TROPICAL ECOLOGY

WBNZ-849

Tropical biodiversity

How can so many species coexist in a tropical rainforest?

Krzysztof Wiąckowski

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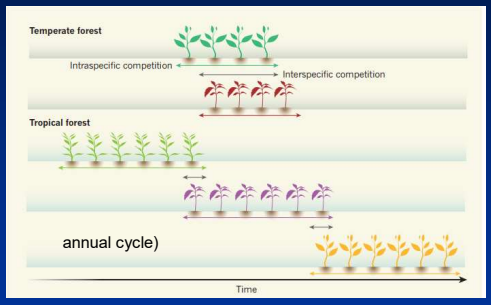
A reminder from the last week

Can lack of seasonality promote tree species coexistence in tropical forests?



Short growing season: strong both itra- and interspecific competition

Long growing season: the intraspecific competition is stronger than interspecific competition

Gary G. Mittelbach 2017
A matter of time for tropical diversity
Nature

colours denote different species

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Competition between plants for pollinators and seed dispersers.

One of its effects is the variation in the flowering and ripening times of fruit (example):

Example 1:

18 species of *Miconia* in Trinidad have flowering and fruiting times shifted so that only a few fruit at the same time...

Kricher, John. The New Neotropical Companion (p. 149). Princeton University Press. Kindle Edition

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Competition between plants for pollinators and seed dispersers.

Example 2:

Plants pollinated by bats in Costa Rica: of the 25 frequently visited species, only about ⅓ bloom at the same time

Kricher, John. The New Neotropical Companion (p. 149). Princeton University Press. Kindle Edition

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Two very different views on tropical rainforest and coral reef communities

Equilibrium theory (niche-based theories)	**Desequilibrium theory** (neutral theories)
They are complex, species-rich communities of coevolved species whose relative abundances are in balanced equilibrium in a stable environment.	**Species-rich communities are not well-integrated, coevolved, "communities" in a balanced stable state.**
Each species has a specific niche of its own, i.e., fulfils a specific role complementary to that of other members of a community.	**To the contrary, they might well be chaotic haphazard collections of species inhabiting a region.**
	Local species composition might be due to a sort of "community drift" resulting from disturbance and dispersal.

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The controversy has a long history in ecology

- ❑ **Frederic E. Clements**
- ❑ **Henry A. Gleason**

The final (climax) stage of ecological succession is usually characterized by:

- ❑ Highest primary production
- ❑ Highest biomass
- ❑ Highest species diversity

But is diversity really highest at the late stage of succession?

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Long term data on ecological succession after cutting down the forest:

- ❑ Species richness increases to the maximum value
- ❑ Then, at later stage it tends to decrease
- ❑ The maximum diversity is not at the late stage …
- ❑ Possible explanation: COMPETITIVE EXCLUSION

→ Analogy to
'Intermediate disturbance hypothesis'

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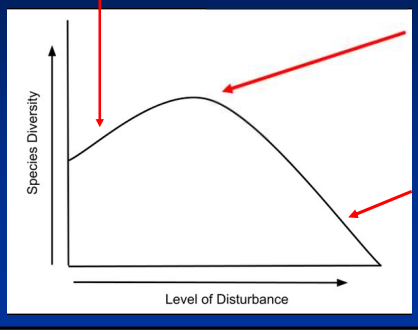
Intermediate Disturbance Hypothesis

At low disturbance level the strongest competitors exclude weaker ones – lower species numbers



The highest species richness can be expected at the Intermediate rate of disturbance –the competitive exclusion is not strong enough …

At high disturbance level many species are affected – high extinction rate – low species richness …

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Is tropical rainforest really in the equilibrium (climax) state?

Sabah, Borneo (Malezja)

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Sabah, Borneo (Malezja)

„FOREST GAP" (or Gaps) – Web-of-Scuence SCI, 2.1.2023: 866 „HITS"

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Meandering rivers constantly destroy banks and create new habitats

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A small tributary of the Amazon River

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Grasses and early succession trees on the newly formed river banks

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Perhaps it is a problem of scale?

