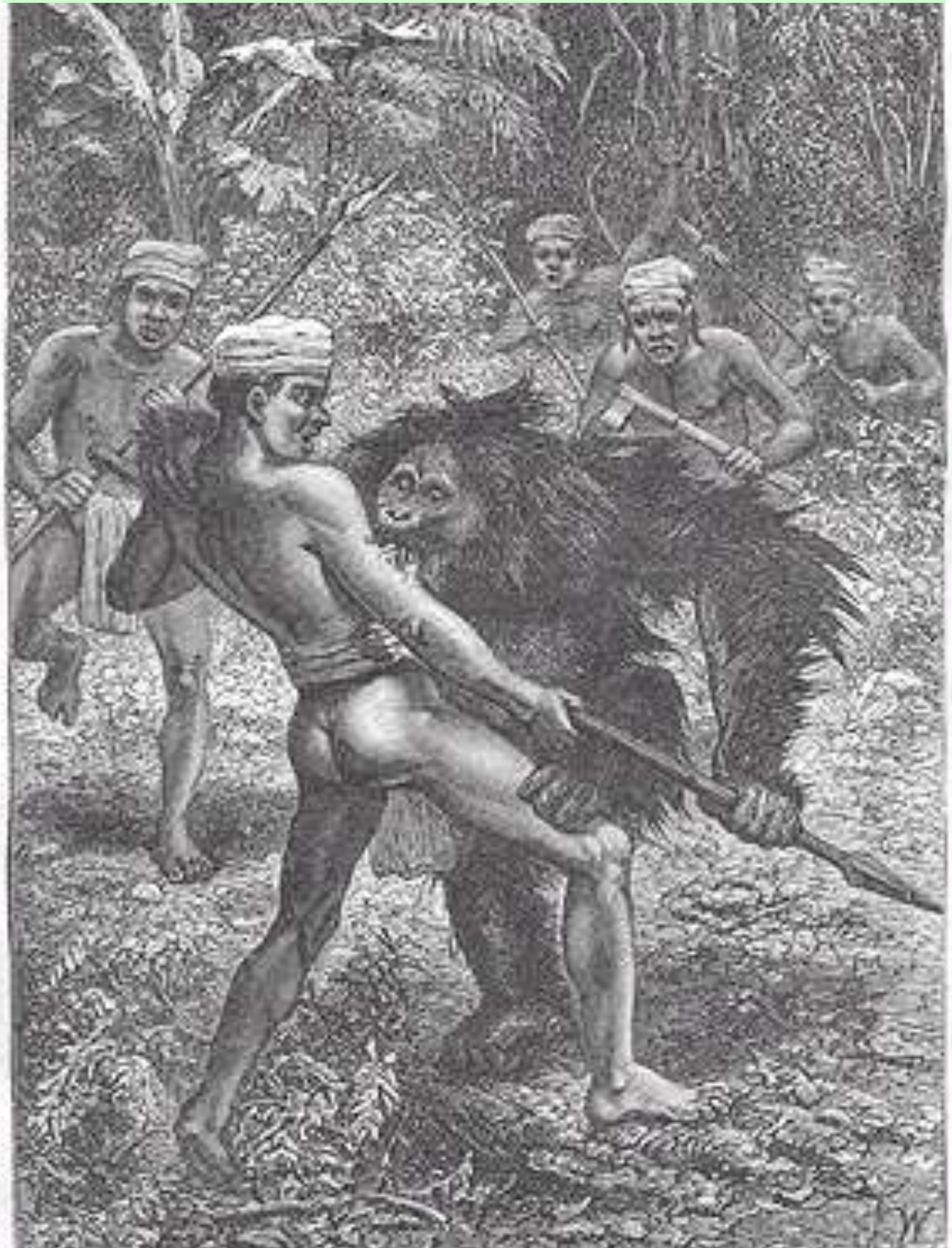
Animals in tropical forests



Ants:
key players in rainforest ecology

Oecophylla smaragdina, New Guinea

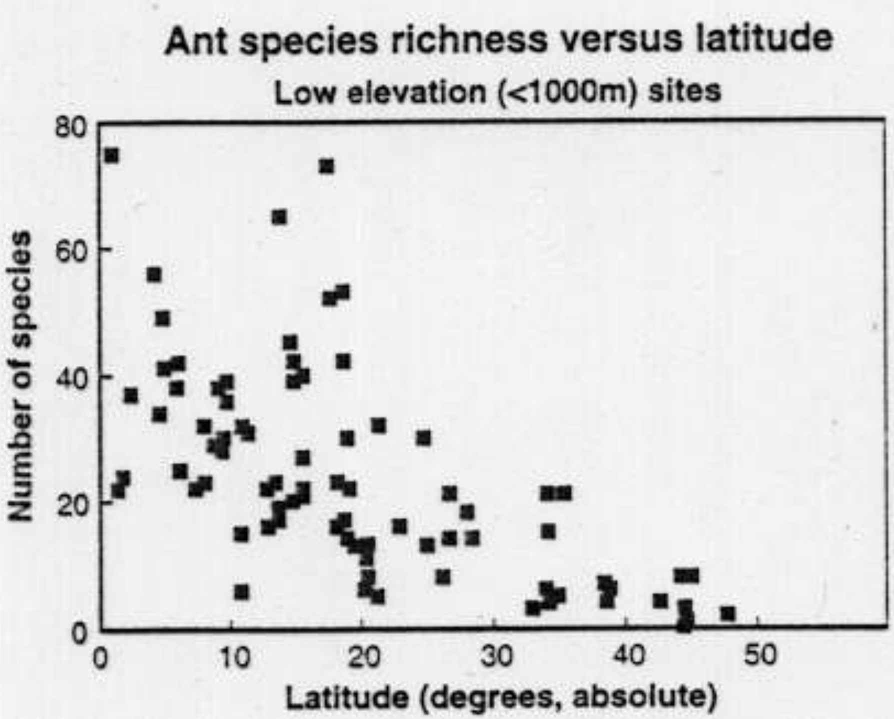
Ants: diversity maximum in tropical lowlands

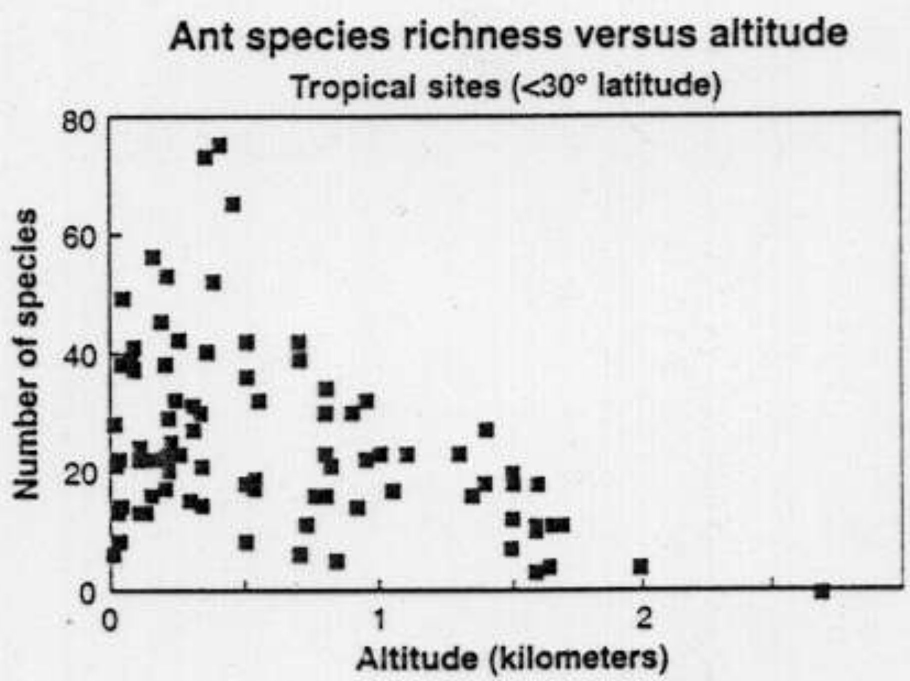
The largest genera in all tropical areas:

Camponotus

Pheidole

Crematogaster





Tropical lowland forests: strong predation pressure from ants

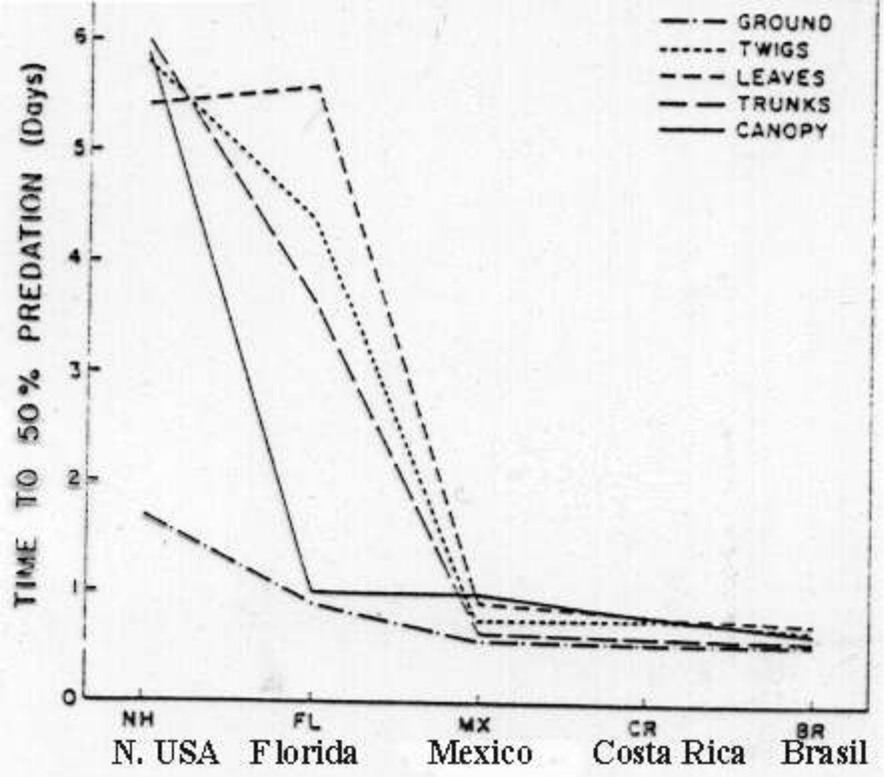


FIG. 7. Latitudinal differences in time to 50% predation on baits in each of five microhabitats in forests. Data based on the following numbers of baits set out (from New Hampshire to Brazil): ground—98, 100, 100, 99, 100; twigs—89,

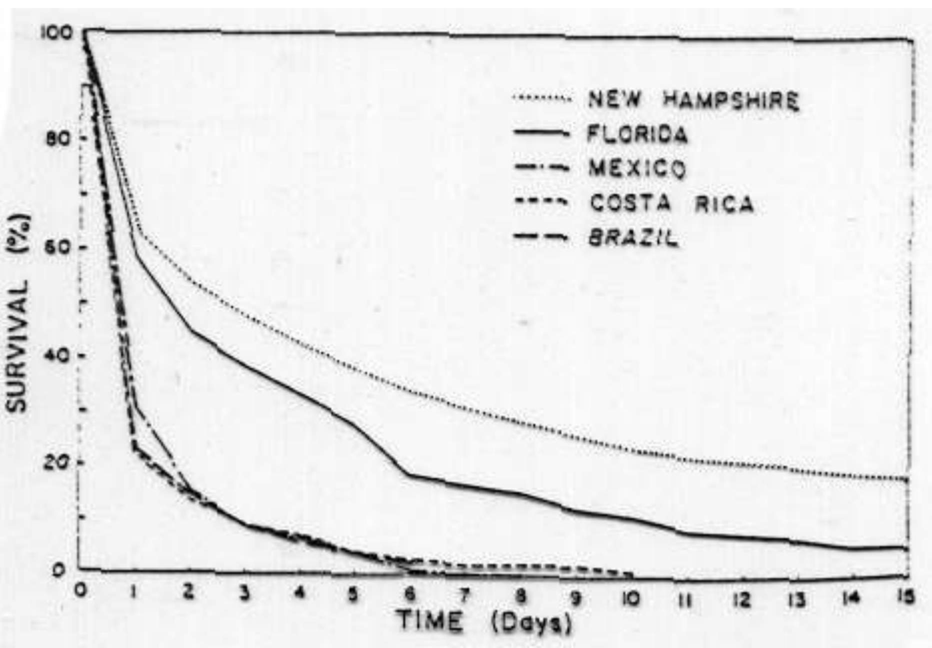


FIG. 4. Survivorship of all baits (except those on buildings) at each of five latitudes. Data based on following numbers of baits set out at each locality: New Hampshire—707; Florida—733; Mexico—742; Costa Rica—746; Brazil—748.

How can we explain the "superabundance" of ant predators in tropical forests?

The extraordinary abundance of ants in tropical rainforest canopies has led to speculation that numerous arboreal ant taxa feed principally as "herbivores" of plant and insect exudates. Based on nitrogen (N) isotope ratios of plants, known herbivores, arthropod predators, and ants from Amazonia and Borneo, we find that many arboreal ant species obtain little N through predation and scavenging. Microsymbionts of ants and their hemipteran trophobionts might play key roles in the nutrition of taxa specializing on N-poor exudates. For plants, the combined costs of biotic defenses and herbivory by ants and tended Hemiptera are substantial, and forest losses to insect herbivores vastly exceed current estimates.

Davidson et al. 2003. Science 300:969

They obtain most of their energy from plants – directly or via mutualisms with homopterans

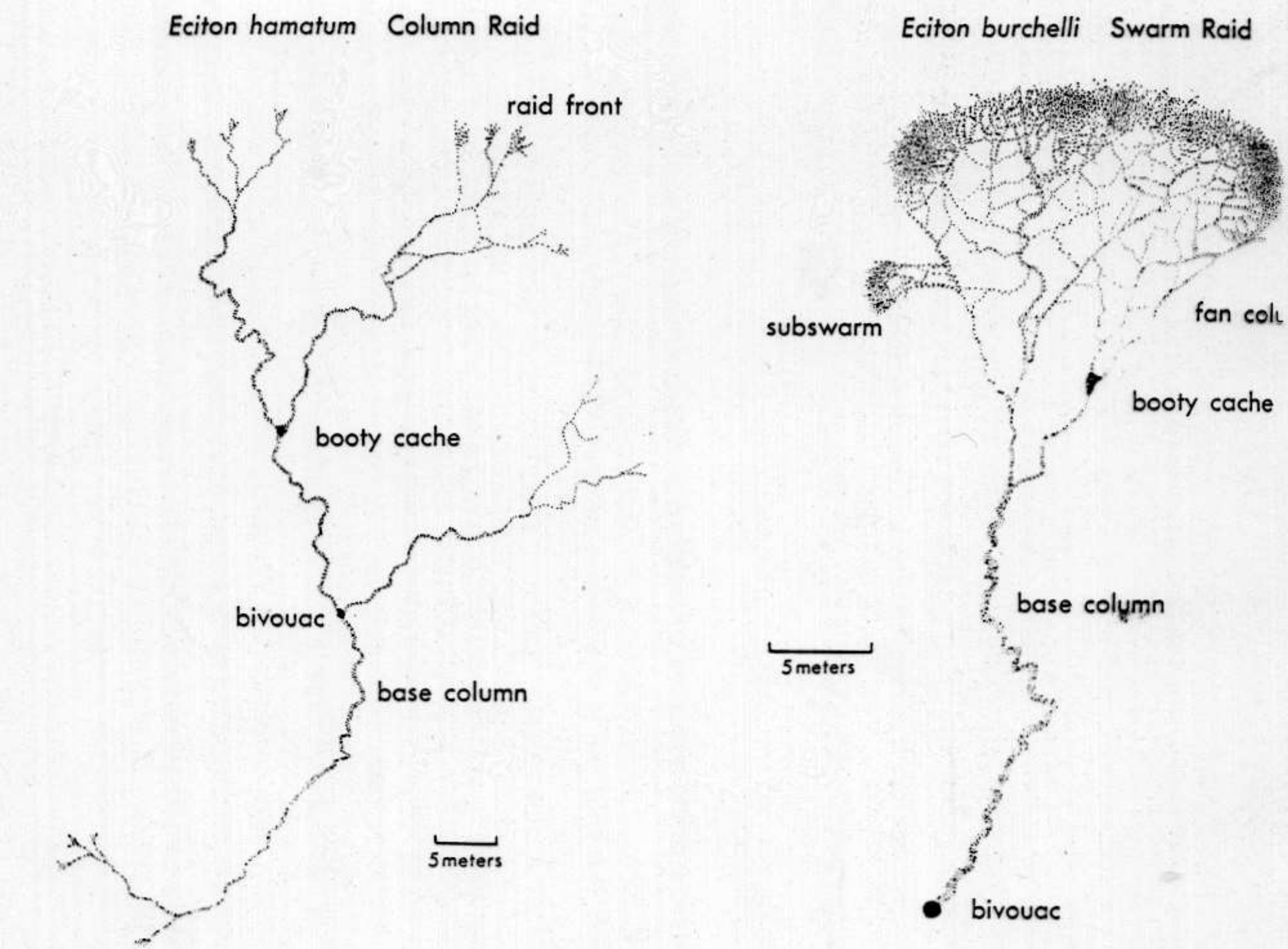
Plants with extra-floral nectaries

% of woody plant spp:
33% Panama
31% Amazon
12% Malaysia

TABLE 4. Previously reported abundances of plants with extrafloral nectaries.

Location and latitude	Mean percent cover	Percent of the flora	Reference
Nebraska, USA 40–43°N	2.4	3	Keeler (1979b)
Northern California, USA *c.* 38°N	0	—	Keeler (1981)
Korean Peninsula *c.* 33–43°N	28.3[1]	4[1]	Pemberton (1990)
Southern California, USA 33.5–35°N	8.5	2.8	Pemberton (1988)
Florida Everglades, USA *c.* 25°N	19.7	8.8	Koptur (1992b)
San Paulo, Brazil 20°S	—	18.3 of woody plants	Oliveira & Leitao-Filho (1987)
Mato Grosso, Brazil *c.* 15°S	—	21.9 of woody plants	Oliveira & Oliveira-Filho (1991)
Jamaica 18°N	28	—	Keeler (1979a)
Costa Rica 8–12°N	42.5	—	Bentley (1976)
Panama 8°N	—	33.3 of woody plants	Schupp & Feener (1991)
Amazon, Brazil 6°S	—	30.7 of woody plants	Morellato & Oliveira (1991)
Malaysian Peninsula 3°N	19.3	12.3 of woody plants	Fiala & Linsenmair (1995)

Army ants



Eciton burchelli - Formicidae - at Barro Colorado Island, tropical forest:
~100,000 ants moving at 6 m wide front 15 m/hod
foraging 13 days, stationary 21 days; 3.6 colonies per km2
every place raided every 400 days, caught 55 kg dry weight prey/km2,
reduce prey density by 50%

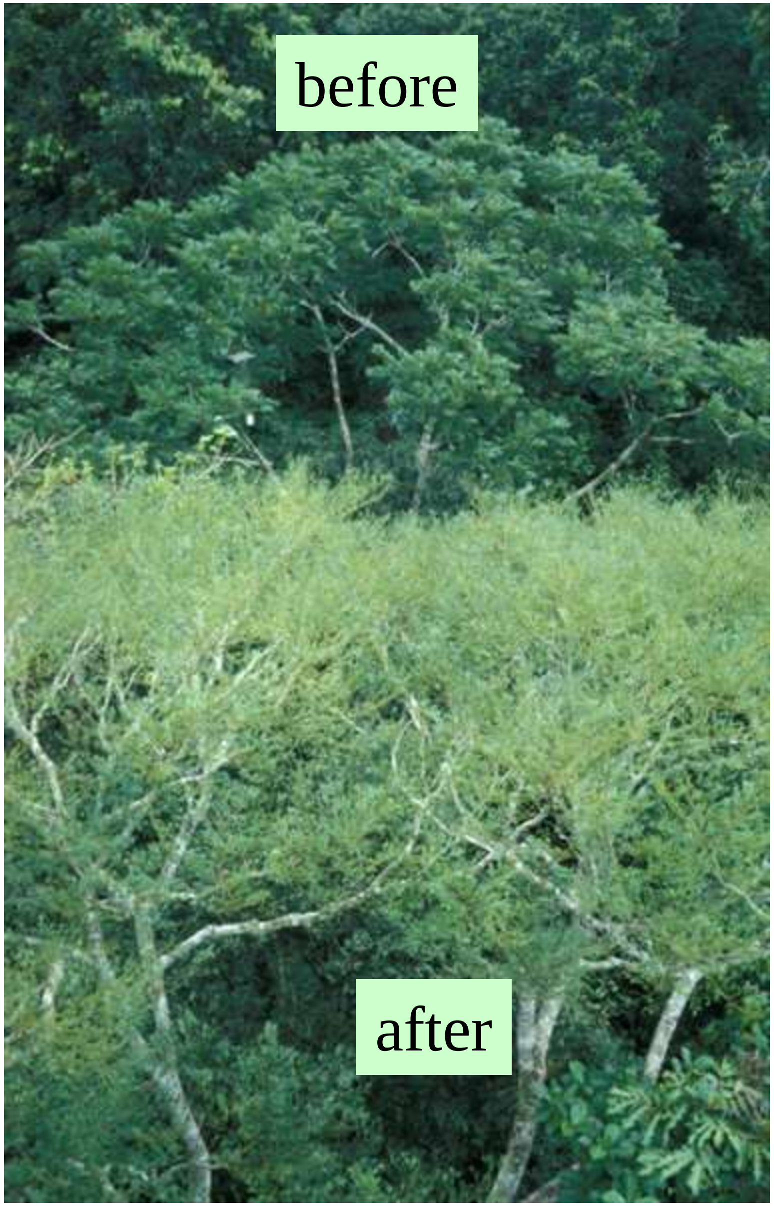
TABLE 4-5. Genera and higher taxa of ants whose species show legionary behavior.

Genus	Distribution	Approximate number of described species	Authority
Subfamily Dorylinae			
Tribe Dorylini			
Dorylus (Subgenera: *Dorylus*, *Alaopone*, *Dichthadia*, *Rhogmus*, *Typhlopone*)	Africa to tropical Asia	20	Emery (1910), Wheeler (1922), Wilson (1964), Raignier and van Boven (1955)
Anomma	Africa	8	Wheeler (1922), Raignier and van Boven (1955)
Aenictus	Africa to tropical Asia and Queensland	50	Wilson (1964)
Tribe Cheliomyrmecini			
Cheliomyrmex	South America to southern Mexico	5	Wheeler (1921a)
Tribe Ecitonini			
Eciton	South America to southern Mexico	12	Borgmeier (1955)
Labidus	South America to Texas	8	Creighton (1950), Borgmeier (1955)
Nomamyrmex	South America to Texas	2	Creighton (1950), Borgmeier (1955)
Neivamyrmex	South America to Iowa and Virginia	100	Smith (1942), Creighton (1950), Borgmeier (1955)
Subfamily Leptanillinae			
Leptanilla	Africa, tropical Asia, Australia, South America	10	G. C. and J. Wheeler (1965), Petersen (1968)
Leptomesites, *Noonilla*, *Phaulomyrma*, *Scyphodon*	Tropical Asia	4	G. C. and J. Wheeler (1965), Petersen (1968)
Subfamily Ponerinae			
Tribe Ponerini			
Leptogenys (*kitteli* and *processionalis* groups)	Tropical Asia to Queensland	10	Wilson (1958b, c)
Megaponera	Africa	1	Wheeler (1936a)
Simopelta	Central and South America	8	Wilson (1958b), Gotwald and Brown (1966)
Tribe Amblyoponini			
Onychomyrmex	Australia	3	Wheeler (1916b), Wilson (1958b)

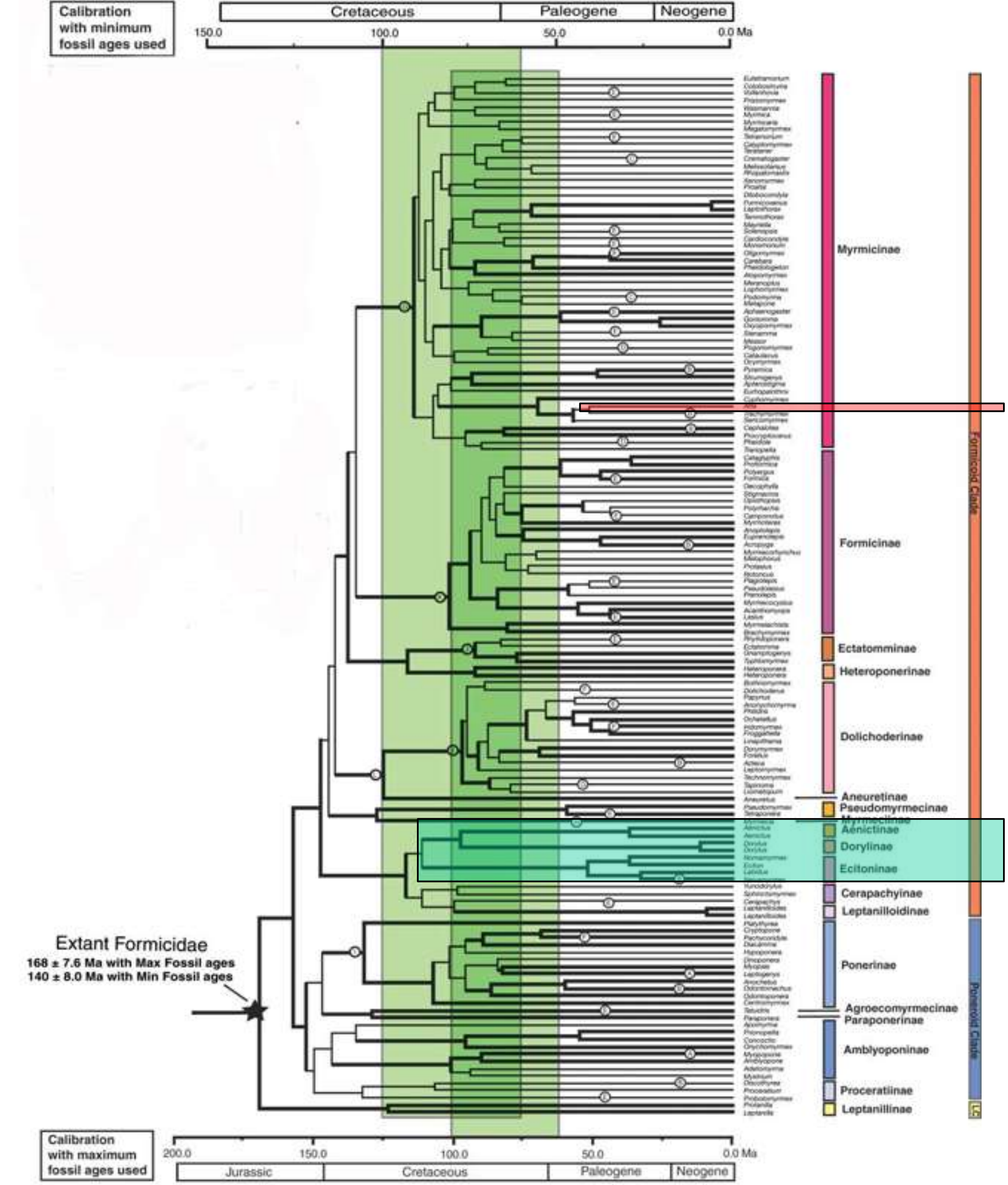
Leaf-cutter ants:
the most important insect herbivores in the Neotropical forests

Atta colombica - Formicidae at Barro Colorado Island, rainforest:
1 colony / 1.7 ha, territorial
collected 134,000 leaf fragments per day = 737 dry weight of leaves and 304 g other plant parts = represents 5% of the total litter fall in the forest
feeding preference: young leaves of various (many) plant spp. with leaves lacking anti-fungal properties


Atta nest


before
after

Leaf-cutter ants: a purely Neotropical phenomenon

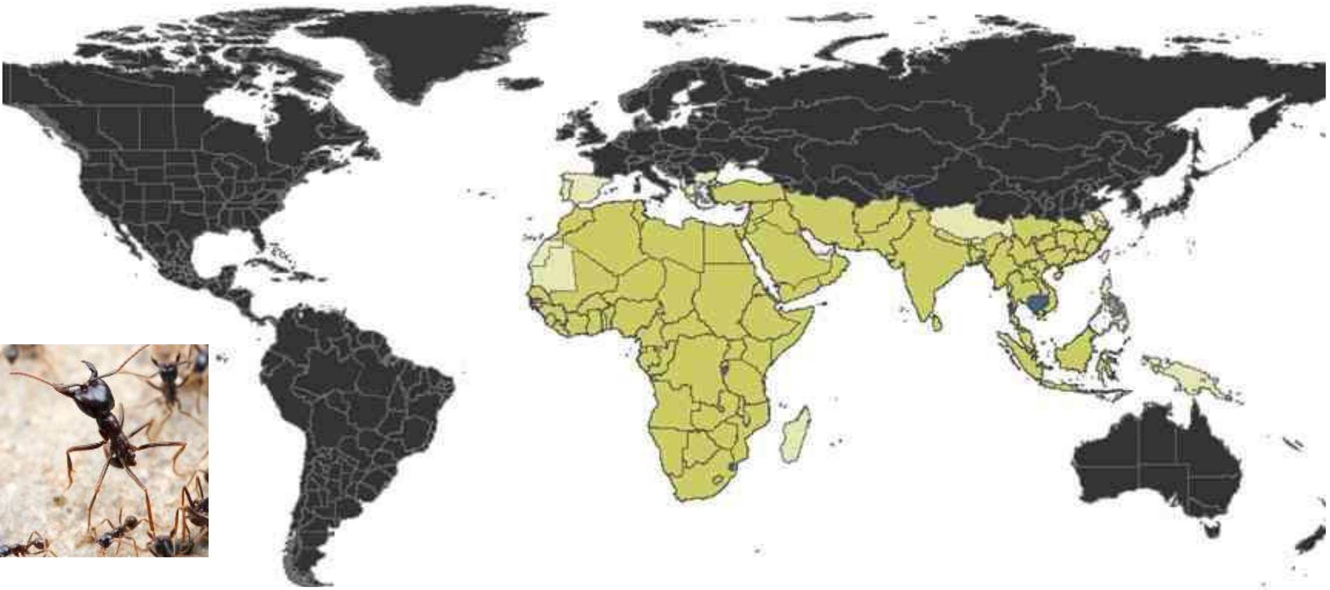


Leaf-cutter ants
50 million yrs ago

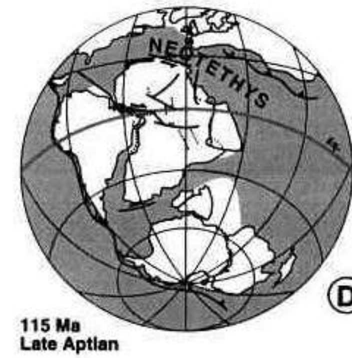
Army ants
95-120 million yrs ago

Moreau et al. 2006, Science 312: 101
Slide courtesy T Fayle

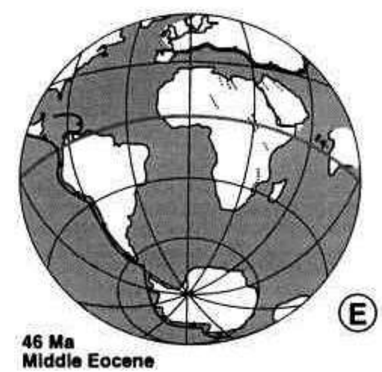
Later origin of leaf cutter ants means that they are restricted to their continent of origin, while army ants were able to spread throughout the tropics before these continents separated



