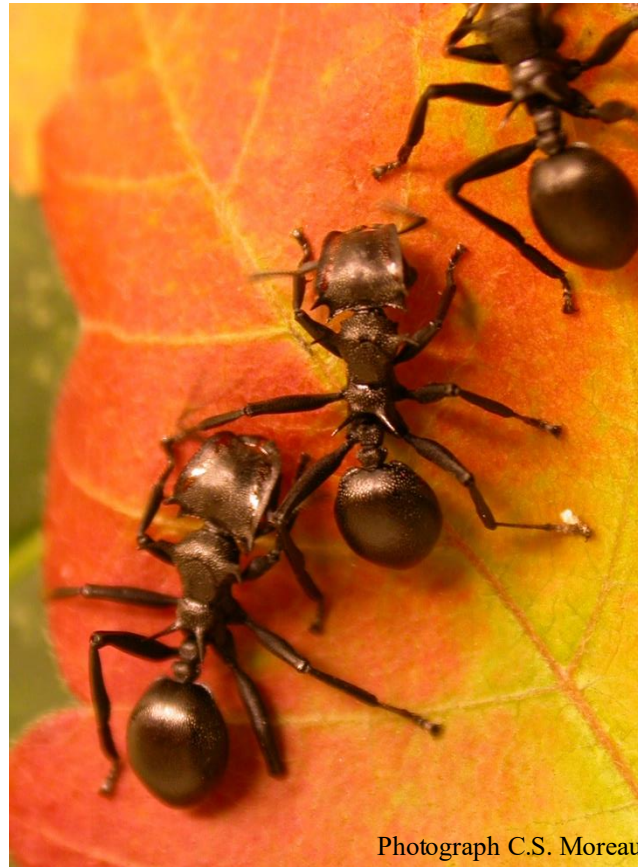


Ant diversification, biogeography, and trait evolution



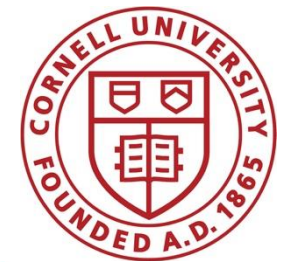
Photograph C.S. Moreau



Corrie S. Moreau (she/her)

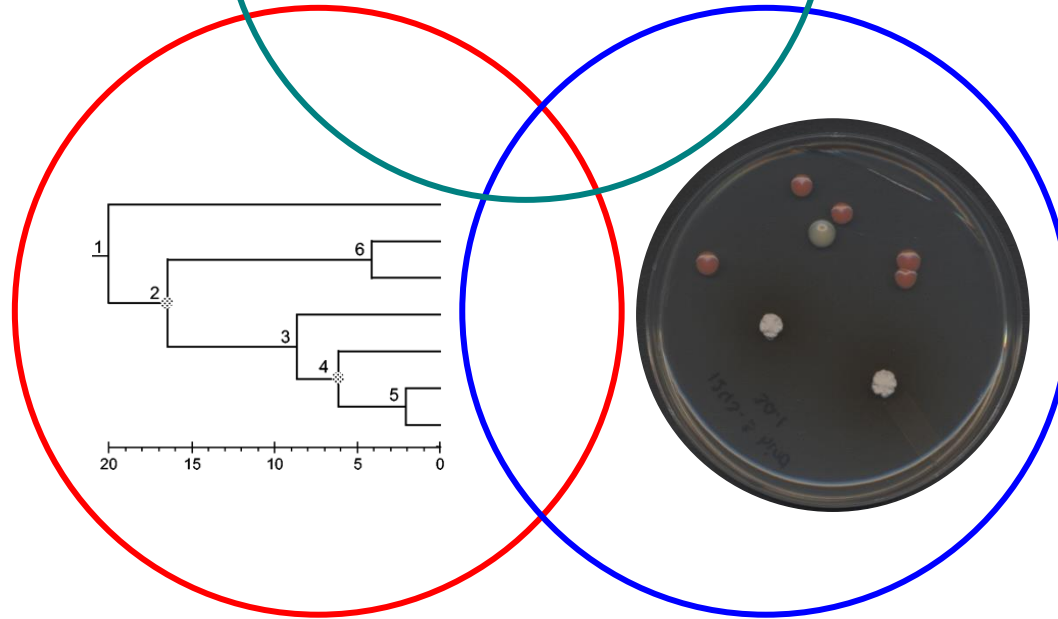
Cornell University
www.moreaulab.org

 @CorrieMoreau



Major themes of my research program

Ant Ecology and Evolution



Macroevolution

Microbiomes

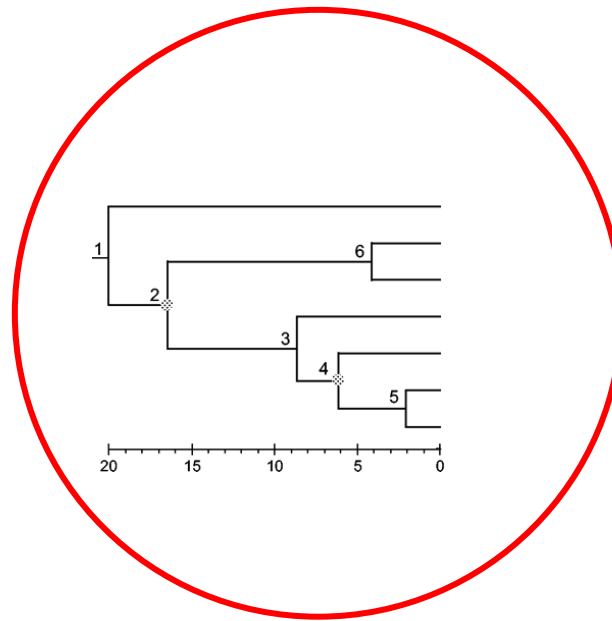
Major themes of my research program

Ant Ecology and Evolution

- Over 15,000 named species
- Found across the planet
- Ecologically successful
- Diverse morphology, ecology, and behaviors
- Engage in symbiotic relationships across the tree of life



Major themes of my research program

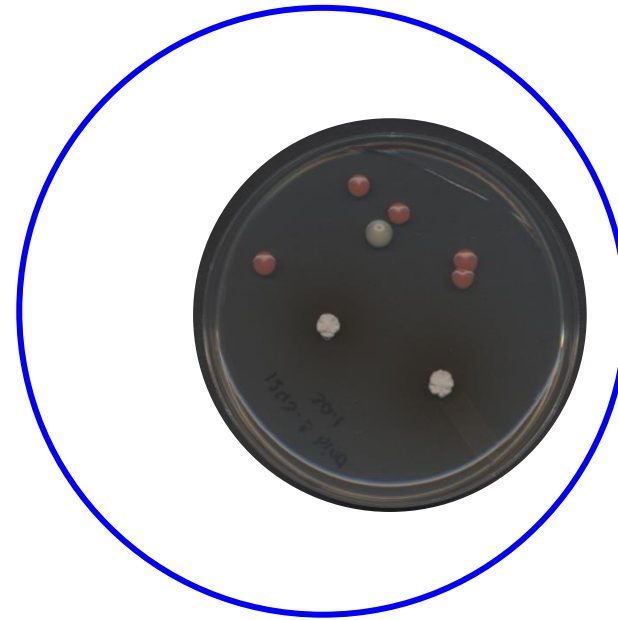


- Phylogenetics
- Divergent dating
- Biogeography
- Trait evolution
- Natural History
- Molecular evolution

Macroevolution

Major themes of my research program

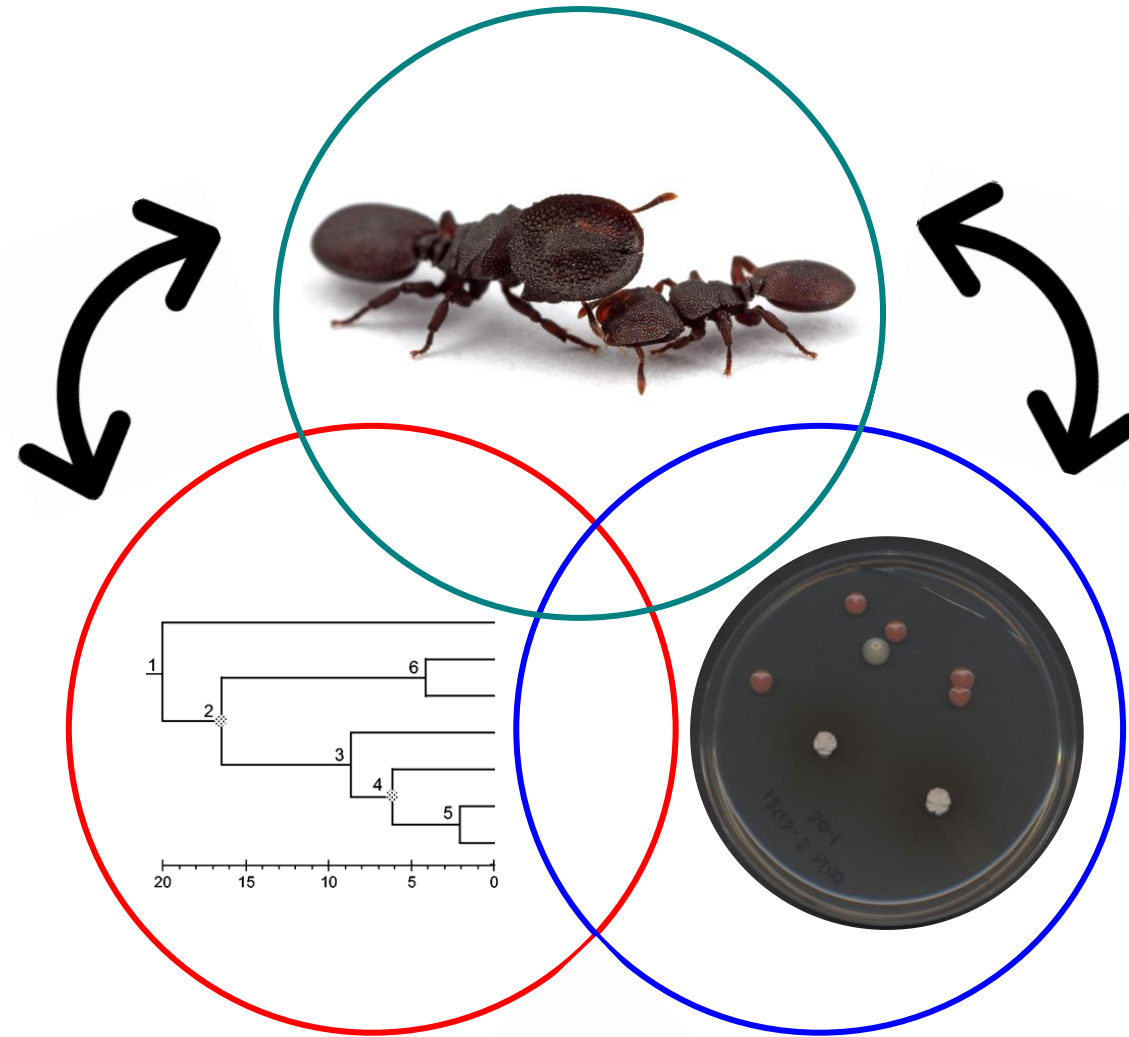
- Document and describe diversity
- Understand host-specificity
- Examine niche specificity
- Co-evolution/co-diversification
- Determine function to host



Microbiomes

Major themes of my research program

Ant Ecology and Evolution



Macroevolution ↔ Microbiomes

Evolution and biogeography of the ants in light of
flowering plant diversification

Feedback with angiosperms driving ant evolution?

PNAS

The rise of the ants: A phylogenetic and ecological explanation

Edward O. Wilson*¹ and Bert Hölldobler*^{2,5}

¹Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138-2902; ²School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501; and ³Theodor-Boveri-Institut für Biowissenschaften (Biozentrum) der Universität, Am Hubland, D-97074 Würzburg, Germany

Contributed by Edward O. Wilson, March 18, 2005



Photograph © Alex Wild

Ant point of view:

1) The influence of angiosperm forest expansion during the Cretaceous on ant diversification

- Wilson and Hölldobler (2005) hypothesized a role for angiosperms in the evolution of ants, but were not able to test these in a analytical phylogenetic framework.

2) Diet changes from away from predation facilitated movement up into the canopy.

OPEN ACCESS Freely available online

PLoS one

Ants Sow the Seeds of Global Diversification in Flowering Plants

Szabolcs Lengyel^{1,2*}, Aaron D. Gove³, Andrew M. Latimer⁴, Jonathan D. Majer³, Robert R. Dunn^{1,3}

¹Department of Biology, North Carolina State University, Raleigh, North Carolina, United States of America, ²Department of Ecology, University of Debrecen, Debrecen, Hungary, ³Centre for Ecosystem Diversity and Dynamics, Curtin University of Technology, Perth, Australia, ⁴Department of Plant Sciences, University of California Davis, Davis, California, United States of America



Photograph © Alex Wild

Plant point of view:

1) Seed dispersal by ants (myrmecochory) evolved independently at least 100 times (present in at least 77 families and 11,000 plant species).

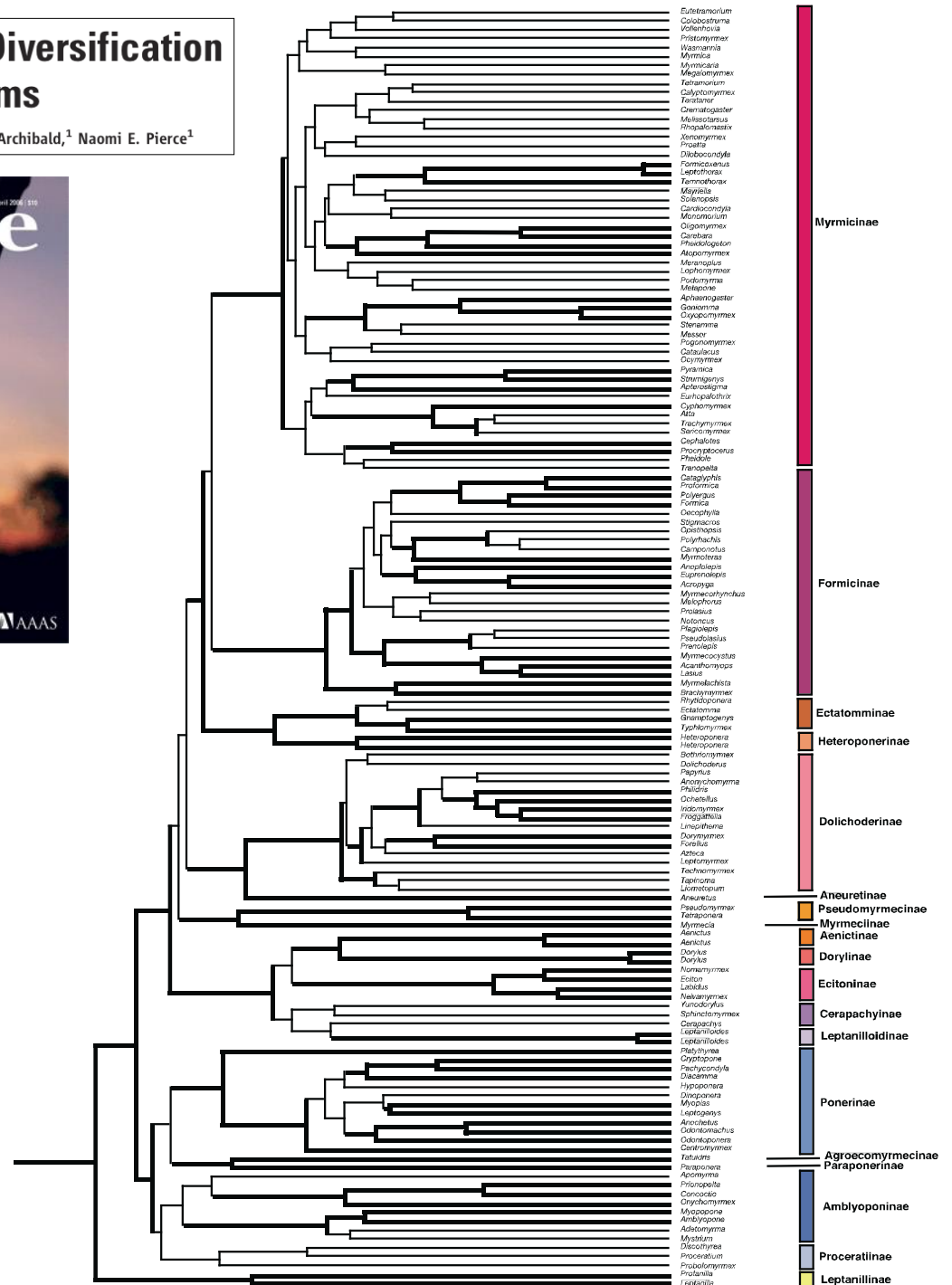
2) Is a key evolutionary innovation and a globally important driver of plant diversity. Myrmecochory provides the best example to date for a consistent effect of any mutualism on large-scale diversification.

Phylogeny of the Ants: Diversification in the Age of Angiosperms

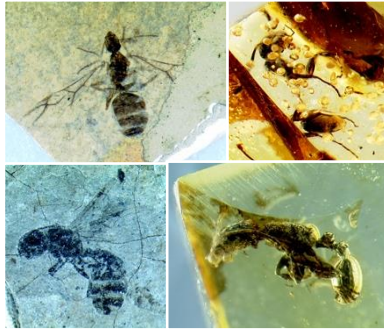
Corrie S. Moreau,^{1*} Charles D. Bell,² Roger Vila,¹ S. Bruce Archibald,¹ Naomi E. Pierce¹



Moreau *et al.* (2006)
Science 312: 101-104.



- 139 of 288 genera included
- (19 of 20 subfamilies)
- Multiple outgroups
- Six gene regions sequenced
- ~ 4.5 kb of sequence data
- Analyzed with maximum likelihood; Bayesian inference
- Thick lines = 100% Bayesian posterior probabilities



Photographs S.B. Archibald

FOXNEWS.COM HOME > SCIENCE

First Flowers Triggered Boom in Ant Diversity

The emergence of flowering plants 100 million years ago may have led to the explosion in ant diversity that occurred around the same time, scientists say.

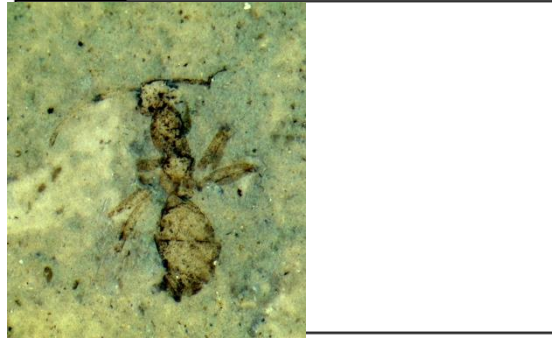
The 11,800 known species of modern ants probably arose from a single species millions of years ago, but scientists previously knew little about ants' evolutionary history.

Researchers analyzed the DNA of fossilized ants trapped in amber and discovered that the ancestors of modern ants first scurried along the ground 140 to 168 million years ago.

These ants, however, were diversifying at a very slow rate. Then flowers, also known as **angiosperms**, sprouted onto the scene.

"An event happened 100 million years ago, and ants started diversifying like crazy," study co-author **Corrie Moreau** of Harvard University told LiveScience. "This is also the time when we start seeing the first angiosperm forests."