- Rainforest is constantly a mosaic of fragments at various successional stages …
- There is no equilibrium at small (local) scale due to frequent disturbances ..
- However, the forest observed at a large scale looks like a stable 'mature' system …
- This would explain the amazing species diversity at the regional scale …

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Examples of evolutionary strategies that are possible only in wet Tropics,

and which directly or indirectly increase species diversity

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Army (nomadic) ants

- Carnivorous ants raiding for food in swarms of hundreds to thousands of individuals…
- They do not build permanent nests …
- Queens are permanently wingless and the whole colony migrates periodically
- All New World army ants belong to the subfamily Ecitoniae (Hymenoptera: Formicidae) with about 150 spp in 5 genera
- Most species are subterranean and only two species forage in large swarms above ground *Eciton burchellii* and *Labidus praedator*
- Only *E. burchellii* ants create temporary nests or bivouacs built of their own bodies …

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Life cycle of *Eciton burchellii*:

An average colony (about 500 000 workers) follows a strict cycle of stationary and nomadic phases:

- During the 20-day stationary phase, the ant pupae and newly laid eggs develop in a temporary bivouac
- Each day, ants raid for food in a different direction …
- When the eggs hatch and the pupae eclose, this ends the stationary and initiates the nomadic phase
- During this phase, the whole colony raids every day spending each night in a new bivouac site ..
- After 15 days the larvae pupate and the colony becomes stationary again…

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The temporary bivouac nests of *Eciton burchellii* are made up of the ants themselves …

Photo: Stefanie Berghof from Rettenmeyer et al. (2011) Insectes Sociaux 58: 281–292

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Colonies of *E. burchellii* can reach sizes of 1.5 million ants and may scour >1000 m^2 of forest floor per day

On average, two raids per km^2 can be observed per day

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ARMY ANTS

Pipeline Road, Panama, 26 July, 2021

The whole raiding columns are usually from 3 to 10 metres wide and 15 m long

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Rancho Grande, Venezuela, 2008

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What army ants have to do with the biodiversity of tropical rainforests?

- *Eciton burchellii* is restricted to Neotropical rainforests (from Mexico to Southern Brazil)
- Why it could not live outside the Tropics?
- More than 550 animal species from different taxa have been observed attending *E. burchellii* swarms
- Of which 300 depend at least in part on army-ants to survive

Rettenmeyer et al. (2011) The largest animal association centered on one species: the army ant *Eciton burchellii* and its more than 300 associates. Insectes Sociaux 58: 281–292

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Most important taxa attending *E. burchellii*

Overall 557 species have been recorded

(most Collembola, mites, staphilinid beetles remain undescribed …)

- Birds – prey upon the escaping animals …
- Butterflies – feed on bird droppings („antbutterfies"); at least 239 species seem to be associated with ant swarms
- Wasps – endoparasitoids of flies and spiders
- Flies – deposit their eggs or larvae on fleeing animals (e.g., crickets, cocroaches)
- plus many more taxa poorly known …

Rettenmeyer et al. (2011) The largest animal association centered on one species: the army ant Eciton burchellii and its more than 300 associates. Insectes Sociaux 58: 281–292

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Flies of the genus *Calodexia* deposit live larvae on cockroaches and crickets fleeing from the ants

Photo: Stefanie Berghof from:

Rettenmeyer et al. (2011) The largest animal association centered on one species: the army ant Eciton burchellii and its more than 300 associates. Insectes Sociaux 58: 281–292

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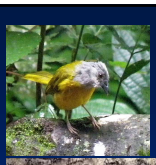

Antbirds

Army-ant following is a specialized foraging strategy that evolved in some birds:

- ❑ The specialization is most developed in the family Thamnophilidae – typical „antbirds" …
- ❑ Birds attend army-ant raids preying upon arthropods and small vertebrates escaping from the ants …

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Army ants provide an important service to the birds:

Many of the flushed prey animals are only nocturnally active or would otherwise stay hidden in the leaf litter

Birds significantly reduce the ants' success rate by reducing the amount of prey captured by the ants

Birds act as kleptoparasites of the army ants

Wrege et al. (2005) Antbirds parasitize foraging army ants. Ecology 86: 555–559

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Three levels of specialization distinguished among Antbirds:

- ❑ **Occasional followers** - those that forage at swarms opportunistically as army-ants move through their territories – 70 species
- ❑ **Regular followers** - follow swarms beyond their territories but also forage independently of swarms – 8 species
- ❑ **Obligate followers** – that appear incapable of foraging independently of swarms – 16-29 species (special adaptations …)

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Army-ant swarms are always attended by numerous antbird species