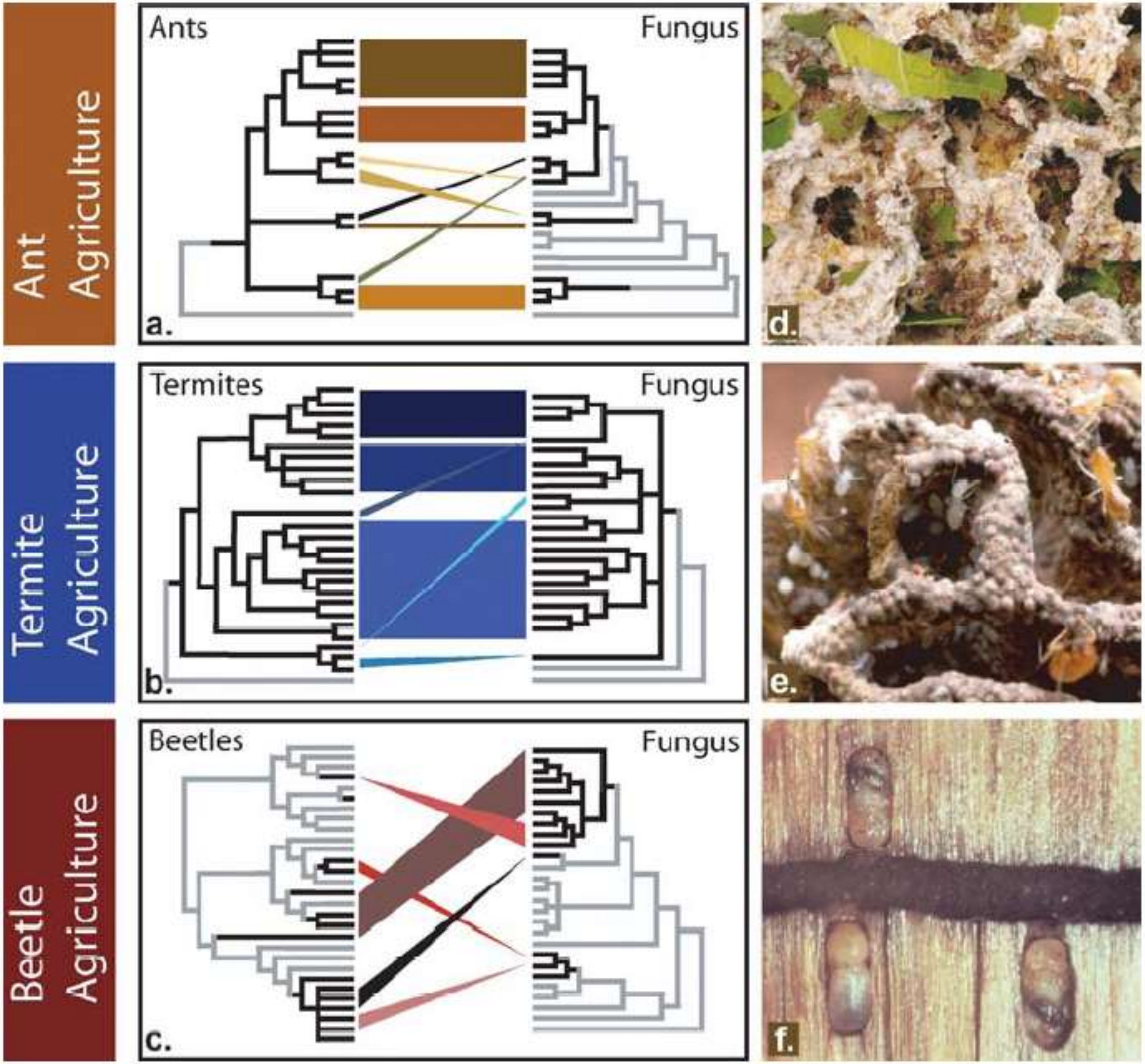
Army ants



Leaf cutter ants



Guenard 2011, antmacroecology.org
Guirauda and Bosworth (1999)



Leaf-cutter ants:

one of three examples of insect agriculture

Annu. Rev. Ecol. Evol. Syst. 2005. 36:563–95

A. macrantha

A. drepanolobium

Ant-plant mutualisms

Cheating in the mutualistic relationship: *Crematogaster nigriceps* on *Acacia drepanolobium* in Africa

- *C. nigriceps* is competitively excluded by 3 coexisting *Acacia* ants
- these ants invade *C. nigriceps*-inhabited tree via their canopy contact
- *C. nigriceps* modifies tree branching to minimize canopy contact
- this modification decreases tree fitness

Stanton et al. 1999

Crematogaster nigriceps

Exclusion of large herbivores [for 10 years]

Reduced investment by Acacia trees to nectaries and domatia

Decline of *Crematogaster mimosae*, increase of *C. nigriceps* and *C. sjostedti* [nesting in cavities caused by wood borers, not domatia]

C. sjostedti

Trees with *C. nigriceps* [pruning their branches] OK

Trees with *C. sjostedti*: increased attack of cerambycid wood borers, slower growth, increased mortality

Palmer et al., 2008, Science 319:192

Hydnophytum (fig.), *Myrmecodia* [Rubiaceae] – Asia, New Guinea, Australia, Pacific

Ant-plants – mostly Palaeotropics:

obtain nutrients (N) from animal remains brought by ants

Table 4. Comparison between the carnivorous and myrmecophilous plants (after Thompson, 1981, modified).

	Insectivorous	Myrmecophilous
Nutritional value of the substratum	very low	very low
Use of animal food	probably nitrogen	probably nitrogen
Duration of life	perennial (few annual)	perennial
Distribution	tropical-temperate (some boreal)	tropical and subtropical
Assimilation system	specialized cells	generally internal roots or trichomes or warts
Situation	aquatic surroundings, bogs, creepers, few epiphytic, mangroves	generally flooded areas, dry or humid forests, mangroves, epiphytic

Devil's gardens

Monospecific stands of *Duroia hirsuta* (Rubiaceae) trees in Neotropical rainforest. Created by *Myrmelachista schumanni* ant killing all other plants by injecting them with formic acid (photo shows leaves developing necrosis along primary veins). D. hirsuta is an ant-plant, providing domatia for the ants. Each garden managed by a single large colony, over as long as 800 years.

Megan E. Frederickson, Michael J. Greene and Deborah M. Gordon
'Devil's gardens' bedevilled by ants. Nature 437, 495-496

Ant gardens

Crematogaster nest with *Dischidia* (Asclepiadaceae, left) and *Aeschynanthus* (Gesneriaceae, right), SE Asia

Arboreal ant nests rich in humus, seeds of certain epiphytes planted in the walls, then grow. Typical for Neotropical forests.

Eva Kaufmann · Ulrich Maschwitz
Ant-gardens of tropical Asian rainforests

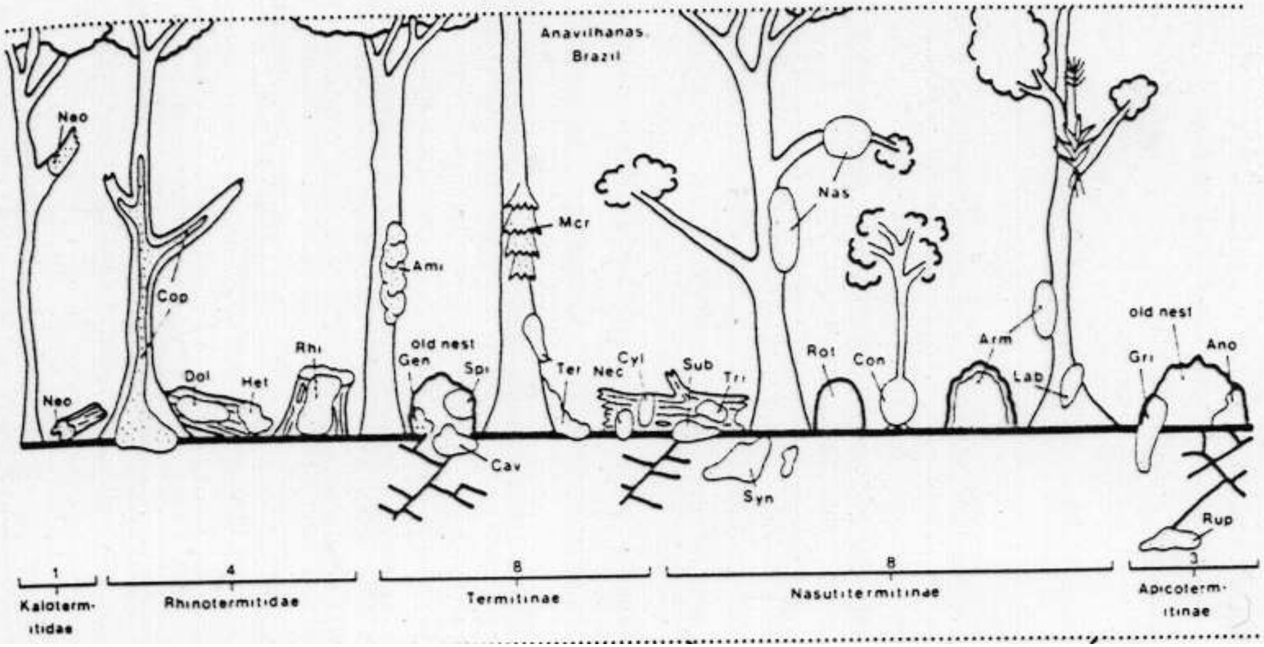
Ants: some of the most troublesome invasive species

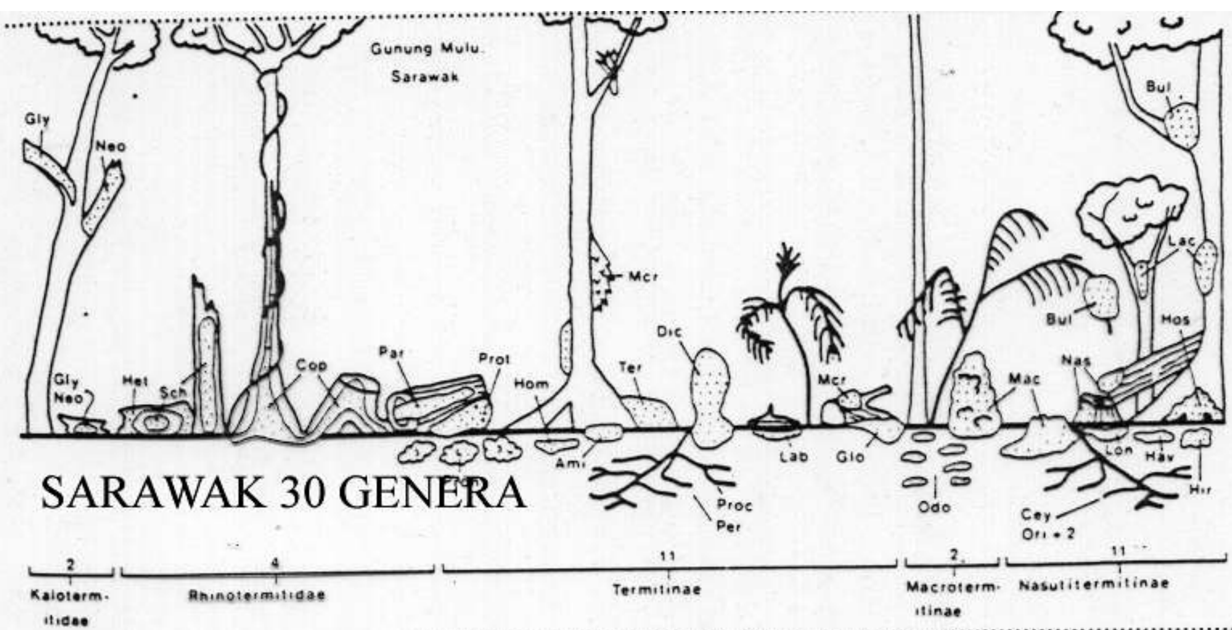
Termites:
key decomposers in tropical forests

LOWLAND EVERGREEN FORESTS - TERMITES

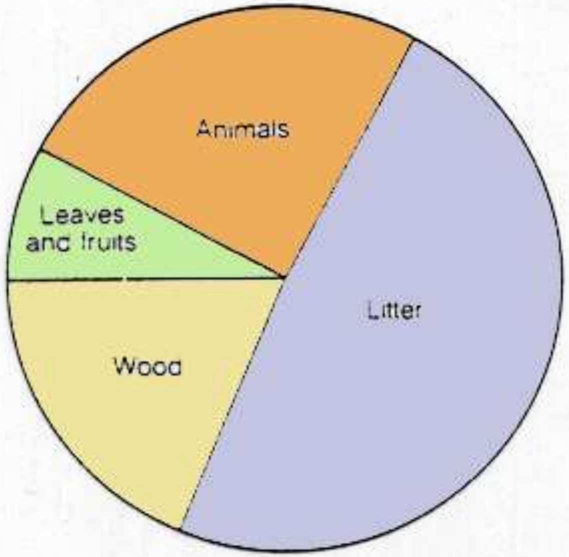
BRASIL 24 GENERA

TERMITES



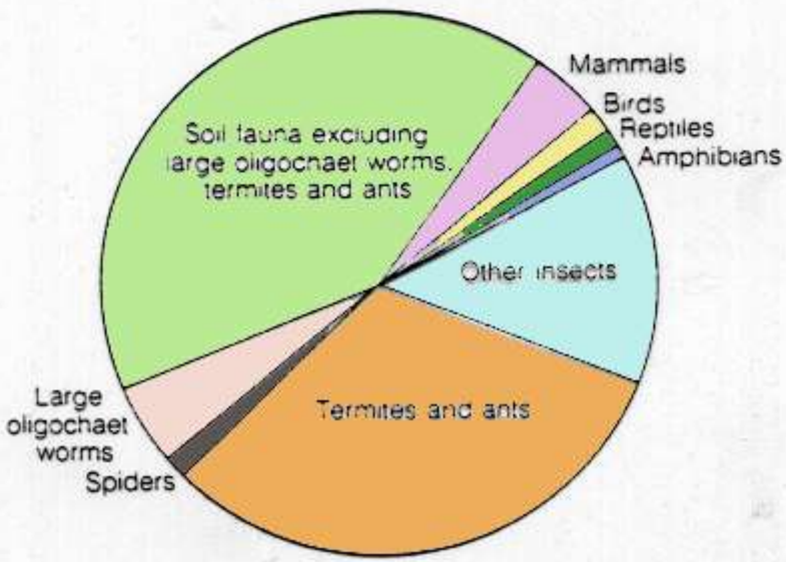


SARAWAK 30 GENERA



Animal food base

BRAZIL



Animal Biomass

Table 7.4 Animal biomass (kg/ha) in

Category	Manaus
All animals	200
Mammals	8.4
Marsupials	2.0
Armadillos	0.5
Sloths	0.8
Anteaters	0.3
Monkeys	0.4
Tapir, deer, peccaries	0.4
Rodents	3.1
Carnivores	0.9
Birds	3.4
Amphibians and reptiles	3.4
Soil Fauna	165
Ants	34
Termites	28
Earthworms	10
Others	84
Other insects	27
Stingless bees	4.7
Wasps (Vespidae)	4.7
Lepidoptera	3.4
Orthoptera	1.1
Hemiptera	2.3
Coleoptera	10.6
Spiders	2.1
Consumers of leaves and fruit	16.0
Mammalian	6.7
Avian	1.8
Arthropod	7.5

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Fittkau and
m E. J. Fittkau
e of the central
973, **5**(1), 8.)

Species richness of termites: maximum in the tropics

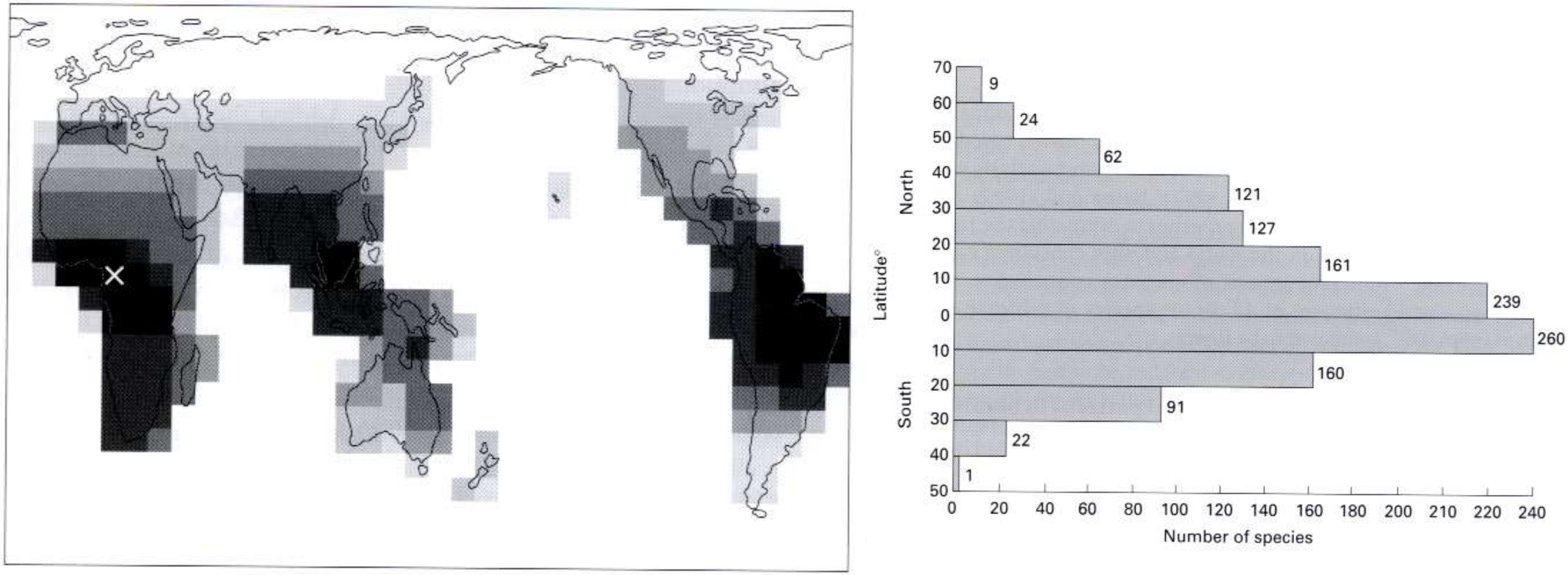
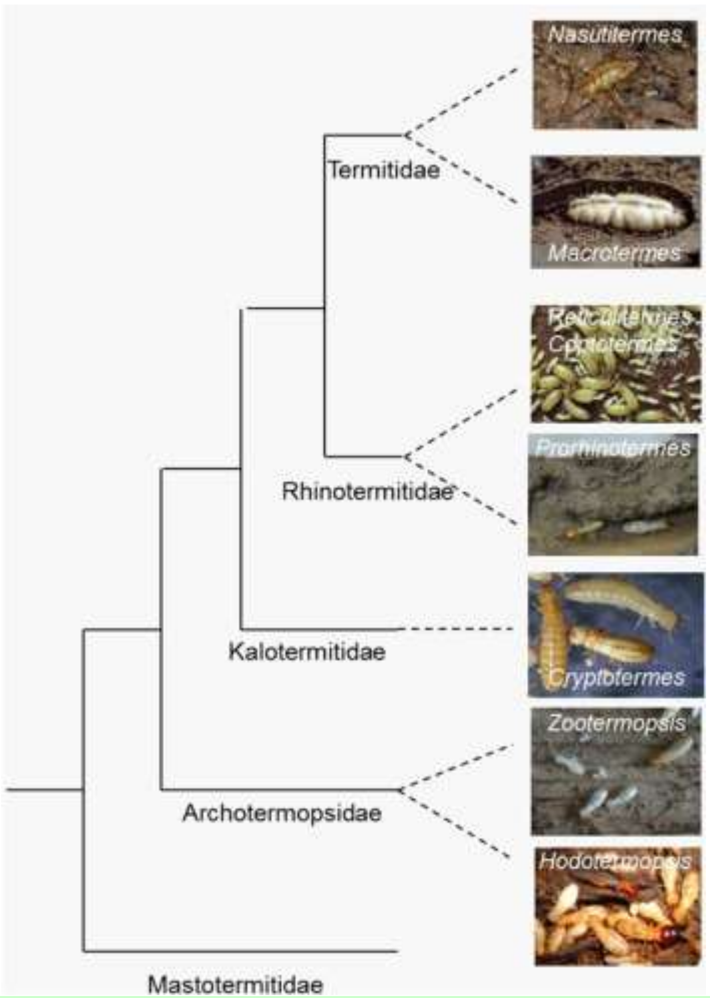


Fig. 8.7 (a) Regional variation in the number of termite genera (represented by a logarithmic grey scale from a minimum (light grey) to a maximum (black with a cross); white, no data). (From Gaston & Williams 1996; data from Eggleton *et al.* 1994.) (b) Latitudinal gradients in the number of swallowtail butterfly species. (From Sutton & Collins 1991.)

Termites:
symbiotic relationships with protozoans,bacteria or fungi



Bacteria, amoebae

Bacteria, fungi

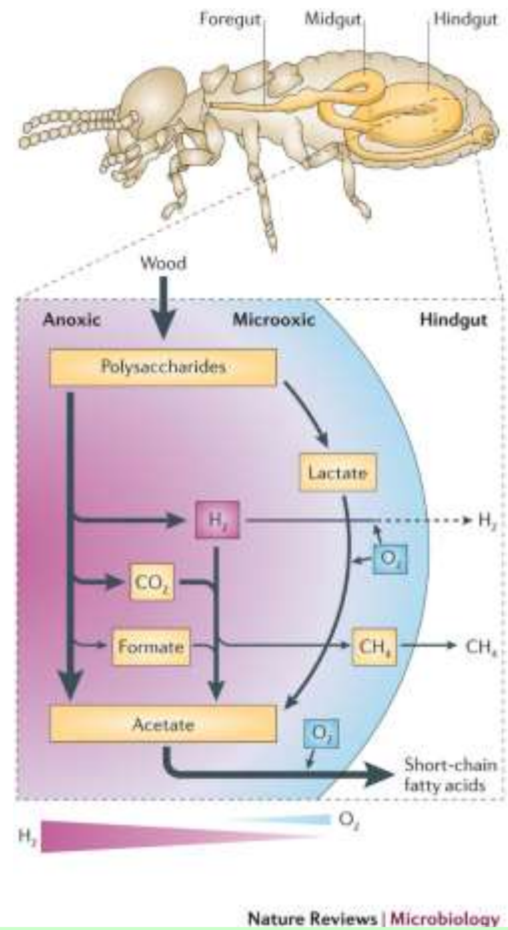
Flagellates

Flagellates

Flagellates

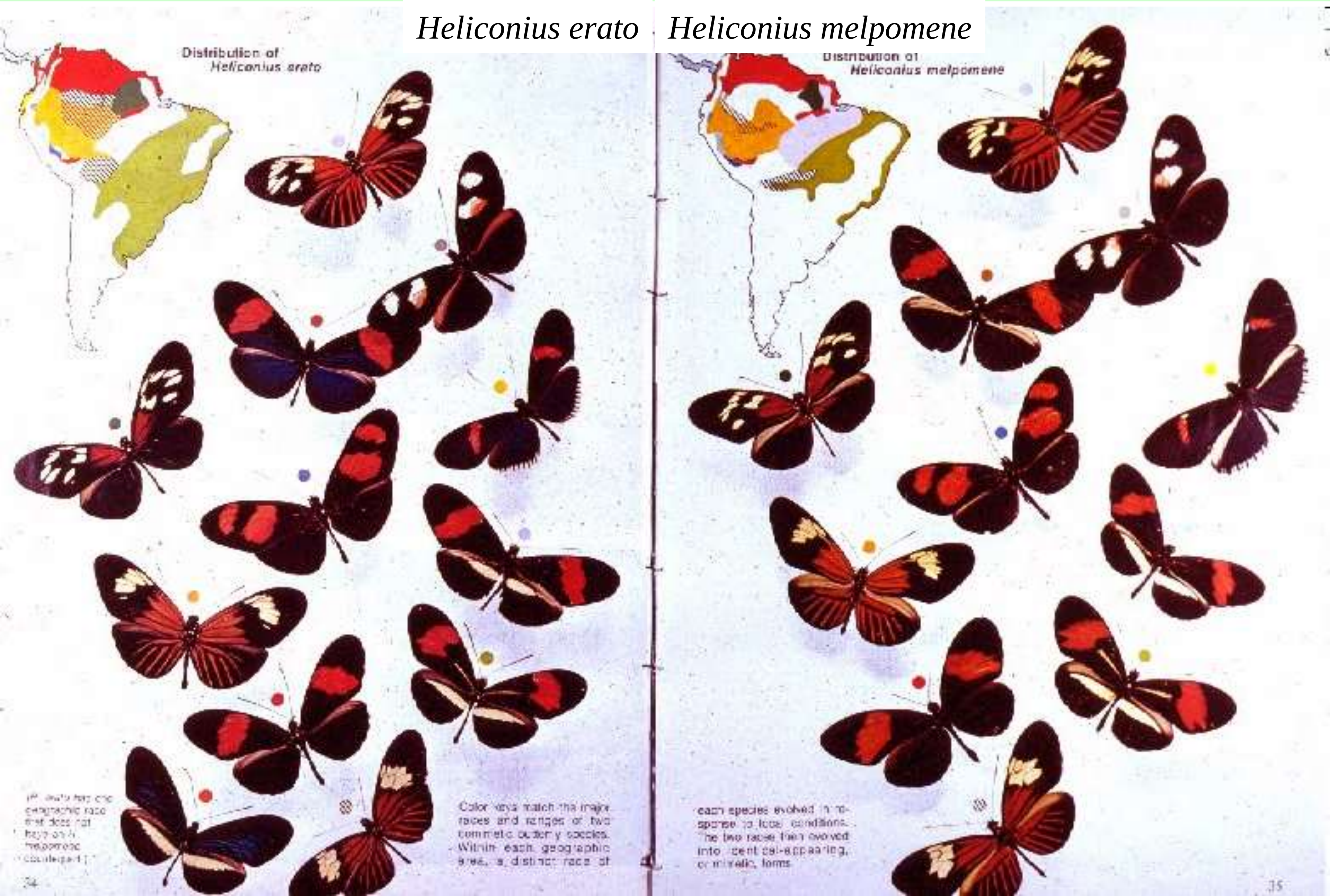
Flagellates

Flagellates

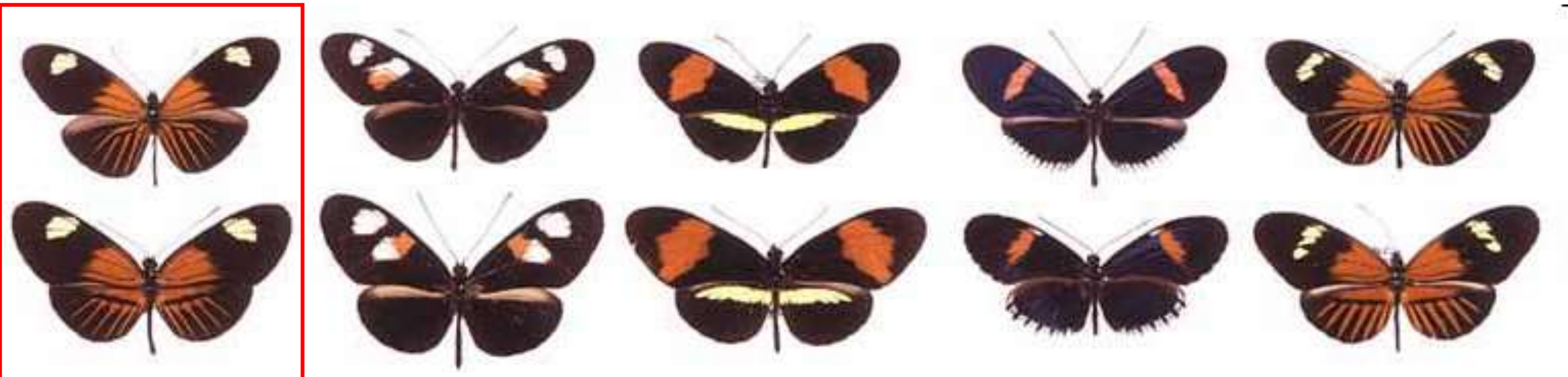


Termites produce 2x more CO_2 than are the emission from burning fossil fuels
28% of primary production ingested
0.8% C emitted as CH_4 [1.5 x 10^8 tons annually]
84% C emitted as CO_2 [5 x 10^{10} tons annually]

Mullerian mimicry: parallel distribution of two dimorphic unpalatable species: *Heliconius erato* and *Heliconius melpomene*



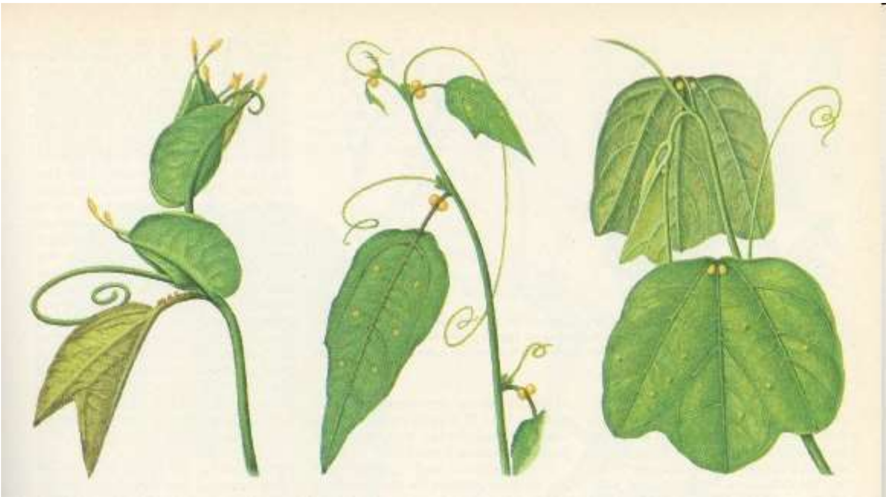
Heliconius erato: various forms, top row



