
Tropical societies, with strong emphasis on ants
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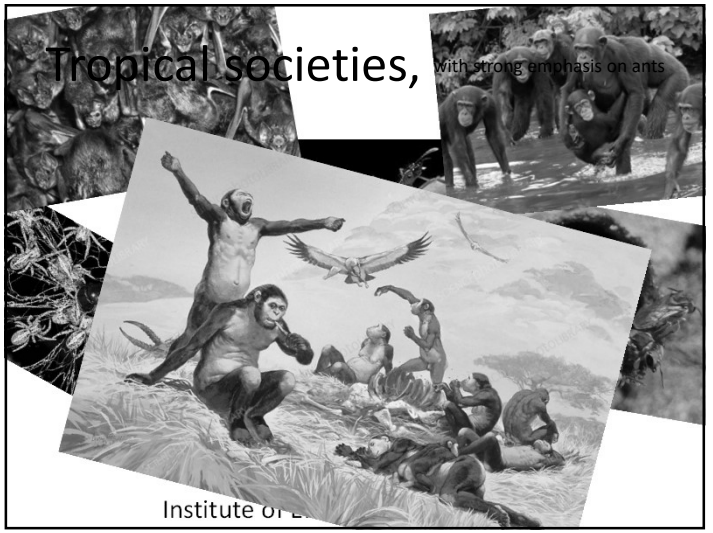
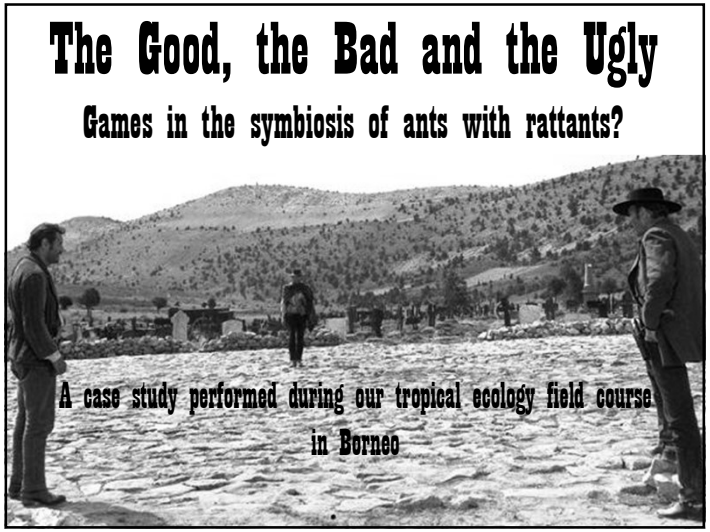
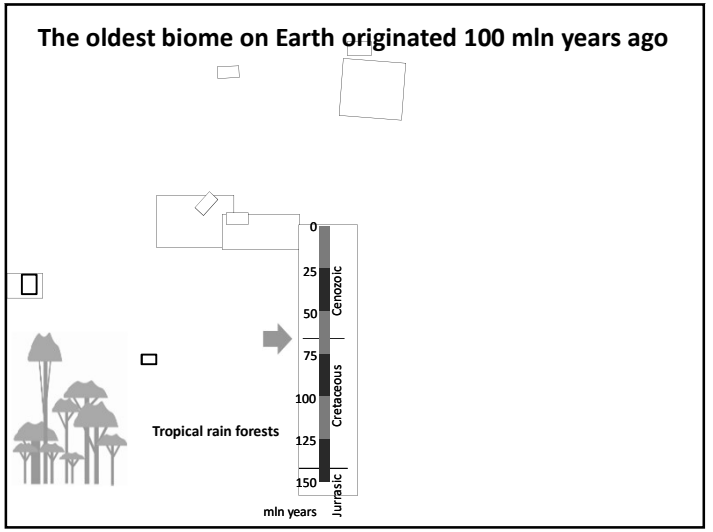
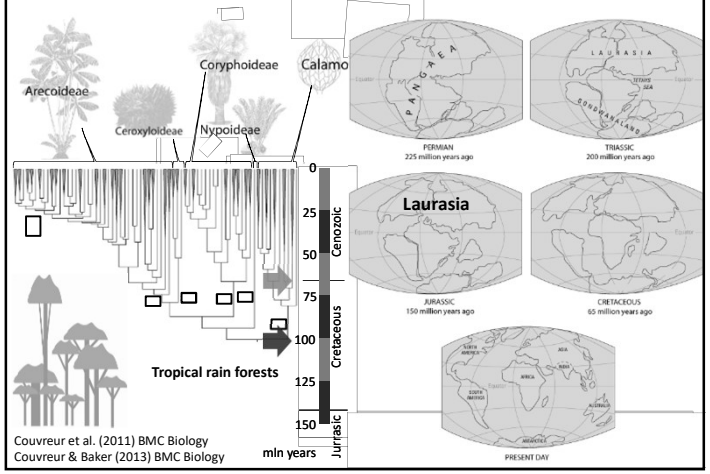

Tropical societies, with strong emphasis on ants


The Good, the Bad and the Ugly
Games in the symbiosis of ants with rattants?
A case study performed during our tropical ecology field course in Borneo

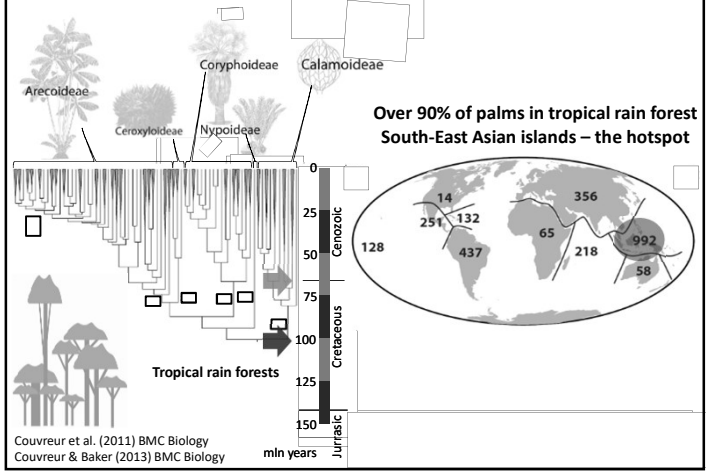

The oldest biome on Earth originated 100 mln years ago
Tropical rain forests
0
25
50
75
100
125
150
Cenozoic
Cretaceous
Jurrasic
mln years

The oldest biome on Earth originated 100 mln years ago



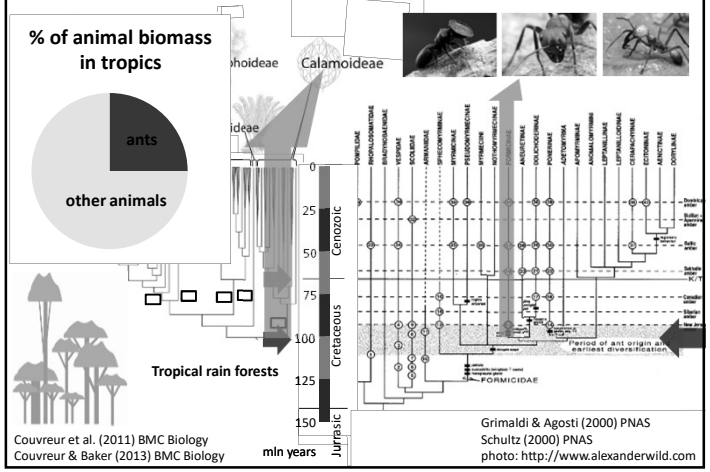
Couvreur et al. (2011) BMC Biology
Couvreur & Baker (2013) BMC Biology