Pipeline Road, Panama, 26 July, 2021

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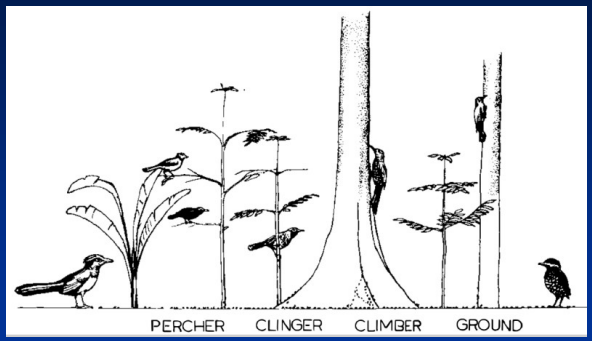
Division of niches by type of perch among antbirds at ant swarms in central Panama



Edwin O. Willis and Yoshika Oniki (1978) Birds and army ants. Ann. Rev. Ecol. Syst. 9: 243-63

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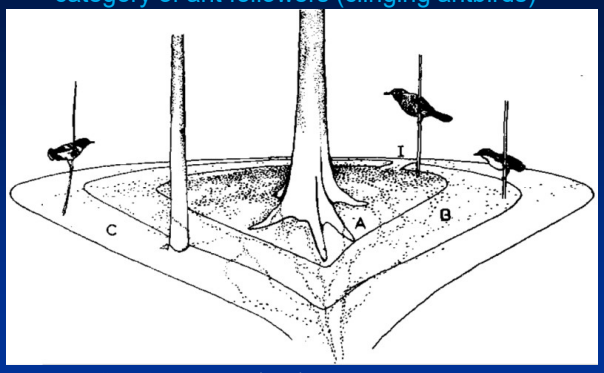
Division of niches by dominance within a single category of ant followers (clinging antbirds)



Edwin O. Willis and Yoshika Oniki (1978)
Birds and army ants. Ann. Rev. Ecol. Syst. 9: 243-63

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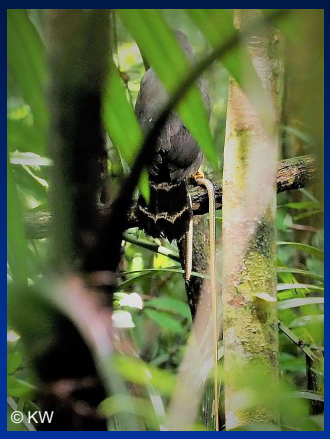

Sometimes larger vertebrates are caught by larger predators

here a bird of prey (Forest falcon?) with a hunted snake

Panama, Pipeline Road, 2021

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Evolution of ant-following behaviour

A detailed molecular phylogenetic analysis of Antbirds (Brumfield et al. 2007) demonstrated that:

- ❑ Army-ant following behaviour is a phylogenetically conserved feature …
- ❑ Regular following evolved only three times
- ❑ Most likely evolutionary progression was from occasional to regular and to obligate specialized state
- ❑ No reversals from the obligate state occurred
- ❑ Molecular dating indicates that army-ant following has persisted in antbirds for more than 5 millions years

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Foraging in mixed-species assemblages is a rule among antbirds

- ❑ Negative and positive interspecific interactions
- ❑ Competiton for food is to be expected …
- ❑ What are the possible positive sides of foraging in mixed-species flocks?
  - ❖ Shared vigilance
  - ❖ Predator dilution effect
  - ❖ Sharing information …

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- ❑ Unpredictability of high-value food resources …
  - ❖ Army ant colonies are widely spaced and mobile
  - ❖ The uncertainty about such resources might increase the value of cooperation (information sharing) …
  - ❖ Large number of birds finds easier ant swarms
  - ❖ Antbirds respond strongly to vocalizations
  - ❖ Positive interspecific interactions (facilitation) favour species diversity

O'Donnell (2017) Evidence for facilitation among avian army-ant attendants: specialization and species associations across elevation. Biotropica 0, 1-10

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Fruits and plant dispersion

- ❑ Fruits are very important food resources for animals in tropical forests …
- ❑ At least half of the rain forest trees produce fleshy fruits targeted at potential animal "spreaders"
- ❑ Why do we lack fruit-eating birds or bats? a very important difference between a tropical forest and a seasonal environment!
- ❑ Fruit-eating opportunists ... using to varying degrees colourful fruits, which mostly contain carbohydrate
- ❑ Specialized fruit eaters ... they consume fruits which, apart from sugar, contain fats and proteins, such fruits most often do not have bright colours

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The possible effect of seasonality on species specialization in resource use

- Organisms in strongly seasonal environments must have relatively general (unspecialized) patterns of resource use
- The broad niches of these generalists limits the number of species that can be packed into a given resource gradient
- Species in less variable environments can specialize on temporally reliable resources
- Idea similar to Rapoport's rule …

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Specialized fruit eaters that eat only fruits

- From 80 to 100 species of mainly fruit-eating primates, bats and birds inhabit the forests of Central America to the Amazon.
- The populations of fruit-eating birds have higher numbers than that of insectivorous birds because of the greater biomass of fruit.
- Fruits are more accessible food than insects, which are often harder to find and catch
- Fruit-eating birds also forage in mixed-species flocks …

Kricher, John. Tropical Ecology Princeton University Press. Kindle Edition.