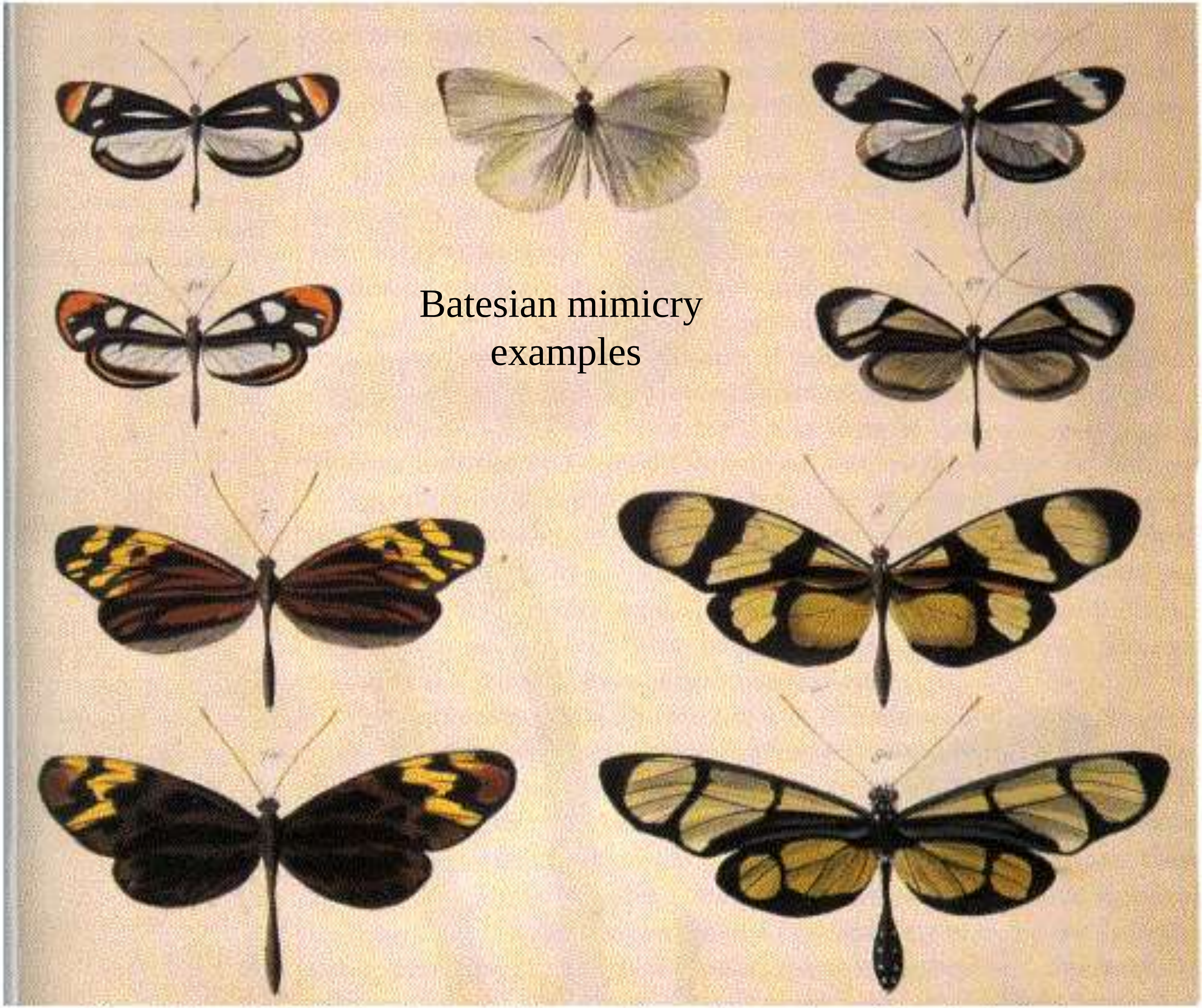
Heliconius melpomene: various forms, top row

similar forms coexist in the same geographic area

Passiflora

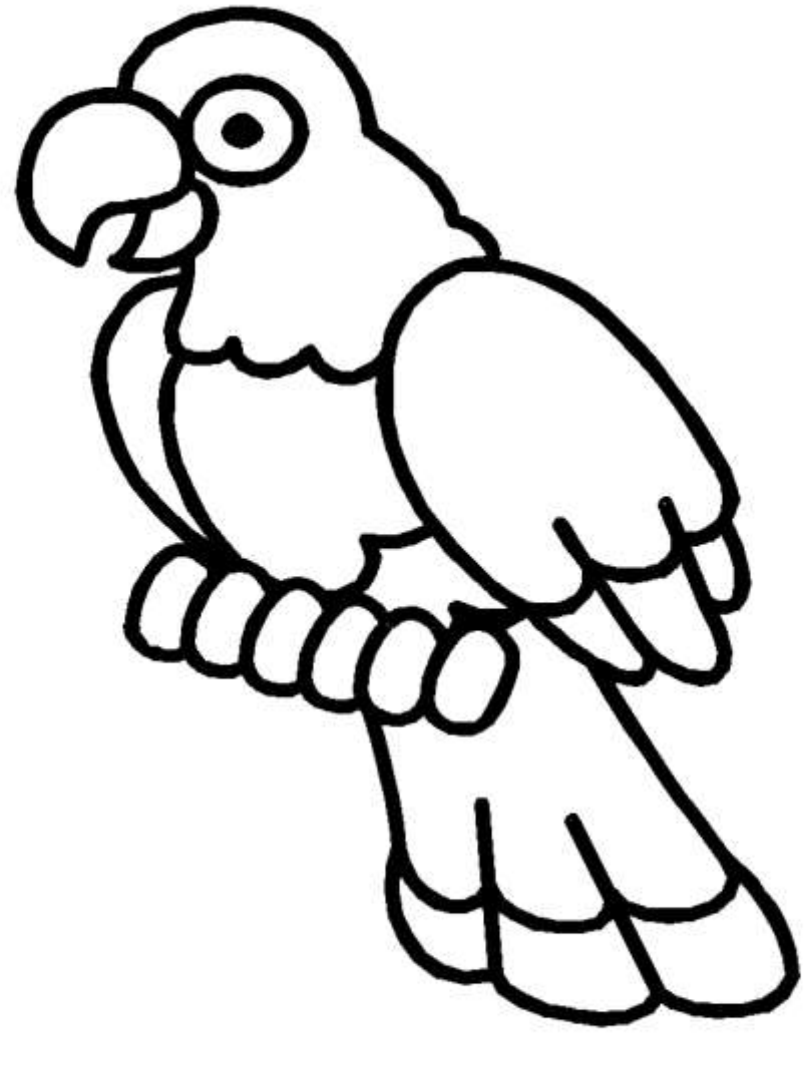


Batesian mimicry examples



Bates' butterflies (1862) showing the distasteful one (above) and its mimic, below.

birds



Species richness of birds [in 1ºx 1º squares]

all species | 25% of spp. with smallest geographic ranges | 25% of spp. with largest geographic ranges

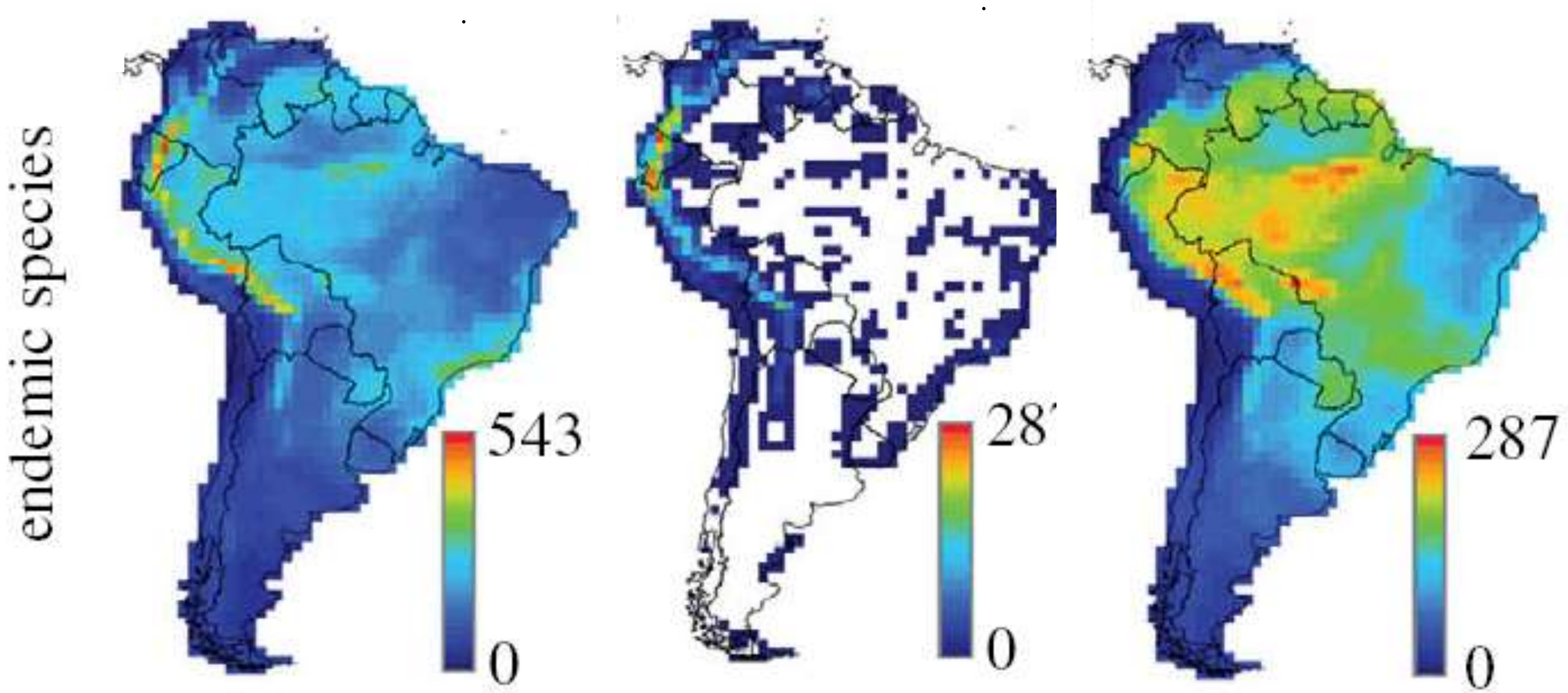
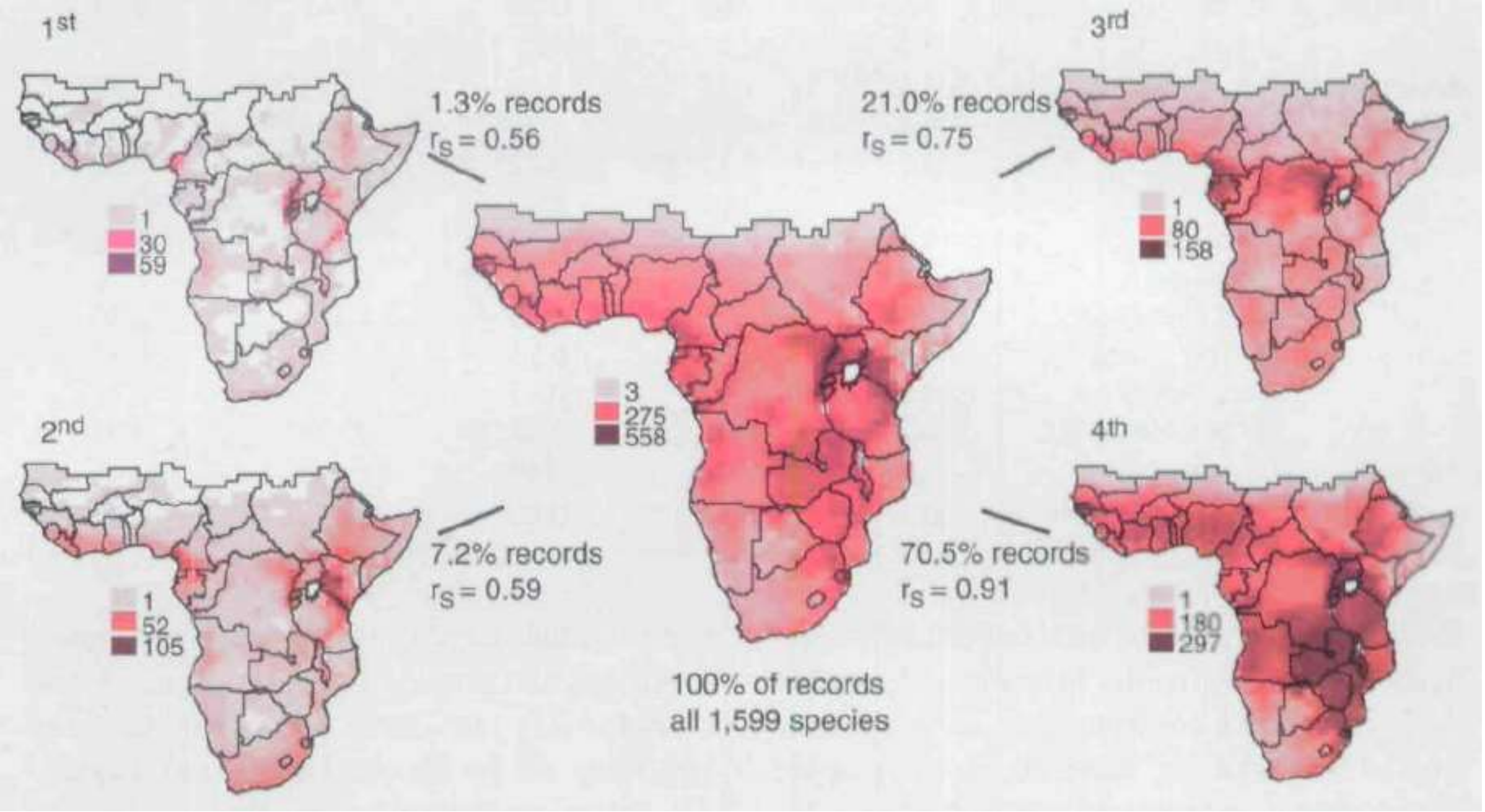


Figure 1. Species richness and environmental variables. (*a–e*) Species richness of endemic birds of South America (n=2248 species) partitioned into geographical range-size quartiles (first, smallest; fourth, largest ranges), at a scale of 1°×1° (latitude–longitude). (*f–m*) Environmental maps used to guide species occurrence probabilities in stochastic models. (*f–j*) Simple variables analogous to traditional single-factor regression analyses. (*k–m*) Composite variables based on published formal models of species richness: species-energy model (Currie *et al.* 2004); water-energy model (Hawkins *et al.* 2003; Currie *et al.* 2004); and temperature-kinetics model (Brown *et al.* 2004; see electronic supplementary material for details).

Predicting continental-scale patterns of bird species richness with spatially explicit models

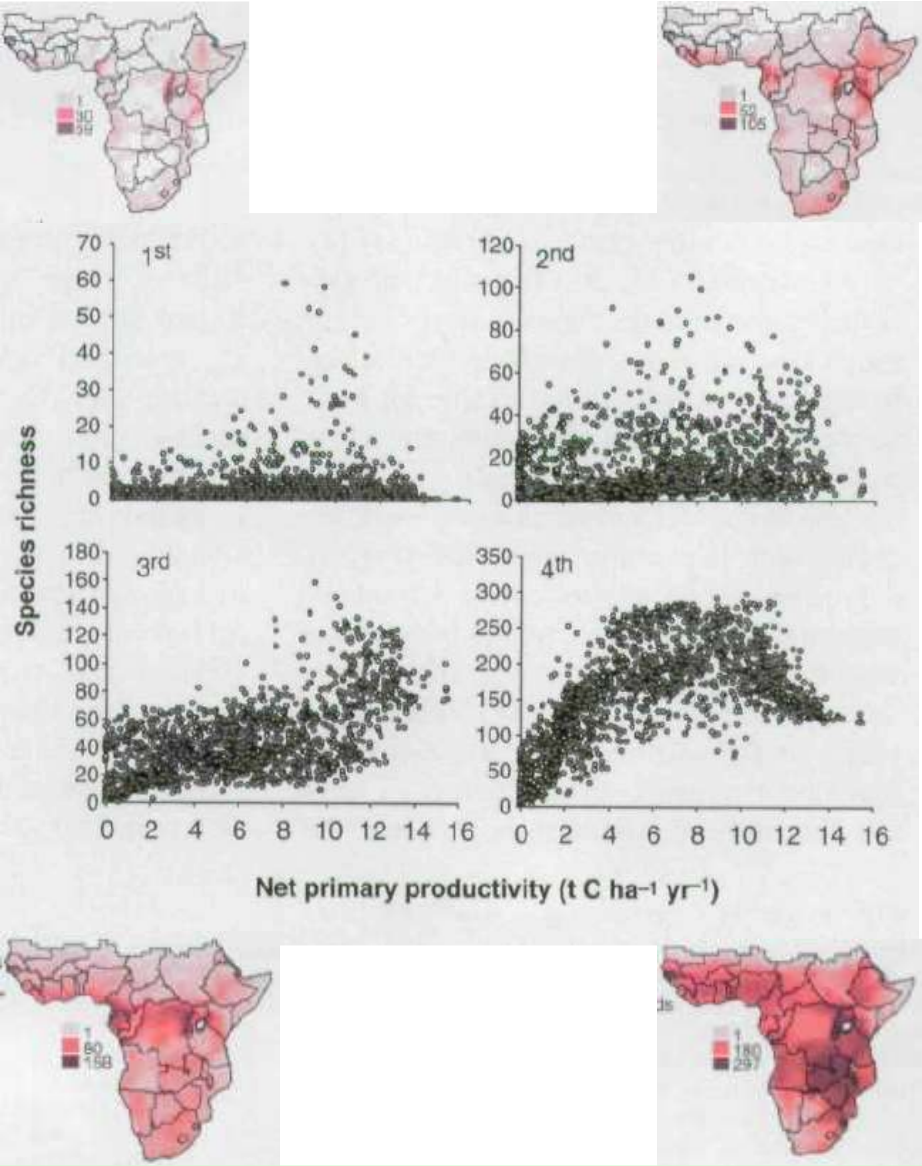
Carsten Rahbek[1,*], Nicholas J. Gotelli[2,*], Robert K. Colwell[3], Gary L. Entsminger[4], Thiago Fernando L. V. B. Rangel[5] and Gary R. Graves[6]

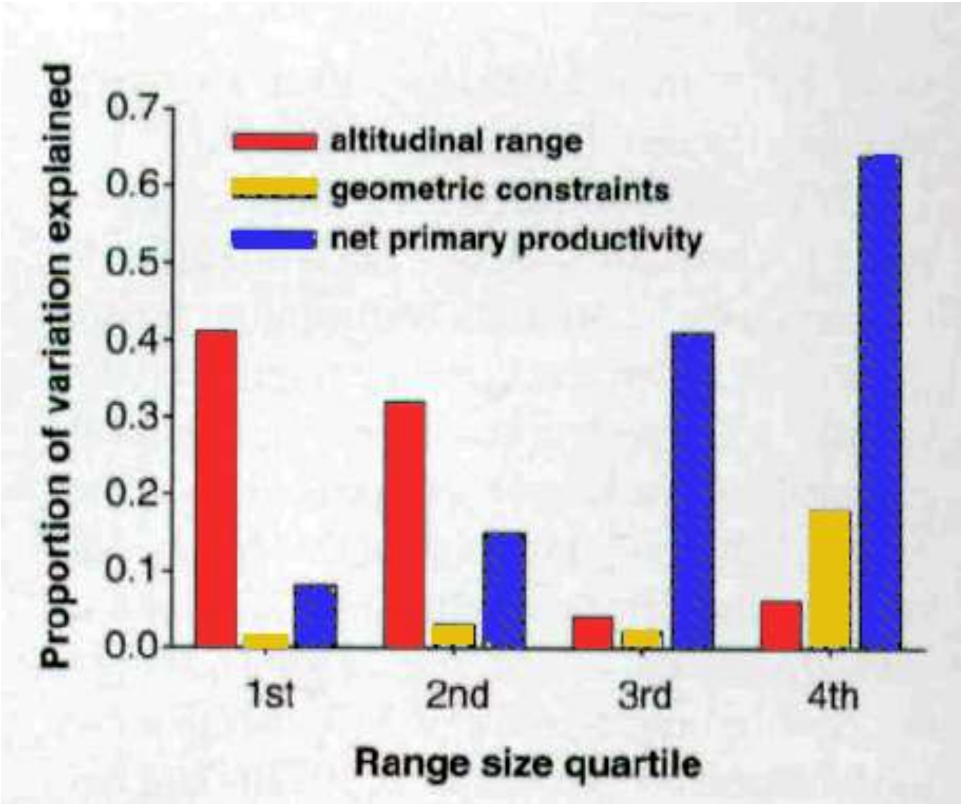
Bird species diversity: total and separated into quartiles by range size [1st quartile = smallest 25% of geographic range sizes]



Jetz & Rahbek 2002, Science 297: 1548

Bird species diversity explained by net primary productivity and altitude

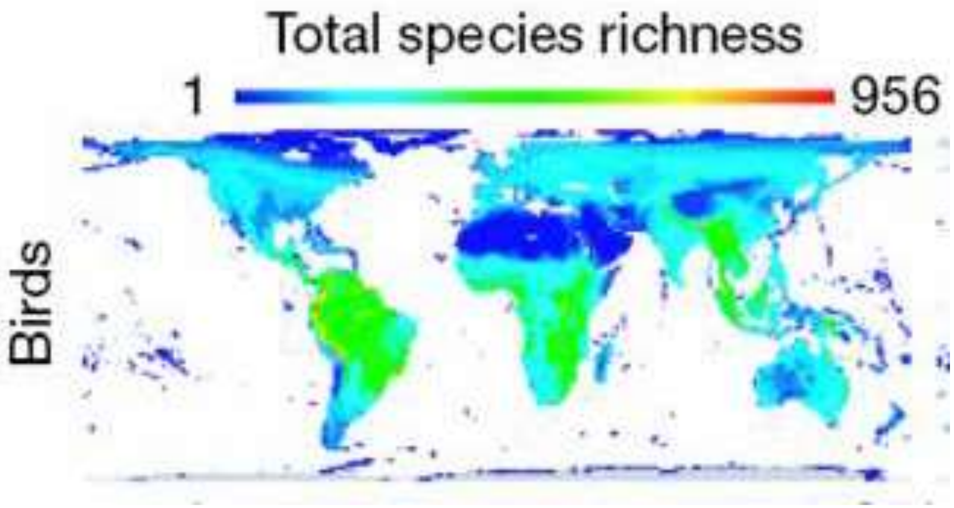


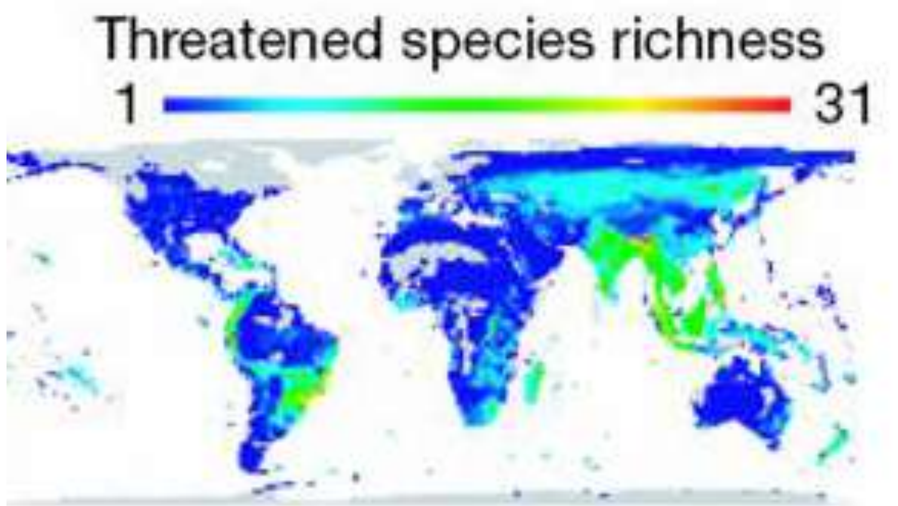


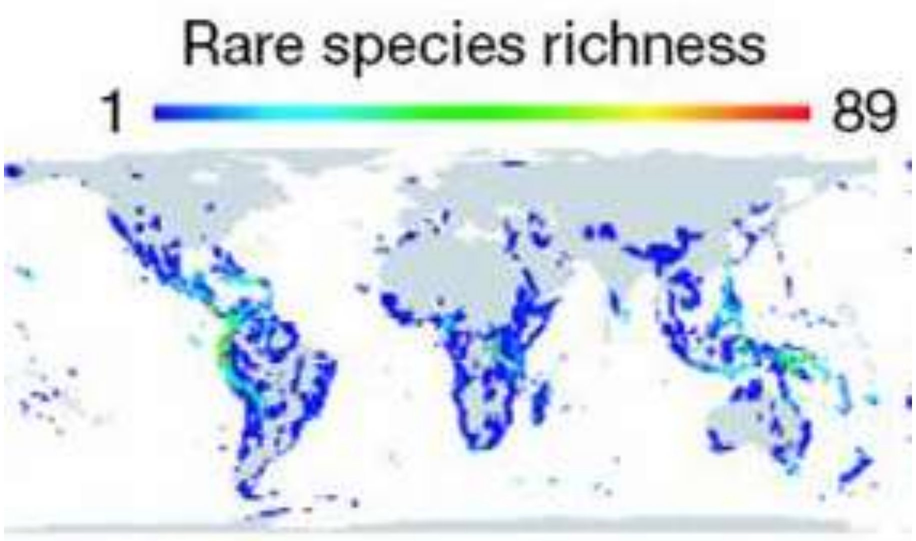
geographic range size quartiles
[1st = smallest]

Jetz & Rahbek 2002, Science 297: 1548

Global distribution of birds







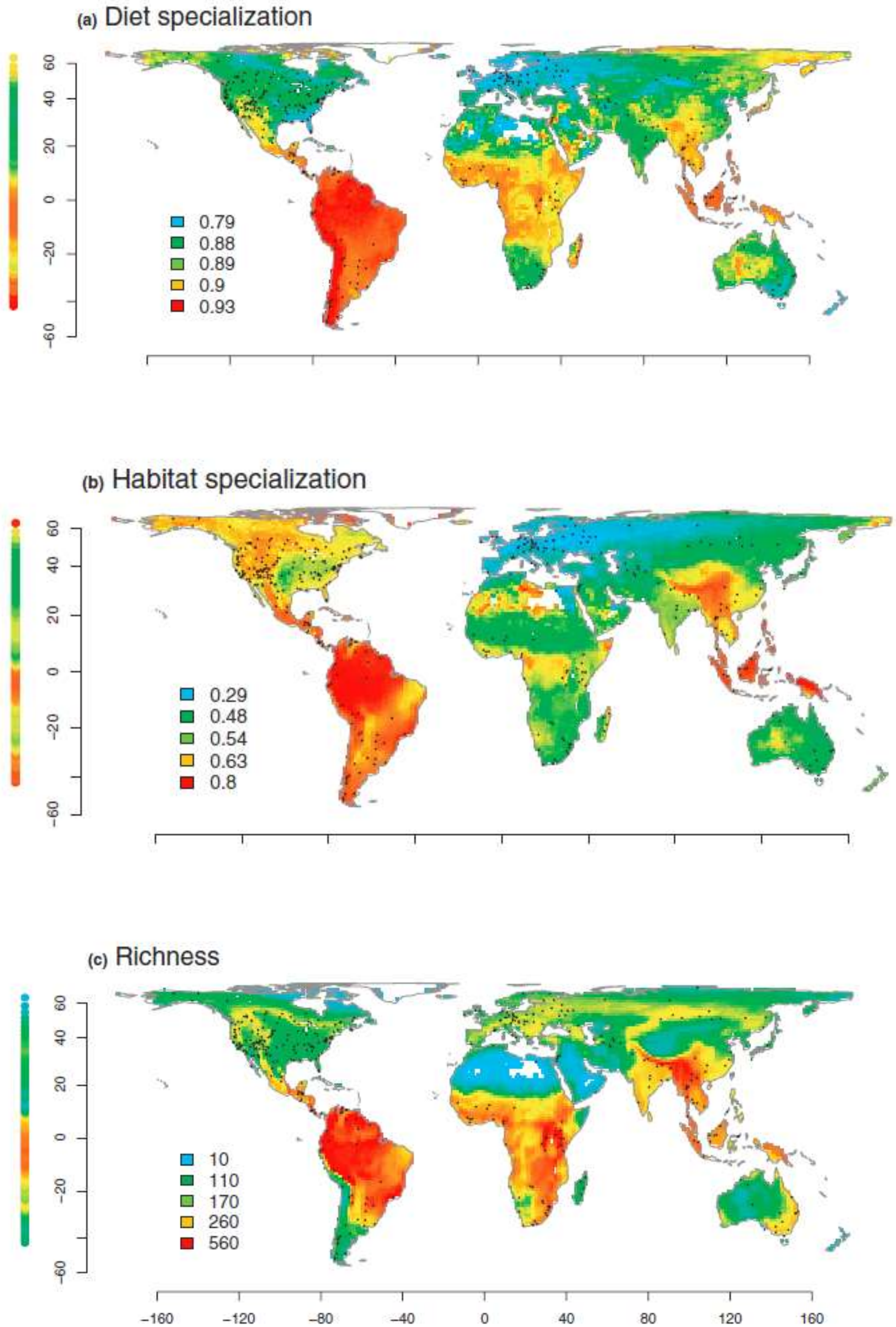
rare species - 25% of species with the smallest geographic ranges
threatened species - IUCN vulnerable, endangered, critically endangered

Global distribution and conservation of rare and threatened vertebrates

Richard Grenyer[1*†], C. David L. Orme[2*], Sarah F. Jackson[3], Gavin H. Thomas[4†], Richard G. Davies[3], T. Jonathan Davies[1†], Kate E. Jones[5], Valerie A. Olson[5†], Robert S. Ridgely[6], Pamela C. Rasmussen[7], Tzung-Su Ding[8], Peter M. Bennett[5], Tim M. Blackburn[4], Kevin J. Gaston[3], John L. Gittleman[1†] & Ian P. F. Owens[2,9]

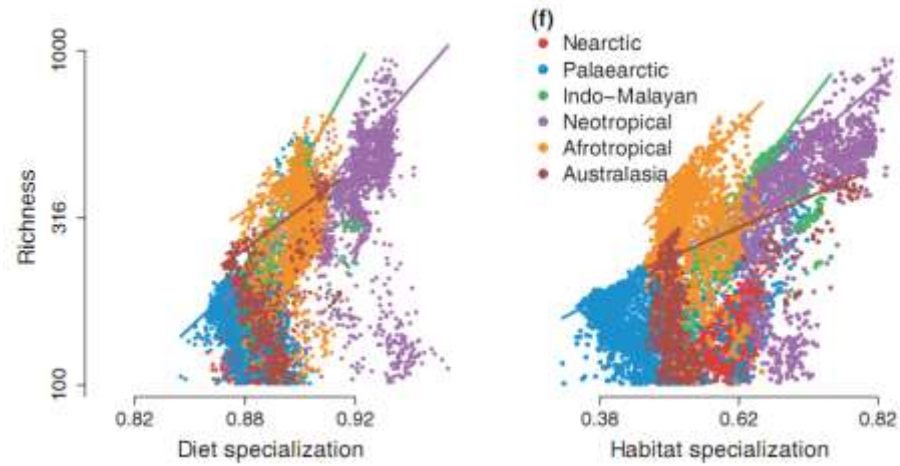
NATURE|Vol 444|2 November 2006

Figure 1 | Global richness maps for birds, mammals and amphibians. Global richness is shown with respect to the three different aspects of species richness used here. Colour gradients are linear with respect to species number.



