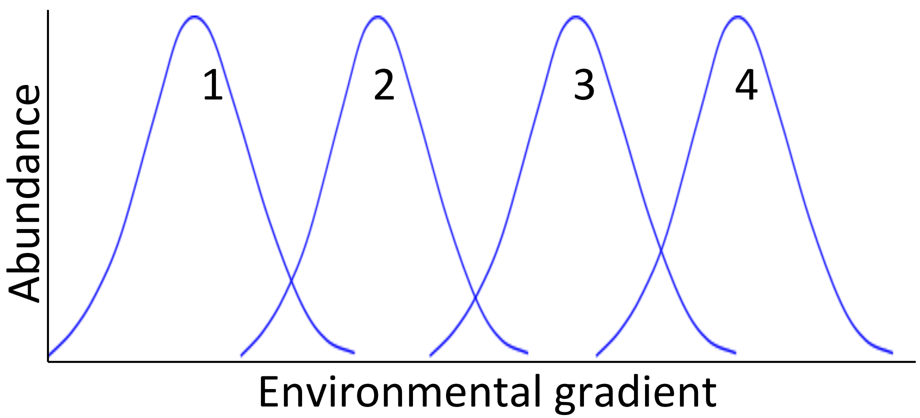
Species interactions and coevolution in the tropics

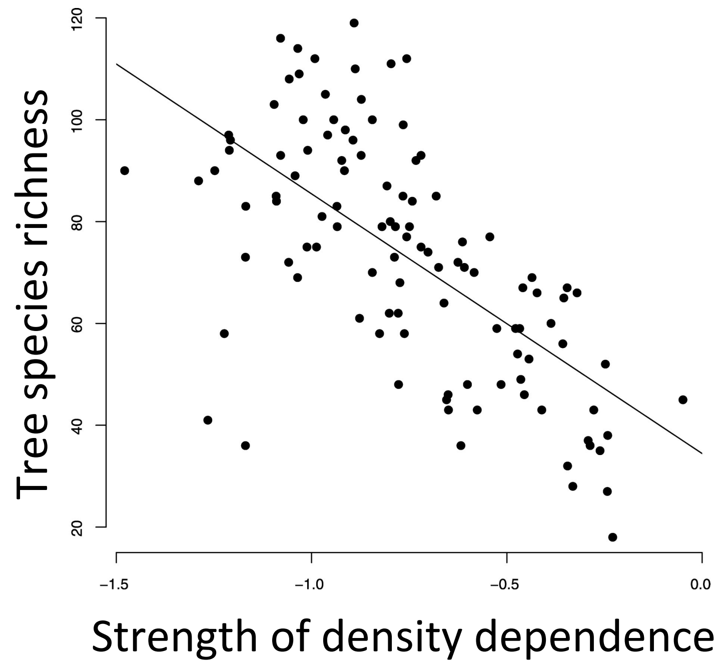
Niche partitioning
Seed shadows and animal dispersal
Seed dispersal and fruit
Pollination by animal vectors

Complex species interactions are a trademark of tropical systems

Niche partitioning

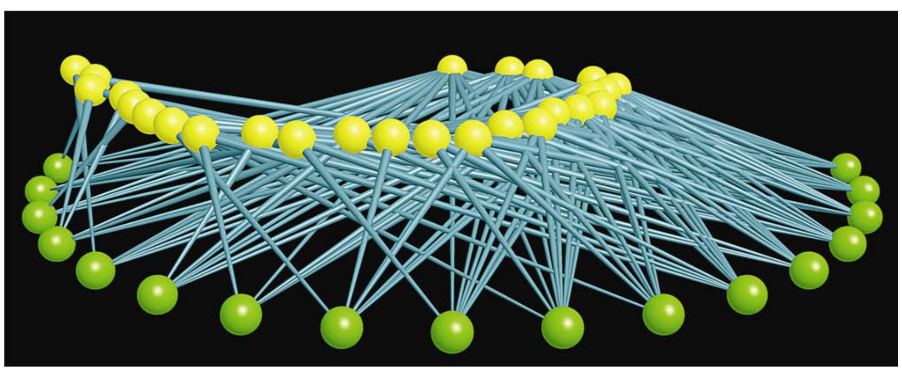


Negative density dependence



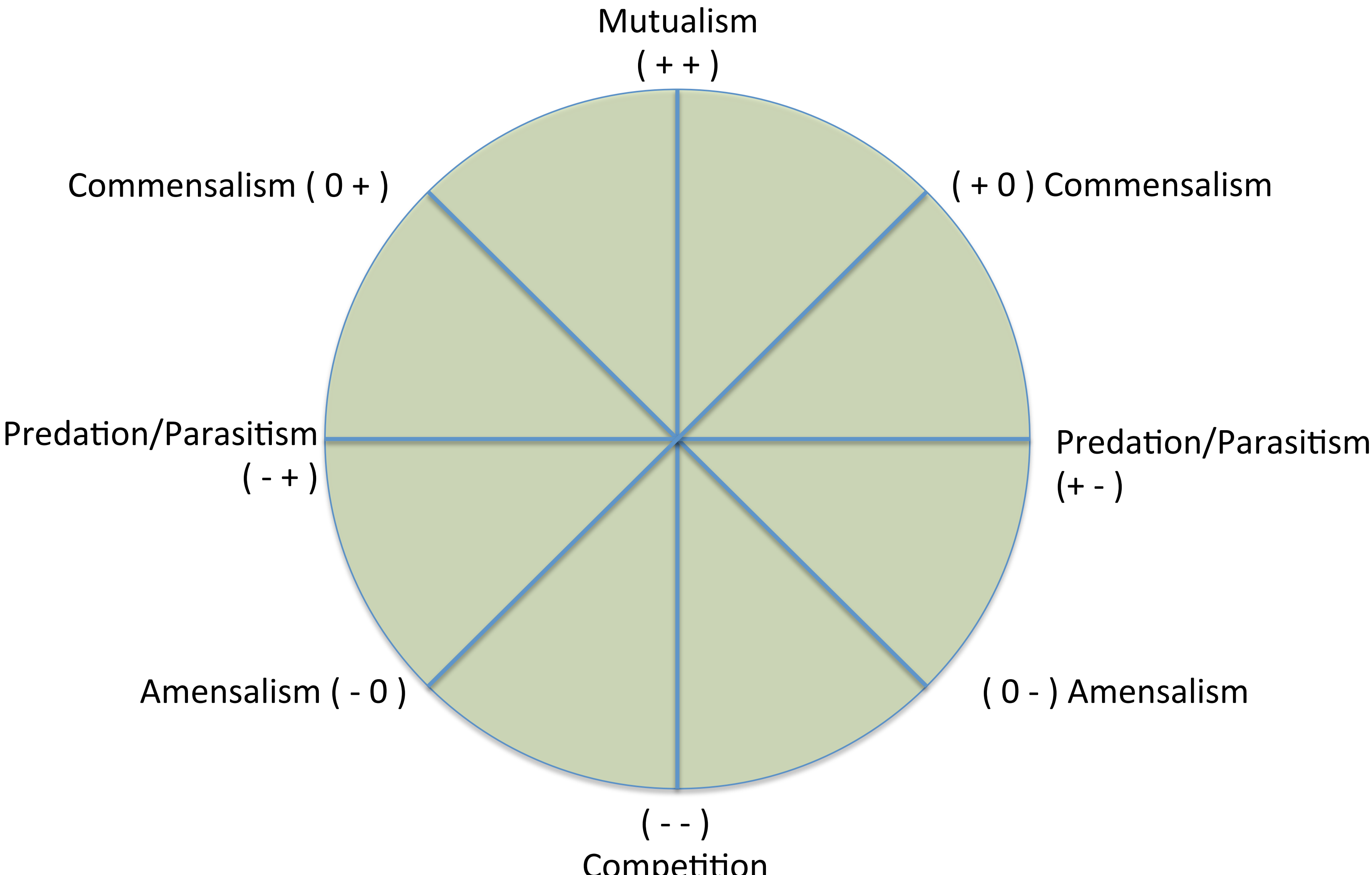
Johnson et al. 2012 *Science*

Coevolution & mutualisms



Plant – animal pollination network

Biotic interactions vary in the direction of interspecific effects



Niche partitioning minimizes interspecific competition

Some species are restricted to special habitat types

Others use different parts of the vertical column of vegetation from the ground to canopy

Species that overlap differ significantly in body size (species partition fruit resources by size)

