Defense and dispersal mutualisms

*Cecropia peltata*  
wattled bellbird
Mutualism review

• Mutually beneficial associations of species (reciprocal parasitism). Benefits of the interaction tend to be context-dependent.

• Horizontally transmitted (partners find each other each generation)

• Vertically transmitted (partnership is inherited from previous generation)
Defense mutualisms

- Many examples of insect-plant defensive mutualisms. Particularly common for fast-growing plant species of high light environments.

- Plant-fungal mutualisms are much more widespread and important, but are much less conspicuous and therefore poorly studied.
Cecropia (Urticaceae)
Neotropics (61 spp)
- Hollow stems inhabited by Azteca ant species
  - prostomata (thin wall)
  - Glycogen rich food bodies (Mullerian bodies) produced at petiole base

Macaranga (Euphorbiaceae)
South East Asia (~300 spp)
- Obligate relationship?
  Crematogaster ants live in hollow stems
  - prostomata (thin wall)
  - Beccarian bodies produced on leaves and stipules
Cecropia prostomata and mullerian bodies
Bull-horn *Acacia* species (Americas, Africa)

*Pseudomyrmex* ants (in central America)

Obligate mutualism?

Ant acacias lack alkaloid defenses present in species lacking ant mutualists

Ants are extremely aggressive predators
Ant-wasp commensalism?
Many other plants have extra-floral nectaries to feed ants
How context-dependent are ant-plant defensive mutualisms?

Chamberlain and Holland (2009) – meta-analysis of the generality of ant effects on herbivory and plant performance.

Effect size describes the magnitude and 95% CI of the difference in treatments (+ or – ants) for different classes of ant mutualisms. Effect is significant when CI does not cross 0.

(see Harrison (2010) “Getting started with meta-analysis”)

![Graph showing effect size of ants on herbivory and plant performance]
Little evidence for context dependency in Chamberlain and Holland analysis

Small latitudinal decline in effect size due to loss of ant plants with domatia outside the tropics
Ant mutualists can also reduce competition.
Tococa shrubs have domatia and provide food bodies for Myrmelachista ants (Morawetz et al. 1992, Renner and Ricklefs 1998)

Ants kill insect herbivores and competing plants!

Tococa grows clonally and is able to form large patches (up to 30 m diameter) completely free of other plant species

Figure 2. Diagrammatic representation of a well developed *T. occidentalis* population and the surrounding forest. To = *T. occidentalis*; s = safety corridor; ma = Maranthaceae.
Seedlings turned to mush in 3 hours!!!!
Duroia hirsuta: The King in the Devil’s garden
Ants not evil spirits create devil’s gardens
(Fredrickson et al. 2005; Nature)

1. Seedlings placed in devil’s gardens
2. In garden; ants excluded
3. No garden; ant exposed
4. No garden; ants excluded

Leaf necrosis
Leaf shedding

![Bar graph showing leaf necrosis and leaf shedding across different treatments.](image)
Why don’t the devil gardens take over?

Although ants reduce competition, they do not reduce herbivory. Fredrickson and Gordon (2007)

More herbivory on *Duroia* in gardens than outside gardens even without the ants.
Endophytic fungi as mutualists

Endophytes = *fungi that inhabit plant parts without causing disease*

Present in all plant species examined: liverworts -> angiosperms

Endophytes are mega-diverse in the tropics:

Arnold et al (2000) isolated 347 distinct genetic taxa of endophytes from 83 leaves from 2 tropical tree species… >50 % of taxa were only collected once...

What are they doing in there???
Most endophytic fungi are horizontally transmitted

Arnold (2003)

Looked at endophytes associated with cacao plants (*Theobroma cacao*)

- Endophytes are *horizontally* transmitted (acquired through the life time of the leaf)

Arnold was able to grow endophytes in the lab and then use them as an inoculum source to infect sterile (uninfected) leaves.
Black pod disease of cacao caused by infection by *Phytophthora capsici*

Black pod and witches broom (a fungal disease) has led to large declines in cacao production

Our chocolate supply is in danger!!!
Asked: Are endophytes effective in protecting cacao plants against pathogens?

Compared incidence of foliar pathogen damage and leaf mortality in cacao plants +/- endophytes and +/- a foliar pathogen *Phytophthora* an important pathogen of cacao (‘black pod’)

A cocktail of 7 endophyte spp applied to leaves significantly reduced severity of pathogen damage
Clay and Holah (1999) Looked at an endophyte in a successional field community

*Neotyphodium coenophialum* is an endophytic fungus that grows intercellularly through Tall Fescue (*Festuca arundinacea*). Fungus is host-specific and *vertically* transmitted with seeds.

