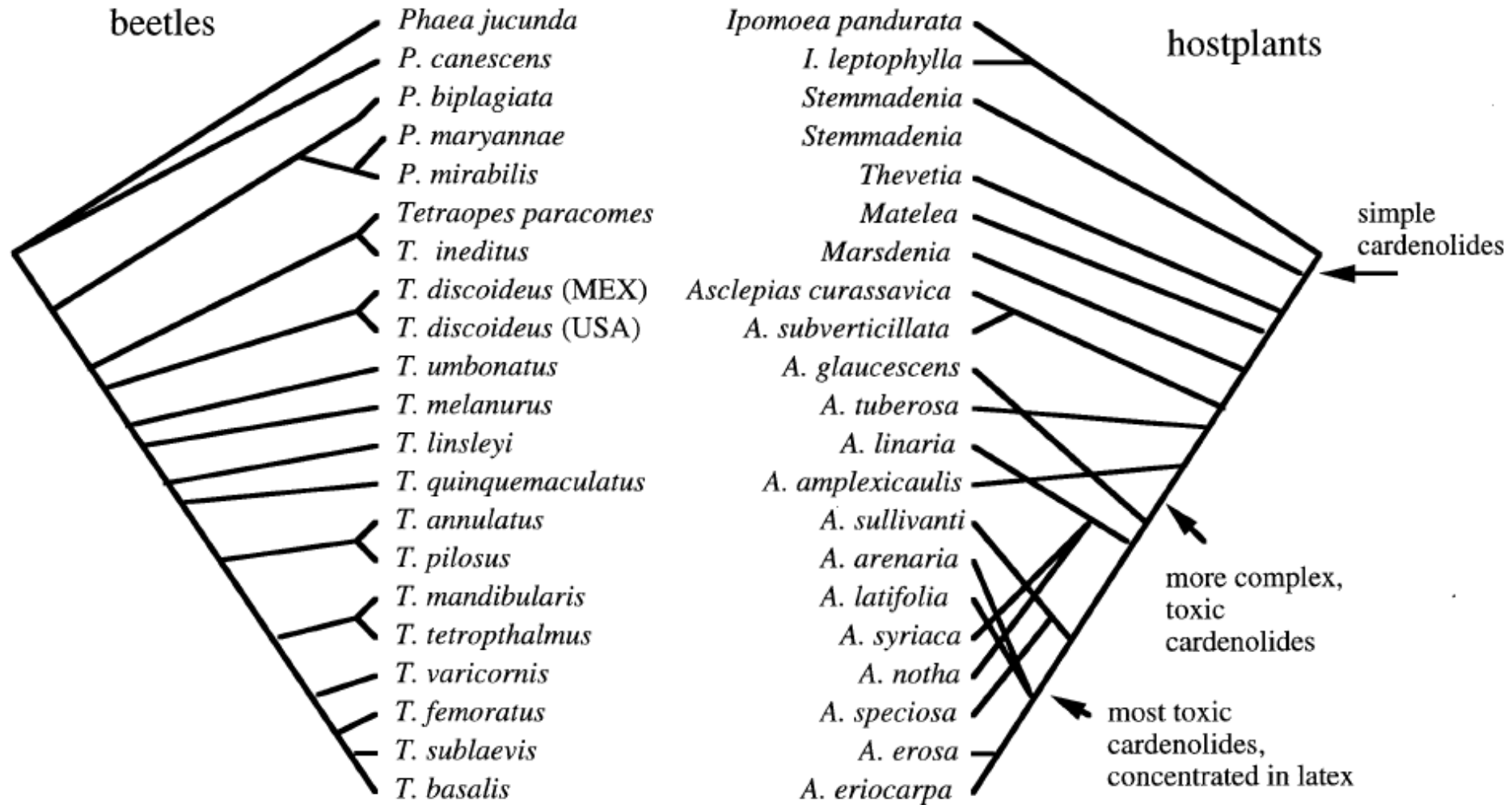
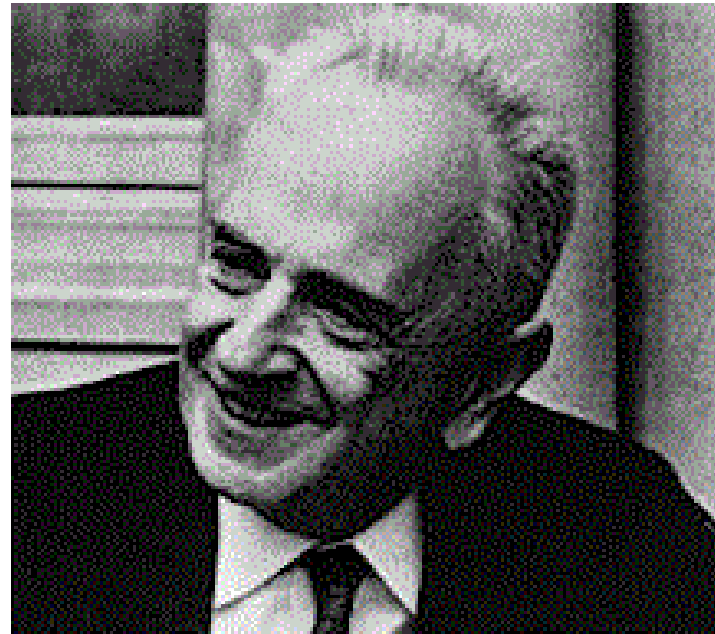


Phylogenetic analysis of community patterns





"Nothing in biology
makes sense except in
the light of evolution."

Theodosius Dobzhansky

Community composition is determined by:

- phylogenetic processes forming regional species pool
- ecological processes recruiting species from this pool

Life history traits in communities are determined by:

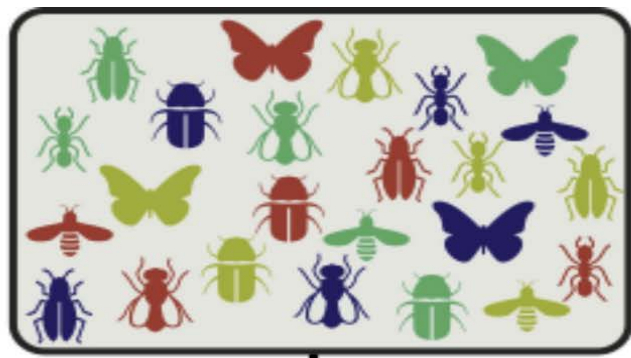
- phylogenetic constraints on life history evolution
- ecological processes selecting for particular traits

The interpretation of community composition has to include

- phylogeny
- ecology

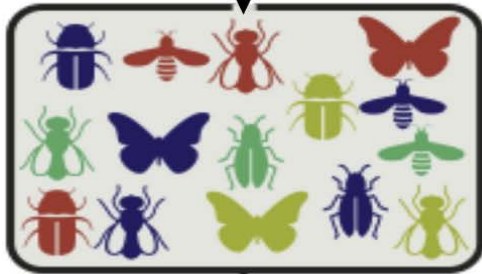
Phylogeny as a statistical nuisance, causing non-independence of species as data points

Phylogeny as explanation of the observed patterns

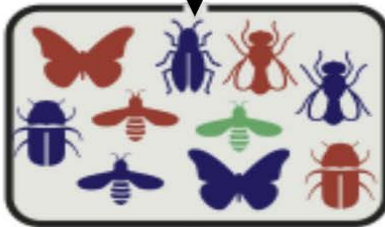


Regional species pool

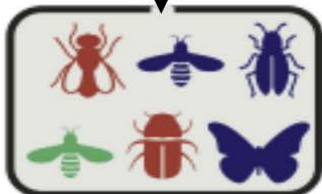
Dispersal filter



Environmental filter



Interaction filter

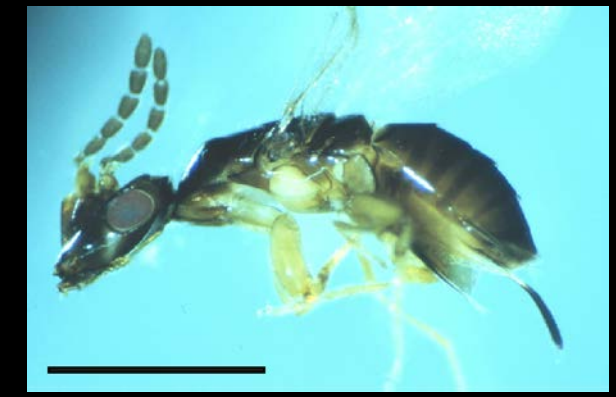
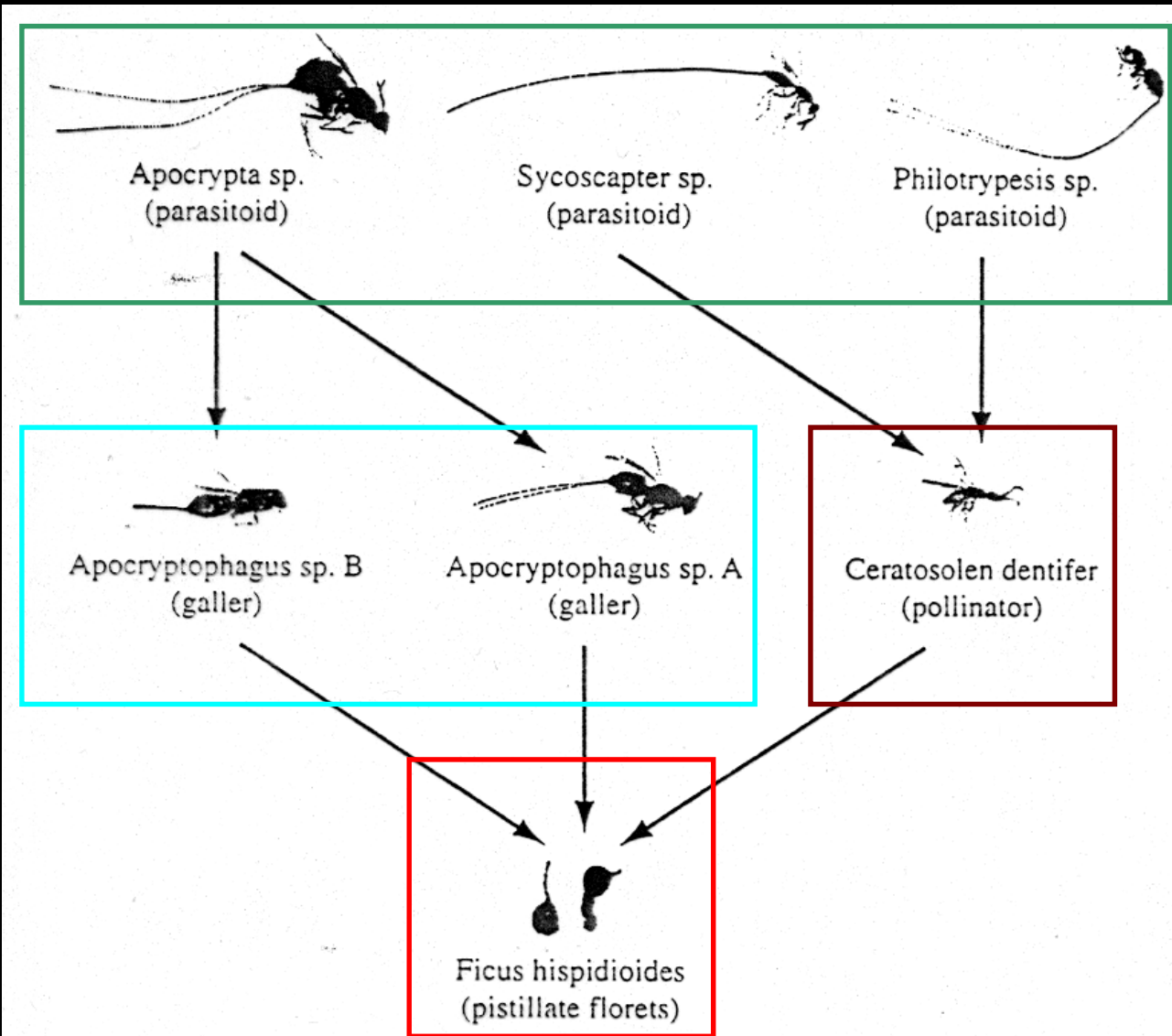


Community

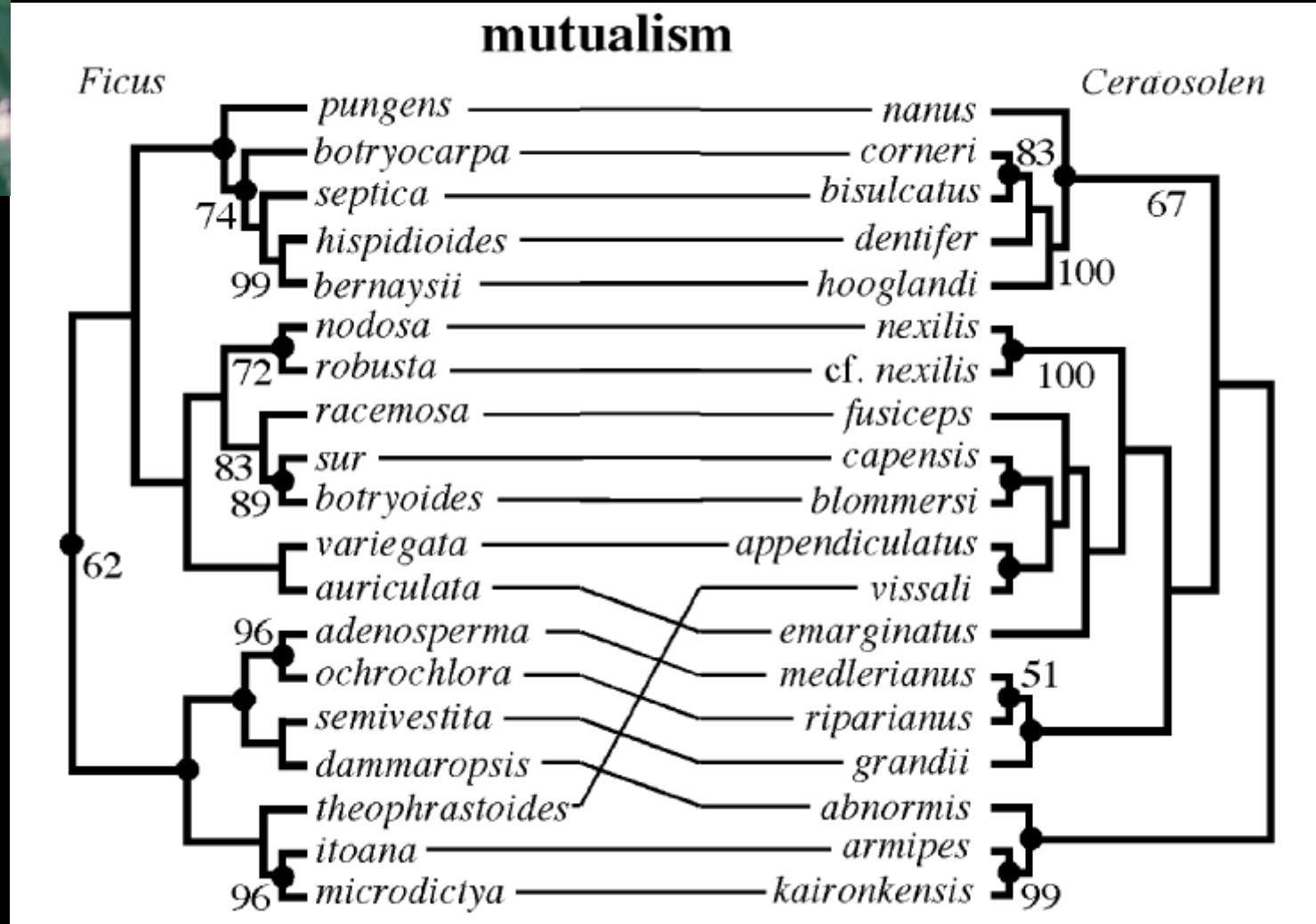
Community assembly from regional species pools

- dispersal,
 - habitat preferences
 - biotic interactions
- all can have a phylogenetic component

Wasps on figs: pollinators, gallers and parasitoids

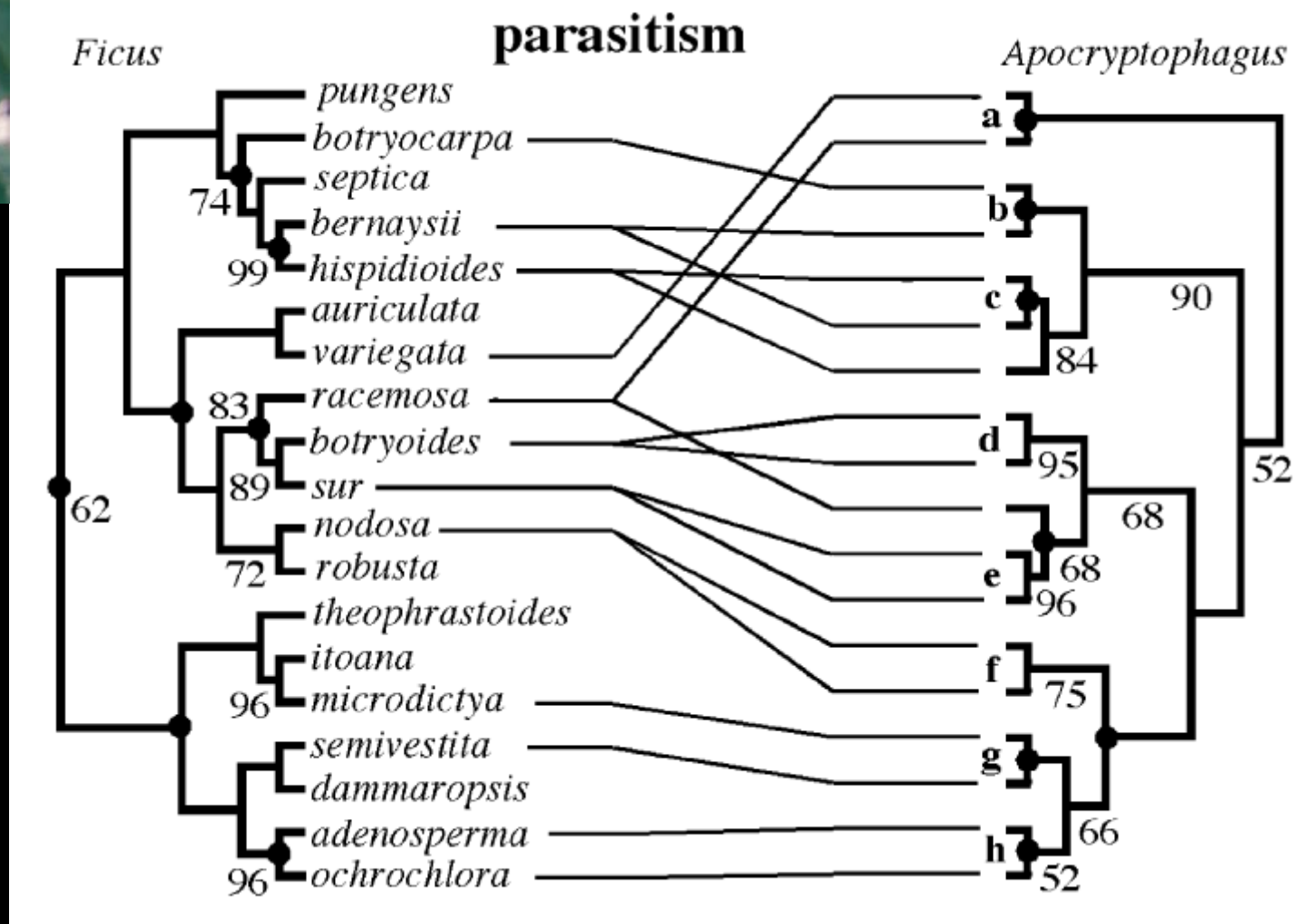


pollinators



Ficus – pollinator interaction web determined by phylogeny

parasitoids

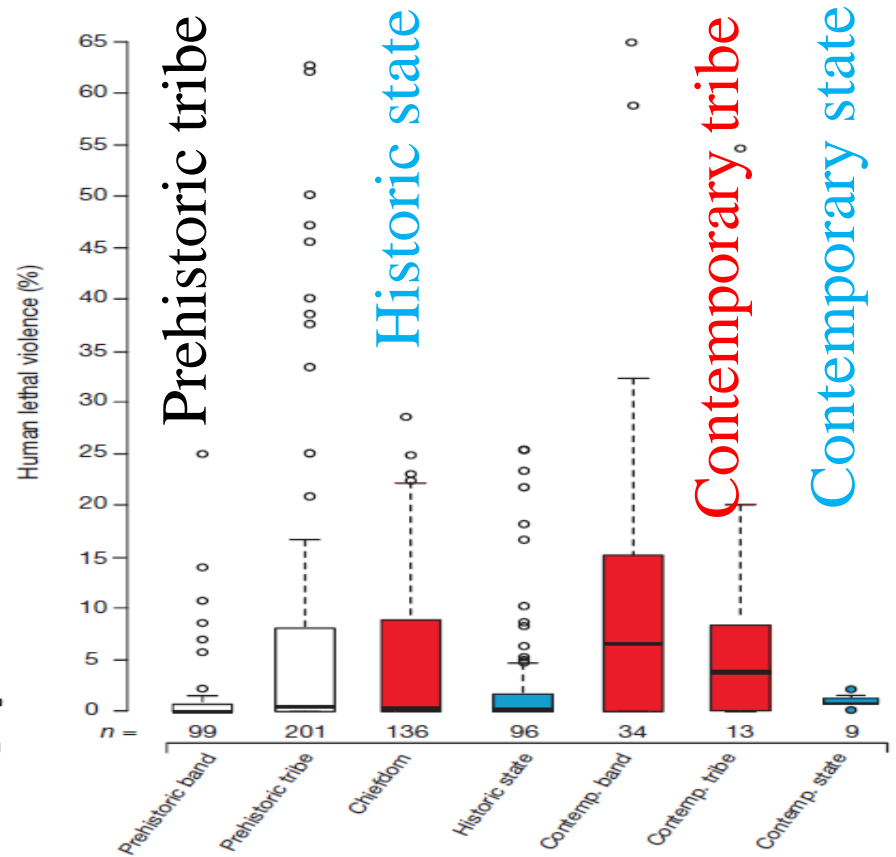
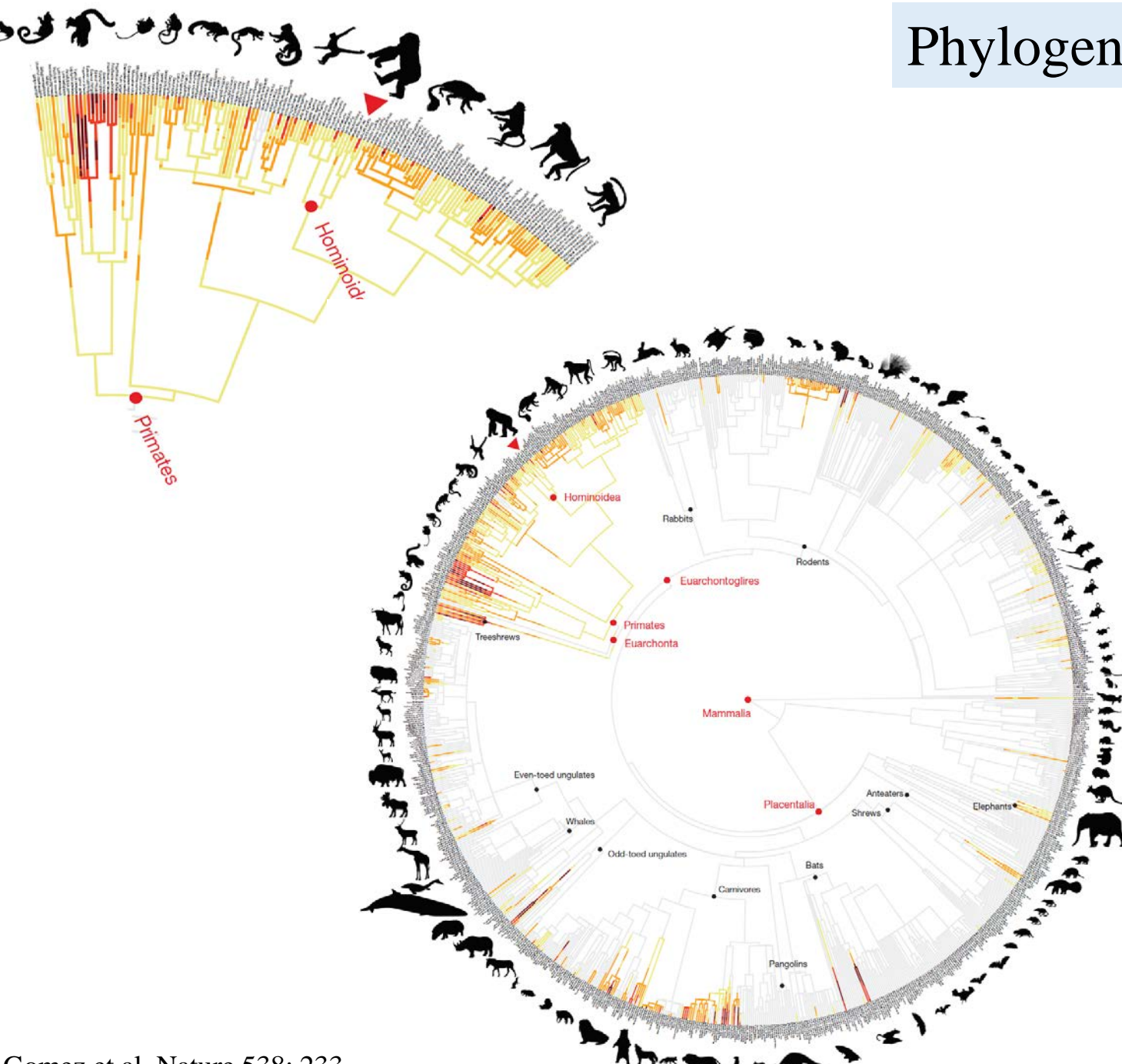


Ficus – parasite interaction web co-determined by ecology

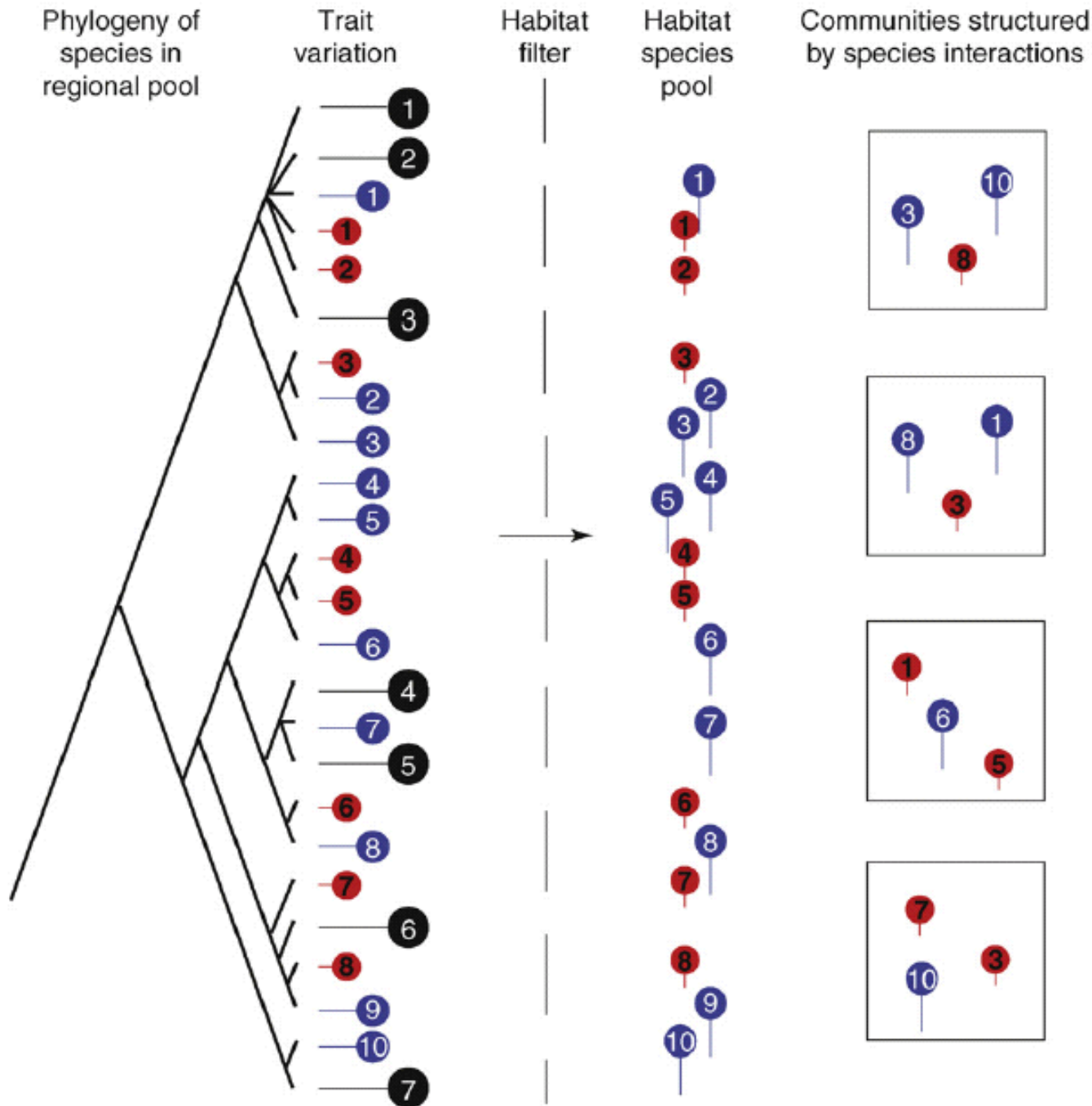
Phylogenetic signal in intraspecific violence

Human tribal societies were well predicted by phylogeny

Lower higher than phylogenetic prediction



Community assembly by environmental filtering and interspecific competition



Environmental filtering:
only species with certain life history traits can survive in a particular environment

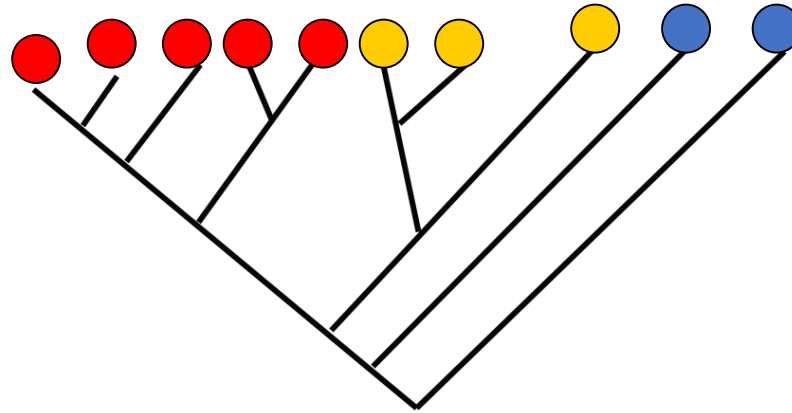
red, blue, black - different life history traits

Figure 2. Community assembly by environmental filtering and interspecific competition. For a given habitat, the pool of species able to colonize that habitat is the subset of a regional species pool, constrained to those species possessing the necessary traits to complete their life cycle within that habitat. The four squares represent geographically discrete but identical habitats that have each been colonized from a regional pool of species. Within the regional pool of species, each species can occupy one of three possible niches. The species traits associated with niche are represented by three different circles (small = red; medium = blue; large = black). Establishment of the seven large black species is precluded by the environmental filter. From among the habitat species pool (blue and red numbered circles), the final species composition of each of the four habitats is dictated by interactions among species. Redrawn and modified with permission from Ref. [44].

