Solo or together? Some background

levels of gregariousness

Single — Aggregation — Supportive group — Society

Two evolutionary drivers of social life (to be continued)

- reciprocal mechanism: mutual benefits - I help you now, you help me later (my fitness **depends directly** on others' fitness)
- kin selection mechanism: by helping relatives, I spread copies of my own genes (inclusive fitness; my fitness **shared with** others' fitness)

Solo or together? Some background

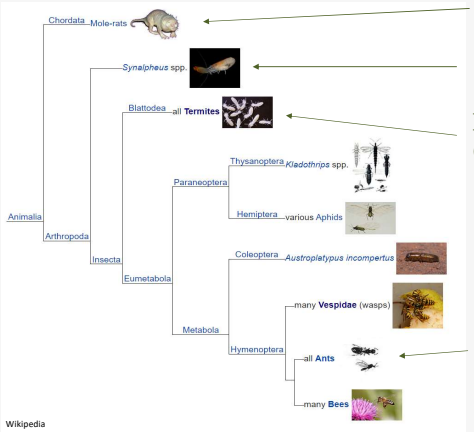
levels of gregariousness

Single — Aggregation — Supportive group — Society

Eusociality (the ultimate form of social systems)

- cooperative brood care, including the care of offspring from other nest members
- overlapping generations of adults in the nest
- division of labor into reproductive and non-reproductive group members („castes" with different behaviour, morphology, „altruistic sacrifice")

Eusociality is extremely rare, and skewed to *Hymenoptera*
Most examples in tropics



Semi-arid grassy areas (dry savanna)
Damaraland mole-rat (South Africa)
Naked mole-rat (East Africa)

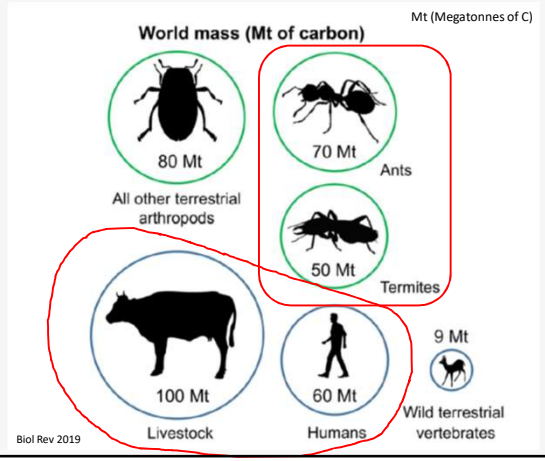
Several species of sponge-dwelling coral reef shrimps
(Central - Western Atlantic)

Termites' diversity peaks in tropics
The oldest eusocial organisms
(150 mln years ago)

Ants' diversity peaks in tropics
Originated more than 100 mln years ago in rainforest

Wikipedia

Enormous part of the animal biomass on Earth is social and peaks in tropics



Biol Rev 2019

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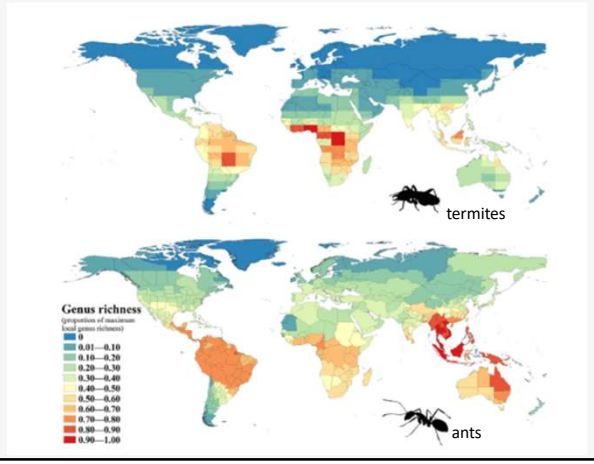
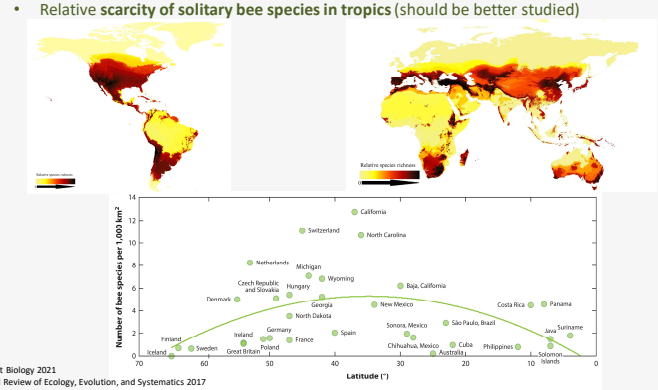


Biol Rev 2019

Only a moderate number of eusocial bee species (many solitary)

- Bee species richness peaks in **xeric and temperate** areas (low species diversity & abundance in tropical forests)
- When forests excluded, plant productivity and richness are important drivers of bee diversity
- Relative **scarcity of solitary bee species in tropics** (should be better studied)



Current Biology 2021
Annual Review of Ecology, Evolution, and Systematics 2017

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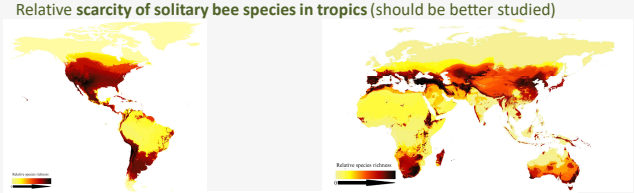


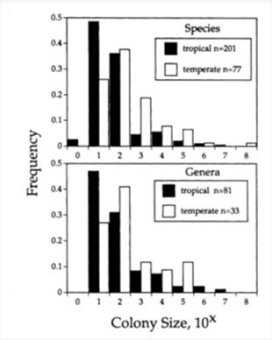
Latitudinal clines in polination ecology (some generalisations)

1) Tropics - polination occurs throught the year; Temperate – seasonal
2) Tropics – flowers last short; Temperate – flowers last long
3) With increasing latitude, polination by vertebrates (birds, bats, rodents) becomes less frequent
4) With increasing latitude, wind polination becomes more frequent

Current Biology 2021
Annual Review of Ecology, Evolution, and Systematics 2017

Towards the equator, ants form smaller colonies, while termites form larger colonies

Tropical vs Temparte ants



Explanations focus on latitudinal clines in

- Climate (unpredictability & stochasticity considered)
- Predation intensity
- Prey size & availability
- Parasites & pathogenes

Highly social systems with many relatives in colonies prone to the spread of pathogenes (genetic homogeneity)

Highly social systems with many relatives in colonies can apply sophisticated forms of anti-parasite behaviours (social distancing, grooming, waste managements etc.). Some ants do this, e.g. leaf-cutter ants!!!