The oldest biome on Earth originated 100 mln years ago



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

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

***Korthalsia furtadoana* rattans**

inhabit lowland dipterocarp tropical rain forest

endemic to parts of Borneo

climbing strategy similar to lianas

lack secondary growth (monocots)

leaf ocrea plays a role in the mechanical properties of the stem

chambers (domatia) formed by leaf ocrea are used by nesting ants

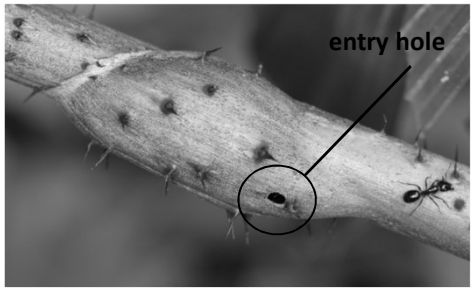
Many palms engage in partnerships with ants, but information on such partnerships is primarily anecdotal

Korthalsia furtadoana **rattans**

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

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

Korthalsia furtadoana **rattans**



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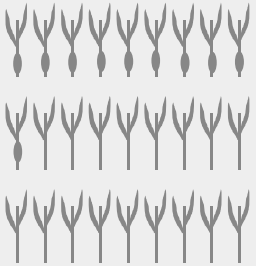
Korthalsia furtadoana **rattans**

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

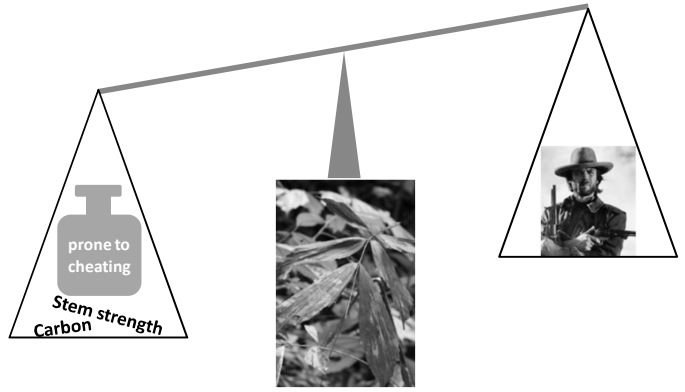


Dransfield (2003)

Partnering with ants, but
do they play the Good, the Bad or the Ugly?

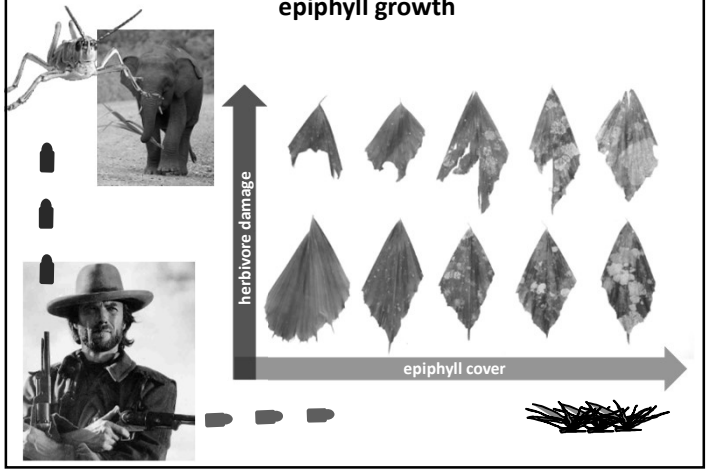
Ugly **Good** **Bad**

Partnering with ants, but
do they play the Good, the Bad or the Ugly?



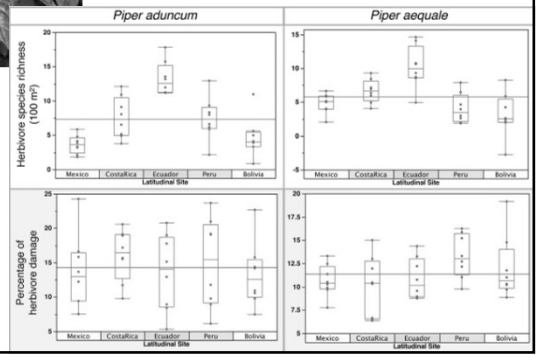
Miler, Yahya & Czarnoleski (2016) Journal of Tropical Ecology
Edwards et al. (2010) Oikos

Leaf health deteriorates due to herbivory and epiphyll growth



Herbivore pressure intensifies in tropics & culminates in lowland rainforest

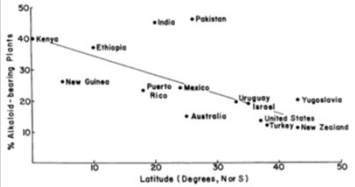
Why herbivore richness increased towards the equator, while the herbivore damage did not?



PNAS 2012

Herbivore pressure intensifies in tropics & culminates in lowland rainforest

In response, plants protect themselves by investing in defences (e.g., alkaloids), including an engagement in the **symbiotic interactions with predatory ants**

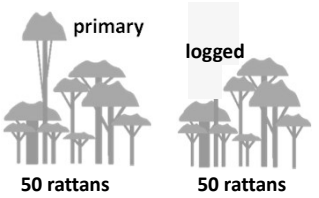


SURVEY OF NEW GUINEA PLANTS FOR ALKALOIDS IN RELATION TO COMMUNITY TYPE

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

Leaf health compared in rattans with and without patrolling ants



ant presence

measuring height

experimental herbivory & epiphyll growth – scoring defensive responses of ants

evaluating leaf health on a leaf sample

Defensive responses of ants to experimental herbivory & epiphyll growth

Herbivory

cutting leaflets

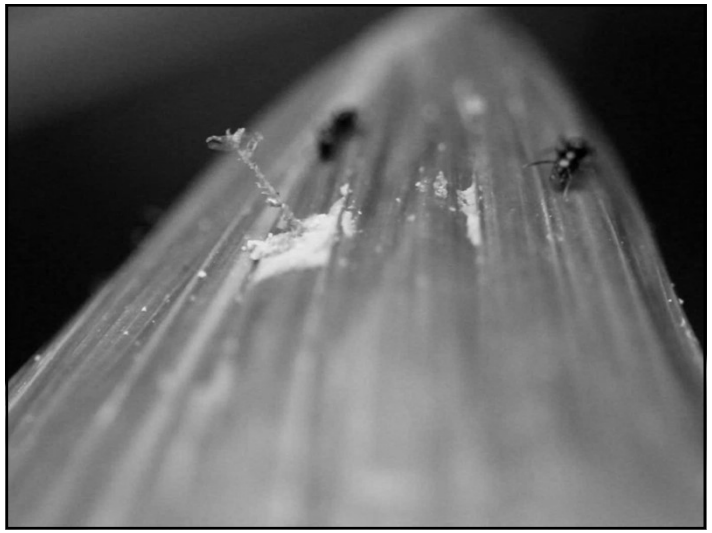
measuring attack rates toward termites placed a leaflet