Sympatric species of African ground squirrel

African giant

Lady Burton’s rope

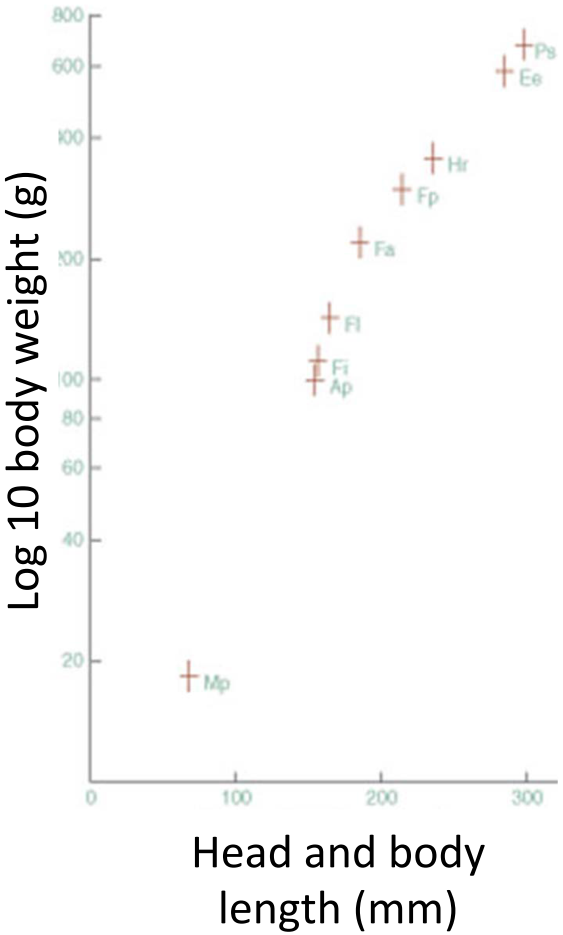
Red-legged sun

Ribboned rope

Thomas’s rope

Western palm

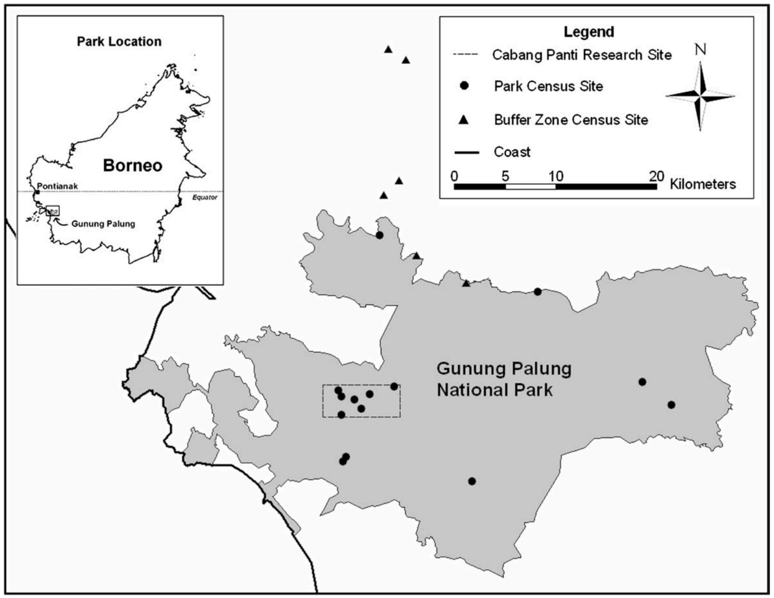
Niche partitioning minimizes interspecific competition



Size distribution of nine squirrel species

SPECIES	HABITAT TYPE	VEGETATION HEIGHT	BODY SIZE	FOOD TYPE	ACTIVE PERIOD
M. pumilio	Mature and disturbed forest	Arboreal	Tiny	Bark scrapings	Long
A. poensis			Small	Some diverse arthropods	Long
H. rufobrachium			Medium		Short
P. stangeri			Large	Hard nuts	
F. lemniscatus		Ground foraging	Small	Many termites	Long
F. pyrrhopus			Medium		Short
E. ebii			Large	Hard nuts, few arthropods	
F. isabella	Dense growth	Lower levels	Small	Leaves, diverse arthropods	Long
F. anerythrus	Flooded forest	All levels	Medium	Many ants	Long

Revisiting negative density dependence

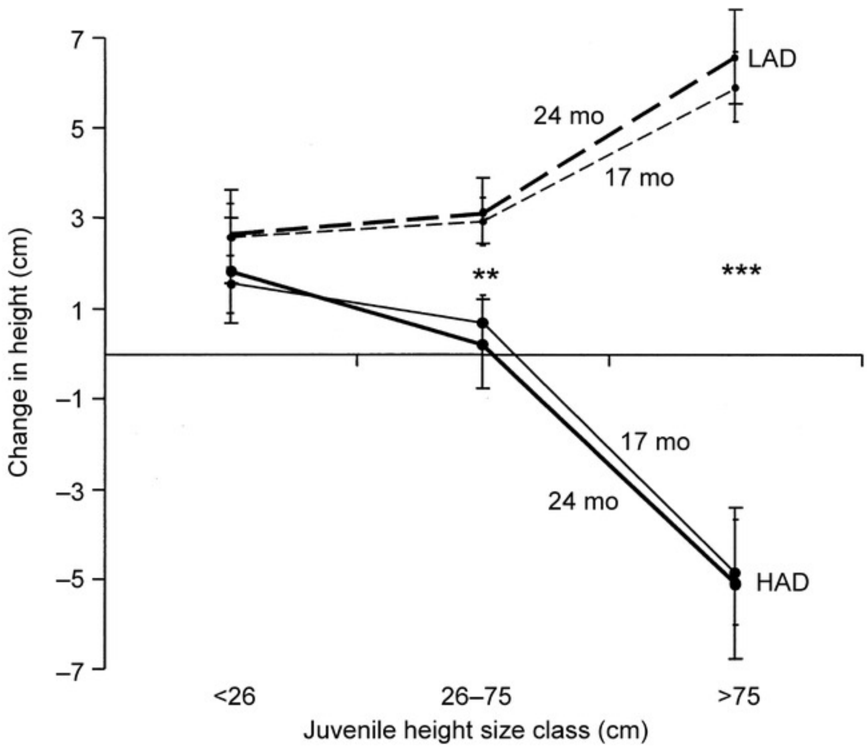


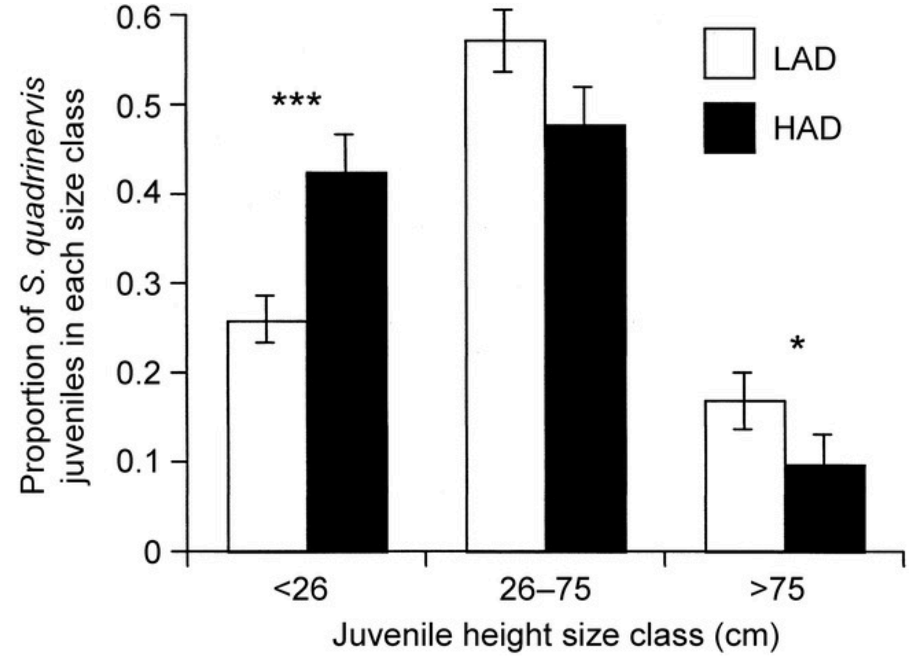
Dipterocarps are the most species rich trees of Southeast Asian tropical forest

Study of *Sorea quadrinervis*, a dominant species of Dipterocarp in Borneo, revealed strong negative density dependence

357 adult trees and 5215 juvenile trees were mapped in areas with High Adult Densities (HAD) and Low Adult Density (LAD)