Phylogenetic distribution of species & traits in a community

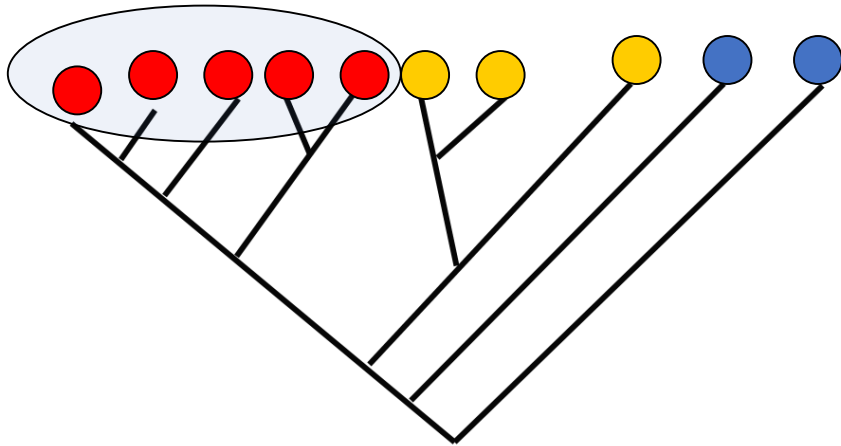
REGIONAL SPECIES POOL

traits are conservative
clustered on cladogram



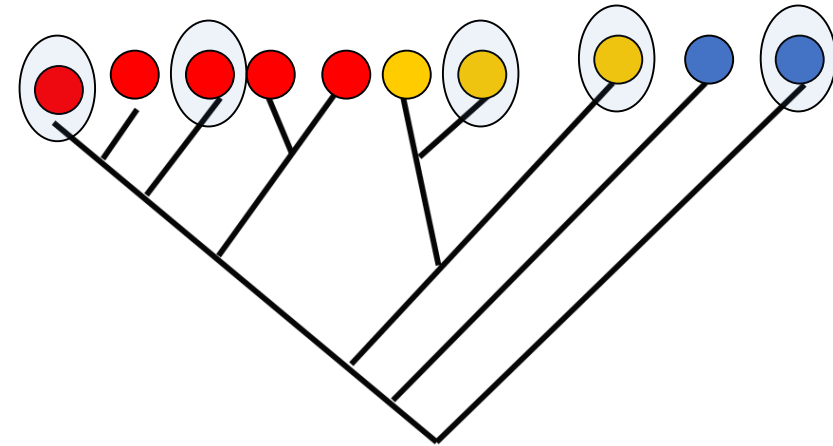
pollination

- bees
- bats
- wind



habitat filtering
[demanding ● trait]

species clustered



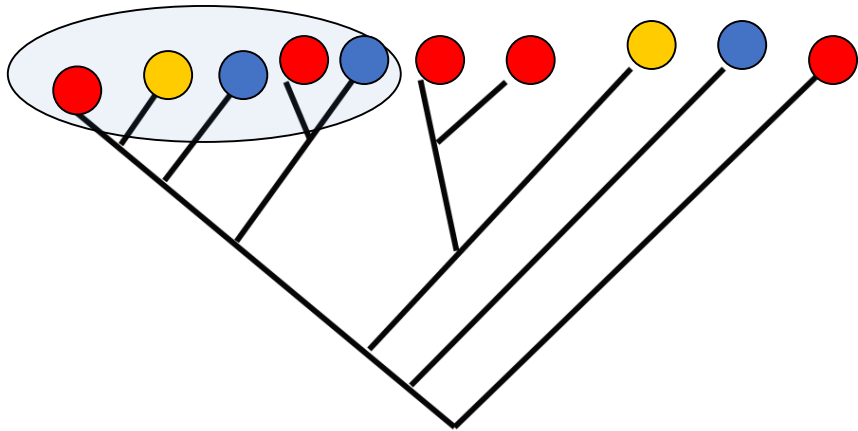
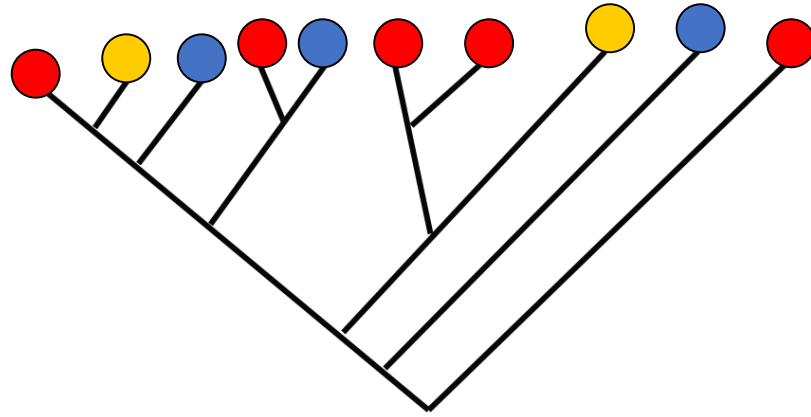
maximum trait differences
facilitate coexistence

species overdispersed

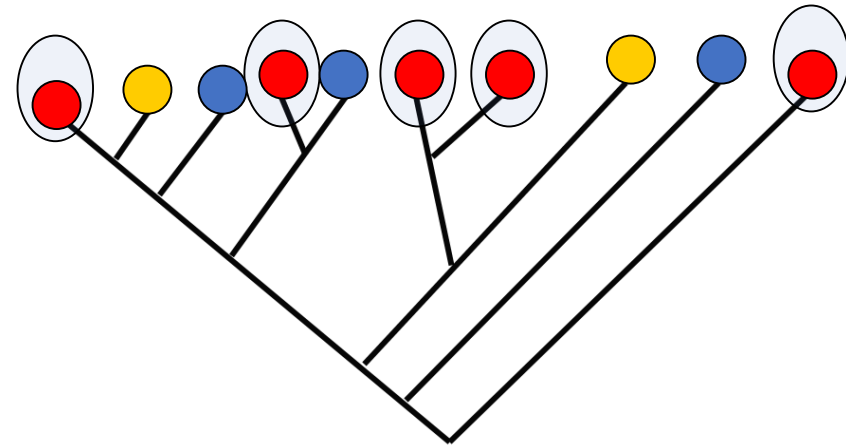
Phylogenetic distribution of species & traits in a community

REGIONAL SPECIES POOL

traits are flexible
overdispersed

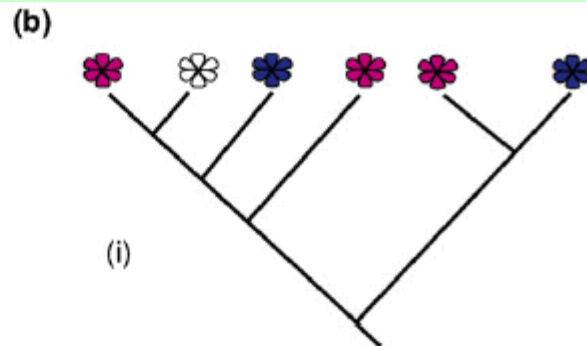
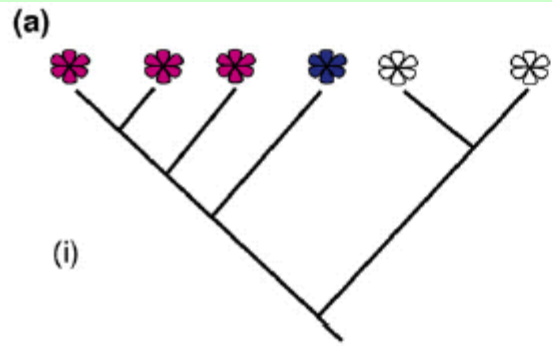


maximum trait differences
facilitate coexistence
species clustered

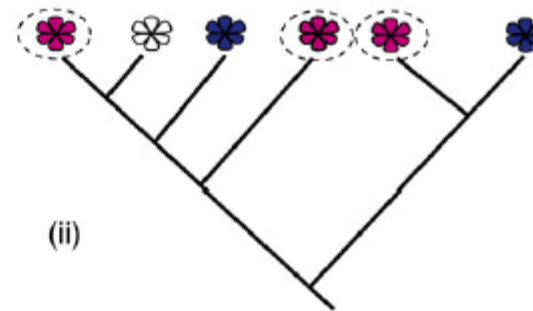
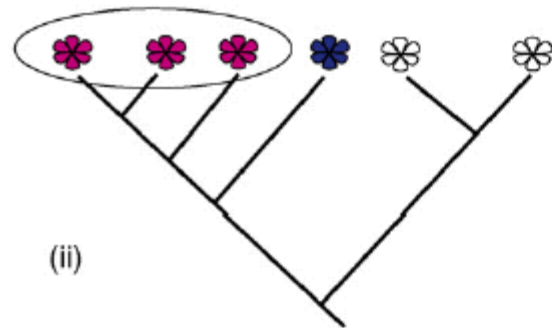


habitat filtering
[demanding ● trait]
species overdispersed

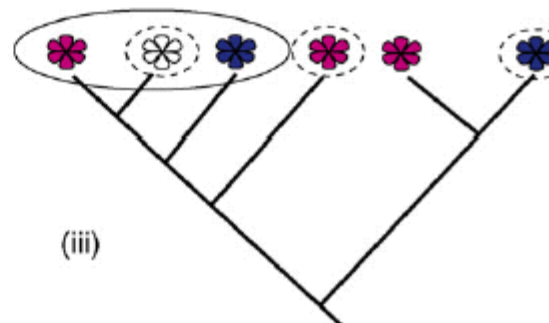
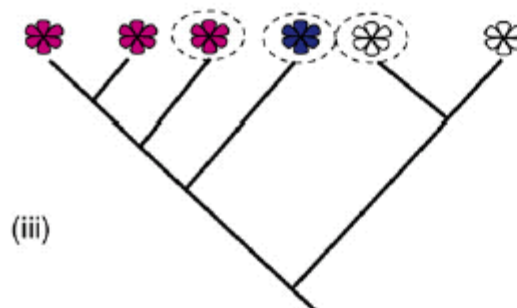
Species trait (flower colour) evolutionary conserved (a) or not (b) community assembly determined by filtering (ii) or competition (iii)



Facilitation/filtering



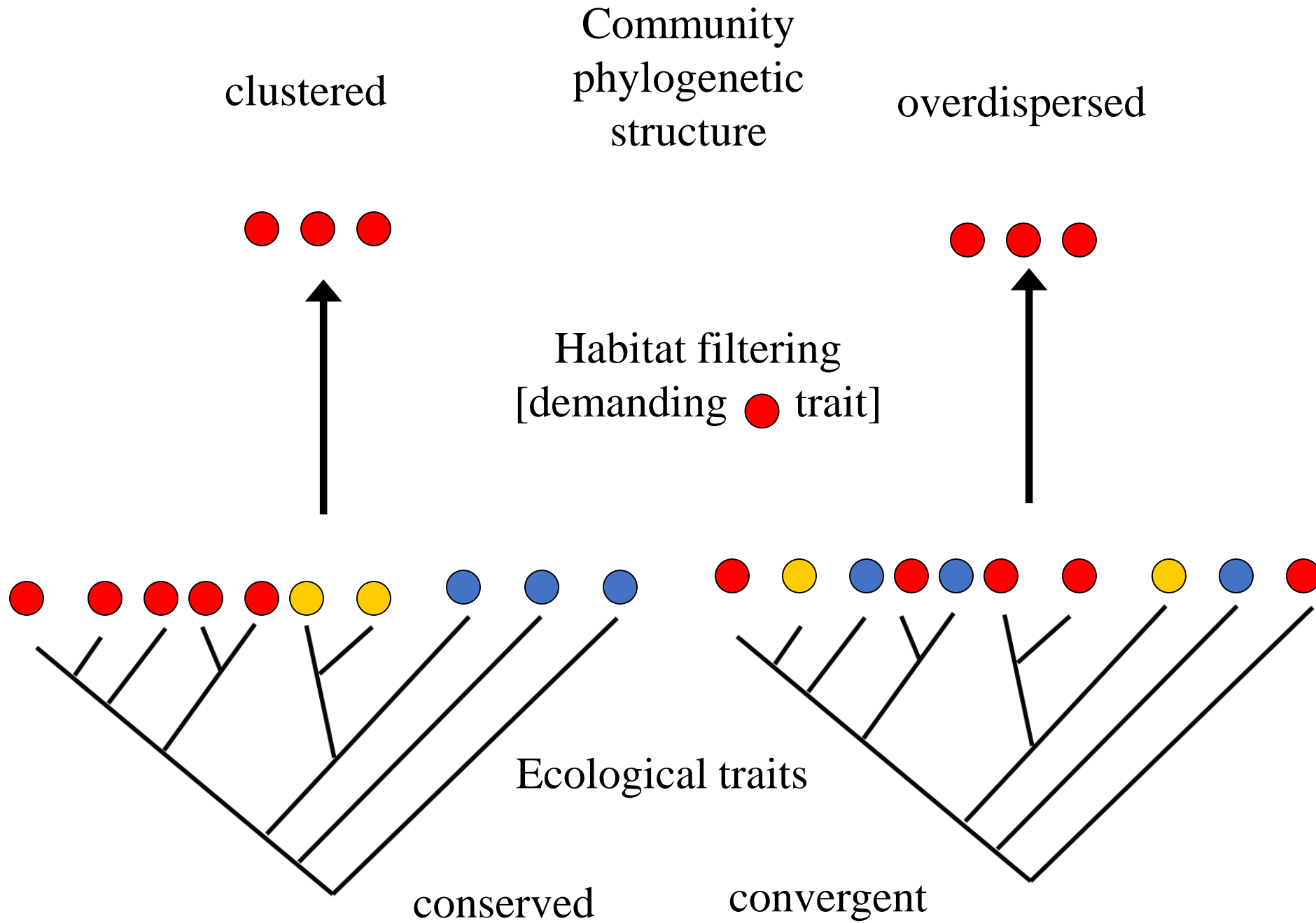
Competition



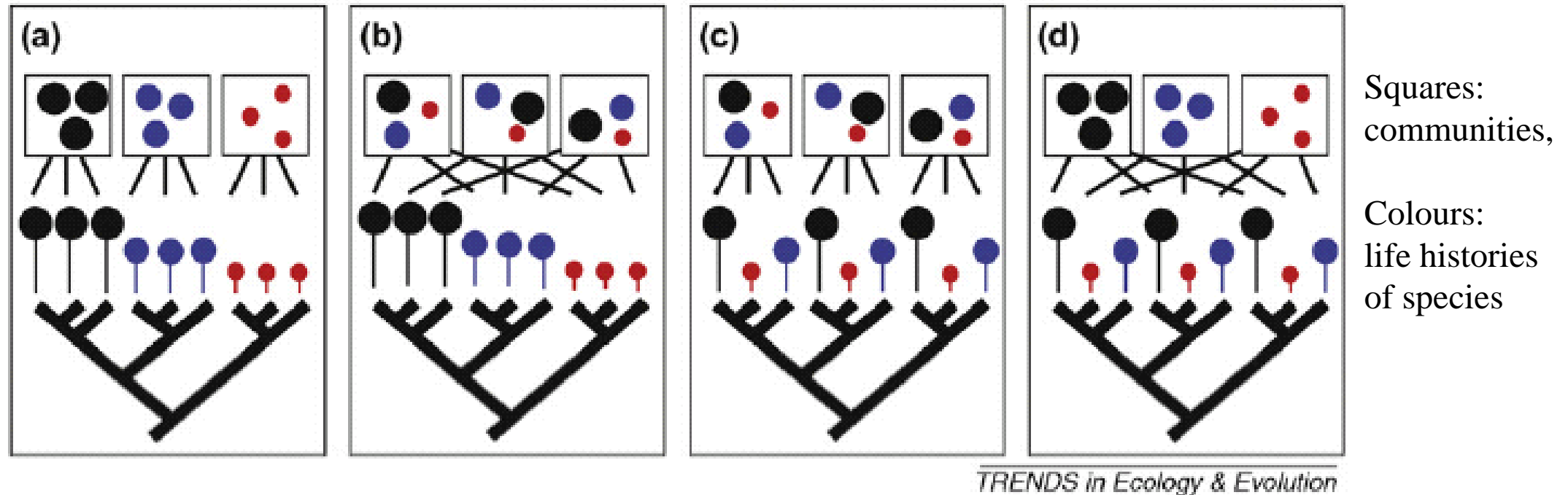
FILTERING

COMPETITION

Figure 3. The pattern of trait distribution on a phylogeny influences the predicted phylogenetic relatedness of species in a community (see Table 1). In panel (a), the flower color trait pattern is evolutionarily conserved, whereas in (b) it is not conserved. Ovals indicate potential three-species communities that are assembled either through the process of facilitation and/or filtering (ii) or through competition (iii). Depending on the trait distribution, the two processes can result in communities of close relatives (solid ovals), as in (a) (ii), communities of distant relatives (dashed ovals) as in (b) (ii) and (a) (iii), or either, as illustrated in (b) (iii).



Phylogenetic and/or phenotypic clustering/overdispersion of species in communities [compared to the regional species pool]



- A: both phylogenetic and phenotypic clustering of spp. in communities
- B: both phylogenetic and phenotypic overdispersion
- C: phylogenetic clustering and phenotypic overdispersion
- D: phylogenetic overdispersion and phenotypic clustering

TABLE 1 The expected distribution of sample taxa on the phylogeny of a pool at a larger spatial scale, given various combinations of phylogenetic trait distribution and ecological process

	Ecological traits phylogenetically	
	Conserved	Convergent
Dominant ecological force:		
Habitat filtering (phenotypic attraction)	Clustered	Overdispersed
Competitive exclusion (phenotypic repulsion)	Overdispersed	Random

Tests of distribution of ecological traits in community vs. regional species pools:

the same procedure as for the tests of local/regional species composition

Habitat filtering:

habitat [biome] choice in lineages is phylogenetically conservative

Crisp et al. 2009. Nature 458:754

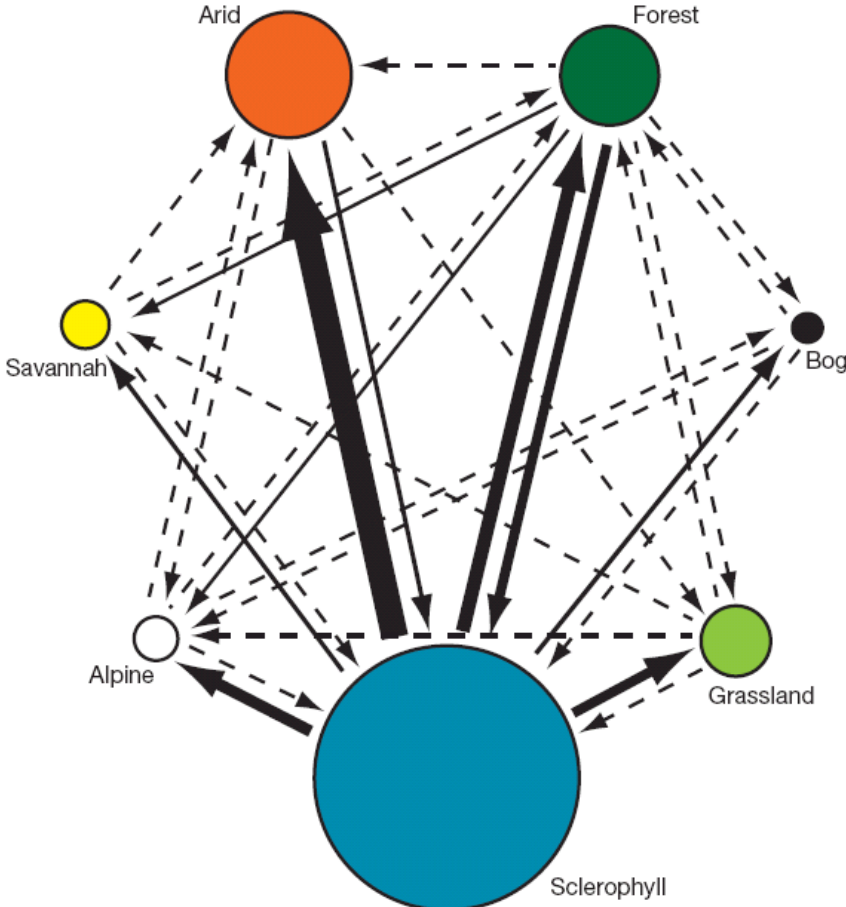


Figure 1 | Biome shifts within landmasses. Shifts occurred with only 356 of 10,800 speciation events within landmasses. Number of species sampled within each biome is proportional to the area of each circle: sclerophyll, 7,250; arid, 1,683; wet forest, 1,005; temperate grassland, 504; savannah, 242; montane, 186; bog, 84. Arrow thickness is proportional to the number of transitions in each direction, ranging from 6 to 95 events; dashed lines indicate 1–5 events and lack of an arrow indicates that there was no event.

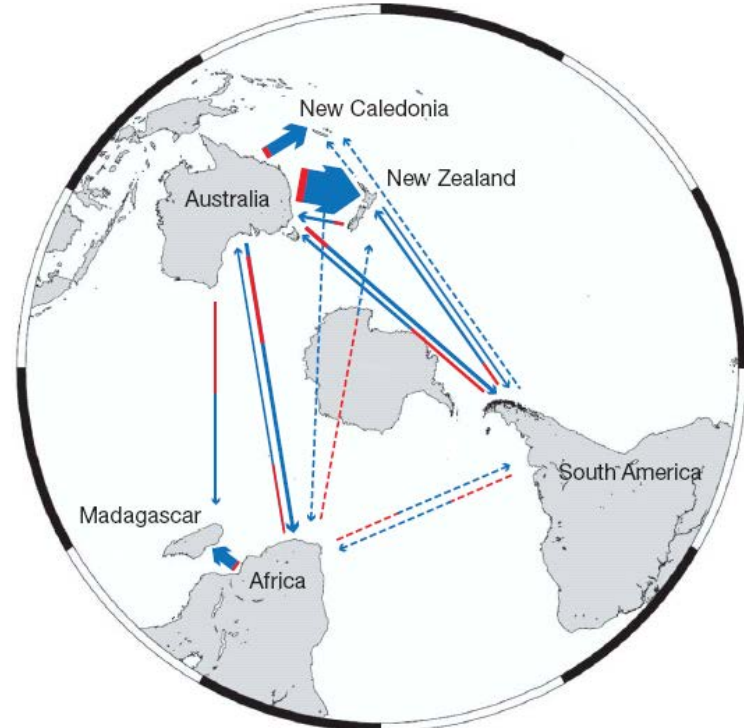
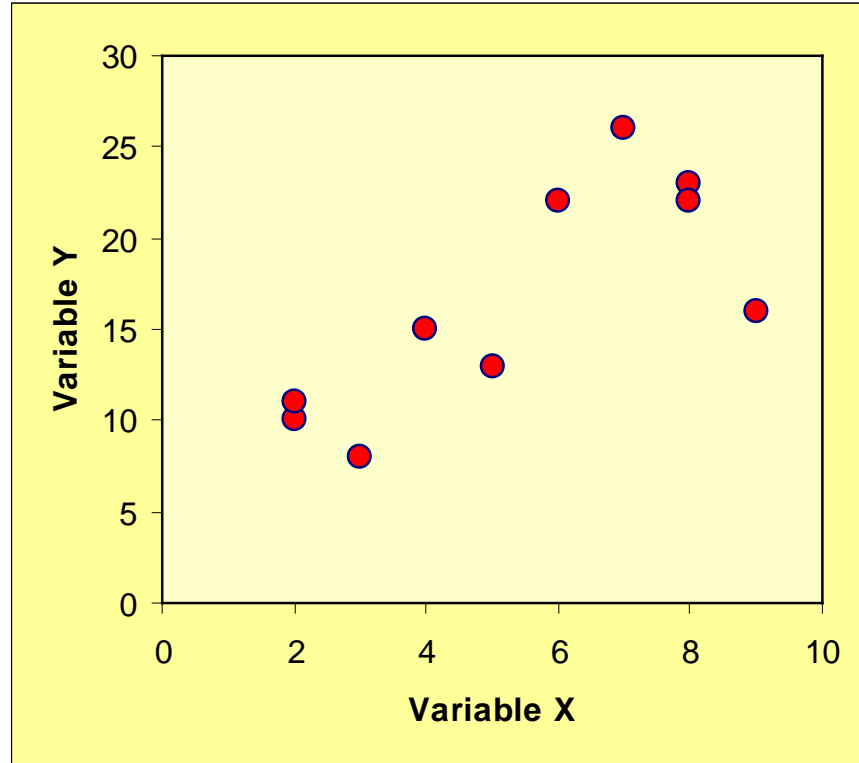
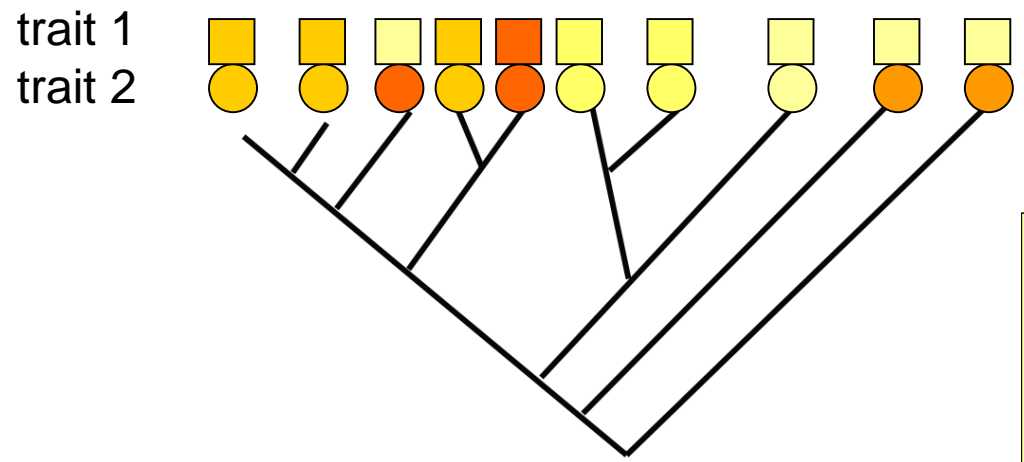


Figure 2 | Biome conservatism in transoceanic plant colonizations around the Southern Hemisphere. Proportion of colonizations into the same (blue) or a different (red) biome are shown along each arrow. Arrow thickness is proportional to the number of colonizations, ranging from 4 to 107 events; dashed lines indicate fewer than 4 events. Four ambiguous colonizations are not shown.

Why species are not
independent data points
and what to do about it

Correlation between ecological traits of species: species are not statistically independent data points

How many independent data points do you see?