Defensive responses of ants to experimental herbivory & epiphyll growth

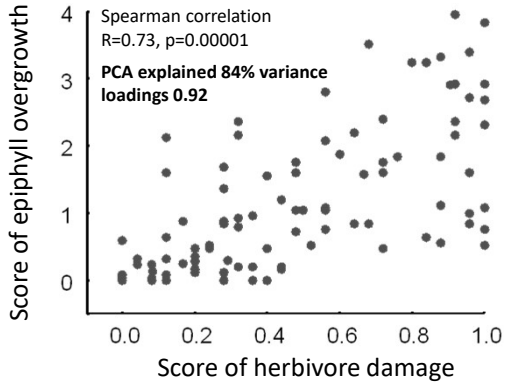
Epiphyll growth

glueing stems of the moss to leaflets with the plasticine

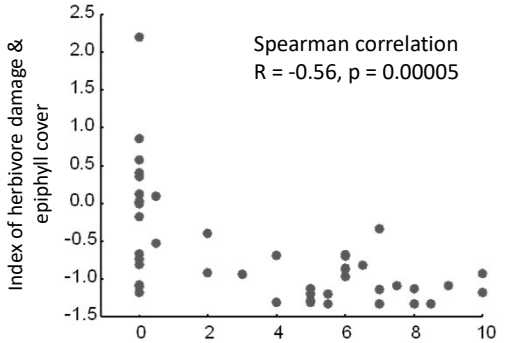
measuring rates of moss removal after 24h



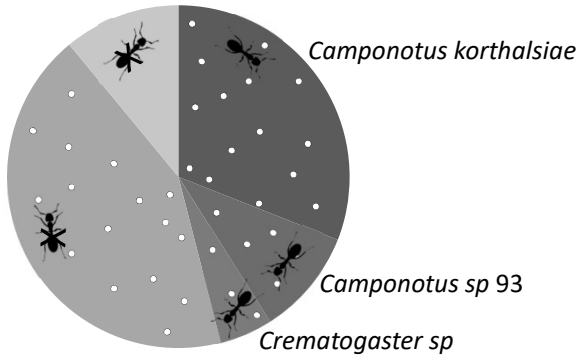
Rattans that were more damaged by herbivores, were also more overgrown by epipylls



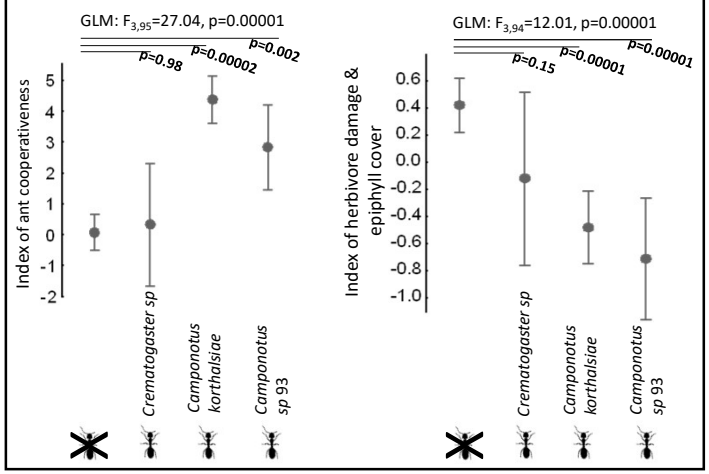
Rattans that partnered with cooperative ants had healthier leaves



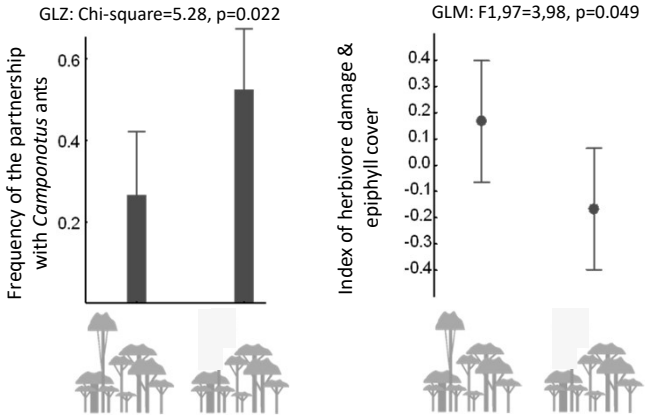
Most rattans had entry holes in domatia, but only ca. 50% rattans had ant partners (3 ant species)

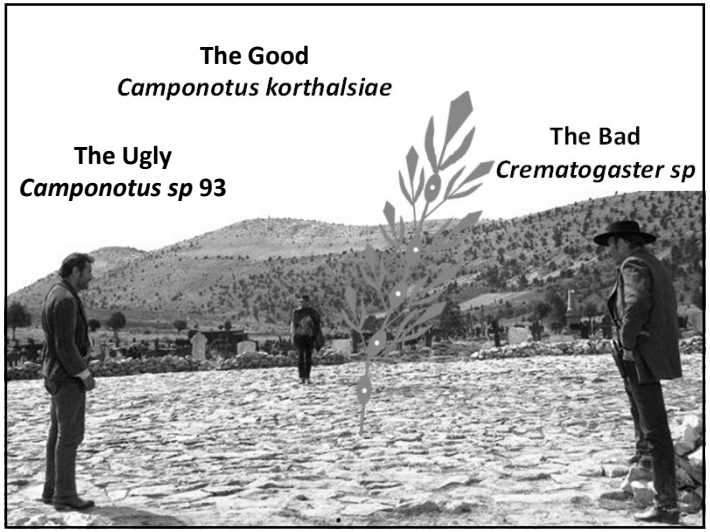


Camponotus ants: cooperative behaviours - healthier leaves



Logged forest: more frequent partnership with *Camponotus* ants & healthier leaves





Solo or together? Some background

Two major evolutionary drivers of social life (to be continued)

- reciprocal mechanism: mutual benefits - I help you now, you help me later (my fitness **indirectly** linked to others' fitness)
- kin selection mechanism: by helping relatives, I spread my own genes (inclusive fitness; my fitness **directly** linked to others' fitness)

Solo or together? Some background

levels of gregariousness

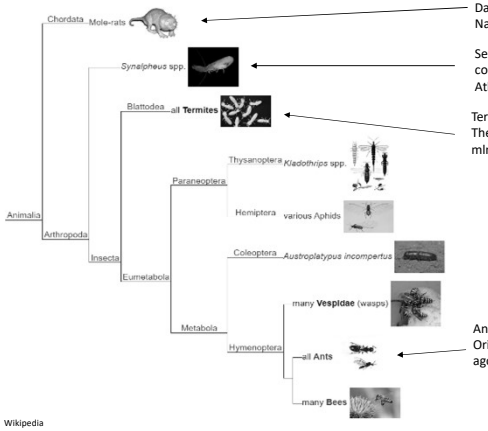
Single | Aggregation | Supportive group | Society

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)

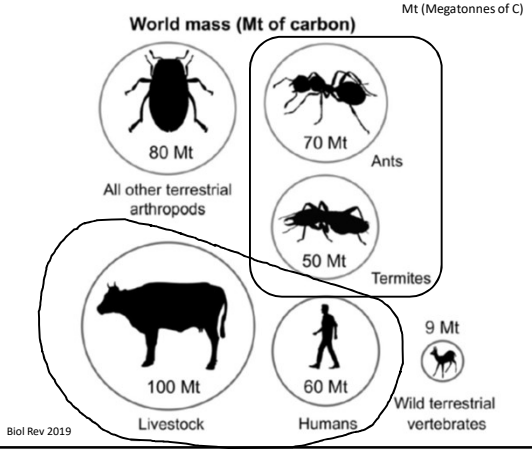
Several species of sponge-dwelling coral reef shimps (Central - Western Atlantic)