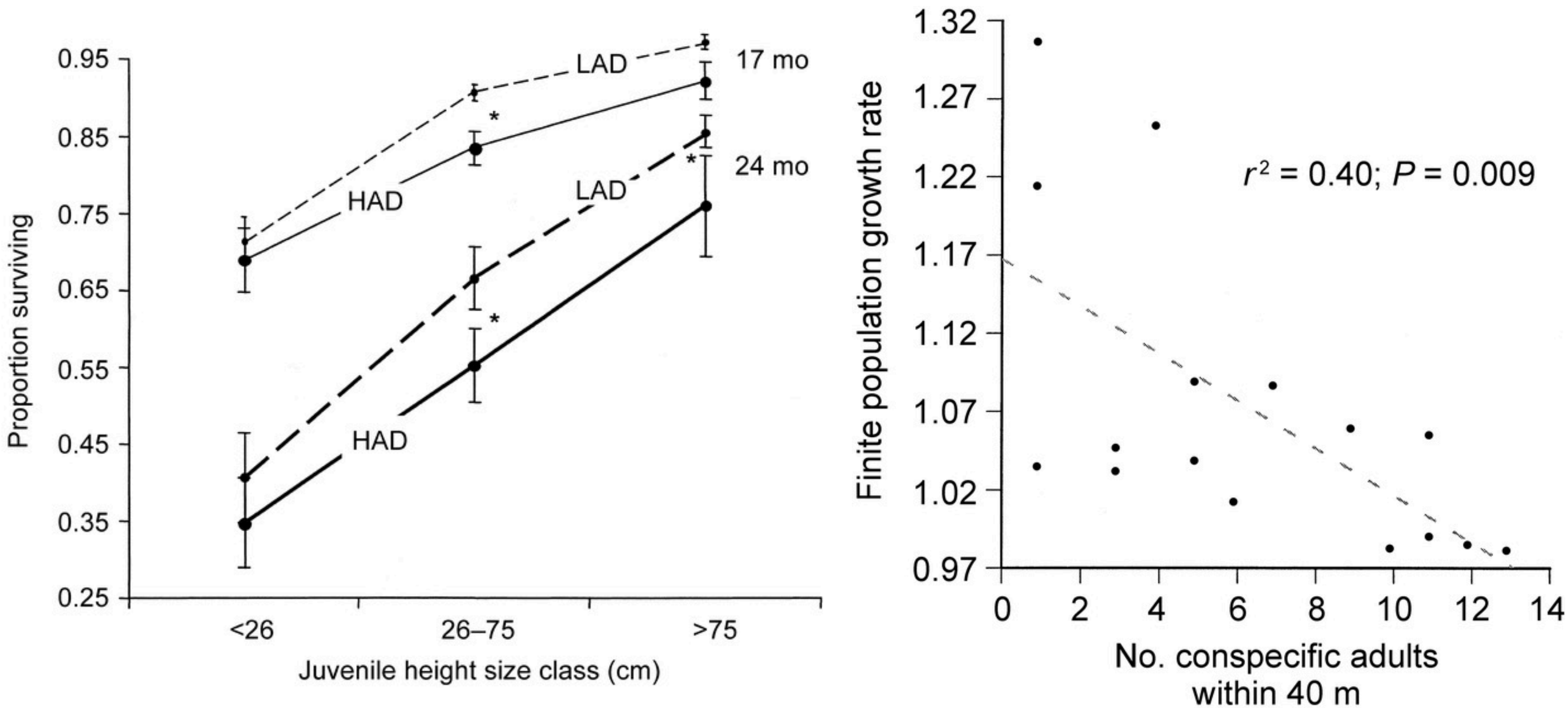
Revisiting negative density dependence





HAD areas had reduced growth in juveniles and a higher number of juveniles in the smallest size class compared to LAD areas

Revisiting negative density dependence



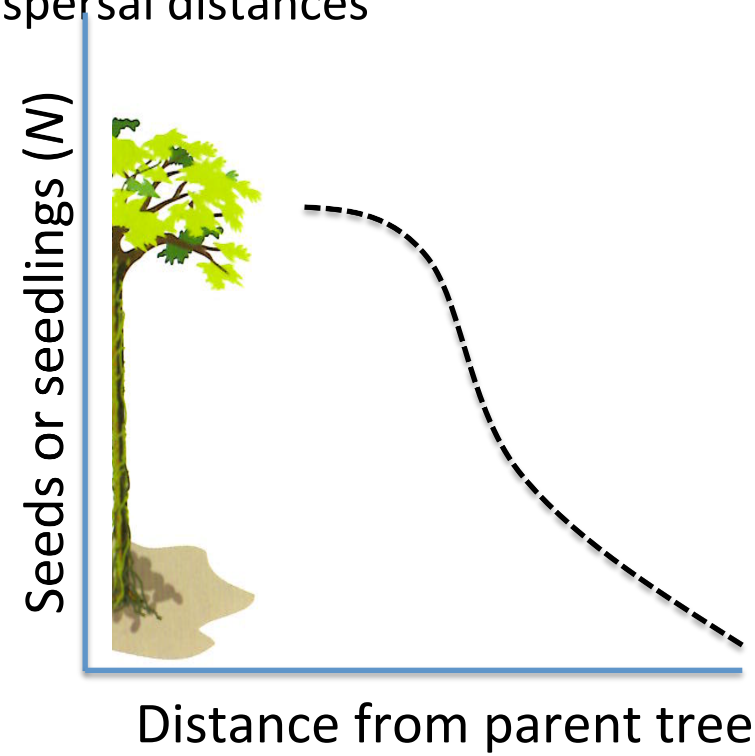
Juveniles in HAD areas were shorter, grew less, had fewer leaves and lower survival than in LAD areas

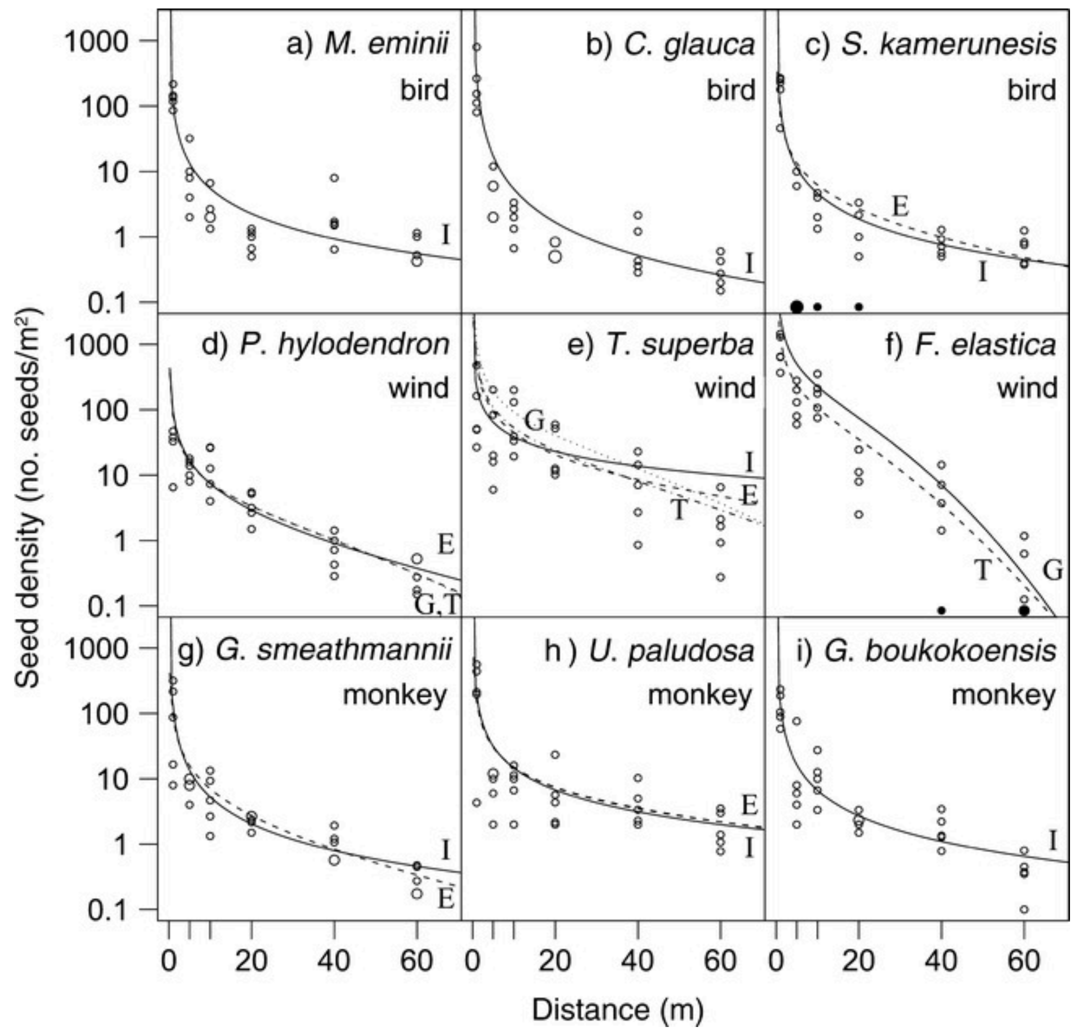
Seed shadows and animal dispersal

Seed shadow effect (Janzen 1970):

Seed density drops sharply with distance from the parent tree

Clark et al. 2005 found that animal-dispersed species have longer mean dispersal distances





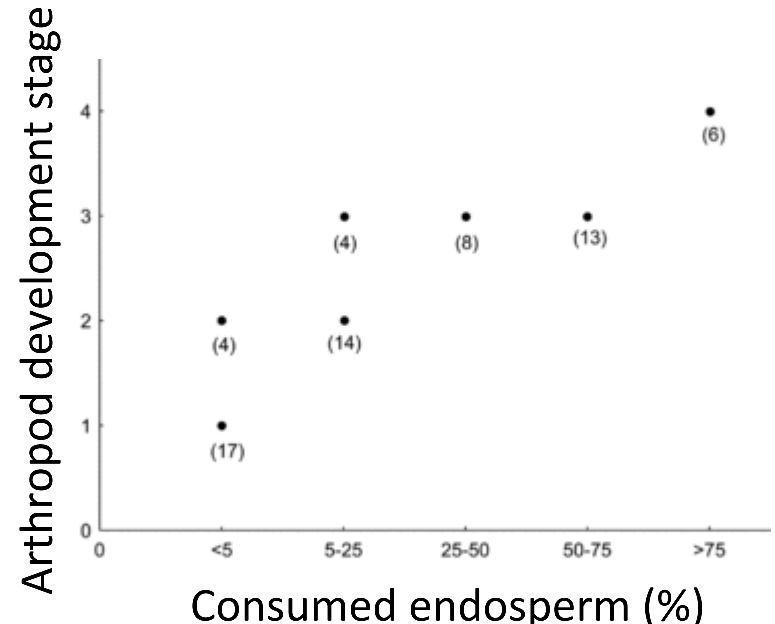
Clark et al. 2005, *Ecology*

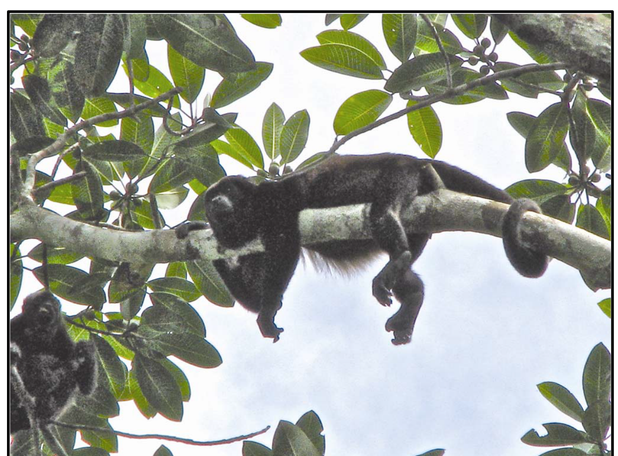
Ingestion of fruits affects seed germination