PHOTOS



STORIES

- Arctic Fossil Bridges Gap Between Fish, Land Animals
- Dinosaur Discovered in Utah Resembled Turkey
- Global Warming Caused Mass Extinctions 247 Million Years Ago
- Medical Students Studying Fossils to Learn History of Disease
- Beetles Used to Strip Animal Carcasses Down to Bones



Sphecomyrma freyi from New Jersey Amber ~92 Mya
Photograph F.M. Carpenter

DIVERSIFICATION

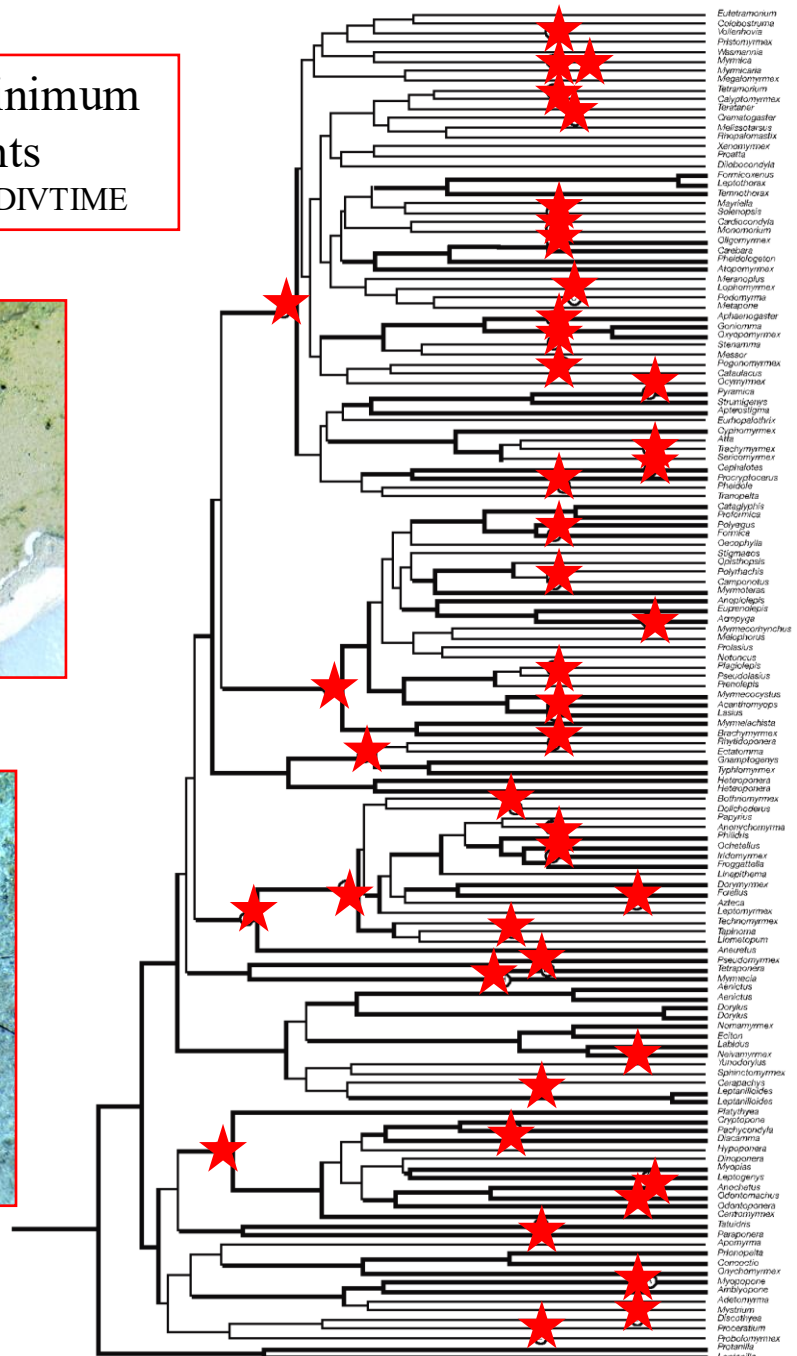
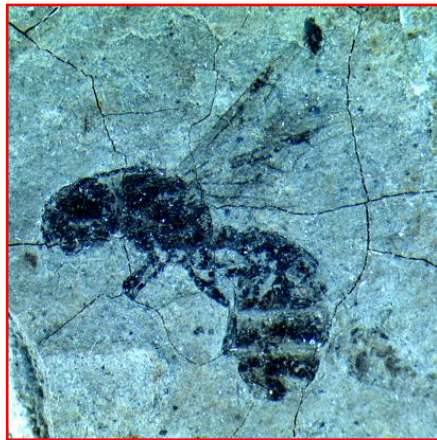
BIOGEOGRAPHY

SILK WEAVING

NECTARIES

SPECIATION

43 fossils used as minimum calibration points
Analyzed with r8s & MULTIDIVTIME



- Myrmecinae
- Formicinae
- Ectatomminae
- Heteroponerinae
- Dolichoderinae
- Aneuretinae
- Pseudomyrmecinae
- Myrmecinae
- Aenictinae
- Dorylinae
- Ecitoninae
- Cerapachyinae
- Leptanilloidinae
- Ponerinae
- Agroecomyrmecinae
- Paraponerinae
- Amblyoponinae
- Proceratinae
- Leptanilloidinae



Photographs S.B. Archibald

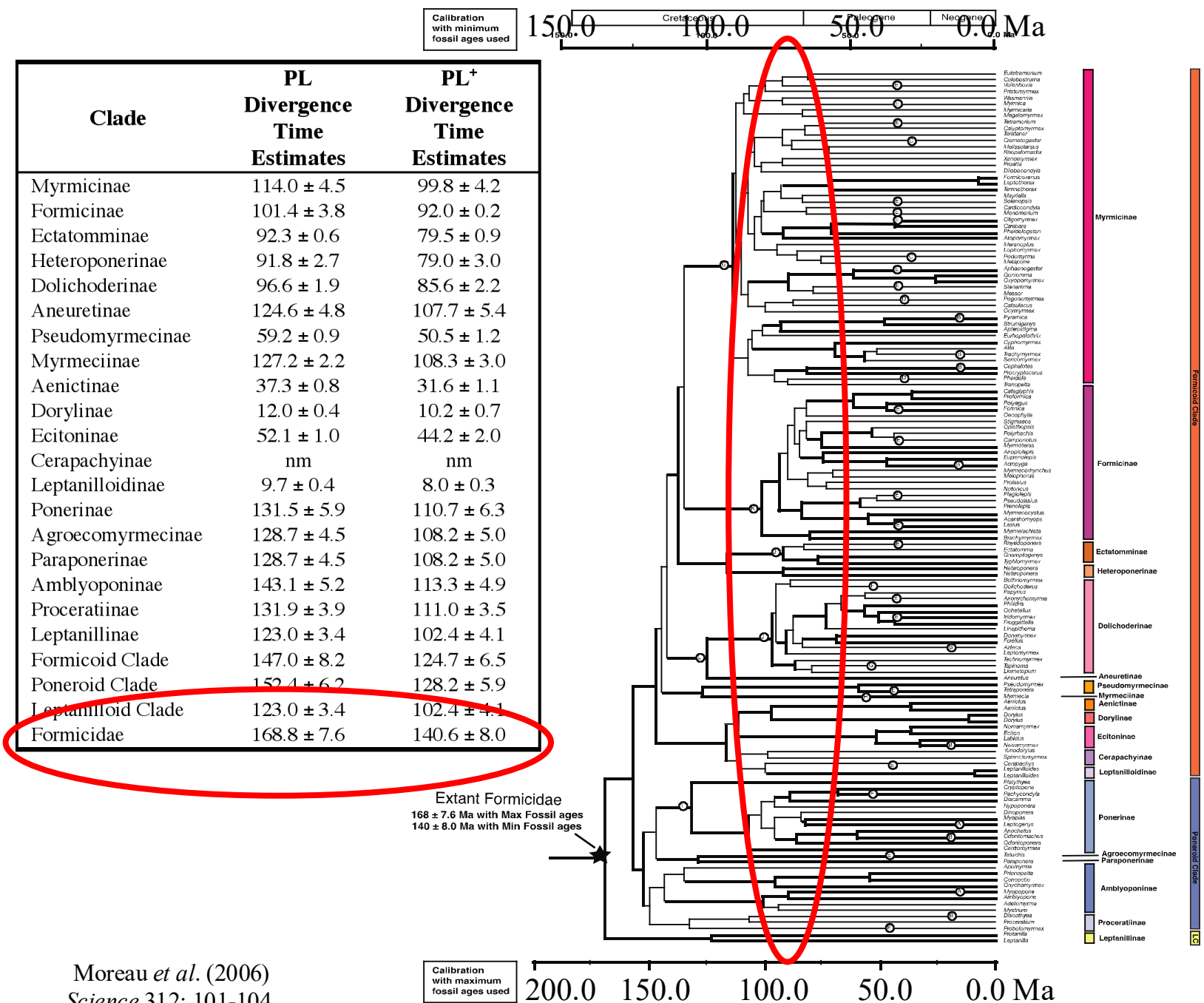
DIVERSIFICATION

BIOGEOGRAPHY

SILK WEAVING

NECTARIES

SPECIATION



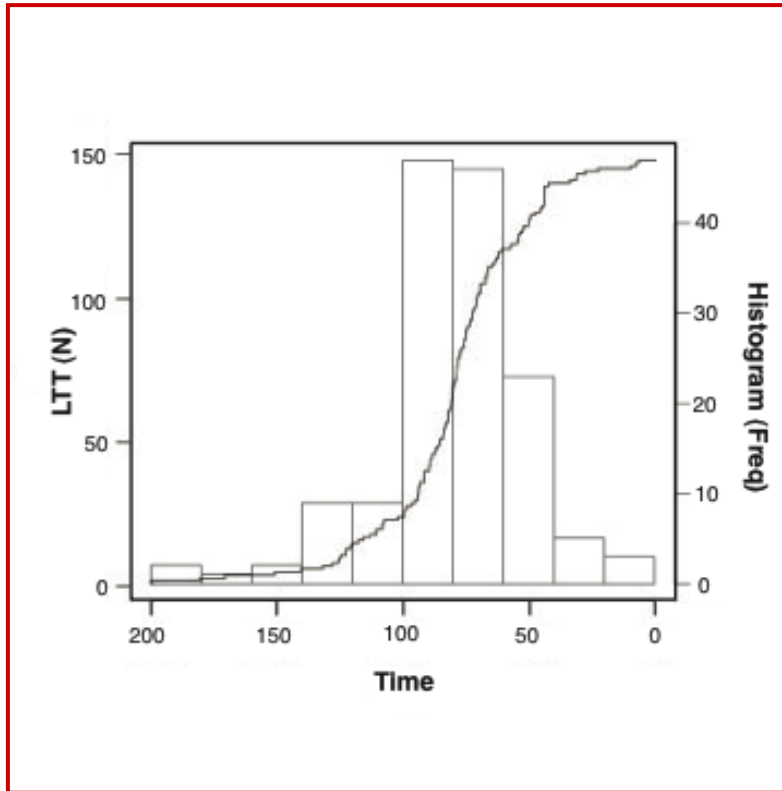


Table S5. Results of fitting three models to ant data. logL=Likelihood, p = parameter. AIC = Akaike information criterion. Comparison of diversification rate models to model A performed with APE v1.4. (see text).

Model	Description		logL	χ^2	P	AIC
A	Constant rate	$\delta = 0.013$	-12358.08			24718.16
B	Variable rate	$\beta = 2.78$ $\alpha = 0.011$	-2960.58	30637.31	<0.001	5917.149
C	Variable rate before and after 100	$\delta_1 = 0.001$ $\delta_2 = 0.006$	-786.64	30637.31	<0.001	1577.283

Model A: Constant rate of diversification throughout time

Model B: Gradual change in diversification throughout time

Model C: Two different rates of diversification before and after a specific breakpoint in time (100 Ma)

Birth-Death model of diversification (Nee *et al.* 1994)

Akaike Information Criterion (AIC) implemented in the program APE v1.4 (Paradis *et al.* 2004)

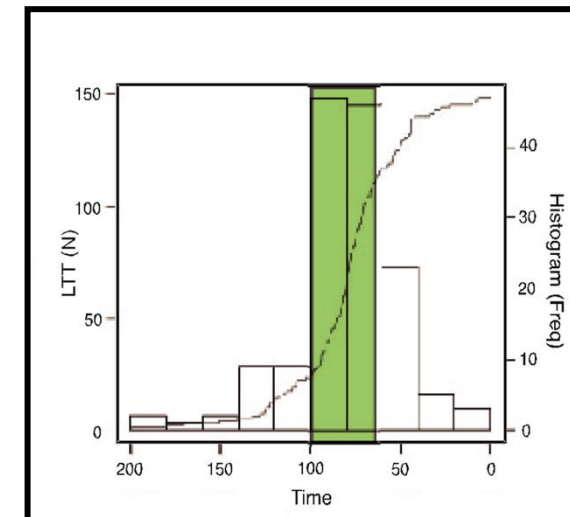
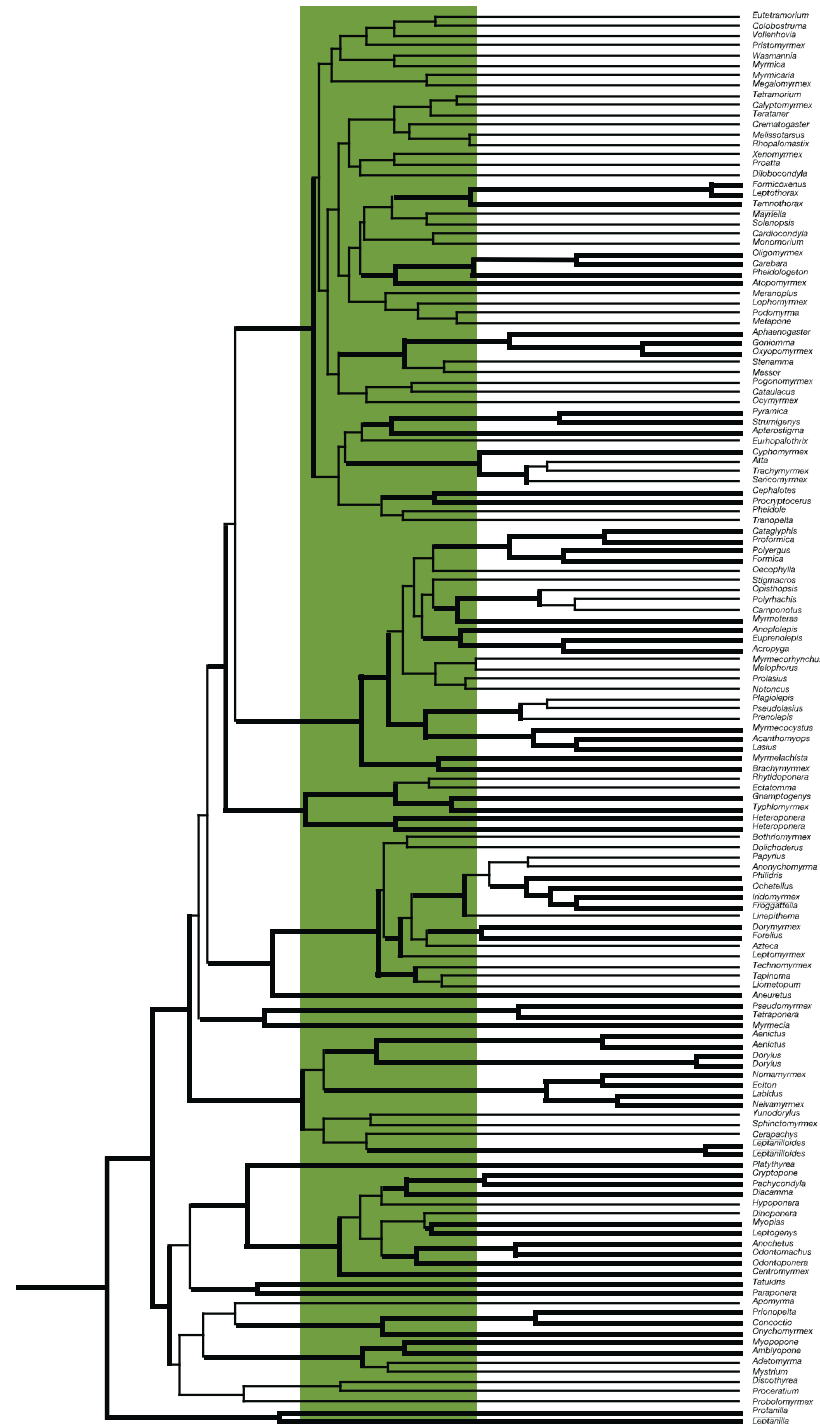
DIVERSIFICATION

BIOGEOGRAPHY

SILK WEAVING

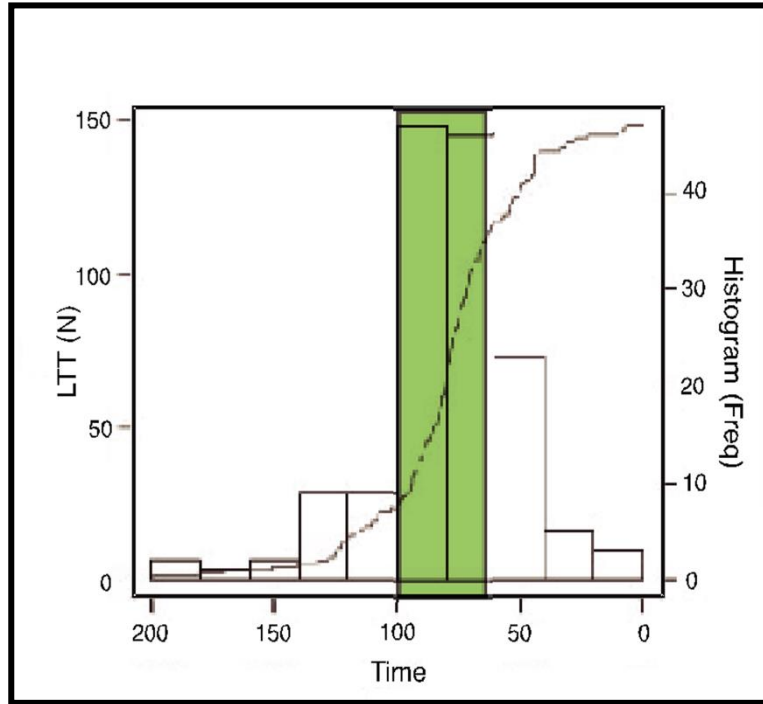
NECTARIES

SPECIATION



Moreau *et al.* (2006)
Science 312: 101-104.

Moreau & Bell (2011)
Entomol. Am. 117: 127-133.



Moreau *et al.* (2006)
Science 312: 101-104.

Moreau & Bell (2011)
Entomol. Am. 117: 127-133.

Moreau & Bell (2013)
Evolution 67: 2240-2257.

The biogeographic origins and spread of ants
across the globe

Where is the majority of biodiversity found and why?

Are the ants tracking the biogeographic expansions of the angiosperms?

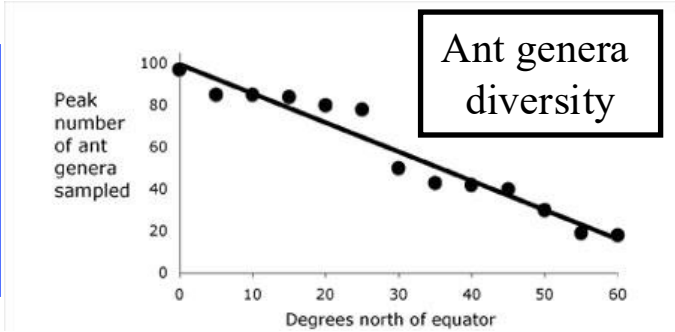
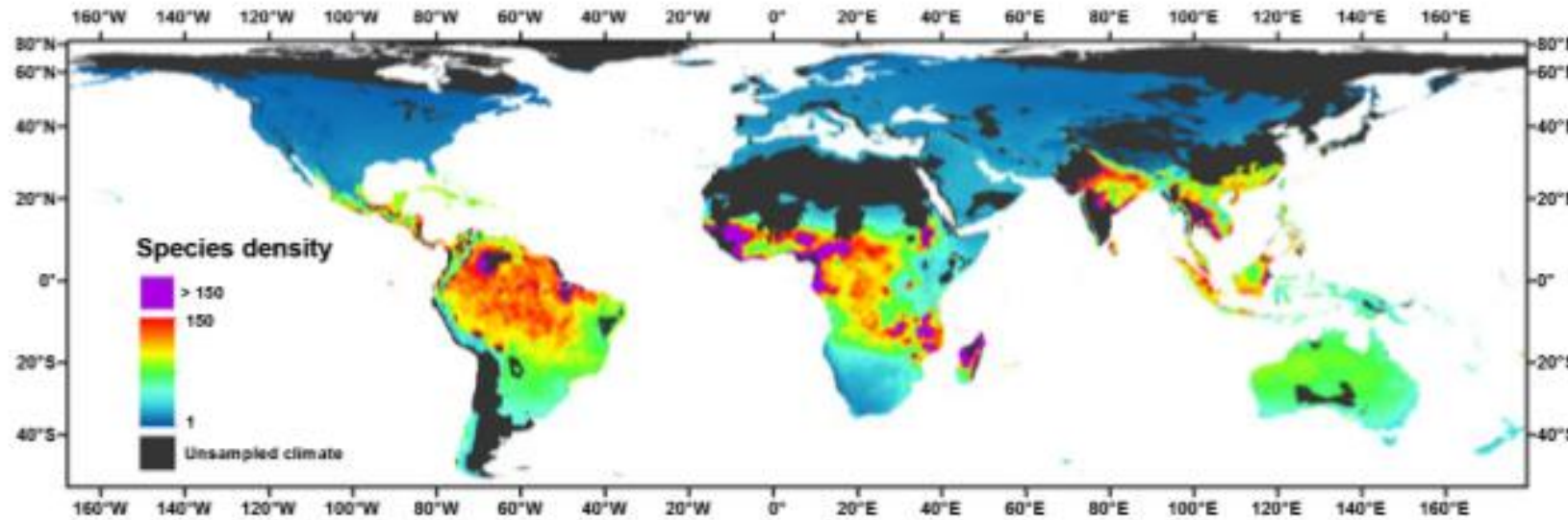


Figure from McGlynn (2010)
Nature Education Knowledge 1:32.