Birds

breeding birds communities in 12,000 km2 areas:
frequency of dietary categories (seeds, fleshy fruits, nectar, invertebrates, carrion, fish, other vertebrates, and other plant materia) and habitat use



Belmaker et al. 2011

Endemic families of tropical birds

Tropical America [13 families]

Tinamidae
Cracidae
Psophiidae
Momotidae
Ramphastidae
Galbulidae
Pipridae
Bucconidae
Dendrocolaptidae
Formicariidae
Thamnaphilidae
Furnariidae
Cotingidae

Madagascar [4 families]

Mesitornithidae
Brachypteraciidae
Philepittidae
Vangidae

Africa [1 family]

Musophagidae

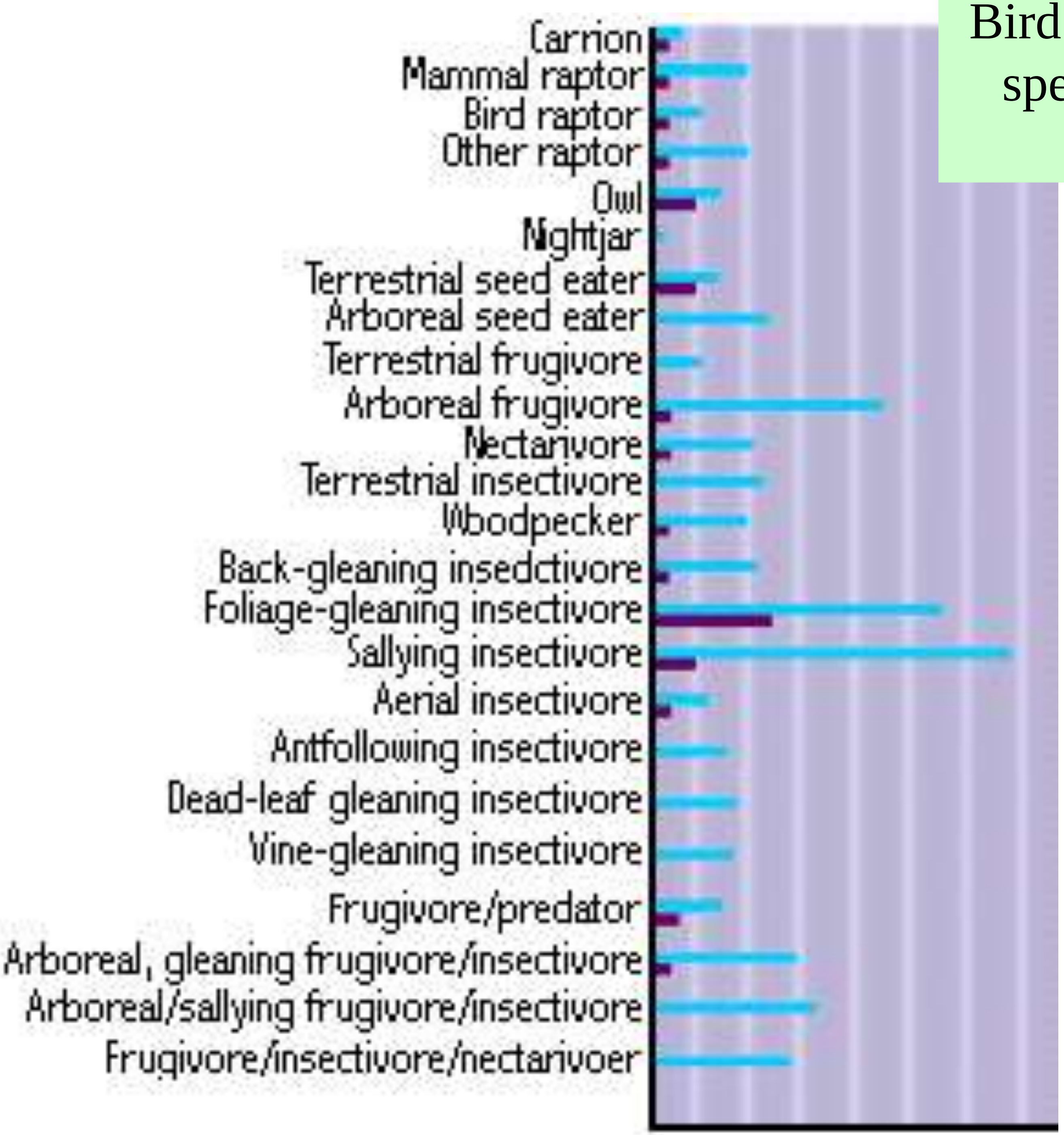
SE Asia [1 family]

Irenidae

Australia/New Guinea [10 families]

Casuariidae
Megapodidae
Menuridae
Ptilonorhynchidae
Maluridae
Meliphagidae
Acanthizidae
Pomatostomidae
Orthonychidae
Paradisaeidae

Bird guilds and ecological specialization (**tropics**, **temperate zone**)



Feeding guilds of temperate and tropical birds

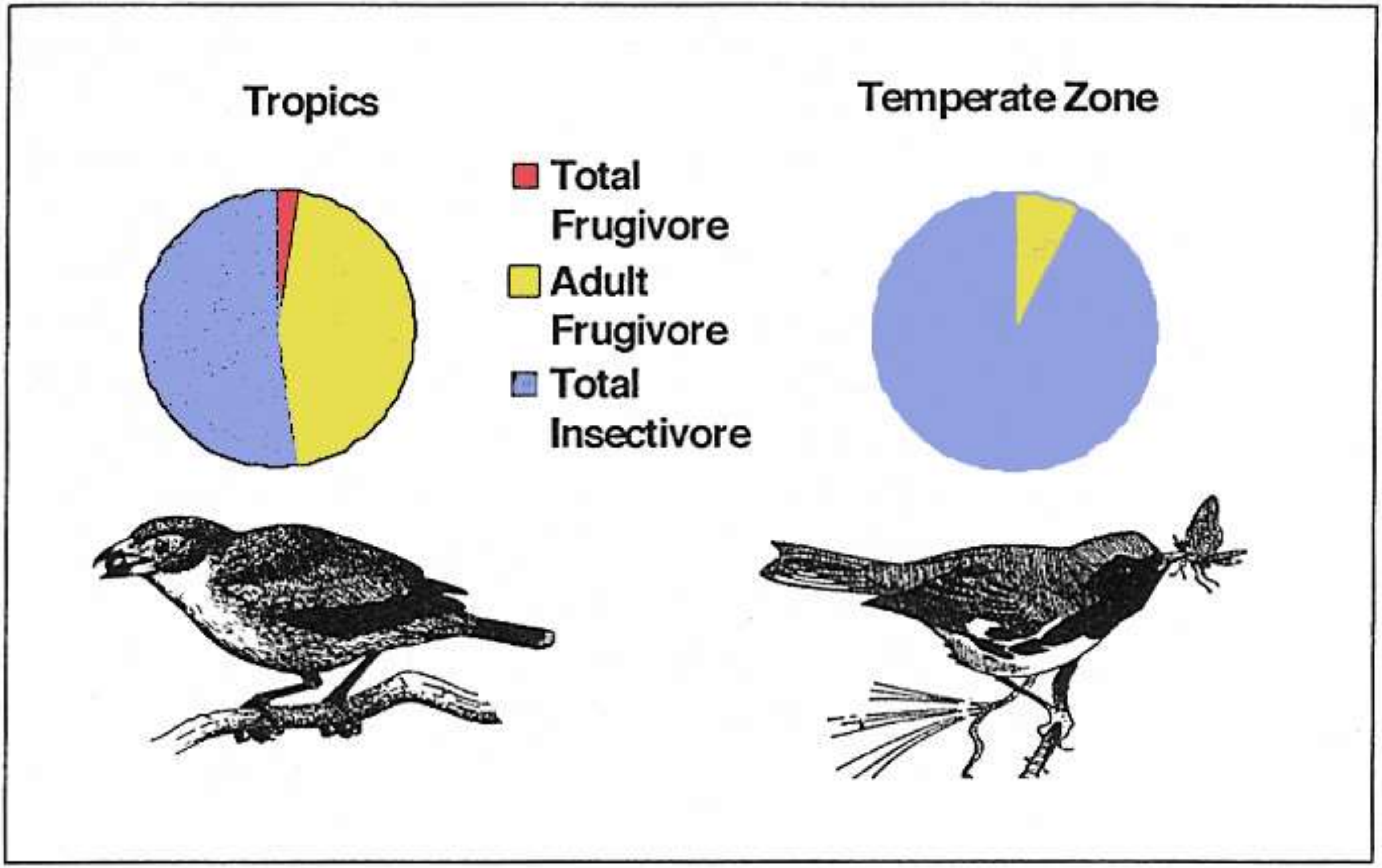
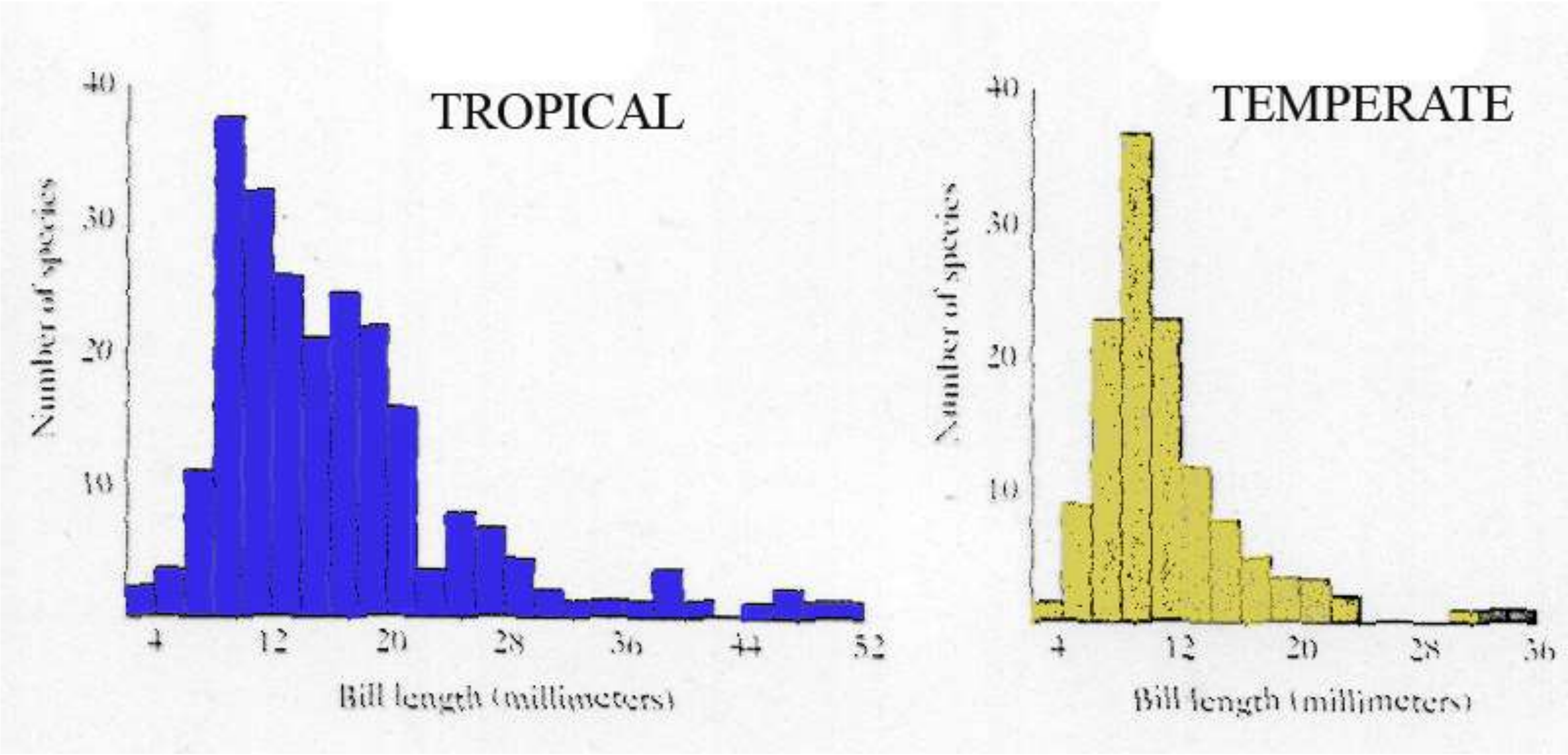


Figure 7.2

Morphological diversity (bill length) of birds in tropical and temperate ecosystems



Territorial systems of birds

Territorial systems of Panamanian passerines compared to North American passerine birds.

Type of Territory[a]	*Number of species*		*Number of genera*[b]	
	Panama	*NA*	*Panama*	*NA*
Breeding	42	224	28	89
Year-long	142	15	84	13
Army ant influenced	11	0	9	0
Mixed species flock	65	0	40	0
Fruit influenced	43	0	20	0
Lek	28	0	19	0
Total	**331**	**239**	**200**	**102**

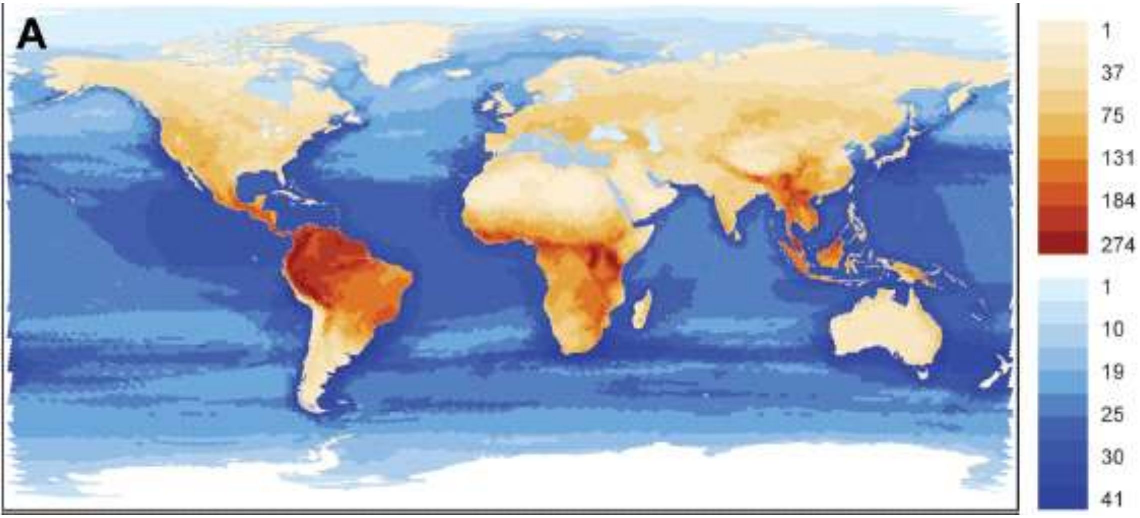
a: See text
b: Species in some genera fit more than one territory type (e.g., *Elaenia*, *Vireo*, *Basileuterus*, *Sporophila*).

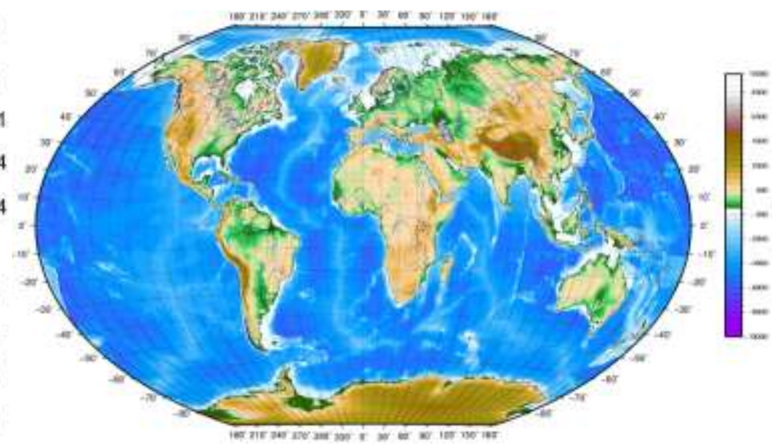
Major bird migration routes.

Only rainforests of SE Asia represent an end-point of a major route.

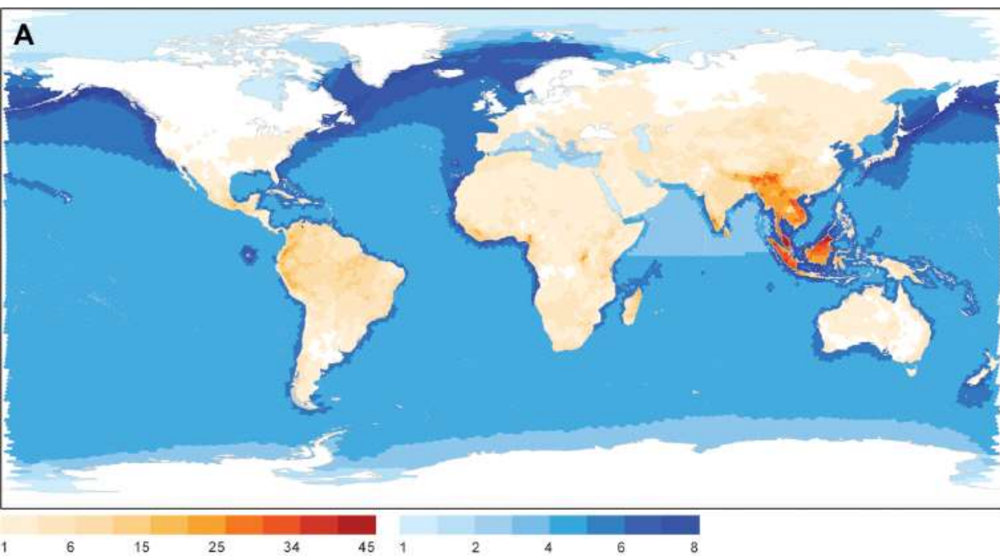
Mammals

Global patterns of species diversity: mammals

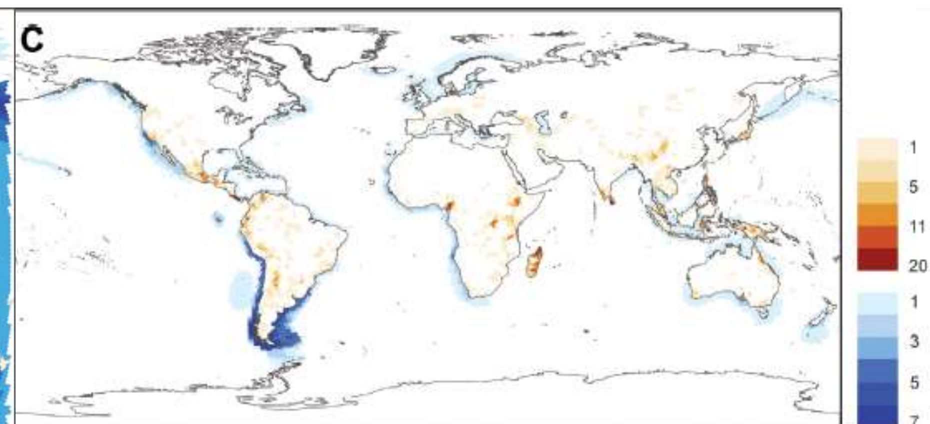




Number of species [per 22,000 km^2 grid units]



No. of threatened species



No. of species with restricted geographic ranges [those 25% spp. with the smallest ranges]

Fig. 1. Global patterns of mammalian diversity, for land (terrestrial and freshwater, brown) and marine (blue) living species, on a hexagonal grid (fig. S2). (A) Species richness. (B) Phylogenetic diversity (total branch length of the phylogenetic tree representing those species in each cell in millions of years). (C) Number of restricted-range species (those 25% species with the smallest ranges). (D) Median range size

Schipper et al. 2008, Science 322:225

Fruit eating bats in the tropics

Old World:
Pteropodidae, Megachiroptera
large size: 15 g – 1.5 kg, up to 1.8 m wingspan
diet: fruits
communal arboreal roosts, flying at sunset long distances
readily colonise and speciate on islands (62% spp. are island endemics)

Neotropics:
Phyllostomidae, Microchiroptera:
small 5-100g
diverse diet: insects, blood, small vertebrates, nectar, fruit
small home range

Feeding guilds – tropical bats

Relative frequency values for the seven trophic roles in the four major rain-forest regions

BATS

Trophic role	Neotropics	Asia	Africa	Australia
Fish-eating	0.9	0.9	0.3	0.3
Blood-feeding	1.4	0	0	0
Other carnivores	1.8	0.6	0.3	1.0
Foliage-gleaning of insects	10.1	15.6	14.3	9.3
Aerial insectivory	43.6	60.5	65.8	48.4
Nectar-feeding	13.3	3.5	5.5	6.4
Frugivory	30.2	19.5	13.8	35.1

Food specialization of Neotropical phyllostomid bats

blood

small vertebrates

nectar

omnivore

fruits

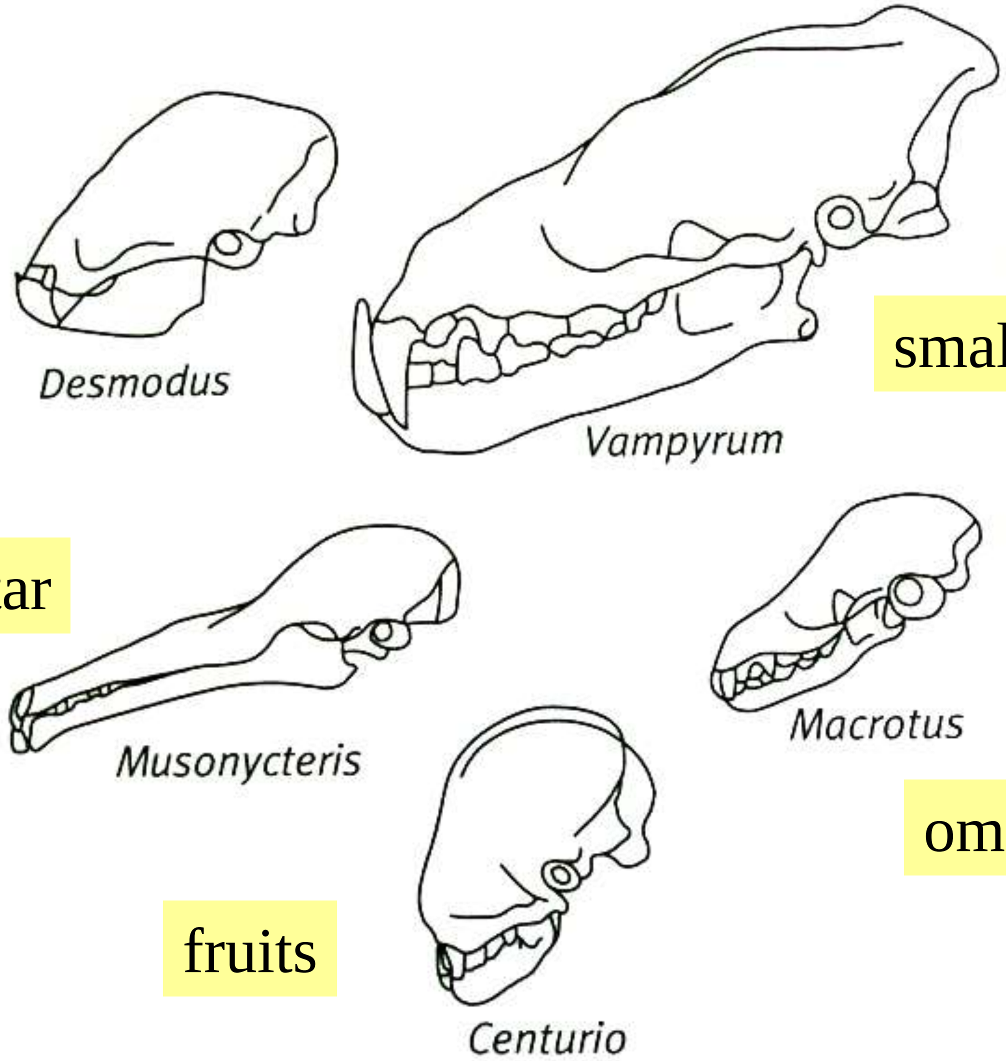
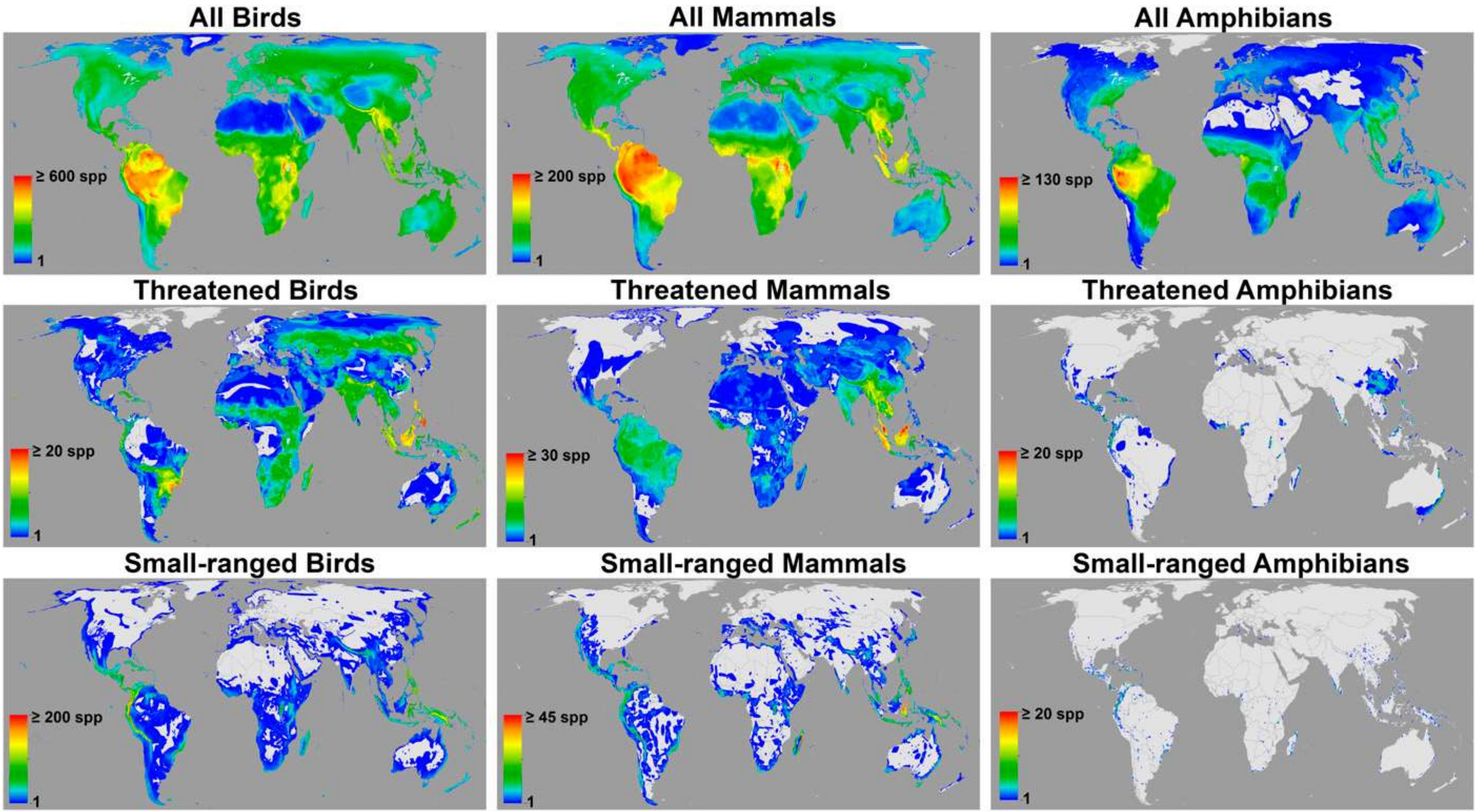


Fig. 6.2 A diversity of skulls from New World phyllostomid bats, illustrating adaptations for feeding on different food types. *Musonycteris* is the most extreme nectarivore, probing into flowers with its long snout. *Centurio* is the most extreme frugivore and probably eats overripe fruit. *Vampyrum* is a large carnivore, eating birds and bats rather than insects. *Desmodus* is a blood-feeder (sanguinivore), while *Macrotus* is a more generalized feeder, eating mostly insects and fruits, and sometimes a bit of nectar. (Courtesy of Patricia W. Freeman.)

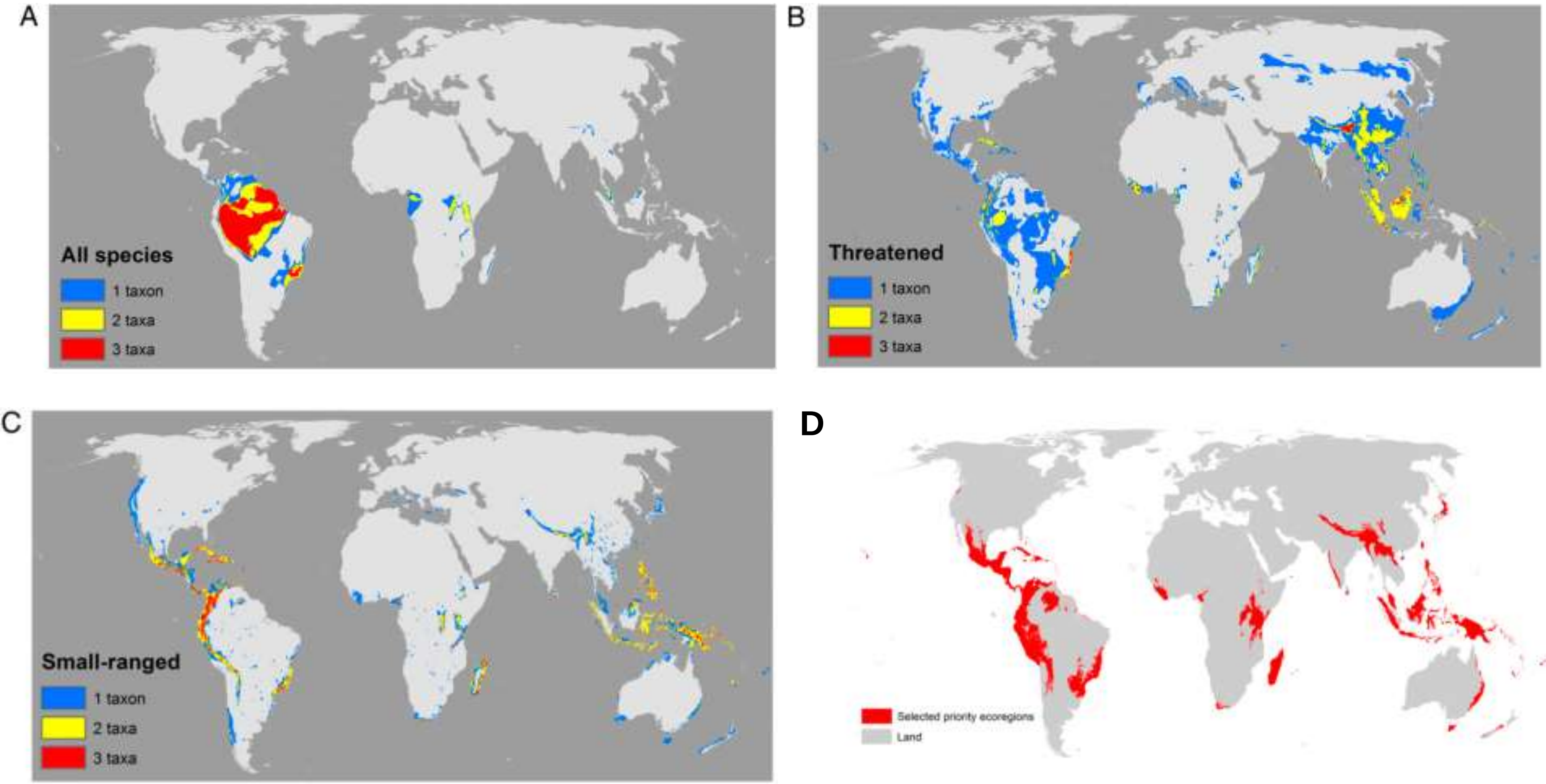
Biodiversity distribution in birds, mammals and amphibians



Threatened species: vulnerable, endangered, or critically endangered in the IUCN Red List.
Small-ranged species: geographic ranges are smaller than the median range size for that taxon.