Species are not statistically independent data points since they share common phylogeny

The problem of ignored phylogeny has been known for a long time

and

Felsenstein (1985) Phylogenies and the comparative method. Am. Nat. 125:1 provided a practical approach to the analysis

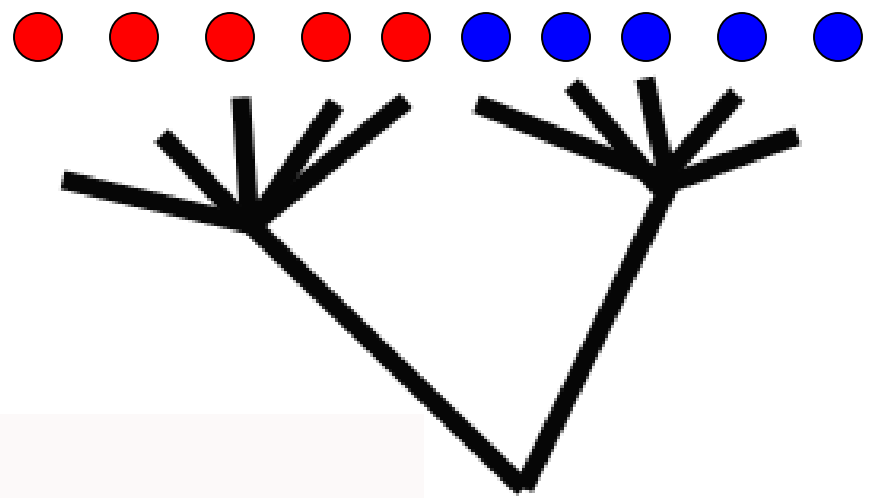
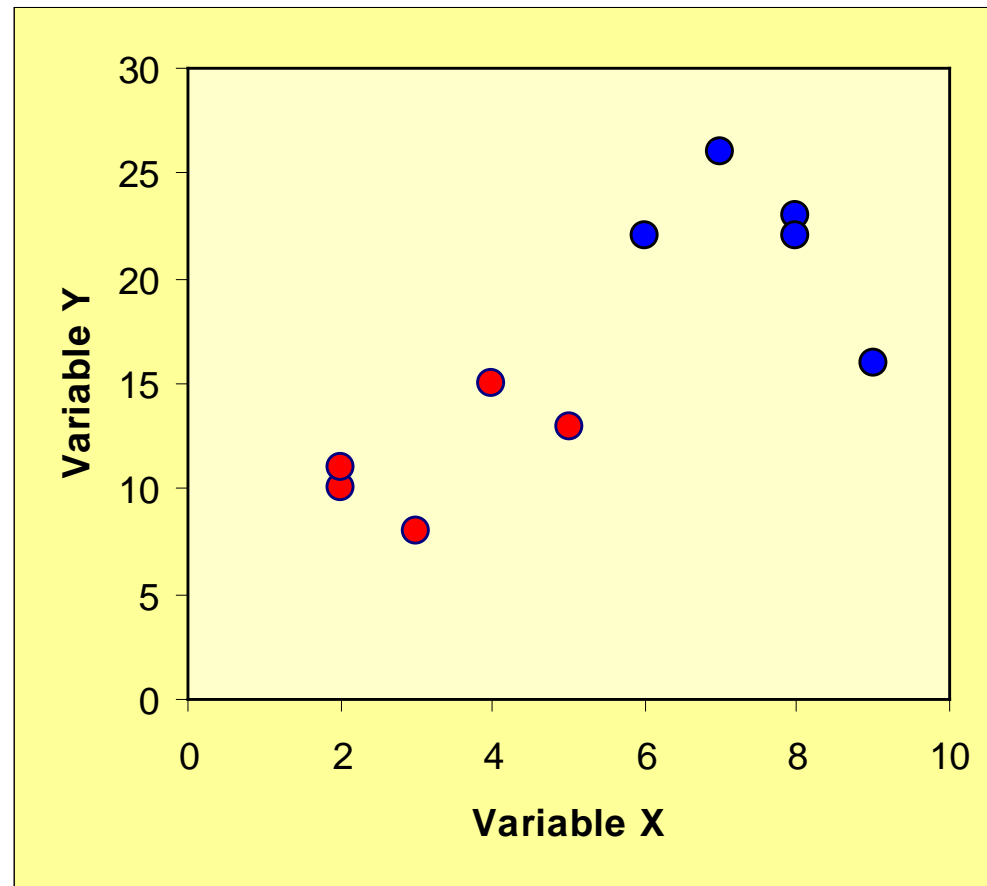
but

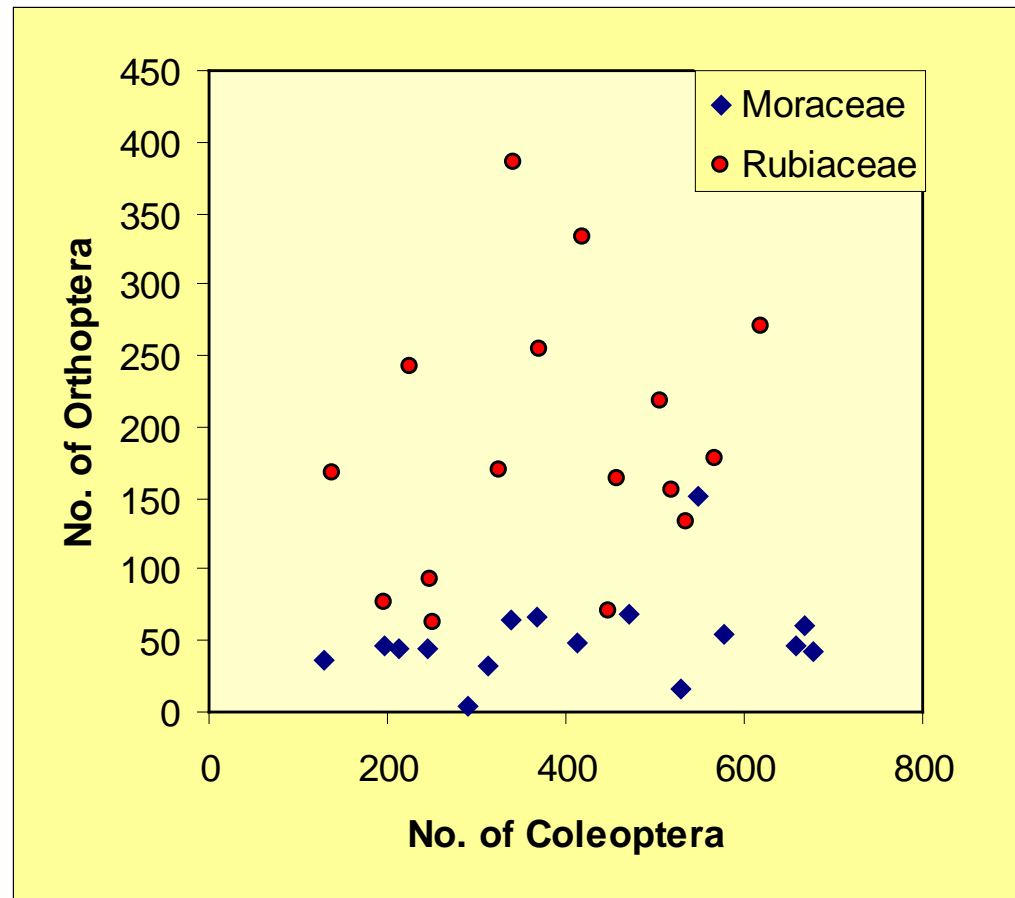
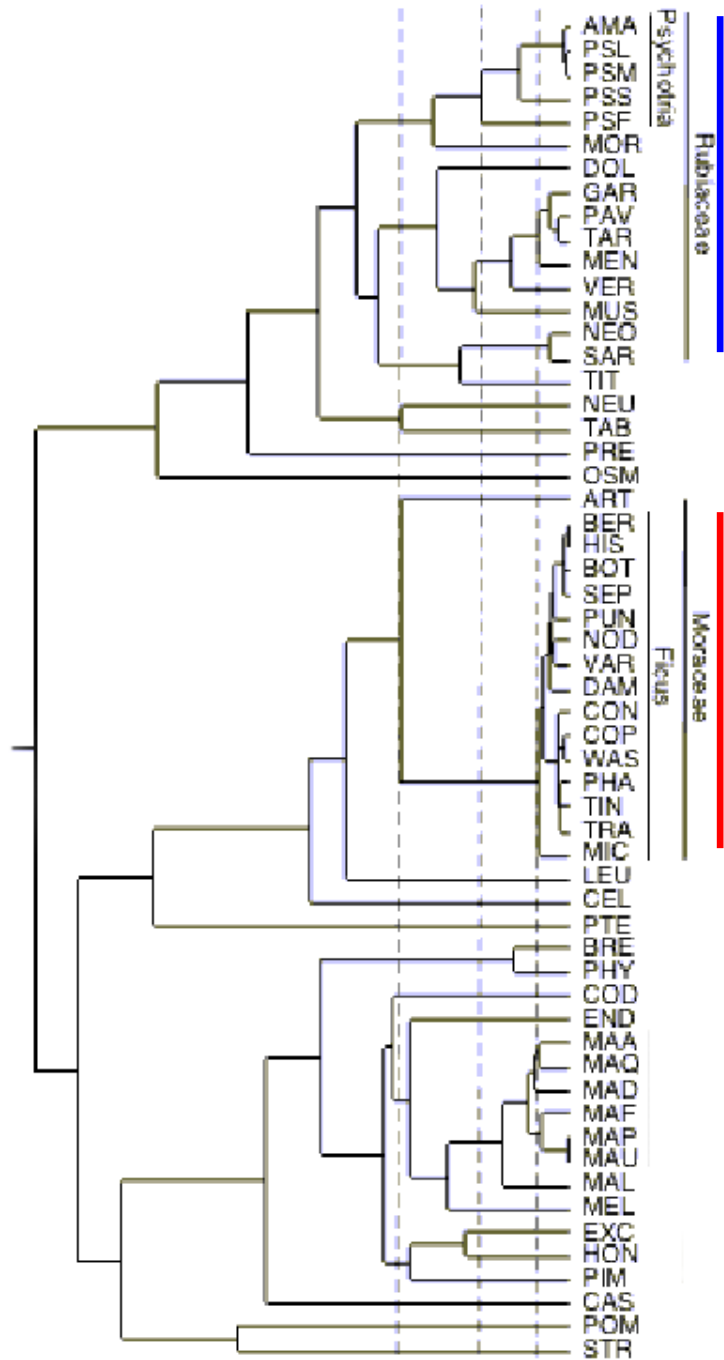
nothing happened because of the lack of phylogenetic information

until

the last 15 years or so when there is an exponential increase in available phylogenies and interest in phylogenetic community analysis

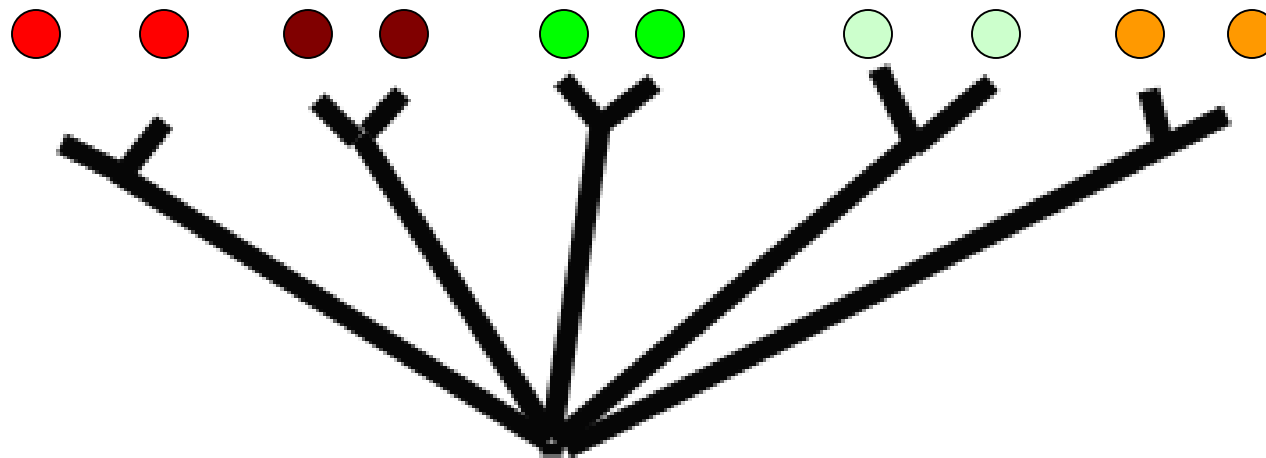
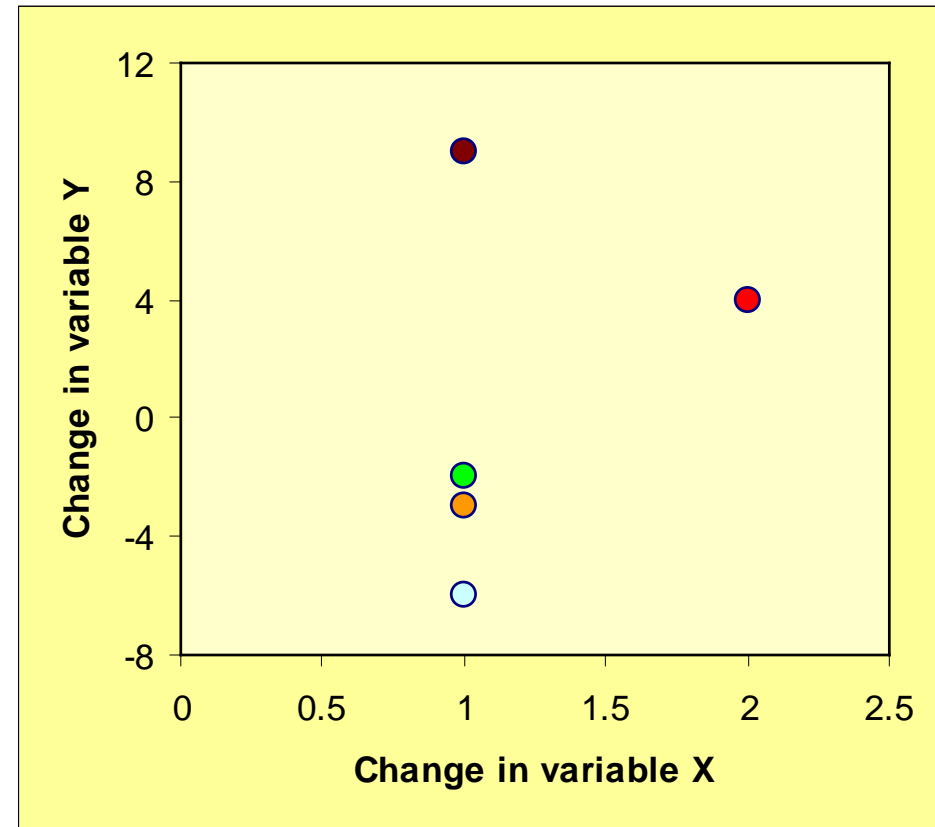
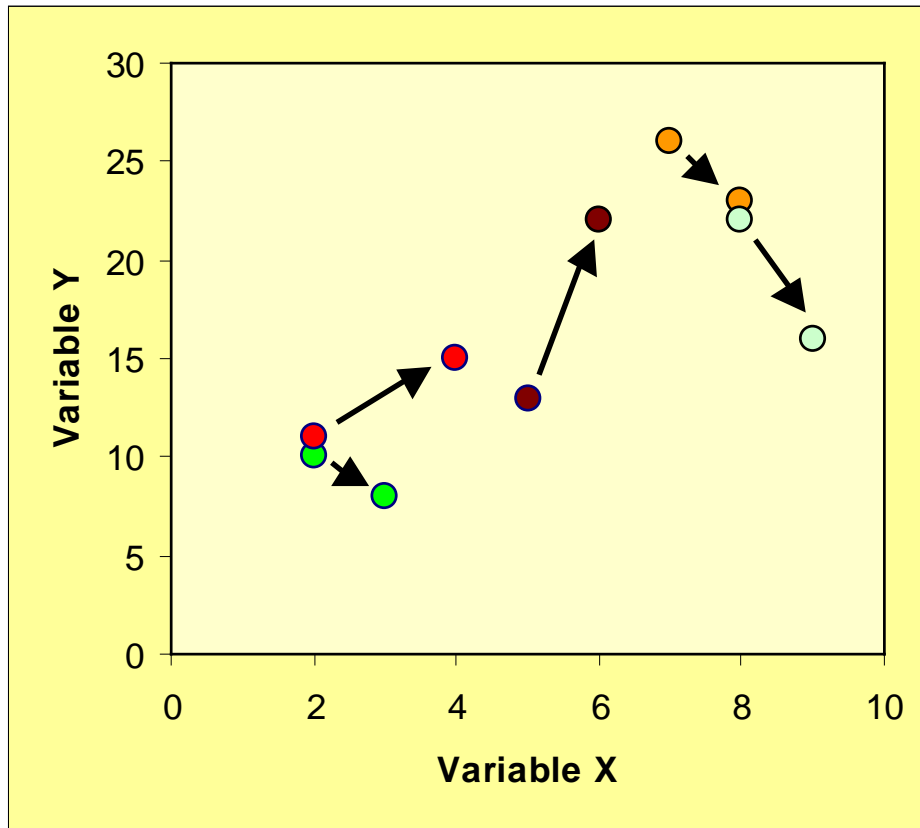
The worst case scenario:
what looks like 10 data points
can in fact be only 2!





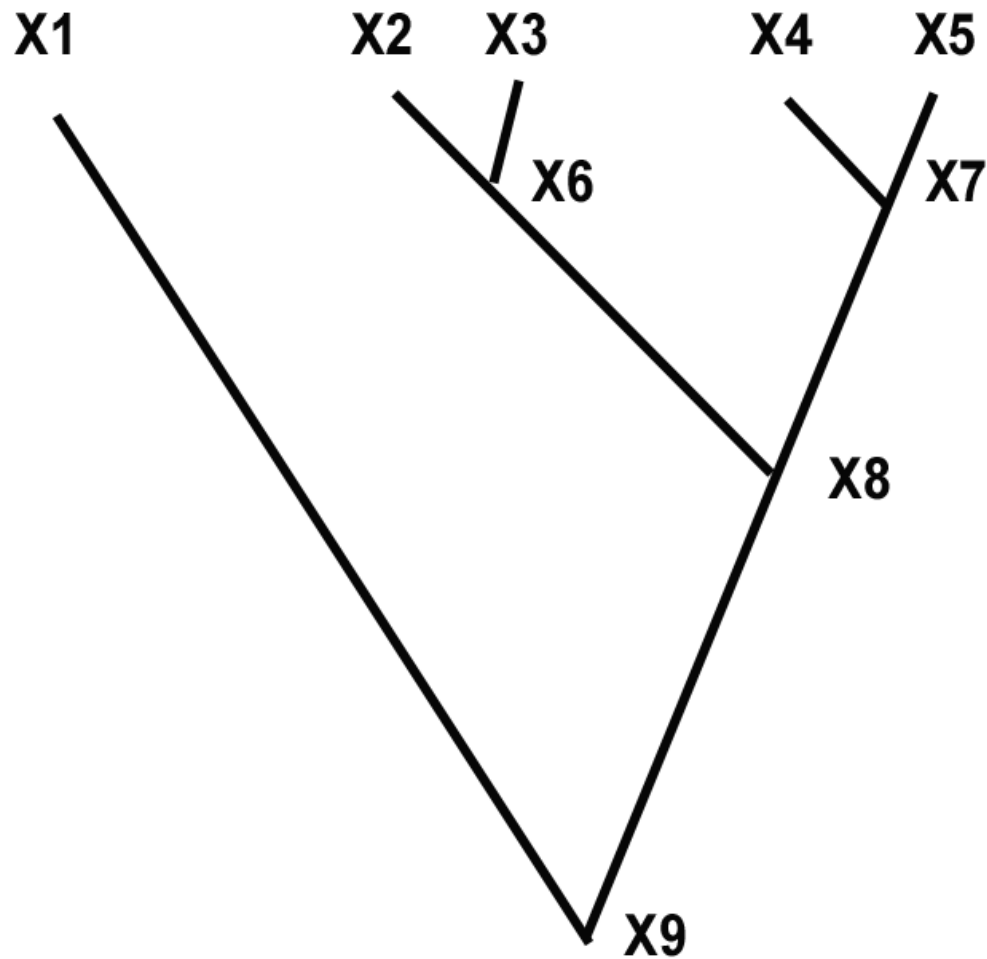
A real world example:
Abundance of different herbivore taxa
on plant species from a New Guinea
rainforest

Independent contrasts, Phylogenetic generalized least squares (PGLS)



Solution:

Covariance of traits X and Y between sister species is mutually independent between different sister species pairs



Independent contrasts
can be calculated
between all nodes:

X4 - X5
X2 - X3
X6 - X7
X1 - X8

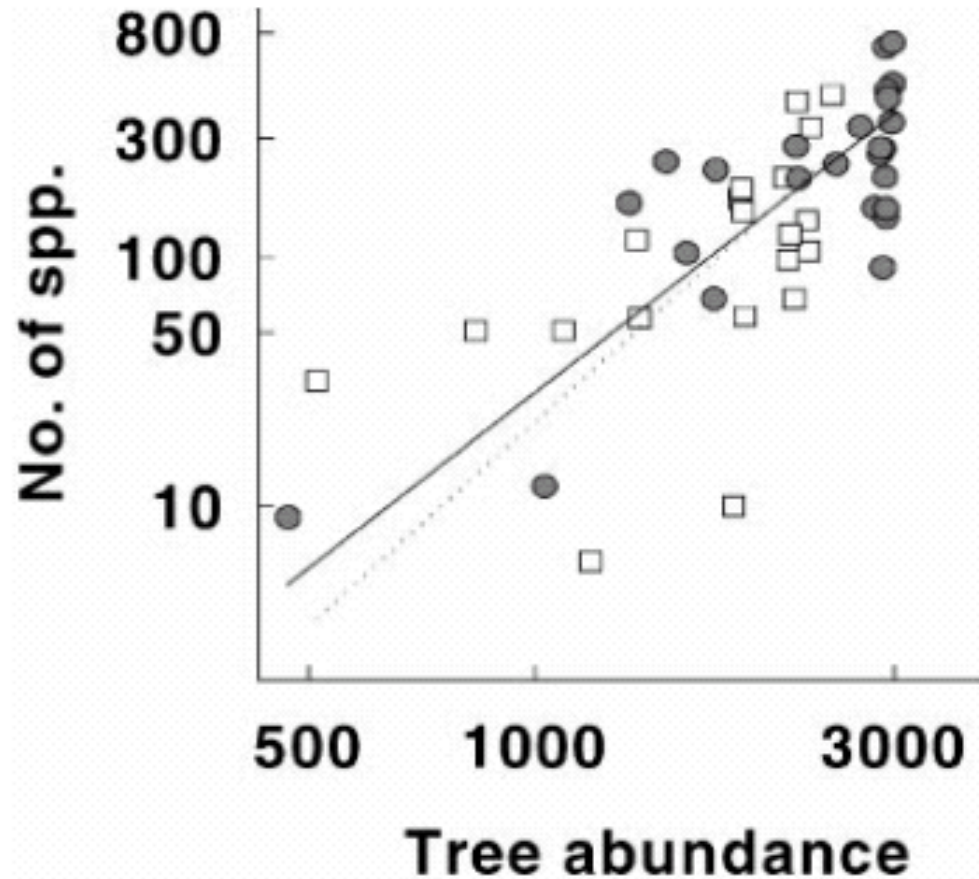
Ancestral reconstruction: tricky

Assumption of a constant rate of evolution along each node -
ancestral value is an average of those for its descendants

$$X6 = (X2+X3)/2$$

different branch lengths - the average is weighted by branch length

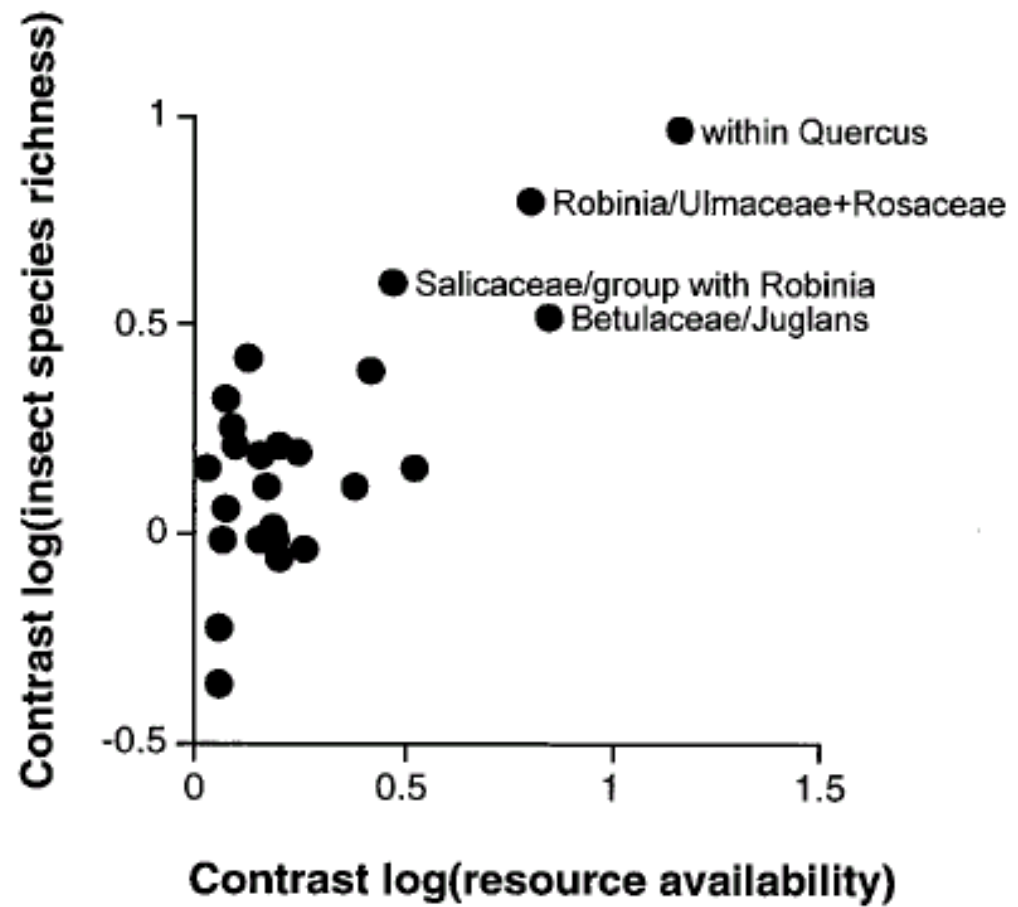
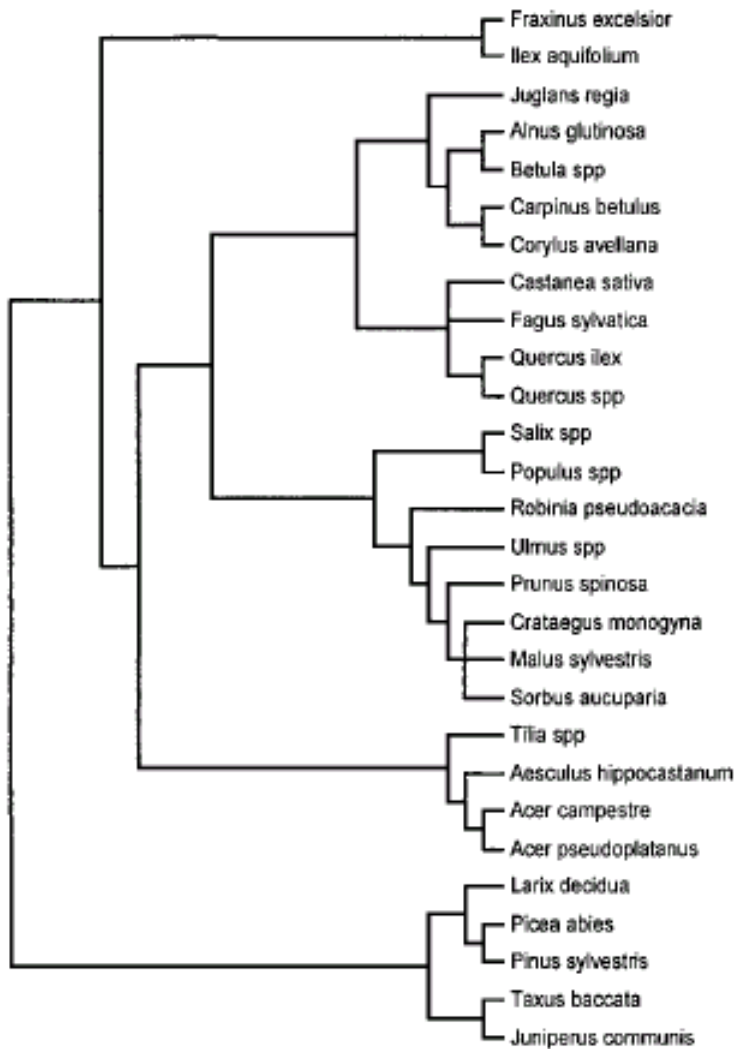
Correlating species traits X and Y across species from a community:
What is wrong with such analysis?