Latitudinal gradient in species richness

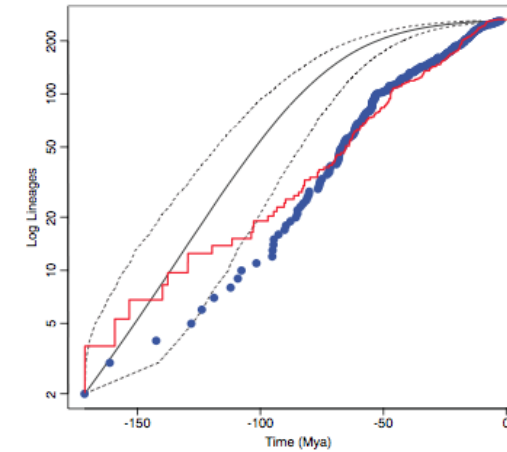
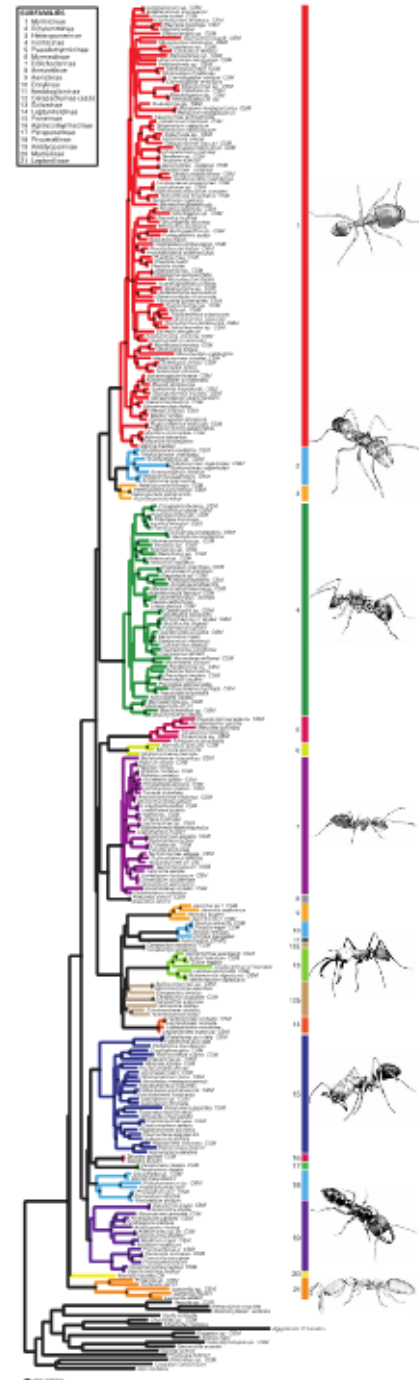


Ant species diversity

Figure from Jenkins *et al.* (2011)
Diversity and Distributions 17:652-662.

**TESTING THE MUSEUM VERSUS CRADLE
TROPICAL BIOLOGICAL DIVERSITY
HYPOTHESIS: PHYLOGENY, DIVERSIFICATION,
AND ANCESTRAL BIOGEOGRAPHIC RANGE
EVOLUTION OF THE ANTS**

Corrie S. Moreau^{1,2} and Charles D. Bell³



311 taxa
 Five gene regions included
 Analyzed with RAxML, & Mr. Bayes
 45 fossils as minimum calibrations
 Analyzed with BEAST & MEDUSA

Combined molecular data from:
 Moreau *et al.* (2006)
 Brady *et al.* (2006)
 Rabeling *et al.* (2008)

Moreau & Bell (2013)
Evolution 67: 2240-2257.

Latitudinal gradient in species richness



Cradle vs. Museum

The tropics were either a cradle, where new life evolved more frequently than at other latitudes, or a museum, where old, ancient life persisted there longer.

-- Stebbins (1974)

Expectations:

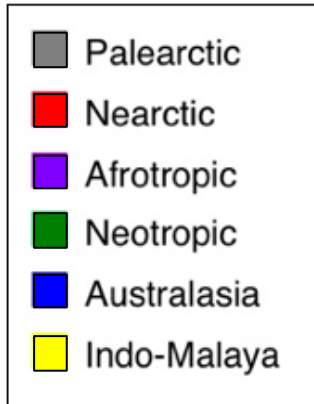
Cradle:

Expect high origination/speciation rates, new adaptive complexes arising within the area, and this region is acting as a center of origin for species diversity.

Museum:

Expect taxa will be older in the tropics, have lower extinction rates, and have larger geographic range sizes (as is often found in the tropics) that positively correlate with their evolutionary persistence.

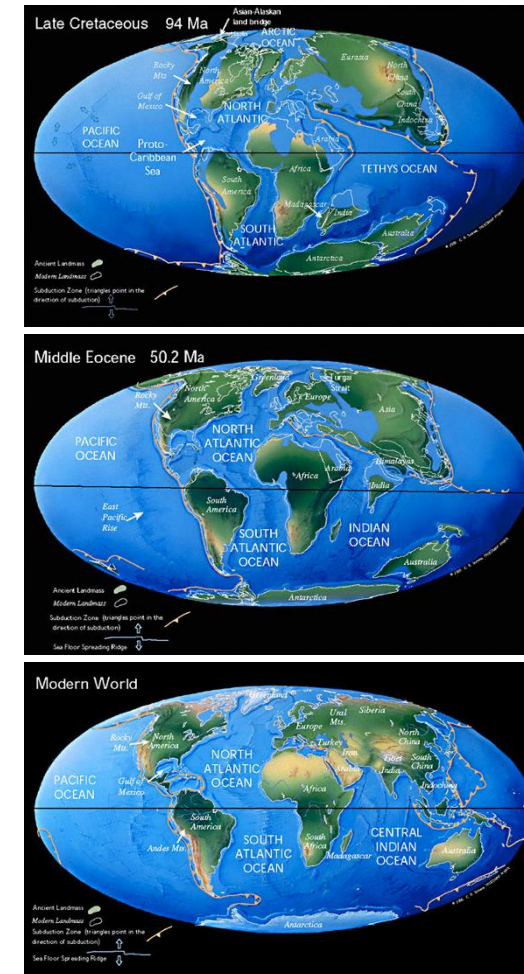
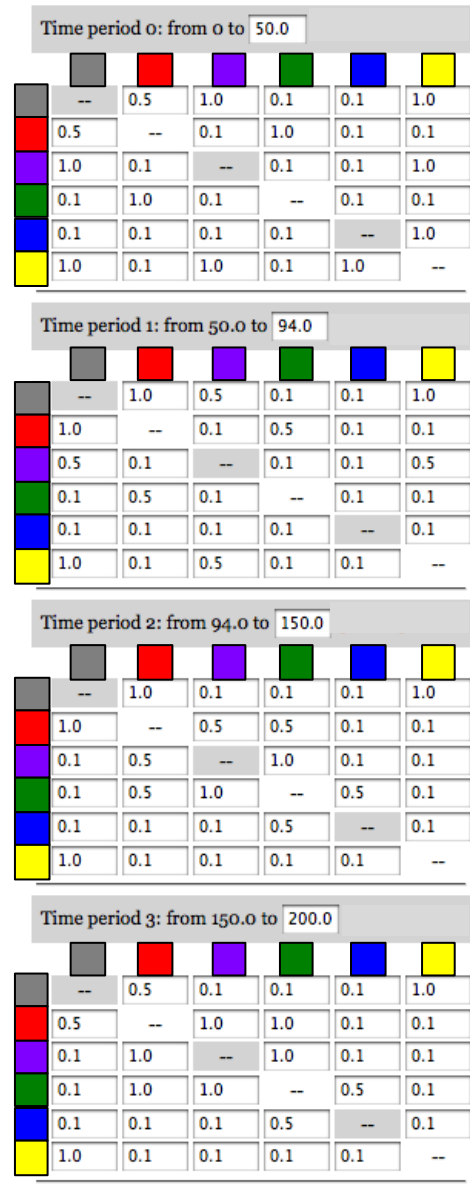
Divergence dating can inform biogeographic reconstructions



Current species distributions

	Grey	Red	Purple	Green	Blue	Yellow
Protanilla_sp_CSM	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Leptanilla_sp_CSM	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Martialis_heureka_CR	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Tetraopona_sp_CSM	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Pseudomyrmex_apache_CSM	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Myrcidris_epicharis	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Myrmecia_fulviculvis_CSM	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Nothomyrmecia_macrops	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Bothriomyrmex_hispanicus_CSM	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Dolichoderus_imitator_CSM	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Azteca_sp_CSM	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Papyrius_nitidus_CSM	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Anonymomyrma_nitidiceps_CSM	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Froggattella_latispina_CSM	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Iridomyrmex_spadius_CSM	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Turneria_bidentata	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Ochetellus_glaber_CSM	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Philidris_cordatus_CSM	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>
Linepithema_keiteli_CSM	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Leptomymex_sp_CSM	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Dorymyrmex_elegans_CSM	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Forelius_sp_CSM	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Tapinoma_opacum_CSM	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Liometopum_luctuosum_CSM	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Technomyrmex_albipes_CSM	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Aneuretus_simoni_CSM	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Cerapachys_augustae_CSM	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Sphinctomyrmex_sp_CSM	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Cerapachys_larvatus	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Cylindromyrmex_striatus	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Acanthostichus_kirbyi	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Simopone_marleyi	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Cerapachys_Yunodorylus_sexspinus_CSM	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Dorylus_mayri_CSM	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Aenictogiton_ZAM02	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
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Eciton_hamatatum_CSM	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Cheliomyrmex_cf_morosus	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Labidus_spininodis_CSM	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Neivamyrmex_nigrescens_CSM	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Aenictus_sp_1_CSM	<input type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Leptanilloides_nomada_CSM	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
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Messor_julianus_CSM	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Aphaenogaster_albisetososa	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
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Messor_denticornis	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Goniomma_hispanicum_CSM	<input checked="" type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

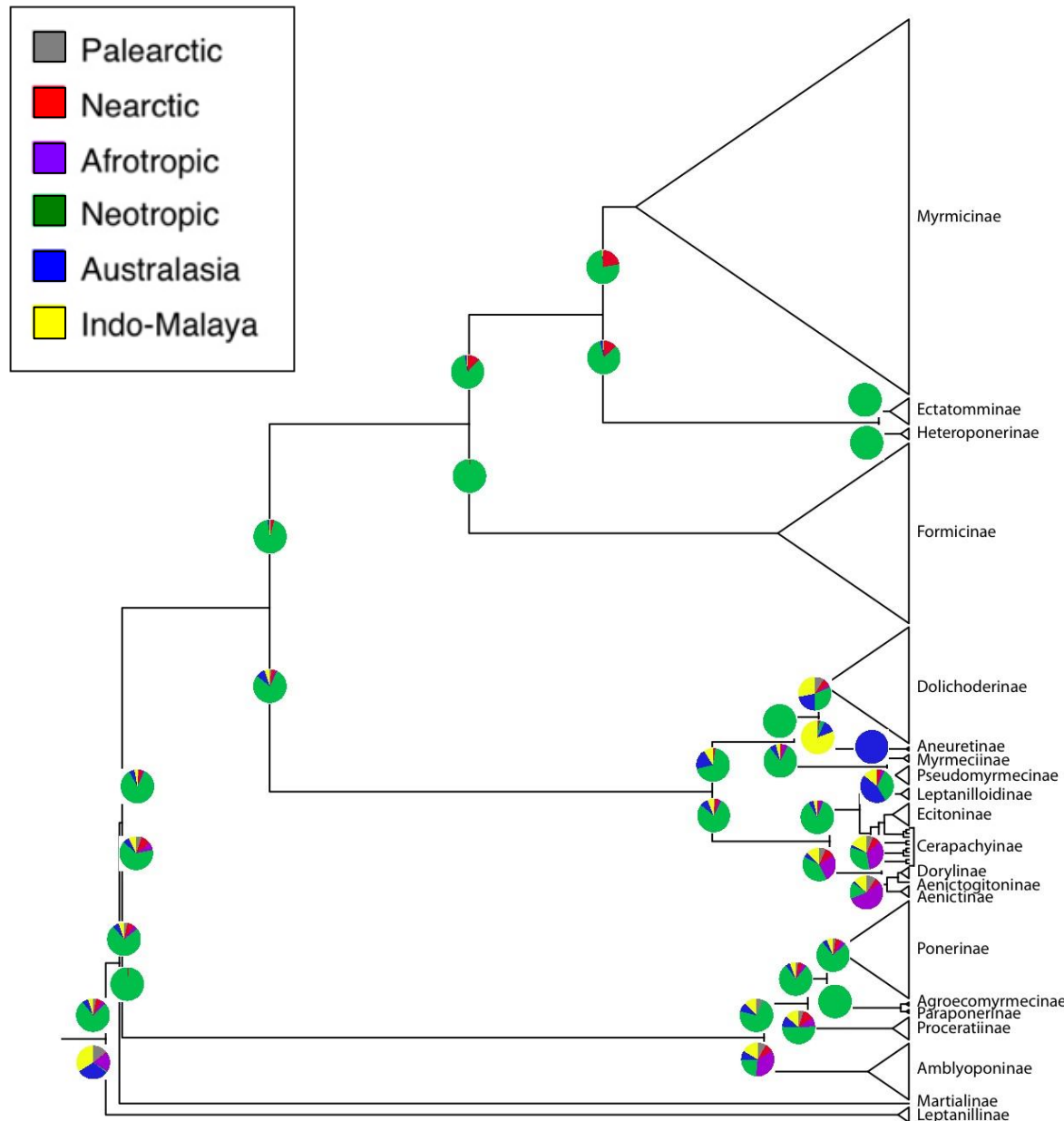
Migration probability between areas over time



<http://www.scotese.com>

Analyzed using Lagrange by Ree & Smith (2008) *Syst. Biol.* 57: 4-14.

Biogeographic range evolution for the ants



Neotropics are currently home to more genera (total number and endemic) and species than any other region.
 - Fisher (2010) in *Ant Ecology*.
 Oxford University Press.

Ants not “tracking” angiosperm biogeography.
 We do not find any significant rate shifts within the ants that correspond to range shifts or to hypothesized movements of plant lineages into or out of the Neotropics.

Neotropics have acted as a museum and cradle for ant diversity

Evolutionary transitions of silk weaving and
arboreal nesting

Silk weaving in ants



Photo from Hölldobler & Wilson (1983)

- The evolution of nest-weaving behavior in arboreal ants has been considered a pinnacle of cooperative behavior (Hölldobler & Wilson 1977, 1983).
- Yet we have a limited understanding of how the actions of numerous individuals underlie this complex-group behavior or the ecological factors that may have been associated with its evolution within ants (Crozier et al. 2010).

Silk weaving in ants

- Typically worker ants use larval silk to “sew” leaves together to build nests
- In some cases the larvae no longer use their silk to make cocoons
- Workers direct where silk is used



The evolution of nesting preference

- The ancestral state is thought to be ground nesting for all ants
- Moving up into trees has evolved multiple times
- Arboreal nesting can involve living in hollow living or dead twigs or among living leaves



The evolution of cooperation in silk weaving in ants

The Evolution of Communal Nest-Weaving in Ants: Steps that may have led to a complicated form of cooperation in weaver ants can be inferred from less advanced behavior in other species

-- Hölldobler & Wilson (1983) *American Scientist* 71: 490-499.

Evolutionary hypotheses for the evolution of nest weaving in ants are currently based on interspecific comparison involving less than two species of each of the four genera containing nest-weaving representatives, along with relevant behavioral and ecological data.

-- Hölldobler & Wilson (1990) *The Ants*. Harvard University Press.



Photograph by C.S. Moreau

The evolution of communal nest weaving

Ant genus	Workers hold spinning larvae
<i>Dendromyrmex</i>	No
<i>Camponotus</i>	Yes
<i>Polyrhachis</i>	Yes
<i>Oecophylla</i>	Yes

-- Hölldobler & Wilson (1983) *American Scientist* 71: 490-499.