Jenkins et al. 2013, PNAS

Overlap in biodiversity centers in birds, mammals and amphibians

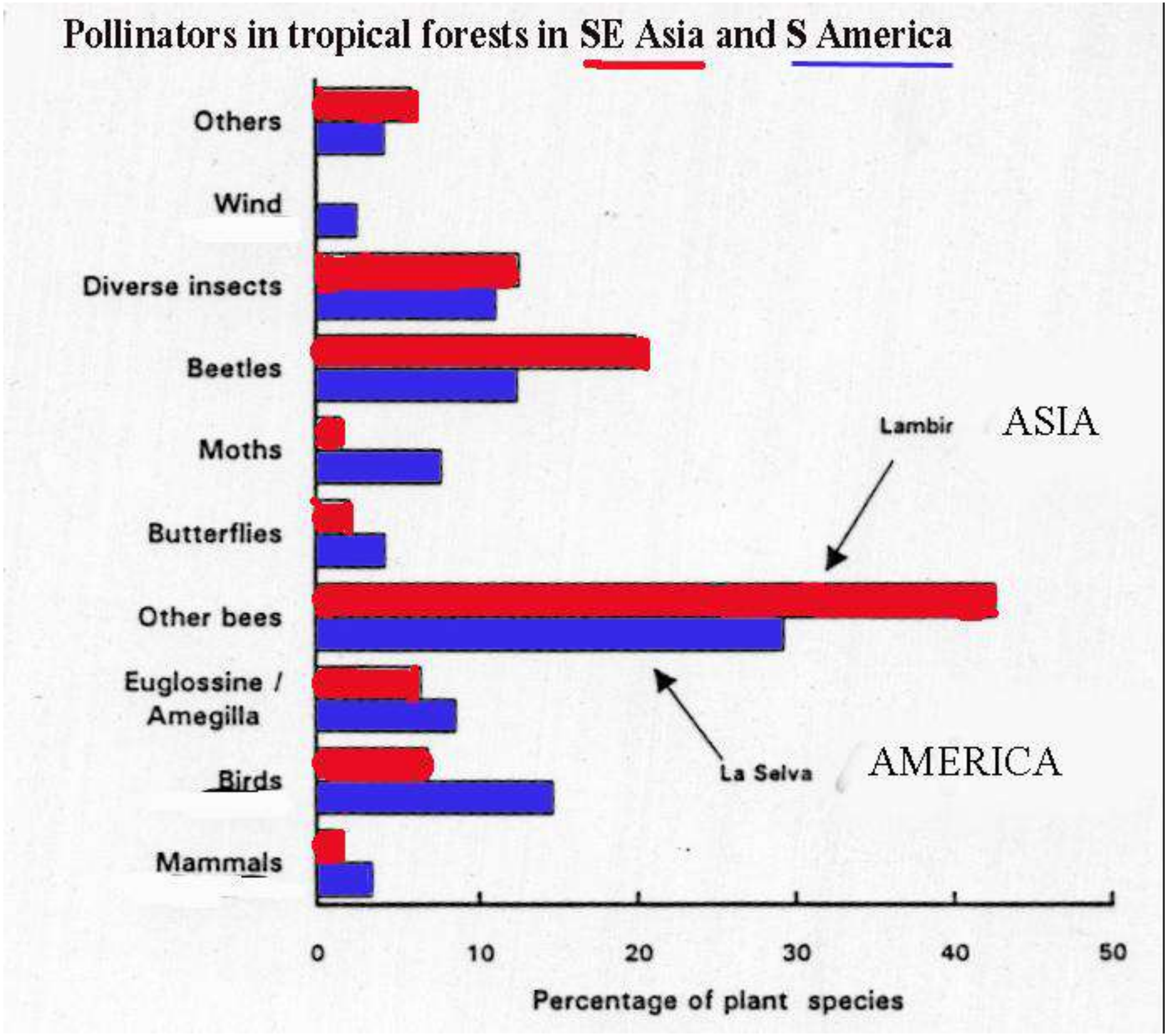


Overlap of species richness centers (centers are among the richest 5% of cells for at least one of the taxa): A: All species, B: IUCN threatened species, C: Small-ranged species. D:.Priority ecoregions based on small-ranged vertebrates

Jenkins et al. 2013, PNAS

Pollination

Modes of pollination in tropical forests of SE Asia and S America



Bees, Apidae

Euglossinae, orchid bees
Meliponinae, stingless bees
Apinae, honeybees

MELIPONINAE - stingless bees

Barro Colorado Island: lowland tropical forest

36,000 meliponine bees per ha
8,300 other bees per ha

polination services = 400 kg sugar per ha annually
which is 6% of primary production

Birds as pollinators

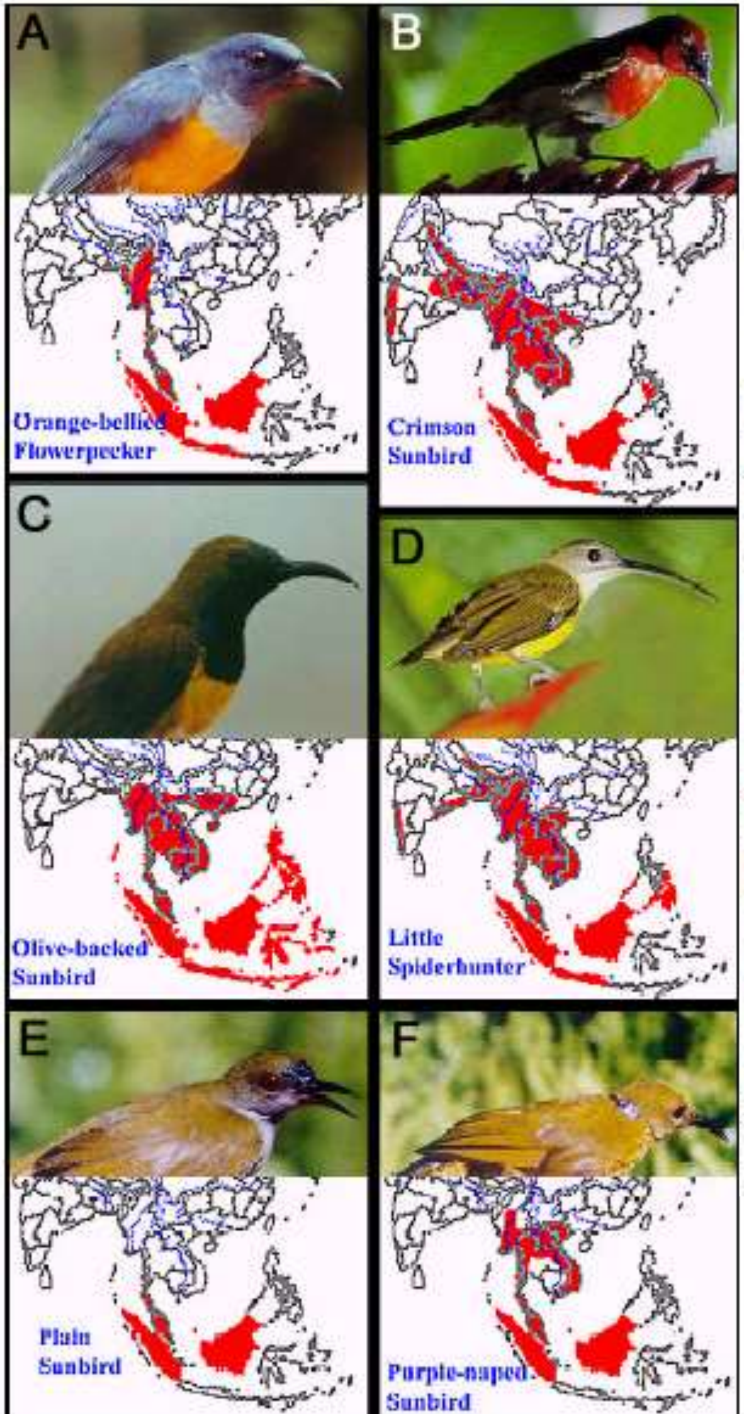
Trochilidae – hummingbirds – Neotropics, 328 species

Nectariniidae – sunbirds – Africa, also Asia

Meliphagidae – honeyeaters – New Guinea, Australia, Pacific

birds are expensive pollinators [high demand on nectar]

most important in Neotropics, but hummingbirds pollinate only herbs, lianas, shrubs, very rarely trees



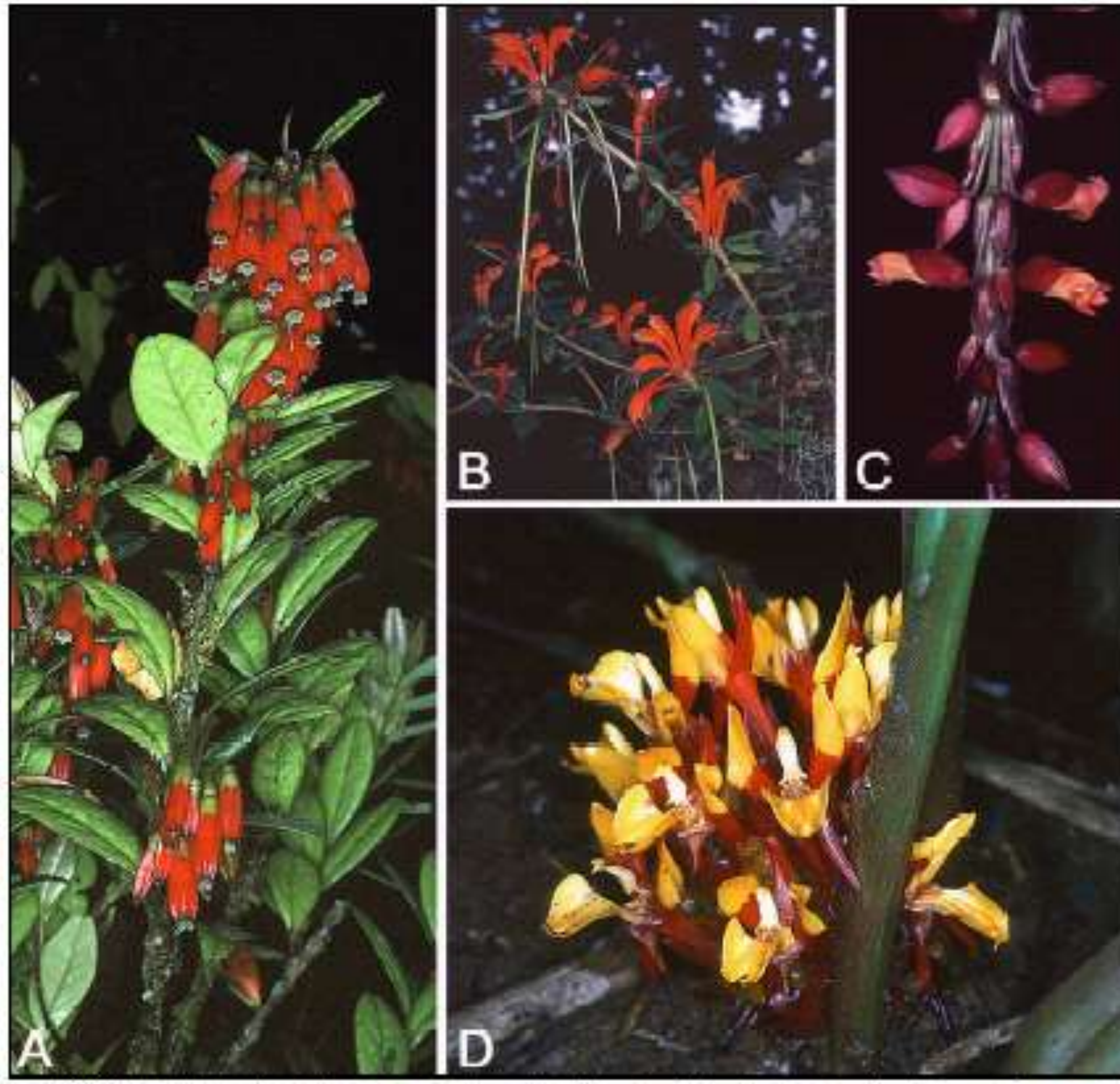
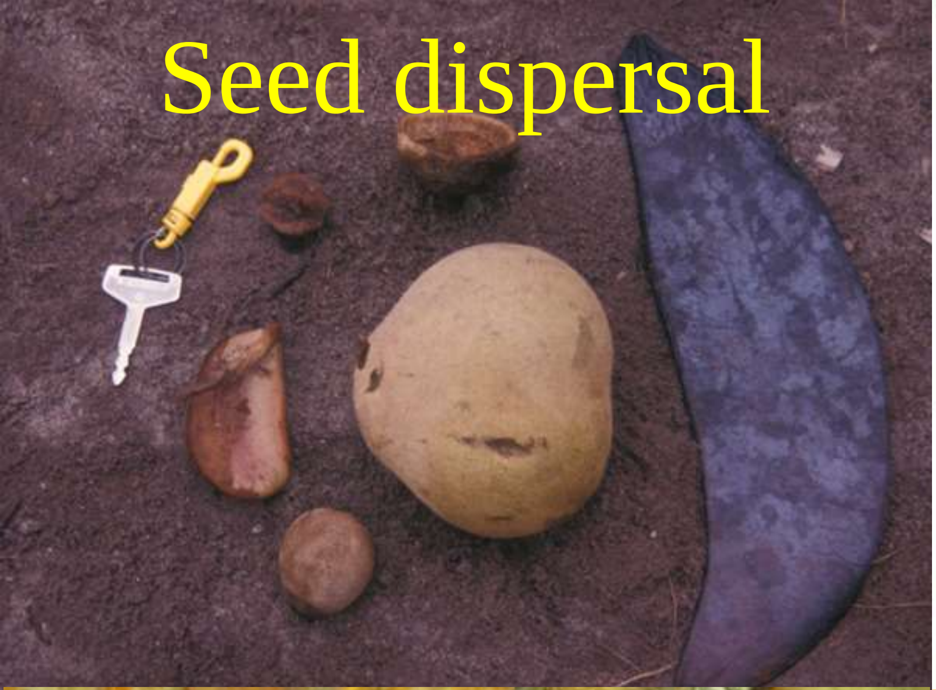
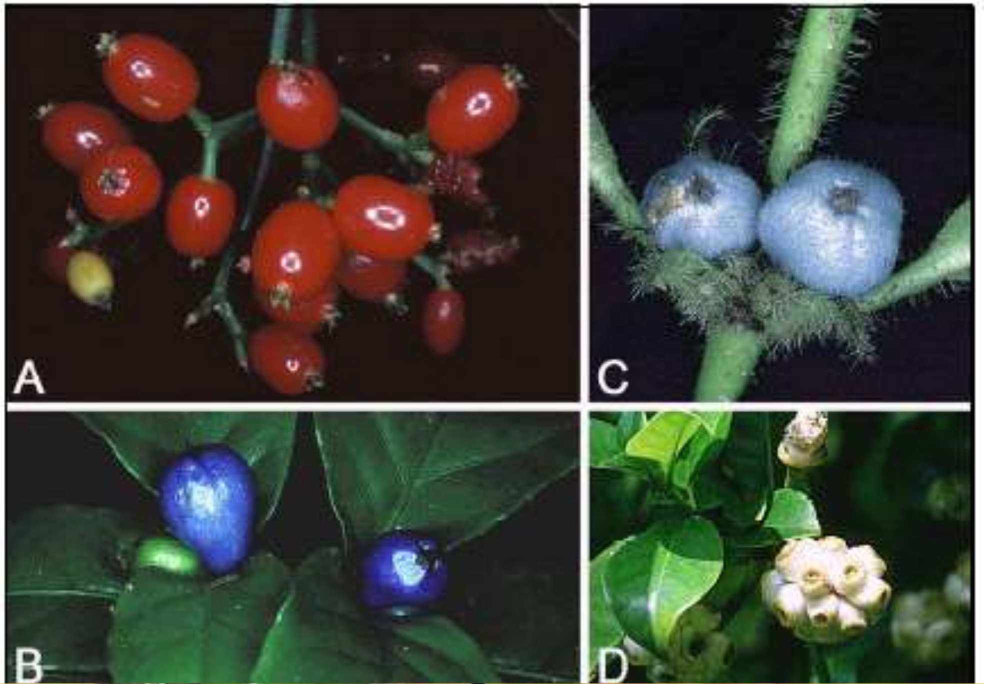


Fig. 1.9.2. Selected bird pollinated taxa from northern and northeastern Thailand. – A, *Agapetes hosseana* (Ericaceae); B, *Aeschynanthus* sp. (Gesneriaceae); C, *Thunbergia coccinea* (Acanthaceae); D, Zingiberaceae, indet. genus. – Further explanations in the text (photos C. Puff)

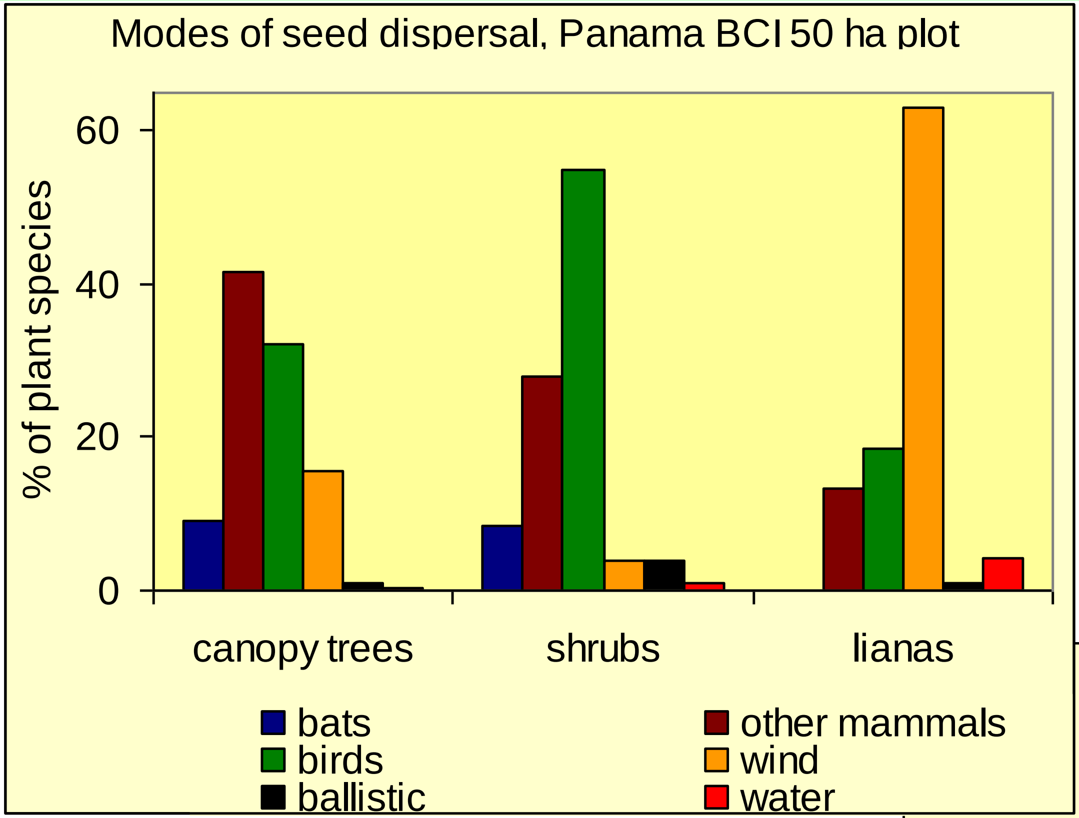
Fig. 1.9.1. Genera and species of Nectariniidae occurring in Thailand and their general distribution ranges. – A, Orange-bellied Flowerpecker (*Dicaeum trigonostigma*). – B-C,E-F, Sunbirds; B, Crimson Sunbird (*Aethopyga siparaja*); C, Olive-backed Sunbird (*Nectarinia jugularis*); E, Plain Sunbird (*Anthreptes simplex*); F, Purple-naped Sunbird (*Hypogramma hypogrammicum*). – D, Little Spiderhunter (*Arachnothera longirostra*) (all bird illustrations from Birds of Sarawak website, all distribution maps from Distribution of Breeding Birds in East Asia web site; see Internet References)

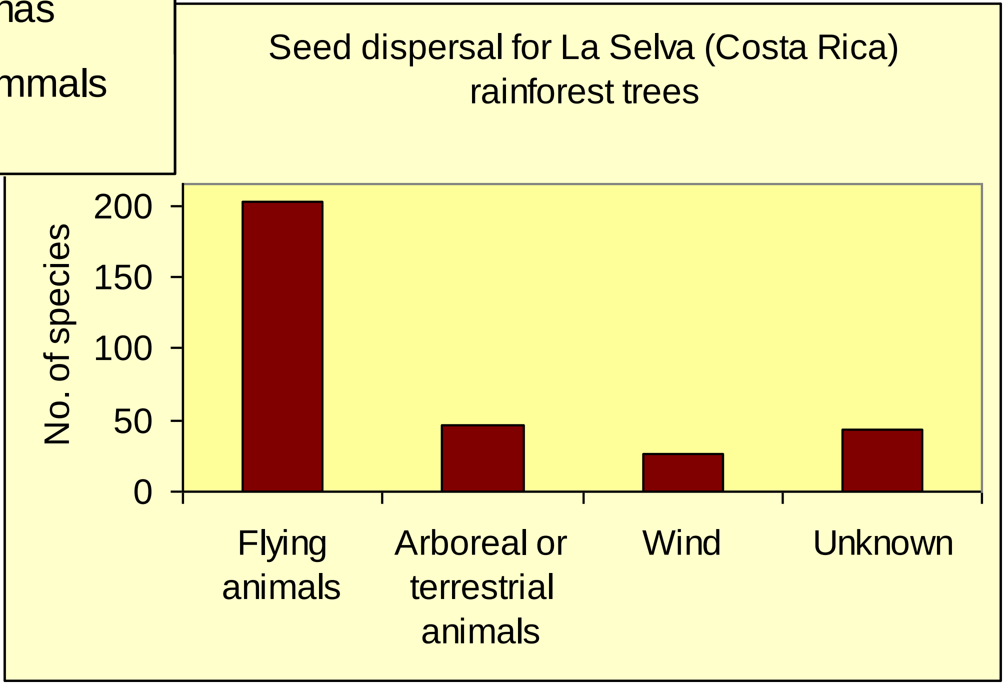
Seed dispersal





Seed dispersal





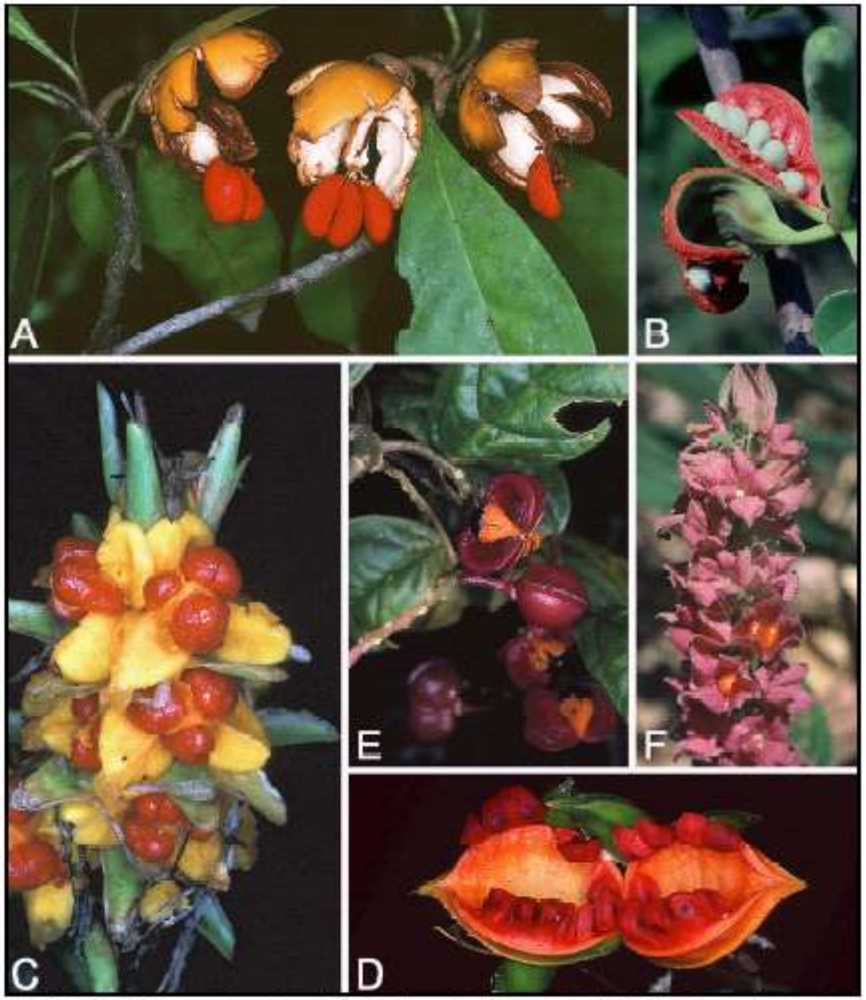


Fig. 1.9.8. Dehisced fruits exposing seeds partially or entirely enclosed by arils or "pulp" (A-E). – A, *Ternstroemia gymnanthera* (Theaceae, or sometimes Ternstroemiaceae), seeds (entirely enclosed by red arils) dangling from dehisced fruits; B, *Xylopia* sp. (Annonaceae), individual carpels of a fruit split open to expose arillate seeds; C, *Hedychium* sp. (a species epilithic on limestone; Zingiberaceae), open fruits exposing seeds almost entirely enclosed by orange "pulp"; D, *Tabernaemontana divaricata* (Apocynaceae), seeds, enclosed in red arils, attached to carpels; E, *Polygala arillata* (Polygalaceae), each carpel with a solitary black seed, basally surrounded by orange aril. – F, fleshy "nutlets" (drupelets) partly exserted from enlarged, colored calyx (*Gomphostemma strobilinum*, Lamiaceae). – Further explanations in the text (photos C. Puff, all from Thailand)

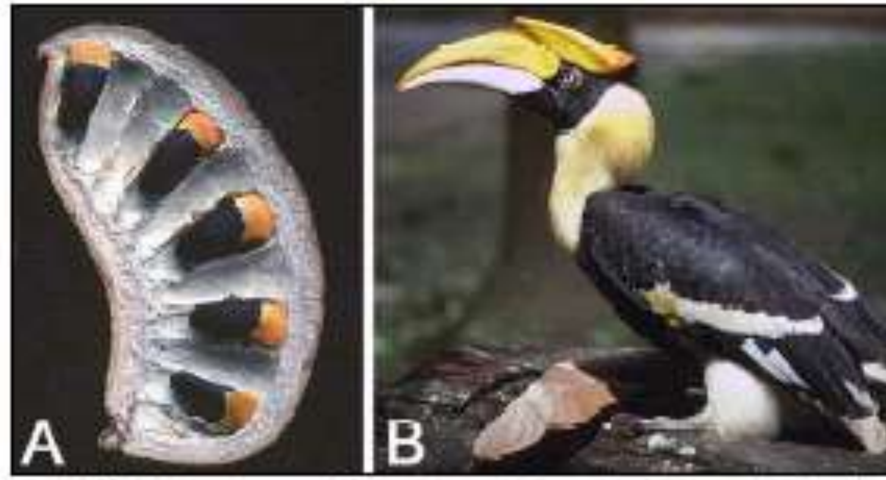


Fig. 1.9.13. *Afzelia xylocarpa* (Caesalpiniaceae). – A woody pod opened to show black seeds and basal yellow-orange arils. Seeds are known to be dispersed by hornbills (B) (photos C. Puff, all from Thailand)

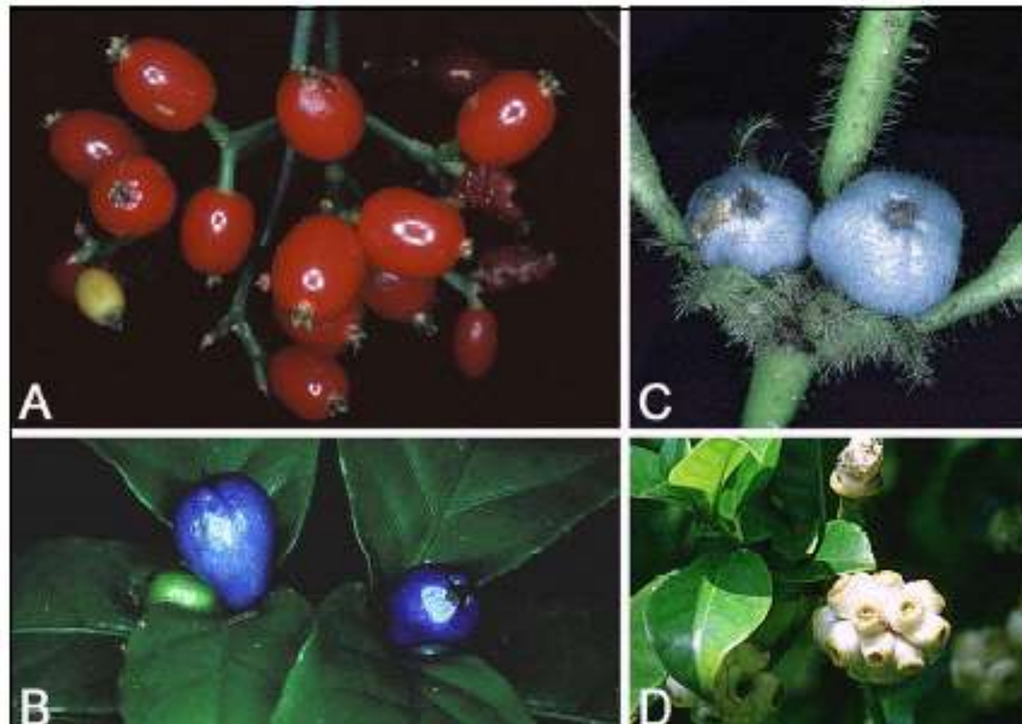


Fig. 1.9.6. Ornithochorous diaspores of selected Thai Rubiaceae (A-C, drupes; D, berry-like fruits in head-like arrangement). – A, *Psychotria rubra*; B, *Saprosma longicalyx*; C, *Lasianthus cyanocarpus*; D, *Schradera polysperma* (syn. *Lucinaea p.*) (photos C. Puff, all from Thailand)