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Adaptation of fruit eating birds

Birds specialized in fruit and nectar consumption have reduced nitrogen requirements and lower nitrogen losses

- evolutionary adaptation to protein-poor food
(the physiological mechanism has not been explained)

Tsahar E. *et al.* (2006) Do nectar- and fruit-eating birds have lower nitrogen requirements than omnivores? An allometric test. The Auk 123:1004-1012.

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Green-billed toucan (Ramphastos bicolorus).
Toucans are typical fruit eaters "gulpers„ …
Iguassu Brazylia

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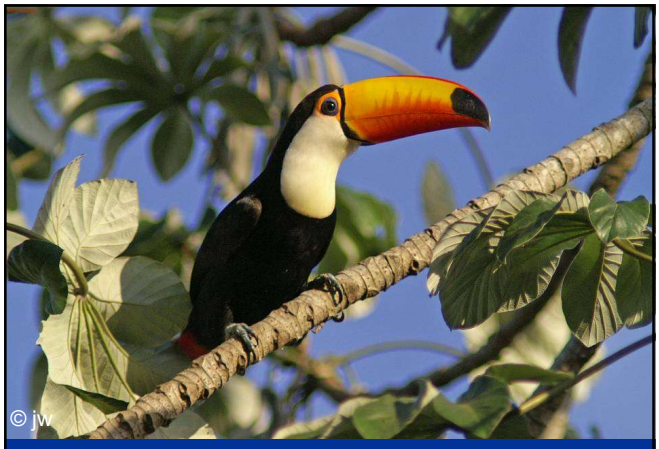

Great Toucan (*Ramphastos toco*)
Pantanal, Brazil

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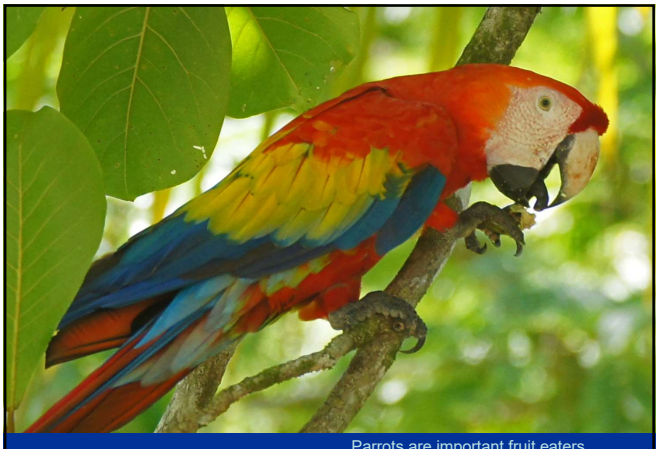

Parrots are important fruit eaters.
Scarlet Macaw, Drake Bay, Costa Rica

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Toucanet (*Aulacorhynchus sulcatus)*

Rancho Grande, Venezuela

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Tanagers (Thraupidae; [Emberizidae])

about 250 species

Tangara arthus
Golden tanager

Thraupis episcopus
Blue-gray tanager

These are „mashers"

Rancho Grande, Venezuela

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Bay-headed tanager (*Tangara gyrola)*

Rancho Grande, Venezuela

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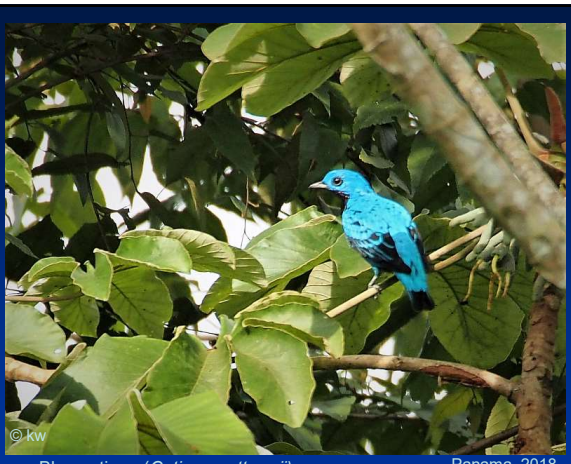