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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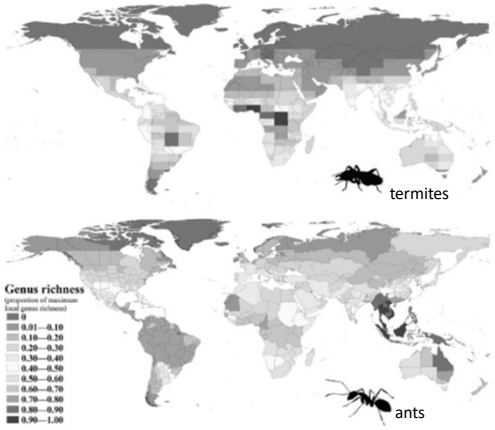
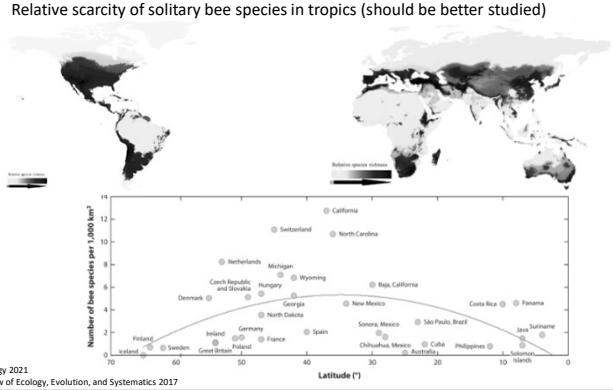


Biol Rev 2019

Only a moderate numer 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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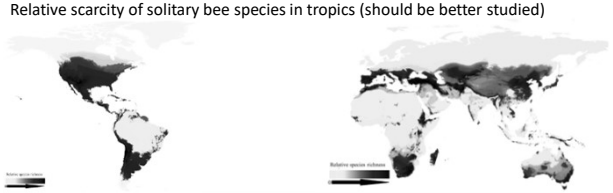


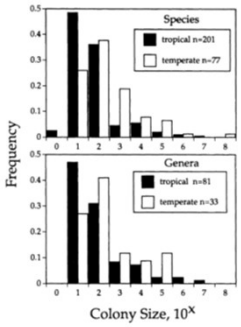
Latitudinal clines in polination ecology (some generalisations)

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

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

Tropics
especially **rich** in the primary ecological drivers of social evolution – threats & enemy (predation, competition, parasitism), and characterised by **patchy** distribution of resources (e.g., recall our discussions on the high level of biodiversity, which also means that representatives of the same species are far apart)

Social life affords colony members **defense against enemies**, and allows them to gain advantage from **superior foraging methods**

Solo or together? Some background

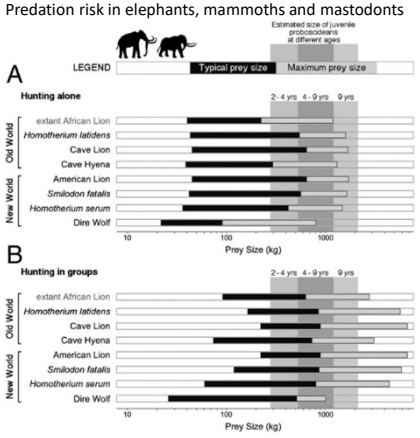
Benefits of staying together
- a member of a cooperating group can more effectively defend itself against enemies and find food

Costs of staying together
- increased intraspecific competition
- risk of parasite spread
- nice and helpful individuals („altruists") are prone to exploitation by „social parasites" - free riding outlaws/egoists



Example: group hunting increases the prey size (now and in the past)

Predation risk in elephants, mammoths and mastodonts



Predicted typical (dark blue) and maximum (light blue) prey size ranges (horizontal bars) for the extant African lion (Panthera leo) and large extinct Pleistocene predators superimposed on the estimated sizes of juvenile proboscideans (mammoths and mastodons) at different ages (vertical stripes).

Prey size ranges are estimated both for (A) solitary hunting and (B) group hunting. Size estimates for mammoths are based on data from living elephants. Prey size ranges for the predators were based on known relationships between prey size and predator body mass for extant large carnivores.

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†

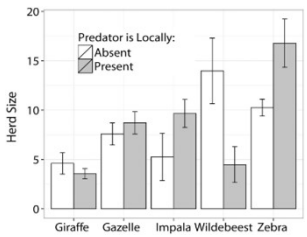
*Department of Ecology, Montana State University, 310 Lewis Hall, Bozeman, MT 59717, USA and †School of Natural Resources and the Environment, University of Arizona, 325 Biological Sciences East, Tucson, AZ 85745, USA

Animal Behaviour

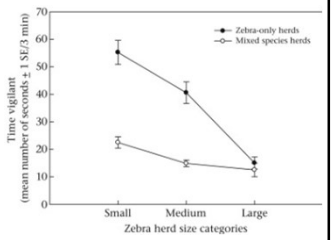
Determining the relative importance of dilution and detection for zebra foraging in mixed-species herds

Melissa H. Schmitt, Kenan Stears, Christopher C. Wilmers, Adrian M. Shrader

Predators induce herding



Larger group, fewer worries



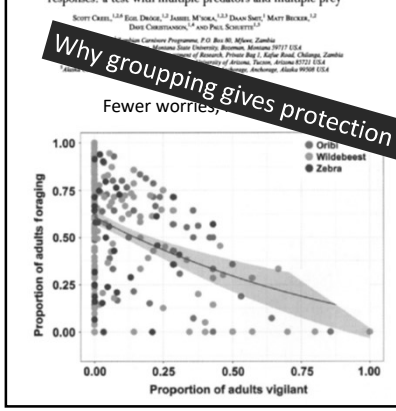
Zebras: 2-9 10-30 31-75

Example: aggregation decreases predation risk

The relationship between direct predation and antipredator responses: a test with multiple predators and multiple prey

Why groupping gives protection against predation?

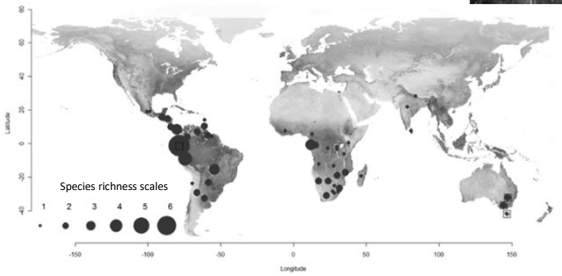
Fewer worries,




Social spiders (mostly tropical)

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

Occur especially in hot arid areas with high productivity (wet nests favour the growth of contagious fungal pathogens)

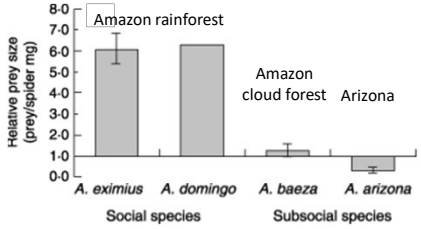


Frontiers in Ecology & Evolution 2015

Social spiders (some generalisations)

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

Cooperative catching of a large grasshopper



Journal of Animal Ecology 2007

Current Biology 2007

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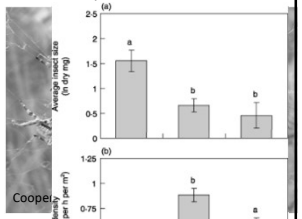
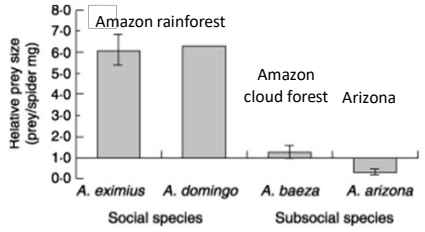
Prey characteristics in habitats



Cooper



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- **Almost no division of labour**, though in some species only a fraction of females in a colony may reproduce
- Too large colonies: increased intraspecific competition & parasitoid pressure (wasps)
- **Female biased sex ratios**, already at the level of eggs (8–17% of the colony is male)
- **Highly inbred**, no migration and exchange of individuals among colonies (strange); in contrast, bees and ants have nuptial flights
- **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: direct sun, water shortage, increased predation – few trees for escape & no canine teetch or claws for defence

