-misrepresents-study-to-claim-plants-will-prevent-dangerous-climate-change/]


“... we asked the following simple question: What are the odds that a given month in the past 5 years was extremely warm (or cold) relative to the base period 1979–2011, for an arbitrary location in either the Northern or Southern Hemispheres? Our definition of extreme here is among the warmest (or coldest) 3 months in this period ... This is a question we can ask observations (here the ERA-Interim 2-meter temperature), as well as the CMIP3 near-surface air temperature, and compare the answers.” [Essex and Tsonis, 2018, p.556]
More generally:

“There are many different types of climate models. Some are purely didactic, for which there is no specific expectation of prediction. The more advanced models are meteorologically based and are presented as “simulations” used for climate “projections”. This common terminology about what climate models are and what they do is telling. A “projection” holds a more modest claim on the future than a prediction, and “simulation” suggests imitation rather than a representation of the thing itself—neither represents the qualities aspired to by a field rooted in rigorous physics. Even “model” is used in a manner different from other fields of science. The standard model of physics, for example, is subject to falsification. If it fails to make correct predictions in controlled experiments, it is false …

“What makes climate models fundamentally different is that they are presented as being unfalsifiable. Even when they deviate from actual observations, they are not superseded by a better competing model. Deviations simply invite some retuning. Moreover instead of replacement by better models retuning leads to all models becoming more alike.

“There are many reasons for this. Some are fundamental features of the field, such as having comprehensive measurements for only a minute time slice of a single realization of the system under study. Controlled experiments are impossible, so falsification in terms of them is also impossible. There is no prospect of a climate analogue to meteorological skill, given only a single, as yet unfulfilled, reali-
zation for any prediction. Also contributing is the nature of the specificity of questions being asked about a physical system that is nonlinear and complex, spanning far too many scales of space and time to be directly treated either computationally or theoretically. Moreover the meteorological theory we begin with calls for data that we do not actually have, but which we optimistically infer (e.g. reanalysis) from substitutes extracted from other copious data sources not properly suited to the task.” [Essex and Tsonis, 2018, p. 556]

- If this is to be believed, climate scientists are engaged in the same sort of trunk wiggling in which Ptolemy and his successors (Kuhn, 1957) engaged for over a thousand years.