Blue cotinga (*Cotinga nattererii)* Panama, 2018

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Oilbird – a very particular frugivore described by Alexander von Humboldt

Steatornis caripensis

Wikipedia

The only nocturnal flying fruit-eating birds in the world

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Oilbirds are related to the nightjars, from which they differ in many respects:

- ❑ Live in very large colonies in caves
- ❑ Use echolocation
- ❑ Nocturnal frugivores feeding exclusively on oil palm and laurel fruits
- ❑ Travel great distances every night in search of fruit (> 150 km)

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Consequences of such a diet:

- These fruits are very rich in carbohydrates and fats, but have little protein ...
- Visibly slower development (birds spend 3 times longer in the nest ...)
- The broods are much larger (four eggs) than other tropical birds ...
- The chicks are highly fat and in the last phase 1.5 times larger than the parents
- The name oilbirds comes from the high fat content ...

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Significance of oilbirds in seed dispersal

At the bottom of the caves a lot of excreted seeds are collected, which germinate but do not grow in the dark ...

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Oilbirds are extremely important in maintaining the plant biodiversity of the forests

According to a study centered in Cueva de Guácharo near Caripe, Venezuela (Roca 1994):

- the entire colony collectively regurgitated about 15 million seeds each month
- a biomass of about 21 tons of seeds
- about 60% of the seeds were dispersed in forest

Kricher, John. Tropical Ecology Princeton University Press. Kindle Edition.

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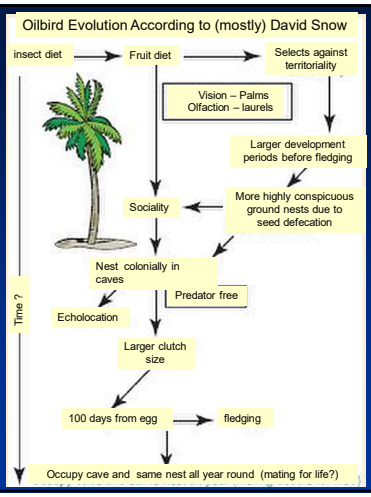

Oilbirds were originally "normal" nightjars feeding on insects.

Shifting to frugivory initiated a cascade of adaptations …

Kricher, Tropical Ecology Princeton University Press. 54

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Lianas

Lianas are among the most characteristic structural elements of tropical rainforests …

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What is a liana?

- Forest plants strongly compete for light …
- Lianas are climbing plants with relatively long, slender, woody stems rooted in soil and extending to the forest canopy, where they produce abundant foliage.
- Like "tree" or "shrub," "liana" refers to a polyphyletic functional group with high structural diversity
- Hundreds of species of lianas exist worldwide, and the liana growth form is represented in nearly all major plant families

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Quantitative significance of lianas

In lowland tropical forests, lianas commonly represent:

- ❑ 25 % of the rooted woody stems
- ❑ 35 % of the woody species
- ❑ up to 40 % of the foliage area of the upper canopy
- ❑ less than 5% of total plant biomass

- ❖ Mature individuals range in length from a few meters to more than half a kilometer
- ❖ and in diameter from a few millimeters to more than half a meter

Yanoviak S.P. and Stefan A. Schnitzer S.A. (2013) Functional Roles of Lianas for Forest Canopy Animals. In: M. Lowman et al. (eds.), Treetops at Risk: Challenges of Global Canopy Ecology and Conservation. Springer Science+Business Media, New York

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Why lianas are so long?

They often extend over several trees, joining their crowns

The extra length and numerous loops is a defence (insurance) against:

- ❑ swinging movements of the trees
- ❑ falling down trees

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Why lianas do not grow outside the Tropics?

- ❑ Water transport in trees
  - pipe system
  - evapotranspiration and capillary action
  - great demand for water
- ❑ Embolism and its causes
- ❑ Lianas, due to their very long stems, are particularly vulnerable to embolism …

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What is the functional role of lianas in tropical rainforests?