Shift to worker control, cocoon loss, increased silk gland size:

- “Simplest type of weaving” = *Dendromyrmex*
- “Intermediate steps” = *Camponotus* & *Polyrhachis*
- “Highest grade of cooperation” = *Oecophylla*

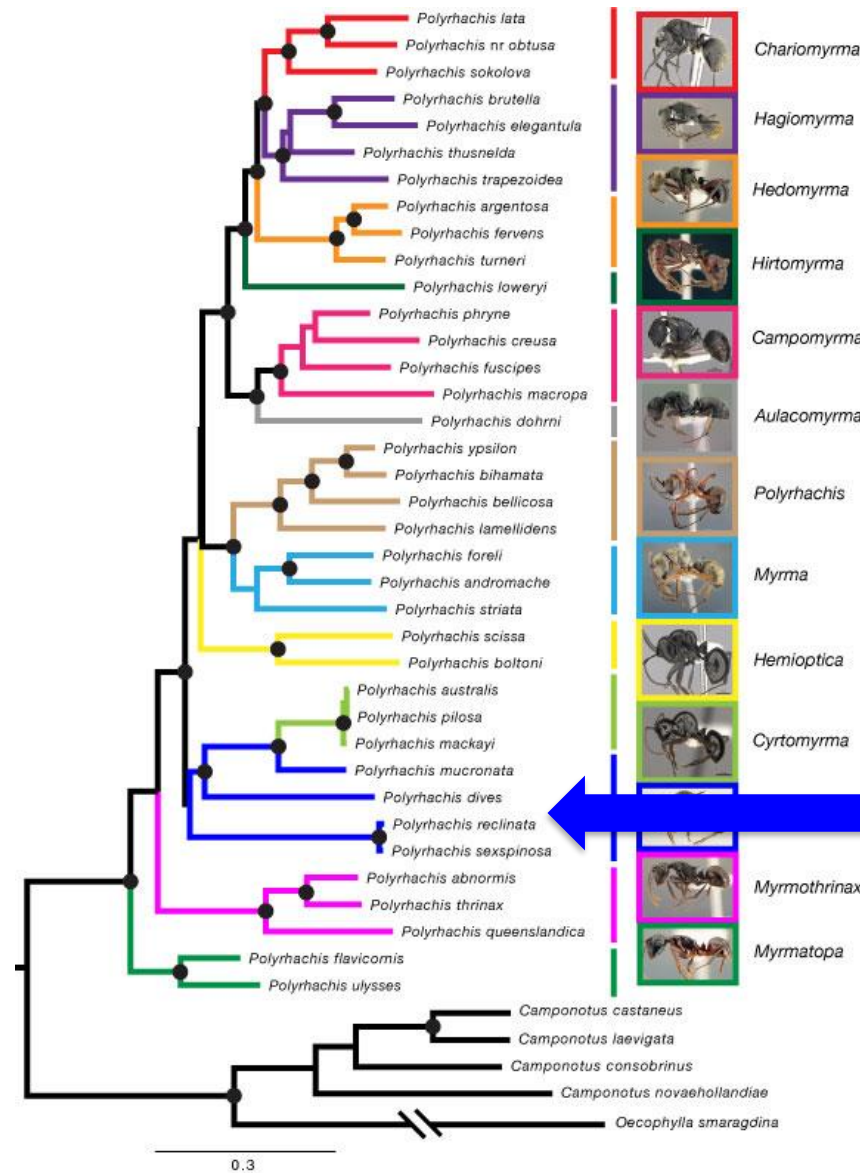
Polyrhachis has over 700 species in 13 subgenera

-- Hölldobler & Wilson (1990) *The Ants*. Harvard Univ. Press

Testing monophyly of genus and subgenera

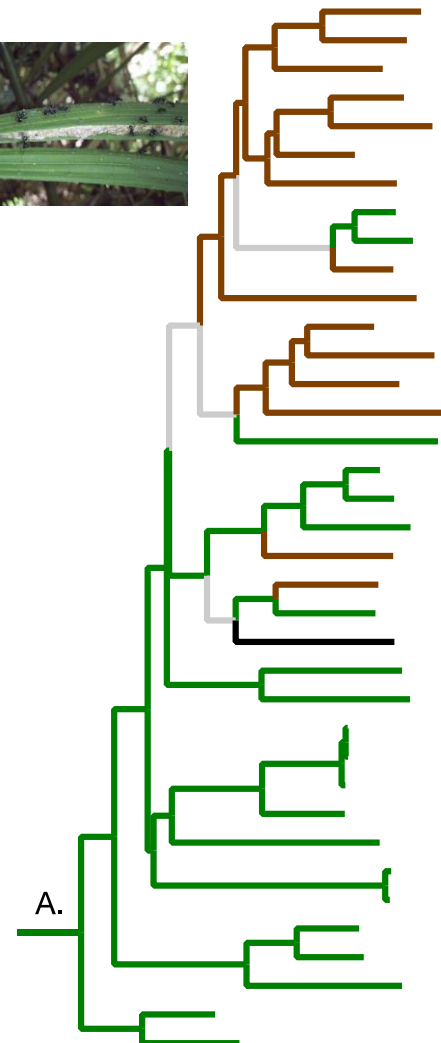
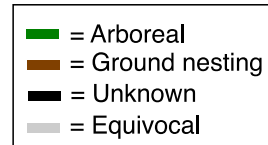
Inferring the phylogeny of *Polyrhachis*

- Members of all 13 subgenera included
- Three mitochondrial and three nuclear genes sequenced
- ~5,000 bp of sequence data
- Bayesian Inference phylogeny with data partitioned for site specific models for each codon of each gene (18 partitions)
- Black dots on nodes ≥ 0.95 BPP



Only *Myrmhopla* recovered as non-monophyletic

Evolution of nest preference



Arboreal nesting is
ancestral in spiny
ants

Ancestral State Reconstruction

- Mesquite (Mk1 likelihood reconstruction method)
- SIMMAP (two-state characters a beta distribution prior was used for the bias parameter and for multi-state characters an empirical prior was used. For all cases the gamma distribution prior of the rate parameter was assigned $k = 90$)
- All clades in green and brown received >95% support in both analyses

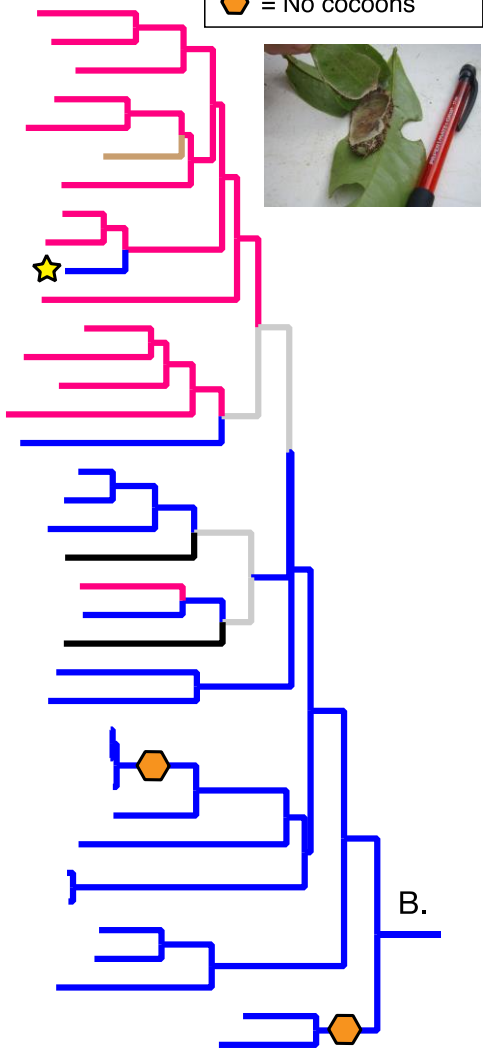
Evolution of silk weaving

Silk weaving is ancestral in spiny ants

Spider silk adopted

Larval cocoons lost

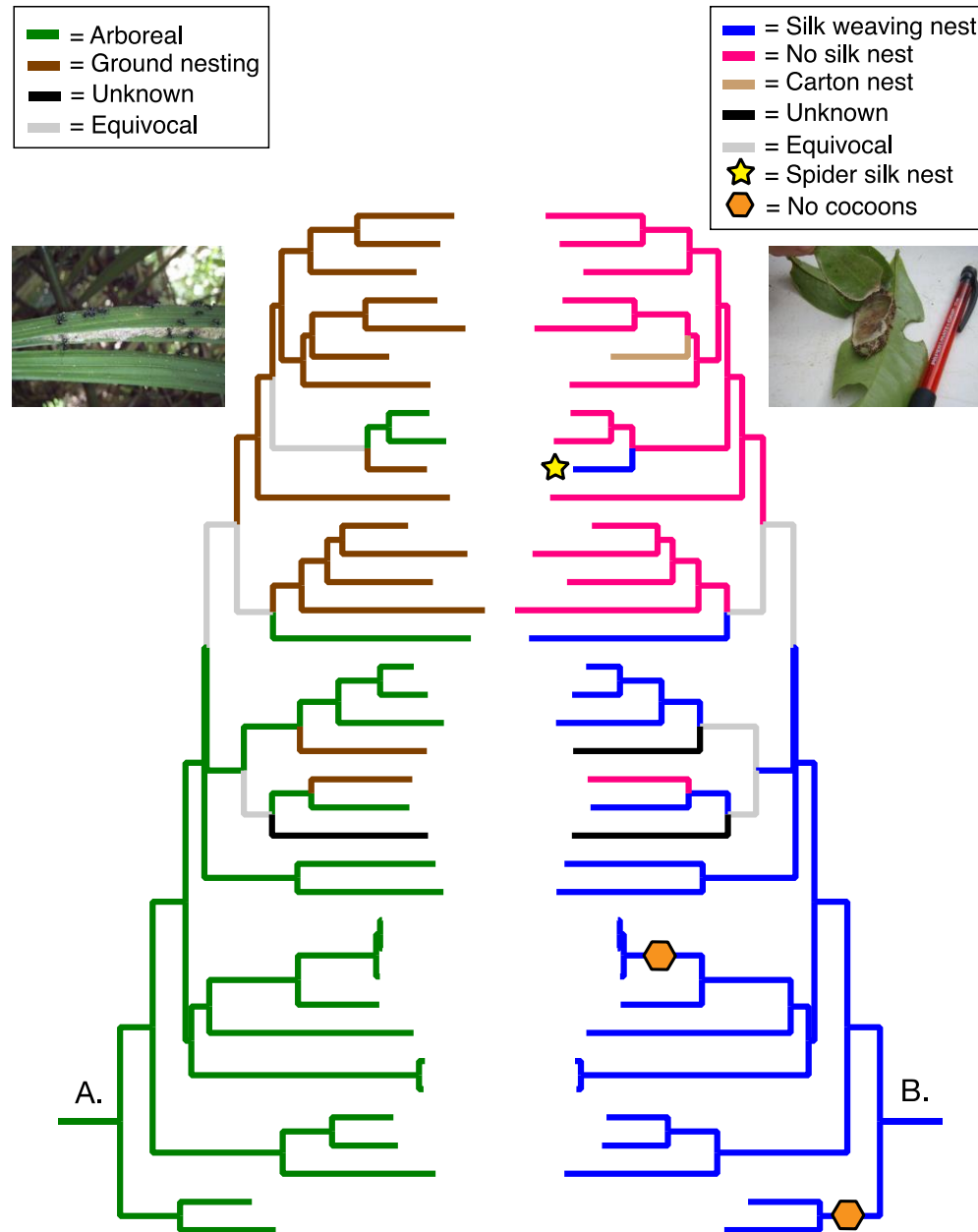
- = Silk weaving nest
- = No silk nest
- = Carton nest
- = Unknown
- = Equivocal
- ★ = Spider silk nest
- ⬡ = No cocoons



Ancestral State Reconstruction

- Mesquite (Mk1 likelihood reconstruction method)
- SIMMAP (two-state characters a beta distribution prior was used for the bias parameter and for multi-state characters an empirical prior was used. For all cases the gamma distribution prior of the rate parameter was assigned k = 90)
- All clades in blue and pink received >95% support in both analyses

Correlation of traits



Tests of correlated characters

- Mesquite using Pagel's 1994 correlation analysis
- SIMMAP using Huelsenbeck et al. 2003 measure of character state associations
- All analyses found $P = 0.00$
- In every case silk weaving and arboreal nesting and no silk use and ground nesting were positively associated with each other

Evolution of silk weaving in *Polyrhachis*

- Contrary to previous hypotheses arboreal nesting and larval silk weaving are the ancestral states in *Polyrhachis*
- These characters are highly correlated
- We see the loss of a complex behavior in weaving ants



Photograph © Alex Wild

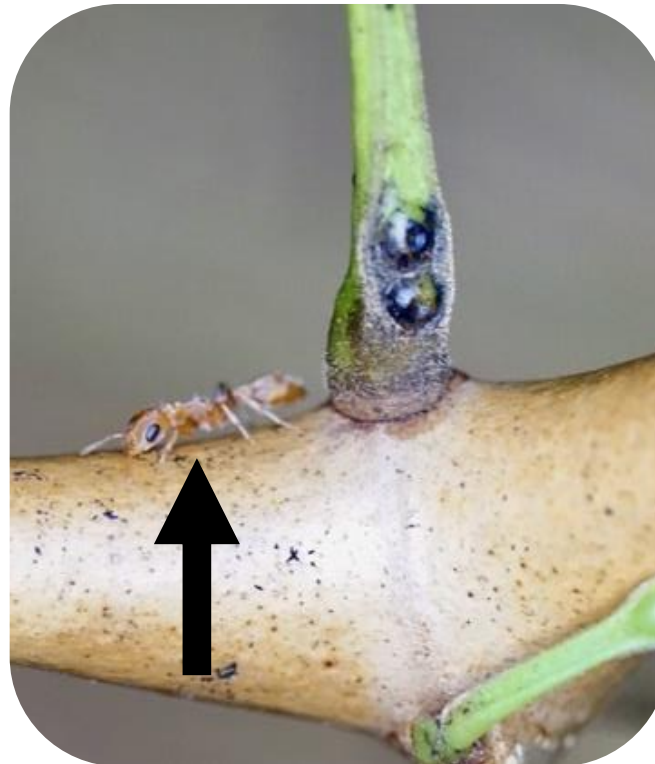
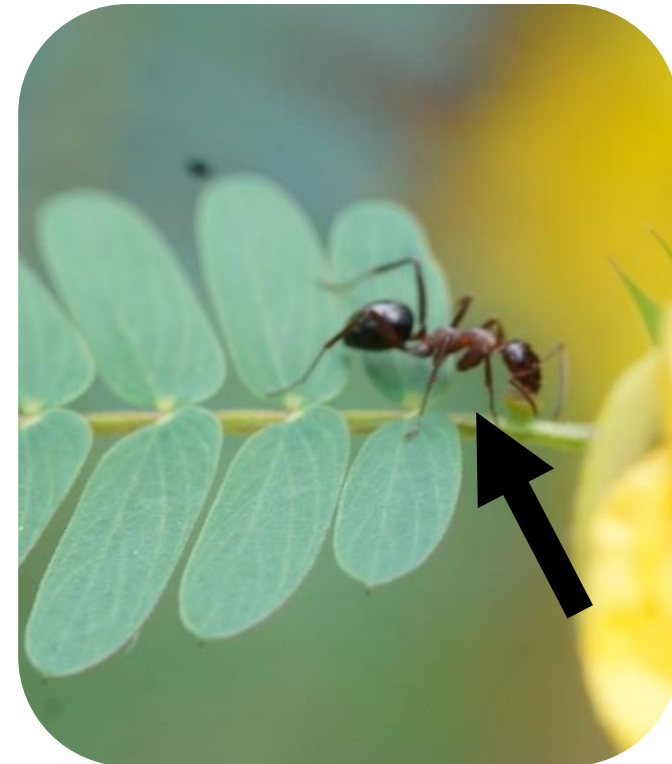
The evolution of nectaries in non-flowering
plants

Jacob Suissa



EFNs as external defense mechanisms

When, why, and how did nectaries evolve outside of non-flowering plants?

Catalpa*Vachellia**Chamaecrista*

Jacob Suissa



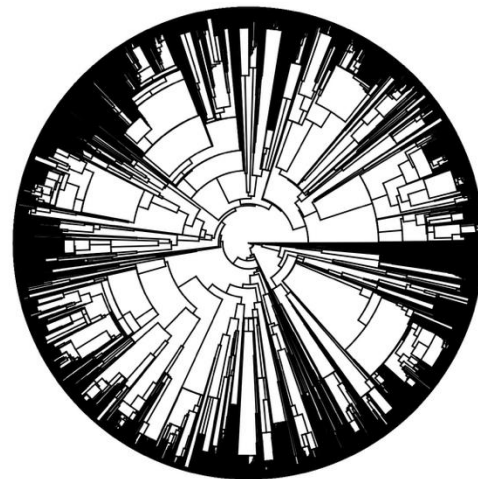
How did we study this?

Ferns



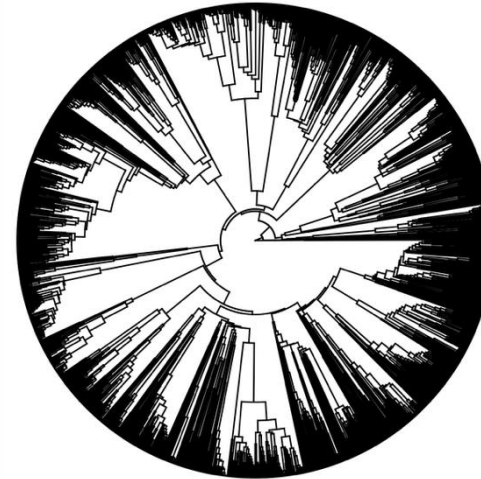
Nitta *et al.*, 2022

Angiosperms



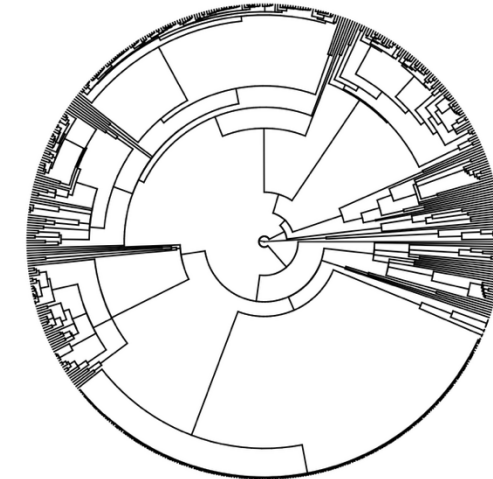
Smith and Brown *et al.*, 2022

Ants



Nelsen, Ree, & Moreau 2018

Fern Herbivores

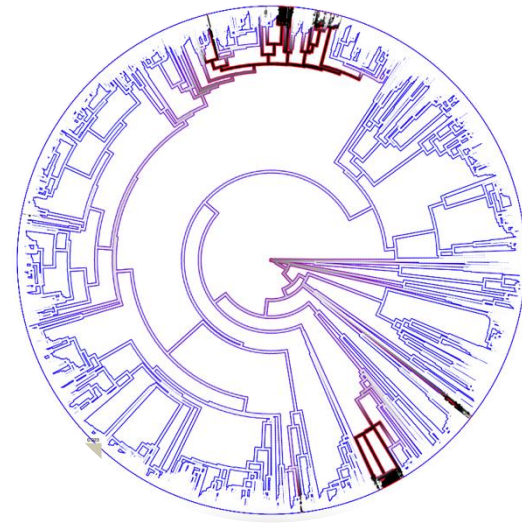
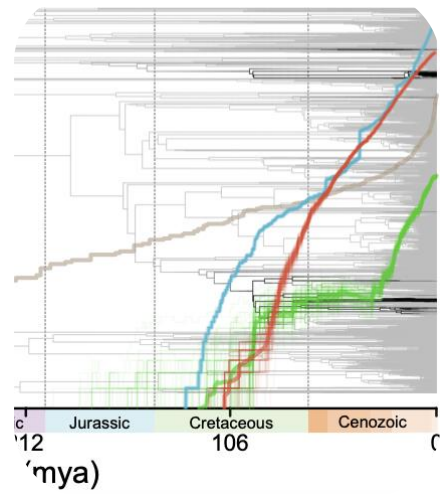
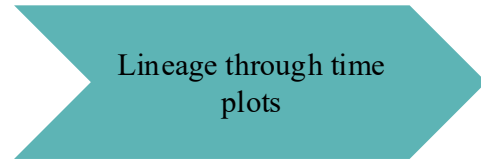
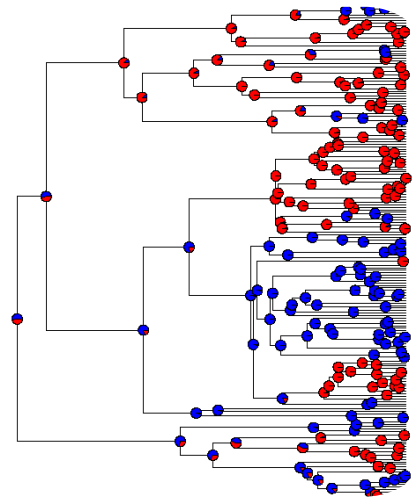
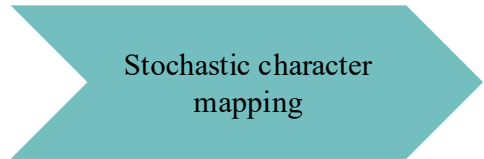
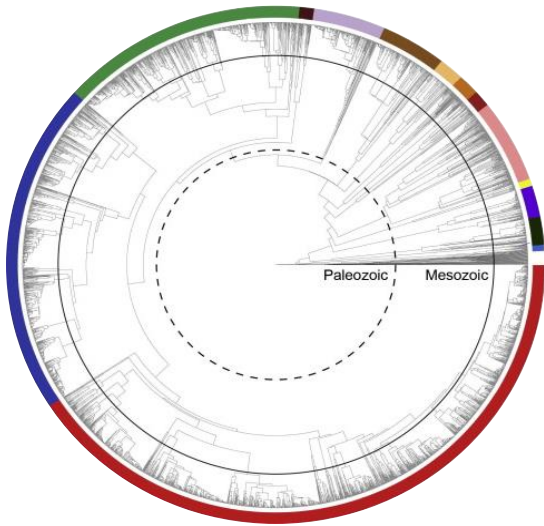
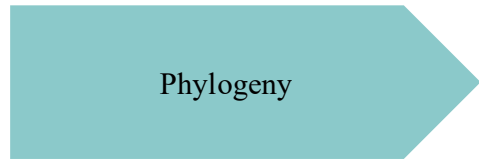