Birds fruits:
small, red colour

Every tropical forest has its big beaks

Ramphastidae – toukans
Neotropics

the two families are unrelated

Bucerotidae – hornbills
Old World

Bird as frugivores (and often seed dispersers):

doves and pidgeons, toucans and hornbills, parrots, birds of paradise, cassowary

Ecological separation of New Guinea pidgeons by fruit size

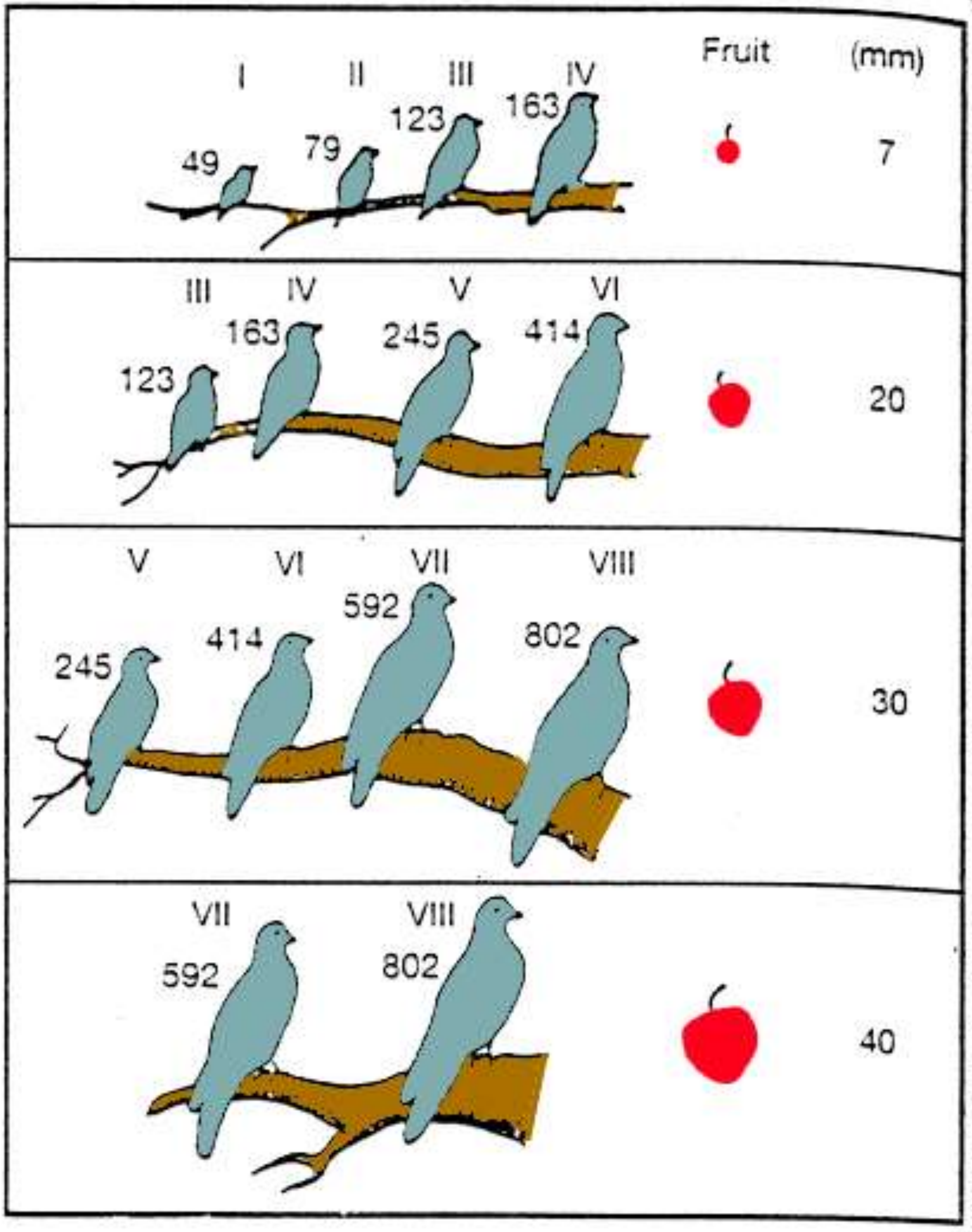
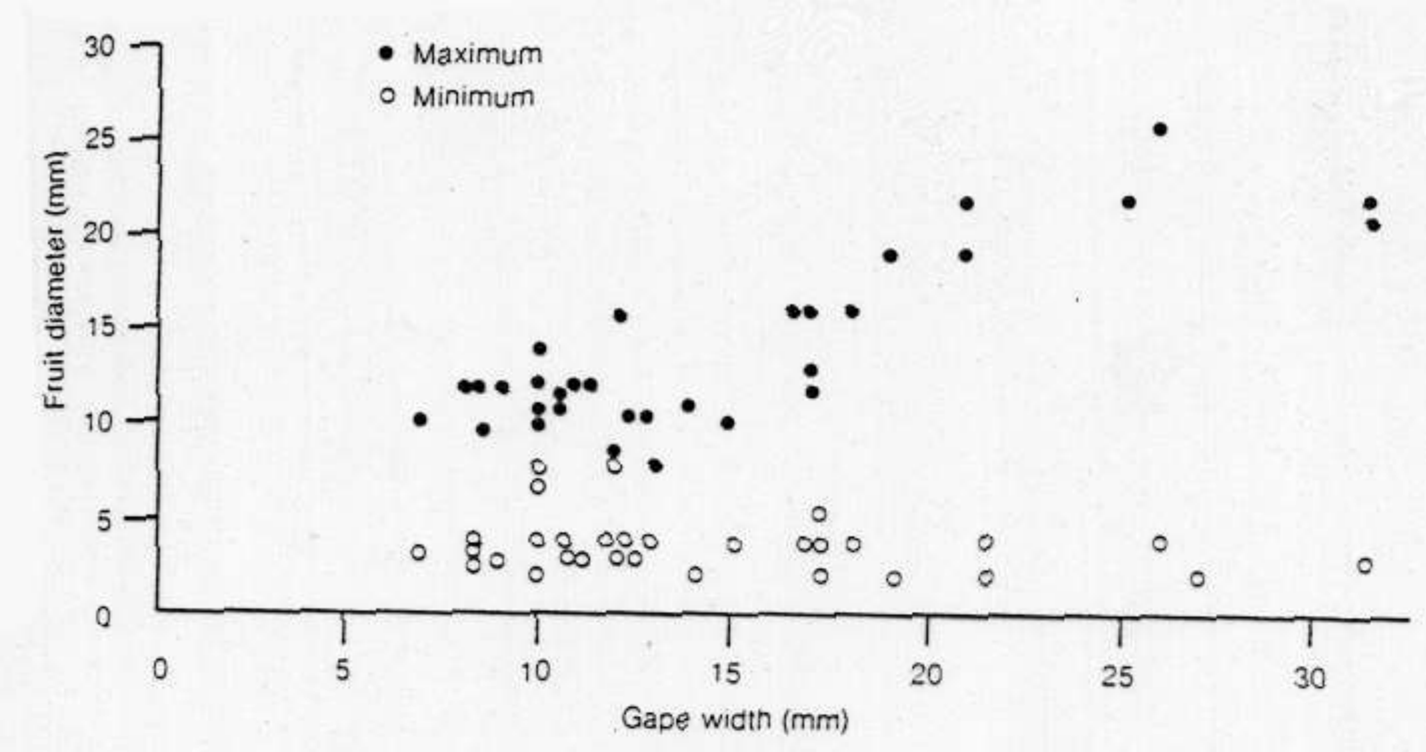


Figure 4.23. Ecological separation by feeding guilds of pigeons in New Guinea forests. Different-sized pigeons take different sizes of rainforest fruits.

Source: Diamond 1973



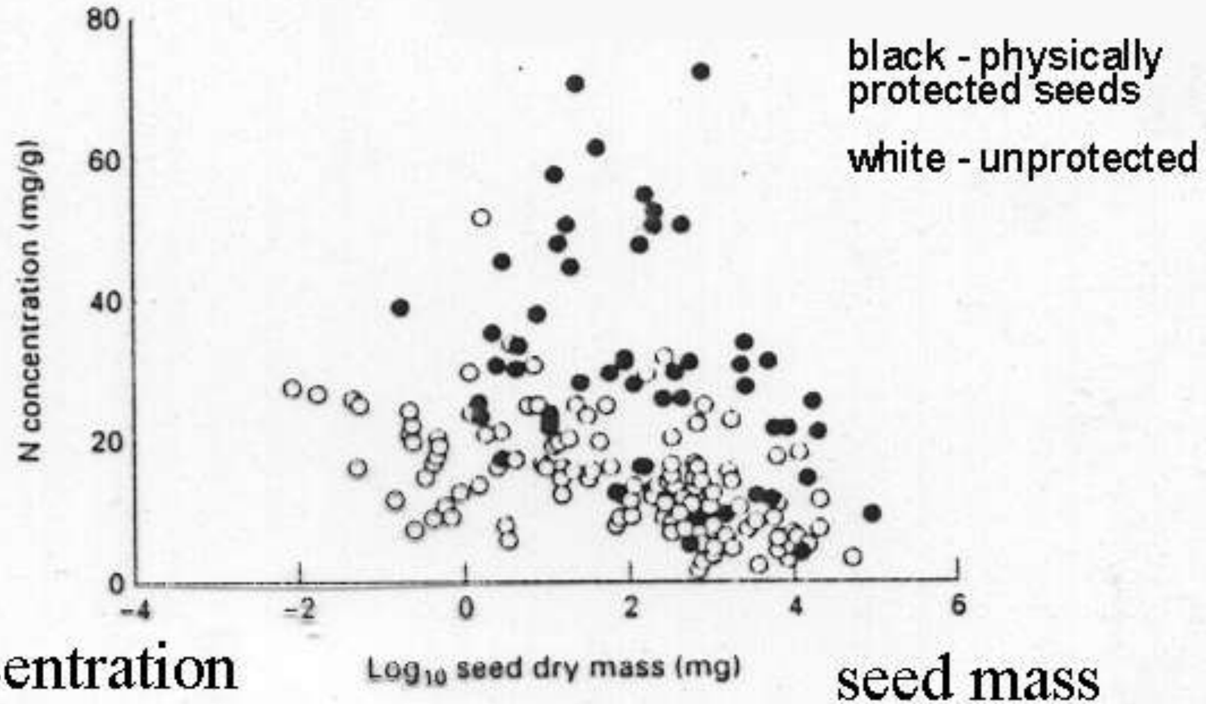
Small fruits are eaten by wider range of bird species than big fruits

Table 7-3 Numbers of birds in feeding assemblages at Central American fruiting trees

Plant Species	Fruit Size (cm^3)	Bird Species (*N*)
Virola surinamensis	2.7	7
Tetragastris panamensis[a]	1.8	12
Virola sebifera	0.7	6
Casearia corymbosa	0.5	22
Guarea glabra	0.2	19
Didymopanax morototoni	0.1	37
Miconia argentea	0.1	46

gape (mouth) width for 36 bird species in
of fruit species included in a diet are
with bird size. Large birds eat fruits in-
birds eat small fruits. After Wheelwright

Seeds with high nutrient concentration are also physically protected



N concentration

seed mass

FIG. 1.4. The mean concentration of N in the seed as a function of the logarithm of mean seed dry mass for seeds from two types of fruit in lowland rainforest in NE Queensland: ●, species with notable physical and/or chemical protection of the seeds by the fruits; ○, seeds not so protected. (From P.J. & E.A.A. Grubb, G.D. Jones & D.J. Metcalfe unpublished data.) The regression for the protected species is $y = -9.89\ (\pm 3.33\ SE) \log x + 63.8\ (\pm 9.6)$, and for the unprotected $y = 6.97\ (\pm 1.80) \log x + 37.5\ (\pm 4.68)$; the slopes are not significantly different but the intercepts (i.e. the y-values when $x = 1$ mg) are ($P < 0.0001$).

Agouti - Dasyprocta punctata

Astrocaryum standleyanum

Tayassu pecari

Astrocaryum palm:
- ripening fruits protected by spines
- many vertebrates feed on fallen fruits
- agoutis peel the fruit, which protects it from bruchids and enables the seed to germinate
- peccaries feed on fruits and suppress thus its population to lower levels than in their absence

Forest elephants as an important ecological factor in African rain forests

Recognised as a species, *Loxodonta cyclotis*
Regular disturbance of vegetation, and dispersal of large seeds
(Parinari exelsa, Balanites wilsoniana, Panda oleosa etc.)

Asian elephants not so important.
Dwarf island version on Borneo:

What were ecological roles or recently extinct megafauna?

Janzen & Martin (1982) NEOTROPICAL ANACHRONISMS: The Fruits the Gomphoteres Ate

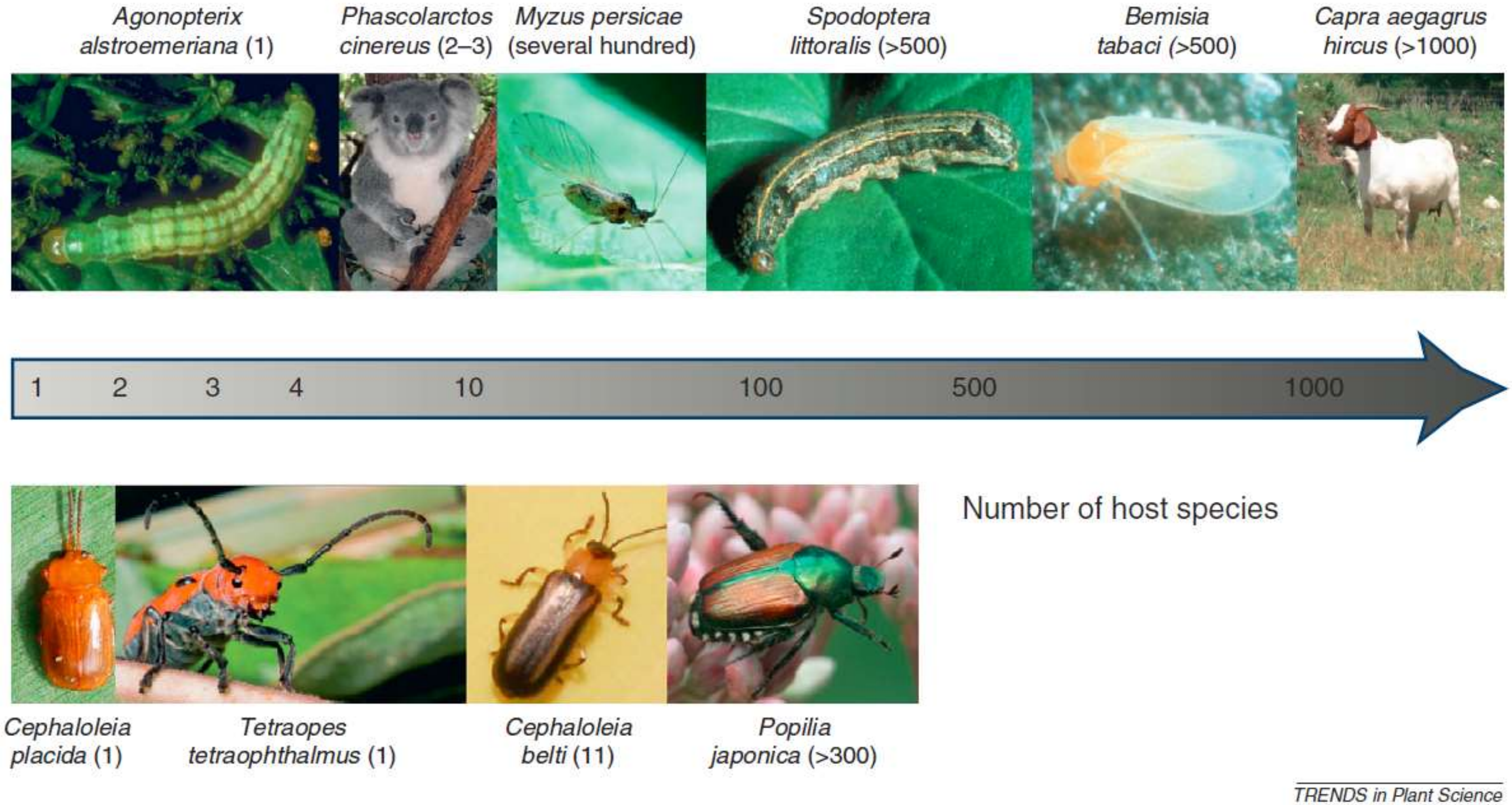
Large recently extinct fauna, such as gomphoteres in S. America, could be important consumers and dispersal agents of large fruits

Crescentia alata

Enterologium cyclocarpum

Similar role played by forest elephants in Africa

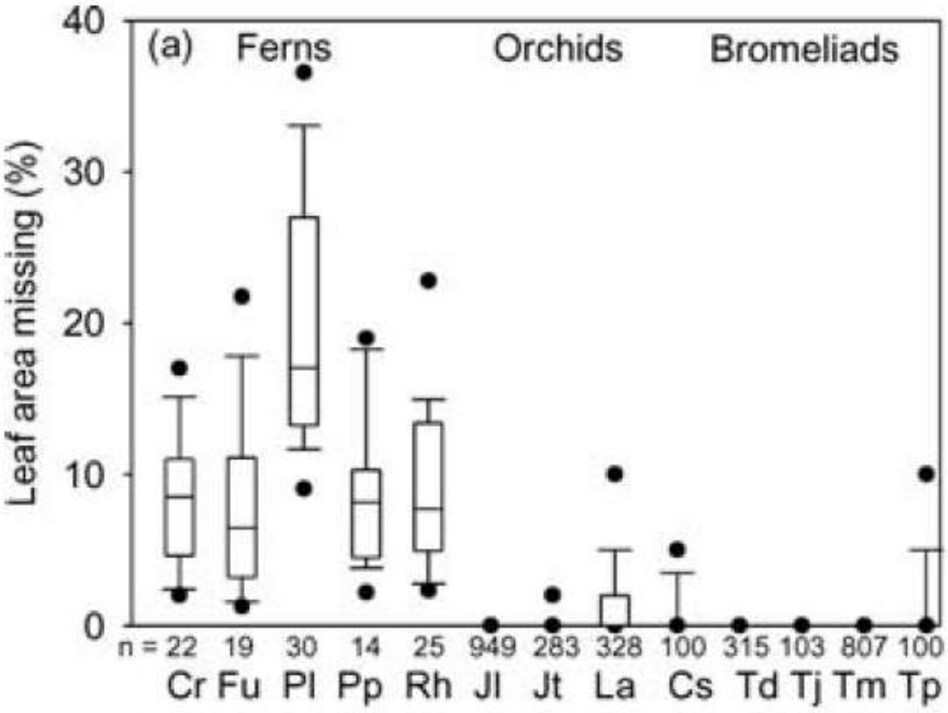
Herbivory



Herbivore host ranges are variable...

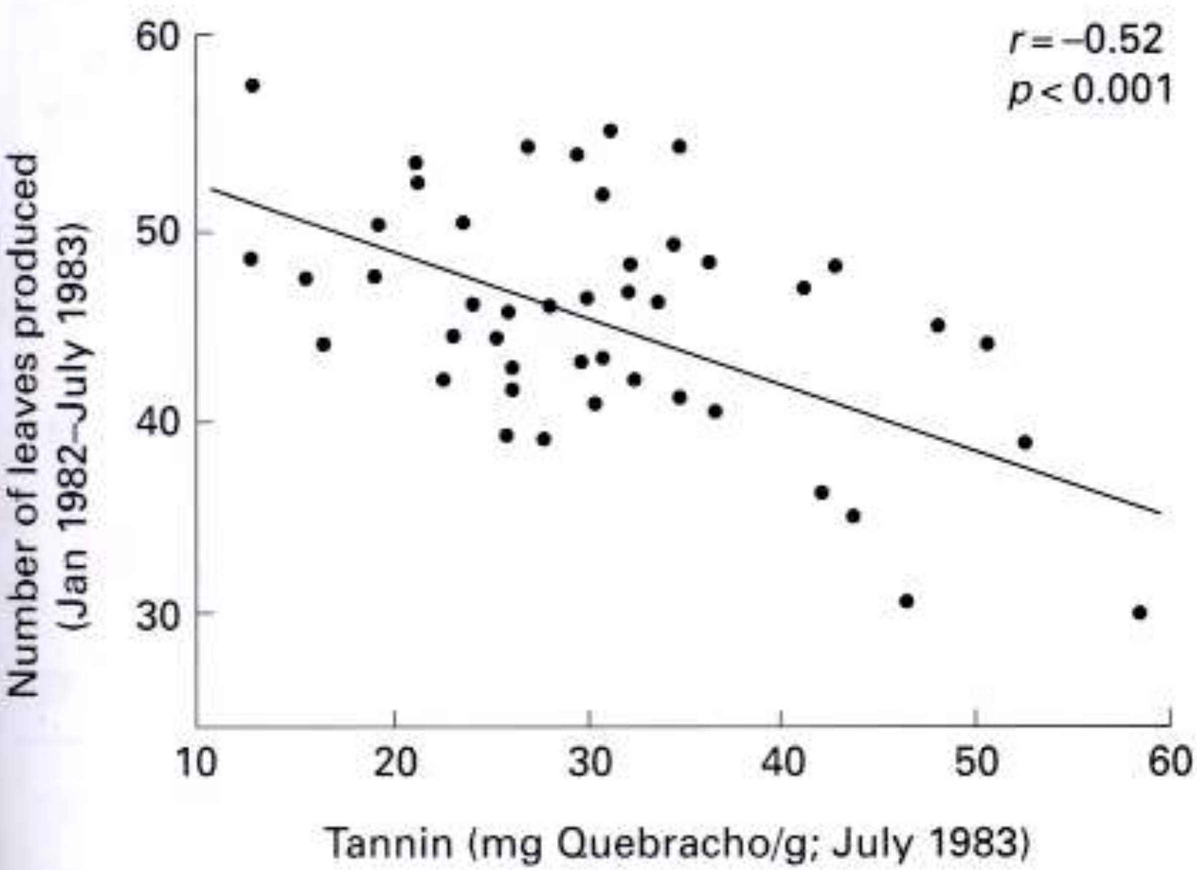
Pioneer apparent plants: the main enemy is other plants; the herbivores are thus “ignored” (and tolerated)

Epiphytic orchids & bromeliads: extremelly well-defended plants in low-resource environment



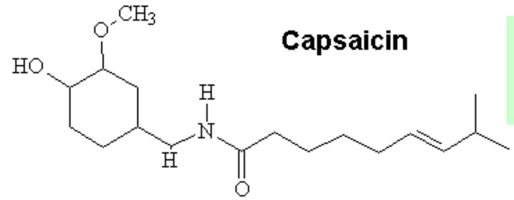
Winkler et al. 2005

Production of secondary metabolites is costly…



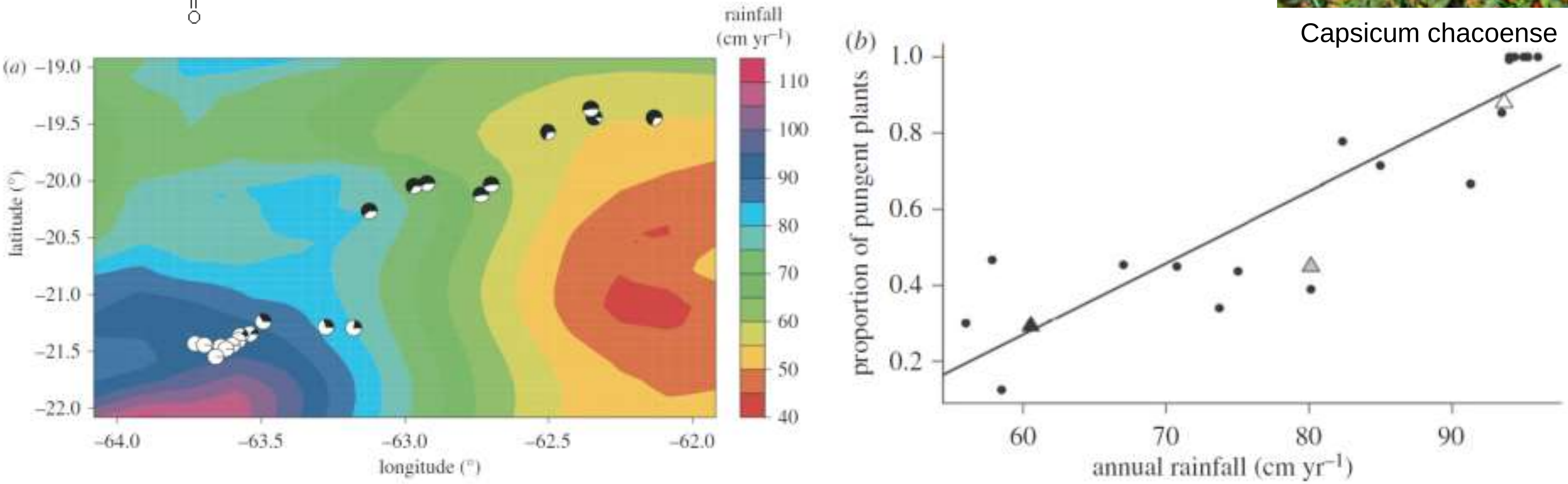
Cecropia

Fig. 3.17 Relationship between tannin concentration in the foliage of *Cecropia* and the number of leaves produced per plant. Investment in tannin appears to occur at the expense of leaf production, and may represent the cost of defence. (From Coley 1986, with permission from Springer-Verlag New York,

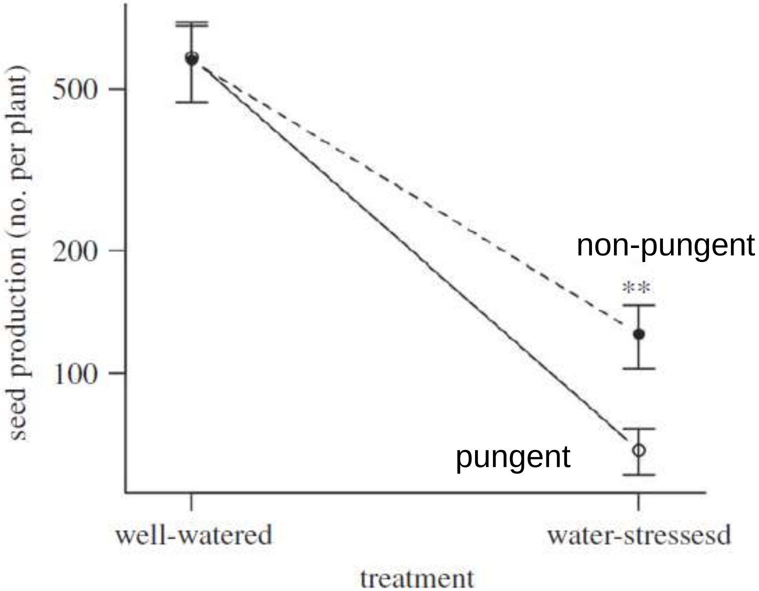


Why are not all chillies hot?

Capsicum chacoense



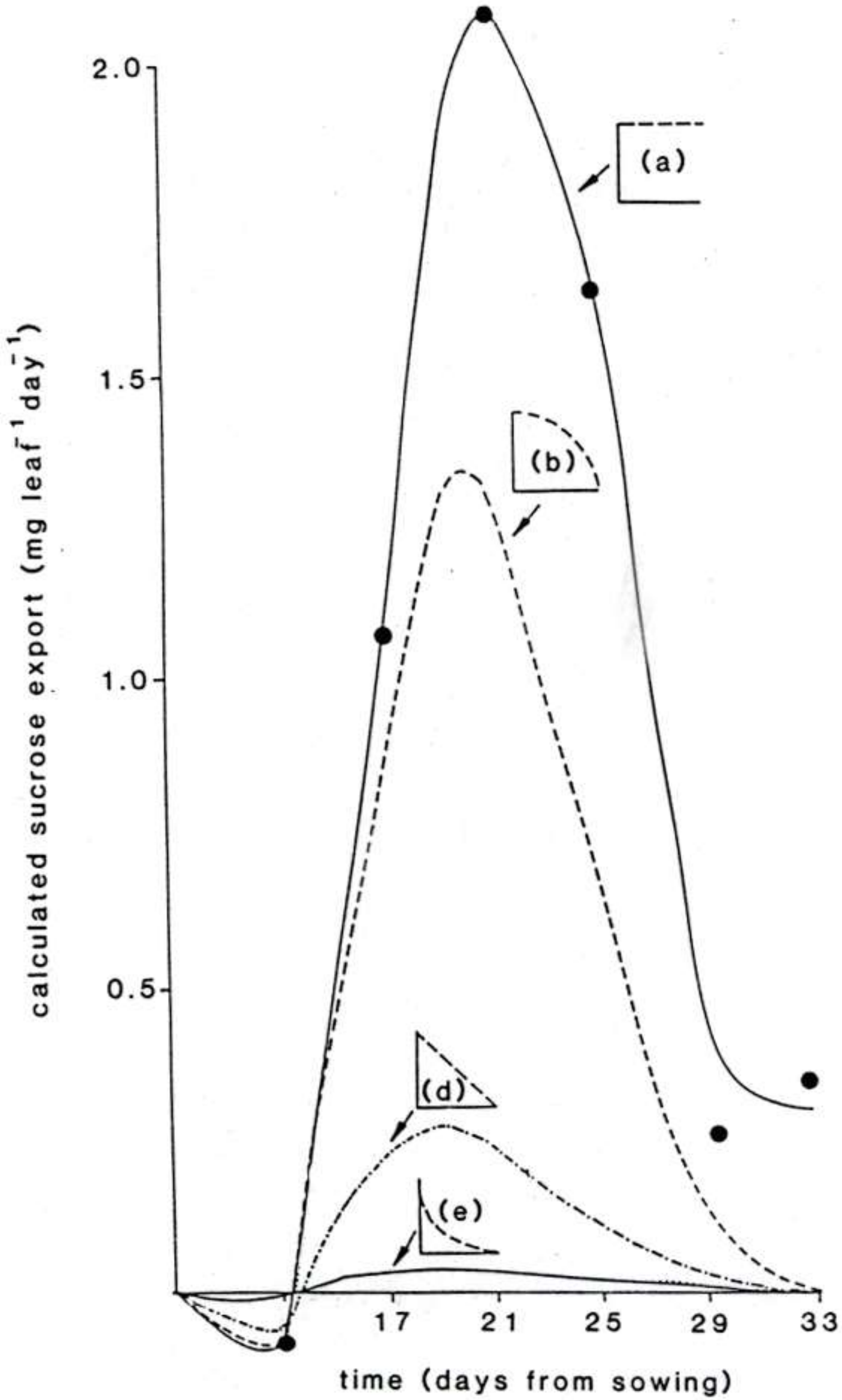
Area in Bolivia with proportion of pungent (white) and non-pungent (black) chillies



Production of capsaicinoids is costly in dry environment where its costs are apparently higher than benefits from protection against herbivory

Haak et al. Proc. R. Soc. B (2012) 279, 2012–2017

Young vs. mature leaves:
unapparent high-quality vs. apparent low-quality resources



Feeding on young leaves is costly for the plant

Photosynthetic production of a population of leaves that

(a) has no mortality

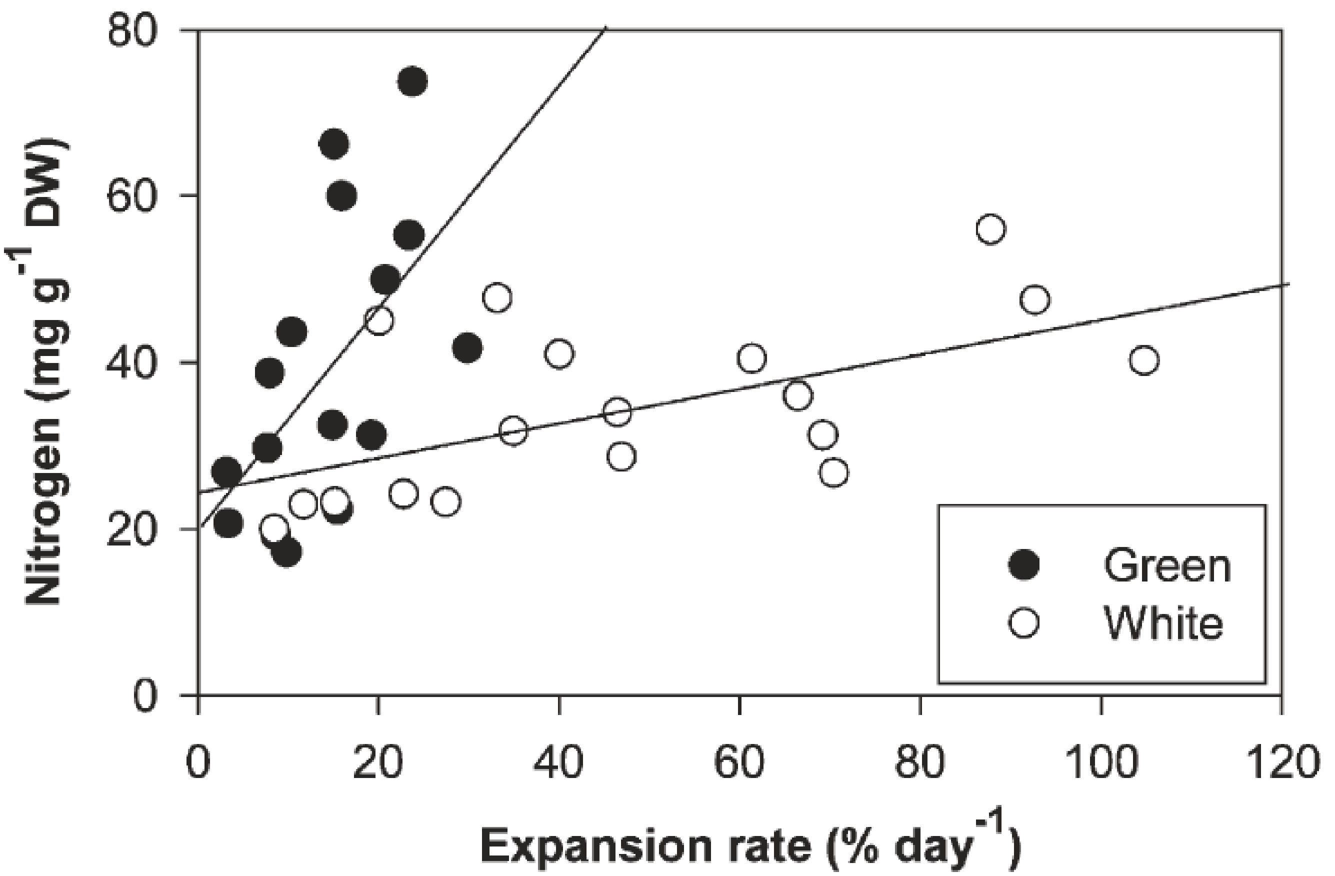
(b) mortality risk increases with leaf age [usual physiological pattern]