Fruits from trees are often infested with insects

As insects develop, they consume the seed endosperm, which can prevent germination

Digestion of *Ocotea diospyrifolia* by black howler monkeys kills insect larvae and increases potential for germination

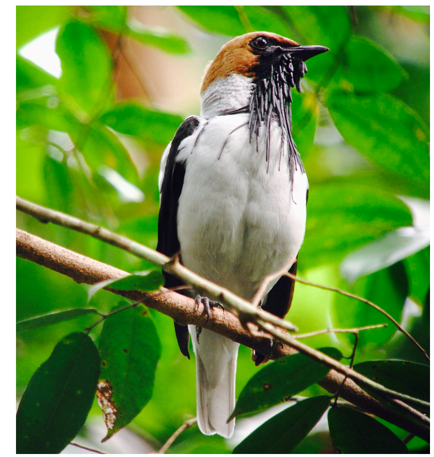




Frugivory and the importance of fruit in the tropics

Entire families of birds depend on fruits



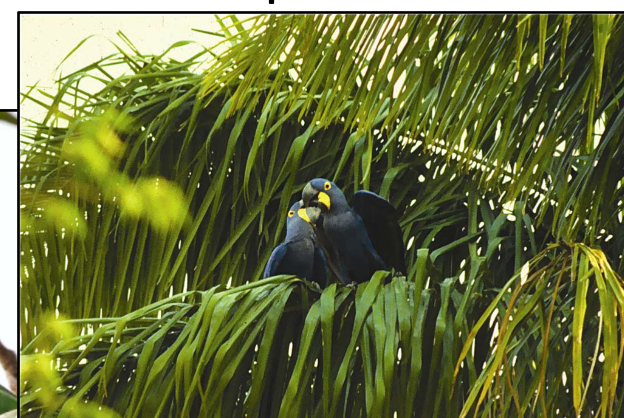



Frugivory and the importance of fruit in the tropics

The evolutionary function of fruit is to be consumed – to advertise itself so it is eaten

Animals derive nutrition from the fruit, and also disperses the seeds – a fundamentally mutualistic relationship

Other species (e.g., parrots), however, digest the seed as well as the fruit, and it does not germinate – these are *seed predators*



Frugivory and the importance of fruit in the tropics

Fruit influences evolutionary patterns in birds

- Fruit may be abundant on a single tree, but trees laden with fruits may be widely spaced

- The temporal and spatial patchiness of this resource selects for social behavior, rather than territoriality

- Fruiting trees are not easy to defend, but resources are locally concentrated and highly available

Frugivory and the importance of fruit in the tropics

Fruit influences evolutionary patterns in birds

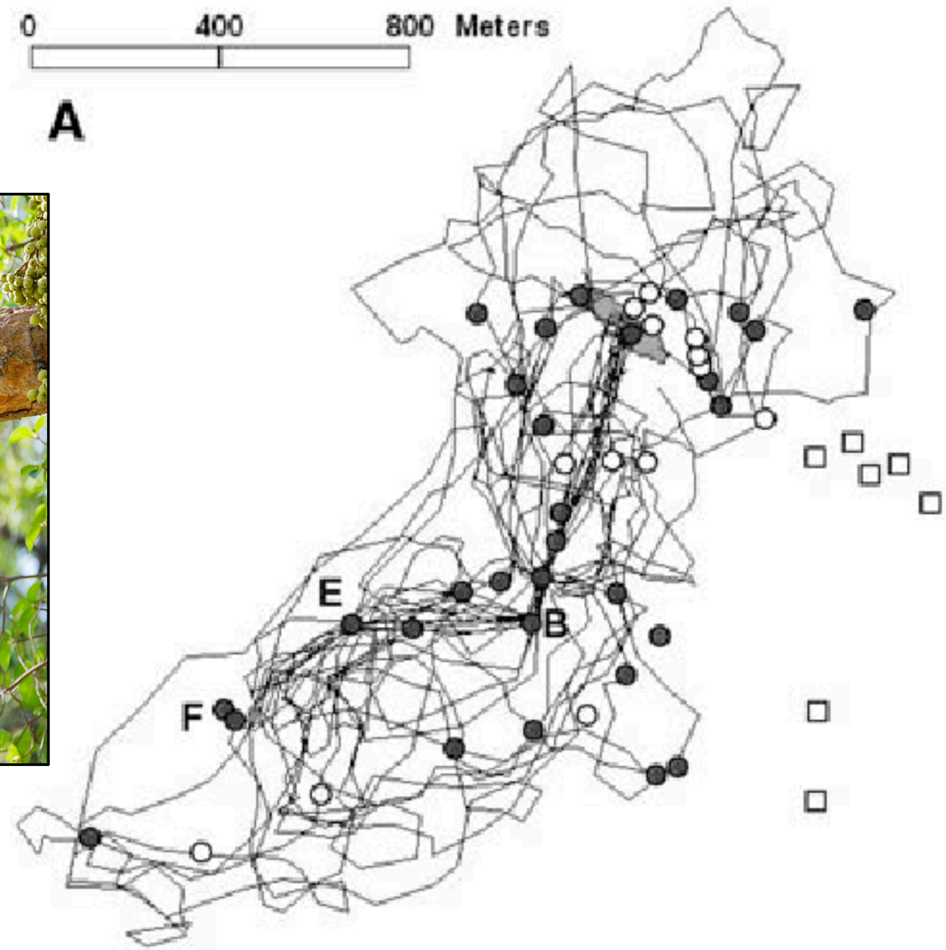
Purple-throated fruit-crows live in communal groups that roam in search of preferred species of fruiting trees.

Group members cooperate in feeding nestling Nests are vigorously defended by the group.

Because fruits are not limiting, there is little competition among the birds, which could have promoted their social organization

Frugivory and the importance of fruit in the tropics

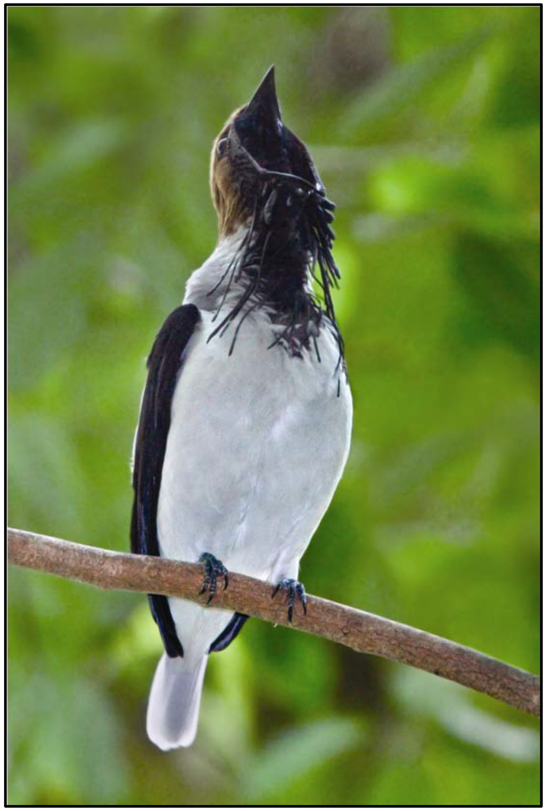
Routes by Wild Chacma Baboons visiting fig trees



Noser & Byrne 2010

Frugivory and the importance of fruit in the tropics

How does fruit influence evolutionary patterns in birds?



Because fruits are generally easy to locate, with little 'capture' effort, frugivorous birds have more 'free time'

E.g., the male bearded bellbird (*Procnias averano*) is entirely frugivorous and spends 87% of its time on a perch calling to females to mate

Frugivory and the importance of fruit in the tropics

How does fruit influence evolutionary patterns in birds?



Because fruits are generally easy to locate, with little 'capture' effort, frugivorous birds have more 'free time'

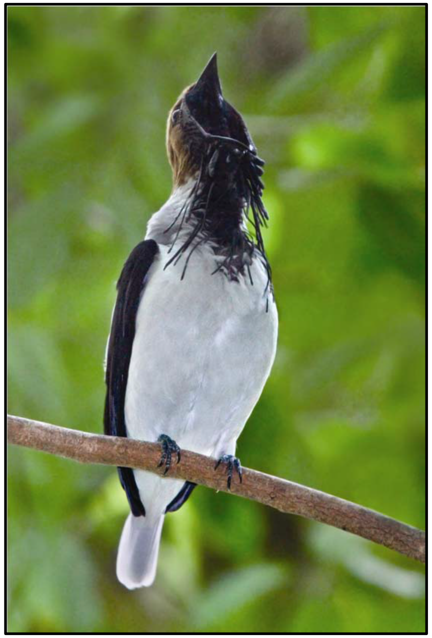
E.g., manakins can spend 90% of their day courting females and displaying (see moonwalking manakin)

Are fruits the evolutionary stimulus for social behaviors and sexual selection?

