Earlier: Unlimited populations grow exponentially.

**Density-dependent regulation** of demographic rates \((b \& d)\) limits pop growth \((r \& mu)\);
if pop growth rate \((r \& mu)\) is low,
\(N\) approaches carrying capacity \(K\);
if pop growth rate is higher, dynamics cyclic or chaotic.

A **biological community** is an assemblage of populations of various species living close enough for potential interaction.

Ecologists define the boundaries of a particular community to fit their research questions.

Begin building **community ecology** by looking at how pair-wise interactions with other species influence demographic rates \((b \& d)\):

- **mutualism** (+/+)
- **commensalism** (+/0, skip this)

Then: consider existence & properties of multispecies communities w/ complex food webs and many indirect interactions.

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A community is any assemblage of populations in an area or habitat.

How can we account for the species found together as members of a community? Two different views on this question emerged among ecologists.

The **individualistic hypothesis** (Gleason) depicts the plant community as a chance assemblage of species in the same area simply because they happen to have similar abiotic requirements - for example, for temperature, rainfall, and soil type.

The **interactive hypothesis** (Clements) ... the community is a group of closely linked species locked together by mandatory biotic interactions that cause the community to function as an integrated unit - as a superorganism.

In most actual cases where there are gradients of env. variation, the composition of plant communities with species more or less independently distributed, ... support the view of plant communities as loose associations without discrete boundaries. (Fig 53.29)

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**Community biodiversity** measures the number of species & their relative abundance. Ecological communities vary extensively in the number of species they contain. Both Wallace & Darwin pointed out that repeatable global patterns: biodiversity is higher in the tropics & on large islands near continents & lower at high latitudes & on small or remote islands.

- 6.6 ha in Malaysia contained 711 tree species.
- 2 ha plots in Michigan forests contained 10-15 species.
- All of Europe north of the Alps has only 50 tree species.

These repeatable biogeographic patterns imply general ecological/evolutionary processes.

What causes **latitudinal gradients** in species richness?

Ongoing debate about:

- but tropics not so stable
- but max diversity at intermediate productivity
- predictability (seasonality) – so far so good
- predation – less competitive exclusion in tropics
- spatial heterogeneity – local adaptation & speciation etc.

**Global Biodiversity Conservation Priorities**

The exponential growth model: \( \frac{dN}{dt} = N \cdot r \)

in incorporate **Intraspecific Competition** w/ density-dependent
- FB on growth rate

The logistic growth model: \( \frac{dN}{dt} = N \cdot \left( \frac{r \cdot (1 - \frac{N}{K})}{K} \right) \)

How can we add a little more realism to this model by incorporating **Interspecific Competition**?

Suppose we can measure the impact of 1 individual of species 2 on the pop growth rate of species 1 relative to the impact of 1 additional individual of species 1?

Call this rate of substitution the ‘interspecific competition coefficient’ \( a_{12} \) (the interspecific coefficients \( a_{11} \) & \( a_{22} \) are implicitly = 1)

The Lotka-Volterra **interspecific competition model**:

\[ \frac{dN_1}{dt} = N_1 \left( r_{1max} \left( 1 - \frac{N_1}{K_1} \right) \right) \]
\[ \frac{dN_2}{dt} = N_2 \left( r_{2max} \left( 1 - \frac{N_2}{K_2} \right) \right) \]

If we ‘do the math’ we find **stable coexistence** of both species 1 & 2 only if \[ (1/K_{1P}) < (1/K_{2P}) \] meaning: \[ (1/K_{2P}) < (1/K_{1P}) \]

implying: diff species use resources differently (different niches).

Otherwise, expect **competitive exclusion** of one of the species.

**Prospects for competitive exclusion** treatment to control salmonellas and other foodborne pathogens in poultry.

**Chlamydomonas** tolerates a broad range of exposure to air (broad fun. niche), but is a:

**Balanus** cannot tolerate long exposure to air (narrow fun. niche), but in lower inter-tidal,

Even though **Chlamydomonas** is concentrated primarily on the upper strata of rocks, when ecologist Joseph Connell removed **Balanus** from the lower strata, the **Chlamydomonas** population

Thus, **Chlamydomonas** could survive lower on the rocks than where it is generally found, were it not for competition from **Balanus**.

Its realized niche is only a fraction of its **fundamental niche**.

Note: coexistence results from tradeoffs: each species better at something.

**Competitive exclusion** is often found in simple lab experiments where 2 diff species are forced to scramble for one limiting resource.