Suissa *et al.*, in review

Jacob Suissa



Methodology



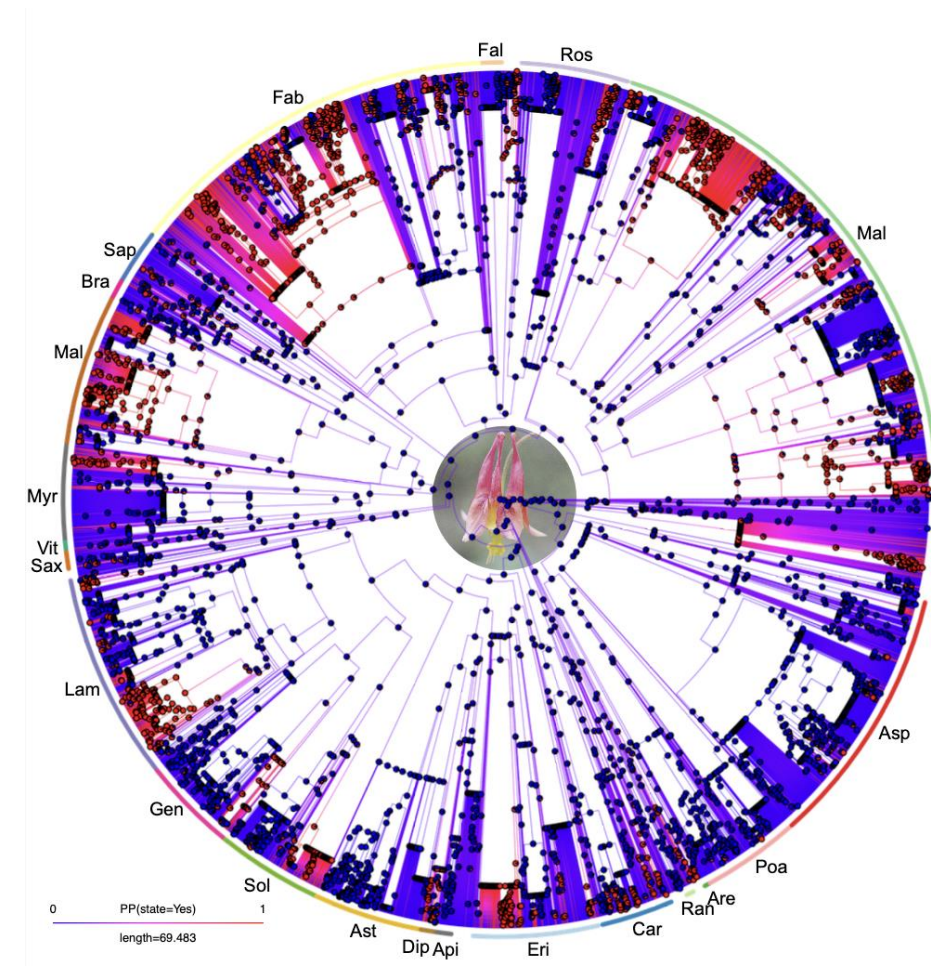
Jacob Suissa



Diversity of EFNs in Angiosperms

1555
gains

2318
losses



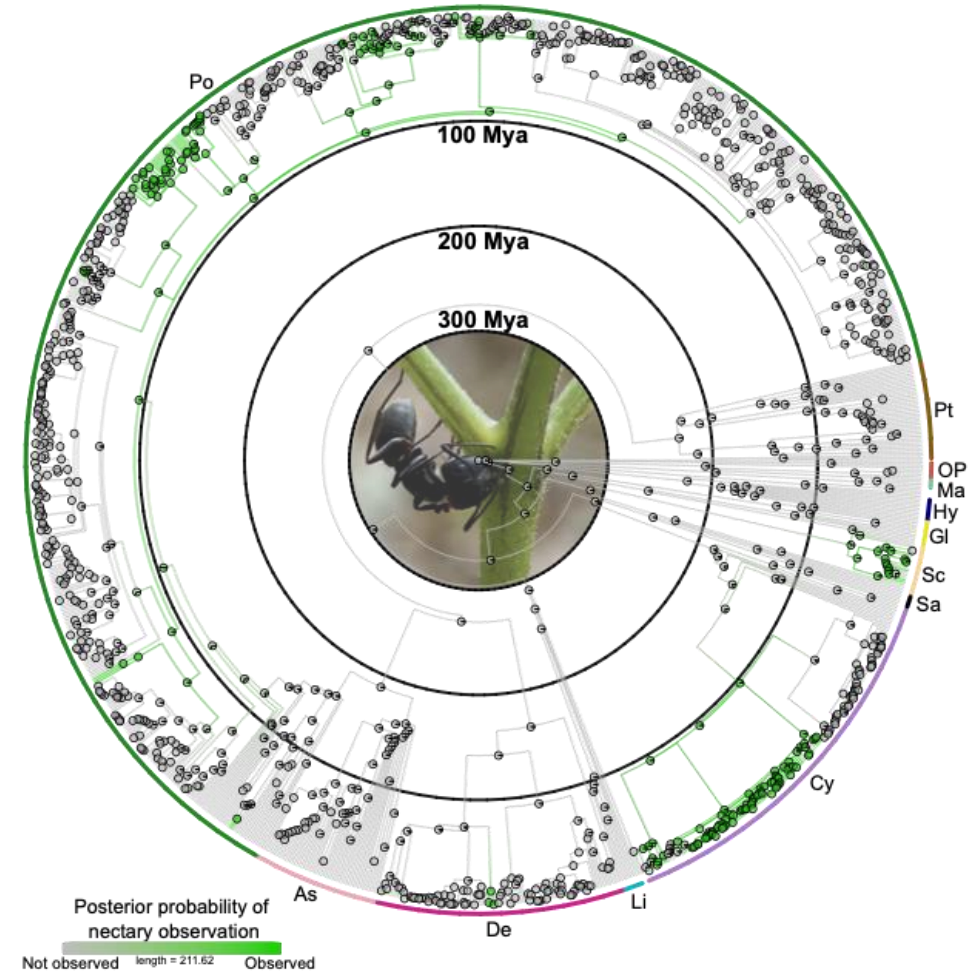
Jacob Suissa



Diversity of EFNs in Ferns

11 gains

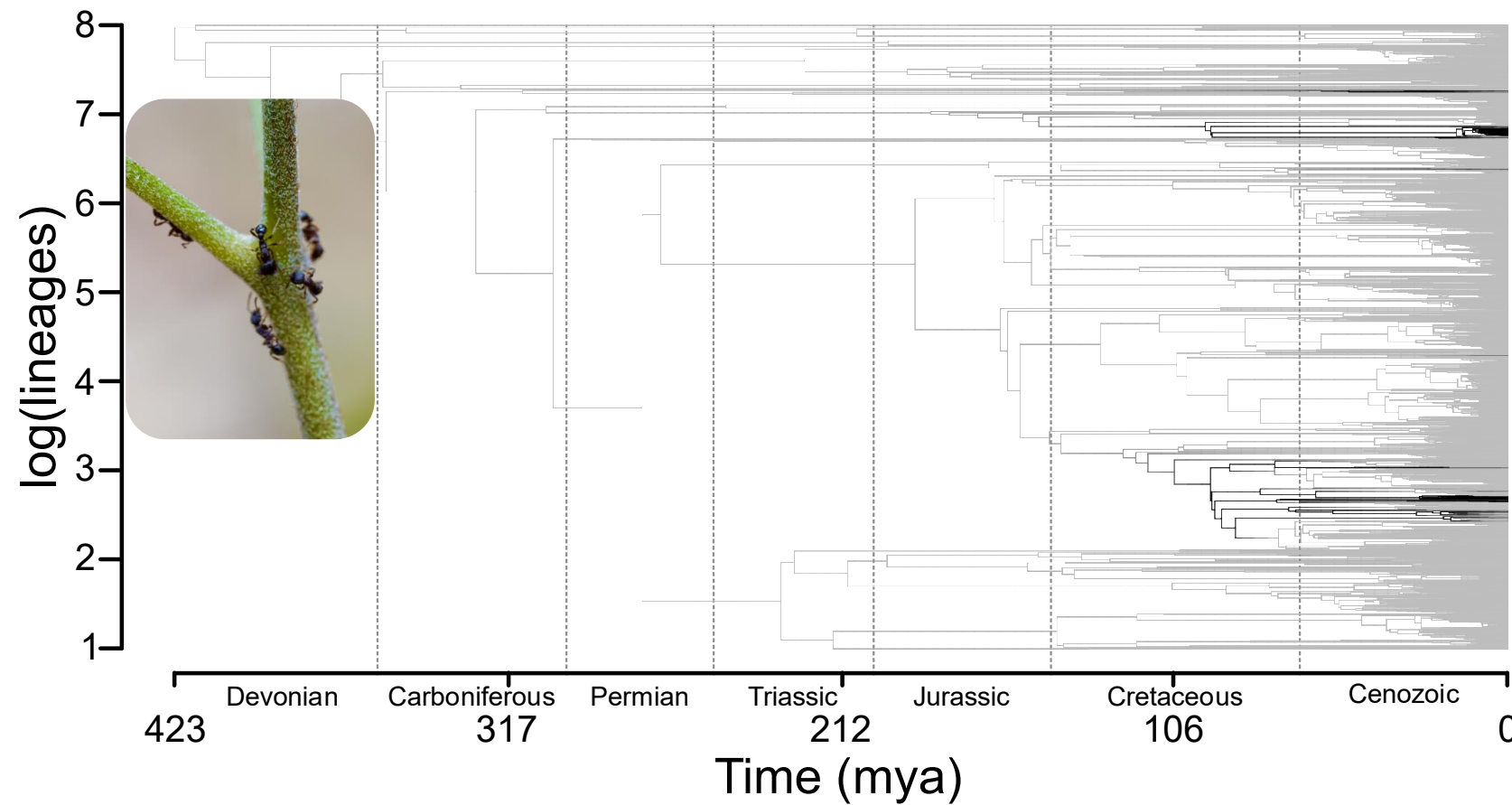
2 losses



Jacob Suissa



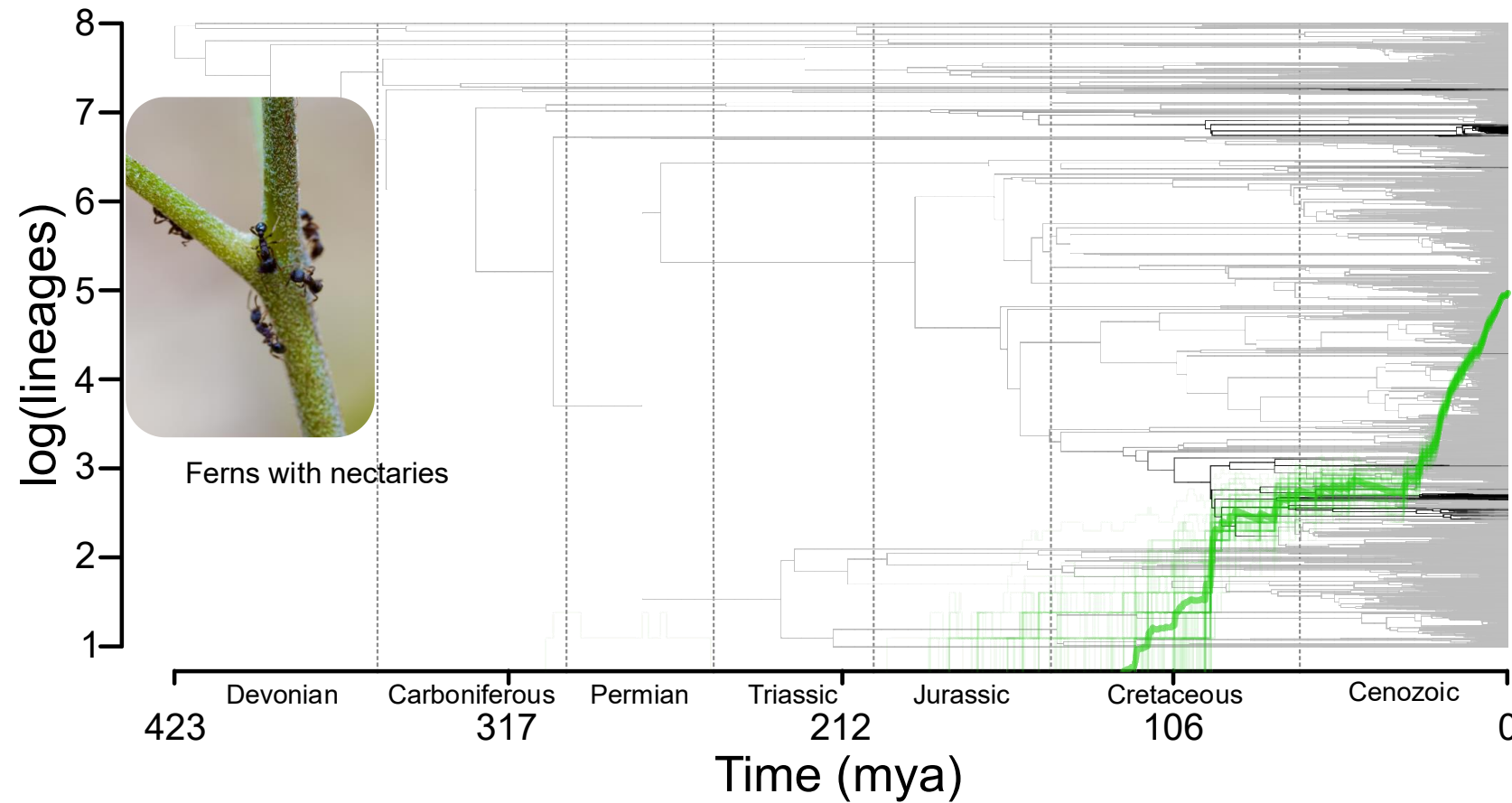
Tempo and mode of nectary evolution



Jacob Suissa



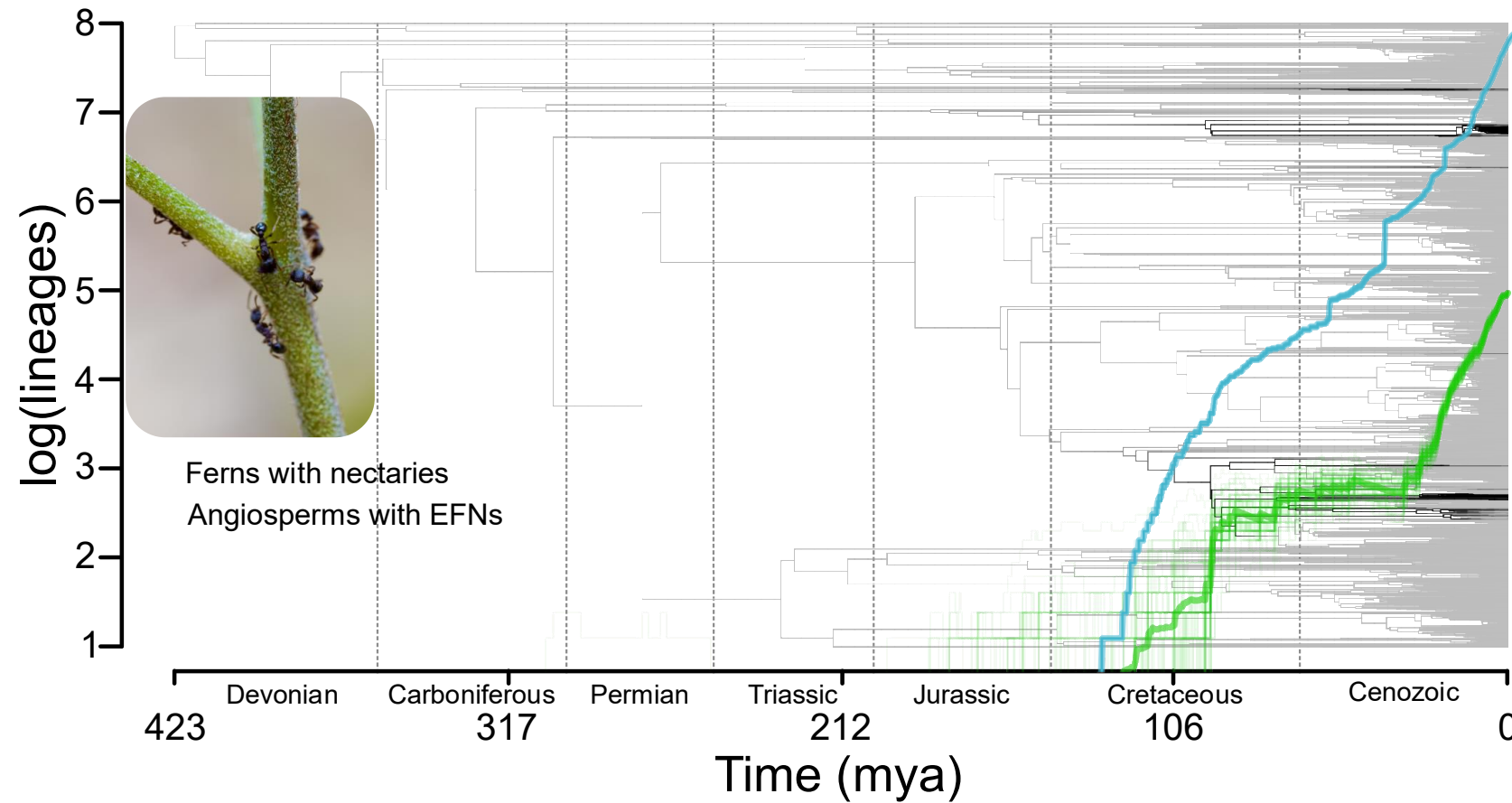
Cretaceous origin of nectaries in ferns



Jacob Suissa



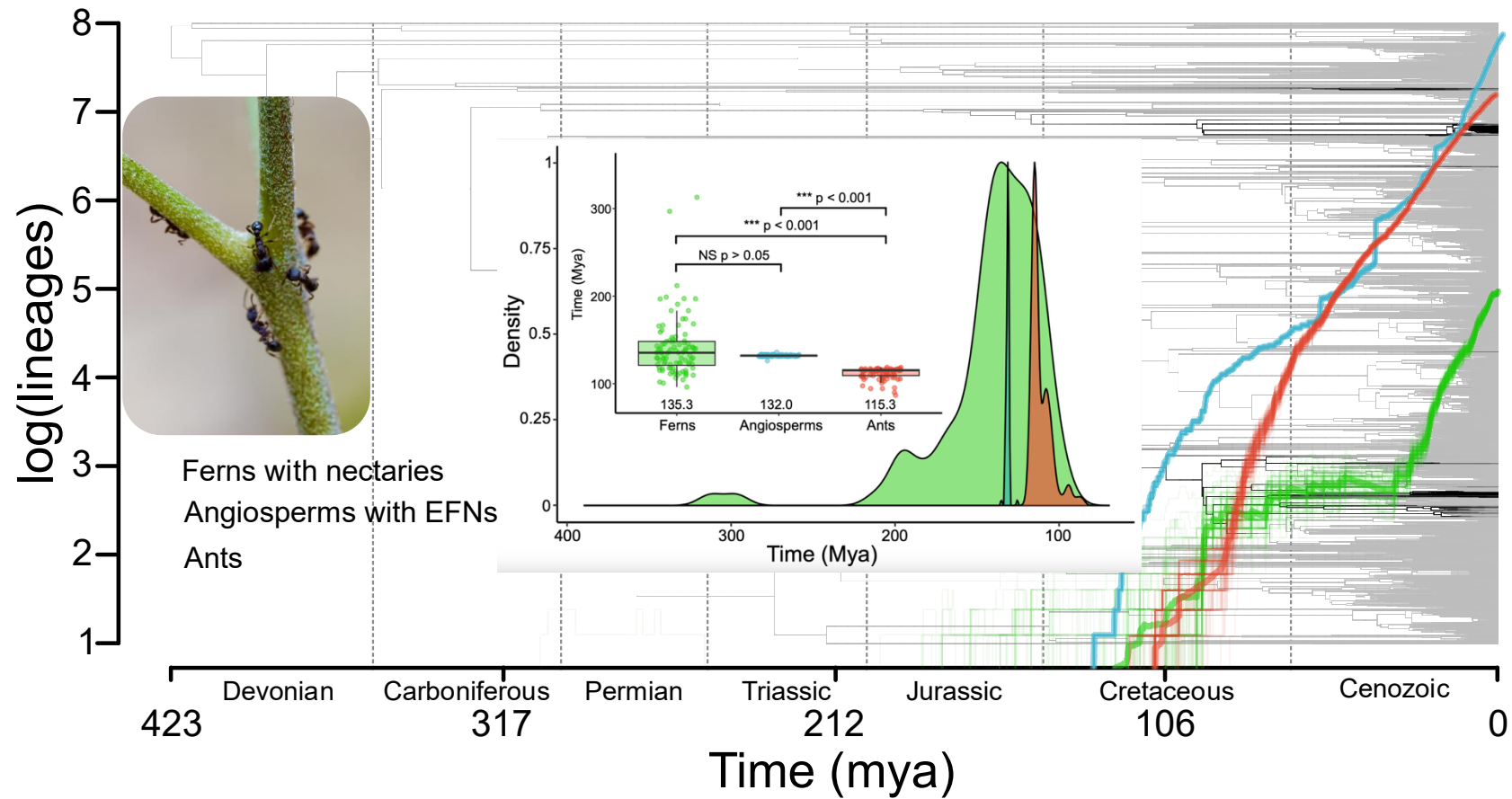
Cretaceous origin of nectaries in ferns and angiosperms