Bearded bellbird: https://www.youtube.com/watch?v=TKgKe24-_G4

Three-wattled bellbird: https://www.youtube.com/watch?v=nnZD3-DJaIQ

Lance-tailed manakin: https://www.youtube.com/watch?v=F9BeTLoDwRw



Frugivory and the importance of fruit in the tropics

How does fruit influence evolutionary patterns in birds?

Frugivorous birds are more locally abundant compared to territorial insectivorous species due to abundance and distribution of resources

The ochre-bellied flycatcher is a flycatcher that now feeds almost exclusively on fruit and has leks for mating – also the most abundant forest flycatcher in lowland forest.

Frugivory and the importance of fruit in the tropics

High biomass of frugivorous birds and mammal species in lowland humid forest (e.g., peccaries, coatimundis, flying foxes)

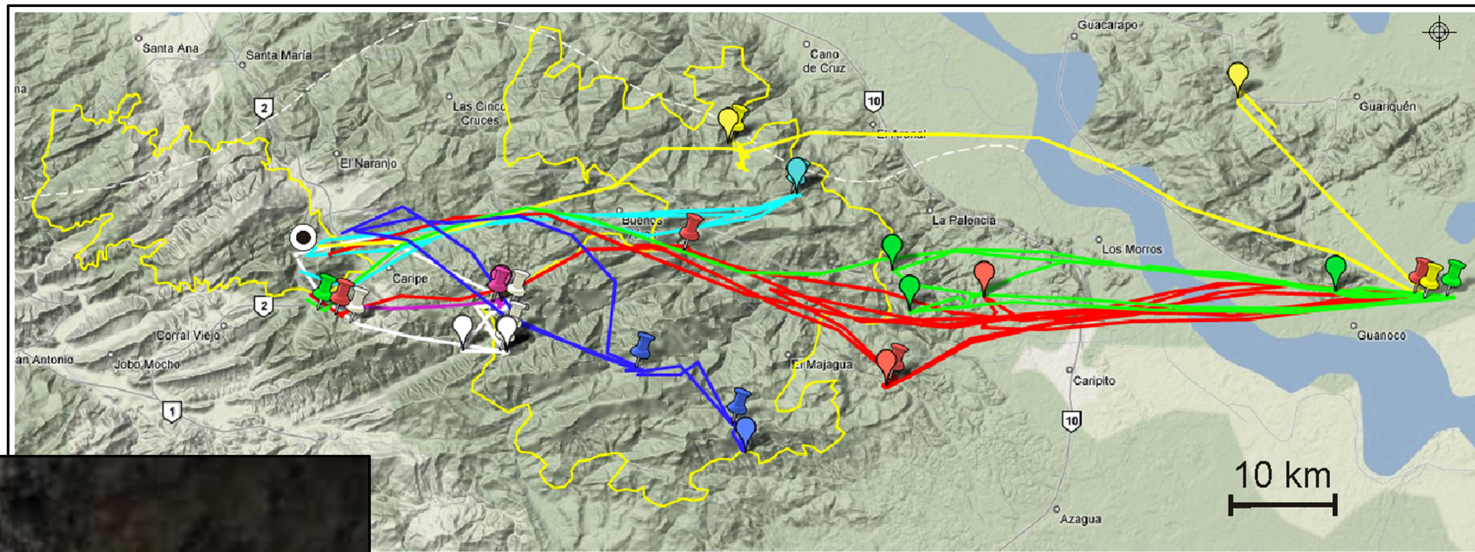
Distribution and defendability of resources favor different social systems and sexual selection pressures

Frugivorous species serve as important seed dispersers of various plant species, utilizing the nutritional rewards offered by fruits

Frugivory in the tropics – revisiting the unique oilbird

The nocturnal oilbird (*Steatornis caripensis*) is a specialist frugivore that consumes fruits from the oil palm and species in the family Lauraceae

Navigate by night using echolocation



Consume fruits high in lipids, though that in the past chicks were captured and boiled to make oil

Frugivory in the tropics – revisiting the unique oilbird

Oilbird cave in Trinidad

Once they hatch, juveniles fatten up on fruits but take a long time to develop due to nutrition imbalance (may outweigh parents by 1.5 times!)

Extended nestling period may have favored nesting in protected areas, like caves

Oilbird evolution (proposed by Snow 1976)

Time?

Insect diet → Fruit diet → Selects against territoriality

Vision – palms
Olfaction - laurels

Selects against territoriality → Larger development period before fledging → More highly conspicuous ground nests due to seed defacation

Fruit diet → Sociality

More highly conspicuous ground nests due to seed defacation → Sociality

More highly conspicuous ground nests due to seed defacation → Nest colonially in caves

Nest colonially in caves → Echolocation

Predator free

Nest colonially in caves → Large clutch sizes → 100 days from egg → Fledging

100 days from egg → Occupy cave and same nest all year (mating occurs for life?)

Frugivory in the tropics – revisiting the unique oilbird

Oilbird cave in Trinidad

Estimated that a colony regurgitated ~15 million seeds/ month, most of which are dispersed in forest

Important for maintaining plant species diversity and merit strict conservation measures, focusing on caves.

Oilbird evolution (proposed by Snow 1976)

Time?

Insect diet → Fruit diet → Selects against territoriality

Vision – palms
Olfaction - laurels

Selects against territoriality → Larger development period before fledging → More highly conspicuous ground nests due to seed defacation

Fruit diet → Sociality

More highly conspicuous ground nests due to seed defacation → Sociality

More highly conspicuous ground nests due to seed defacation → Nest colonially in caves

Predator free

Nest colonially in caves → Echolocation

Nest colonially in caves → Large clutch sizes → 100 days from egg → Fledging

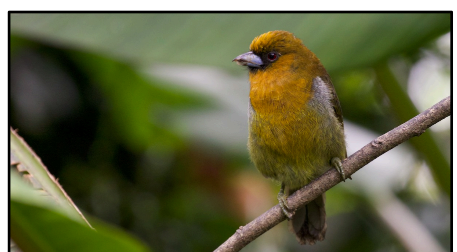
100 days from egg → Occupy cave and same nest all year (mating occurs for life?)

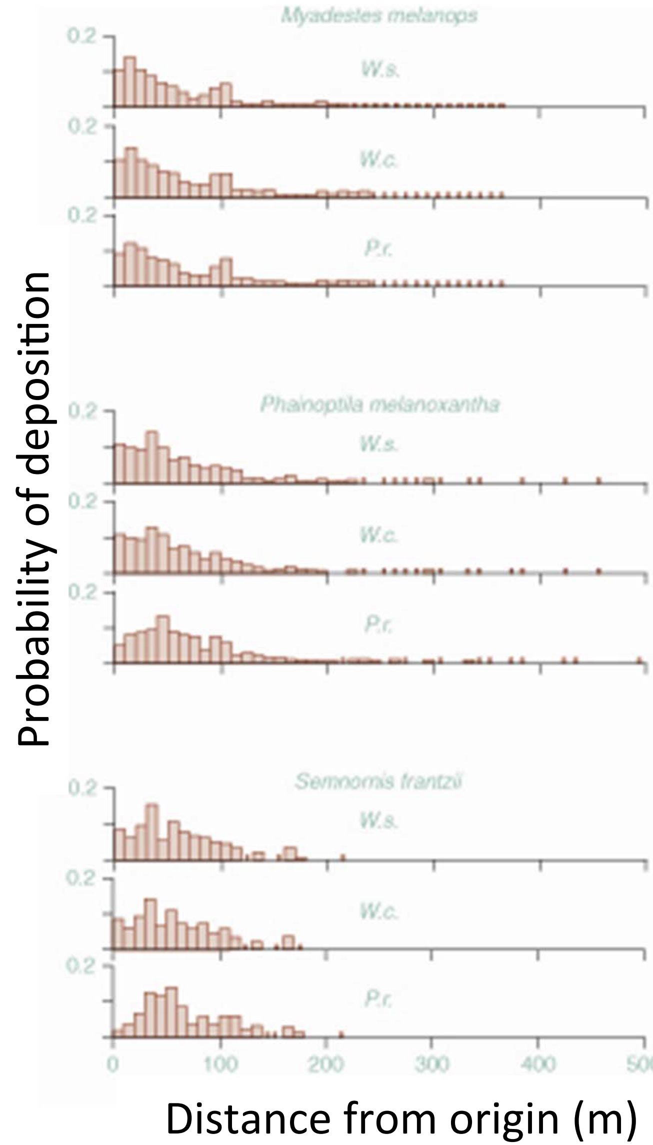
Dispersal distance from origin by different frugivorous species

Some frugivores are more effective at dispersing seeds far from the parent tree

Depends largely on foraging behavior and mobility of species

Fruit represents an important resource for a large component of the community, but only a subset of these frugivores may serve as key dispersers for the plant species