Tree abundance
(no. of 10x10km squares)
vs.
number of its herbivore species
Britain (squares) and Germany (circles)

Each point represents one tree species

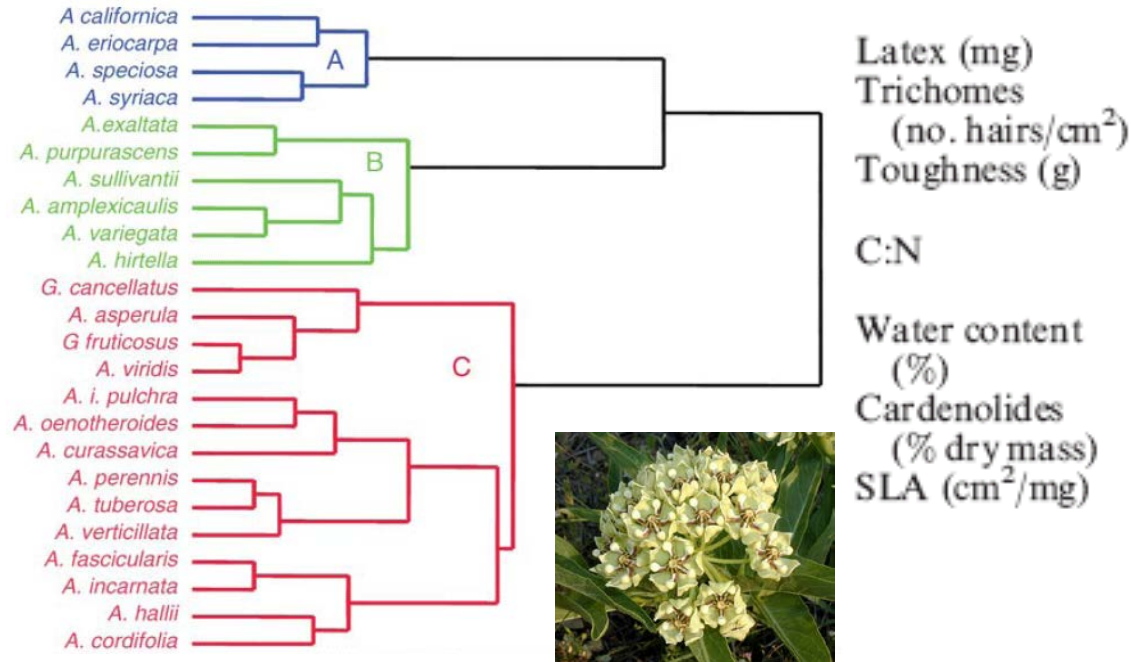
Fig. 3. Species–area relationship for the number of phytophagous insect and mite species on native British trees ($n = 20$, quadrates, dotted regression line) and on native German trees ($n = 25$, circles, solid regression line). Present tree abundance was measured as the number of 10×10 grids occupied in Britain and the number of 11×11 -km grids occupied in Germany. Britain: $n = 20$, $r^2 = 0.30$, $P = 0.011$, $b_{RMA} = 2.72$, 95% confidence limits 1.02–7.26; Germany: $n = 25$, $r^2 = 0.65$, $P < 0.001$, $b_{RMA} = 2.34$, 95% confidence limits 1.70–3.25. Axes are \log_{10} -transformed. Note that regression lines are reduced major axis regressions.



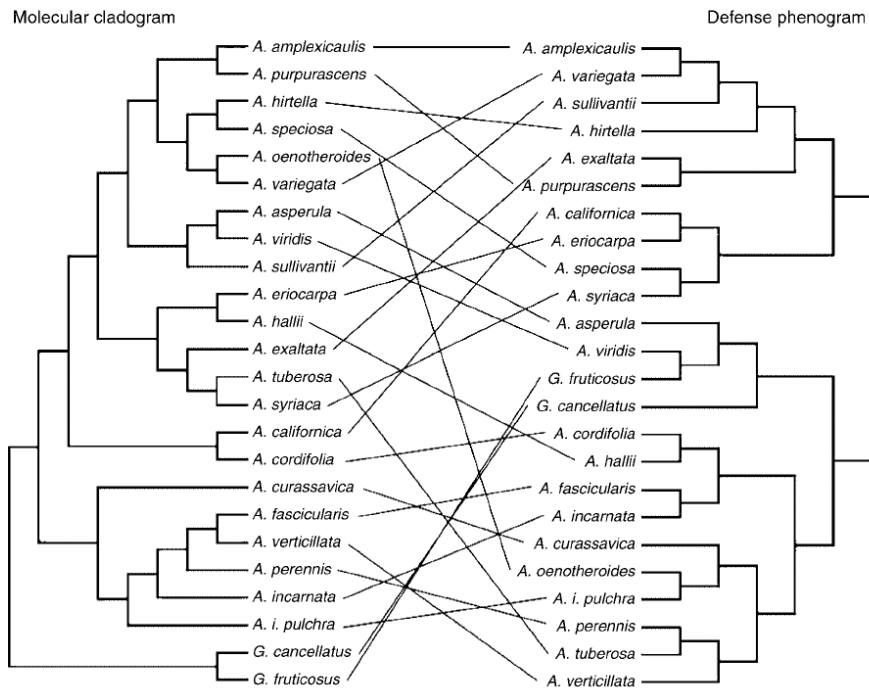
Kennedy & Southwood 1984. J.Anim. Ecol. 53:455
 Kelly & Southwood 1999. PNAS 96:8013

ABSTRACT The data on the number of species of insects associated with various trees in Britain have been reanalyzed to factor out possible bias from phylogenetic effects. It was found that tree availability (range and abundance) continues to provide a good predictor ($r = 0.852$) of insect-species richness, slightly better than straightforward cross-species analyses. Of the two components of tree availability, tree abundance gives a much better prediction than tree range. The species richness on trees of major taxa with similar trophic habits (Lepidoptera and Hymenoptera/Symphyla and the two suborders of the Homoptera—Auchenorrhyncha and Sternorrhyncha) shows positive correlations; there is thus no evidence of competitive exclusion at this taxonomic level.

Tree abundance x herbivore richness relationship revisited:
 Independent contrasts re-analysis of
 of herbivore species richness on
 British trees: no new insights



When independent contrasts are not needed:
Asclepias plant traits cluster in 3 defence strategies (A, B, C) which do not correspond to plant phylogeny



raw correlation $r=0.60$
 independent contrasts $r=0.62$

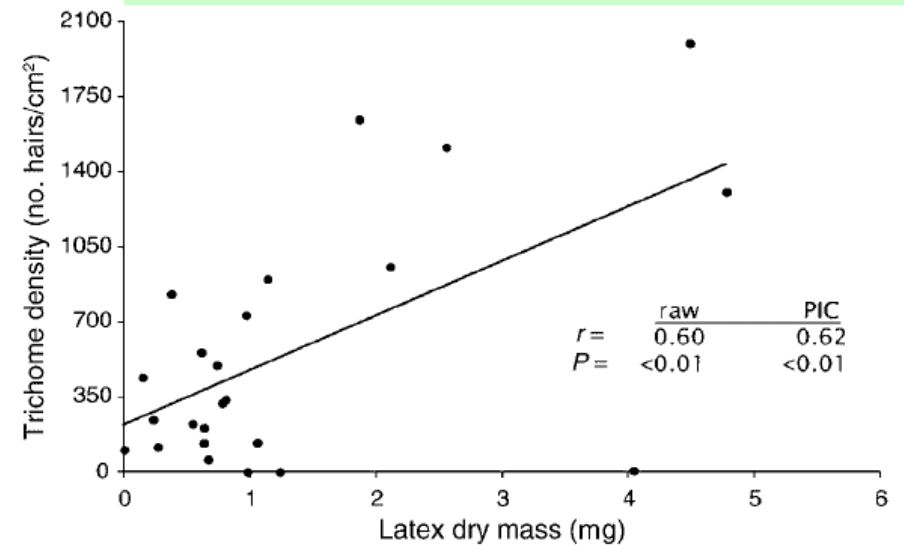


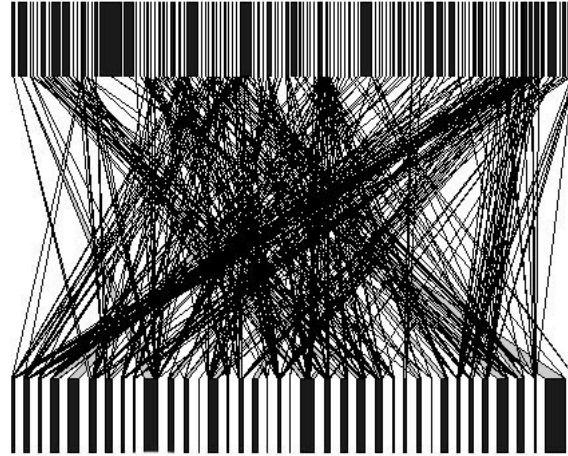
FIG. 5. Schematic depiction of the lack of congruence between the molecular phylogeny of *Asclepias* and the defense trait phenogram (see Fig. 4).

Correlation in species diversity between folivorous guilds:

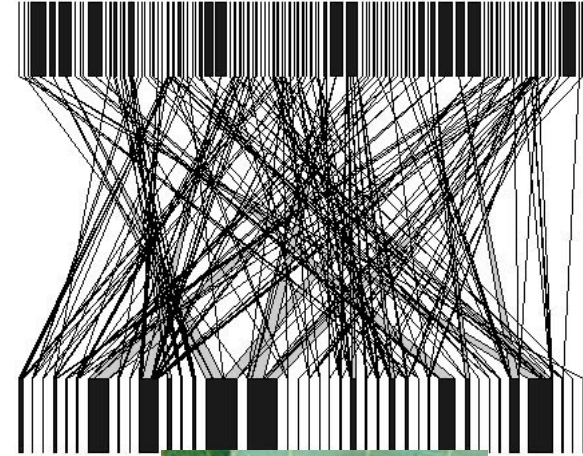
mobile chewers



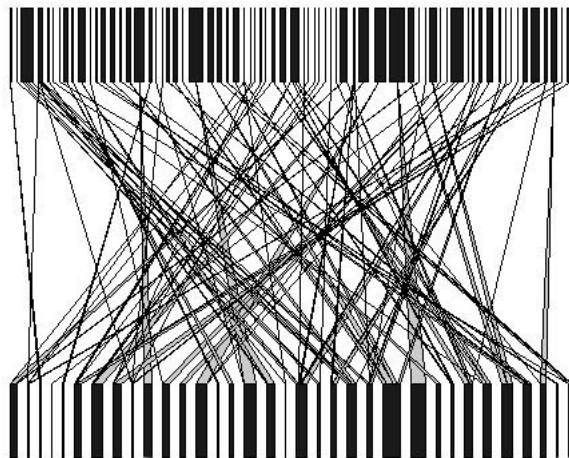
semi-concealed chewers



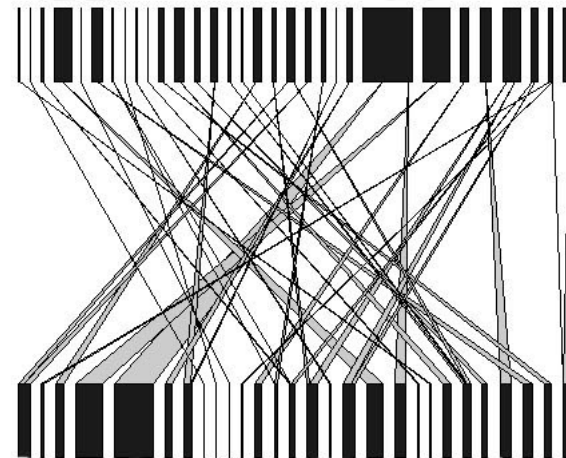
exposed chewers



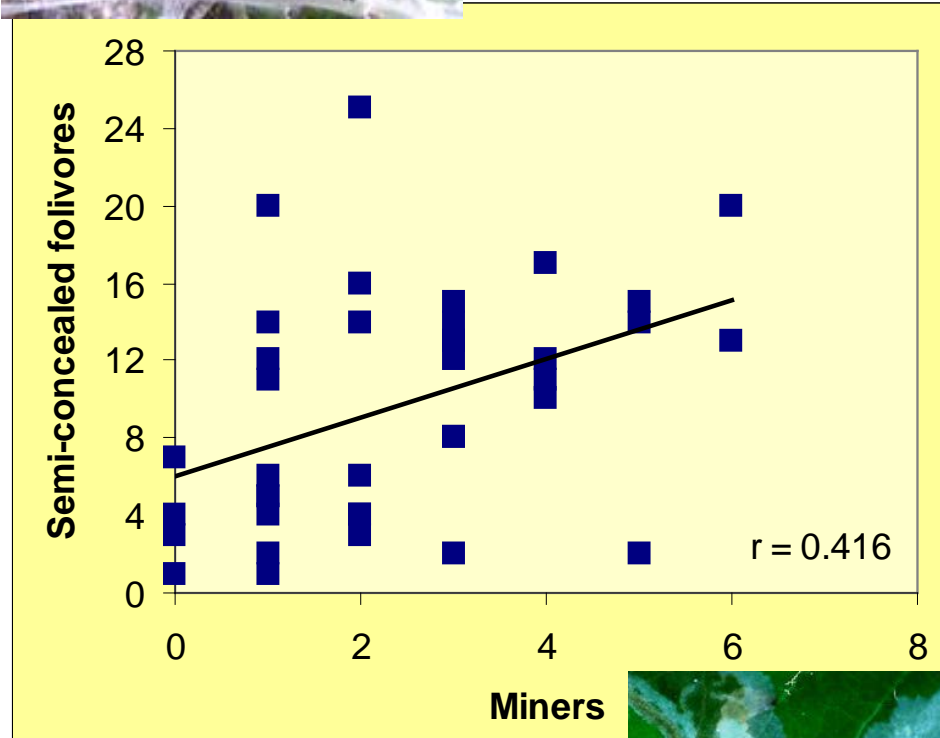
miners



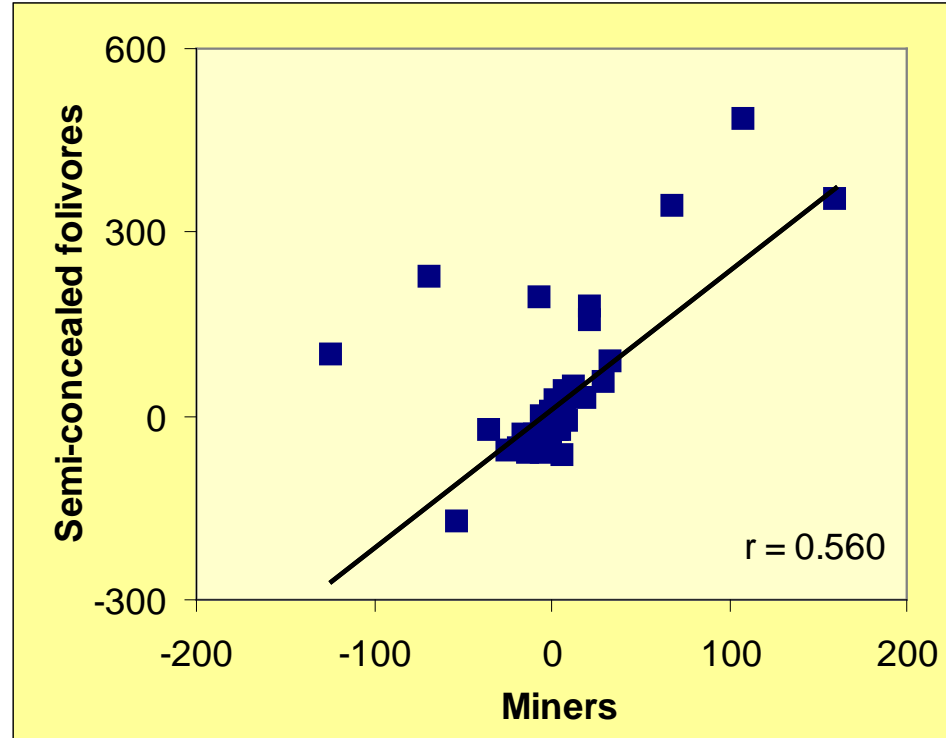
mesophyll suckers



Species richness of semi-concealed (leaf-tying, rolling) caterpillars and miners



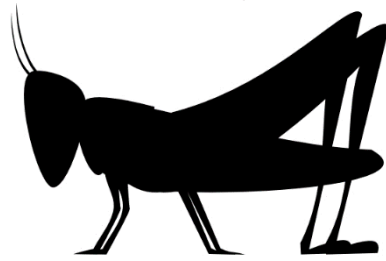
tree species as data points



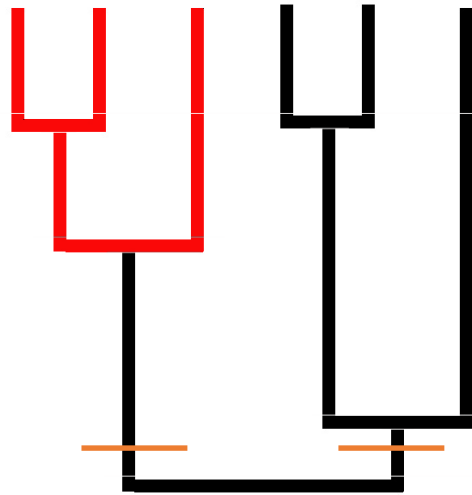
independent contrasts

Measuring resource use on host phylogeny

Host specialization in phylogenetic context:
from counting host species (and genera, and families)
to more precise measures

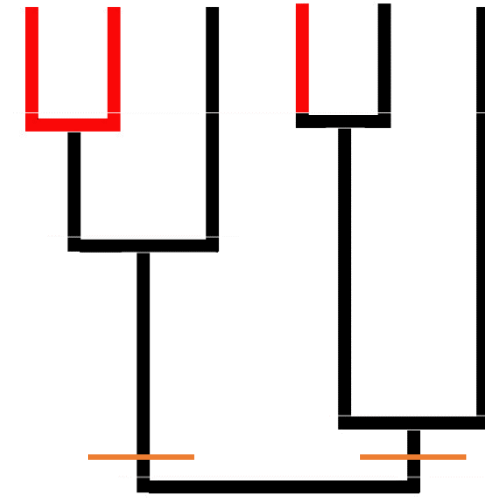
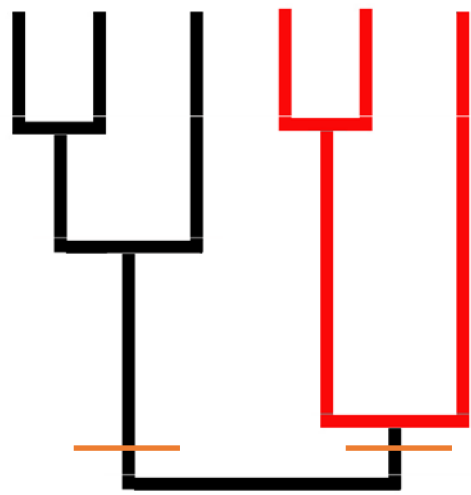


Mean pair-wise phylogenetic distance MPD:
between all pairs of host plant species



genus A

genus B



ECOLOGY LETTERS

Ecology Letters, (2014)

doi: 10.1111/ele.12347

An integrated framework to improve the concept of resource
specialisation

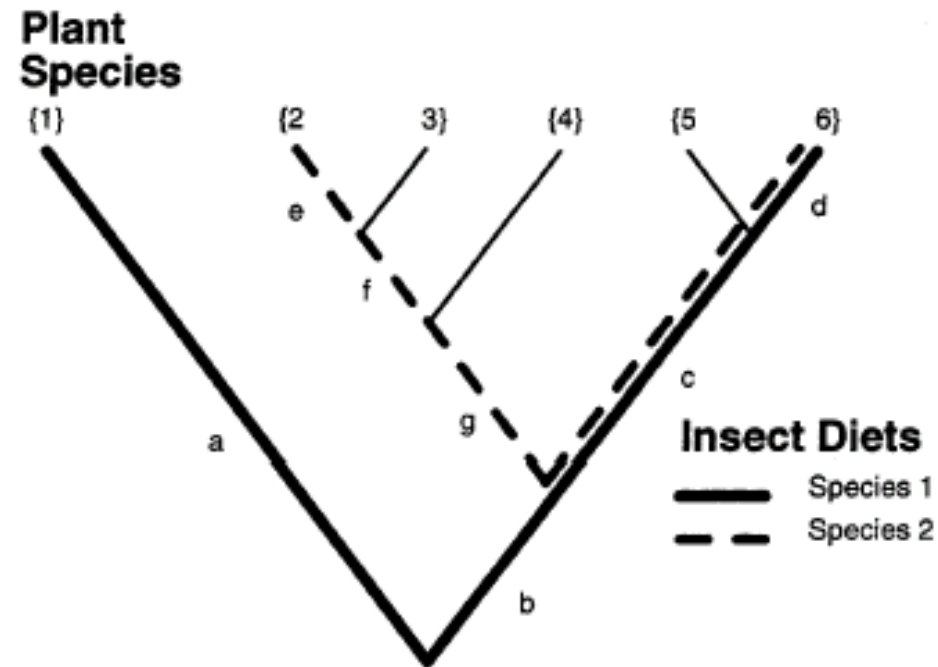
Leonardo R. Jorge, Paulo I.
Prado, Mário Almeida-Neto and
Thomas M. Lewinsohn

Net relatedness index (NRI):

$$\text{NRI} = - (X_{\text{net}} - X(n)) / \text{SD}(n)$$

X_{net} is the mean phylogenetic distance between all pairs of n host plants sharing a herbivore

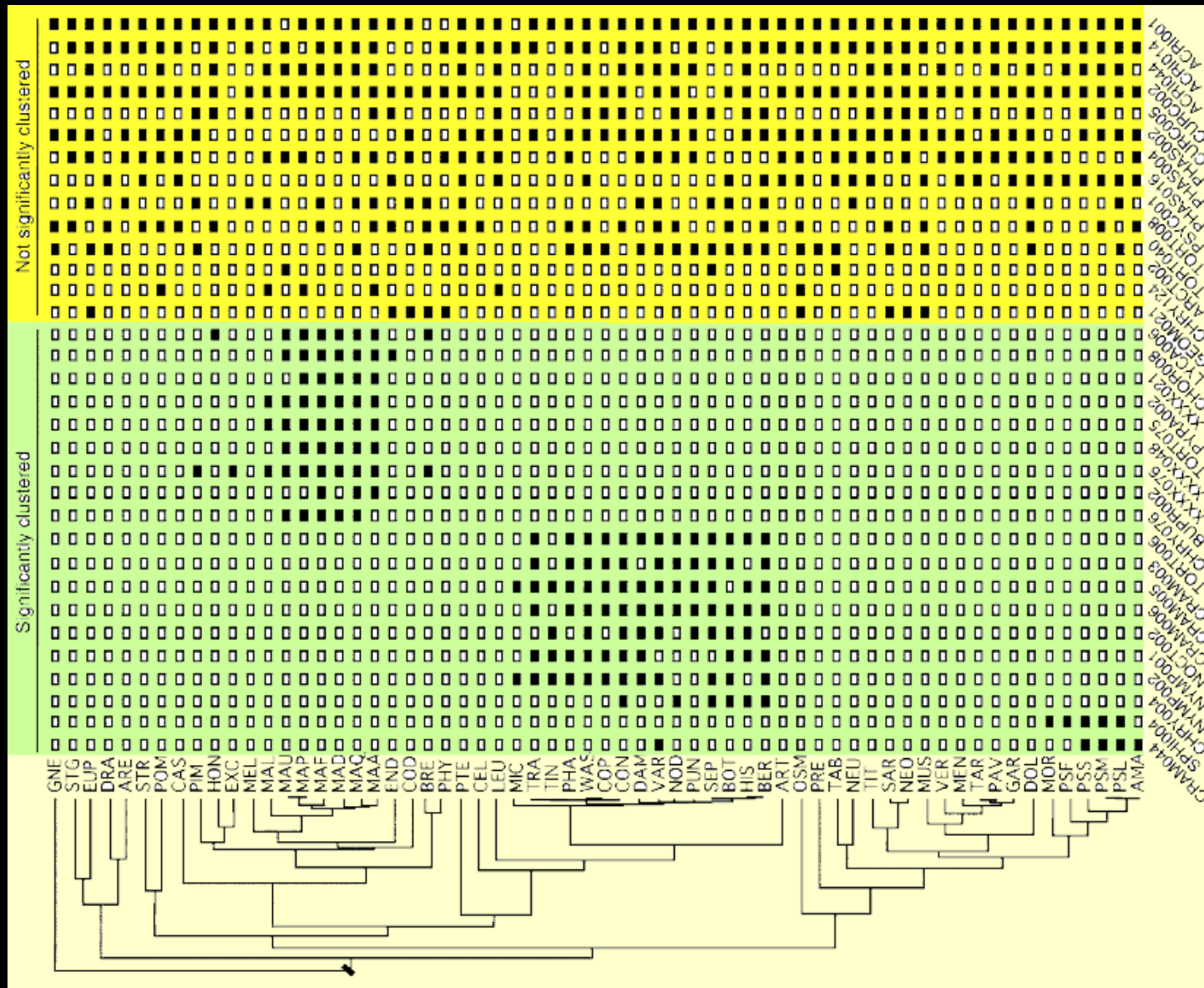
$X(n)$ and $\text{SD}(n)$ are the mean and standard deviation of phylogenetic distance for n host plants randomly distributed on the phylogeny, obtained by multiple iteration