American Naturalist 1995
Biological Reviews 2011

Solo or together? Some more generalizations & background

Tropics are especially rich in the primary ecological drivers of social evolution

- **threats & enemies**: predation, competition, parasitism
- **patchy distribution of resources** (recall that the high level of biodiversity also means that representatives of the same species are far apart – large distances)

In response to these challenges, social life style can offer colony members

- **increased defense against enemies**
- **increased foraging performance**

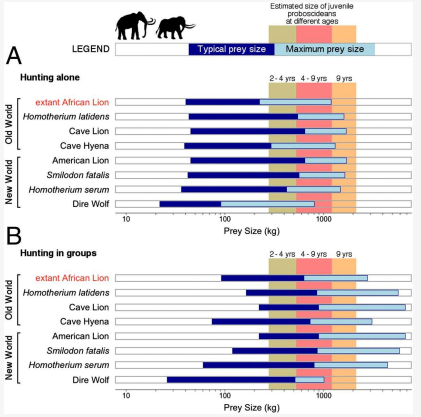
But staying together has costs

- **increased intraspecific competition**
- **risk of parasite spread**
- **exploitation by selfish egoists** - nice and helpful individuals („altruists") are prone to exploitation by „social parasites"



Example: group hunting increases the prey size

Predation on elephants (now), and mammoths and mastodonts (past)

Valkenburgh et al. 2016 PNAS

Example: aggregation decreases predation risk

Original Article

Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community

Scott Creel,* Paul Schuette,* and David Christianson†

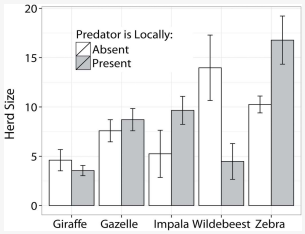
*Department of Ecology, Montana State University, 310 Lewis Hall, Bozeman, MT 59717 USA and †School of Natural Resources and the Environment, University of Arizona, 325 Biological Sciences East, Tucson, AZ 85765, USA

Animal Behaviour

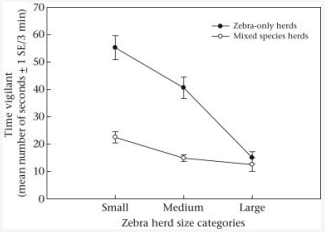
Determining the relative importance of dilution and detection for zebra foraging in mixed-species herds

Melissa H. Schmitt, Keenan Strain, Christopher C. Wilmers, Adrian M. Shrader

Predators induce herding



Larger group, fewer worries



Zebras: 2-9 10-30 31-75

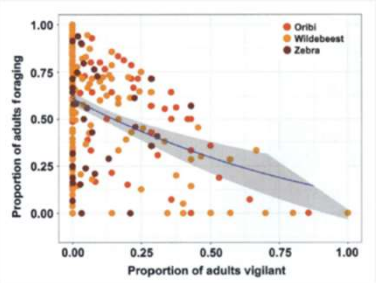
Example: aggregation decreases predation risk

Why groups give protection against predation?

The relati… responses: a test with multiple p…

Scott Creel, Egil Droge, Jamie M'soka, Dean Sam, Matt Becker, Dave Christianson, and Paul Schuette

Fewer worries, more food

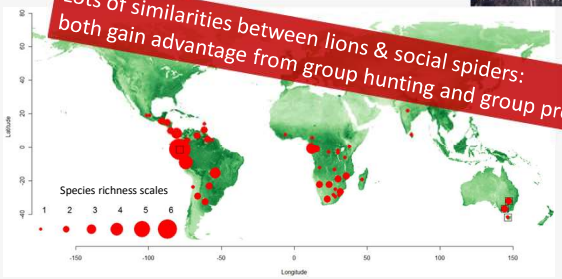


Social spiders (mostly tropical)

- Evolved independently many times (but rare among spiders)
- Occur especially in **hot arid areas with high productivity** (wet nets favour growth of contagious fungal pathogens)
- **Cooperative hunting of larger prey, antipredator protection** (e.g., against tree ants)

Example: a colony of the social spider *Stegodyphus dumicola*, Namibia

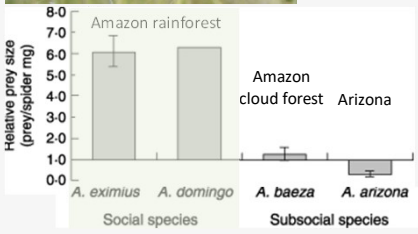
Lots of similarities between lions & social spiders: both gain advantage from group hunting and group protection



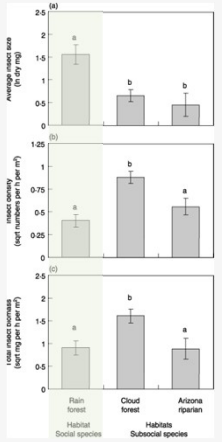
Frontiers in Ecology & Evolution 2015

Social spiders are hunt larger prey than nonsocial spider

Cooperative catching of a large grasshopper



Prey characteristics in habitats



Journal of Animal Ecology 2007

Social spiders (more info)

- **Female biased sex ratios**, already at the level of eggs (8–17% of the colony is male)
- **Almost no division of labour**, though in some species only a fraction of females in a colony may reproduce
- Too large colonies suffer from increased intraspecific competition & parasitoid pressure (wasps)
- **Highly inbred and isolated**, no migration and exchange of individuals among colonies (strange!!!); in contrast, bees and ants have nuptial flights (a bee queen has sevaral sexual partners)
- **Colonies reproduce by budding** (like yeast), which leads to genetic differences between colonies (genetic drift, divergence)
- Colonies suffer a very **high failure rate**, 'spider plagues' are commonplace (e.g., in *Anelosimus eximius* from South America, 20–70% of colonies per generation are lost!!!)