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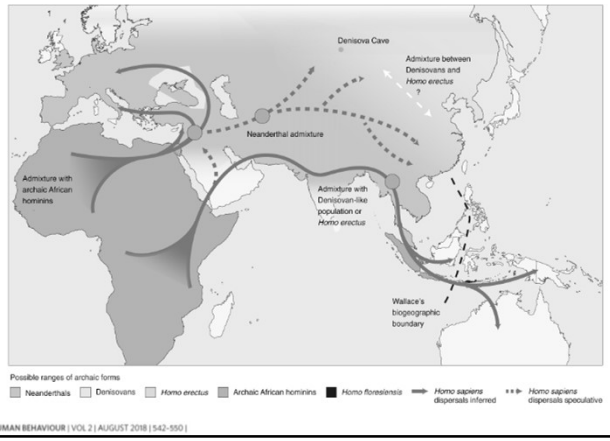
Evolutionary response:

- 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
  antipredator defence
  communal hunting
  between-group interactions (bands)

Communal net hunting in nomadic Aka pygmies (Central African Republic)

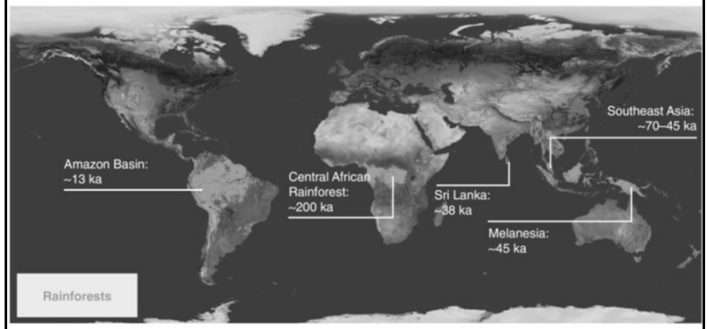
- dense tropical forest decreases visual communication during communal hunts
- hunt coordination with a help of songs

Re-entering tropical rainforests
African savanna-adaped *Homo sapiens* expanded worldwide



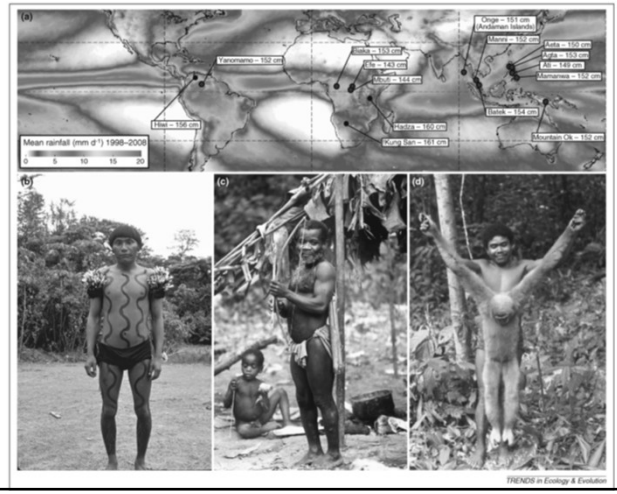
NATURE HUMAN BEHAVIOUR | VOL 2 | AUGUST 2018 | 542–550 |

Re-entering tropical rainforests
African savanna-adaped *Homo sapiens* expanded worldwide

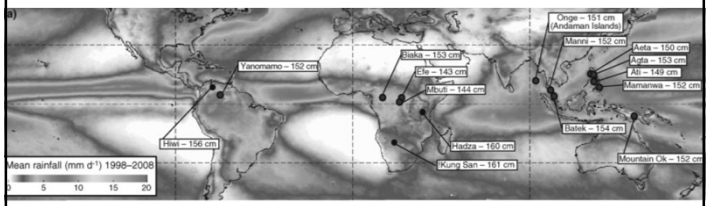


NATURE HUMAN BEHAVIOUR | VOL 2 | AUGUST 2018 | 542–550 |

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



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

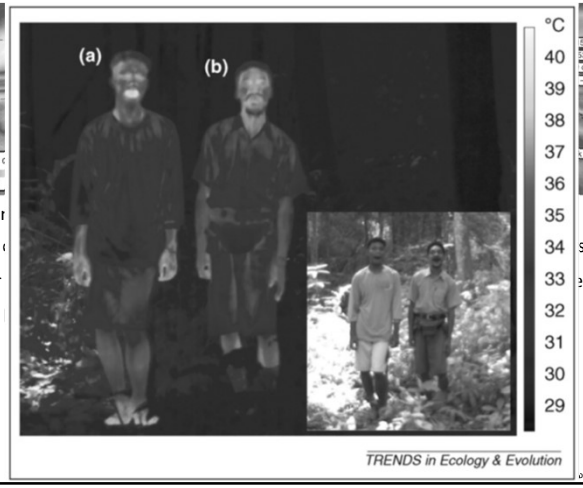


But, why reduced body size in rainforest?

- 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)

Trends in Ecology & Evolution 2009

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



But, why r
- lower
- better

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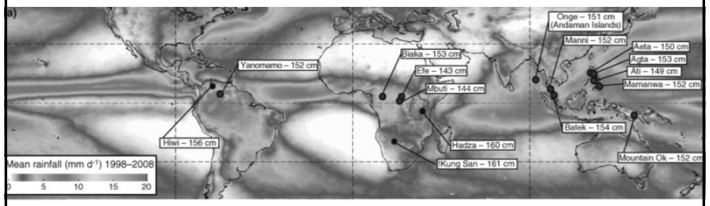
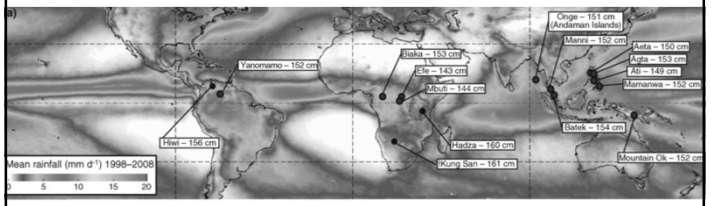


But, why reduced body size in rainforest?

- lower caloric requirements (rainforests as poor food source for hunter-gatherers)
- better thermoregulation (rainforests are hot and humid, small size gives relativelly 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)
- an adaptive life history response to increased mortality

Trends in Ecology & Evolution 2009

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



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

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

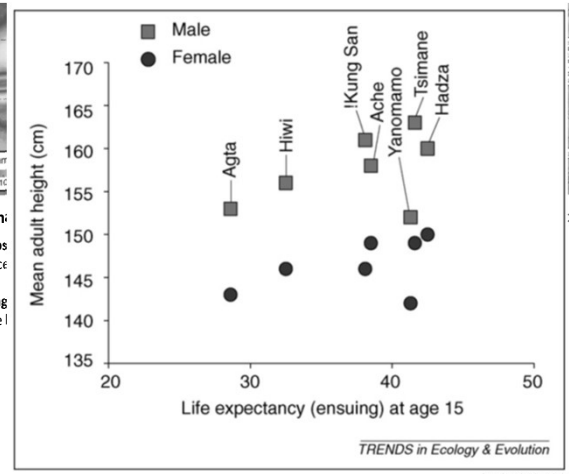
the chances of surviving to age 15 are **30-51% in rainforest** vs **59-76% in non-rainforest** areas