(d) mortality risk is constant

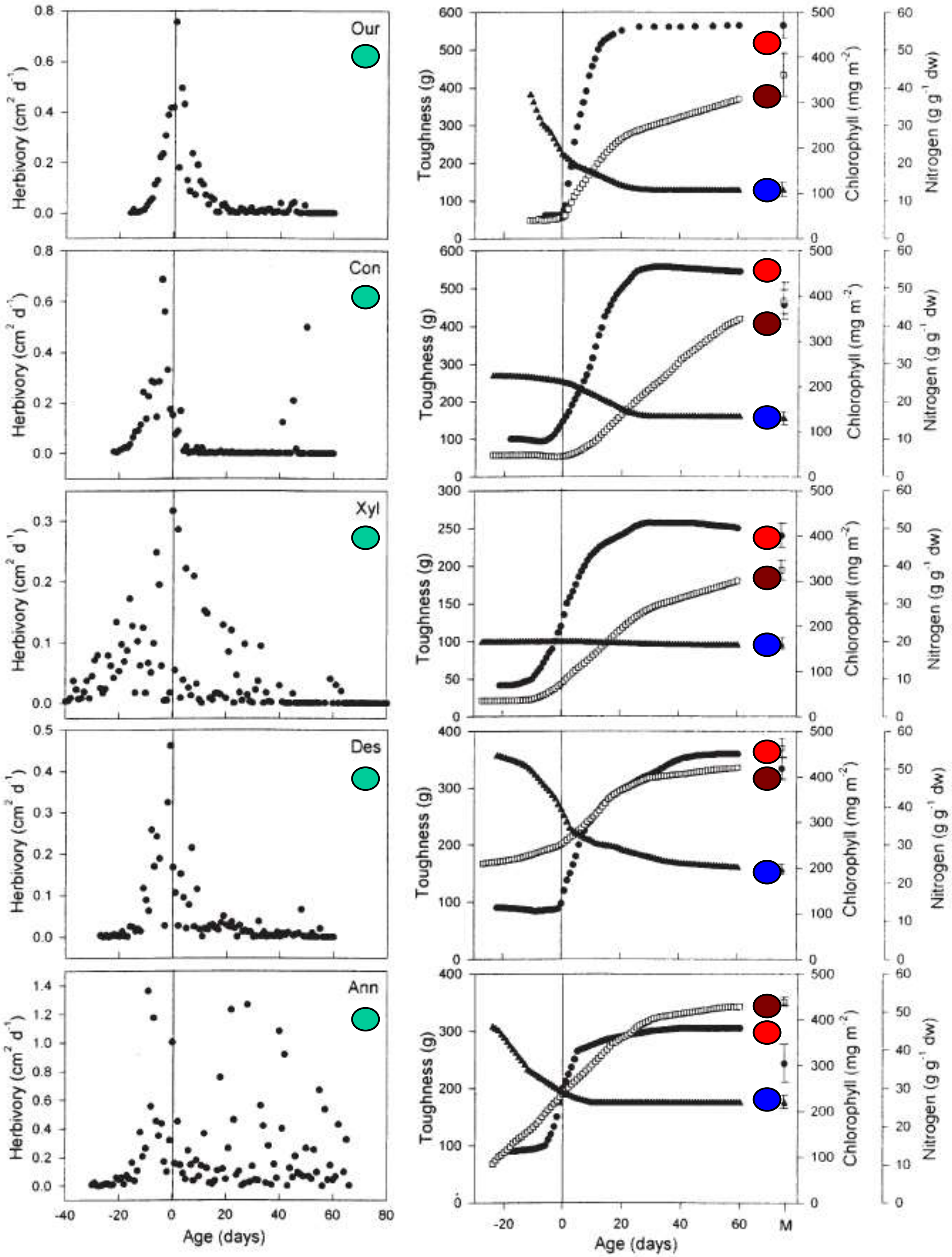
(e) mortality decreases with leaf age [high herbivory pattern]

Fig. 3. The effects that different patterns of leaf survivorship l(*x*) would have on the rate of "reproduction" of fixed carbon. The survivorship curves are shown on a logarithmic scale. **a** There is no significant risk of death until the leaf loses its capacity for carbon export. **b** The risk of death increases continuously with age of the leaf. This appears to be the most common form of survivorship for leaves that do not suffer predation or other external causes of death (Harper 1987). **c** The survivorship curve ressembles that in Fig. 3b except that the risk of death declines among very old leaves. **d** The risk of death is constant throughout the

Delayed greening: faster expansion with lower N concentrations



Kursar & Coley 2003



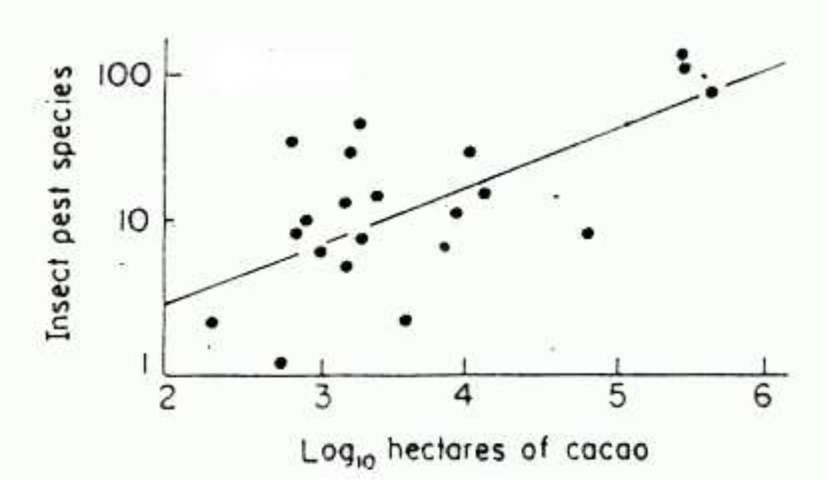
Leaf:

- damage
- toughness
- nitrogen
- chlorophyll

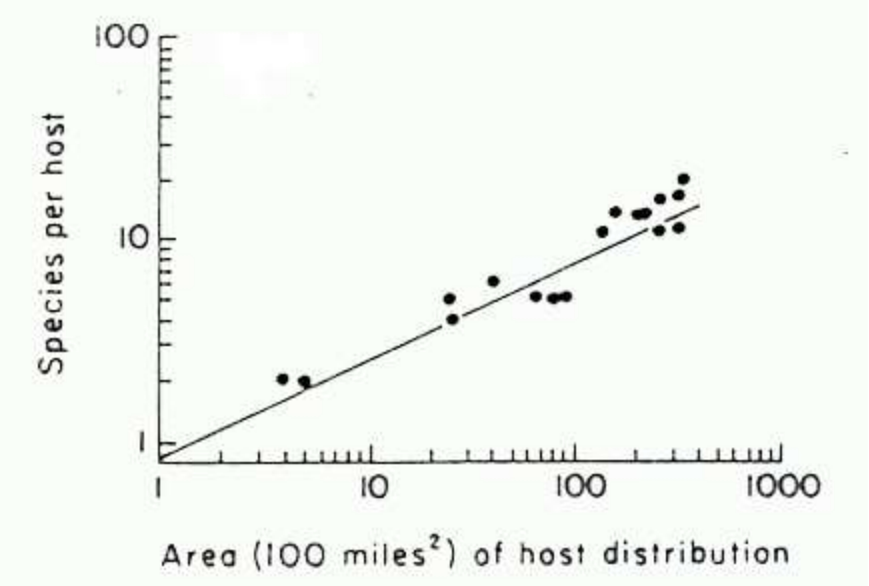
Kursar & Coley 2003

Species richness of herbivore communities: determined by plant abundance

Species richness of insect pest species on cocoa plantations in various countries

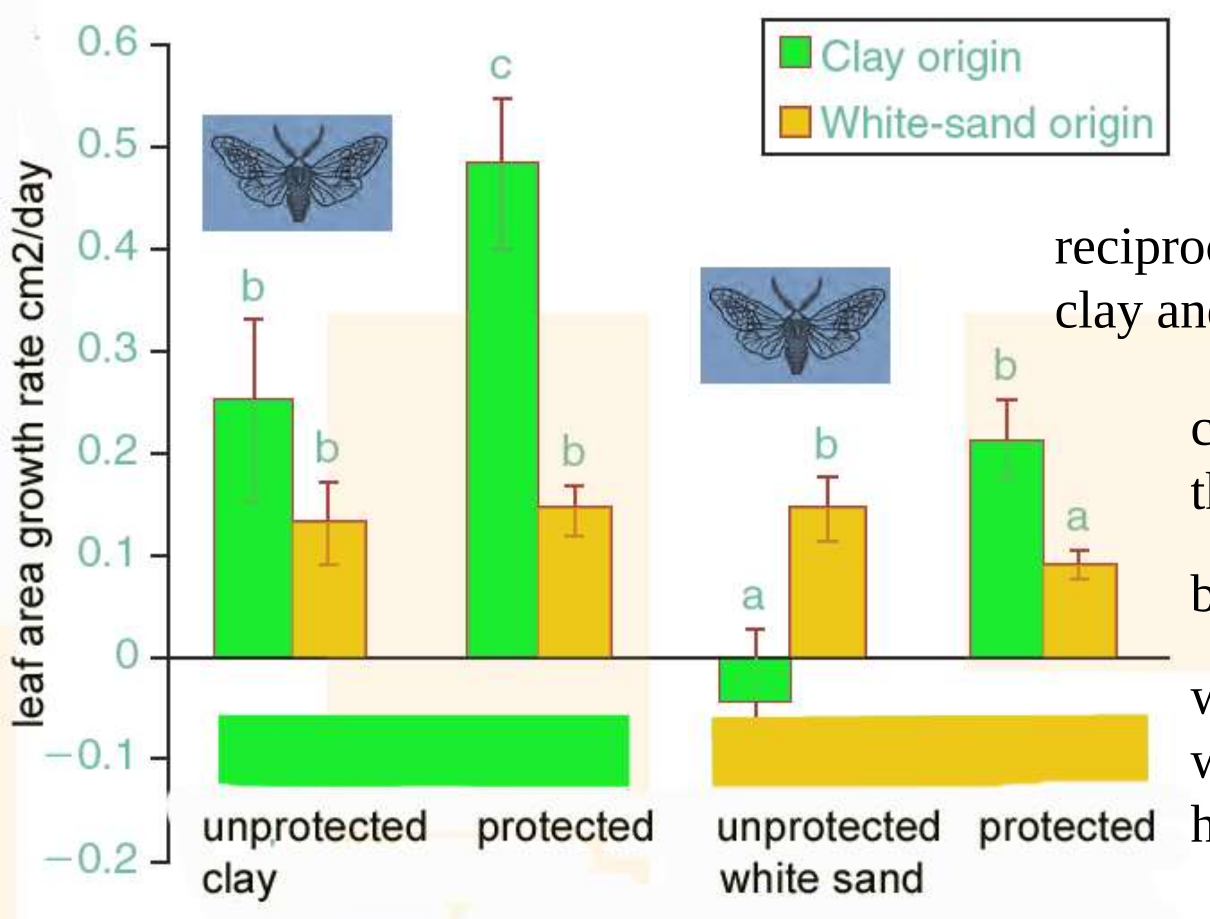


Species richness of leaf miners on various oak species in California



Strong et al. 1977 Opler 1974

Herbivores determine competitive hierarchy

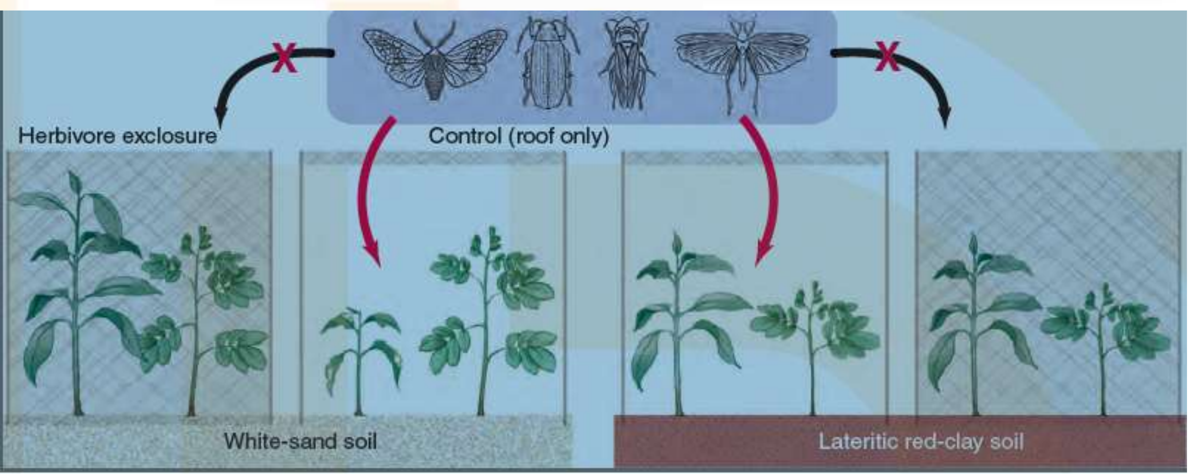


reciprocal transplants of plants between clay and white sands in tropical forest

clay plants do better on clay than white-sand plants

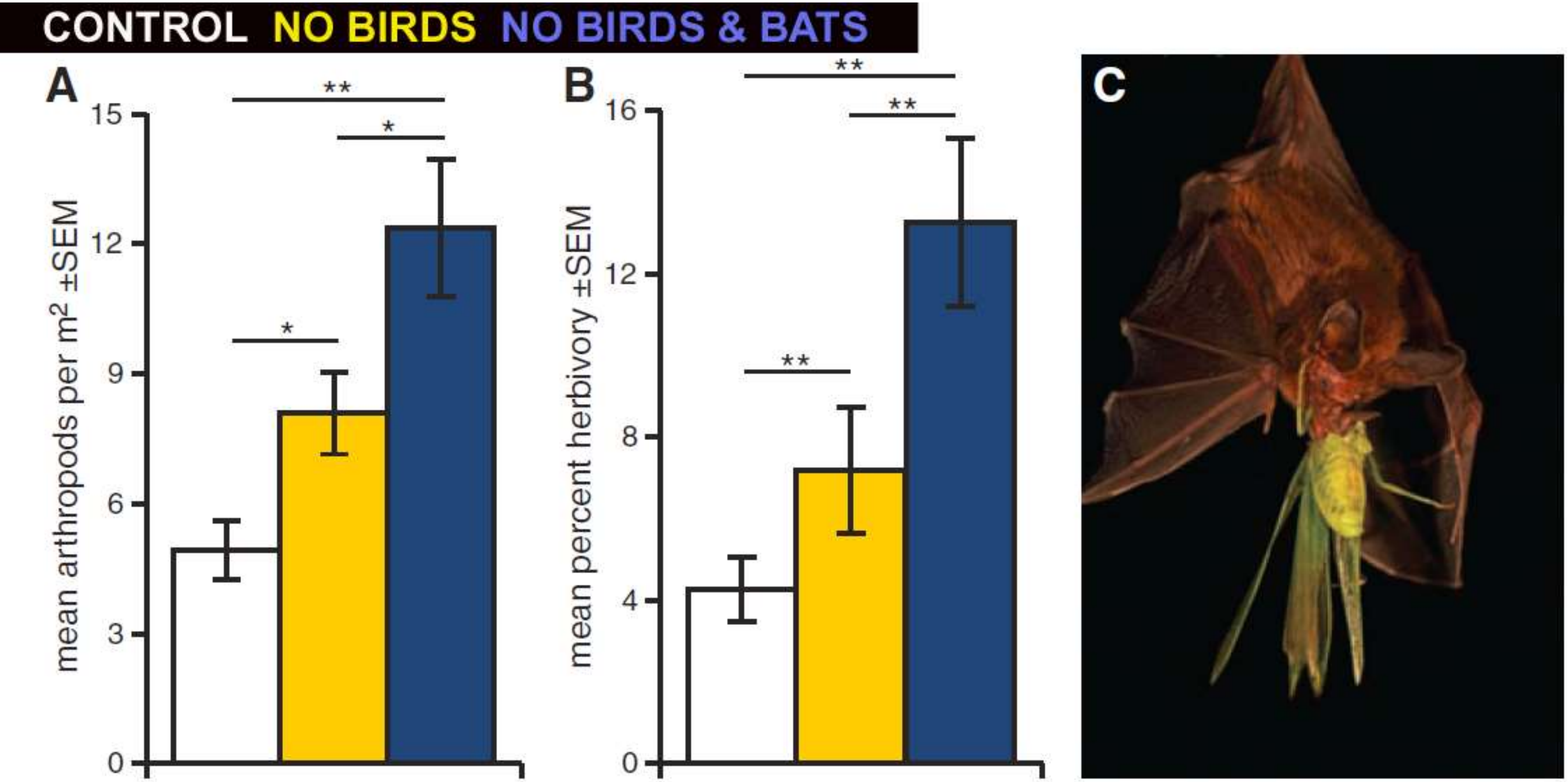
but

white-sand plants do better on white-sand only when insect herbivores are present



Fine et al. 2004, Science 305: 663

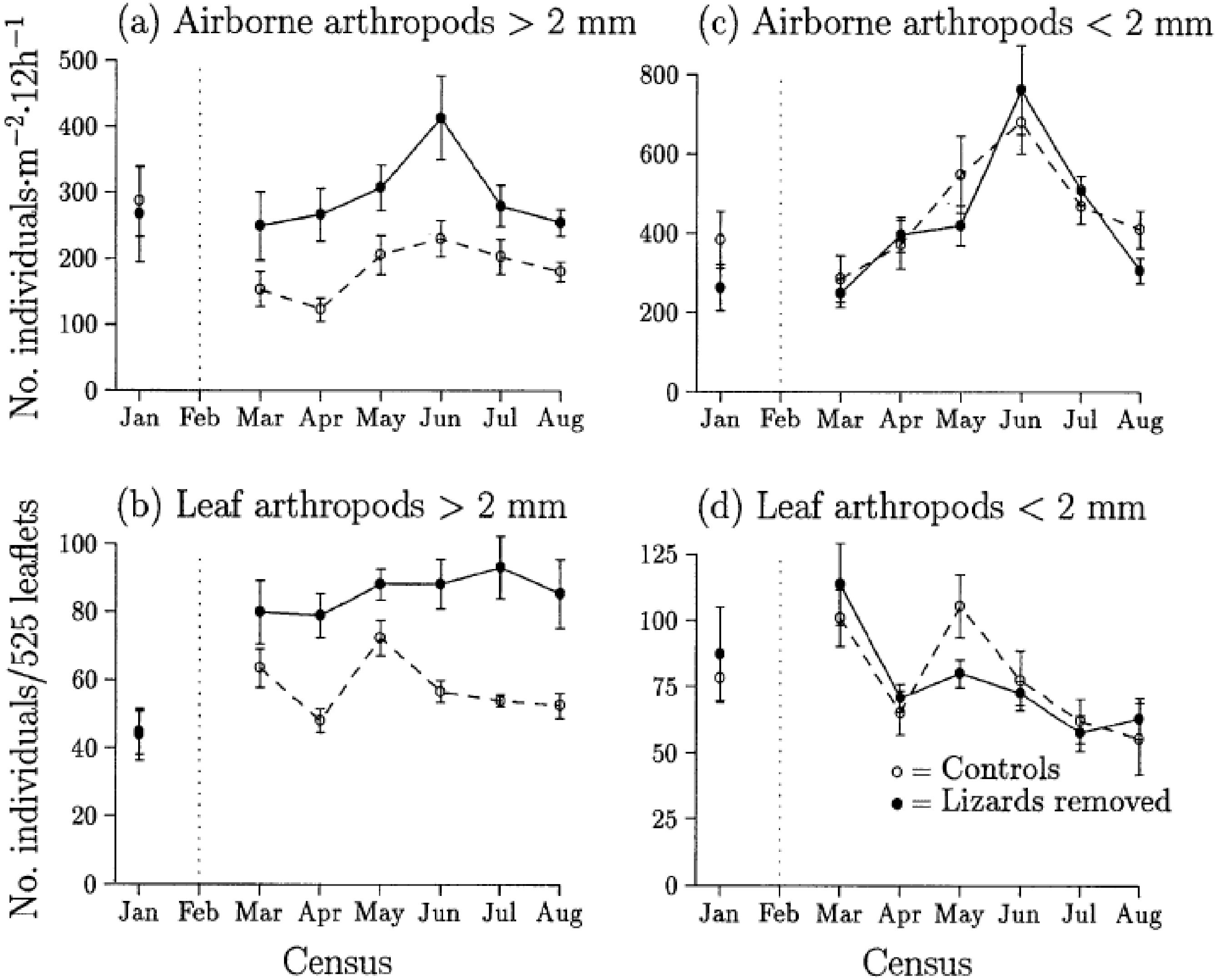
Top-down control:
birds and bats control arthropods on tropical foliage



(A) Mean number of arthropods per m2. (B) Mean herbivory as percent of total leaf area.
(C) Micronycteris microtis consuming a katydid. Barro Colorado Island, Panama.

Kalka et al. 2008. Science 320: 71

Responses of arthropods to lizard removal: rainforest in Puerto Rico



In arthropods >2 mm, predatory (spiders), parasitic (Hymenoptera), and nonpredatory (Diptera, Coleoptera, Orthoptera, and Blattaria) spp. responded to lizard removal.

Dial & Roughgarden 1995. Ecology, 76: 1821-1834

Why are there host specific herbivores?

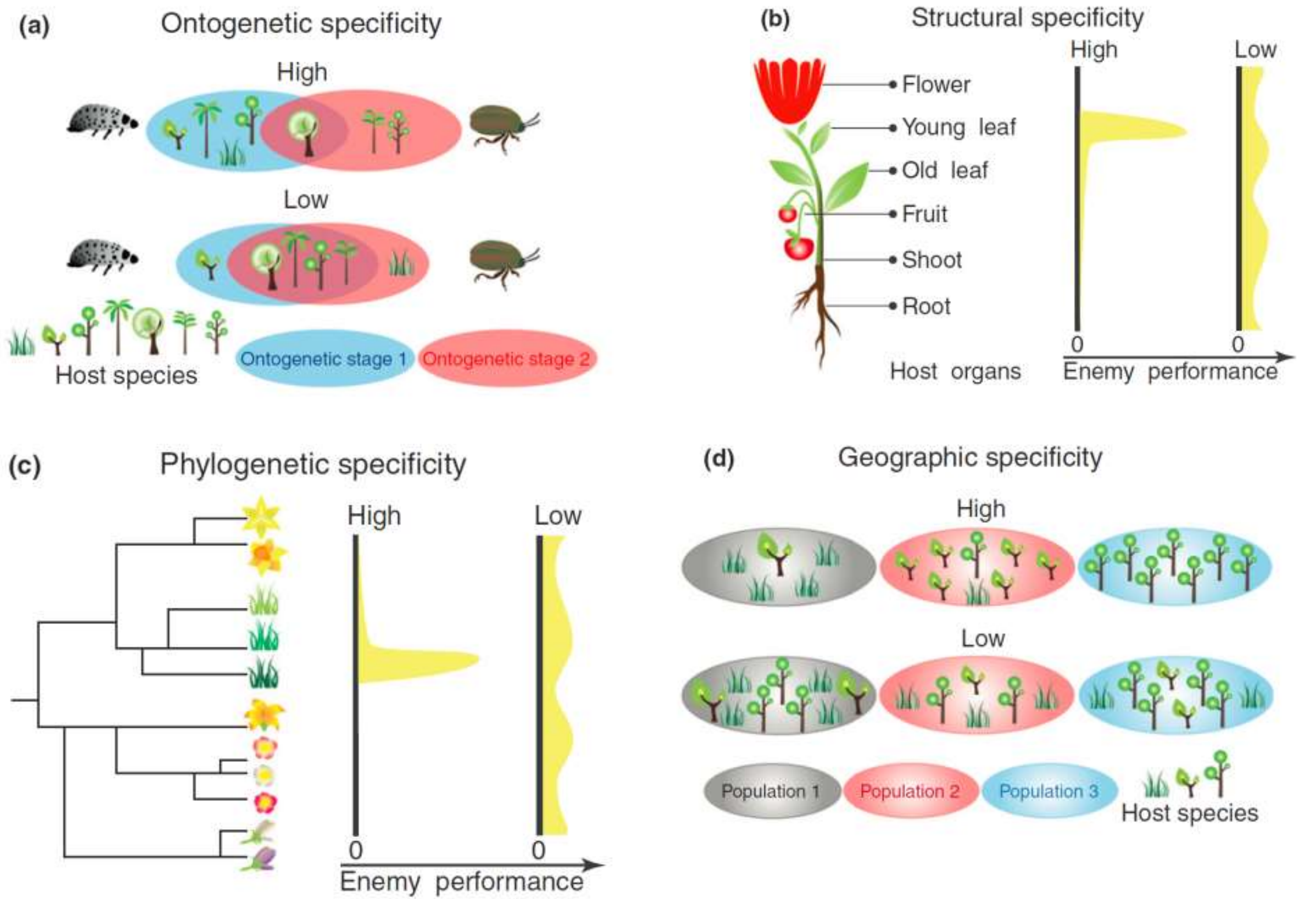
- genetically based trade-offs in performance between host species
- interspecific competition for food or enemy-free space
- increased resistance to generalist predators on some host plants
- similarity of some hosts to unsuitable hosts
- facilitated mate finding
- facilitated defence against enemies [sequestering plant metabolites]
- ability to aggregate and overwhelm plant defences

Why are there generalists?

- hosts are rare, unpredictable, unapparent
- small plants favouring larval grazing
- risk spreading strategies due to temporal/spatial variability in host quality
- intraspecific competition
- predator and pathogen functional/numerical response

Jaenike, J. 1990. Annu. Rev. Ecol. Syst. 21:2

Multiple meaning of host specificity



Tropical leaf-chewing insects: feeding on multiple species of a single genus

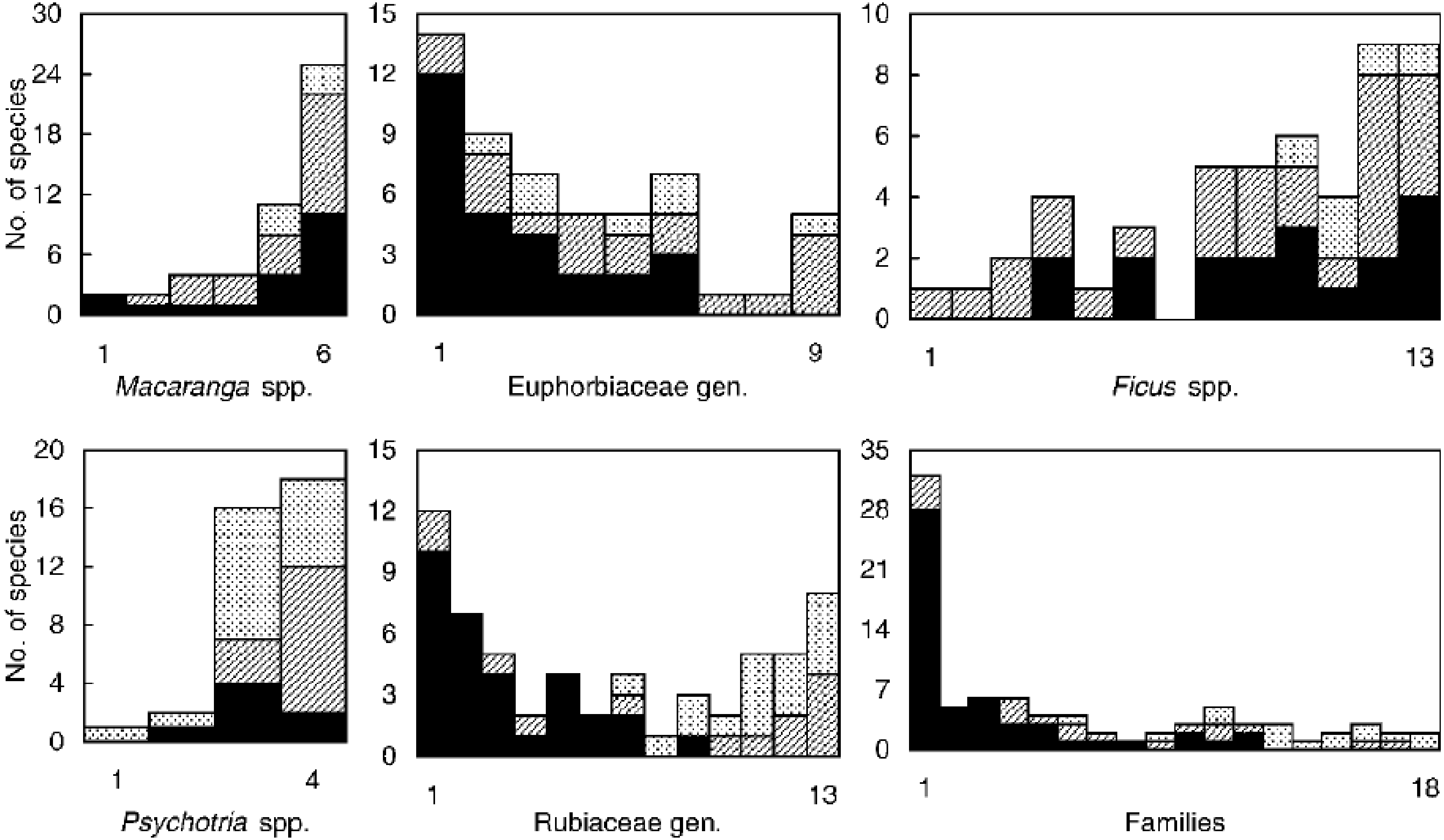
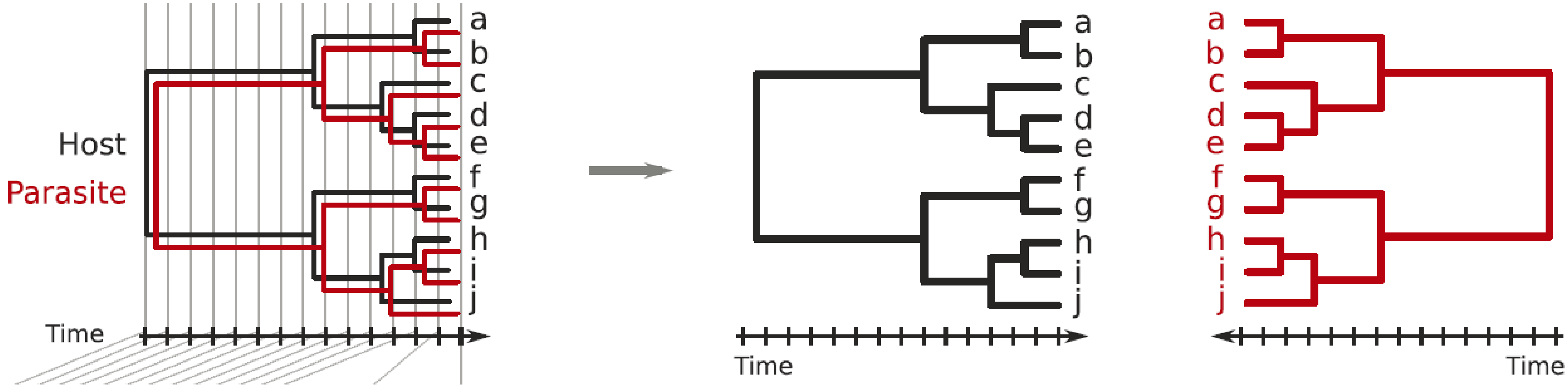
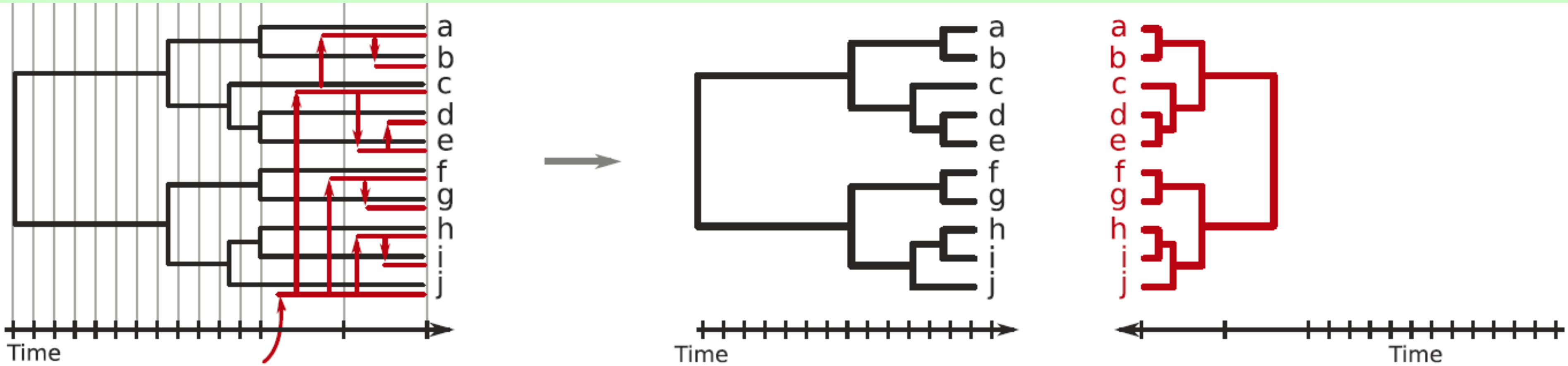


Fig. 2. Host plant range of leaf-chewing insects on congeneric species of *Macaranga*, *Psychotria* and *Ficus*, on confamilial hosts from different genera of Euphorbiaceae and Rubiaceae, and on hosts from different families of flowering plants. Lepidoptera (black), Coleoptera (hatched), orthopteroids (stippled).