Current Biology 2007

Apes that „came down tropical forest trees to live on savanna"

Around 7 mln years ago: one of the branches of Apes (*Hominoidea*) started to utilize more intensivelly savannas (climate changes caused droughts and shrinking of tropical forests)

New challenges: open grasslands, direct sun, water shortage, increased predation – few trees for escape & no canine teetch or claws for defence

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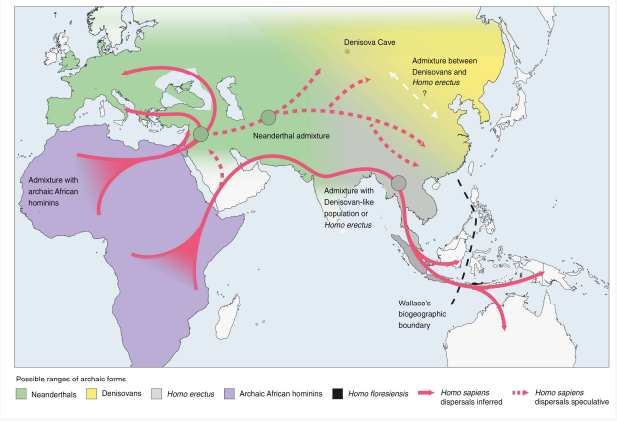
Evolutionary response:

- Vertical posture (cooling down the brain, larger horizon), which ultimatelly affected our ability to use tools (free hands)
- Good tolerance of water shortage
- Cooling down by sweating
- **Living in larger groups**
  increased antipredator defence
  increased hunting efficiency
  increased competitiveness with smaller groups

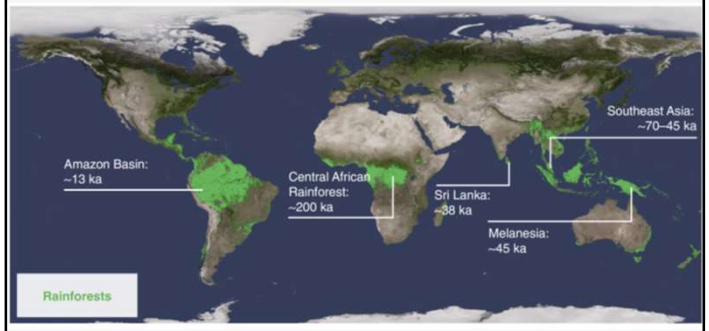
African savanna-adaped *Homo sapiens* expanded worldwide (70–50,000 years ago?), with some migration pathways through tropics

re-entering tropical rainforests led to new adaptations



NATURE HUMAN BEHAVIOUR | VOL 2 | AUGUST 2018 | 542–550 |

For how long *H. sapiens* has inhabited tropical rainforests?



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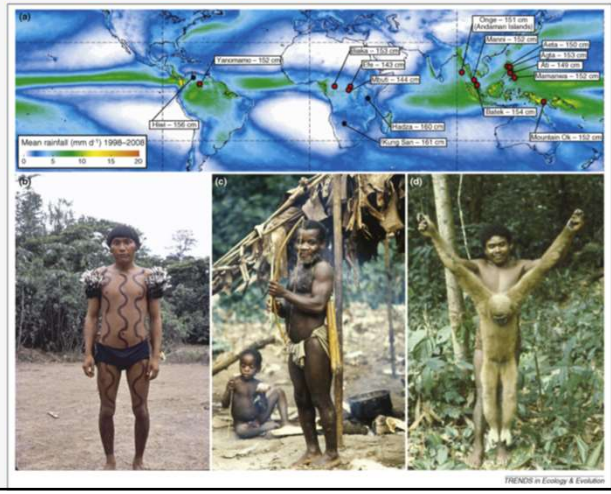
Re-entering tropical rainforests led to new adaptations: smaller size



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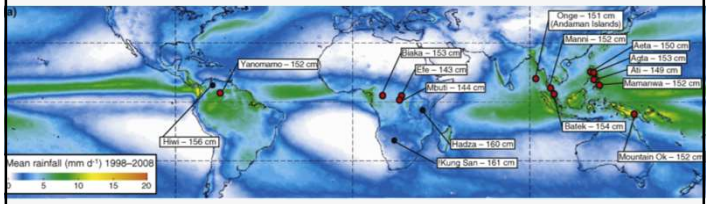
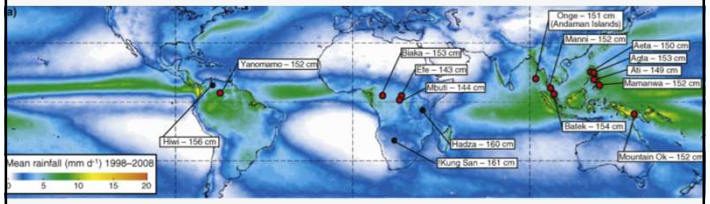


But, why smaller body size in rainforest?

- lower caloric requirements (rainforests as poor food source for hunter-gatherers)
- better thermoregulation (rainforests are hot and humid, small size gives relatively larger body surface area)
- better mobility & foraging, including tree climbing for honey (lower costs of locomotion – no need for crouched posture, lower mass while climbing, fewer injuries while falling down)

Trends in Ecology & Evolution 2009

Re-entering tropical rainforests led to new adaptations: smaller size



But, why smaller body size in rainforest?

Adaptive life history response to high mortality rates in rainforest

Trends in Ecology & Evolution 2009

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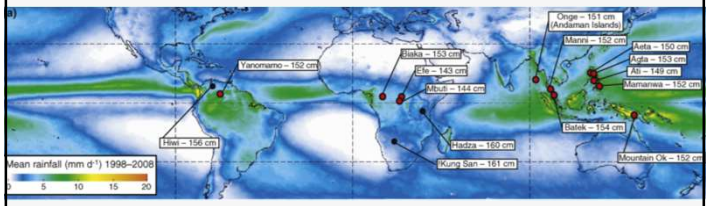


Earlier maturation at smaller size: an adaptive life history response to shorter life perspective

- **Groups of hunter gatherers from Africa & Southeast Asia**

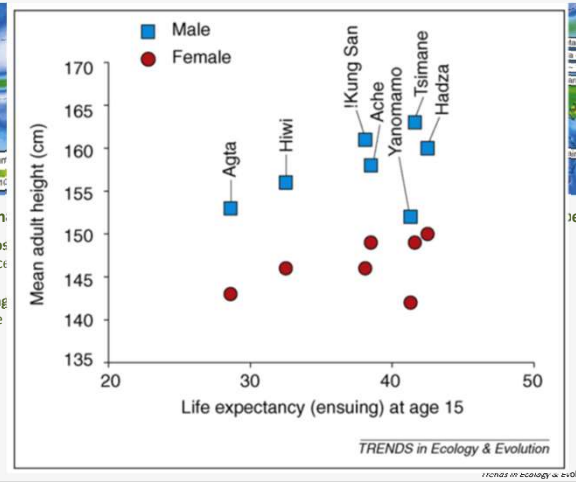
the chances of surviving to age 15 are **30-51% in rainforest** vs **59-76% in non-rainforest** areas