(it’s difficult to maintain stable pairs in simple environments w/ exploitation competition).

A classic illustration is from **Gause’s exp’s w/ paramecia** competing for bacteria in chemostats (w/ fixed input of food).

When grown separately each species does fine (note: **P. aurelia** has smaller r but larger K)

When grown in competition:

**Competitive exclusion** is expected from details of L-V competition model, but there is a simpler interpretation (from D.Tilman):

- Note that **P. aurelia** has a bigger carrying capacity \( K \) than **P. caudatum**.
- This means that each **P. aurelia** can... \((1/K_{2P}) < ((1/K_{1P})\)... of the resource base).
- The growing pop of **P. aurelia** can drive resources out of the system.

**Lactobacillus as a probiotic for preventing** against bacterial pathogens in poultry.

**La Ragione et al. 2004. Letters in Applied Microbio**

protection against salmonellas and other foodborne pathogens in poultry, but in lower inter-tidal,

**Chlamydomonas** protects the vagina from colonization by pathogens by ...

blocking their attachment to the vaginal epithelium and producing substances that inhibit their multiplication.

**My enemy’s enemy is my friend!**
There are two possible outcomes of competition between species with identical niches:

- either the less competitive species will be driven to local extinction,
- or one of the species may evolve to use a different set of resources. This differentiation of niches is called resource partitioning.

We can think of resource partitioning as "the ghost of competition past" - circumstantial evidence of earlier interspecific competition resolved by the evolution of niche differentiation.

Niche differentiation is often evident from morphological [character displacement] & in the seeds that they can eat most efficiently.

The Galápagos finches provide a good example of [resource partitioning].

Evolution of Character Displacement in Darwin's Finches
PR Grant & BR Grant (14 July 2006) Science 313 (5784), 224. | Full Text

Parasites & disease influence the distribution and abundance of organisms

The African trypanosome, Trypanosoma brucei, is an important pathogen of humans and livestock. … the parasite and the subsequent disease in cattle renders much of Central Africa refractory to raising high-yielding beef and dairy cows; indirectly, this has the most profound effect on the human economy and nutrition in the area. (& explains why holsteins haven’t yet displaced wildlife) The reservoir hosts are wild game animals. Humans become infected when they invade the territory of the tsetse fly. The Food and Agricultural Organization of the UN states, ‘Trypanosomiasis is probably the only disease which has profoundly affected the settlement and economic development of a major part of a continent.” (keystone species)

Of the approximately 7-10 million km² of land that are infested by tsetse fly, only 20 million cattle are raised. Under different circumstances, this land could support more than 140 million cattle.

It is apparent that predation influences the distribution and abundance of prey species - most obviously by killing some and scaring the rest.

Predators can actually increase biodiversity, by preventing competitive exclusion: by preferentially killing the most abundant (dominant) competitor. (R. Payne, Fig 53.16)

Are invasive species a major cause of extinctions?

Numbers of species affected by different threats believed to be responsible for causing population declines: Wilcove et al. (2002).

Invasive exotic species are causing dramatic changes in ecological systems worldwide, and there is no question that invasive species are profoundly altering many communities and ecosystems.

Zebra mussels are currently considered to be the major threat to North American freshwater unionid bivalves. Of a historic 281 species, 19 are known to be extinct, 21 are thought to be extinct, 77 are endangered, 43 are threatened, and 72 are of special concern.
Competition between the gypsy moth, *Lymantria dispar*, and the northern tiger swallowtail, *Papilio canadensis*: interactions mediated by host plant chemistry, pathogens, and parasitoids.

Redman AM, Scriber JM - *OECOLOGIA* 125: (2) 218-228 OCT 2000

... interspecific competition among insect herbivores probably involves more frequently than direct battles over food ...

Typically, indirect competition between species occurs when the activity of one species induces a *chemical response in its host plant*, affecting other species feeding on the same plant. *(inducing defenses, like scaring away prey, makes resource less available)*

Examples of indirect competition mediated by *pathogens* have been reported for a great many species ... but not, as far as we know, for herbivorous insects. *(increasing abundance of shared predators & pathogens is "apparent competition")

... *predators and parasitoids* may also mediate indirect competition ...

The attraction of polyphagous natural enemies to visual cues or ... host damage can negatively affect neighboring herbivores.

We investigated interspecific competition in a study system involving the northern tiger swallowtail and the gypsy moth, feeding on quaking aspen. The northern tiger swallowtail, *Papilio canadensis* is native to North America. ...