- Lianas are detrimental to trees via mechanical loading and competing for light and nutrients
- Their leaves and fruits are important food resources for many animals
- They strongly affect rainforest diversity by:
  - their large species numbers
  - providing food (leaves and fruits) …
  - creating structural complexity …

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Physical elimination of lianas from experimental areas led to significant reduction of animal species diversity

- Birds …
- Insects (in particular not flying ones – e.g., ants)

When climbing ropes were extended where lianas have previously been eliminated, diversity increased again …

Yanoviak and Schnitzer (2013) Functional role of lianas for forest canopy Animals. Springer

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Epiphytes

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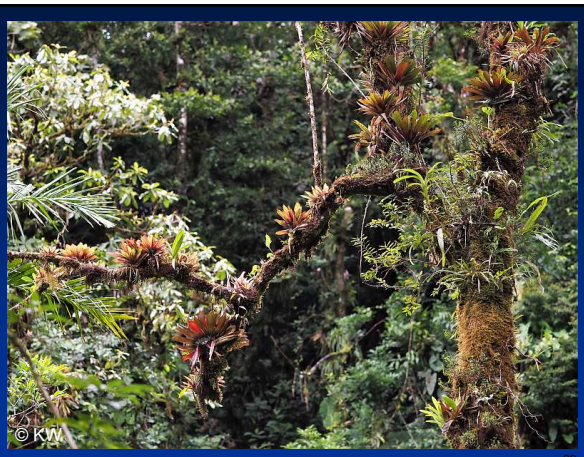

Boquete, Panama, 2021 69

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Phytotelmata

Contained aquatic habitats formed naturally by a plant and populated by aquatic organisms

telmata = ponds, wetlands (grec., plural form)
A term proposed by Ludwig Varga (1928)

Other terms used in the literature:

Container habitats
Inquiline communities
(from Latin: inquilinus)

„hanging aquaria"
(in old literature)

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Bromeliads

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Zbiorniki w liściach Bromeliaceae

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Bromeliads

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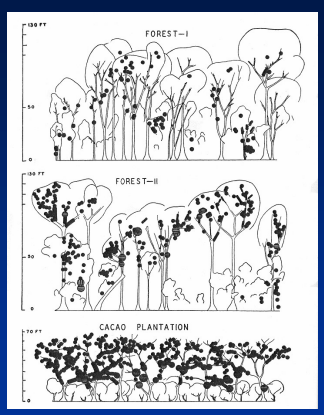

Distribution of Bromeliads in two types of forest and in cacao plantation (Trynidad)

Kitching (2000)

The average density of epiphytic bromeliads in a Colombian cloud forest has been estimated as 17,5 individual bromeliad per m^2 of the forest surface.

Each plant contained on average 250 ml of water
(Sugden & Robins 1979)

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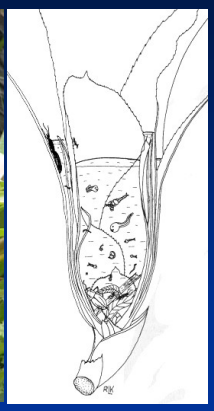
Bromeliads



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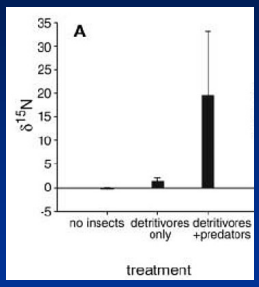
How Bromeliads depend on aquatic predators

Ngai and Srivastava (2006) Predators Accelerate Nutrient Cycling in a Bromeliad Ecosystem. Science 314: 963



Nitrogen content in fresh bromeliad leaves: without detritivores; with only detritivores; and with both detritivores and predators (damselflies)

Bromeliad damselfly larvae *Mecidogaster Modesta.* Occurs in water tanks > 100 ml
https://www.earthmagazine.org/
Edd Hammill

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Studies on phytotemata concern general ecological issues

Why predators are often more sensitive to habitat size than their prey and frequently occur in only the largest habitats?

Small habitats:

(a) do not have enough energy to support higher trophic levels;

(b) are less likely to contain particular prey required by specialist predators;

(c) are risky for predators with slower life histories and/or large body sizes;

(d) are numerically unlikely to be colonized by regionally rare species, such as predators.