- **Among different groups of hunter gatherers from rainforest**

A positive link between body size and life expectancy

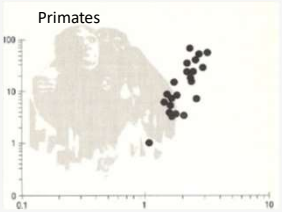
Trends in Ecology & Evolution 2009

Re-entering tropical rainforests led to new adaptations: smaller size



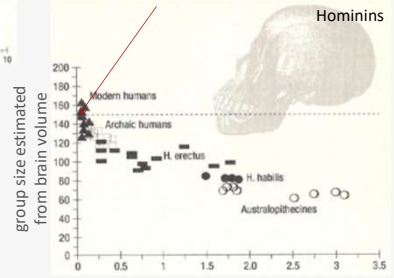
Trends in Ecology & Evolution 2009

Social life requires larger brains (social brain hypothesis)

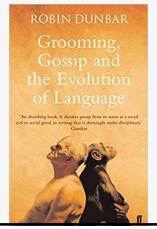


Neocortex is a brain part built of 6 layers, which occurs exclusivelly in mammals

A group of 150 people is the so-called Dunbar's number



Robin Dunbar
1947, UK



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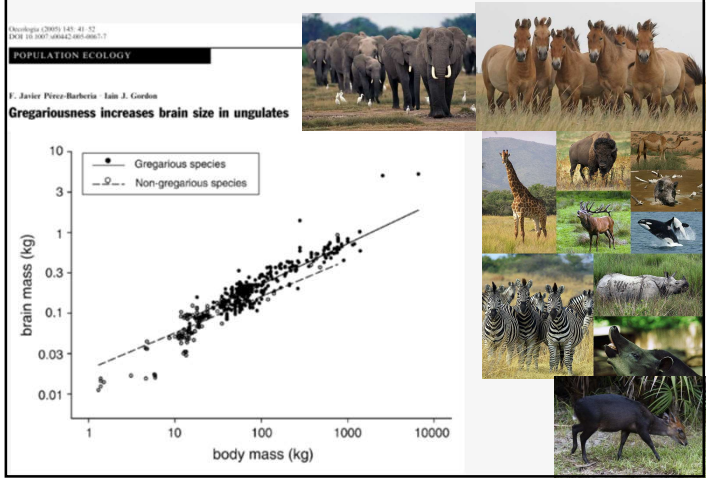

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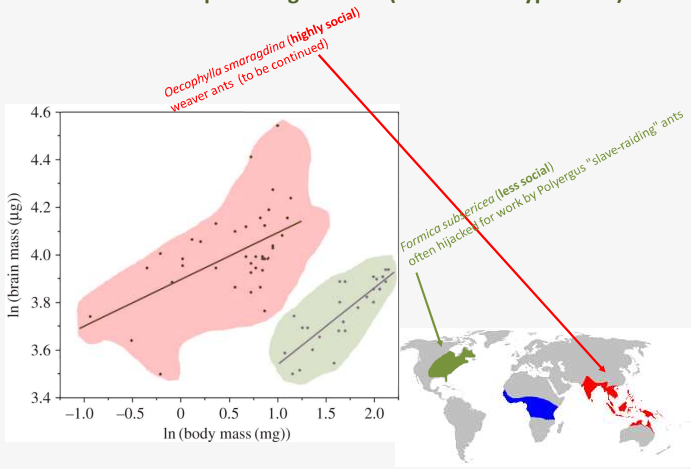


Proc.R.Soc. B 2016

But why large brain in social life?

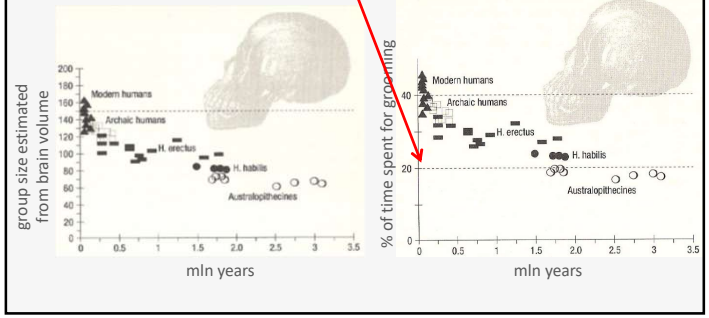
- Groups with complicated social structures (not gorups of anonymous individuals e.g. schools of sardines)
- Group members have to know each other, remember and understand interactions within a group
- Group living requires a mechanism that creates bonds, builds companionships & coalitions, reinforces social structures, resolves conflictcs and punishes freeriders

The **evolution of language** created a new method of grooming, which allowed *Homo sapiens* to **increase the size of groups**

Gossiping in groups of 3 people brings back the „grooming time" to the acceptable level of 20%

Brain size and group size were increasing in tandem

As groups grew in size, more time was required for „keeping bonds", limiting the maximum size of a group



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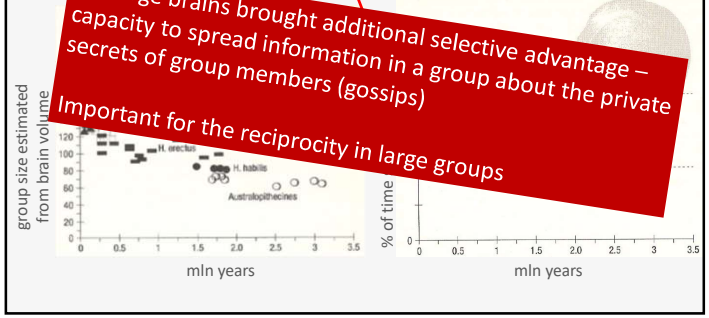
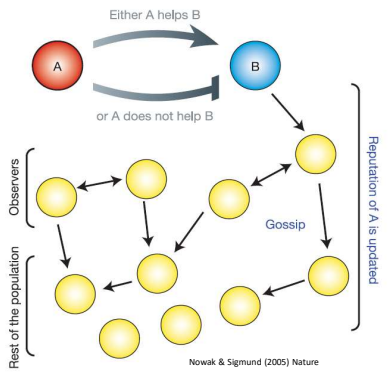
So, large brains brought additional selective advantage – capacity to spread information in a group about the private secrets of group members (gossips)