Herbivore species as plant ecological traits

random

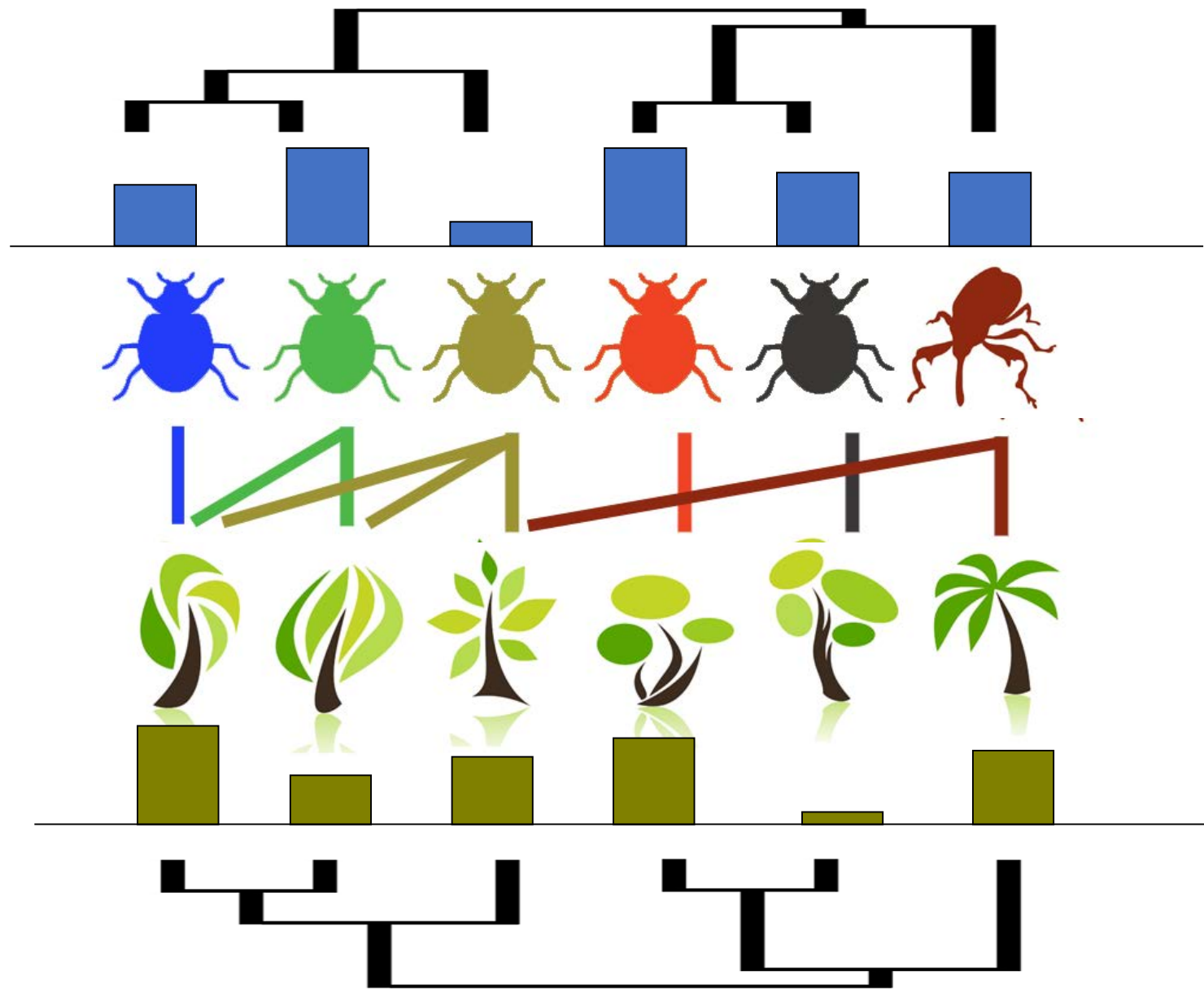
clustered



plant species

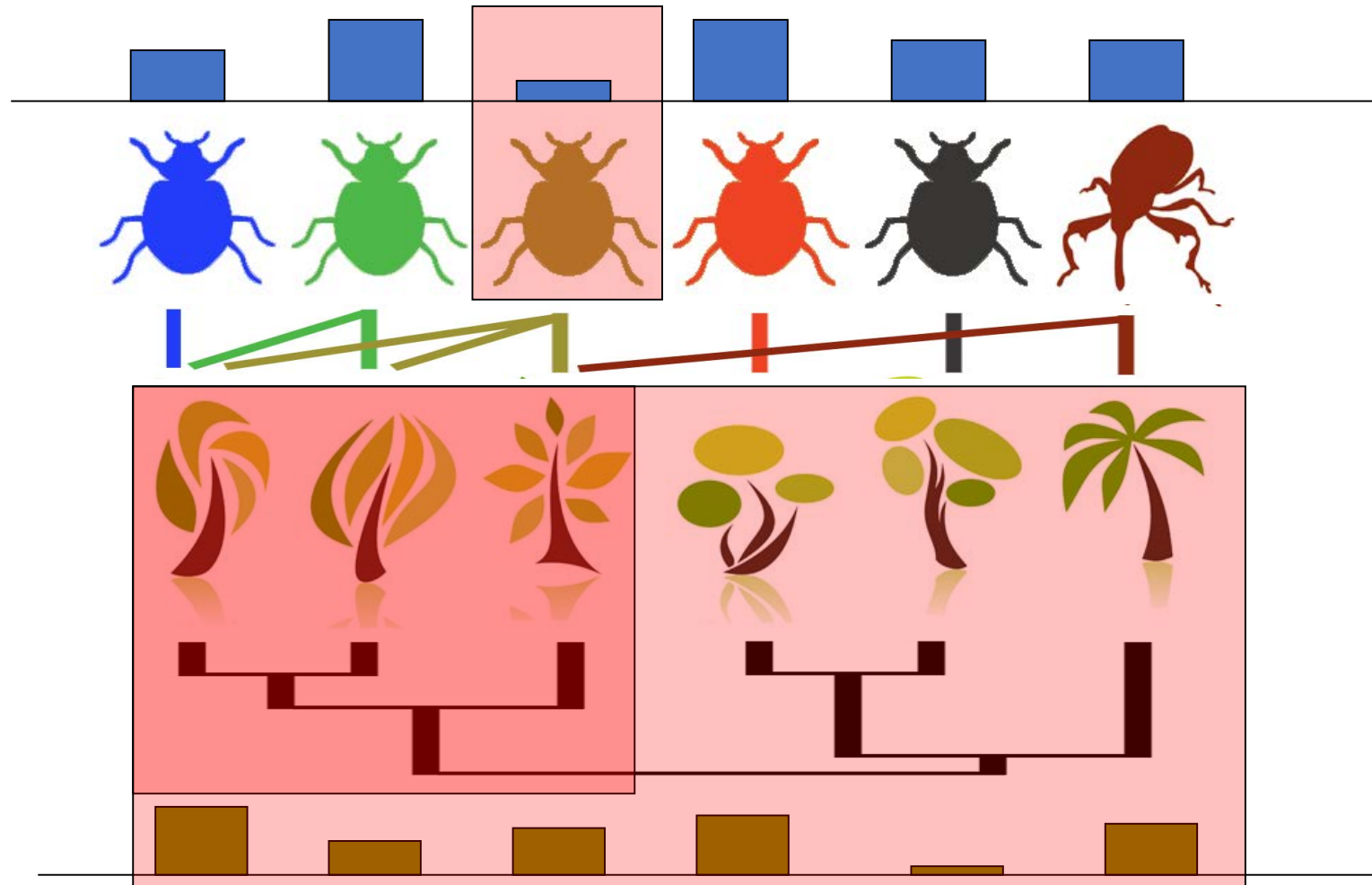


herbivore species

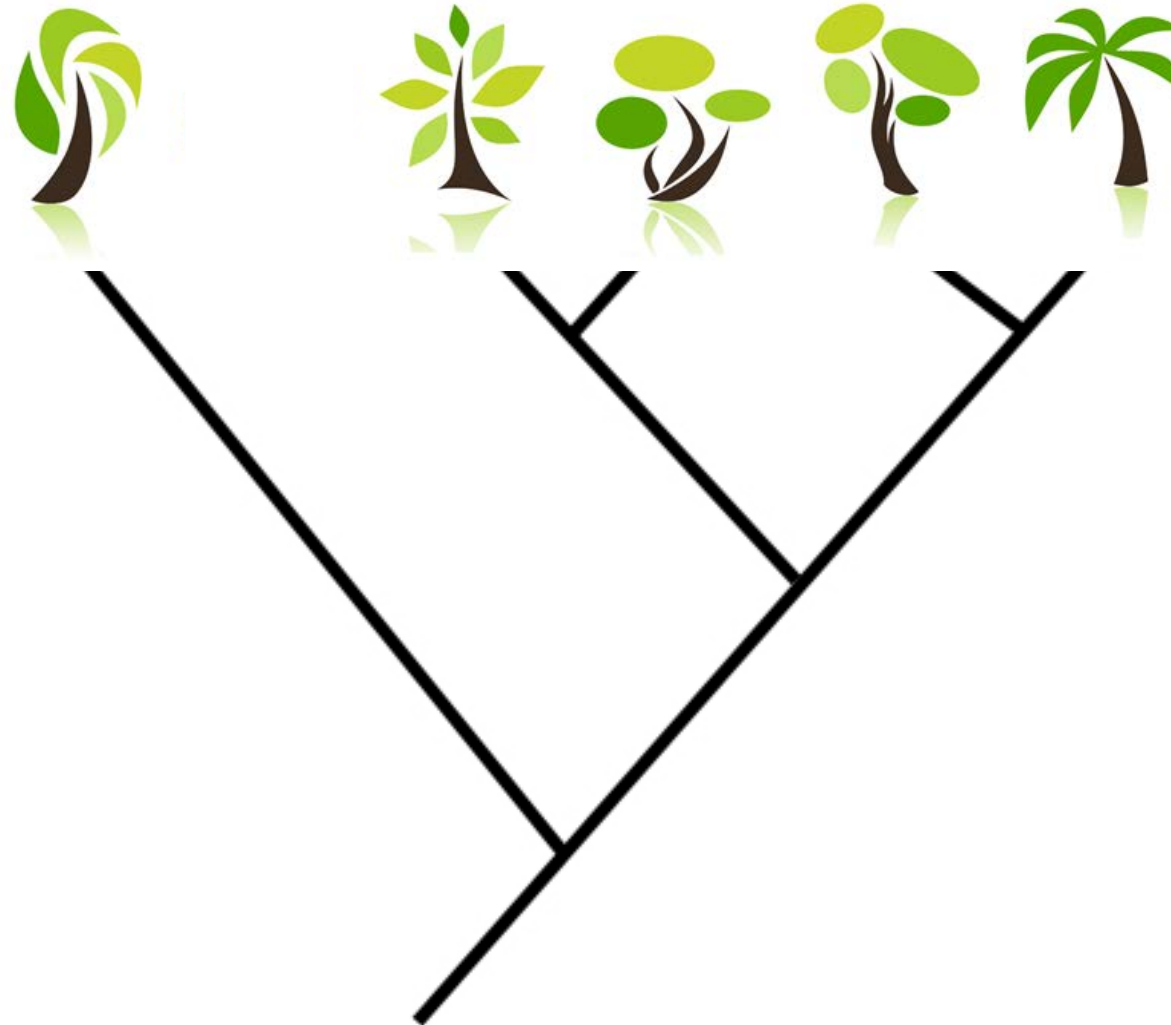


Food webs and phylogeny

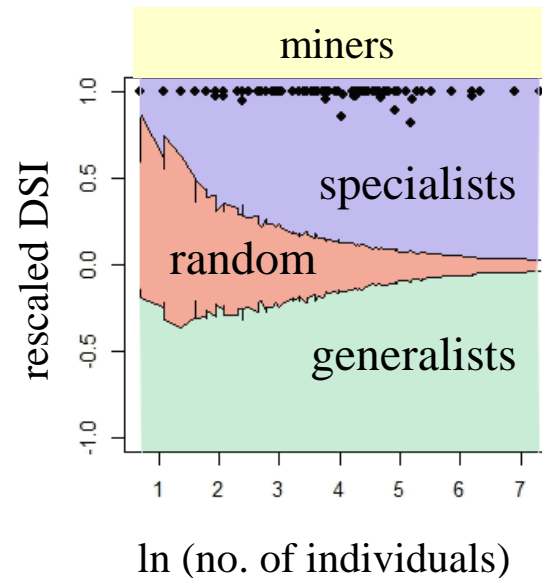
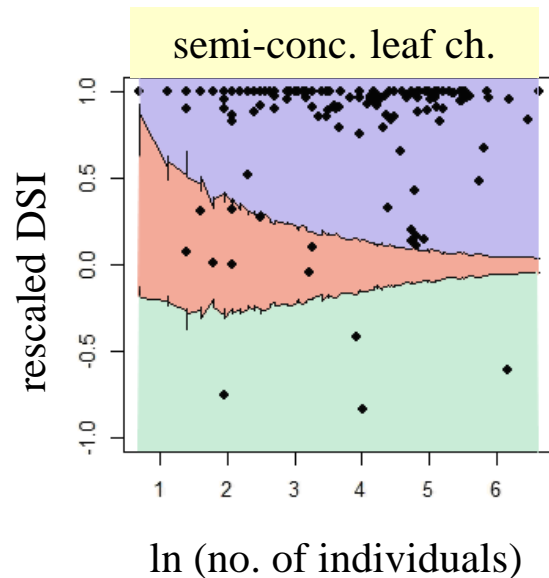
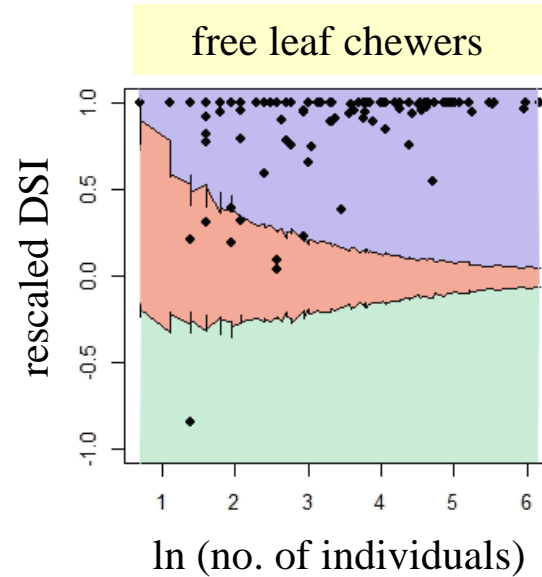
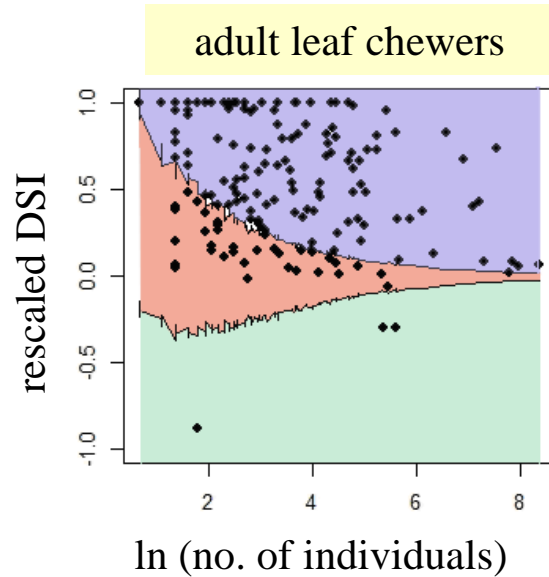
Mean phylogenetic distance (MPD) based on the distribution of individual insects on the host plants is compared with MPD generated by random distribution of these insects among all available plant species, reflecting plants' relative abundance (Z-score) and rescaled from minimum to maximum possible mean phylogenetic distance (MPD) for a given sample size. This **distance-based specialization index (DSI)** is a quantitative analogy to the net relatedness index (NRI, Webb et al. 2002).



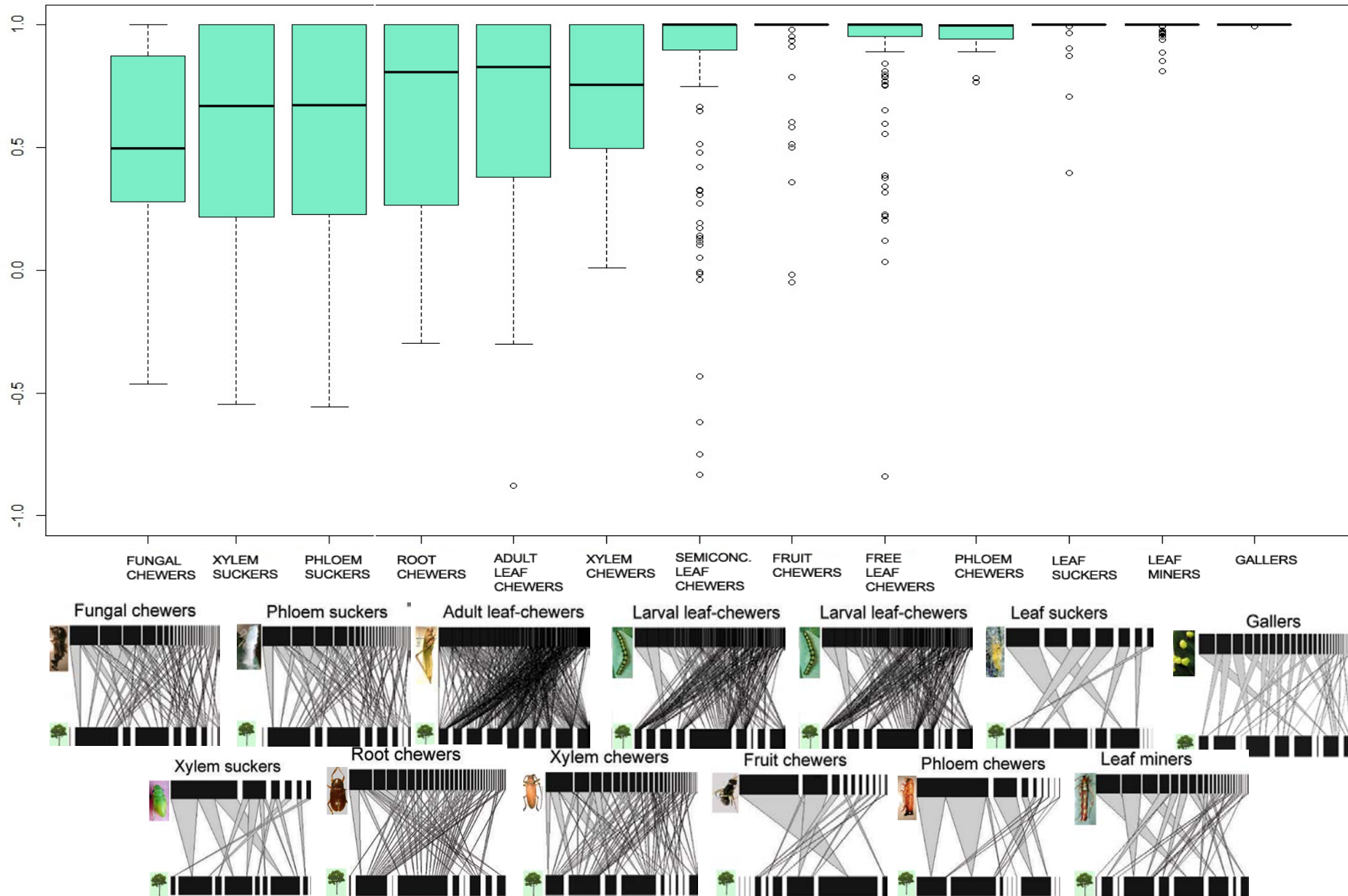
How to distribute insects to maximize their mean phylogenetic distance?



DSI rescaled from minimum to maximum possible mean phylogenetic distance (MPD) for a given sample size



Rescaled DSI can be used to characterize host specificity in different herbivorous guilds



Food web parameters: purely functional approach

Generality, vulnerability, conectance, diversity, modularity, and other assorted ahistoric indices describing web structure and functions



Japan

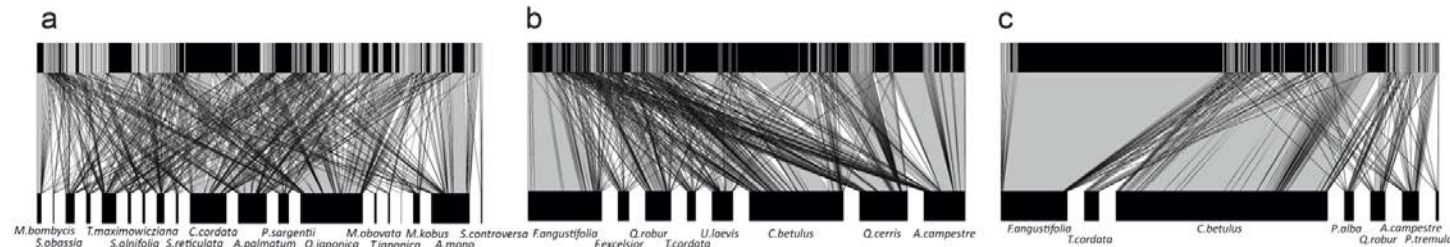


C. Europe 1

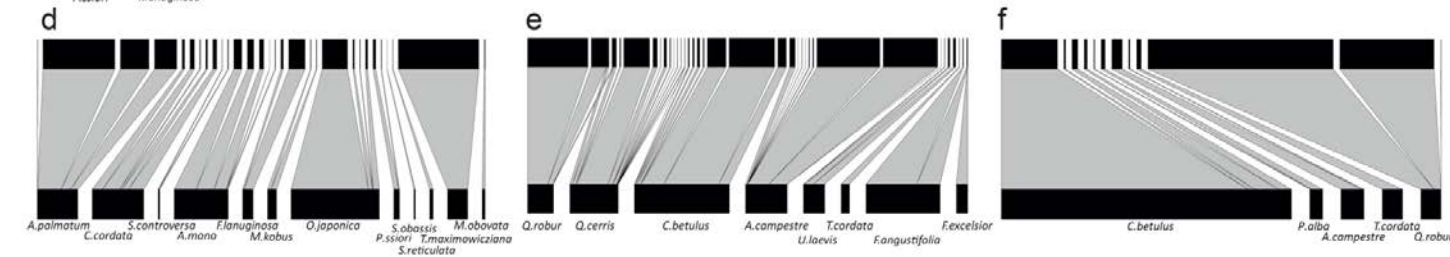
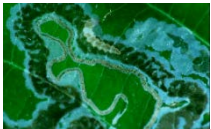


C. Europe 2

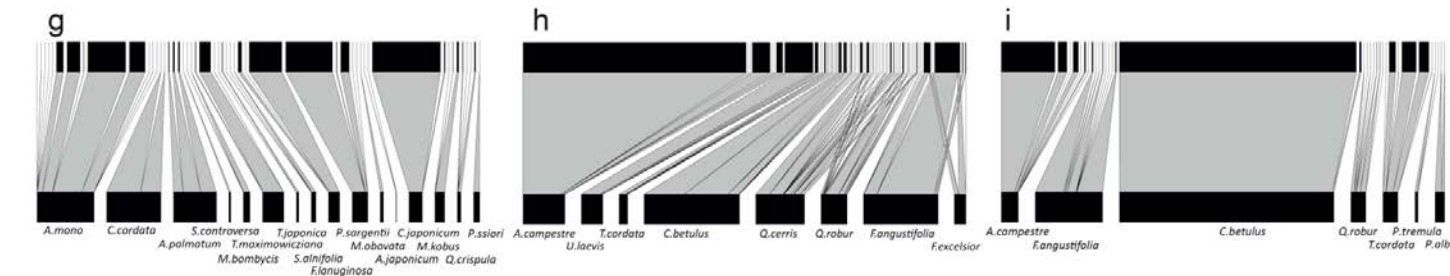
Chewers



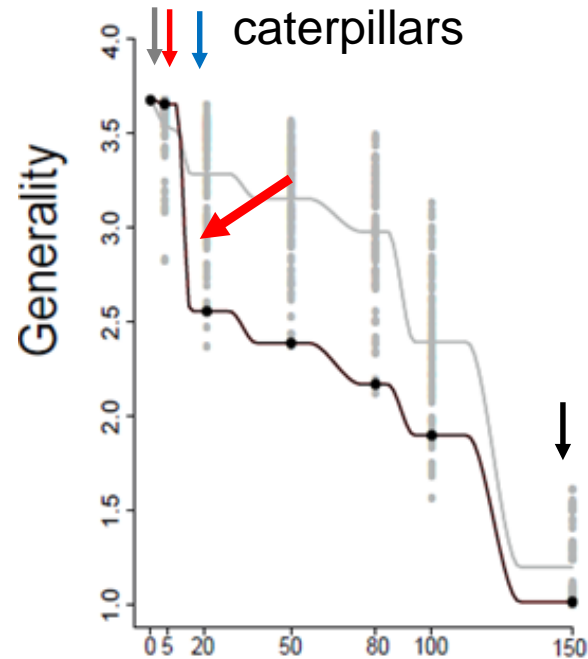
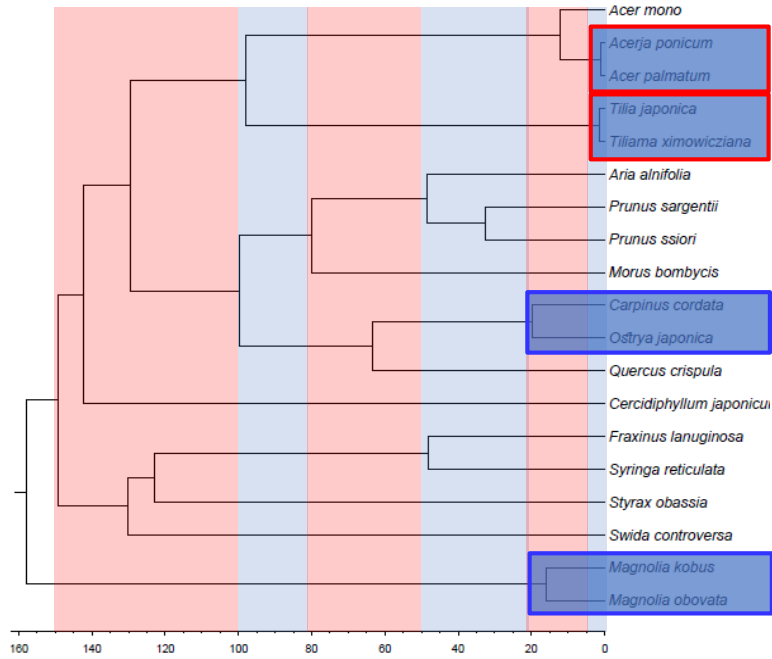
Miners



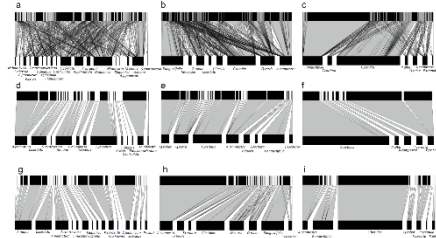
Gallers



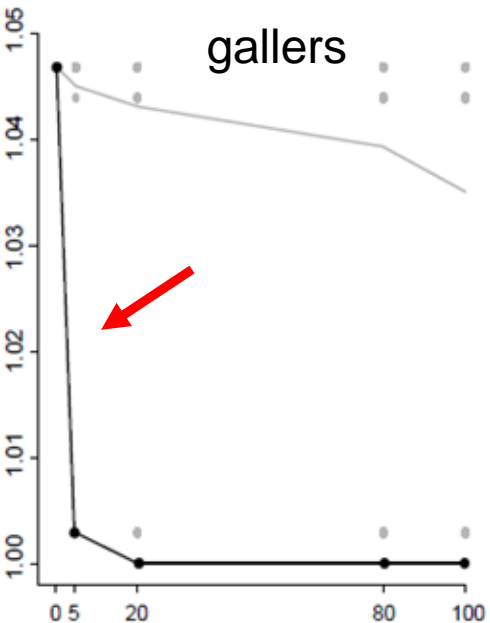
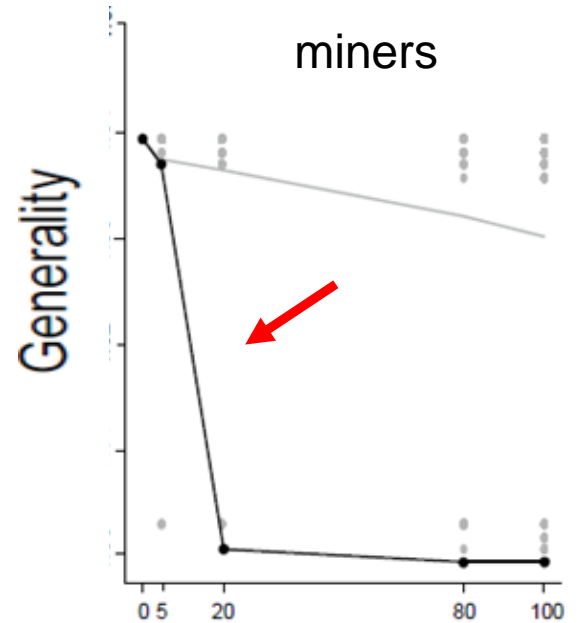
Exploring the effect of plant diversification on host specificity



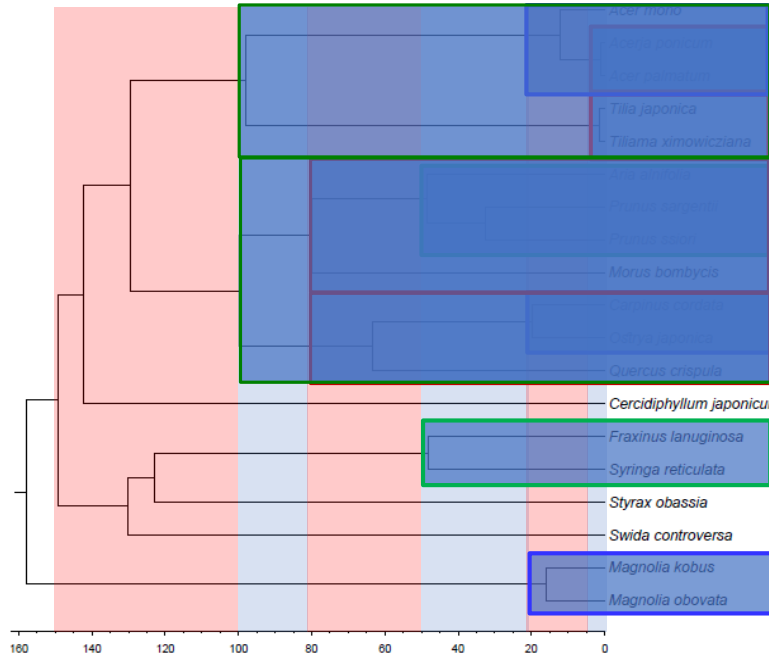
Martin Volf et al.
J. Anim Ecol. 86, 556



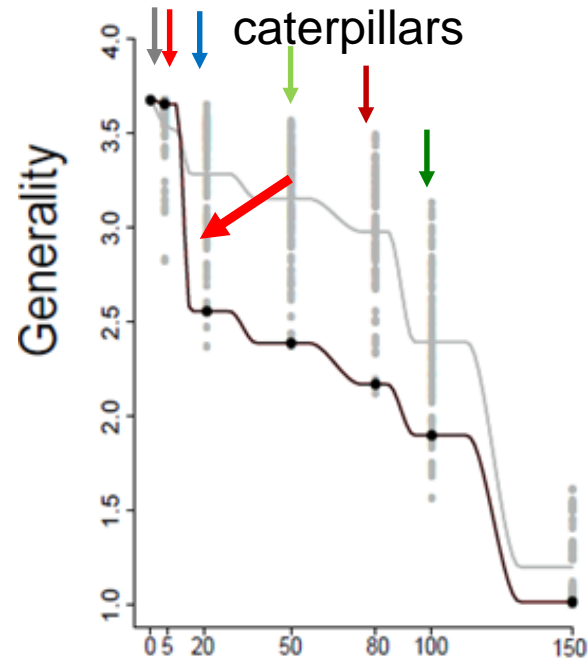
Steep decrease in plant-caterpillar food web generality (= how many herbivores eat a given plant sp.) when the plant diversity generated during the past 20 - 50 myr



