Competition trade-offs

Diversity could be maintained if species partition resources ($R^*$, warblers, mongooses) or if differences in competitive ability trade-off with other abilities.

Many examples exist of competition-dispersal or competition-colonization trade-offs (Daphnia, insects, fungi, plants)

Traits that confer high competitive ability come at a cost – associated with speed of development, dispersal ability, persistence.
Example of a colonization-competition trade-off: Neotropical *Drosophila* species (Sevenster and Van Alphen 1993; Krijger et al. 2001)

Diverse assemblages of *Drosophila* species coexist on decaying fruits in tropical forests (feeding on yeasts).

*Species differ markedly in larval development time*

Experiment: Pairwise competition trials between 7 species varying in development times.

Result: Species with long development times suffered greater interspecific competition, but had greater survival times (potentially an advantage in finding new food resources).
Fig. 1. The starvation time of adults (experiment B5) versus developmental period (experiment B1) for 18 species. Circles indicate means, bars their standard errors. $\tau$ is Kendall's rank correlation on the means. Line fitted by linear regression (see
In *Drosophila* speed of development is traded off with:

- *Resistance against abiotic stresses* (e.g., desiccation, temperature extremes)

- *Adult survival*. A long adult life improves the probability of colonizing a new breeding site (decaying fruit)

- If resource availability fluctuates through the year, or if flies are specialized on different fruit types with different abundances then variation in development time can maintain species diversity.
Testing mechanistic models for resource partitioning is difficult!

Observational studies are (sometimes) consistent with the hypothesis that coexistence is linked to resource heterogeneity.

Some evidence also supports limits to the similarity of coexisting species.

Challenges to a competition-centric view of community assembly comes from species-rich communities where the number of coexisting species far exceeds the number of limiting resources or the scale of their heterogeneity.
Mutualisms

Fig wasps, ectomycorrhiza
*Rhizobium, Acacia*
Mutualisms

- Reciprocally positive interactions between species (contrast with competition), and commensalisms which show unidirectionally positive effects. 
  Better to think of most mutualisms as ‘reciprocal parasitism’

- Many kinds of associations exist influencing energy uptake, nutrition, protection, and transport

- Lots of classifications. Relationships range from:
  - Facultative mutualisms: non-essential, but positive effects on fitness to:
  - Obligate mutualisms: co-evolved relationships in which neither member of the association can persist without the other.
Lots of papers on mutualisms, but…

Little emphasis on mutualism as a form of interaction with emphasis on ecological or evolutionary dynamics.

Competition models (e.g. Volterra model) that predict species coexistence cannot be applied to mutualisms.

Species 1: \( \frac{dN_1}{dt} = r_1 N_1 \left( \frac{(K_1 - N_1 - \alpha_{12} N_2)}{K_1} \right) \)
Species 2: \( \frac{dN_2}{dt} = r_2 N_2 \left( \frac{(K_2 - N_2 - \alpha_{21} N_1)}{K_2} \right) \)

Where \( \alpha_{ij} \) = competition coefficient for the effect of species j on species i.

Mutualism models are problematic because mutualisms tend to be context-dependent.
What conditions lead to the development of mutualistic interactions among species?

Bertness and Calloway (1994), and Calloway (2002) considered this for sessile organisms

Suggest that mutualisms common in **stressful environments**: e.g., prevalence of lichens in nutrient poor sites

  e.g., neighbourhood habitat amelioration (*facilitation* of the establishment of *Juncus* by *Spartina* in salt marshes). Some species can take the role of space-holders, buffering neighbours from stressful conditions (temperature, dessication, low nutrients, osmotic stress, disturbance).
Bertness and Calloway view of mutualisms

- Physical stress
- Consumer pressure
- Mutualistic interactions
- Defense
- Habitat amelioration
- Competitive interactions
- Physical stress
From an evolutionary perspective also important to classify mutualisms as vertically and horizontally transmitted.

Harmony! Evolutionary interests of mutualists are aligned.

Vertical transmission

G₁

G₂

G₃

Wolbachia

Atta: leaf-cutter ants
Leaf-cutter (Attine) ants and fungi (*Leucoprinus* spp)

Large group of ant species restricted to neotropical/temperate forests.

Fungus breaks down the leaves and produces food bodies from hyphal tips on which ants feed.

Second mutualism between ants and an antibiotic producing bacteria (*Streptomyces*) carried on the ants cuticle. Bacteria controls growth of a parasitic fungus (*Escovopsis*). Currie et al. (1999)
From an evolutionary perspective also important to classify mutualisms as vertically and horizontally transmitted.

Horizontal transmission

G₁

G₂

G₃

Conflict! Each mutualist should benefit most by cheating its partner ("tragedy of the commons")
What stops mutualists from cheating??


*Rhizobia* provide fixed N to host, and take resources from host (carbohydrate and O₂).