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

A positive link between body size and life expectancy

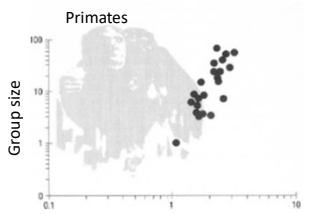
Trends in Ecology & Evolution 2009

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



Trends in Ecology & Evolution 2009

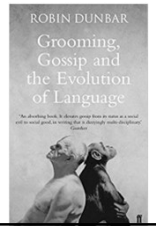
Social life requires larger brains (social brain hypothesis)

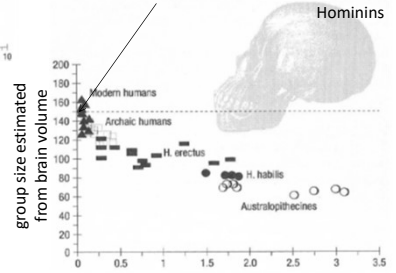


Neocortex is a brain part built of 6 layers, which occurs exclusivelly in mammals

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

Robin Dunbar
1947, UK





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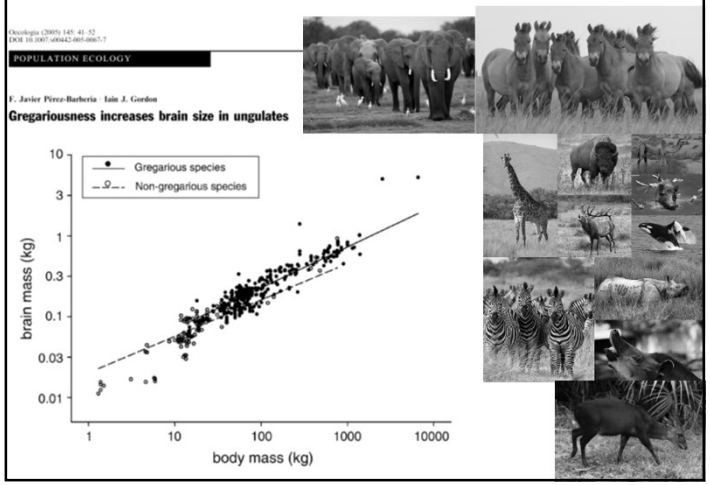
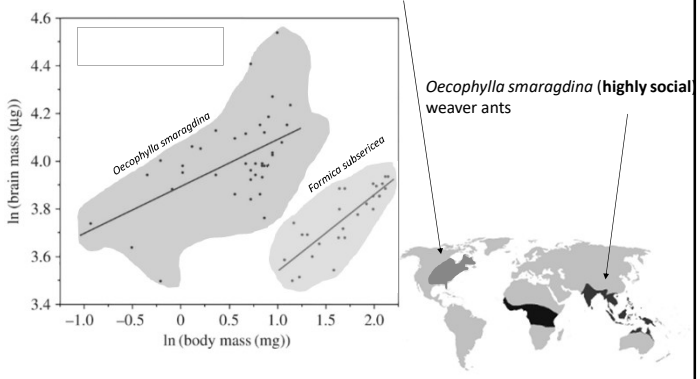


Social life requires larger brains (social brain hypothesis)

Formica subsericea (**less social**)
often hijacked for work by Polyergus "slave-raiding" ants

Oecophylla smaragdina (**highly social**)
weaver ants



Proc.R.Soc. B 2016

Weaver ants

- Rainforest, mobile, tree canopies
- 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)
- Nests built by binding leaves together with silk (weaving) produced by larvae
- Predators & gatherers of honeydew from sap-feeding insects (aphids, scale insects)

Oecophylla smaragdina

Oecophylla longinoda

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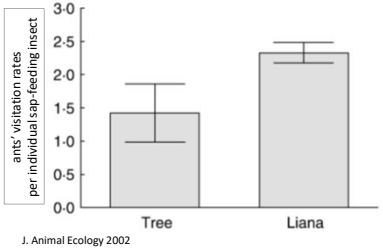
O. smaragdina prefered honeydew produced by insects feeding on the sap of lianas (compared to trees, more and higher quality sap)



Oecophylla smaragdina

Oecophylla longinoda

J. Animal Ecology 2002

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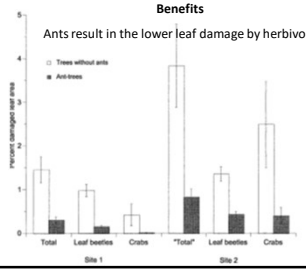
Trees associated with *O. smaragdina* have 3-20 time higher benefits than costs (data for mangrove forest, Thailand)

Benefits

Ants result in the lower leaf damage by herbivory



Costs

Host plants do not invest in the production of domatia or ant attractants, but still suffer costs:

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

Biotropica 2004, 2006

Why large brain in social life?

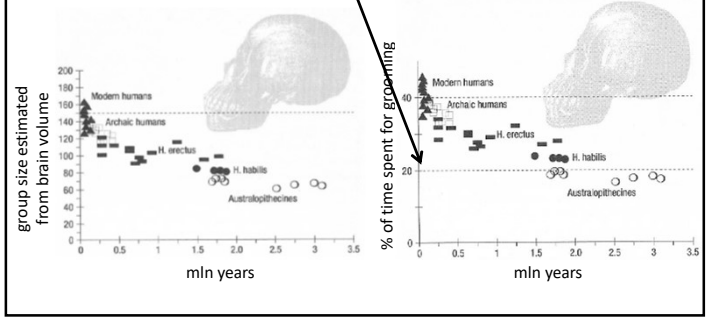
- We are talking here about groups with complicated social structures (not about gorups of anonymous individuals e.g. schools of sardines)
- Group members have to know each other, remember and understand interactions within a group
- Group living requires a mechanism that creates bonds, builds companionships & 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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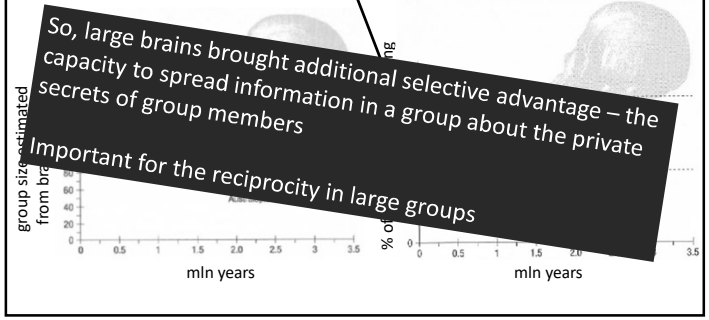
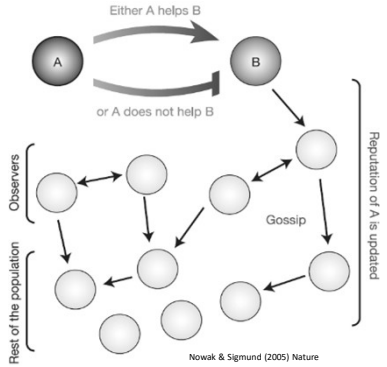
So, large brains brought additional selective advantage – the capacity to spread information in a group about the private secrets of group members

Important for the reciprocity in large groups



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



Nowak & Sigmund (2005) Nature

- Cooperative and altruistic acts require reciprocity and punishment
- Larger groups of cooperative individuals prone to selfish free-riders („social parasites")
- Gossiping is a **social punishment/reward system** that maintains indirect reciprocity

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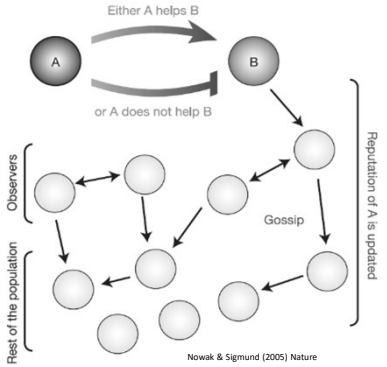

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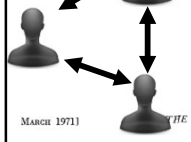
- Gossiping is a **social punishment/reward system** that maintains indirect reciprocity
- **Gossiping shapes reputation**, which becomes a prescious resource (difficult to build up, but easy to lose)
- Origin of moral values, religions with „Big Gods", justice, honor, prestige, „co ludzie powiedzą", police, law, prisons, Facebook/Youtube emojis, etc.