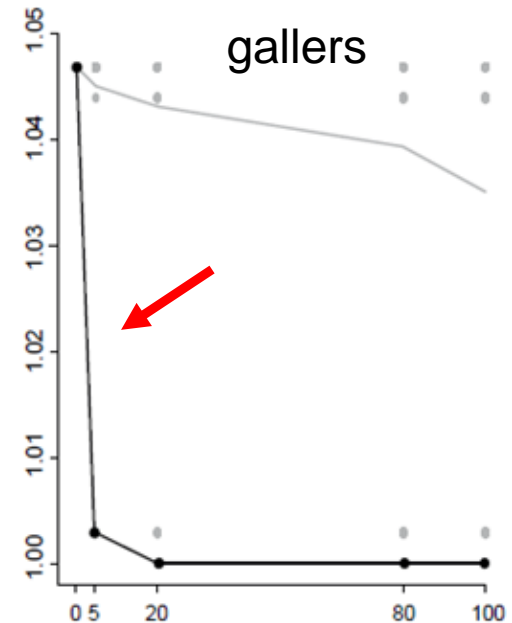
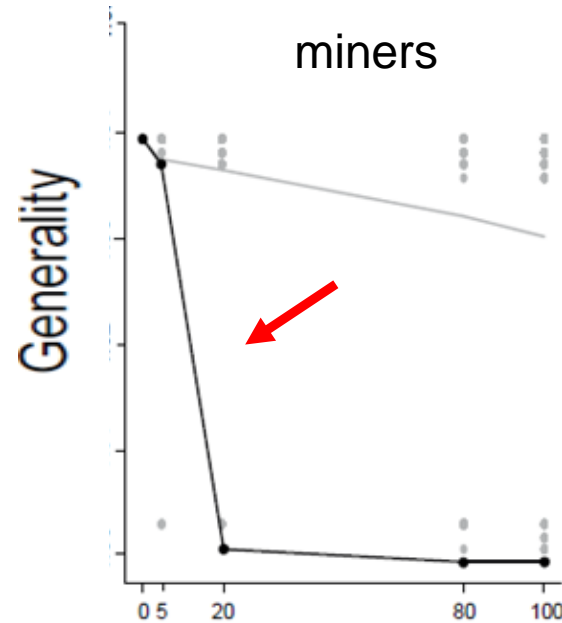
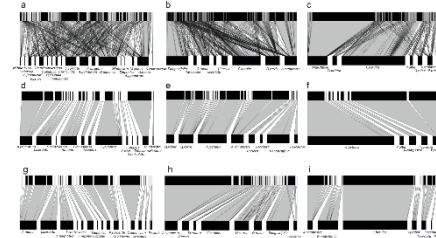
Exploring the effect of plant diversification on host specificity



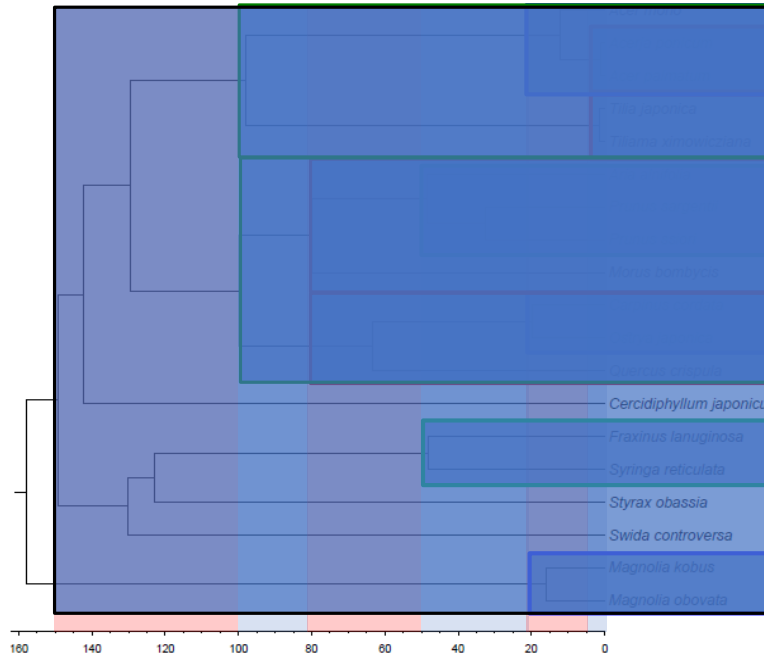
Steep decrease in plant-caterpillar food web generality (= how many herbivores eat a given plant sp.) when the plant diversity generated during the past 20 - 50 myr



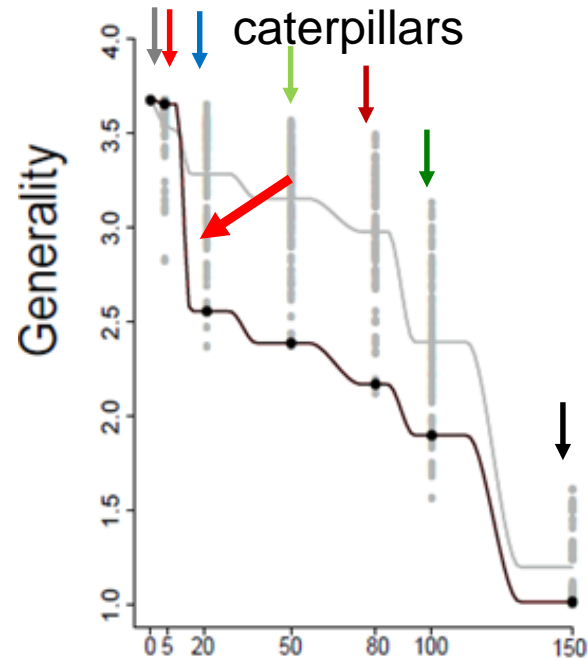
Martin Volf et al.
J. Anim Ecol. 86, 556



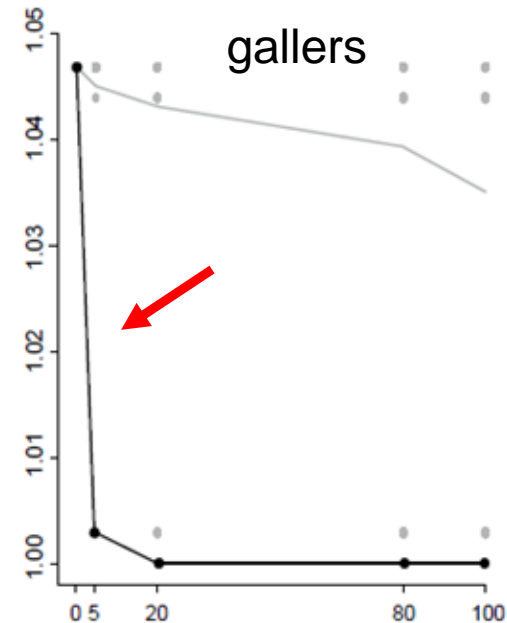
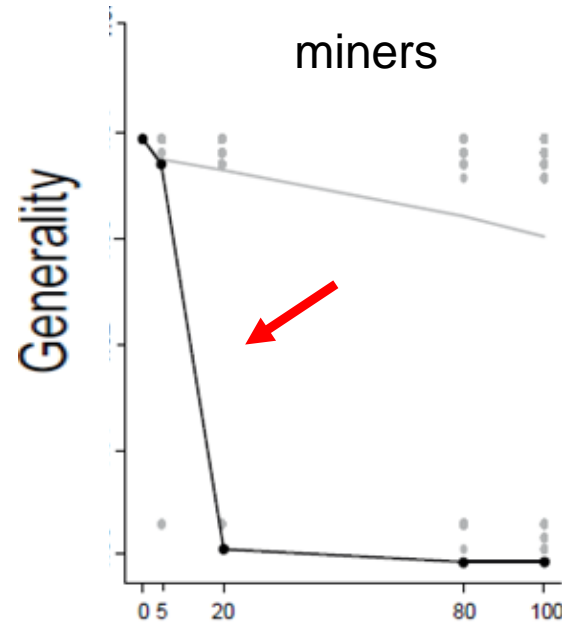
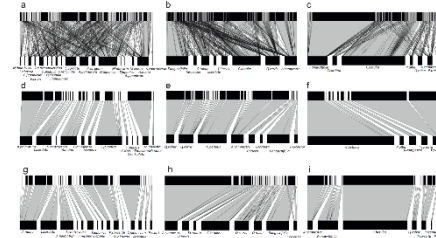
Exploring the effect of plant diversification on host specificity



Steep decrease in plant-caterpillar food web generality (= how many herbivores eat a given plant sp.) when the plant diversity generated during the past 20 - 50 myr



Martin Volf et al.
J. Anim Ecol. 86, 556



Predicting plant-caterpillar food webs in a lowland rainforest

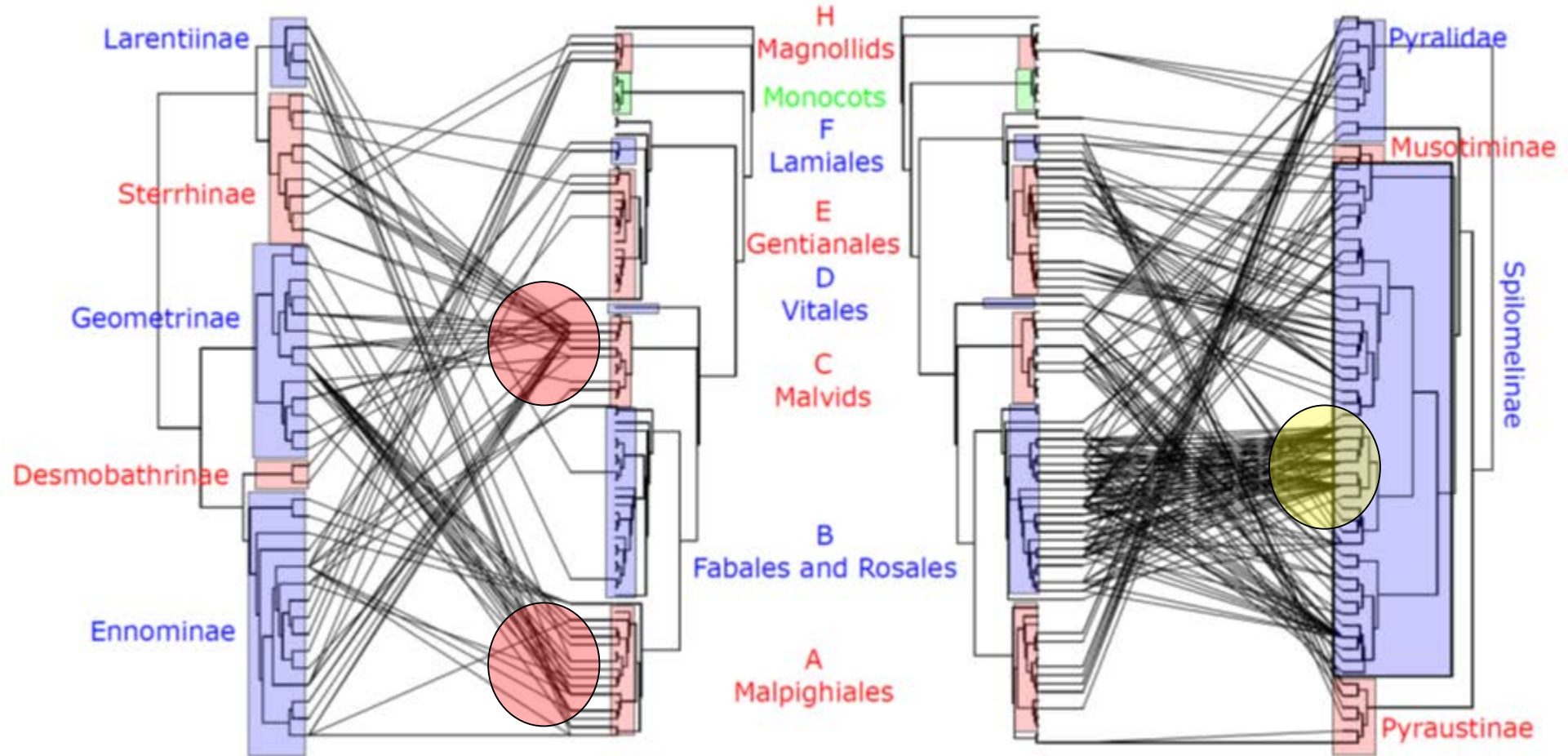


Geometrids



Pyraloids

Geometrids:
plants better predictor of interactions than moths
Pyraloids:
moths better predictors than plants



Plants $d=0.51$

Insects $d=0.35$

Plants $d=0.12$

Insects $d=0.63$

Ives & Godfray 2006 (Am. Nat 168: E1) Parameter d as a measure of phylogenetic signal in food webs

$d=1$ Brownian motion phylogeny, $0 < d < 1$ stabilizing selection, $d < 0$ absence of phylogenetic correlation ("star" phylogeny)

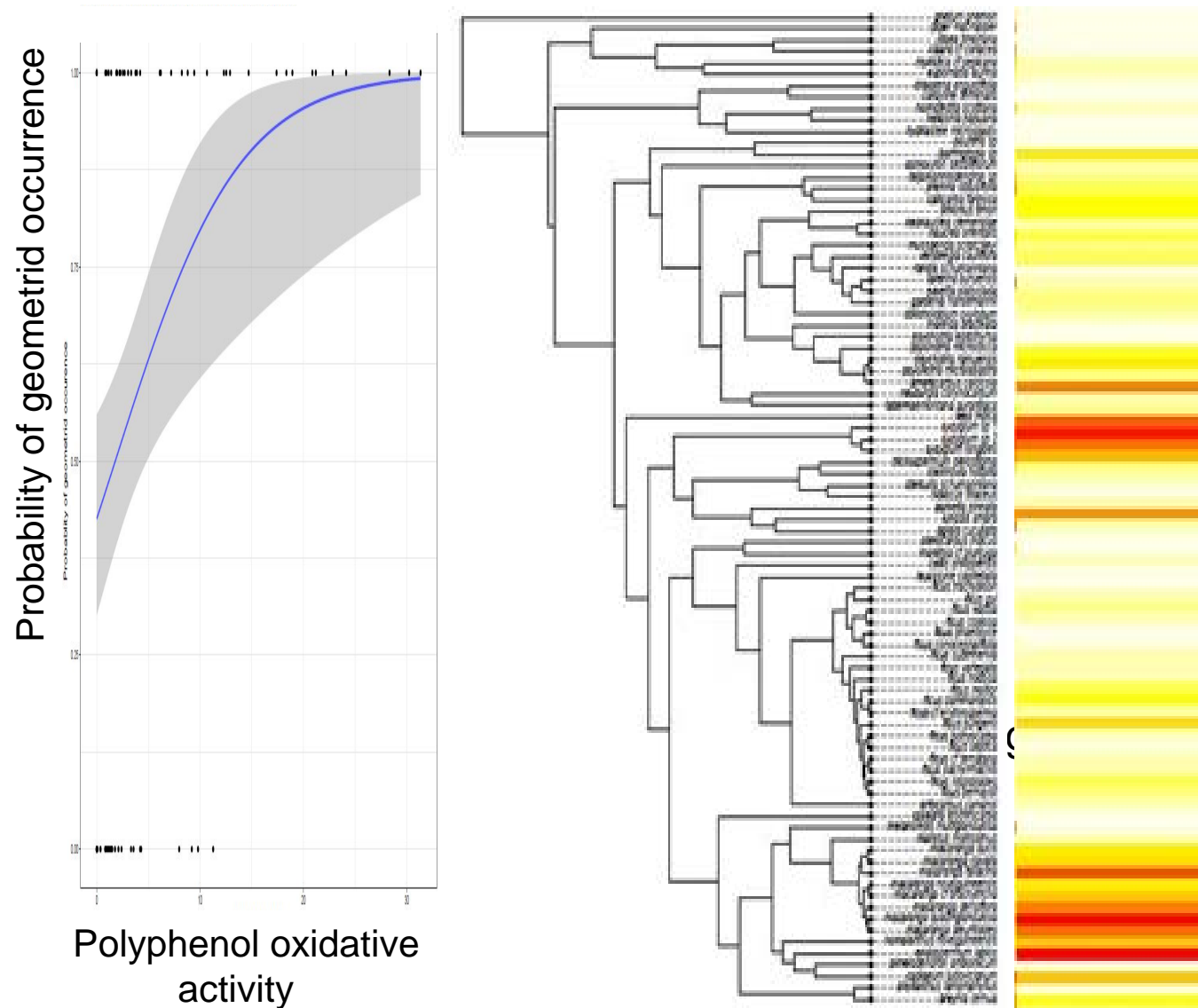
Simon Segar et al.
Proc RS 2017



Next step: prediction from plant secondary metabolites

Geometrids and oxidative activity of polyphenols

Geometrid abundance
Oxidative activity OBSERVED MODELLED



Phylogenetic structure in communities



primary forest



secondary forest 2.5 yrs

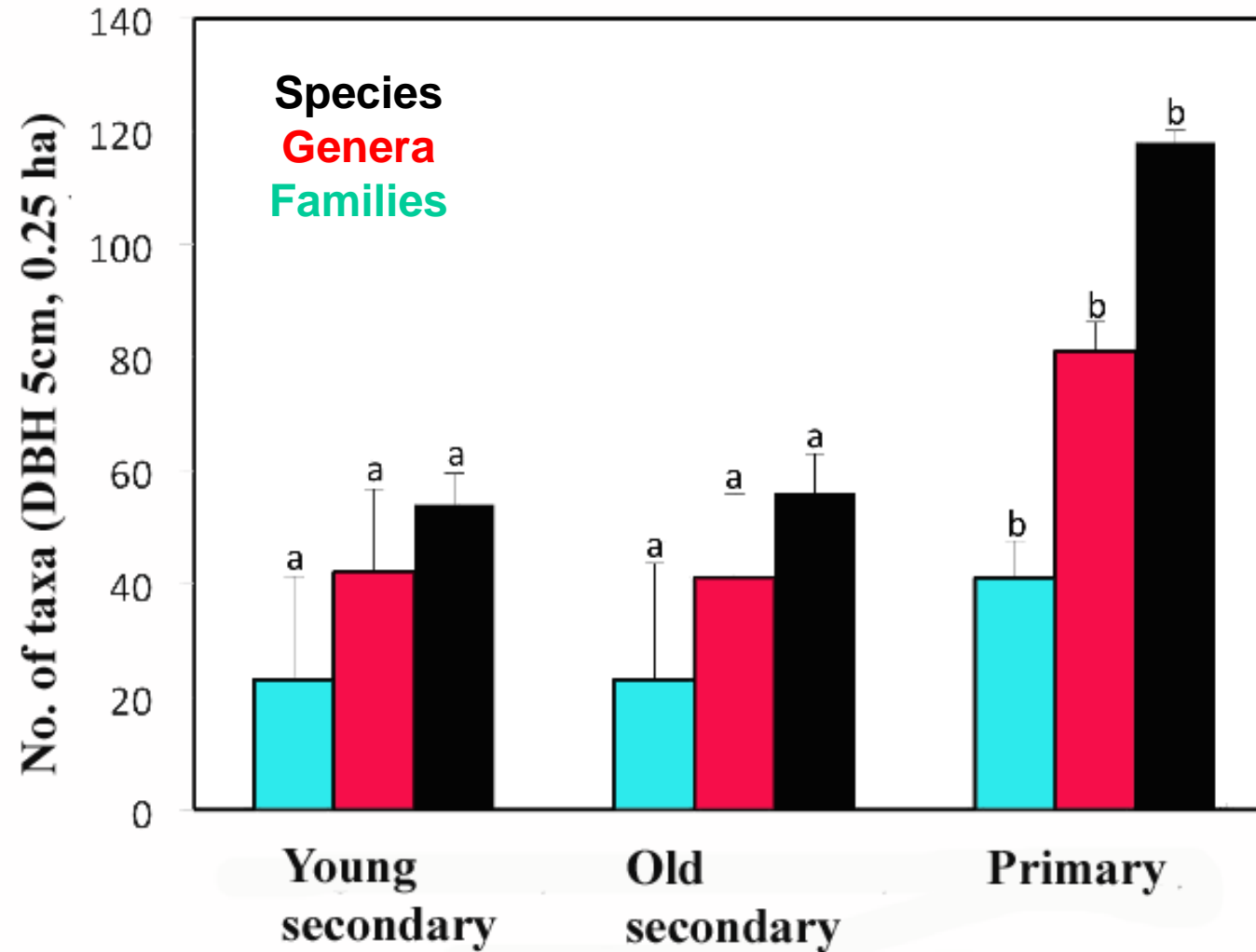


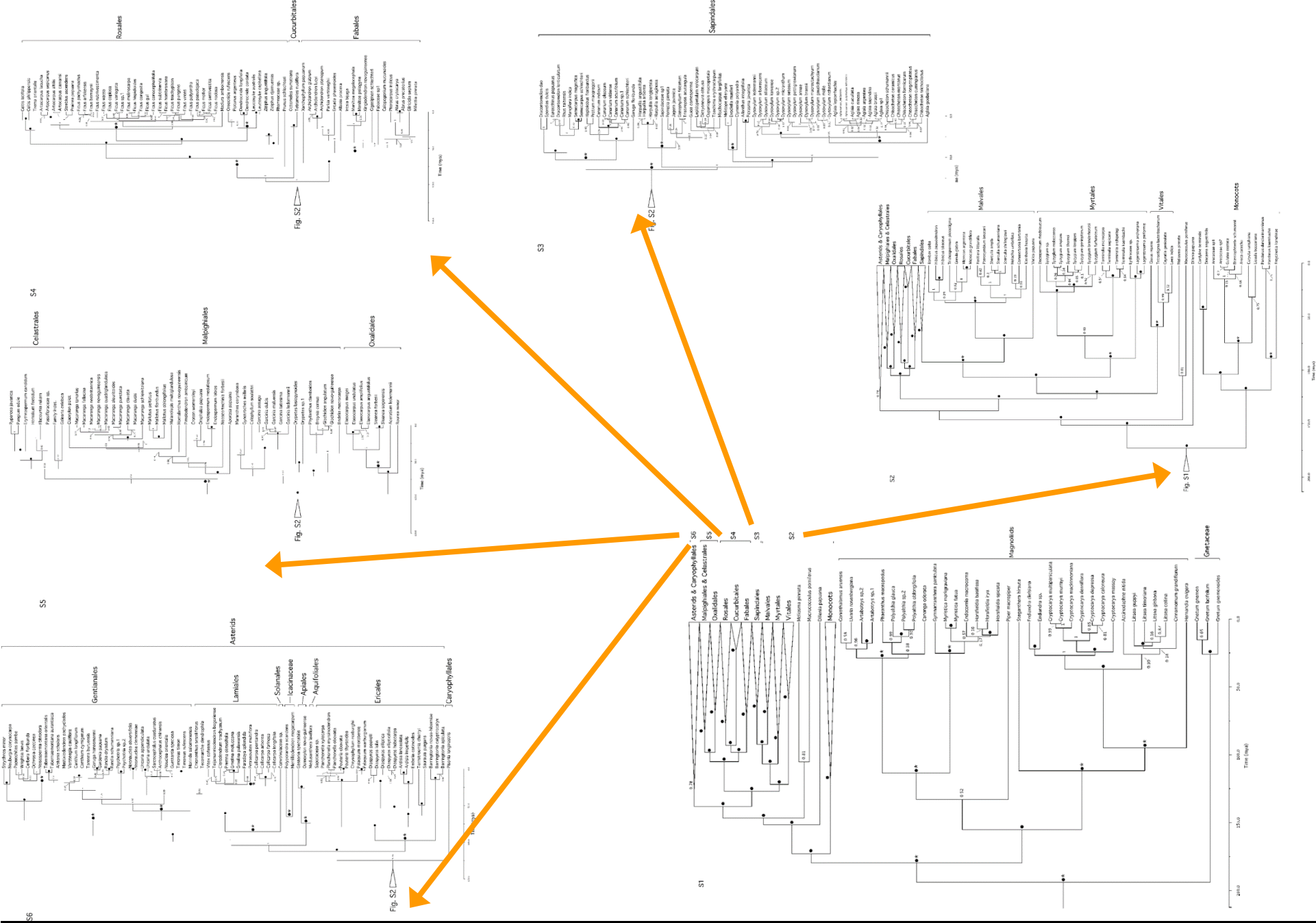
5.5 yrs



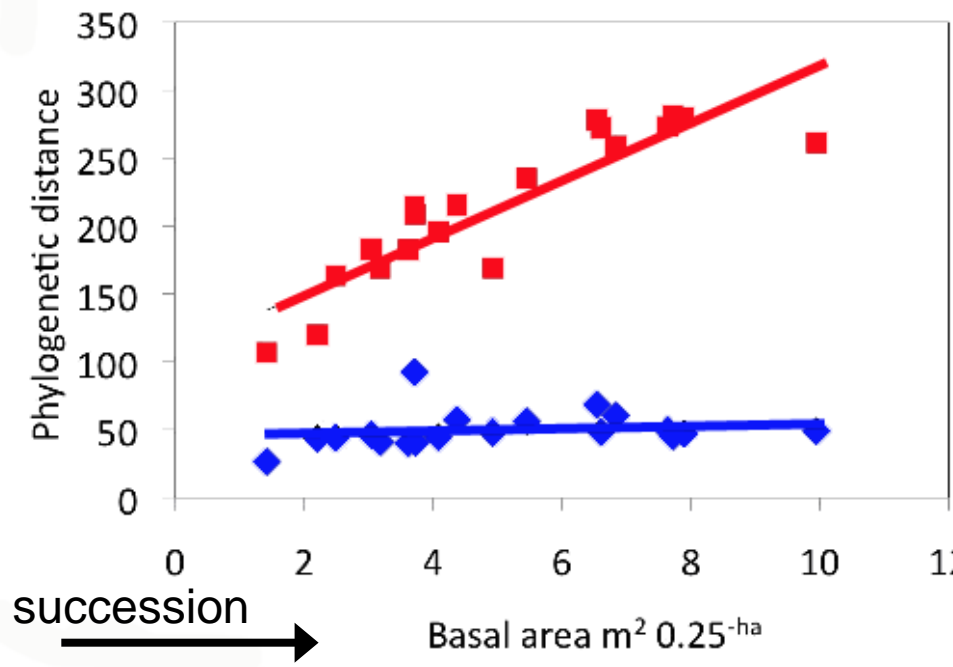
19 plots 0.25 ha each
plants with DBH>5cm

Plant phylogenetic diversity during rainforest succession





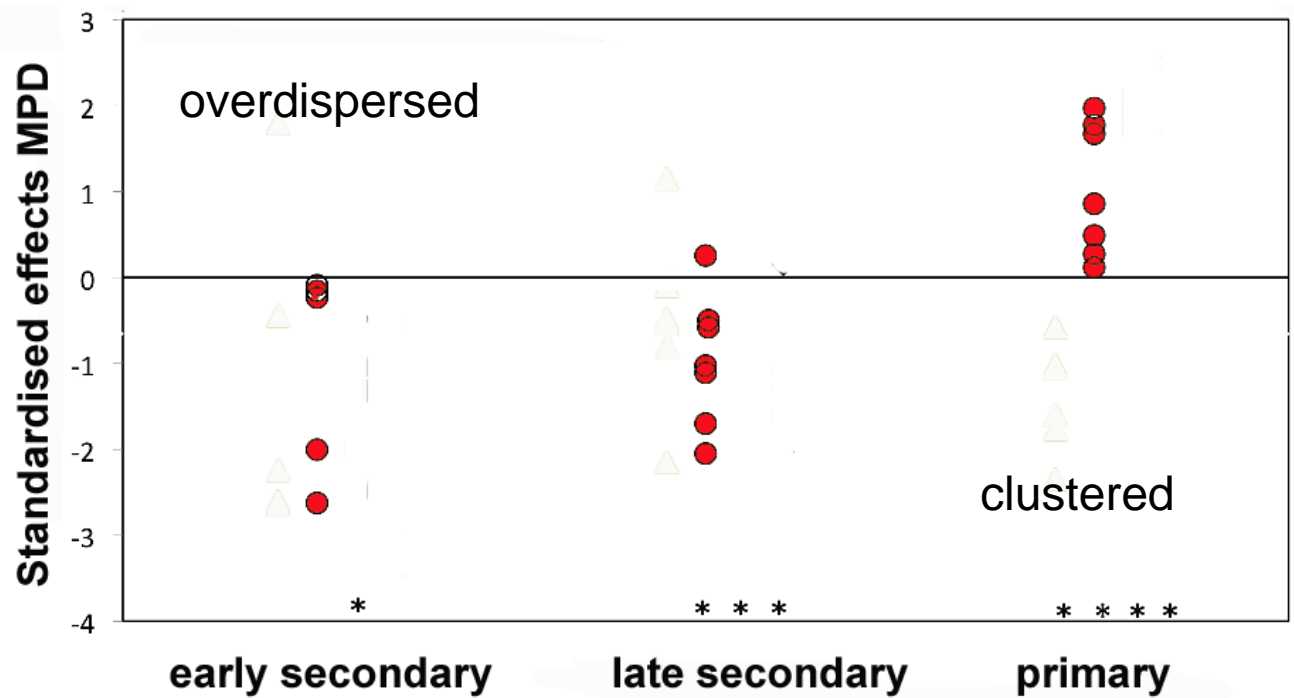
Phylogeny of 349 local plant species ≥ 5 cm dbh



Phylogenetic distance between coexisting plant species increases during succession