Individual host plants are colonized by multiple rhizobium genotypes

*Rhizobia* are *horizontally transmitted* (each new plant has to be infected by contact in the soil)
Kiers: test of ‘Sanctions hypothesis’: hosts are able to reward cooperation or punish cheating

Mostly difficult to test because most symbioses are hard to manipulate

Force rhizobia to cheat by replacing air (N₂:O₂ 80:20 v/v) with (Ar:O₂ 80:20 v/v). Apply gas mix to whole plants, half a plant or individual nodules

**Predictions**

*No sanctions from host*: predict higher growth and reproduction of *Rhizobia* receiving no N₂ (divert resources to own growth)

*Sanctions from host*: predict higher growth and reproduction of N₂ receiving nodules
Lower reproduction of rhizobia under zero N$_2$
(Note: *Rhizobia* are not directly N limited as they import N from the phloem)
Heath and Tiffin (2009) Test of the “partner-choice” hypothesis

Explored stability of a wild legume-rhizobium partnership

Compared growth and infection of different genotypes of *Medicago* infected with different strains of rhizobium

Positive correlation between fitness to the plant of particular rhizobium strains and the frequency with which they were infected by those strains.
Mycorrhizal associations: plant fungal associations influencing nutrient uptake (and more).

Often considered to be classical mutualisms because experiments show that both fungi and plants benefit from *reciprocal exchange of mineral and organic resources*… however can find positive, neutral or negative plant growth responses to infection: depends on ontogeny, environment, identity of fungus (Johnson et al. 1997)

Mostly horizontal transmission (orchid mycorrhiza is an exception)

Stability is enforced by a ‘biological market’ – each mutualist can reward those that provide the ‘best exchange’ (Kiers et al. 2011)
Mycorrhizal mutualisms are important from a community ecology perspective because they influence nutrient uptake in nearly all higher plants.

**Ectotrophic/sheathing mycorrhiza:**
Very common among temperate forest trees.

![Image of mycorrhizal structures]

Outer sheath of hyphal strands and intercellular network of hyphae

Cells of host not normally penetrated.

Fungi = Agricales and Russales
Only about 3% of higher plants, but ecologically important ones
Endotrophic mycorrhizas

More diverse than ectomycorrhizas and common on fertile soils
3 types: Vesicular-arbuscular (AMF), ericoid and orchidaceous

AMF
Intracellular hyphal network

4 Genera of fungi (Zygomycotina)
*Glomus*, *Gigaspora*, *Acaulospora*, *Sclerocystis*
How much exchange?

*Carbon*
4-20 % of plants total C budget goes to mycorrhizas

*Nutrients*
Estimated that AMF can deliver up to 80 % of plants P and 25 % of plants N (perhaps more)

AMF communities not particularly diverse <50 species at a single site?

A single fungus can infect a wide variety of hosts therefore specificity is low…
Benefits of AMF vary. Trade-off between competitive ability of a mycorrhizal fungus (AMF) and benefit to the host.

Scutellospora calospora is strongest competitor colonizing roots of Plantago but gives no benefit to host.

Presence of particular AMF could therefore significantly affect plant performance.
Mycorrhizas: The wood-wide web!

Simard et al. (1997)
Used reciprocal labeling with $^{13}$C and $^{14}$C to examine potential transfer of carbon between ectomycorrhizal birch (*Betula papyrifera*) and Douglas fir (*Pseudotsuga menziesii*)

*Plant trees together with AM tree species arbor vitae (Thuja)*

2 growing seasons

Expose replicates to 3 light treatments (full sun, partial shade, full shade)
Experiment: $^{13}\text{CO}_2$ and $^{14}\text{CO}_2$ given to either birch or fir. Followed movement of isotopes over next 9 days

Results:

Year 1: Movement, but no net transfer

Year 2: Strong net transfer to fir from birch depending on light environment. Deeply shaded plants received 10% of total isotope fixed; partially shaded received 5%; full sun 4%.

13% of isotope received by fir retranslocated from roots to foliage

Very little transfer to AMF plant (arbor vitae) - indicates that transfer occurred through the ectomycorrhizal hyphal net.
Other studies have shown translocation of nitrogen from N-fixing plants of similar magnitude through ectomycorrhizas (e.g. Arnebrandt 1993) and of carbon between canopy and understory plants (e.g. Booth 2004), and carbon from adults to seedlings of the same species (McGuire 2007)

More recent papers suggest similar hyphal networks facilitate carbon fluxes between AMF species, but results still controversial (Bever et al. 2011, Walder et al. 2012).
Carey et al. (2004) Mycorrhizal transfer of carbon from a native grass to an invasive weed

Spotted knapweed, *Centaurea maculosa*, is an invasive species in native prairie in NW USA dominated by native bunchgrass *Festuca*
Grew *Centaurea*, *Festuca* and a C4 species together +/- AMF

Found that growth of *Centaurea* greatest in presence of *Festuca*

*Figure 1.* Total plant mass of *Centaurea maculosa* grown in competition with either *Bouteloua gracilis* or *Festuca idahoensis* and with or without arbuscular-mycorrhizal (AM) fungi. Different letters indicate differences between means (P < 0.05). Each bar is the mean (± 1SE) of 12 plants.
Argue that *Centaurea* benefits from presence of *Festuca* through a link for C transfer through the AM fungi:

- Increased growth of *Centaurea* + AM and + *Festuca*
- Carbon isotope ratio of *Centaurea* more like that of *Festuca* when *Festuca* present, but only +AM
- Increase in *Centaurea* biomass accompanied by decrease in photosynthetic rate for same plants
Conclusions – Mutualisms Part 1

Little theoretical treatment of how mutualisms influence species coexistence (cf predation, competition)

Most mutualisms are horizontally transferred, which can result in large variation in the benefits provided by individual associates. Benefits can be context-dependent

In turn, variation in benefits can influence community dynamics if performance is tied to mutualist identity (e.g., plant growth and AMF identity)

Common mycorrhizal networks may also link plants together altering competitive interactions