*P. canadensis* ... typically exhibits a strong preference for quaking aspen, *Populus tremuloides* ...

Females ... oviposit on newly expanded leaves during the first few weeks of June, and larvae grow throughout the summer, pupating in mid- to late August.

**Quaking aspen**, which supports a large number of herbivores, is defended primarily by the phenolic glycosides salicortin and tremulacin, and secondarily by tannins.

When leaf tissue is removed ... refoliation replaces nearly 90% of damaged foliage with leaves that tend to be ... Damaged leaves themselves also tend to contain elevated levels of these compounds.

The European gypsy moth, *Lymantria dispar* was brought to Massachusetts from France in 1868, and has since radiated ... over most of the eastern United States. Gypsy moth outbreaks are ecologically dramatic events, and it is difficult to imagine that many species remain unaffected. *Gypsy moth defoliation* ...

*Gypsy moth outbreaks are associated with high densities of* ...

At least some of these natural enemies ... are known to use alternative hosts.
We conducted a long-term growth trial to determine if defoliation by gypsy moths decreased the quality of quaking aspen leaves for *P. canadensis*. This assay consisted of 40 *P. canadensis* neonates on each of four treatments:

1. Leaves from undefoliated stands,
2. Leaves from resistant trees in defoliated stands,
3. Regrowth leaves from defoliated stands, and
4. Partially eaten leaves from defoliated stands.

All defoliation treatments severely reduced survival... when leaves from defoliated areas were sterilized, whereas sterilization of leaves from undefoliated stands had no effect on survival.

We also tested for the presence of pathogenic substances in gypsy moth body fluids themselves. We collected the cadavers of gypsy moth larvae from an intensely defoliated quaking aspen stand... We ground the cadavers with a mortar and pestle, diluted them with distilled water and painted approximately 1 ml of the resulting solution on quaking aspen leaves... Leaves painted with gypsy moth body fluids and water resulted in 100% mortality of swallowtail caterpillars... However, when we autoclaved the body fluid solution, the effect on survival nearly disappeared.

We set up a field experiment to test whether gypsy moth larvae attracted parasitoids that attacked *P. canadensis* larvae as well. Swallowtails were subjected to two treatments: quaking aspen stands artificially infested with gypsy moth larvae, and paired uninfested control stands. When we placed swallowtail caterpillars on trees in areas that had been artificially infested with gypsy moths... the incidence of parasitism...
Our data suggest that indirect competition between gypsy moths and tiger swallowtails can occur. ...

gypsy moth-defoliation significantly depressed the quality of quaking aspen leaves for Papilio caterpillars, even when leaves were sterilized; thus, leaf chemistry appears to have reduced swallowtail performance.

... pathogens or other lethal agents associated with gypsy moth body fluids ... could potentially devastate wild tiger swallowtail populations. We observed 84% mortality in a very short period of time on unsterilized leaves ... and 100% mortality on leaves painted directly with gypsy moth body fluids.

... as a result of proximity to gypsy moths, parasitism rate was significantly altered.

Studies such as this ... stand not only to illuminate the basic mechanisms and consequences of interspecific interactions but also to enhance our ability to manage pests responsibly.

Community Effects of Climate Change
Most forecasts of ecological responses to climate change assume that these can be based on individual species tolerances for changing moisture or temperature ... Suttle et al. challenge this assumption. In a 5-year experiment, they examined the consequences of alternative climate change scenarios in a grassland ecosystem in California, USA. Manipulation of rainfall over replicated 10-m diameter plots showed that higher-order species interactions dictate responses throughout the community. The effects on plant and arthropod abundance and diversity were the reverse of what would have been predicted based on individual species responses.

Species Interactions Reverse Grassland Responses to Changing Climate
K. B. Suttle et al. 2007. Science 315 (5812), 640. PDF

Indirect effects of climate on species will commonly lag behind direct effects, but their importance makes system-level interactions crucial to climate change forecasting ... {indirect interactions make predicting ecosystem responses very challenging!}

In ecology, as w/ gravity, ‘everything is connected to everything else’ - the trick is figuring out which interactions are ‘trivial’ & can be ignored.

Studies such as this ... stand not only to illuminate the basic mechanisms and consequences of interspecific interactions but also to enhance our ability to manage pests responsibly.

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The Concluding Passage from The Origin of Species by Charles Darwin

It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us. ... There is grandeur in this view of life ...