Infected plants are more vigorous, more drought resistant than uninfected plants, and TOXIC (cattle and horse poisoning).

Tall Fescue is a European grass introduced to N. America. Becomes dominant in pastures it invades.
In Indiana established 8 plots (20 x 20 m) mown and cleared, sown with infected (+E) or uninfected (-E) Fescue. Grassland community established composed of Fescue and other spp germinated from seed bank.

Species diversity declined in +E plots overtime relative to -E plots, 6 species were restricted to -E plots after 3 yr
Gallery et al. (2007) Endophytic fungi may also protect seeds against pathogens
Freeman and Rodriguez (1993): The heart-warming tale of a reformed pathogen...

Notorious filamentous fungal pathogen: *Colletotrichum magna* wanted for causing anthracnose disease in cucurbit plants.

Member of a large group of pathogens capable of infecting the majority of agricultural crops worldwide

Infection occurs when spores adhere to host tissue, enter a cell and subsequently grow through the host leaving a trail of necrotic tissue. Plants die within a week.
*path-1*: a single locus mutant of the wild type of *C. magna* infects the host and spreads (albeit more slowly) through out the host without killing it and without necrosis. *path-1* does not sporulate and lives as an endophyte

Plants infected with *path-1* were subsequently protected from disease symptoms produced by the wild-type, and were immune to disease caused by an unrelated pathogenic fungus, *Fusarium oxysporum*

A single gene *sakA* also switches *Festuca* endophyte to a pathogen. Are endophytes attenuated pathogens?
Eaton et al. (2010) Looked at *Festuca* endophyte system of Clay

Single gene sakA in endophyte switches interaction from mutualistic to pathogenic

- Changes in host morphology
- Large downstream changes in transcriptome of fungus and host
- Hydrolytic enzyme production in fungus
- Upregulation of pathogen defenses in the host.

Considerable potential to tailor endophytes as biocontrol agents?

Transport Mutualisms

Pollinator mutualisms:

Wind pollination is quite restricted (prevalent in grasses).

Benefits to pollinators include pollen, nectar, fragrances (Euglossine bees), oviposition site and food supply for larvae

Pollination mutualisms could be significant to community structure if pollination limitation occurs.

Some evidence that certain groups are pollen limited: ephemeral spring flowers in eastern USA (Motten 1983)
Competition for pollinators can be sufficiently intense to drive character displacement in plants (Smith and Rausher 2008).

When two morning glory vine species grow together, selection drives tighter clustering of stamens of *Ipomoea purpurea*. Clustering increases self-pollination rate, which may increase seed production if pollinators are scarce or if most pollen is from the competing species.

*Ipomoea* (morning glory)
Competition for dispersers is often intense

“Dispersal limitation” is an important mechanism structuring plant communities. Plants cannot disperse their seeds everywhere - either too few seeds or too few dispersers…

Most plants use many dispersers. Mutualisms are diffuse. Although dispersal ‘syndromes’ recognized (flower and fruit characteristics predictive of the principle taxa of pollinators or dispersers), predictive power is weak.

A few traits are somewhat predictive (colour, size, scent) of guilds of pollinators/seed dispersers
*Ficus* spp and fig wasps (Agaonidae) (Herre 1996)

Fig inflorescence = synconium

Individual flowers are on the inside

Female wasp enters the fig carrying pollen deposited on some flowers in the fig

Wasp also lays eggs on a proportion of the flowers in the fig. The developing wasps induce galls which nourish larval development.
Phenomenally complicated system:
Tight coevolution: single wasp species per fig species.

Pollination mutualism (wasps get food for development, fig gets extraordinarily effective pollinator - gene flow >100 km)  
(Nason et al. 1998)

Mutualism costs:  
Provisioning of larval development (seed losses)  
Maintaining fig temperature optimal for wasp development (Herre and West 1997)

Mutualism conflict: production of fig seeds and fig wasps are negatively correlated. How is it stabilized?
Mutualisms – summary

Represent reciprocal parasitism or exploitation

Consequences for community function/diversity are poorly understood.

Maintenance of mutualisms may dependent on environmental conditions (resource supply rates), and in horizontally transmitted mutualisms may switch from beneficial to antagonistic.

Horizontally transmitted mutualisms are inherently unstable, but can be stabilized by sanctions and partner choice (where one partner controls the mutualism) or by ‘biological markets’ (or ‘trading partnerships’).