Jacob Suissa



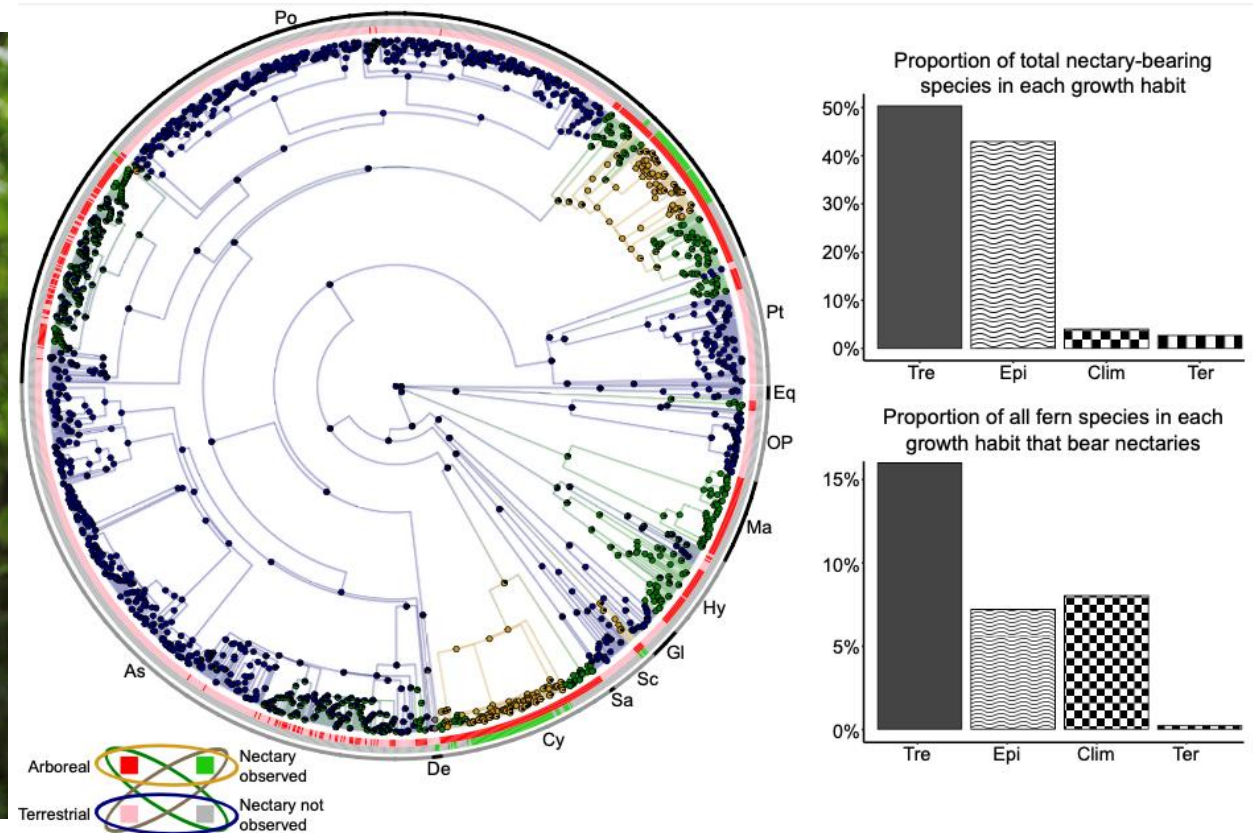
Origin of nectaries corresponds to the rise of arboreal ants



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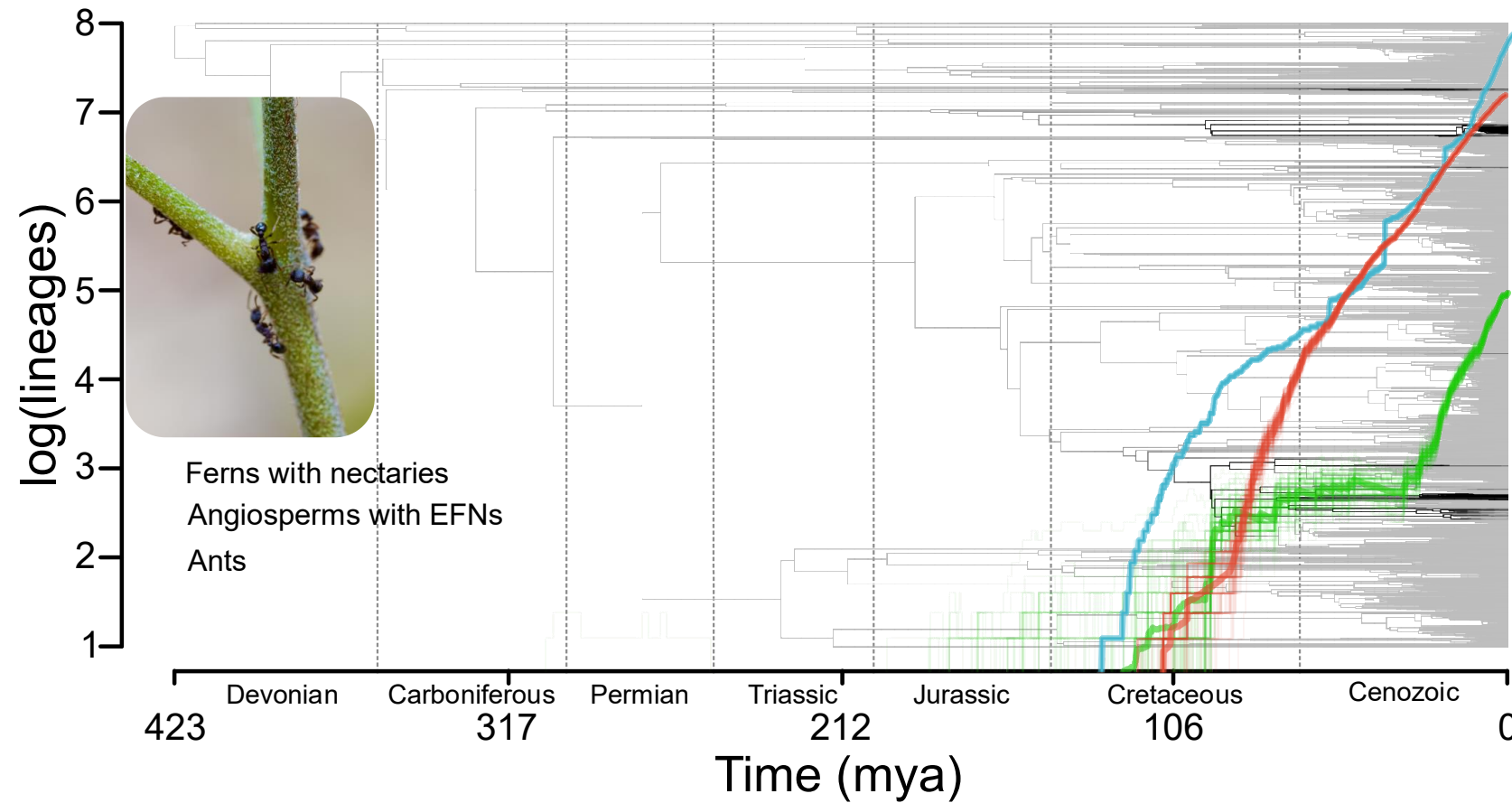
Proximity is key in fern-nectary evolution



Jacob Suissa



Lag of nectary diversification in ferns



Jacob Suissa



Increased herbivory during the Cenozoic, a general pattern

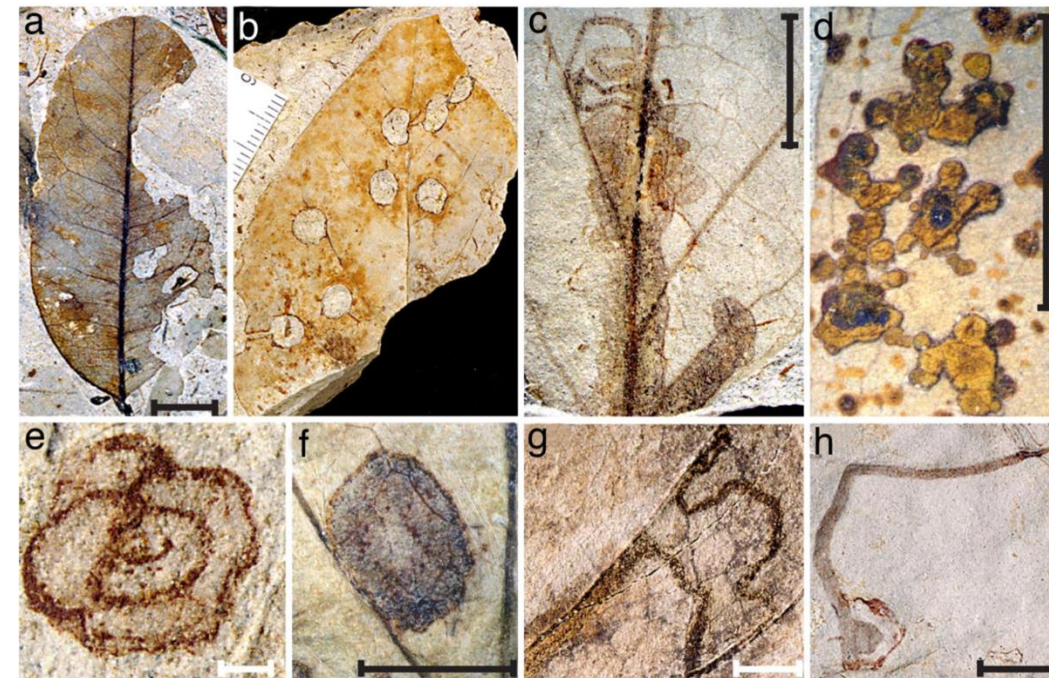
PNAS

Sharply increased insect herbivory during the Paleocene–Eocene Thermal Maximum

Ellen D. Currano^{*†‡}, Peter Wilf^{*}, Scott L. Wing[†], Conrad C. Labandeira^{*§}, Elizabeth C. Lovelock[¶], and Dana L. Royer^{||}

^{*}Department of Geosciences, Pennsylvania State University, University Park, PA 16802; [†]Department of Paleobiology, Smithsonian Institution, Washington, DC 20560; [‡]Department of Entomology, University of Maryland, College Park, MD 20742; [§]Department of Earth Science, University of California, Santa Barbara, CA 93106; and ^{||}Department of Earth and Environmental Sciences, Wesleyan University, Middletown, CT 06459

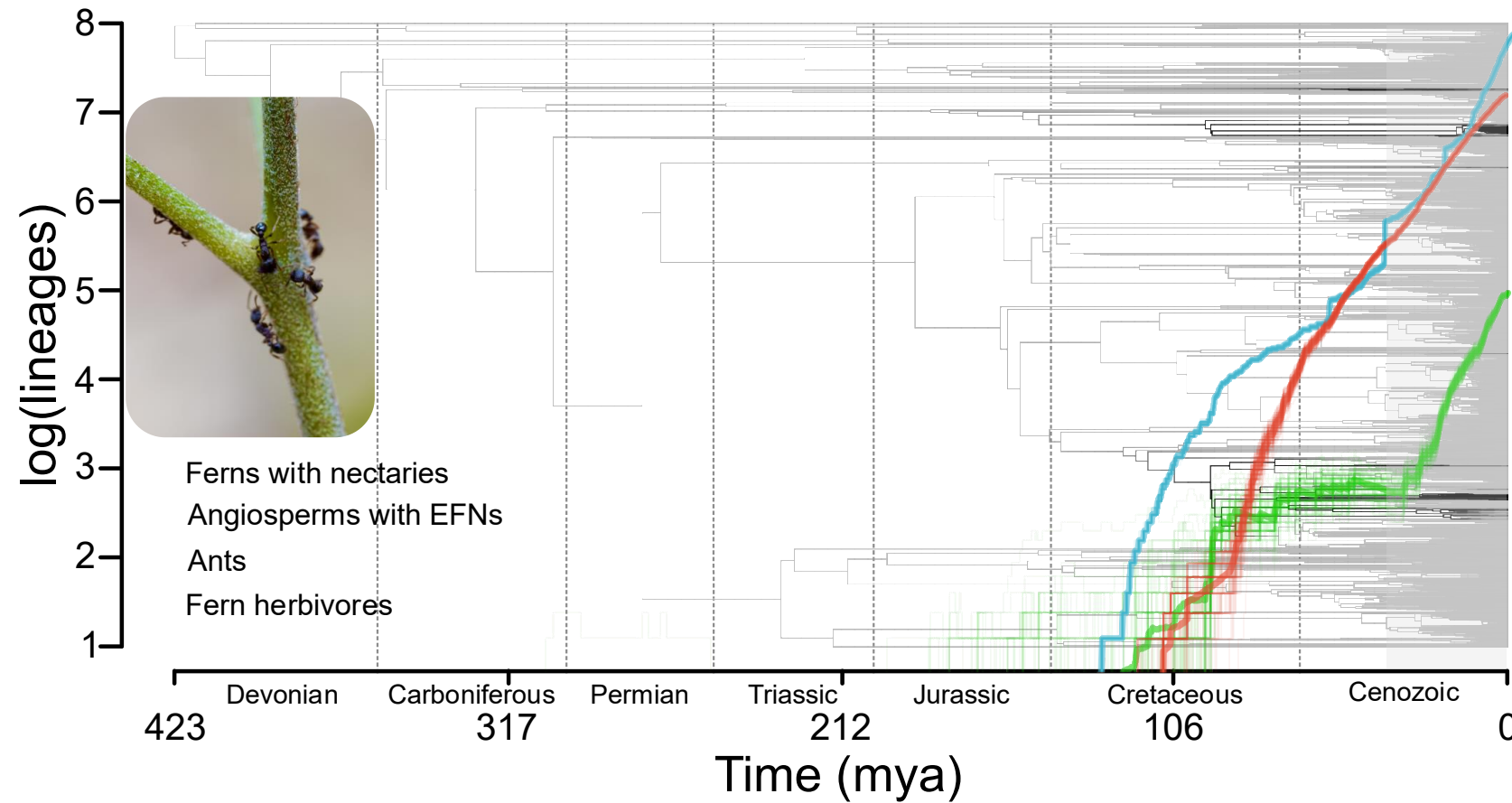
Edited by May R. Berenbaum, University of Illinois at Urbana–Champaign, Urbana, IL, and approved December 3, 2007 (received for review September 11, 2007)



Jacob Suissa



What about fern herbivores?



Fern nectary evolution

- Convergent evolution of fern nectaries
- Nectaries are more prevalent in canopy ferns
- Facilitated independent recruitment of ant-bodyguards from flowering plants
- Lag in evolution of nectaries may be the result of increased herbivores

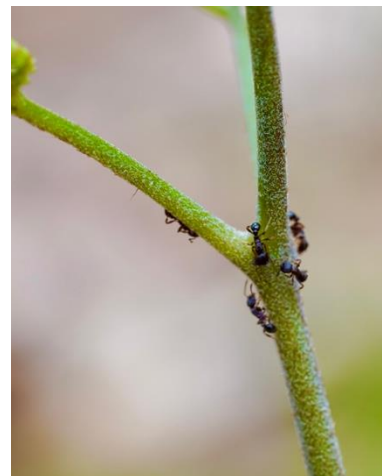


Photo by Jacob Suissa

Early and dynamic colonization of Central America
drives speciation in Neotropical army ants

Central America Colonization Models



Neotropical Army Ant Genus: *Eciton*



Photographs © Alex Wild

- Keystone invertebrate predators
- Poor dispersers due to wingless queens
- Cannot colonize across water
- Wide geographic distribution
- 12 species in genus (3 known only from males)



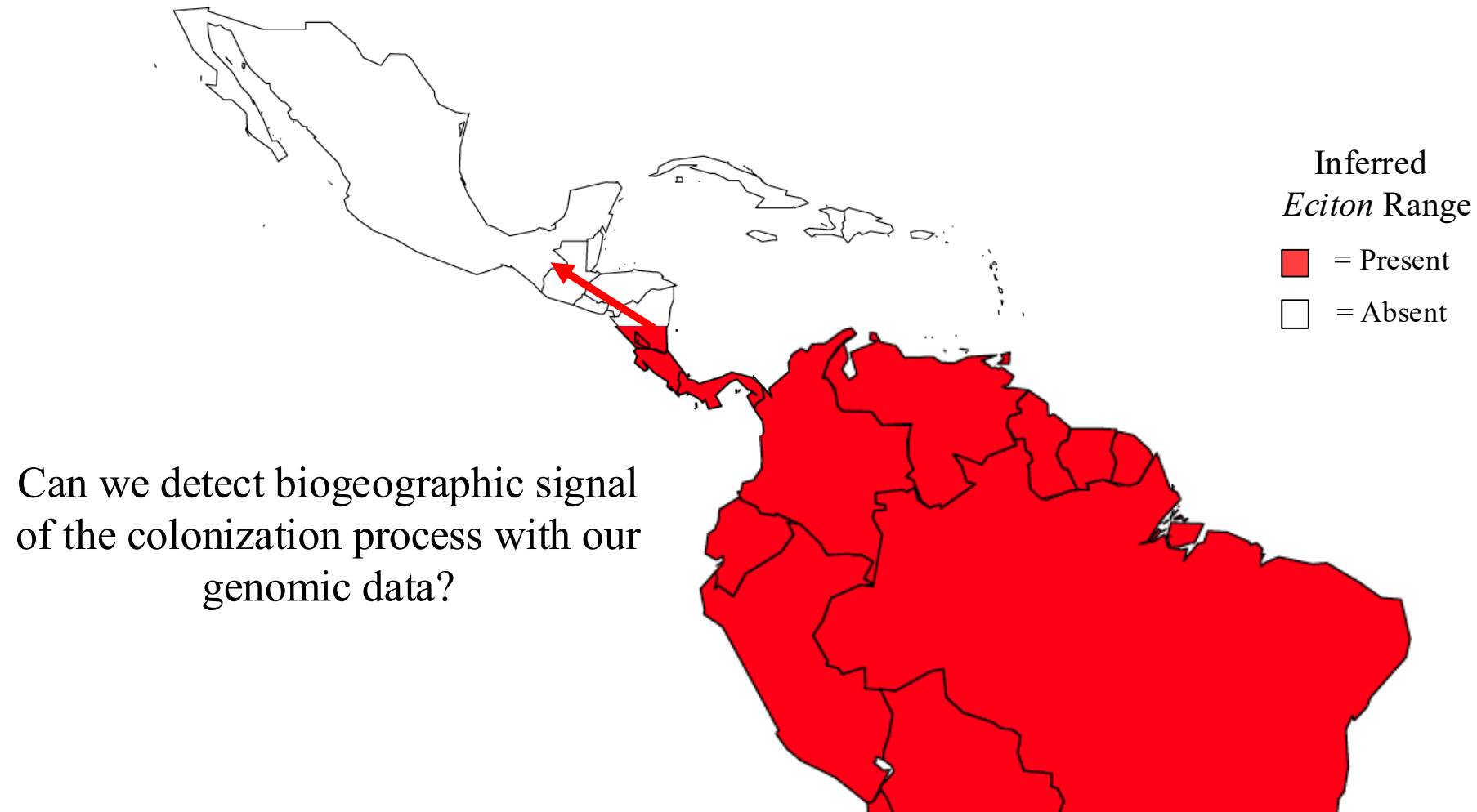
Panama provides land bridge for Central American
colonization [3.0 Ma - Today]