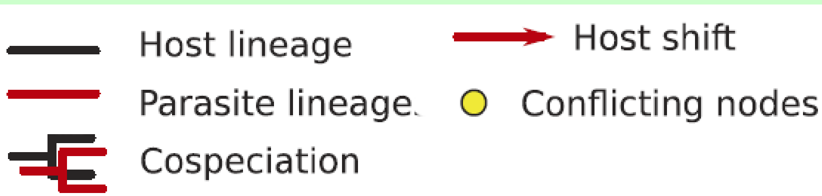
Novotny et al. 2002



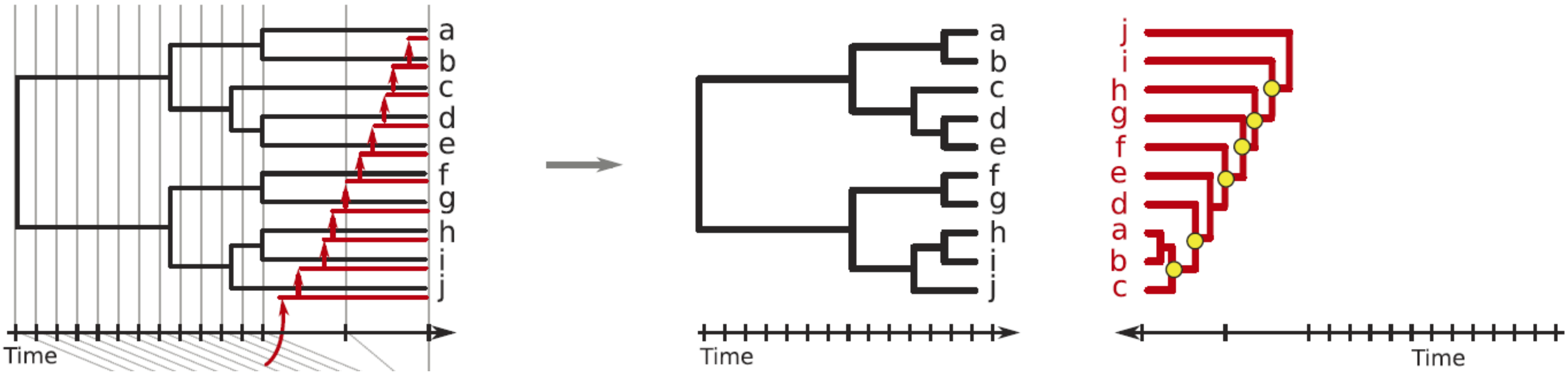
Cospeciation resulting in congruent phylogenies.



Host-shift speciation resulting in congruent phylogenies, but with shorter branches in the parasite lineages



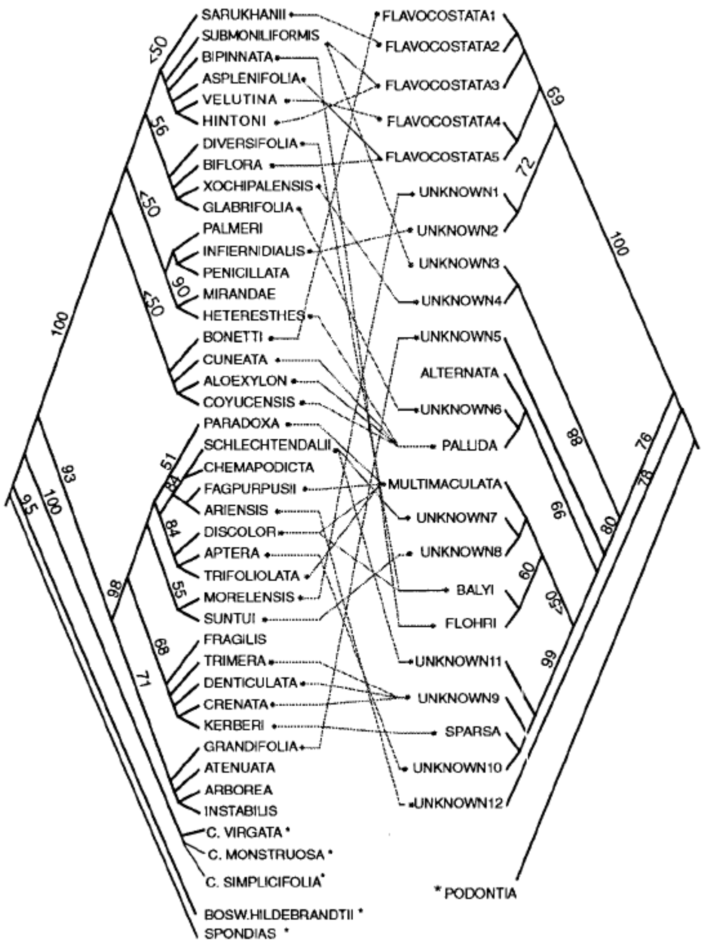
de Vienne et al. New Phytologist (2013)
doi: 10.1111/nph.12150



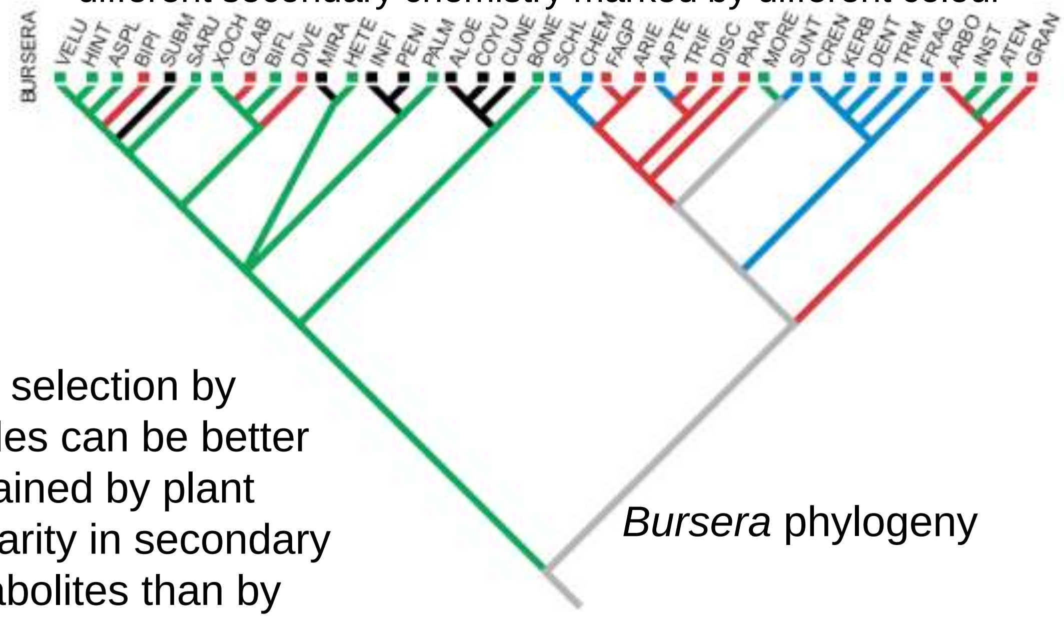
Host-shift speciations, resulting in incongruent phylogenies.

de Vienne et al. New Phytologist (2013)
doi: 10.1111/nph.12150

Blepharida beetles on *Bursera* plants: secondary chemistry explains multiple host colonizations



different secondary chemistry marked by different colour

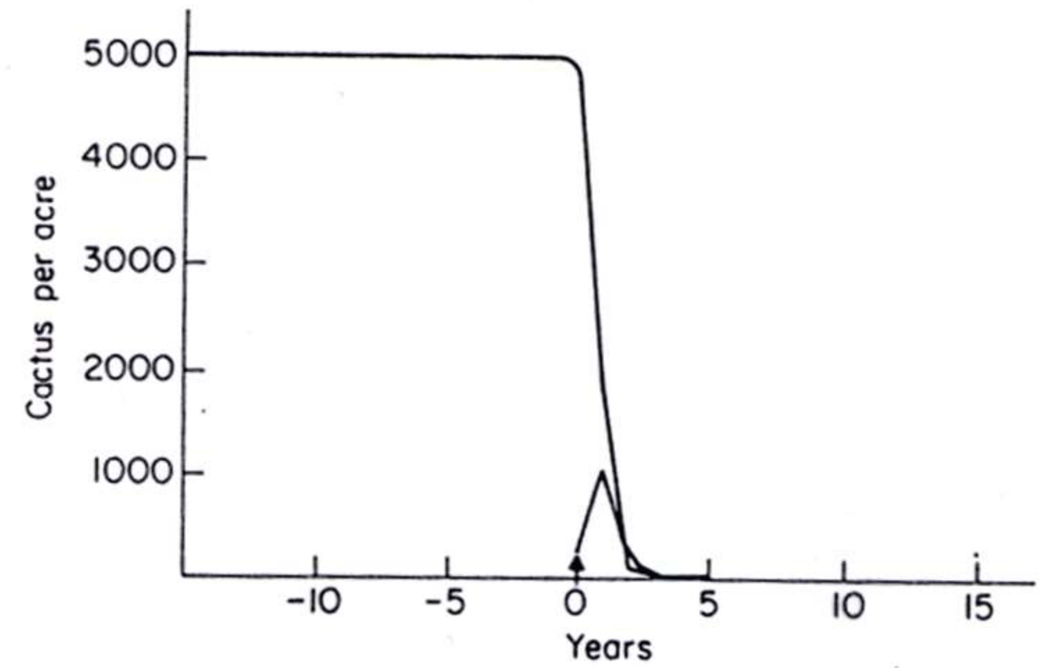


Host selection by beetles can be better explained by plant similarity in secondary metabolites than by plant phylogeny

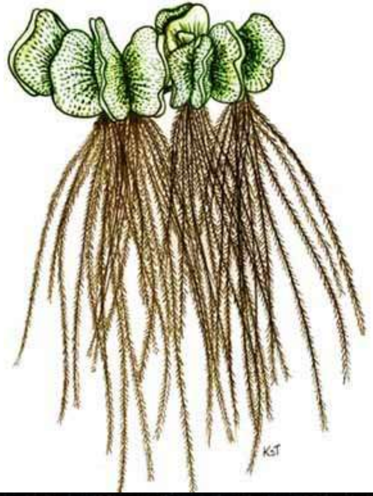
Bursera phylogeny does not correspond with phylogeny of its beetles

Becerra 1997

Biological control of plants by herbivores:
the success story of *Cactoblastis cactorum* controlling *Opuntia* (Australia)

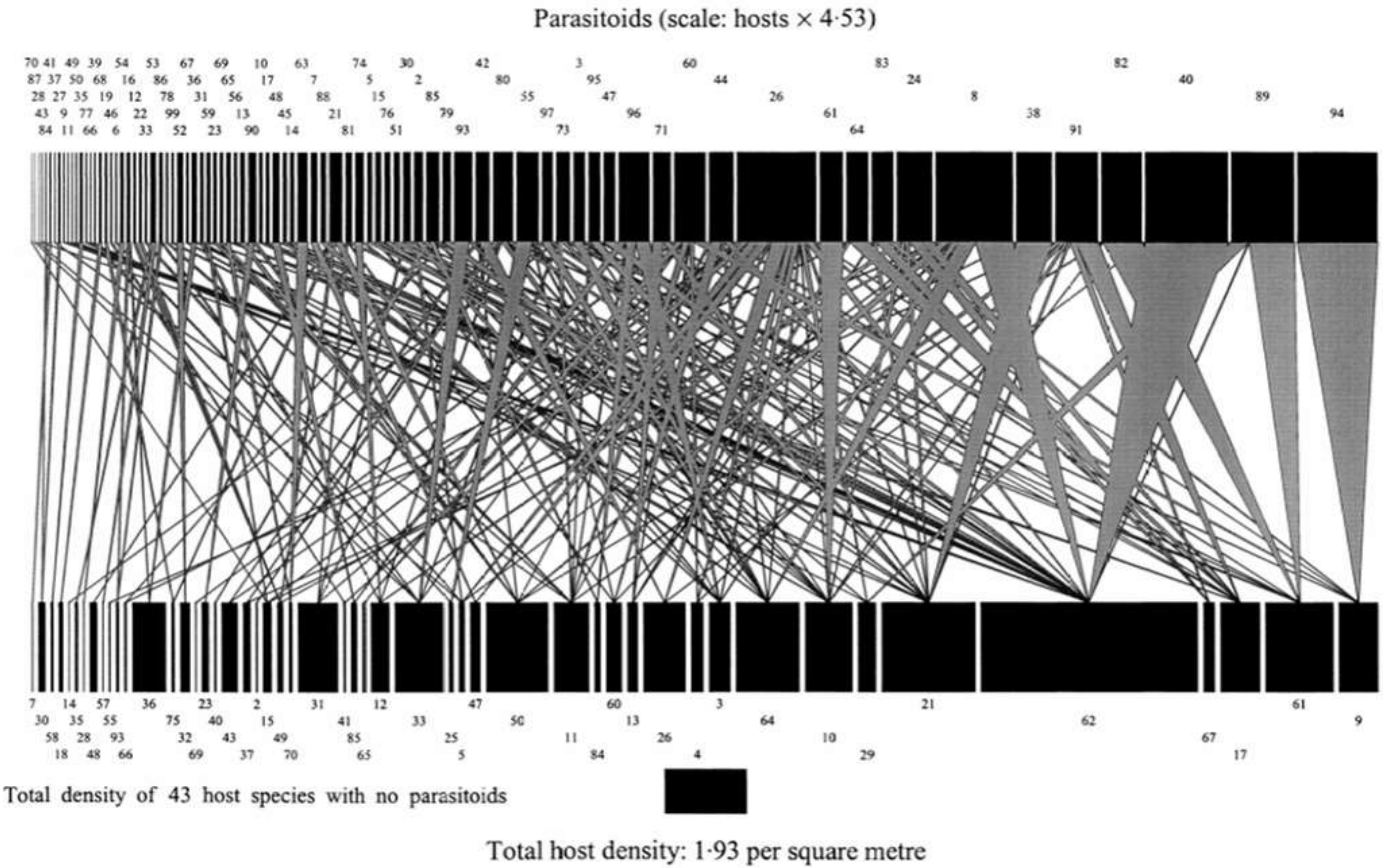


The model of Caughley and
population from its pre-release
f only 11 plants per acre within
curve = moth numbers after
n in the text.

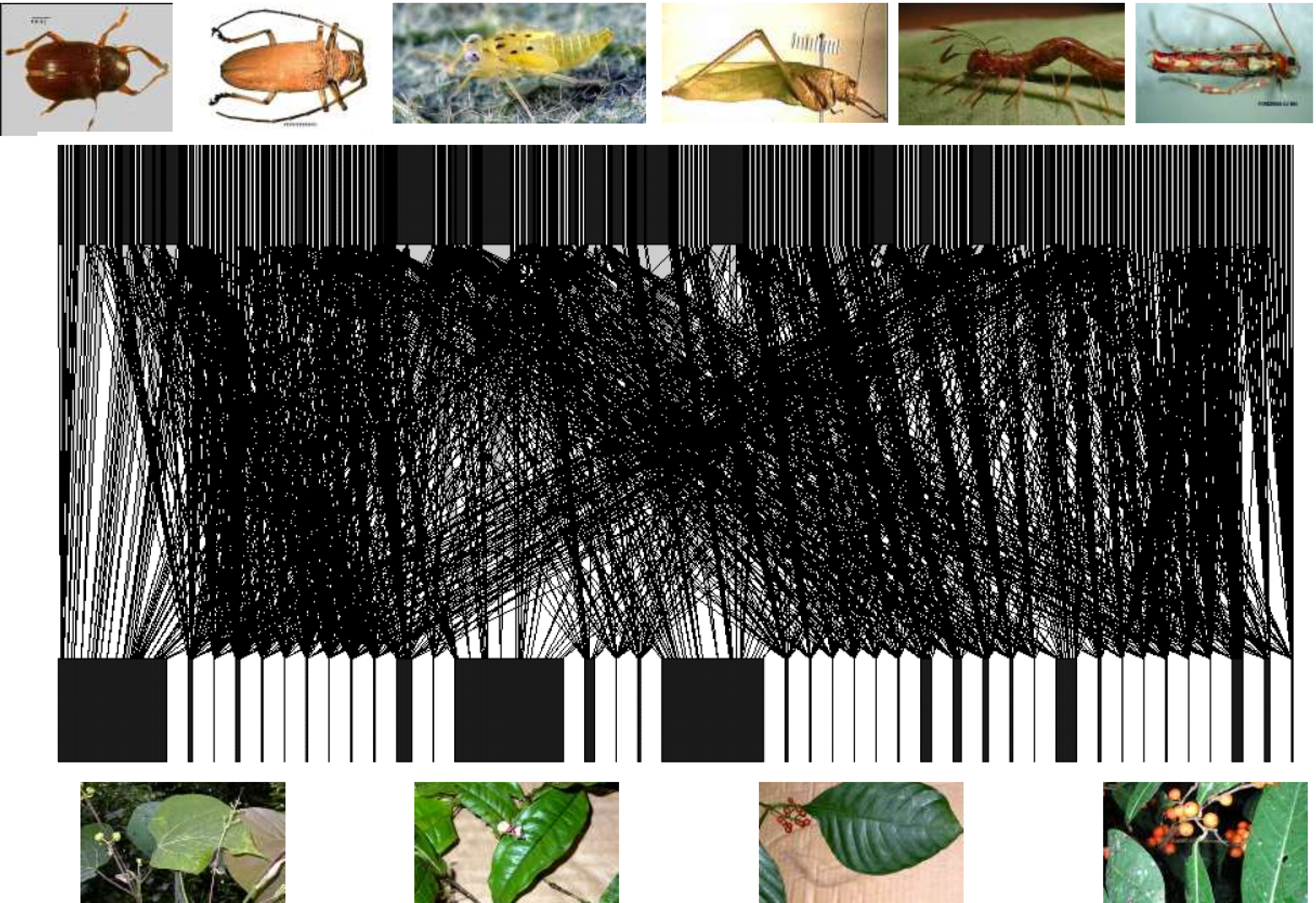


Salvinia molesta
and
Cyrtobagous salviniae

Leaf-miners and their parasitoids in lowland rainforest in Belize: tropical food webs are rather complex



Food web including folivorous herbivores on 38 tree species in a New Guinean rainforest



Plant-leaf miner-parasitoid food web in a forest understorey in Belize

Removal of a single host plant species will eliminate its specialist leaf-miners (hatched) but is also expected to affect other spp. (blue and red) via shared parasitoids

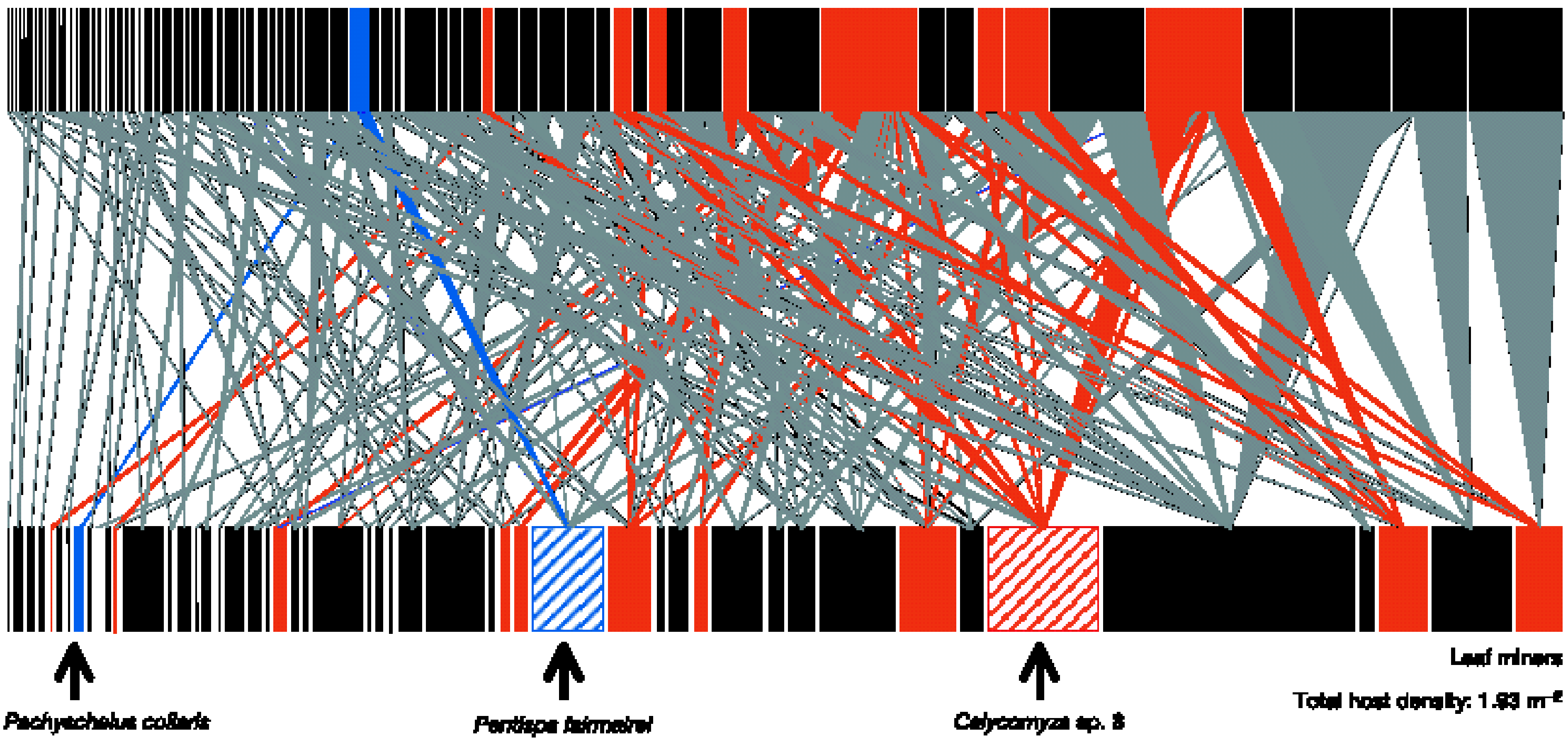
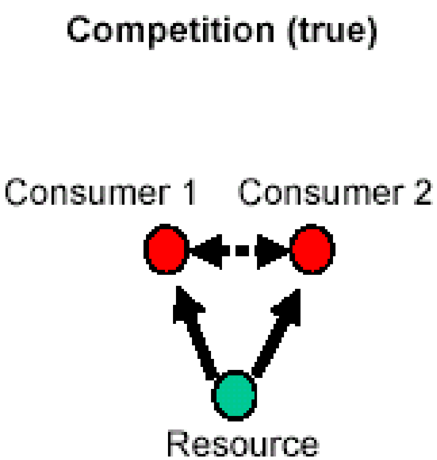
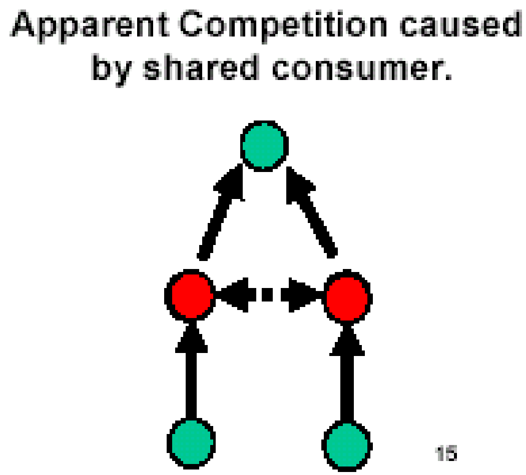


Figure 1 Quantitative food web[17] showing leaf-miner species (bottom bars), parasitoid species (top bars), trophic links among them, and the species predicted to be affected by the manipulation. *Calycomyza* sp. 8 and *P. fairmairei* were directly affected by host plant removal. Dipteran leaf-miner species present during the sampling period and predicted to be affected indirectly via parasitoids shared with *Calycomyza* sp. 8 are shown in red. The beetle *P. collaris* (blue) was also predicted to be affected indirectly by the manipulation through parasitoids that it shares with *P. fairmairei*. Only hosts from which parasitoids were reared are shown in the web.

Morris et al. 2004. Nature 428:30

Apparent competition





Indirect interaction: an effect of one species on another, mediated through the action of shared natural enemies.

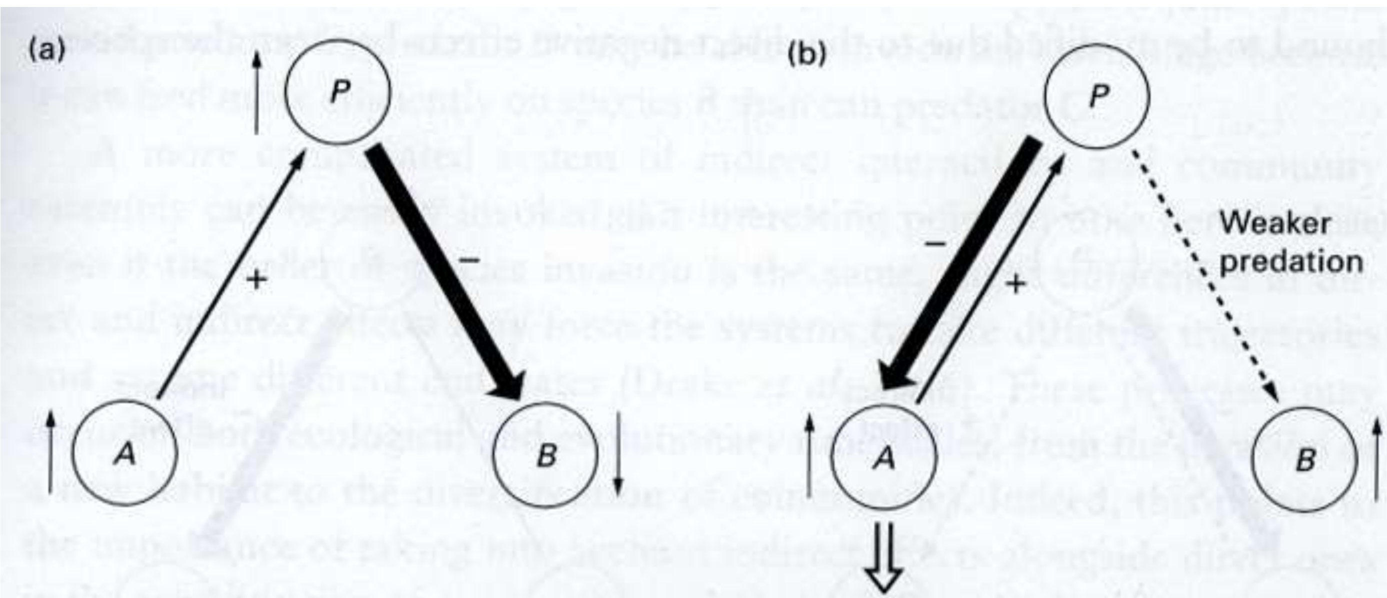
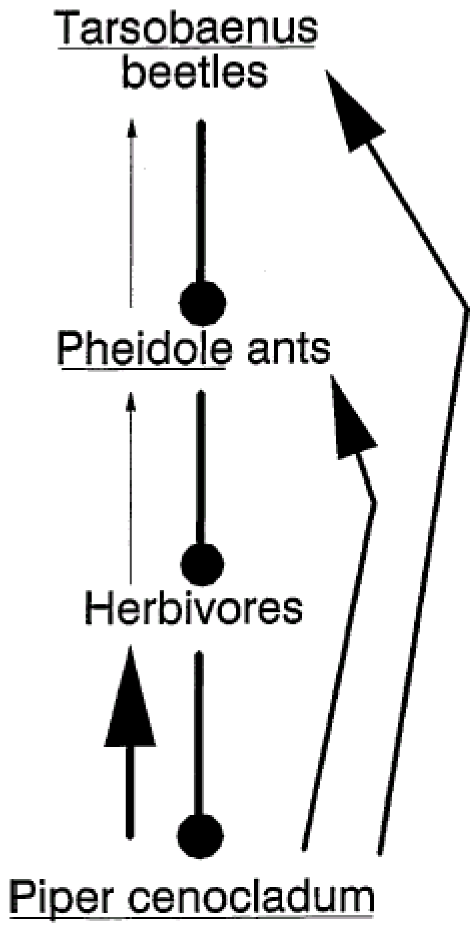


Fig. 9.6 Apparent competition between two species *A* and *B* through their shared predator *P*. In (a), an increase in *A* leads to an increase in *P*, which, in turn, feeds more heavily on *B*. In (b), an increase in *A* prompts *P* to feed more heavily on *A*, resulting in the latter's overall decline, whilst *B* suffers less predation.

Complex interaction along a rainforest food chain



Tarsobaenus added

↓

Fewer ants

↓

More herbivores

↓

Smaller plants

↑ interaction increases abundance

interaction produces mortality

Fig. 1 Summary of the trophic interactions between *Piper cenocladum* and associated arthropods. *Bulletheads* indicate that the interaction results in mortality of individuals, *arrowheads* indicate a positive contribution to the biomass of individuals, and *line thickness* indicates the importance of the interactions (based on natural history observations). For example, although clerid beetles may derive relatively more of their biomass from plants (by way of consuming food bodies produced in the petioles) than they derive from consuming ants, they inflict a relatively large amount of mortality on the ants that they encounter, and they do not kill plants

Dyer et al. 1999. Oecologia 119:2