Reciprocal altruism can evolve as an adaptation, if:
- detecting & punishing selfish outlaws/freeriders possible
- need for help occurs frequently

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

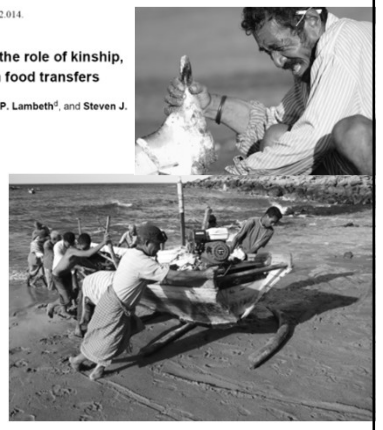
Biological Laboratories, Harvard University, Cambridge, Mass. 02138

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

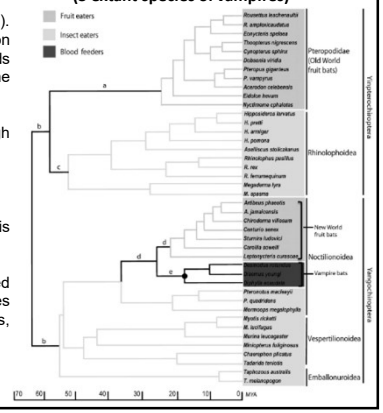
Vampire bats from South America share blood meals

- Mutual benefits – reciprocity (it is not real altruism)
- Small & stable groups (only females)
- Hunting individually
- No blood means 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 outlaws – suspension of help

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

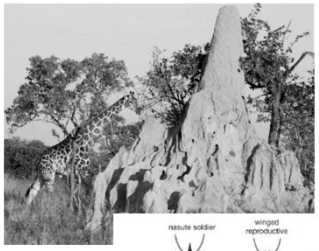
Blood feeding evolved in bats only once, ca 20 mln (3 extant species of vampires)

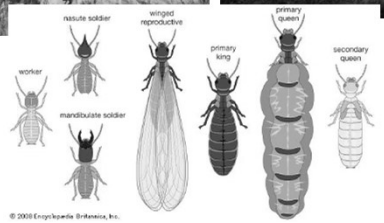
- Unclear origin (a kind of parasitism). Perhaps their ancestors were feeding on insects that were attracted to the wounds of mammals, and this way they „tasted the blood"
- Physiological adaptations to cope with high doses of iron, proteins & liquids
- Can walk & jump (no other bats do this)
- Lost 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**)



Mol. Biol. Evol. 2010

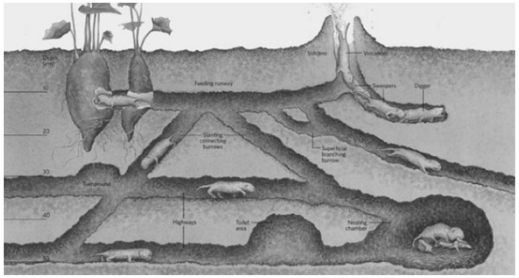
Eusocial animals – the extreme example of gregariousness explained by **kin selection & inclusive fitness**

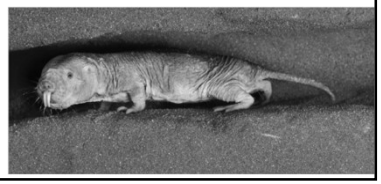




Agriculture communities of termites

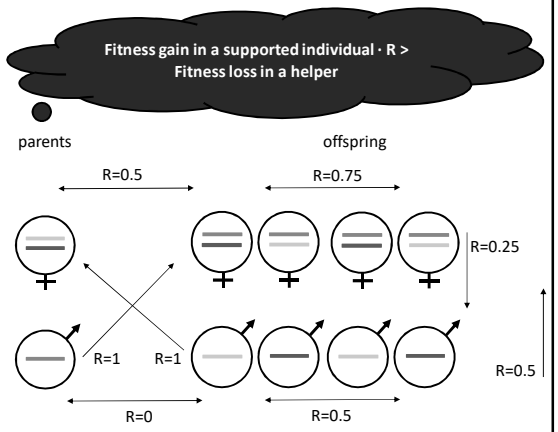
African mole-rats (2 species) are the only eusocial mammals





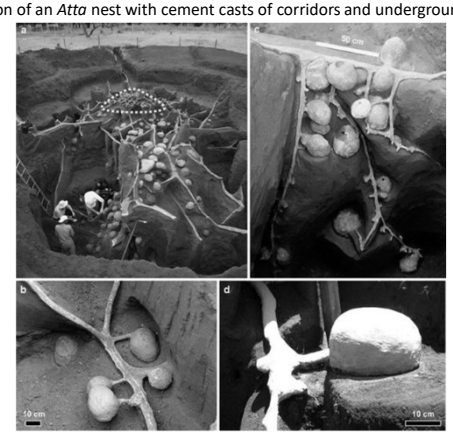
Hymenoptera (ants, bees, wasps, bumblebees) have a haplo-diploid system of sex determination & evolved eusociality many times independently

Bill Hamilton
1936-2000, UK



Leaf cutting _Atta_ ants (Neotropics) form huge eusocial colonies (10^3–10^6 workers) with many castes

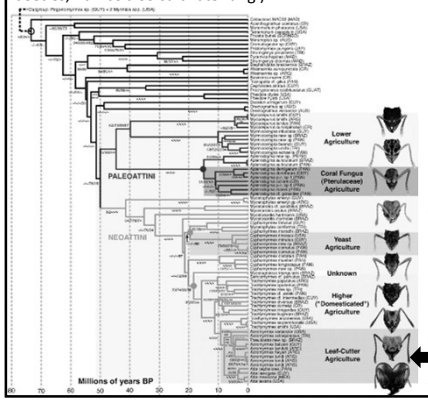
Excavation of an _Atta_ nest with cement casts of corridors and underground chambers



Insect. Soc. 2012

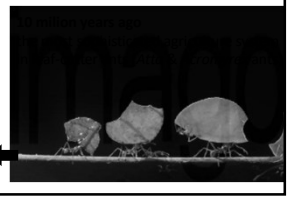
Agriculture (a kind of symbiosis) evolved independently in humans, bark beetles, termites and ants

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)

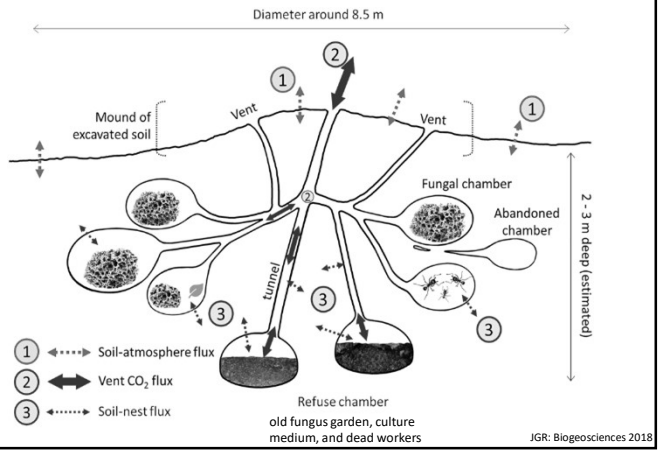


Some general characteristics of the leaf-cutter ant strategy

- Obligate mutualism with fungi
- Fungi endemic to 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



Specialized workers harvest leaves and manage the nest (queen, larvae, fungus gardens, wastes, air ventilation, parasites, etc.)