Complex emergence of Panama [8.0 – 3.0 Ma]



Given the possibility of early colonization of Central America over ephemeral land bridges before full closure of the isthmus



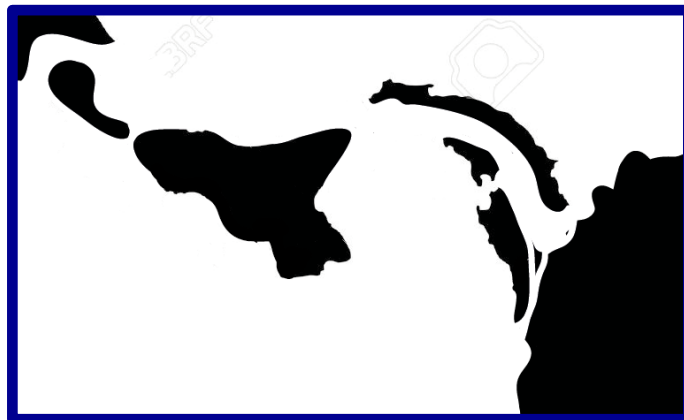
Central America Colonization Models

Expectations



Full Closure Colonization (FCC)

- Colonization after full closure (3 Ma)
- No increase of diversification in CA
- Divergence times on isthmus less than 3 Ma
- Secondary contact zones randomly distributed



Early Dynamic Colonization (EDC)

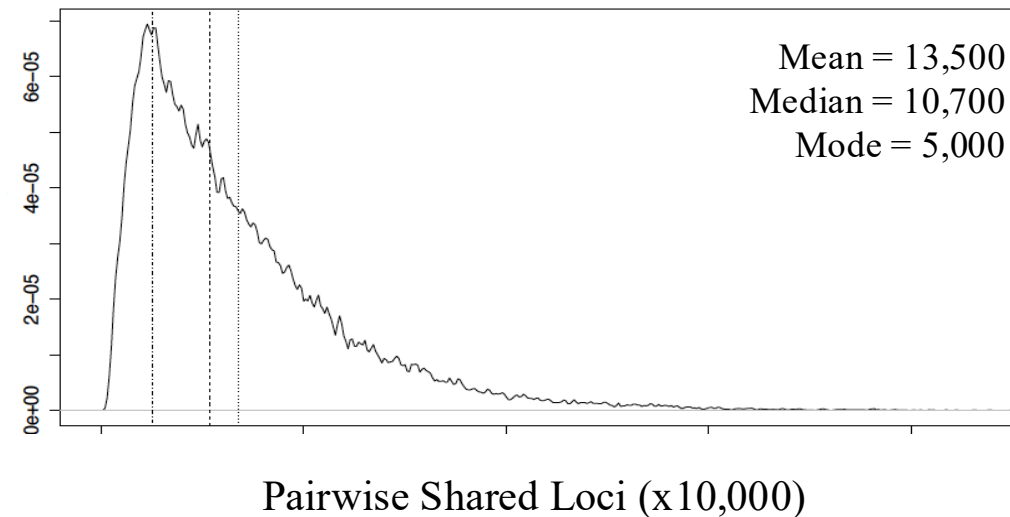
- Colonization across early land bridge (3 – 8 Ma)
- Increase of diversification in CA
- Divergence times between 3 – 8 Ma
- Secondary contact zones potentially coincident

De novo locus assembly of 630 million barcoded reads from 146 army ant samples

Max Winston



All samples had over 10,000 loci ($N = 146$)



Loci assembly: pyRAD pipeline

- Employs *vsearch* algorithm
- *De novo* read clustering
- 1-2 weeks split on 40 cores

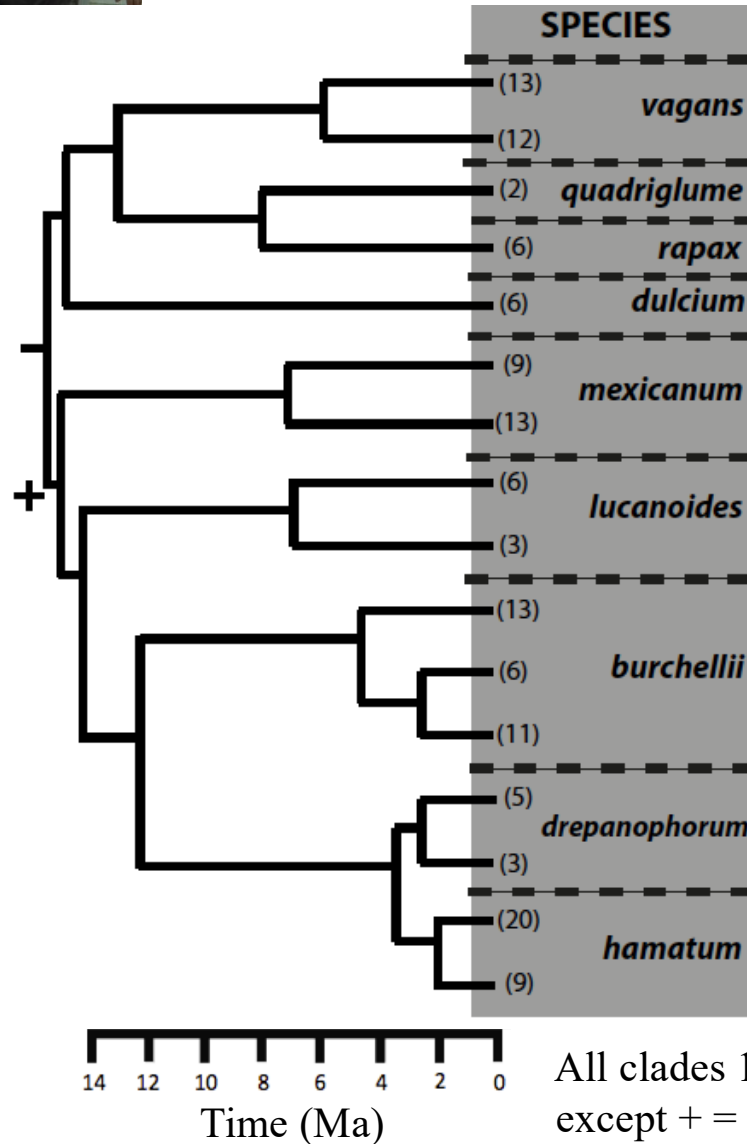
506,759 parsimony informative loci

- 100bp length
- Shared by at least 4 taxa
- Minimum 10x coverage ($\mu \approx 20$)

Max Winston



Phylogeny, Divergence Dating, and Biogeographic Inference

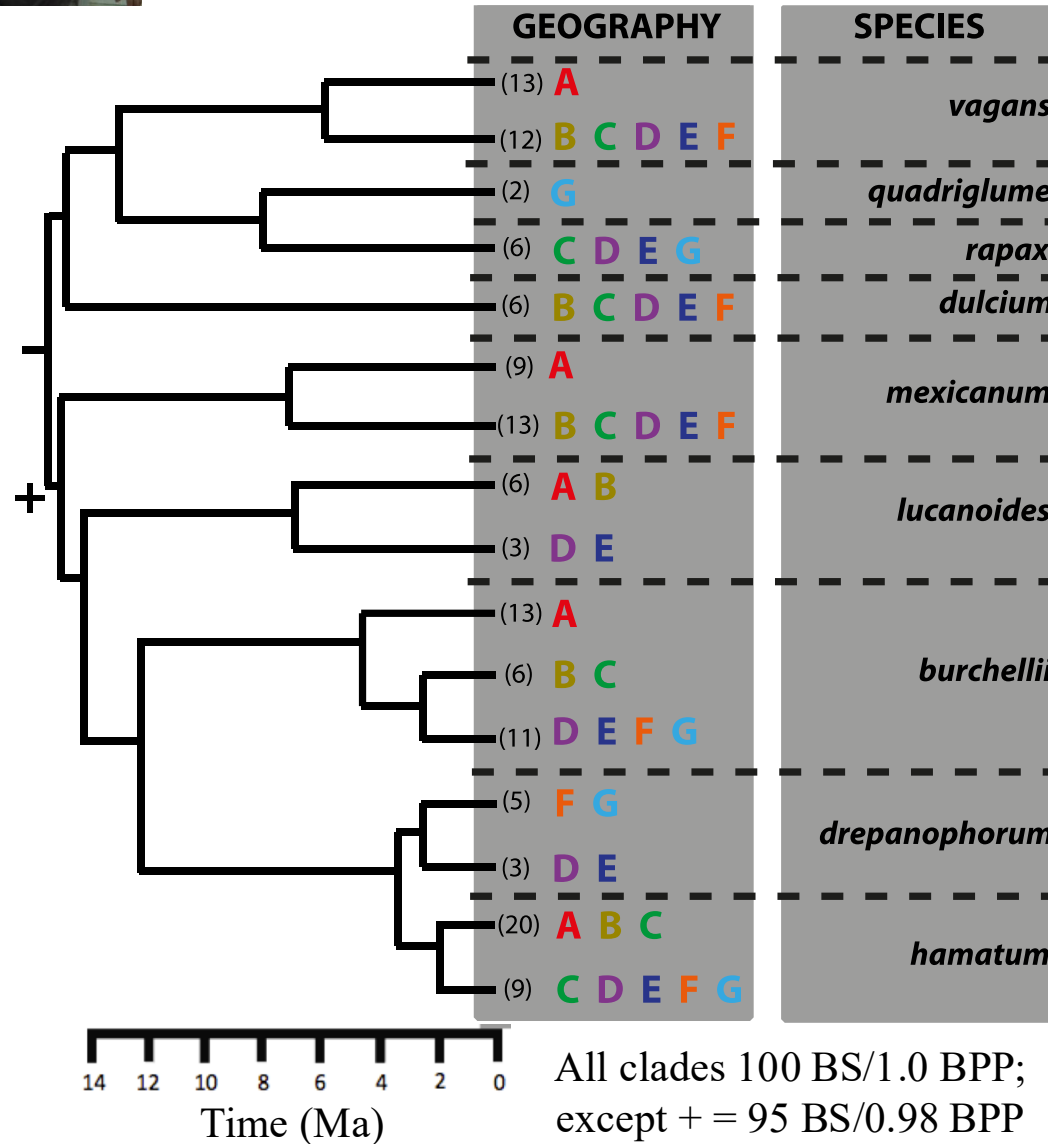


- Maximum likelihood and Bayesian inference converge on same well-supported topology
- All species recovered as monophyletic
- Many subspecies designations supported
- Multiple pairs of biological and technical replicates included

Max Winston



Phylogeny, Divergence Dating, and Biogeographic Inference

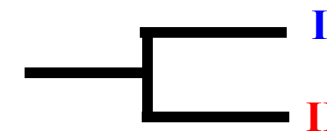
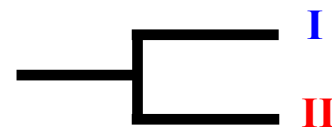
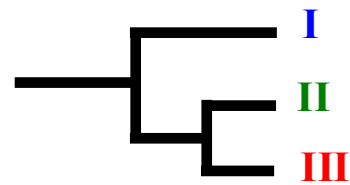
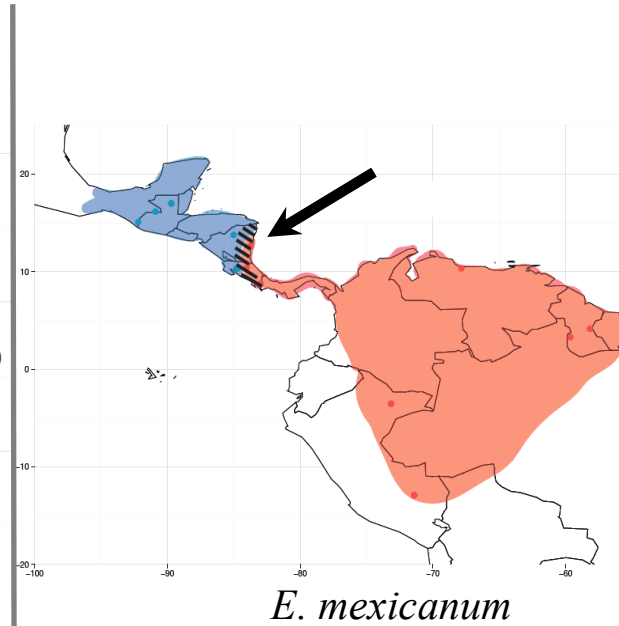
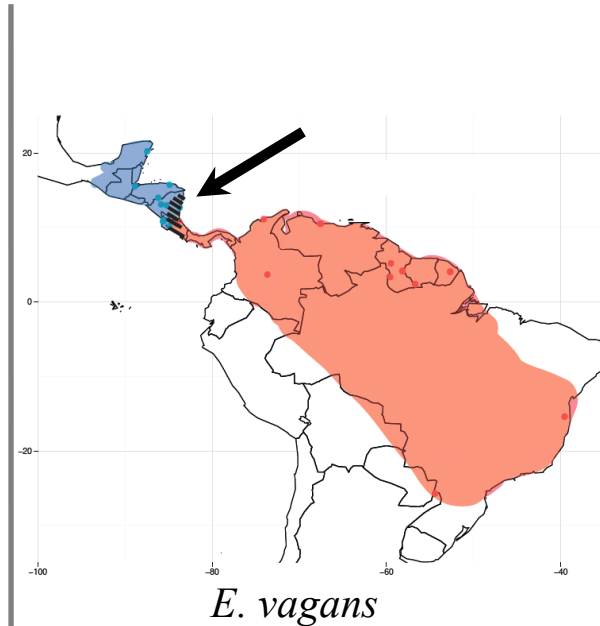
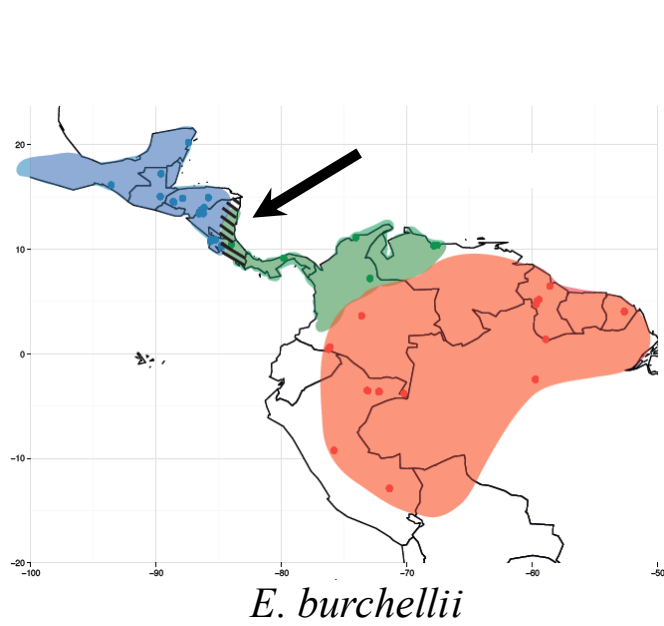


Max Winston



Coincident Secondary Contact Zones

▨ = Secondary Contact Zone



Max Winston



Phylogenomics and population genomics provide clear evidence for speciation in multiple army ant lineages that colonized Central America

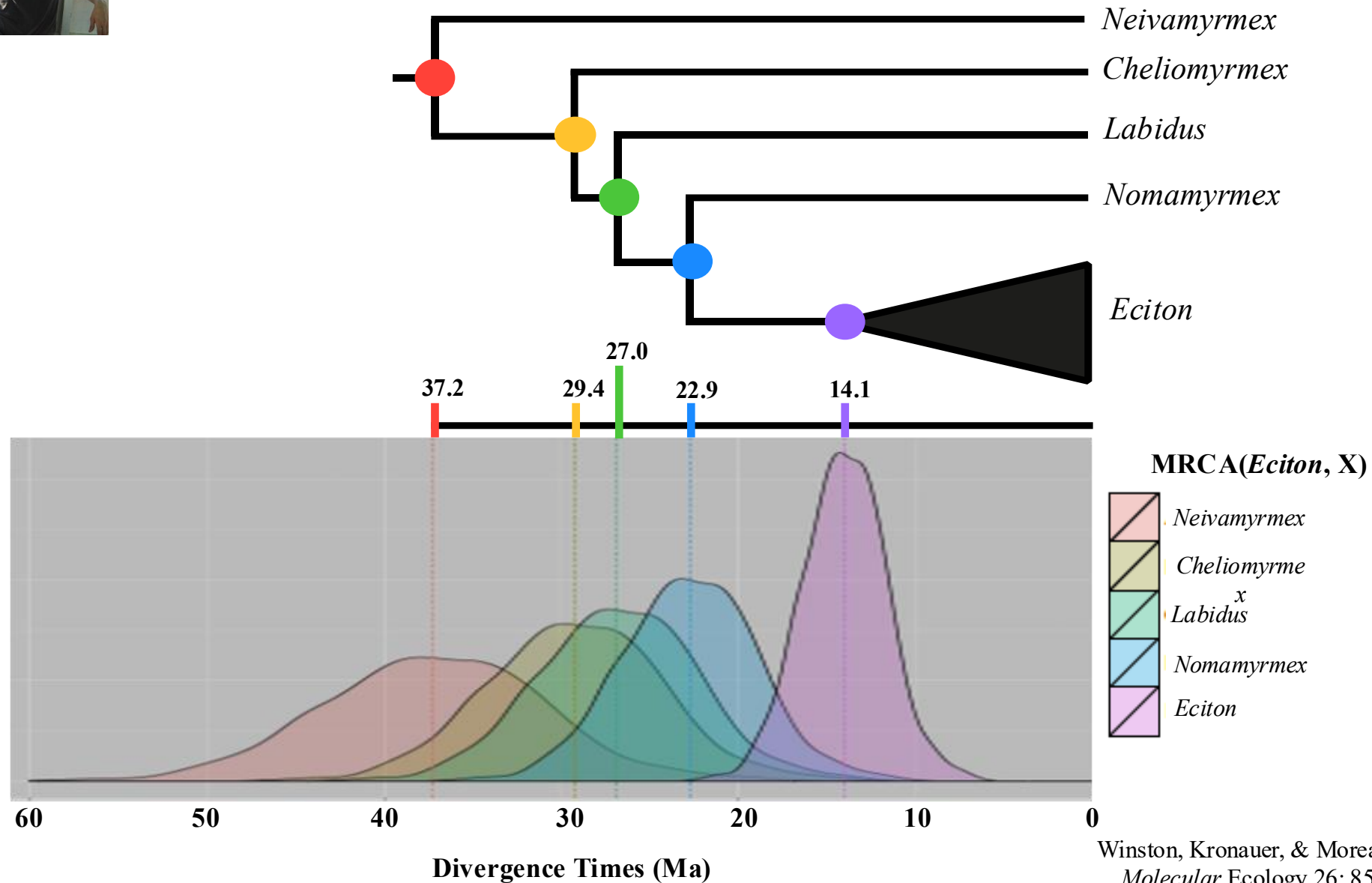


When did this speciation occur?