Srivastava et al. (2020) Habitat size thresholds for predators: Why damselflies only occur in large bromeliads *Biotropica* 52: 1030–1040

Bromeliad damselfly larvae *Mecidogaster Modesta.* Occurs in water tanks > 100 ml
https://www.earthmagazine.org/
Edd Hammill

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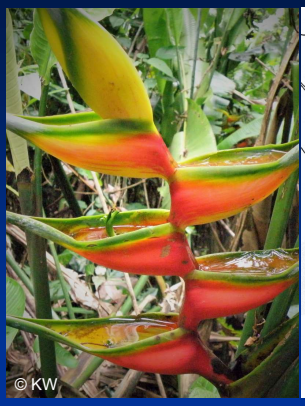
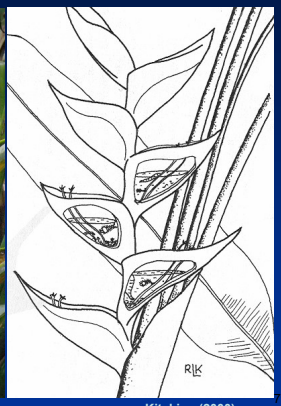
Floral bracts of *Heliconia bihai*





Kitching (2000)

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Floral bracts of *Heliconia bihai*

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Heliconia sp.

Water-drinking animals are possibly an important means of dispersing small aquatic organisms among these habitats

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Floral bracts of *Calathea* sp.

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Floral bracts of *Calathea* sp.

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Sarraceniaceae

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84

Pitcher plants - *Nepenthes spp*

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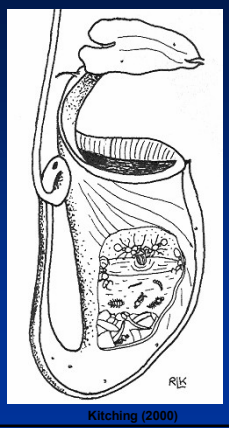
Pitcher plants - *Nepenthes spp*



Kitching (2000)

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Mount Kinabalu, 4 095 m asl (Borneo, Sabah)

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Can phytotelmata be used for testing hypotheses on biogeographic gradients?

A general hypothesis:

Aquatic communities in phytotelmata should reflect the biogeographic history of a given plant taxon

Prediction 1:

If plants have a well-defined geographical range, we can expect that their food webs should differ from the centre towards the edge of the range ... (Centre of origin hypothesis)

Prediction 2:

The food web within a particular type of reservoir will be richer in species and more complex if there are more habitats of a similar type in the same area ... (Island biogeography model)

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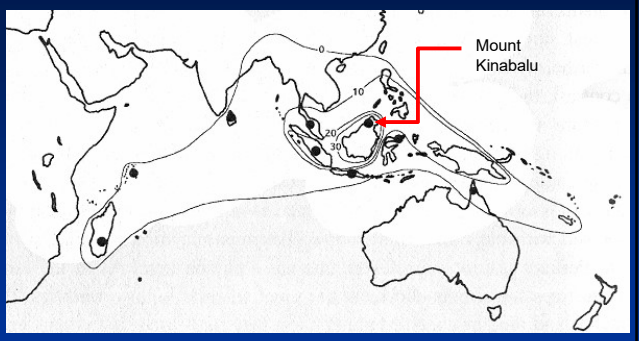
Geographic range of the genus *Nepenthes*

Centre of species divesity – Massif Kinabalu (Borneo)



Sampling locations and isopleths for the numbers of coexisting species

From: Kitching (2000)

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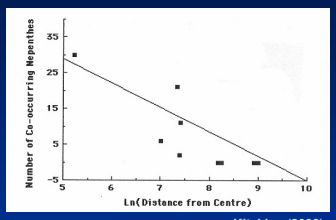
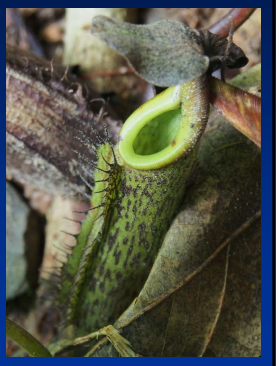
Dependence of the number of co-occurring *Nepenthes* species on the distance from the genus biodiversity centre



Kitching (2000)



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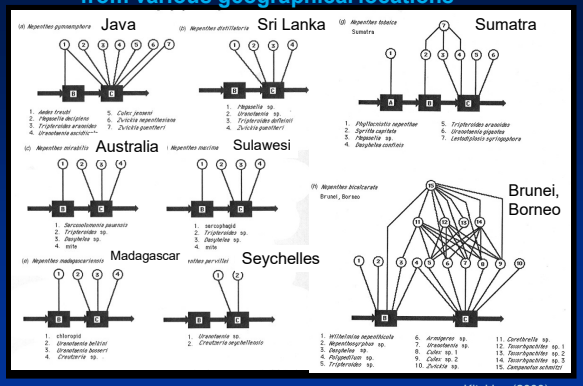
Examples of pitcher plant food webs from various geographical locations