Seed dispersal and facilitation of succession

Can exotic plants assist the reestablishment of forest?
A special case with guava (*Psidium guajava*)

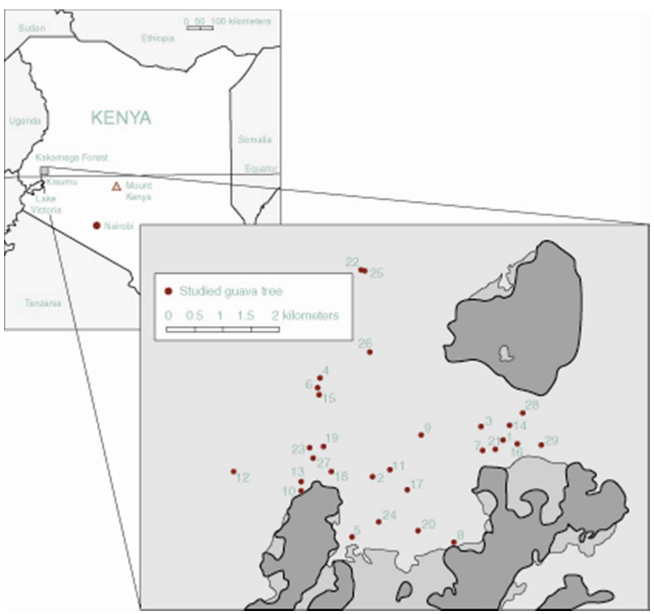
Common to the Neotropics, but has been widely introduced in Africa, Australia and the Pacific islands.

Usually invasive species are ecologically undesirable

Seed dispersal and facilitation of succession

Can exotic plants assist the reestablishment of forest?
A special case with guava (*Psidium guajava*)

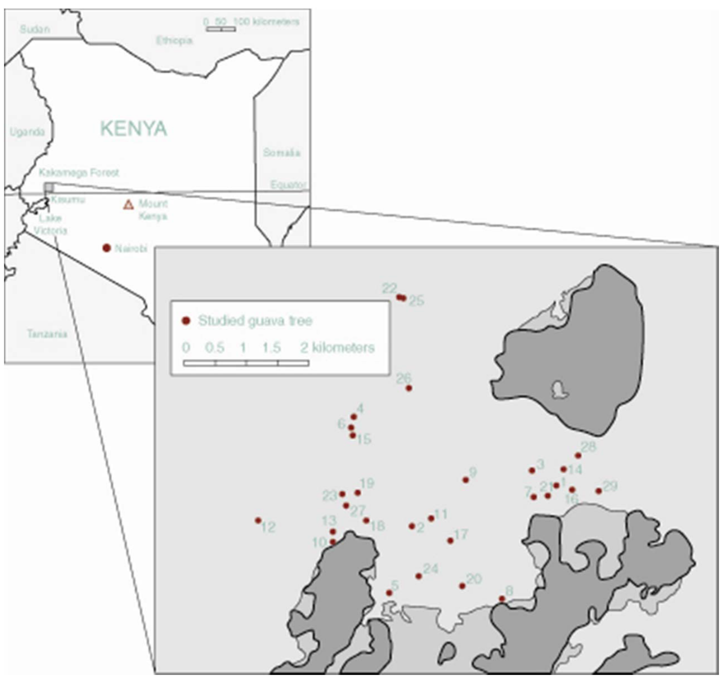
In Kenya, researchers studied the bird species feeding on 29 fruiting guava trees and examined the seed rain beneath the trees



Seed dispersal and facilitation of succession

In Kenya, researchers studied the bird species feeding on 29 fruiting guava trees and examined the seed rain beneath the trees

61 bird species fed from guava trees (attracting strong fliers like hornbills)



Seed rain included 12 other species that were bird dispersed

57% were late successional species

36% were early successional species

7% were exotics

Exotic guava trees act as food magnets for many frugivorous species; input of seeds from distant areas may facilitate regrowth of forest

Figure shows area of Kakamega Forest, Kenya, with location of 29 study trees in farmland between primary/secondary forest fragments

Fish: Seed dispersers in the Amazon

Floodplain forests (varzea) are periodically inundated by annual flood cycles (2-10 months of the year)

At least 2400 species of fish inhabit these waters (40% of those described belong to characins and catfish)

During flood cycles, fish have direct access to forest, and many consume fruits and seeds (flooding facilitates a frugivorous diet)

Tambaquis (left) and Amazon catfish (above) are among the most important seed dispersing fish in Amazon flooded forest

Tambaqui feed almost exclusively on fruits for the first five months of the flooding season

Fish: Seed dispersers in the Amazon

A study of two frugivorous species (Tambaqui and Pacu) showed that fruit made up 78-98% of the diet during the peak flood months, including 27 species of woody plants

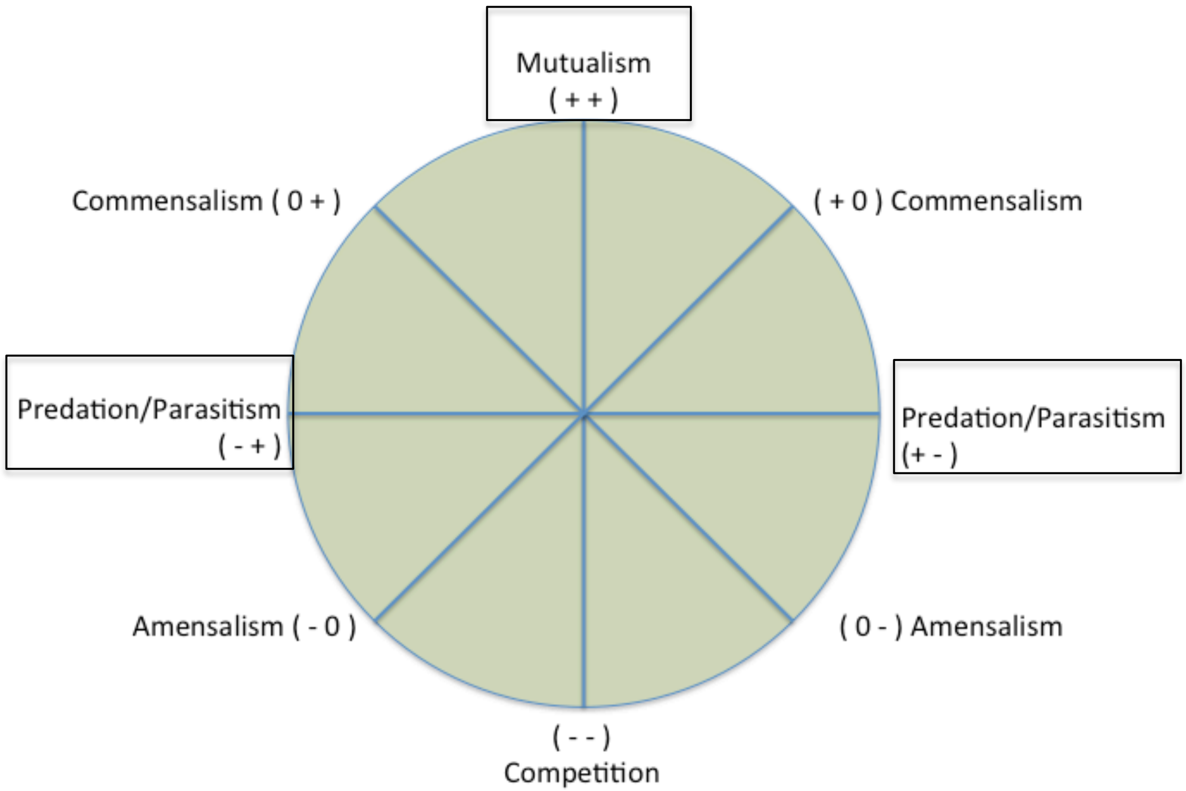
Abundance of fruit correlated closely with the flood cycle, facilitating access to fruits by fish

Pacus are routinely overfished, which could very negatively impact seed dispersal

Lucas (2008) *Biotropica*

Galetti et al. (2008) *Biotropica*

Biotic interactions are selection pressures that determine evolutionary directions



When one species exhibits a trait with a selection pressure on another species, and the second possesses a trait as a counter-selection pressure on the first, evolutionary fates can become permanently locked.