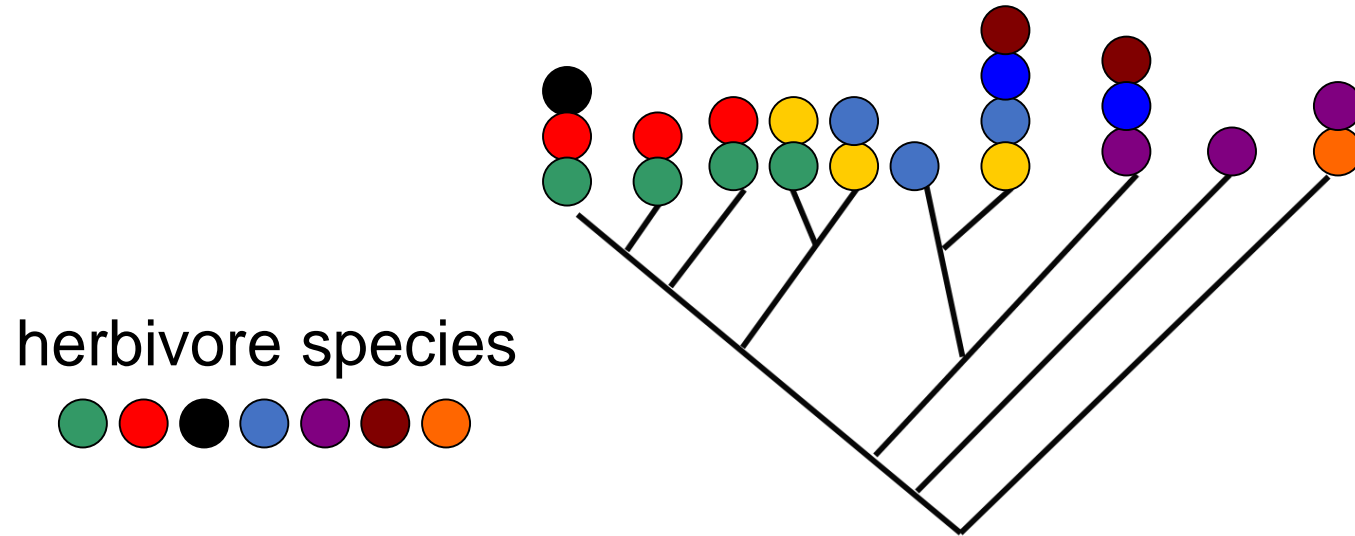
MPD = mean pair-wise distance

MNTD = mean nearest taxon distance



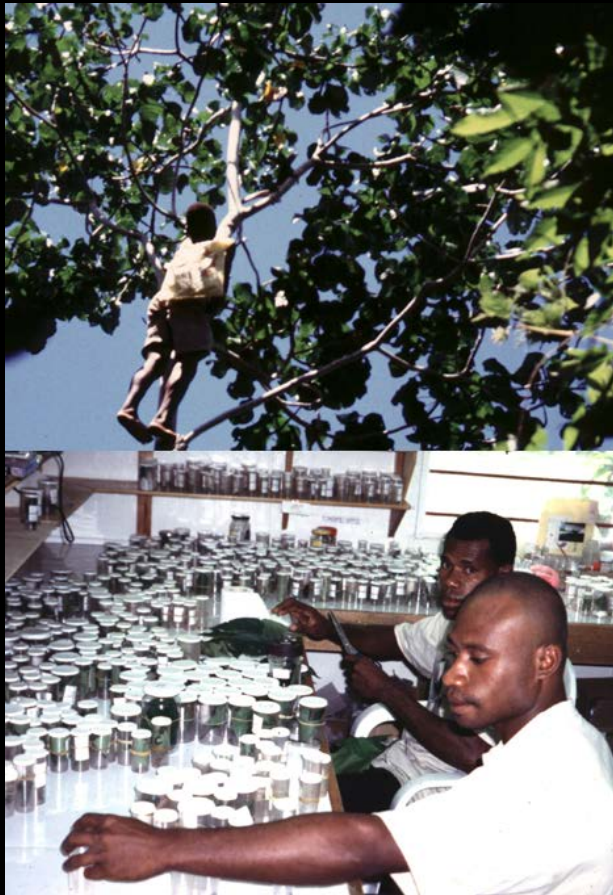
Secondary plant species are phylogenetically clustered, primary plant species overdispersed

Phylogenetic distance of species and their ecological similarity

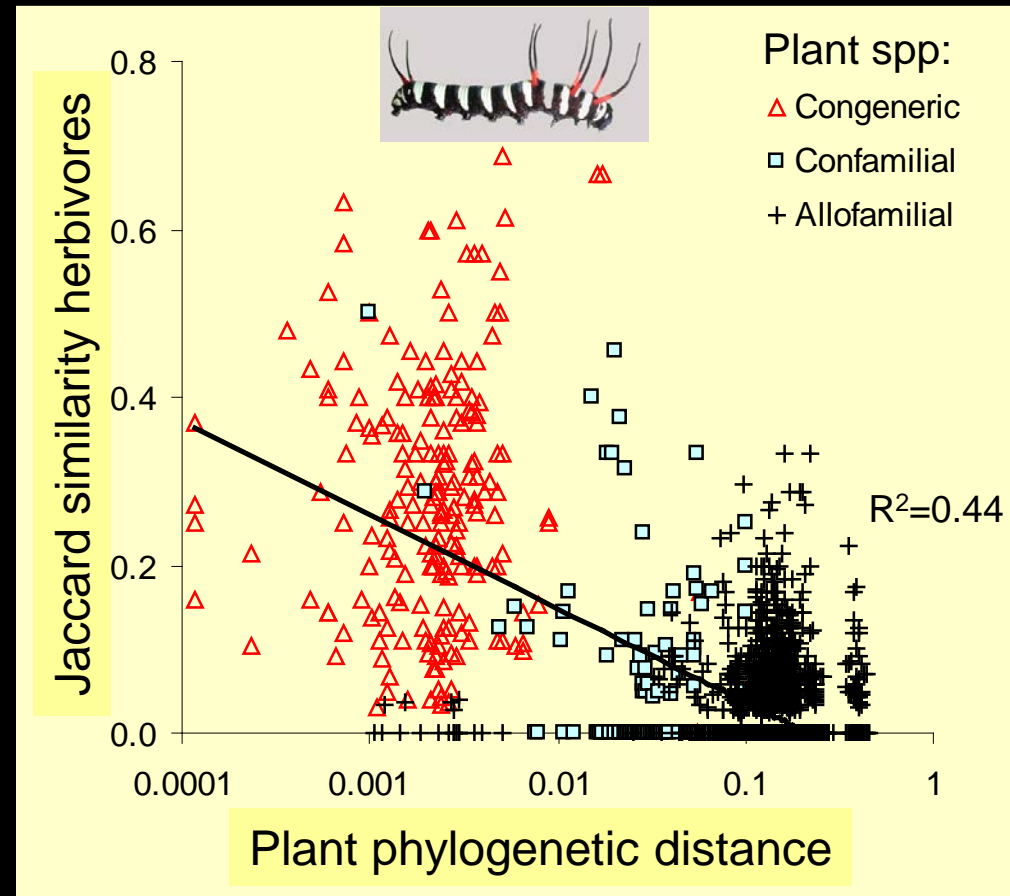


Example:
plants species and their herbivorous communities

Phylogenetic distance of plants matters to herbivores [but not very much: 44% of variance explained]



Caterpillars on
65 rainforest tree species

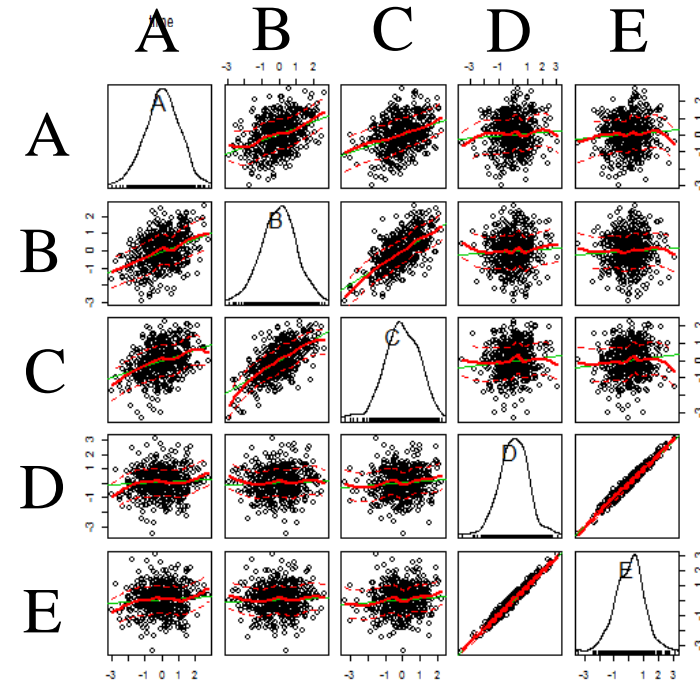
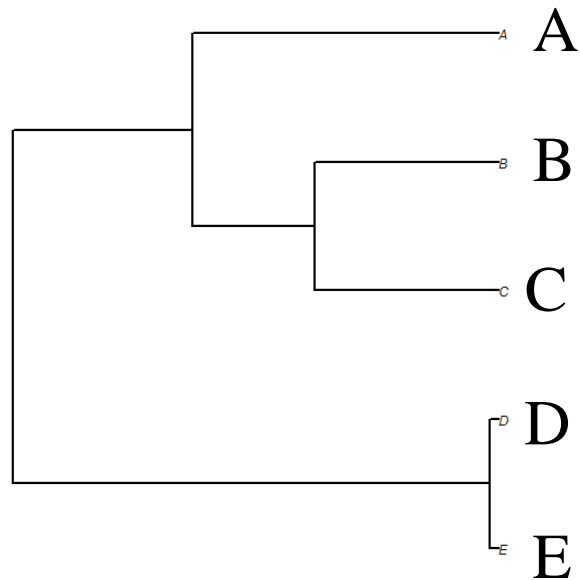
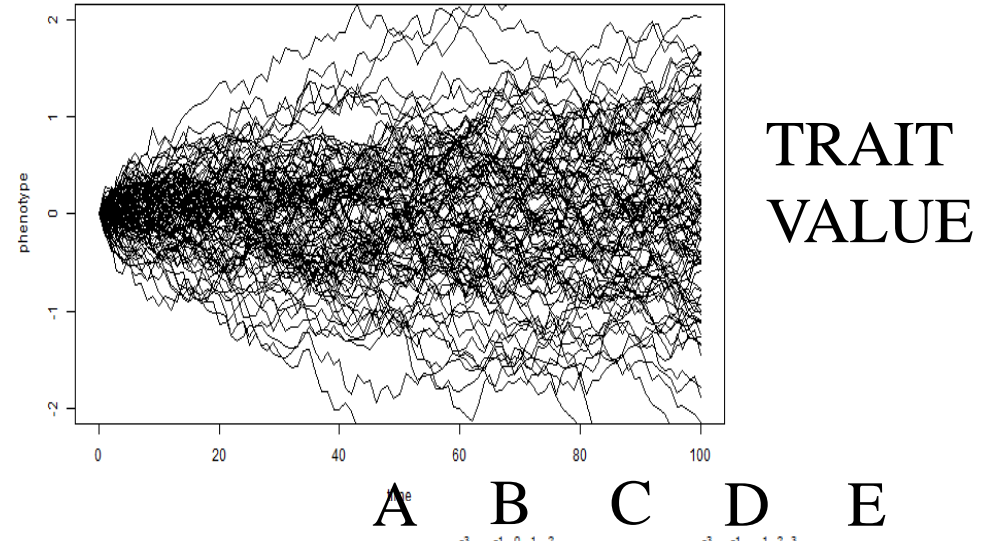
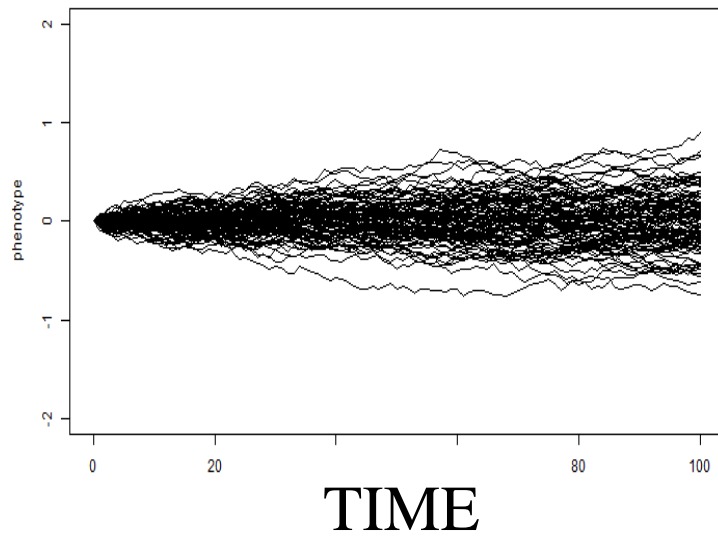


congeneric, **confamilial**, **allofamilial**
tree species pairs

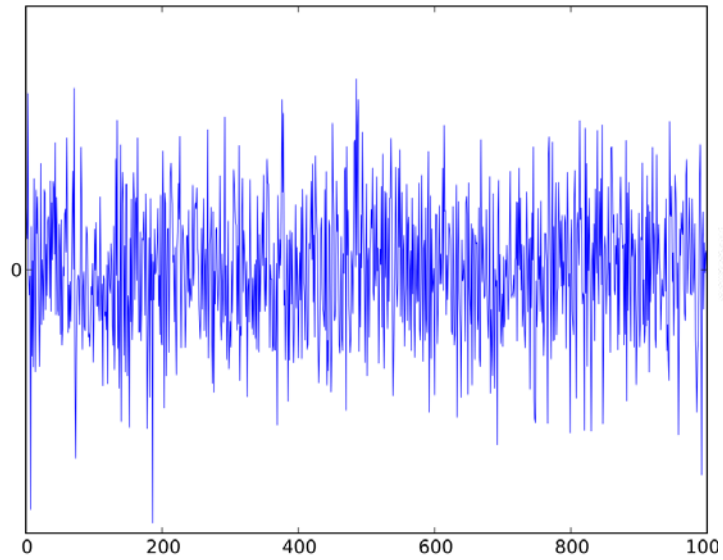
Evolutionary scenarios for ecological traits

Brownian motion model

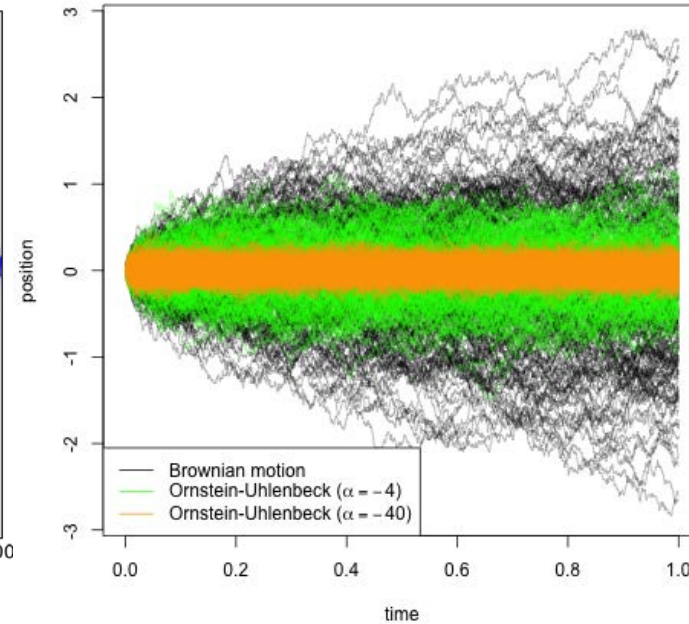
Random walk along each lineage, the change in each unit of time is drawn from a normal distribution with mean = 0 and variance σ^2 . The variance term describes the rate at which the trait values of related species will diverge from each other.



White noise



Ornstein-Uhlenbeck: stabilizing selection



Brownian

O-U

O-U

Bloomberg's K measures the similarity among relatives compared with expectations of the Brownian model. $K=1$ matched Brownian model, $K<1$ means low phylogenetic signal (closely related species differ from each other than expected), $K>1$ means stronger phylogenetic signal (closely related species are more similar than expected). It is a ratio of the variance among species over the independent contrasts variance (which will be low if phylogenetic signal is high).

Pagel's λ is a scaling parameter for the correlations between species, relative to the correlation expected under Brownian evolution.

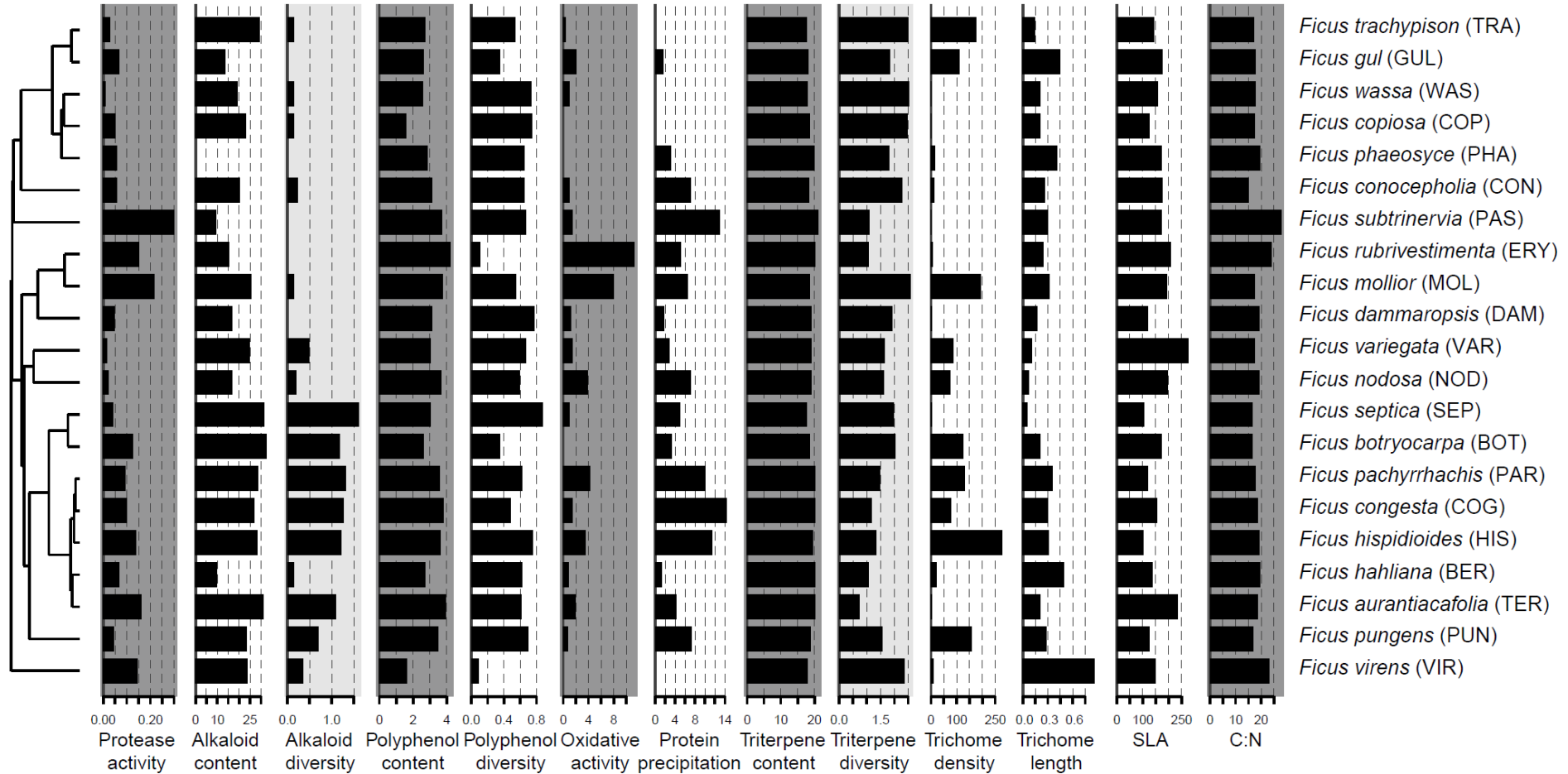


Phylogenetic distribution of plant defence traits on *Ficus* trees

Brownian motion

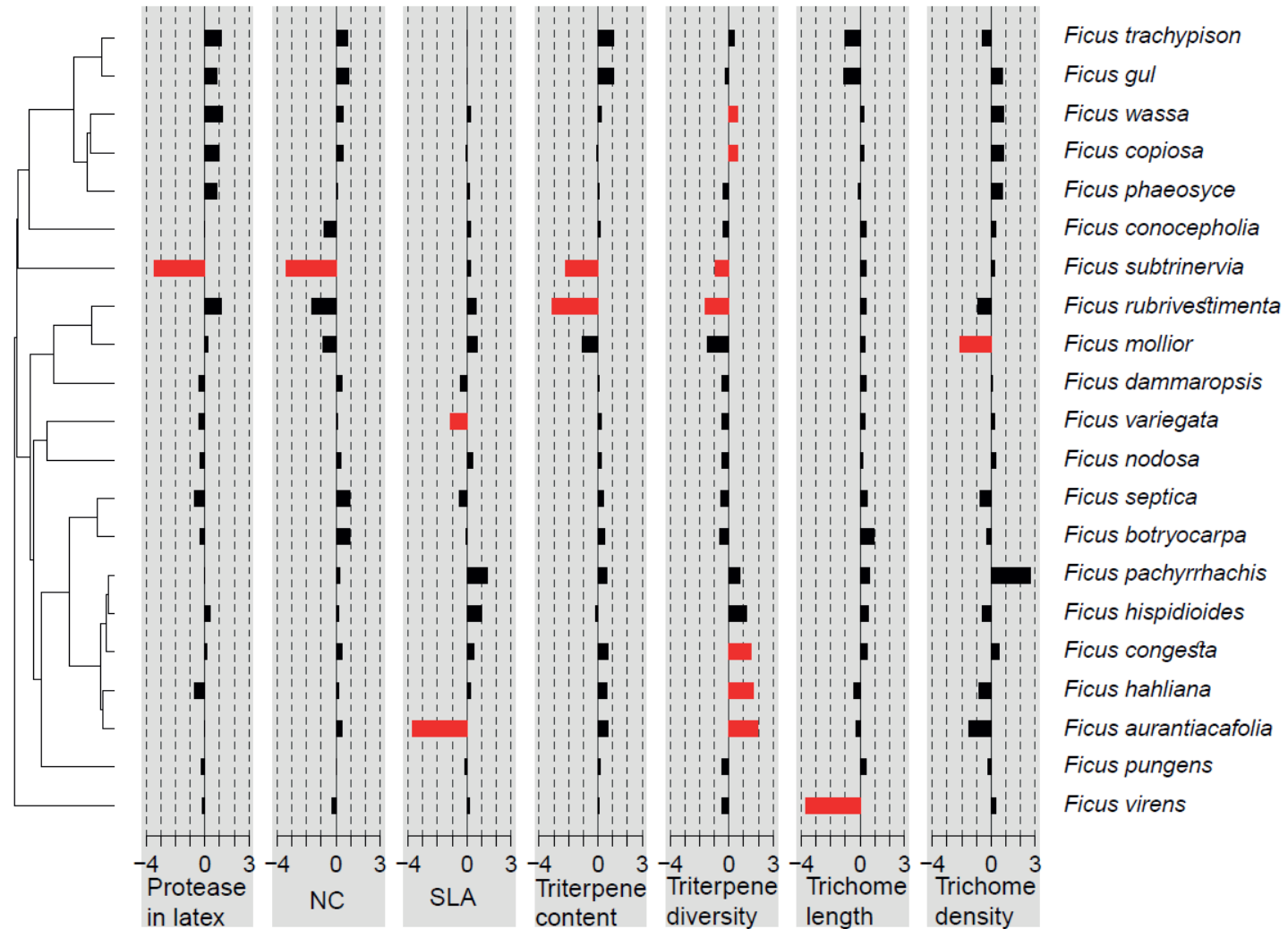
White noise

Phylogenetic signal



Plant traits: habitat filtering vs. divergence facilitating coexistence

Distribution of defensive traits along *Ficus* phylogeny

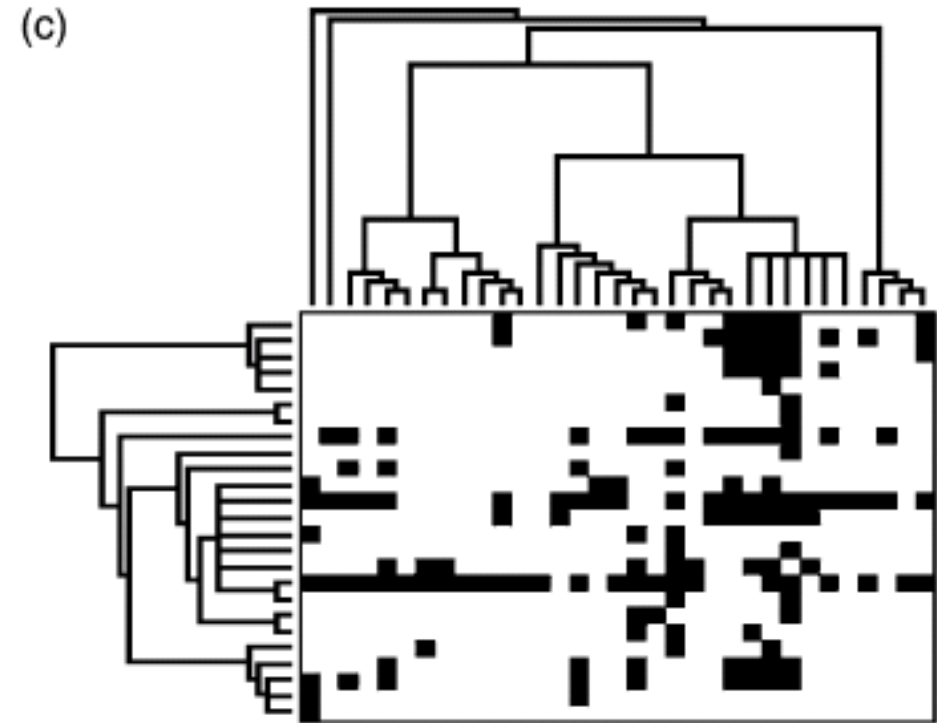
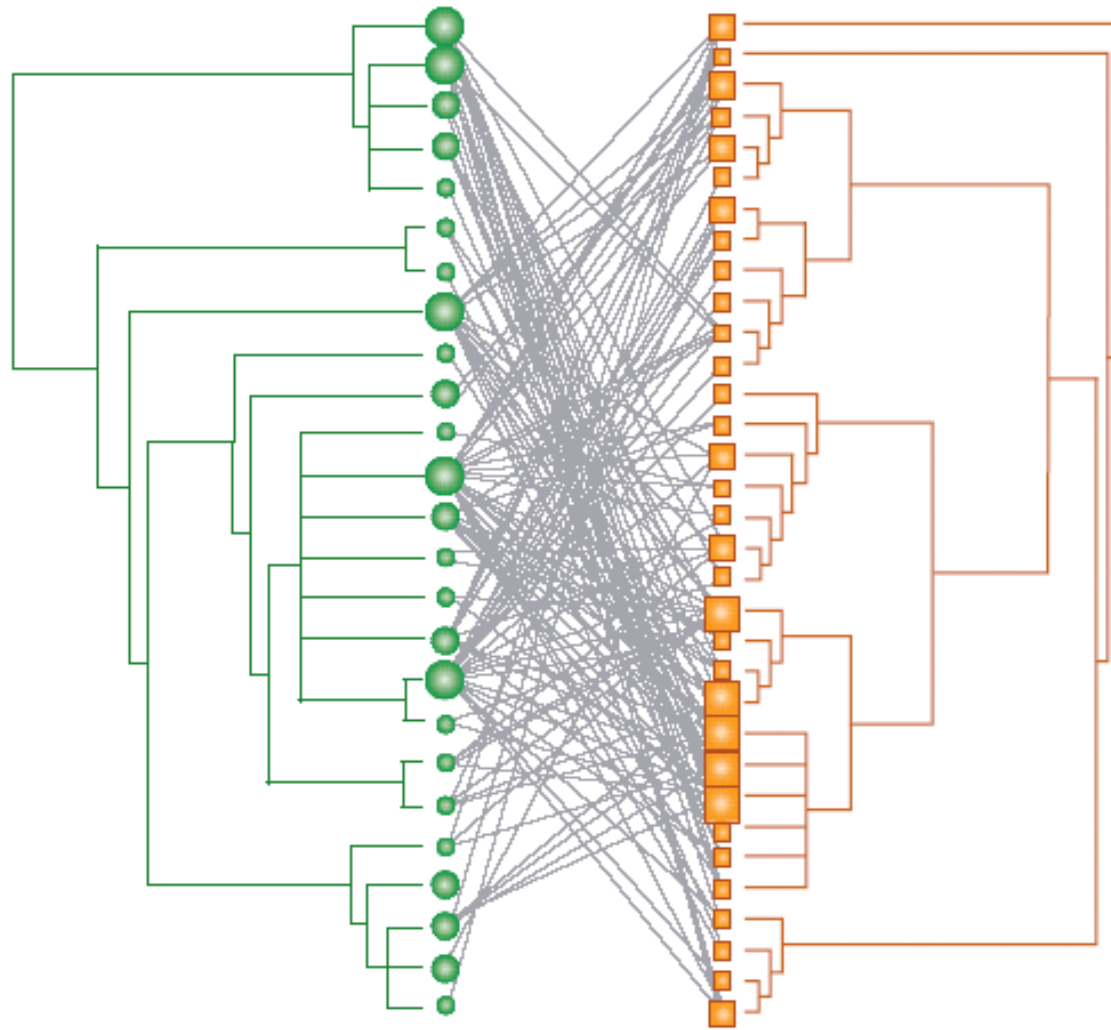


Volf, Segar et al.
2018 Ecology
Letters 21: 83



Closely related species are dissimilar in important defensive traits

Why we need to know phylogenetic relationships of interacting species?