Species richness and food-web complexity correlate with the distance from the centre of the range

Kitching (2000)

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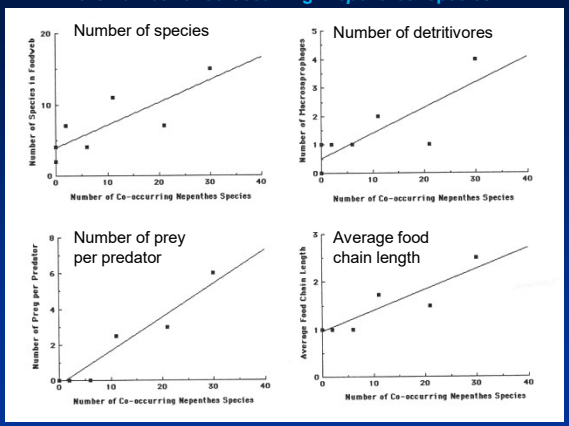
Dependence of some properties of food webs on the number of co-occurring *Nepenthes* species



Kitching (2000)

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Aquatic communities in water-filled tree holes

Rancho Grande, Venezuela

93

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Aquatic communities in water-filled tree holes

Kitching R.L. (2000) Food webs and container habitats:
The natural history and ecology of phytotelmata.
Cambridge University Press

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Coconut shells filled with rain water

long lasting aquatic microhabitats in a rainforest

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Fallen palm bract leaves filled with rain water

96

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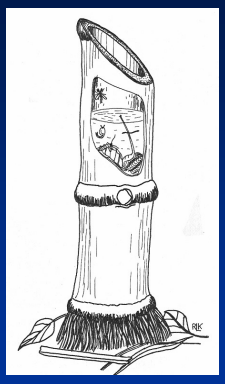
Water reservoirs in the internodes of broken or cut bamboo stalks



Another example of a popular aquatic microecosystem formed by plants

97

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Microecosystems (microcosm method)

experiments on community-level phenomena

Advantages of laboratory microcosms

- ❑ Precise control of external conditions
  (thanks to very small size)
- ❑ High number of replicates possible
  (high statistical reliability)
- ❑ Often large populations in experiments
  (due to small size of the organisms)
- ❑ The experiments are short-lived ...
- ❑ Simplified systems allow for a thorough examination of specific mechanisms ...
  (easier interpretation)

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Phytotemata as natural microecosytems

They provide most of the advantages of laboratory microcosms

- ❑ Small size
- ❑ Simplified communities - easier interpretation
- ❑ Many independent replicates possible
- ❑ Experiments under field conditions are certainly more difficult …

Can experiments in phytotemata have any advantages over laboratory microcosms?

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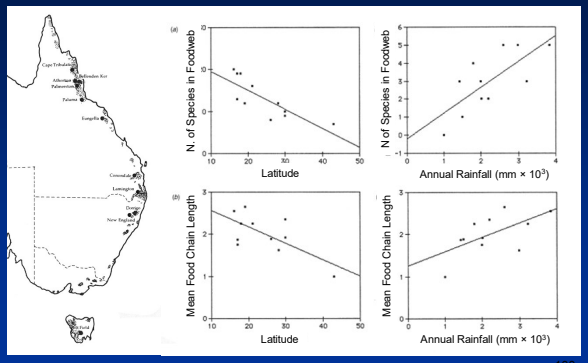
Species richness in water-filled tree holes

in a latitudinal gradient along the eastern coast of Australia (from Queensland to Tasmania)



Kitching R.L. (2000) Food webs and container habitats: The natural history and ecology of phytotelmata. Cambridge University Press.

100

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Practical task:

Please, indicate specific ecological and evolutionary mechanisms possibly responsible for this gradient …

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Possible mechanisms for higher species richness towards the tropical zone:

- ❑ **Higher productivity** (higher rate of decomposition under higher temperature)
- ❑ **Higher numbers and biomass of all aquatic organisms in tree holes**
- ❑ **More trophic levels** (top predators may decrease competition among their prey species …)
- ❑ **Higher stability of climatic factors** (e.g., temperature)
- ❑ **Higher precipitation** (lower probability of drying out)
- ❑ **Higher stability is more important for predators** (larger size and longer generation times makes them more vulnerable to drying)
- ❑ **Higher diversity of trees in the area – more different types of tree holes** (larger regional species pool …)
- ❑ **In addition to the tree holes also other phytotelmata in the tropical zone** (larger regional pool of species …)

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