Important for the reciprocity in large groups



In the course of evolution, *Homo sapiens* accumulated genes responsible for taking care about **REPUTATION**

- Cooperative social life requires reciprocity and punishment of egoists
- Larger groups of prone to „social parasites" (high anonymity)
- Gossiping is a **social punishment/reward system that maintains indirect reciprocity**



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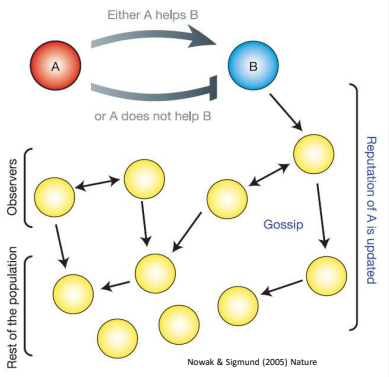


- **Reputation** as a prescious resource (difficult to build up, but easy to lose)
- Building repution in social media by collecting „likes", origin of moral values, religions with „Big Gods", justice, honor, prestige, „co ludzie powiedzą", police, law, prisons, etc.

Helping each other can evolve as an adaptation, even among unrelated group members, via a reciprocal mechanism if:

- detecting & punishing „social parasites" is possible
- [illegible] looking for help is an „everyday problem"

Polish proverb (similar sayings in your country?)
Jak Kuba Bogu, tak Bóg Kubie

Robert Trivers
born 1943, USA

MARCH 1971] THE QUARTERLY REVIEW OF BIOLOGY [VOLUME 46

THE EVOLUTION OF RECIPROCAL ALTRUISM

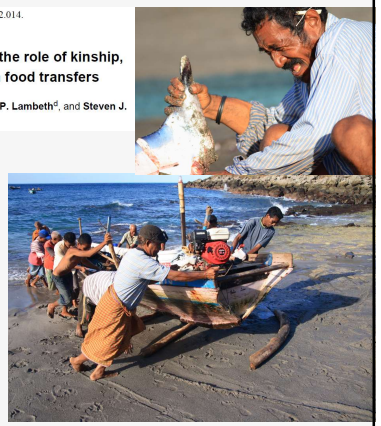
BY ROBERT L. TRIVERS

Biological Laboratories, Harvard University, Cambridge, Mass. 02138

Anim Behav. 2013 May ; 85(5): 941–947. doi:10.1016/j.anbehav.2013.02.014.

Chimpanzees share food for many reasons: the role of kinship, reciprocity, social bonds and harassment on food transfers

Joan B. Silk[a,b,*], Sarah F. Brosnan[c,d], Joseph Henrich[e], Susan P. Lambeth[d], and Steven J. Shapiro[d]



Chimpanzees: unrelated group mambers often **share food**, and one of the reasons is reciprocication & building social bonds

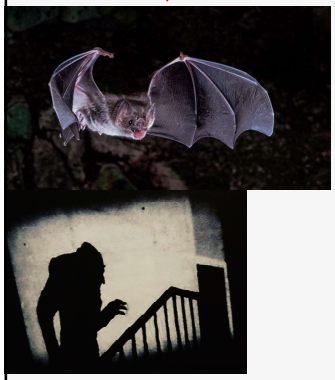
Indonesia: Lamalera whalers hunt communally and they **share prey** according to their involvement in hunting and family bonds

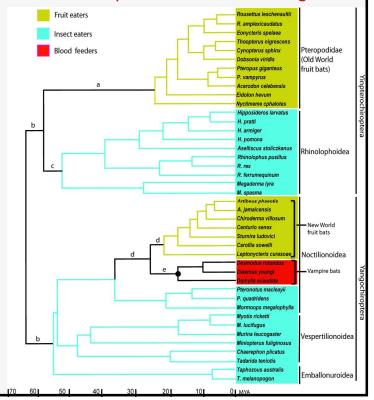
Vampire bats from South America share blood meals

- Mutual benefits – reciprocity (it is not real altruism)
- Small & stable groups (only females)
- Hunting individually
- No blood means rapid death
- You must be lucky to find a host - the need for help occurs frequently
- Cognitive capacity to remember neighbours & their behaviours
- Mechanism of sanctioning egoists – suspension of help

Vampirism is a highly specialised feeding strategy - the only mammal that feeds exclusively on blood

Blood feeding evolved in bats only once, ca 20 mln years ago
3 extant species of vampires and all in tropical forest
so ... the Transylvanian Nosferatu from a mountain temperate forest must be a legend





Mol. Biol. Evol. 2010

Vampirism is a highly specialised feeding strategy - the only mammal that feeds exclusively on blood

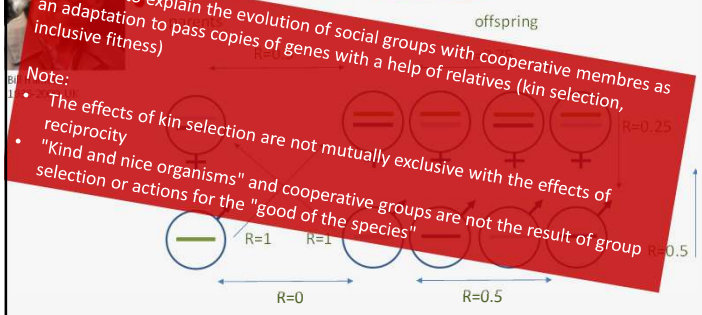
- Unclear origin (a kind of parasitism). Perhaps their ancestors were feeding on insects that were attracted to the wounds of mammals, and this way they „tasted the blood"
- Physiological adaptations to cope with high doses of iron, proteins & liquids
- Can walk & jump (no other bats do this)
- Lost the sweet taste receptor (the gene is silent – pseudogene)
- Echolocation, but also use odour & infrared sensing (the only other vertebrates detecting infrared radiation are boas, pythons and pit vipers, **all tropical**)

Hymenoptera (ants, bees, wasps, bumblebees) have a haplo-diploid system of sex determination & evolved eusociality many times independently

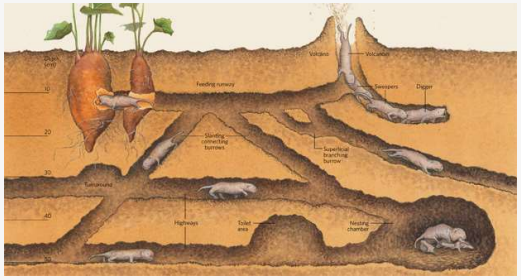
My equation:
Fitness gain in a supported individual · R > Fitness loss in a helper