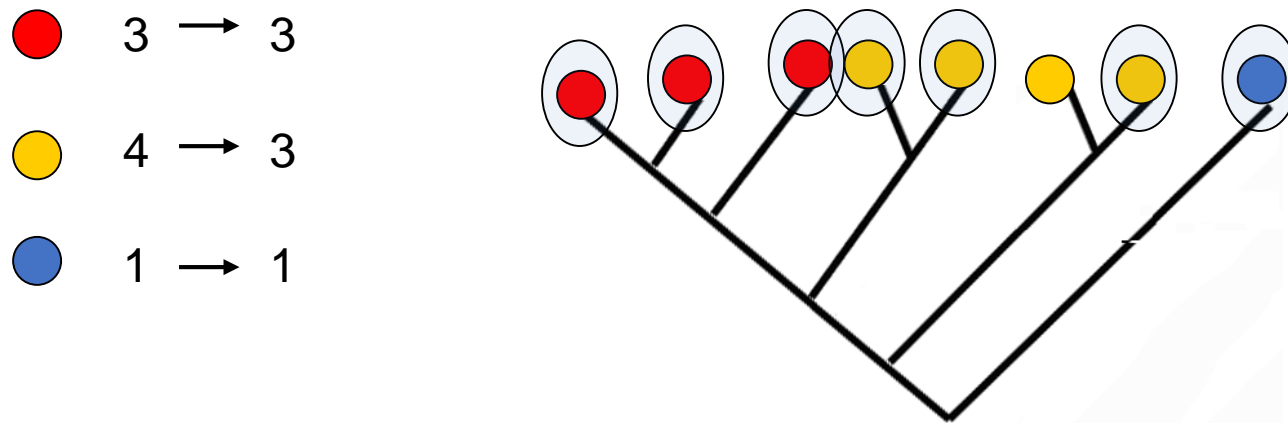
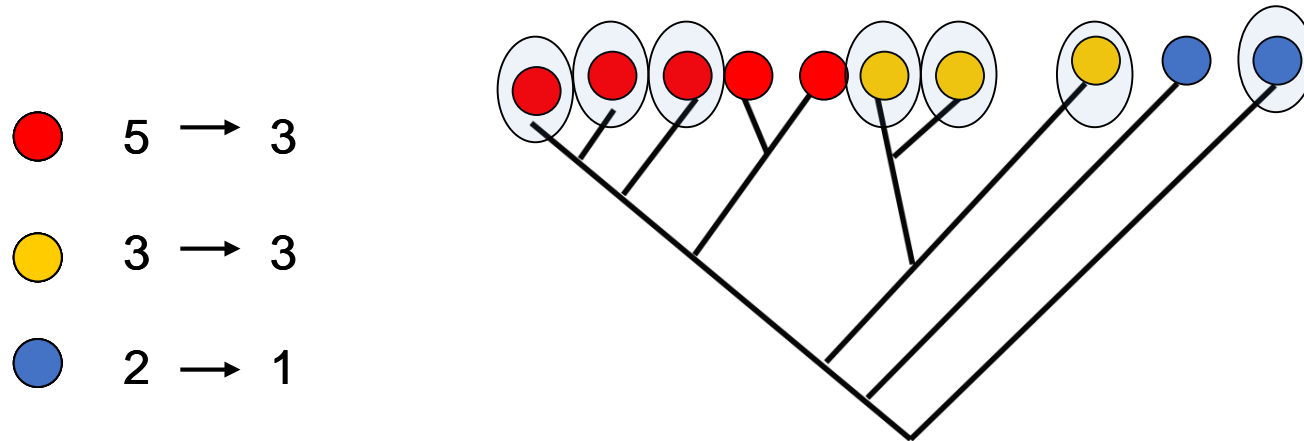


Nestedness and phylogenetical signal: are related frugivores feeding on related plants?

Plants and frugivores in Spain

Standardizing phylogeny for ecological analysis

Distribution of ecological traits in communities with unequal phylogenetic diversity



original → standardized

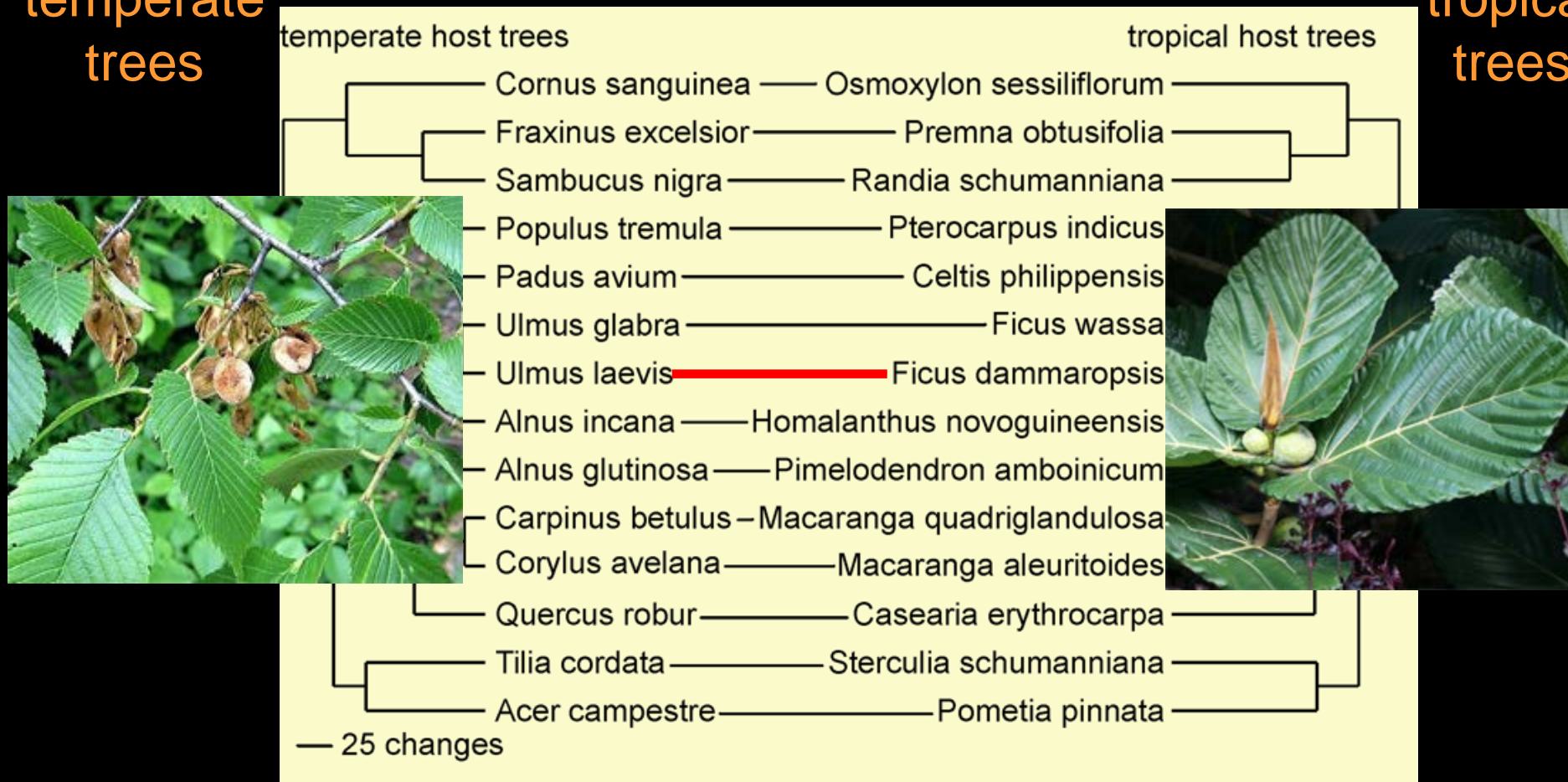
Comparing apples and oranges:
standardising phylogenetic diversity between
temperate and tropical forests



Standardization of plant phylogenetic diversity between temperate and tropical forests

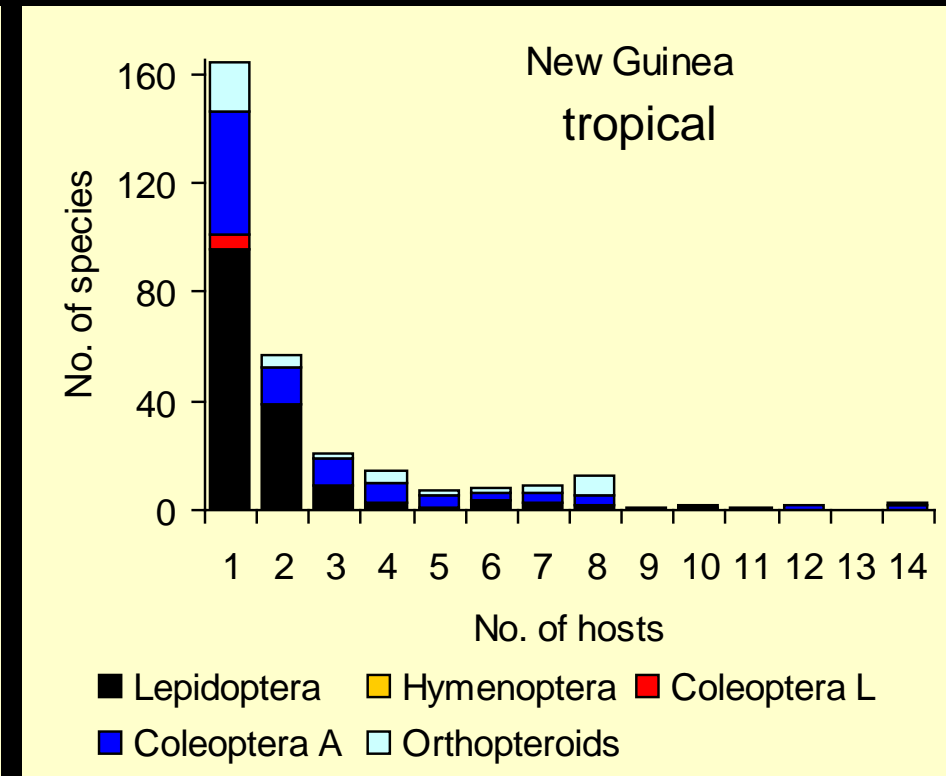
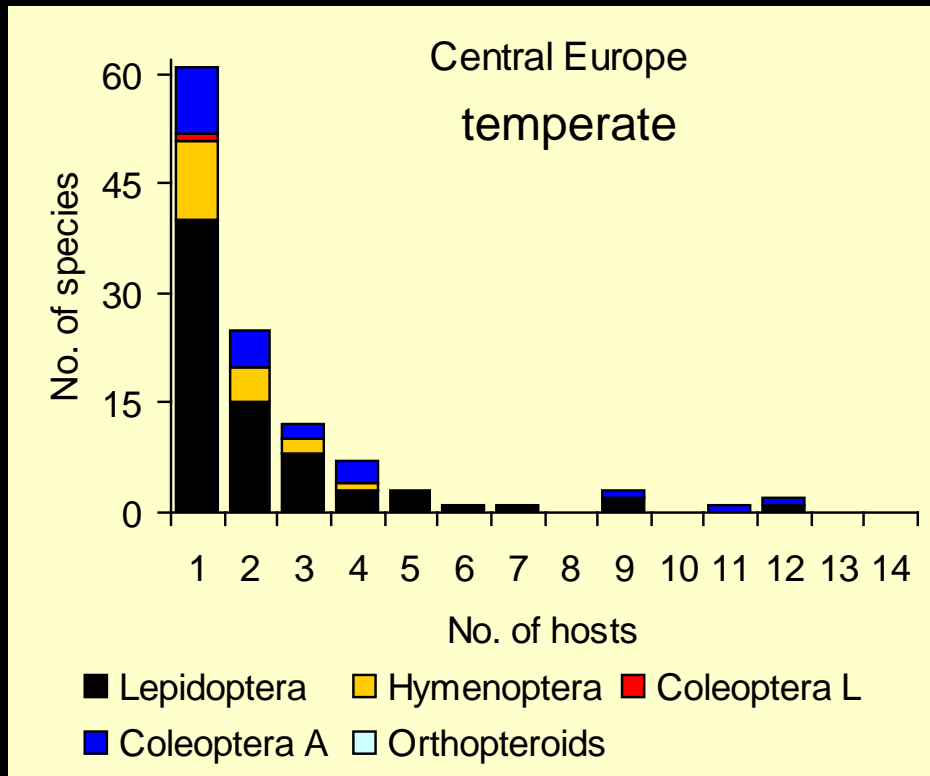
temperate
trees

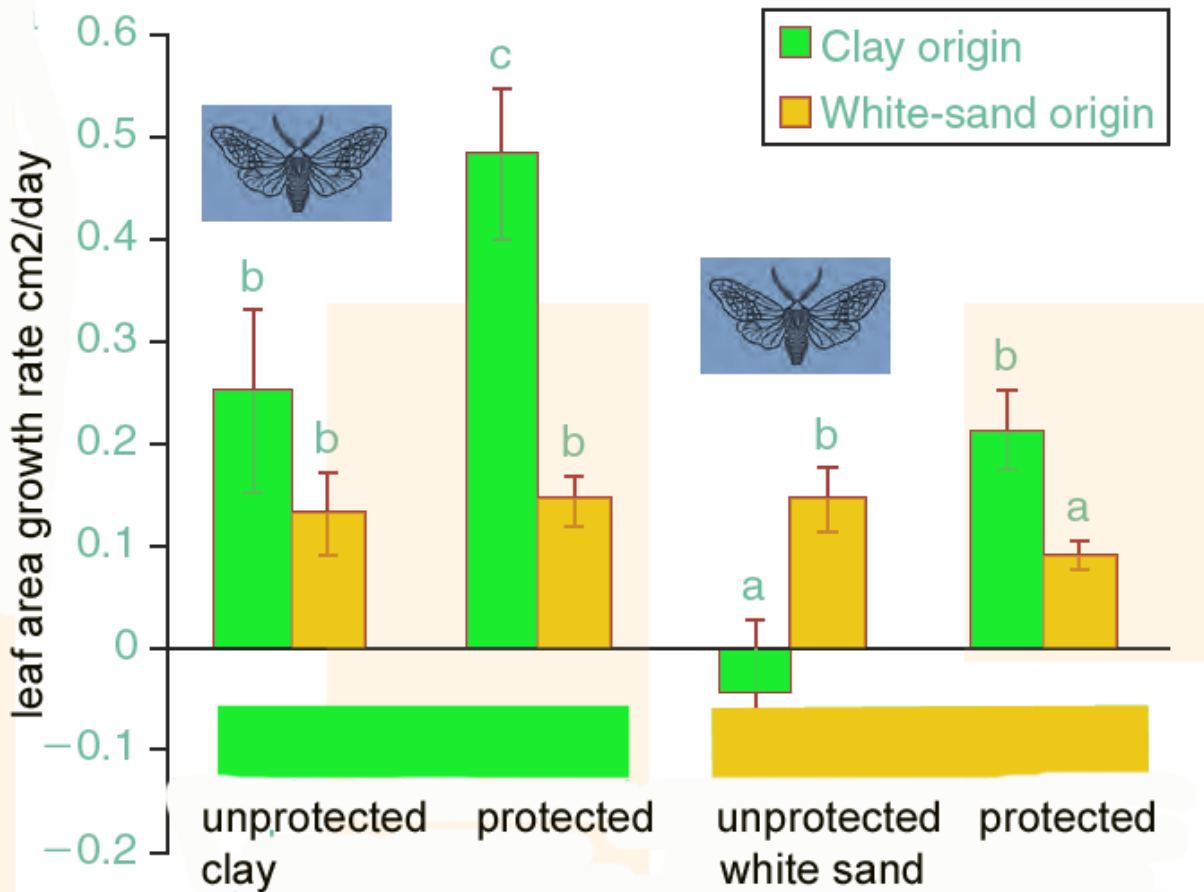
tropical
trees



Cladogram topography and branch lengths standardized,
but individual lineages not matched between the forests

Host specificity of leaf-chewing herbivores on two sets of tree species with equal phylogenetic diversity





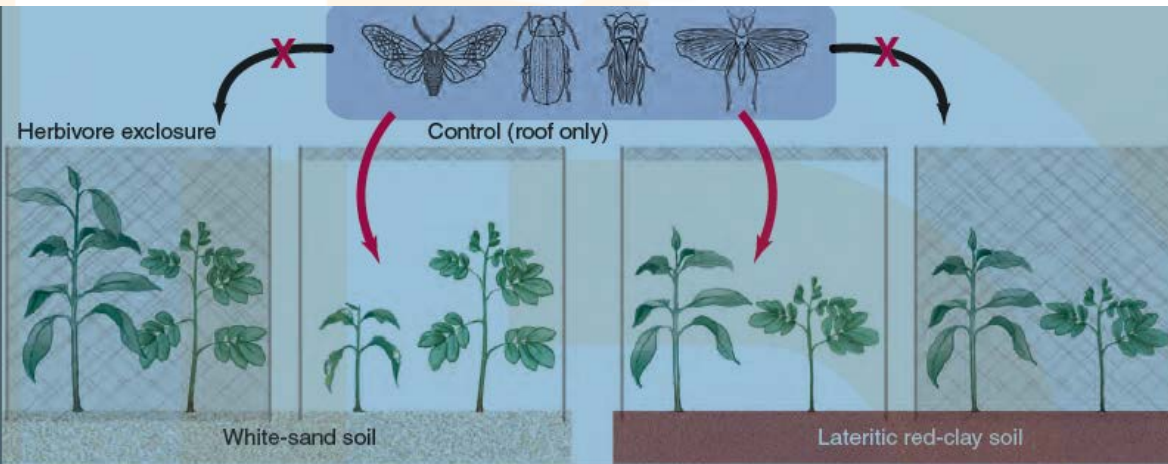
Herbivores determine plant competitive hierarchy

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



Herbivores Promote Habitat Specialization by Trees in Amazonian Forests

Paul V. A. Fine,^{1,2*} Italo Mesones,³ Phyllis D. Coley¹

In an edaphically heterogeneous area in the Peruvian Amazon, clay soils and nutrient-poor white sands each harbor distinctive plant communities. To determine whether a trade-off between growth and antiherbivore defense enforces habitat specialization on these two soil types, we conducted a reciprocal transplant study of seedlings of 20 species from six genera of phylogenetically independent pairs of edaphic specialist trees and manipulated the presence of herbivores. Clay specialist species grew significantly faster than white-sand specialists in both soil types when protected from herbivores. However, when unprotected, white-sand specialists dominated in white-sand forests and clay specialists dominated in clay forests. Therefore, habitat specialization in this system results from an interaction of herbivore pressure with soil type.

	Family	Genus and species	Soil type (origin)
	Annonaceae	<i>Oxandra xylopioides</i> Diels	Clay
	Annonaceae	<i>Oxandra euneura</i> Diels	White sand
	Burseraceae	<i>Tetragastris* panamensis</i> (Engler) Kuntze	Clay
	Burseraceae	<i>Protium subserratum</i> (Engler) Engler	White sand
	Burseraceae	<i>Protium nodulosum</i> Swart	Clay
	Burseraceae	<i>Protium paniculatum</i> Engler	White sand
	Burseraceae	<i>Protium opacum</i> Swart	Clay
	Burseraceae	<i>Protium calanense</i> Cuatrec.	White sand
	Burseraceae	<i>Protium trifoliolatum</i> Engler	Clay
	Burseraceae	<i>Protium krukoffii</i> Swart	Clay
	Burseraceae	<i>Protium heptaphyllum</i> subsp. <i>ulei</i> (Swart) Daly	White sand
	Burseraceae	<i>Protium hebetatum</i> Daly	Clay
	Malvaceae (Bombacoid)	<i>Pachira insignis</i> (Swartz) Swartz ex Savigny	Clay
	Malvaceae (Bombacoid)	<i>Pachira brevipes</i> (Robyns) Alverson	White sand
	Euphorbiaceae	<i>Mabea pulcherrima</i> Müll. Arg.	Clay
	Euphorbiaceae	<i>Mabea subsessilis</i> Pax & Hoffmann	White sand
	Fabaceae (Faboid)	<i>Swartzia arborescens</i> (Aublet) Pittier	Clay
	Fabaceae (Faboid)	<i>Swartzia cardiosperma</i> Spruce ex Benth.	White sand
Fabaceae (Mimosoid)	<i>Parkia multijuga</i> Benth.	Clay	
Fabaceae (Mimosoid)	<i>Parkia igneiflora</i> Ducke	White sand	

Things we will never know

Is body size in sap-sucking insects determined by feeding niche?

We will never know as cell-feeding originated only 1x and xylem-feeding only 1-2x in the entire group - not enough for statistics!

Cell-feeders: Typhlocybae

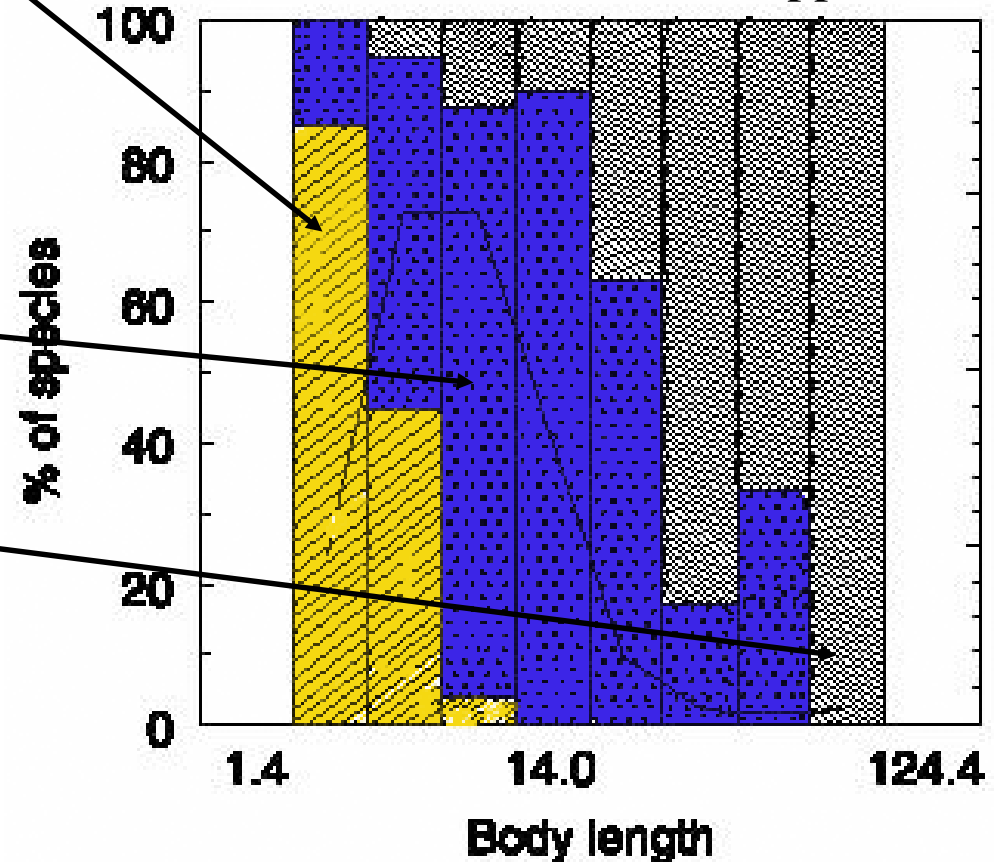


Phloem feeders: various taxa

Xylem-feeders:
Cicadidae, Cercopidae



Vietnam rainforest leafhoppers



Phylogenetical constraints on the composition of herbivore communities: leaf-cutting ants are the most successful herbivores, but exist only in the Neotropics



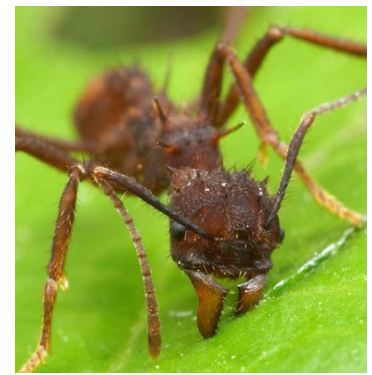
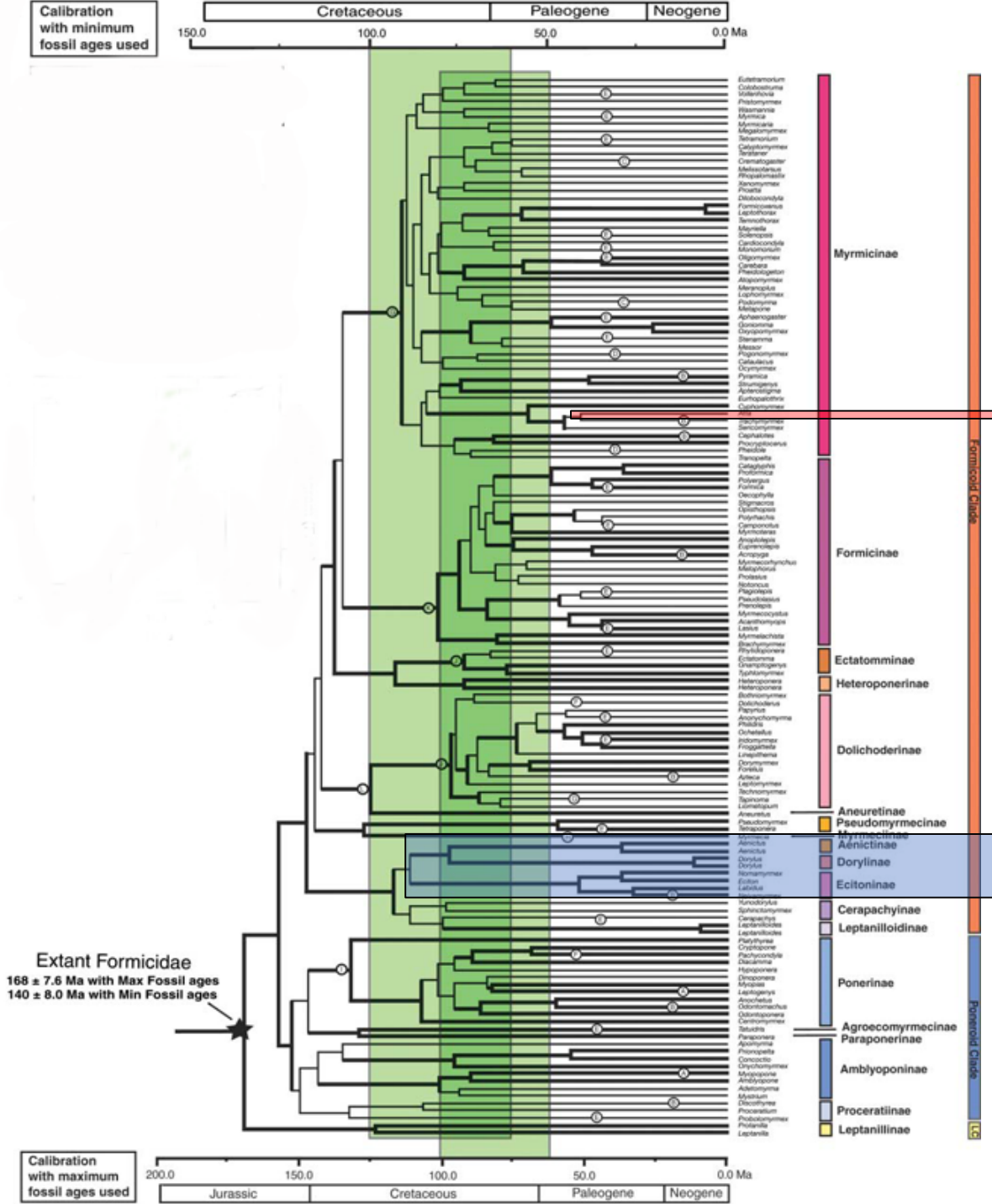
Atta colombica - Formicidae at Barro Colorado Island, rainforest:

1 colony / 1.7 ha, territorial

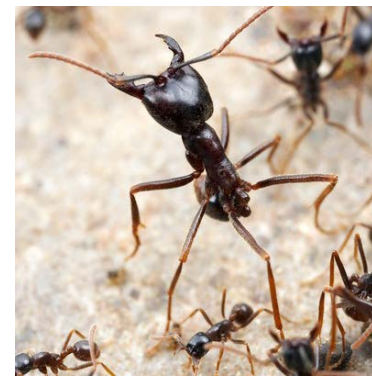
collected 134,000 leaf fragments per day = 737 dry weight of leaves and 304 g other plant parts = represents 5% of the total litter fall in the forest

feeding preference: young leaves of various (many) plant spp. with leaves lacking anti-fungal properties





Leaf-cutter ants
50 million yrs ago



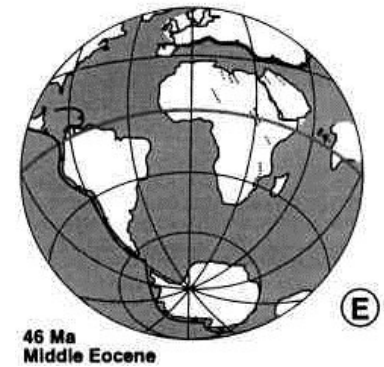
Army ants
95-120 million yrs ago

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



Leaf cutter ants



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

Conclusions:

(i) phylogeny is an important factor shaping community composition

(ii) ecologists can see phylogenetic effects either as a nuisance that needs to be filtered out from their analyses or as a focus of their analyses; either way, these effects cannot be ignored

(iii) despite the previous statement, the phylogeny has been ignored by ecologists until very recently; it remains to be seen whether and how the recent (after yr. 2000) proliferation of phylogenetic analysis changes our perception of ecological processes