Pollination of plants is a widespread example of coevolution

This typically happens with reciprocal arms races in parasitic/predatory interactions, or when both species gain from the interaction (mutualisms)

Pollination by animal vectors

Many flowering plants depend upon insects, birds and bats for fertilization, and animals use nectar as a food source

Common in rainforests (often where wind pollination would be ineffective) in contrast to open savannas (where grasses and sedges are largely wind pollinated)

Pollination by animal vectors

Insects:	Birds (whole families):
Bees	Hummingbirds (332 species)
Flies	Sunbirds (127 species)
Beetles	Flowerpeckers (44 species)
Butterflies	Sugarbirds (2 species)
Moths	Honeyeaters (174 species)

Many insects move long distances, ensuring effective cross pollination (Euglossine bees, carpenter bees)

Coevolution and sexual dimorphism in a hummingbird species

In Purple-throated Caribs (*Eulampis jugularis*) males have shorter bills than females

On St. Lucia Island, there is coevolution between hummingbird sexes and the flowers they feed on

E. Jugularis is the only pollinator of two *Heliconia* species

Males feed on *H. caribaea*

Females feed on either *H. caribaea* or *H. bihai* (which has longer corollas)

Males exclude females from *H. caribaea* flowers

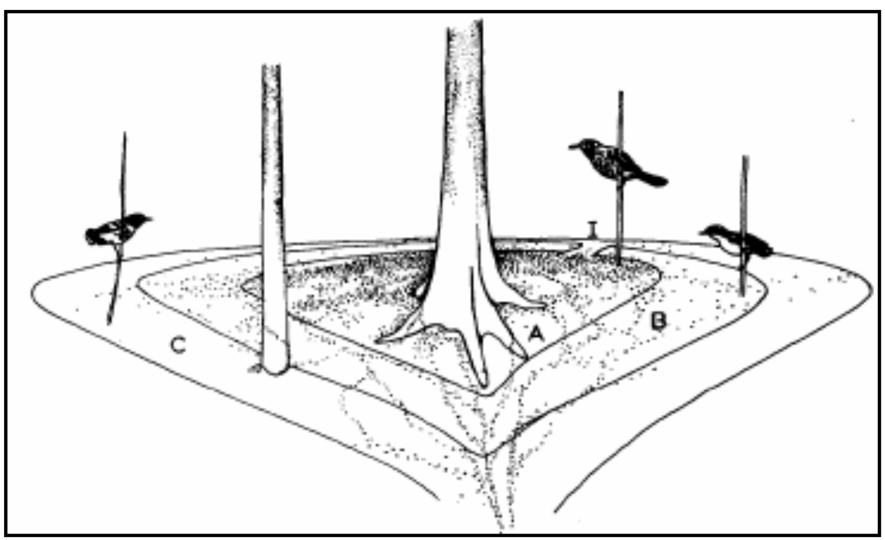
Pattern is switched on island of Dominica – *H. caribaea* has evolved yellow flowers and longer corollas, which female caribs feed from!

Coevolution in heterospecific social groups: mixed species flocks

Unlike mixed species flocks in the temperate zone, which are highly seasonal, flocks in the tropics form stable associations of individuals, with consistent membership over years

One proposed benefit of flocking is protection from predators:

Key species – "sentinels" – give alarm calls to alert other flock members



Willis & Oniki 1978

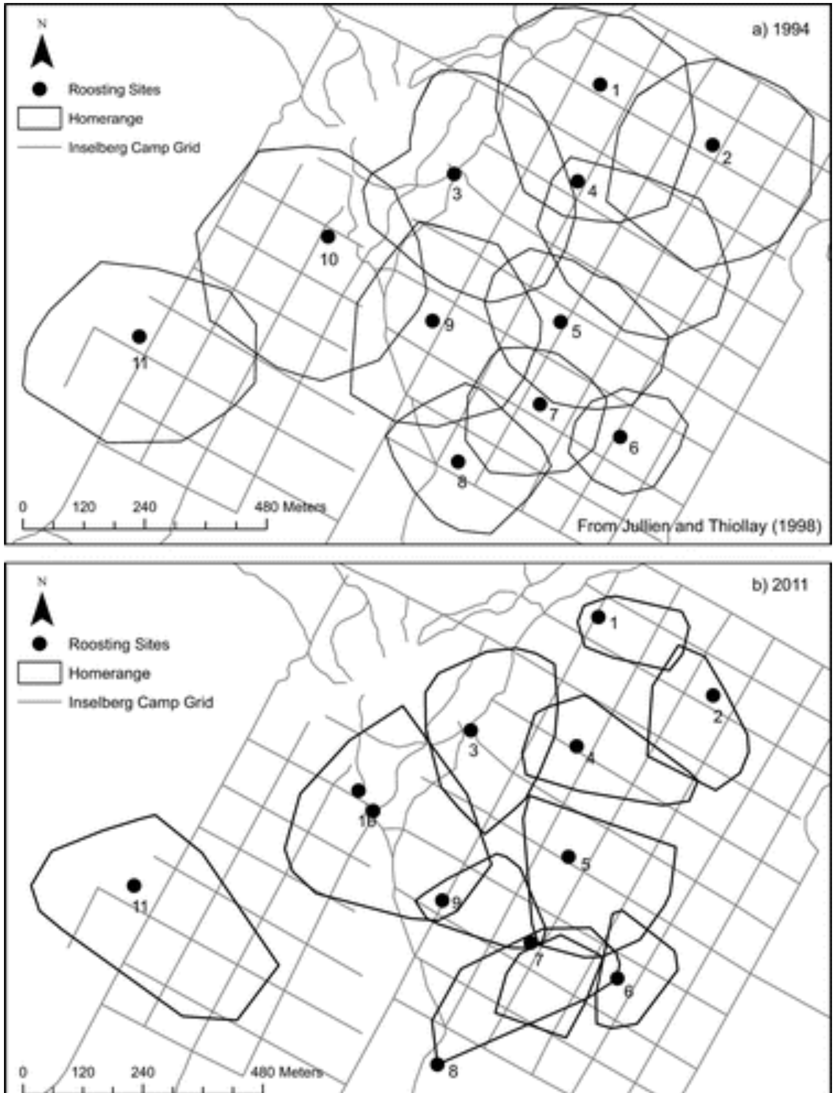
Mixed species flocks and territoriality

Only some flocks exclusively follow ant swarms − others are simply foraging in the understory and canopy, but hold territories, which are defended against other ***flocks***

Lowland canopy obligate members

Lowland understory obligate members

Mixed species flocks and territoriality



A group returned to map the position of flock territories after 17 years in a lowland forest in French Guiana

7 of 11 of the roosting sites for flock territories were identical

Coevolution in heterospecific social groups: mixed species flocks

Deception in mixed foraging flocks?

White-winged tanagers occasionally trick flock members by giving false alarm calls --

Sometimes sentinel species, which usually give alarm calls against predators, are deceitful.

Can give false alarm calls when no danger is present − causes momentary hesitation by other birds and an opportunity to steal prey: *kleptoparasitism*

Other coevolved mutualisms: Figs and fig wasps

Figs and fig wasps have a long established symbiosis dating back 60 million years

Most figs (~700 species) are pollinated by one or a few wasp species

Male/female reproduction of wasps occurs within the figs, and pregnant females leave the syconium to find another fig to deposit eggs

Other coevolved mutualisms: Leaf cutters as fungus garden ants


Attini ants and fungus relationship dates back to ~50 mya

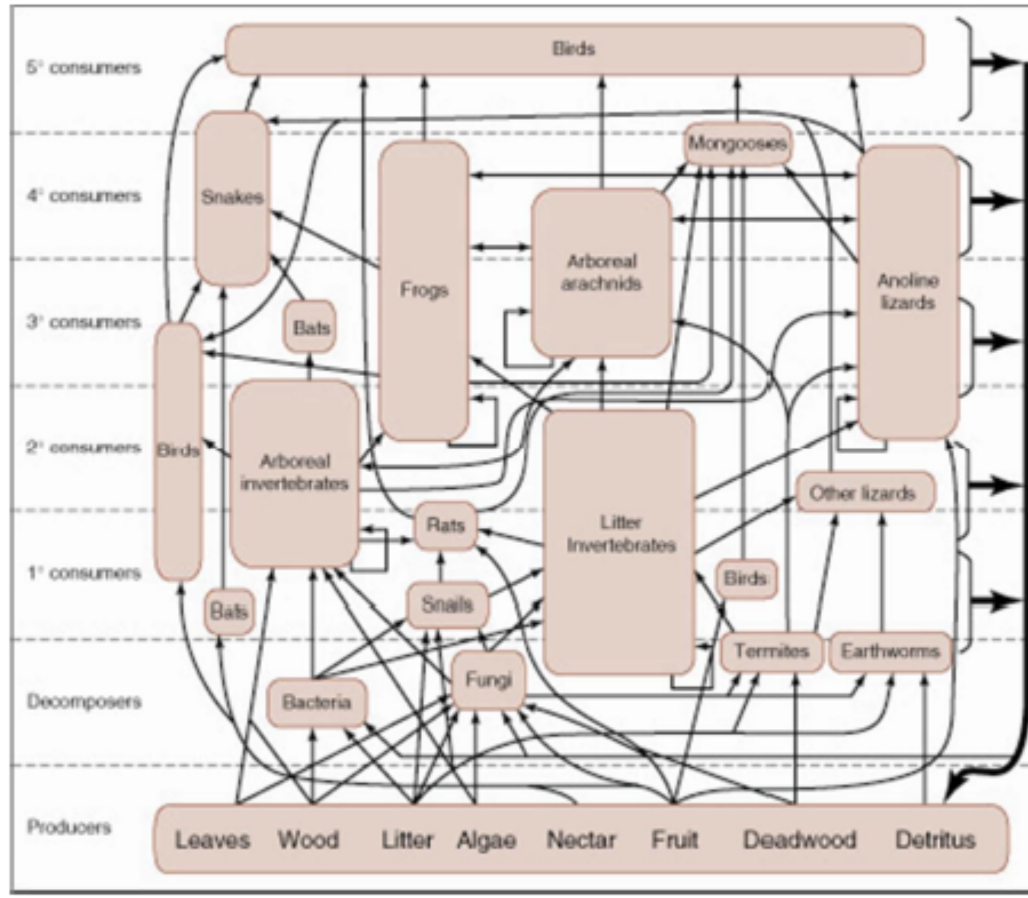
Ants bring neatly clipped pieces of leaves back to underground colonies


In the colony, they convert the leaves to a *cultivar*, to culture a specific fungus. Ants constantly weed the colony to promote a single species of fungus, which cannot grow outside the colony.