It is easier to explain the evolution of social groups with cooperative membres as an adaptation to pass copies of genes with a help of relatives (kin selection, inclusive fitness)

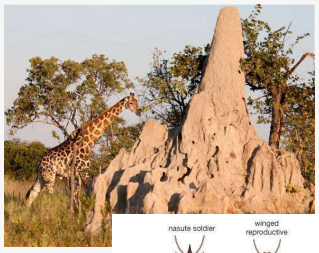
Note:
- The effects of kin selection are not mutually exclusive with the effects of reciprocity
- "Kind and nice organisms" and cooperative groups are not the result of group selection or actions for the "good of the species"

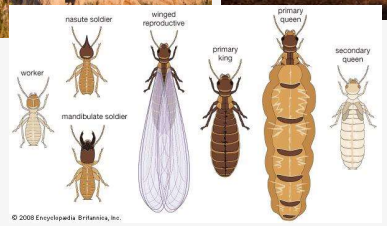


African mole-rats (2 species) are the only eusocial mammals



Eusocial animals – the extreme example of gregariousness explained by **kin selection & inclusive fitness**





Agriculture communities of termites

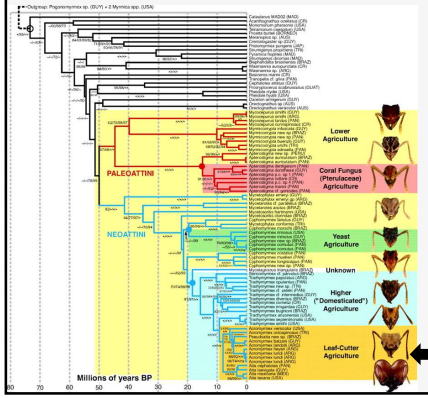
Leaf cutting *Atta* ants (Neotropics) – eusocial societies with agriculture and domestication

Excavation of an *Atta* nest with cement casts of corridors and underground chambers
Atta ants form huge colonies (10^3–10^6 workers) with many castes

Insect. Soc. 2012

Agriculture (a kind of symbiosis) evolved independently in humans, bark beetles, termites and ants

Among ants
agriculture originated 50 million years ago in a tribe of Attini from Neotropics
food source – cultivated fungi („fugus gardens" – convergent evolution with termites & bark beetles, humas also cultivate fungi)

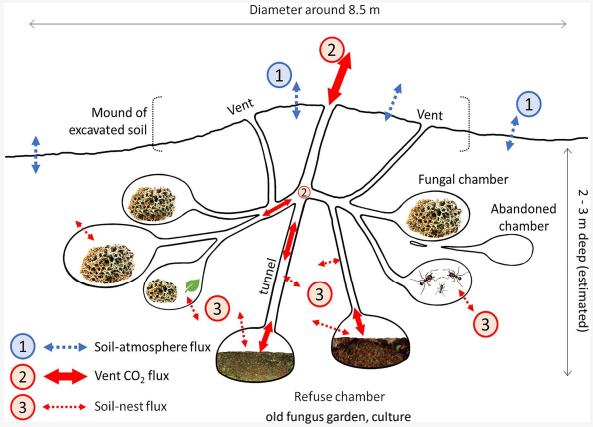


Some general characteristics of the leaf-cutter ant strategy

- Obligate mutualism with fungi
- Fungi species endemic to ant nests (total dependence)
- Cultivated fungi (cultivars) specific to each colony (high genetic divergence among colonies)
- Queens bring a sample of the native cultivar when founding new nests

10 milion years ago
the most sophisticated agriculture system in leaf-cutter ants (*Atta* & *Acromyrex* ants)

Atta leaf-cutters: specialized workers harvest leaves and manage the nest (queen, larvae, fungus gardens, wastes, air ventilation, parasites, etc.)



JGR: Biogeosciences 2018

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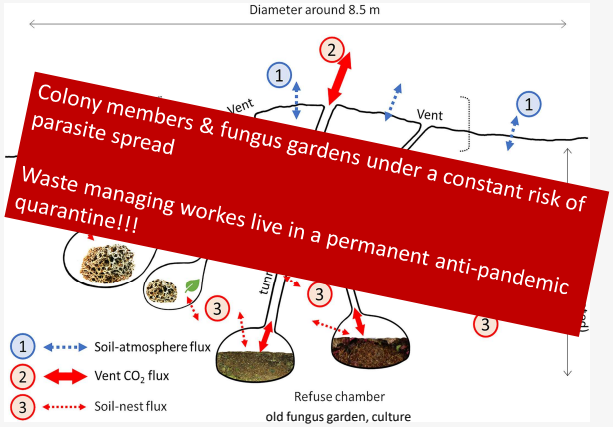


Colony members & fungus gardens under a constant risk of parasite spread

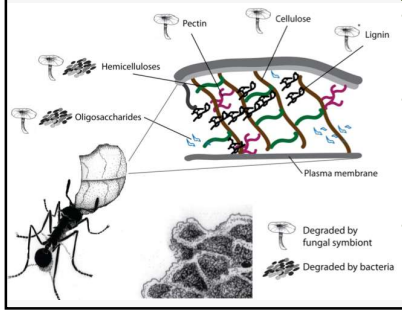
Waste managing workes live in a permanent anti-pandemic quarantine!!!

JGR: Biogeosciences 2018

Plant polymer degradation in *Atta* fungus gardens

Fungi - a dominant role in breaking down cellulose, lignin, and pectin

Bacterial community & fungi - break down simple oligosaccharides and hemicelluloses



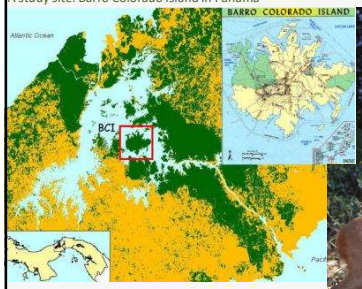
Ants

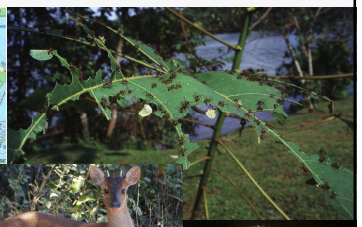
- Feed & disperse the fungus, selecting plants that do not produce toxins harmful to the fungus
- Supply the fungus with nitrogen sources (they put rectal fluid on leaves, which contains amino acids & enzymes that help to generate more nitrogen supplies)
- Protect fungi from parasites (fungus *Escovopis*)