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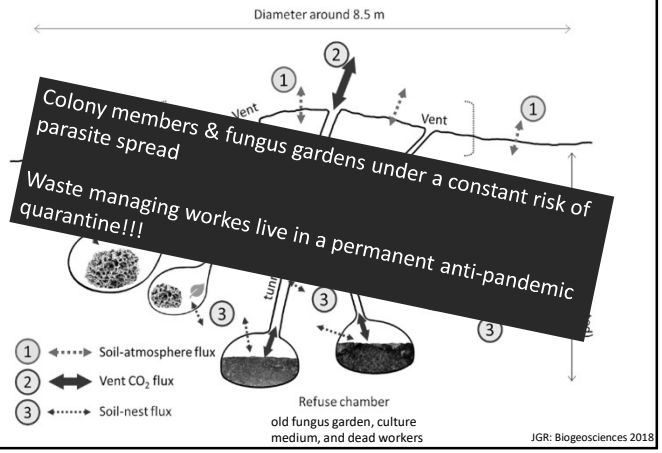
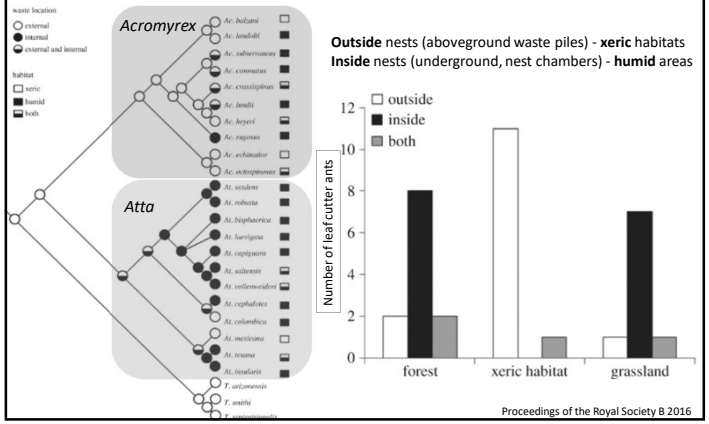


Colony members & fungus gardens under a constant risk of parasite spread

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

Hygienic challenges of social life - waste management

„Outside nest" waste management – an ancestral state in the evolution of leaf cutter ants (*Atta* & *Acromyrex*)



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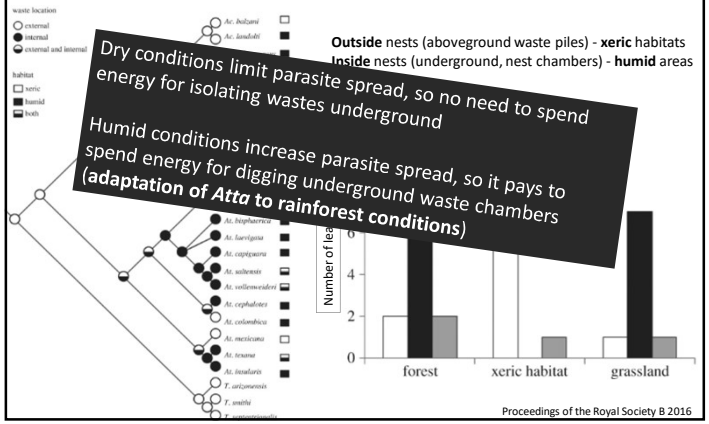


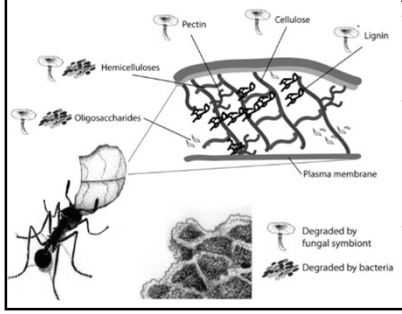
Dry conditions limit parasite spread, so no need to spend energy for isolating wastes underground

Humid conditions increase parasite spread, so it pays to spend energy for digging underground waste chambers (**adaptation of *Atta* to rainforest conditions**)

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



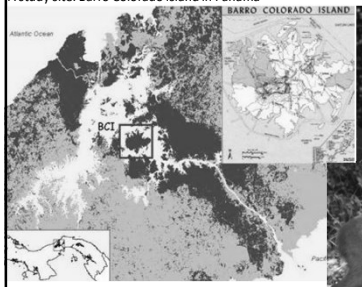
Ants

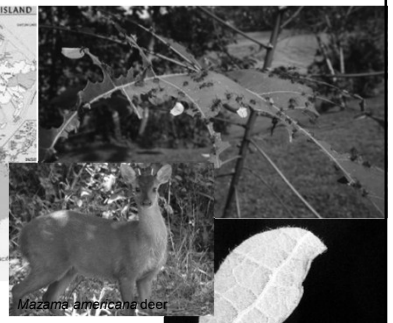
- Feed & disperse the fungus, selecting plants that do not produce toxins harmful to the fungus
- Supply the fungus with nitrogen sources (they put rectal fluid on leaves, which contains amino acids & enzymes that help to generate more nitrogen supplies)
- Protect fungi from parasites (fungus *Escovopis*)

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



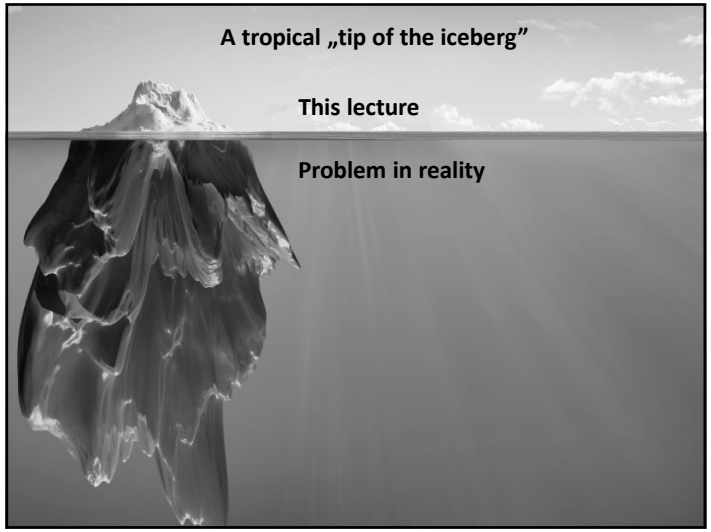


Colonies of *A. colomica* in the island

- 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



Some final thoughts

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2) Bright & dark sides of social life

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

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1) Enormous part of the animal biomass on Earth is social & peaks in tropics

2) Bright & dark sides of social life

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

3) Social behaviour is an adaptation, not true altruism (sacrifice) - mutual benefits

- Reciprocity (genetic relatedness not important)
- Inclusive fitness (genetic relatedness important)

Some final thoughts

1) Enormous part of the animal biomass on Earth is social & peaks in tropics

2) Bright & dark sides of social life

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

3) Social behaviour is an adaptation, not true altruism (sacrifice) - mutual benefits

- Reciprocity (genetic relatedness not important)
- Inclusive fitness (genetic relatedness important)

4) Mutualistic symbioses (*Camponotus* ants – rattans or *Atta* ants – fungi) also driven by reciprocity, so in princile, they are not fundamentally different from e.g. bat vampirism