When queens found a new colony, she takes some of the fungus with her…so fungus and ants disperse together.

Trophic dynamics and coevolution

All food webs are made up of complex combinations of top-down and bottom-up forces



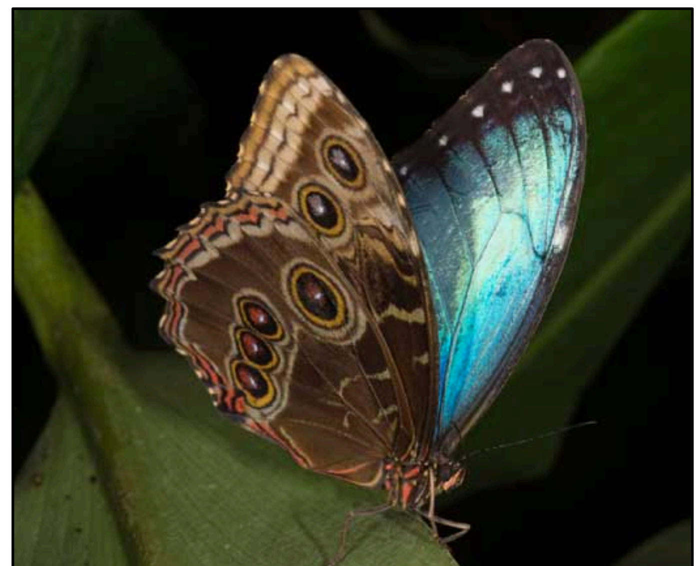
Example from a 'simple' community – El Verde, rain forest on island of Puerto Rico

Complexity in trophic dynamics results from selection pressures exerted on species to evolve strategies to avoid being detected:

Antagonistic predator-prey interactions

Trophic dynamics and coevolution

Cryptic coloration



Cryptic coloration of boa constrictor on forest floor, and underwing coloration of blue morpho butterflies

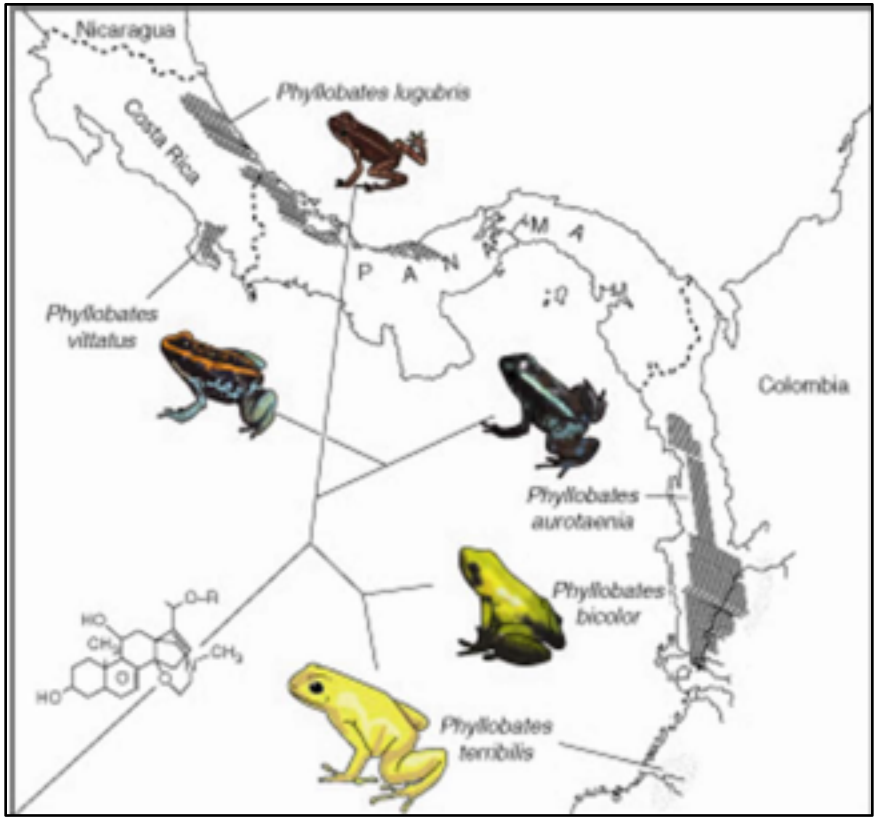
Trophic dynamics and coevolution

Cryptic coloration

Various species of the same insect group (Orthoptera – katydids) are cryptic against different backgrounds

Trophic dynamics and coevolution

Warning (aposematic) coloration



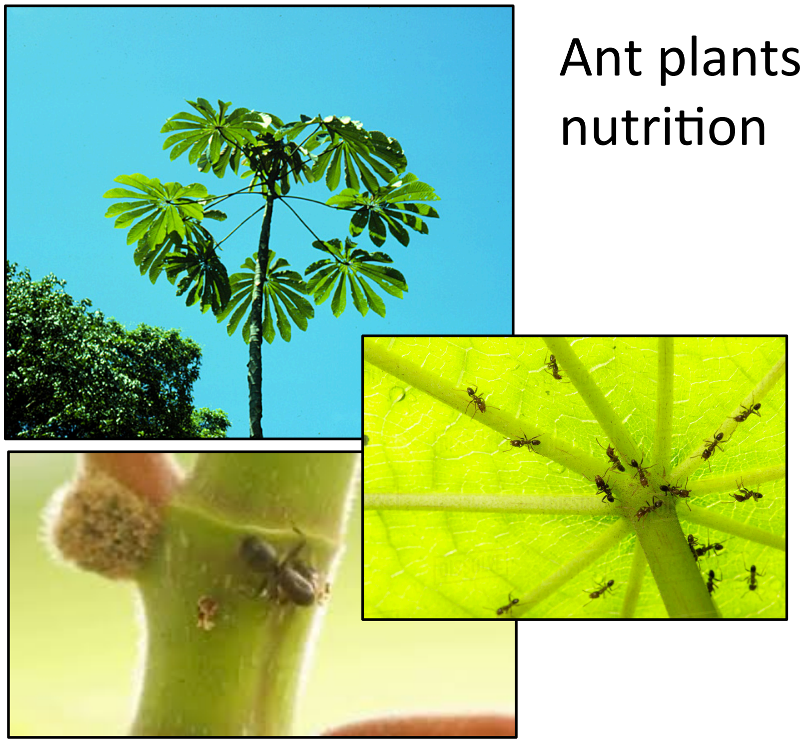
Poison-dart frogs (Dendrobatidae) contain toxic alkaloids in their skin secretions, characterized by bold color patterns



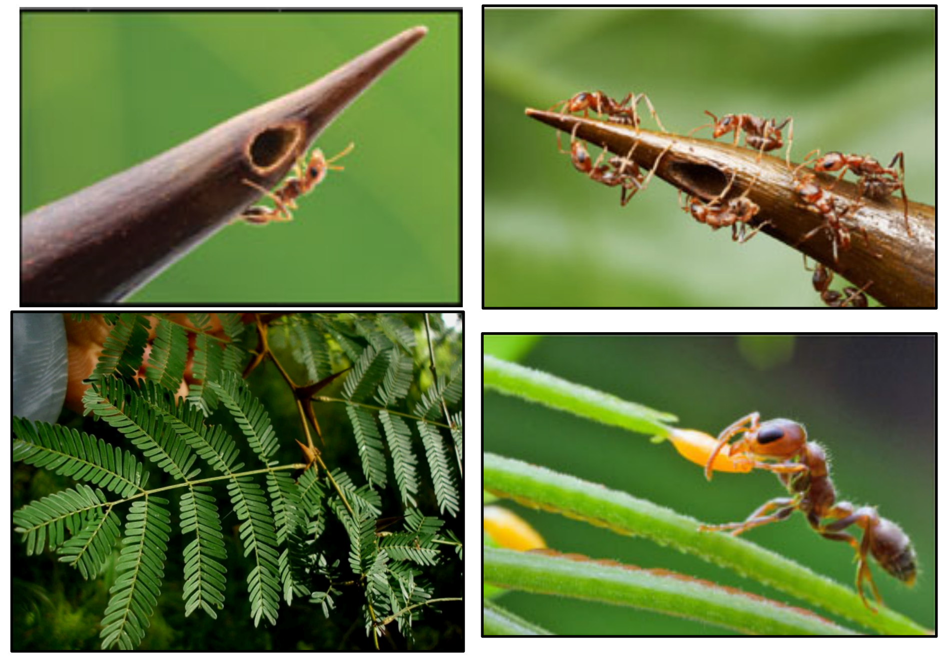

Adaptations at lower trophic levels affects would-be predators at upper trophic levels

Trophic dynamics and coevolution

Ant plants and extrafloral nectaries (EFNs)



Ant plants usually have ant *domatia* and provide nutrition



Host plants benefit from presence of protectionist ants, and those that benefit most also offer food bodies and domatia to the ants

Summary points of species interactions and coevolution

- Niche partitioning, negative density dependence and coevolution networks are each important in maintaining or generating tropical diversity
- Frugivory is a major kind of species mutualism that generates (through dispersal) the patterns of seedling establishment
  - Other forces, like niche partitioning and negative density dependence operate on these patterns to determine community structure
- Other evolved mutualistic interactions and trophic interactions result from selection pressures on either member's own best fitness interest