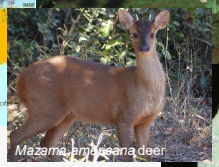
Applied and Environmental Microbiology 2013

Atta ants are important, but not dominant herbivores in Neotropics (against some earlier views)

A study site: Barro Colorado Island in Panama







Colonies of *A. colomica* in the island

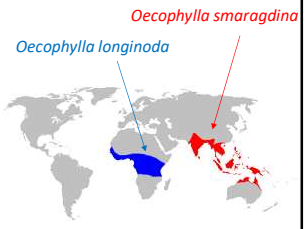
- harvested 13.2 tons of biomass per year
- deposited 9.4 tons of refuse material per year
- annual consumption 266 kg/colony = annual consumption of a single *M. americana* deer

Total herbivory rate estimated as 1.7 % of the annual biomass leaf production in the island

Biotropica 2007

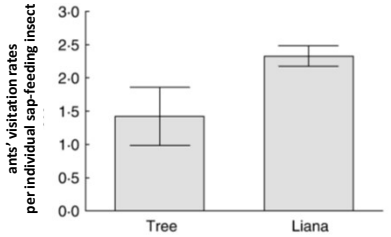
Weaver ants (highly social, big brains)

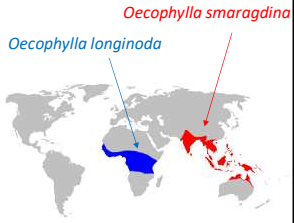
- Rainforest, mobile hunter-gatherers, occupy tree canopies
- Temporary nests built by binding leaves together with silk (**weaving**) produced by larvae
- Independent of plant-produced domatia and food rewards, and often associate with nonspecialized host plants
- Polydomy: many spatially separated nests occupied by a single colony – similar to the *Camponotus* from rattans (to be continued)
- Predators & collectors of honeydew from sap-feeding insects (aphids, scale insects)



Weaver ants

O. smaragdina prefered honeydew produced by insects feeding on the sap of lianas
Lianas provide more sap and higher quality sap than trees





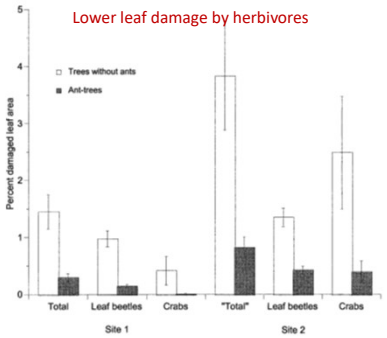
J. Animal Ecology 2002

Weaver ants

Interestingly, trees associated with *O. smaragdina* have 3-20 times more benefits than costs
(data for mangrove forest, Thailand)

Benefits imposed by wevaer ants

Lower leaf damage by herbivores



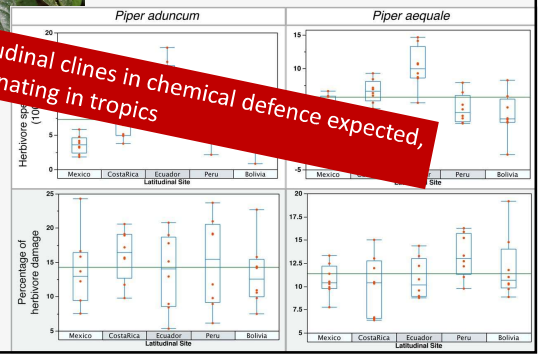
Costs imposed by weaver ants

- loss of sap (ants exploit sap-feeders)
- loss of leaves caused by nest building

Biotropica 2004, 2006

Herbivore pressure intensifies in tropics & culminates in lowland rainforest

Why herbivore richness increased towards the equator, while the herbivore damage did not?



Latitudinal clines in chemical defence expected, culminating in tropics

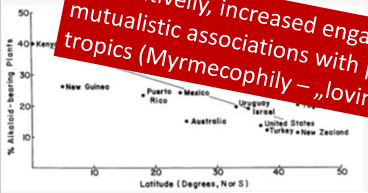
PNAS 2012

Herbivore pressure intensifies in tropics & culminates in lowland rainforest

Yes, indeed!

In ... protect themselves by investing in defences (e.g., alkaloids)

Alternatively, increased engagement of plants in mutualistic associations with predatory ants expected in tropics (Myrmecophily – „loving the ants")



Survey of New Guinea Plants for Alkaloids in Relation to Community Type

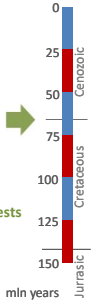
Community	Species Tested for Alkaloids: Positive	Species Tested for Alkaloids: Negative	Alkaloid-bearing Species (%)	Mean ± SE Alkaloid Content (% Dry Wt)*
Weed	3	47	6.0	...
Ocean strand	7	51	12.1	.06 ± .03
Monsoon forest	5	38	11.6	.17 ± .13
Lowland rain forest	58	212	21.5	.57 ± .18
Foothill rain forest	38	272	12.2	.34 ± .11
Montane rain forest	68	368	14.6	.22 ± .07
Montane cloud forest	3	54	5.3	...
Subalpine forest and scrub	0	12	0.0	...
Secondary alpine grassland	0	86	0.0	...

American Naturalist 1976

How old is myrmecophily? Is it linked to tropics?

The oldest biome on Earth originated 100 mln years ago

Tropical rain forests



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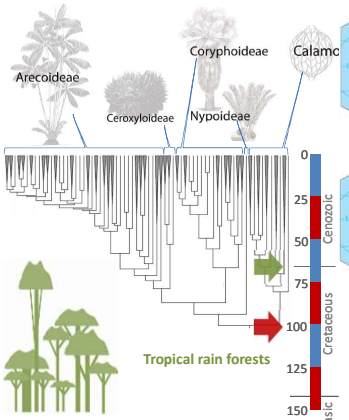
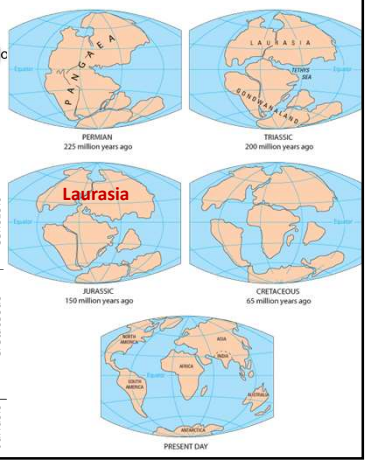


Tropical rain forests



Couvreur et al. (2011) BMC Biology
Couvreur & Baker (2013) BMC Biology

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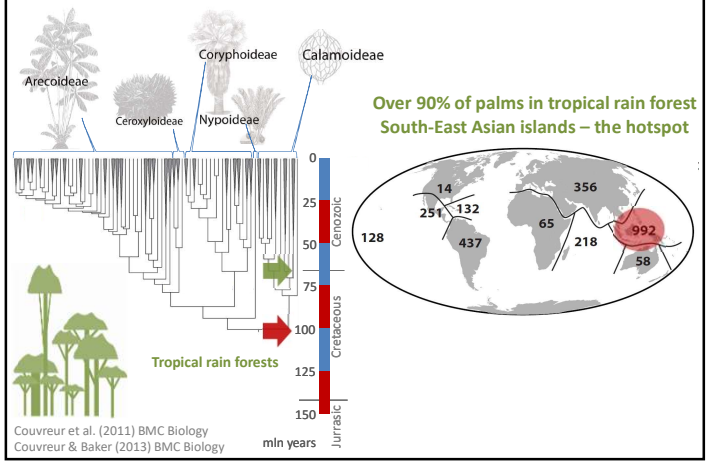
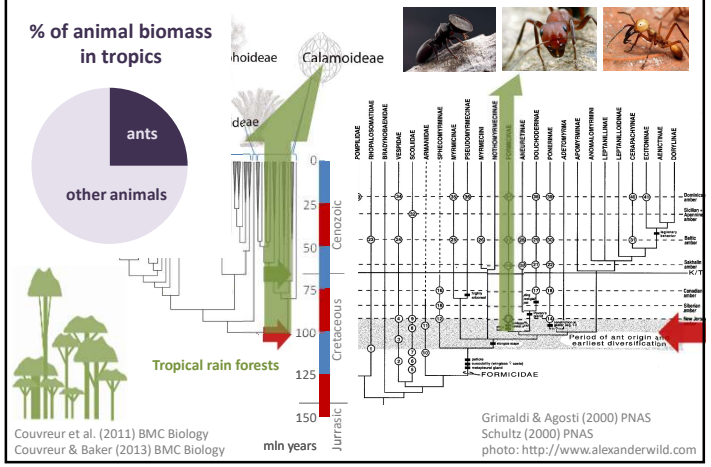


Couvreur et al. (2011) BMC Biology
Couvreur & Baker (2013) BMC Biology

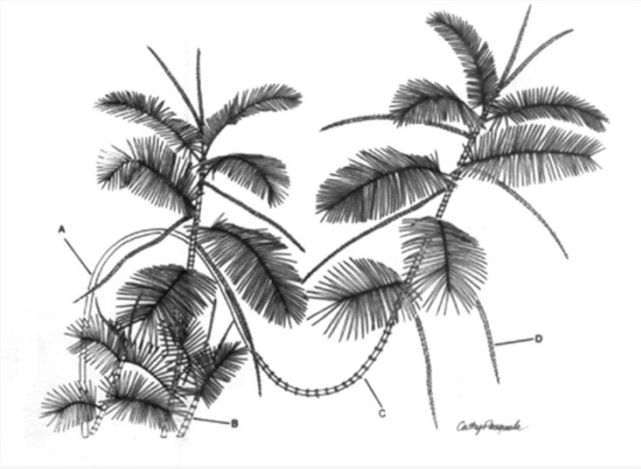
Palms and ants have coevolved for 100 mln years



Couvreur et al. (2011) BMC Biology
Couvreur & Baker (2013) BMC Biology

Grimaldi & Agosti (2000) PNAS
Schultz (2000) PNAS
photo: http://www.alexanderwild.com

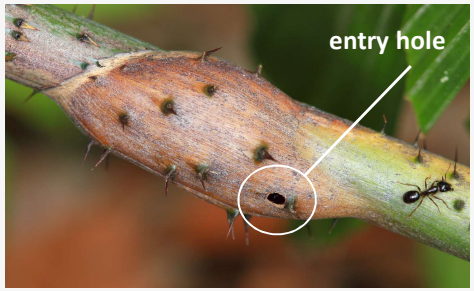
Lina-like palms - rattans (only South-East Asia)



Many palms associate with ants, but information on such partnerships is primarily anecdotal

Korthalsia furtadoana **rattans with their partner ants (ants have multiple nests inside small domatia - polydomy)**

A case study from our tropical field courses in Borneo



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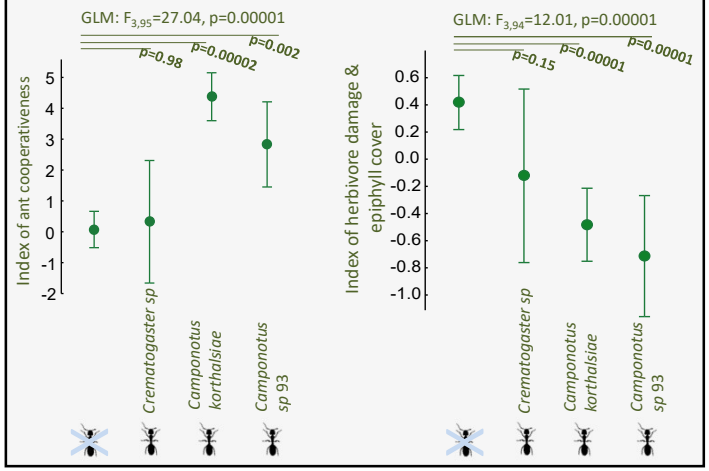
***Korthalsia furtadoana* rattans**

Domatia evolved independently in 10 out of 27 rattan species of *Korthalsia*

Dransfield (2003)

Camponotus ants: cooperative behaviours - healthier leaves



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- Bright: defense against enemies and resource acquision
- Dark: intraspecific competition, epidemics, exploitation by free riders

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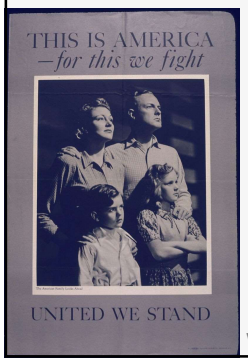
4) Mutualistic associations between species (*Camponotus* ants – rattans or *Atta* ants – fungi) also driven by reciprocity (relatedness for sure not involved here). So in princile, they are not fundamentally different from e.g. cooperating vampire bats

Some final thoughts

Tropics are especially rich in the primary ecological drivers of social evolution:



- **enemy**: **predators, parasites, competitors**
- **patchy distribution of resources**

Unfortunatelly, still valid

World War II - American slogan