Max Winston



Divergence Times of Sister Lineages
Across Central American Isthmus

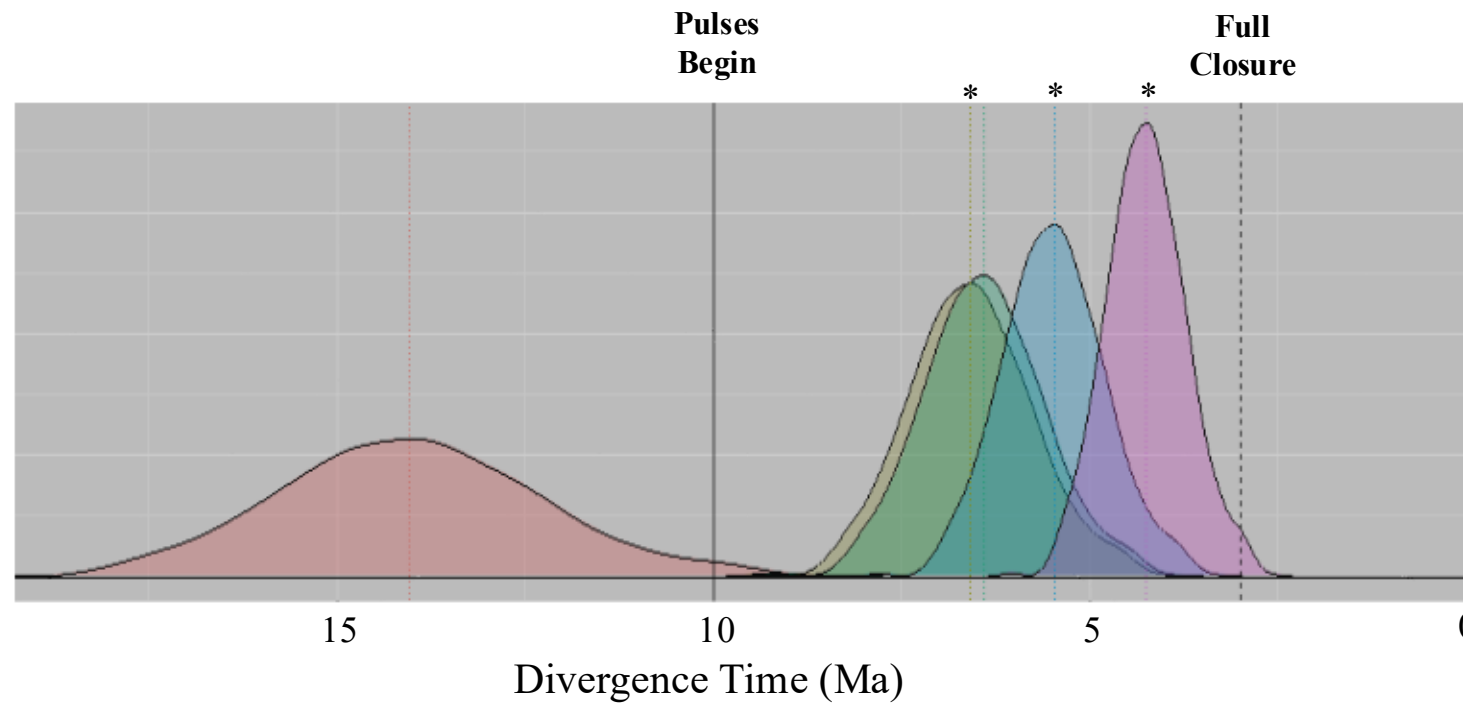
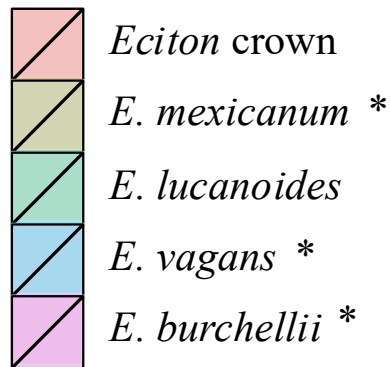
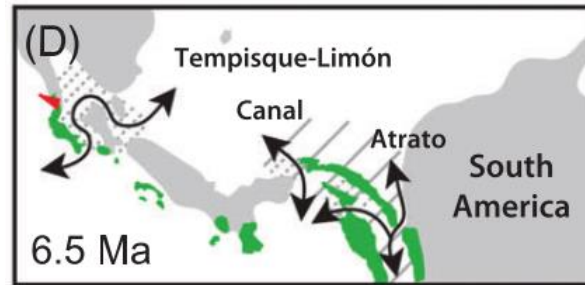


Winston, Kronauer, & Moreau (2017)
Molecular Ecology 26: 859-870.

Max Winston



Divergence Times of Sister Lineages *Across Central American Isthmus*



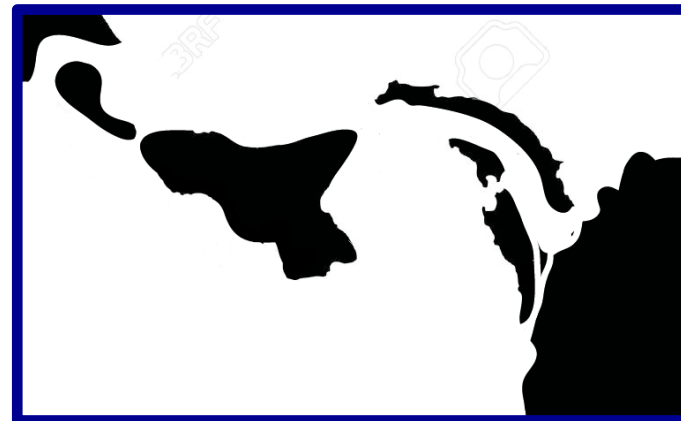
* = indicate lineages with geographically coincident species boundaries across Costa Rica, Nicaragua and Panama

Which model does the evidence support?

FCC = Full Closure Colonization model

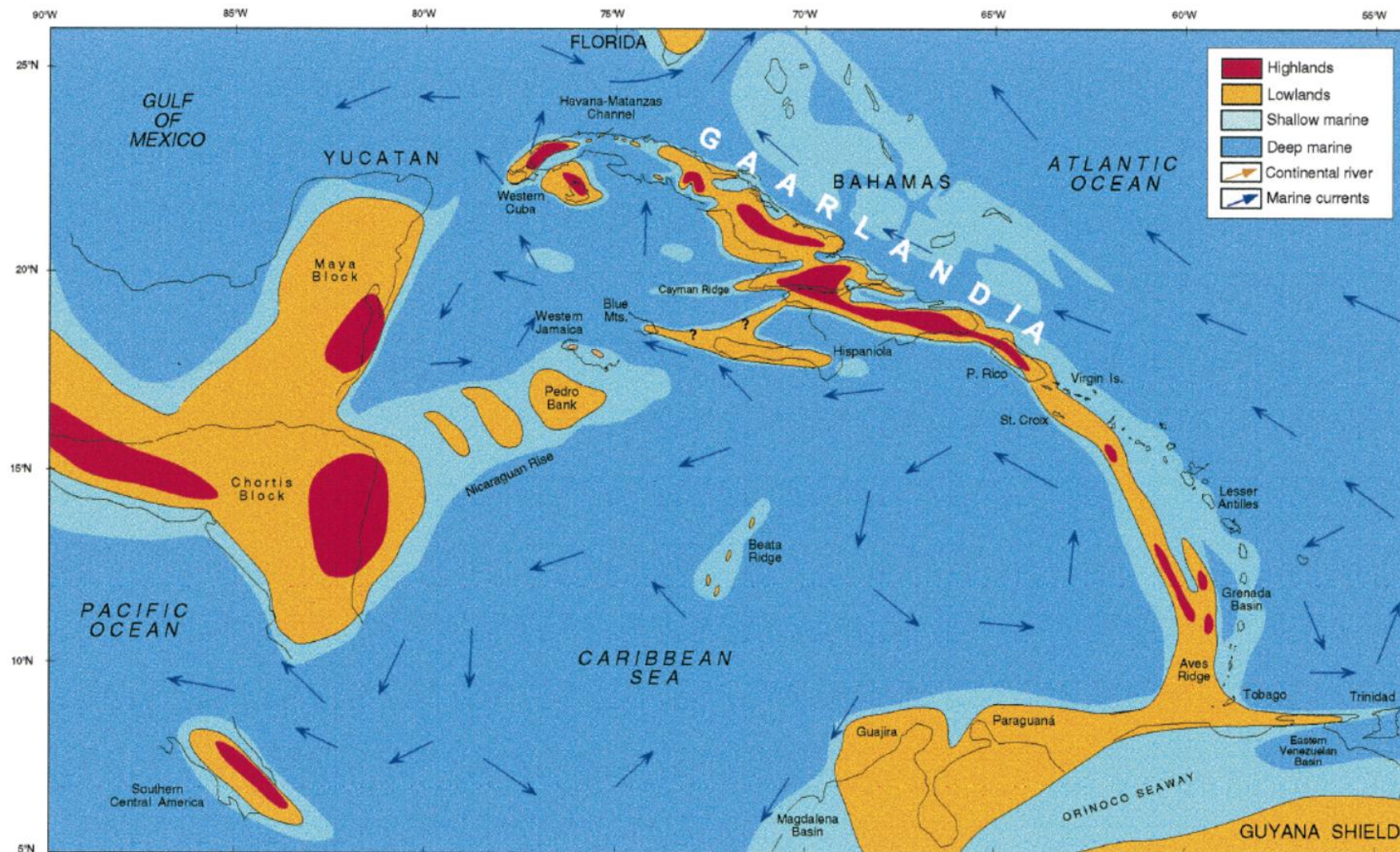
EDC = Early Dynamic Colonization model

	FCC	EDC	<u>Evidence Support</u>
<i>Diversification</i>	No effect	Increase	
<i>Divergence Times</i>	Less than 3 Ma	4 – 8 Ma	
<i>Parapatry Coincidence</i>	Random	Yes	



Early Dynamic Colonization (EDC)

GAARlandia land bridge

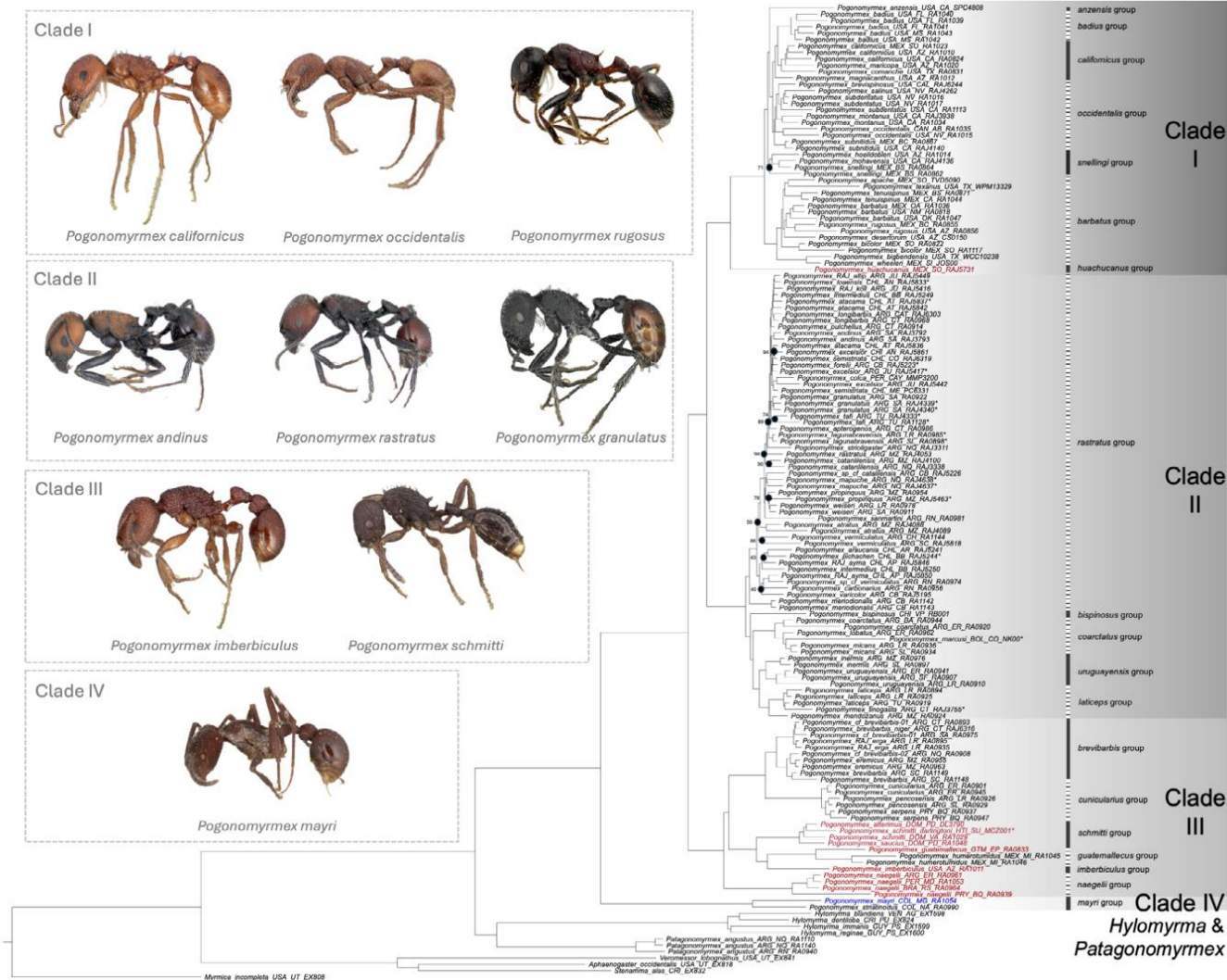


GAARlandia land-bridge model of
 Iturralde-Vinent and MacPhee (1999) *Bulletin of the American Museum of Natural History*, 238, 1–95.

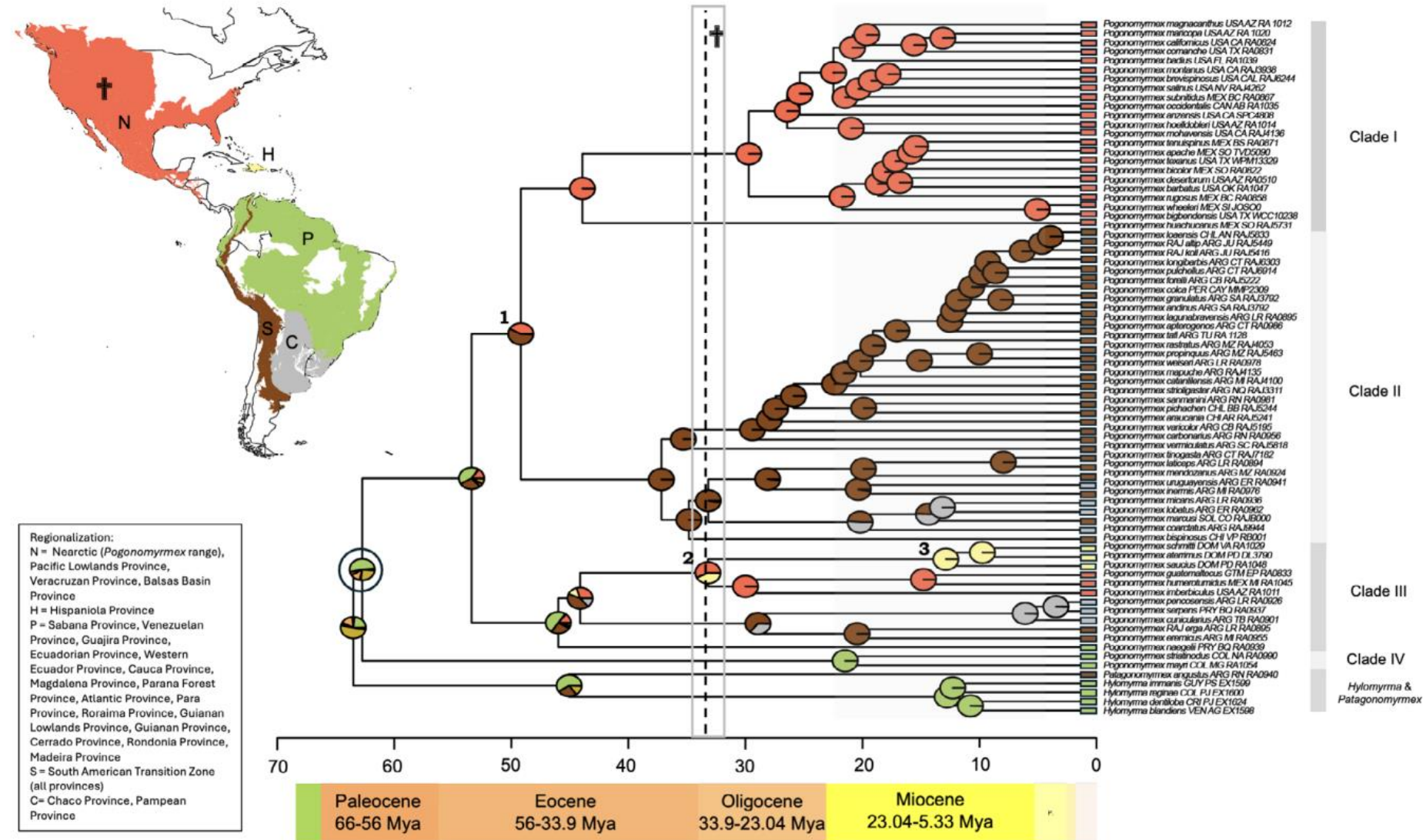
Multiple Transcontinental Dispersals of the Amphitropical Harvester Ant Genus *Pogonomyrmex*

153 samples representing 77 of the 93 described *Pogonomyrmex* species

1423 UCE loci
1,039,348 base pairs



Harvester ants dispersed before the closure of the Isthmus of Panama

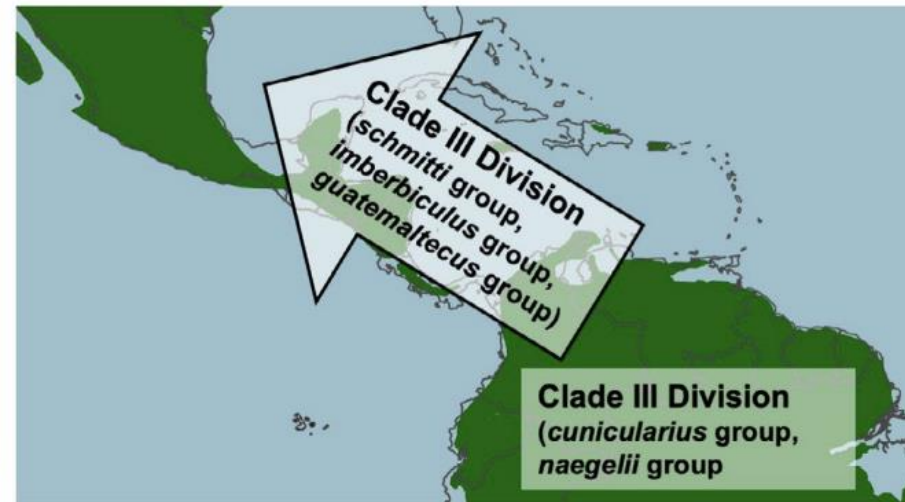


Multiple waves of migration northward

(A) Eocene dispersal, 49-44 Mya



(B) Eocene-Oligocene dispersal, 44-33 Mya



(C) Oligocene-Miocene dispersal, 24 - 13 Mya





Conclusions



Ant evolution is complex and driven by ecology and geography

- Ants are an old group that likely diversified in response to the rise of the flowering plants
- The tropics played an important role in the evolutionary history of the ants
- Silk weaving in ants evolved in complex ways
- Ferns co-opted ants from flowering plants
- Army ants and harvester ants inform the complex history of the colonization of Central America

Acknowledgements

Collaborators on this work:

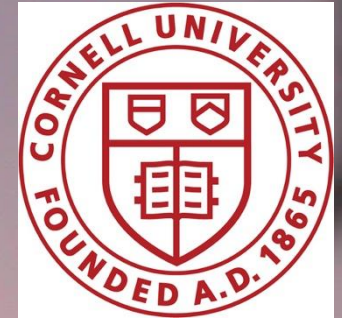
Bruce Archibald (Simon Fraser University)
Charles Bell (University of New Orleans)
Daniel Kronauer (Rockefeller University)
Fay-Wei Li (Boyce Thompson Institute)
Naomi Pierce (Harvard University)
Simon Robson (James Cook University)
Jacob Suissa (University of Tennessee at Knoxville)
Roger Vila (Universitat Autònoma de Barcelona)
Max Winston (University of Chicago)

Moreau lab members:

Yareli Alvarez (Ph.D. student)
Guilherme Azvedo (Visiting postdoctoral researcher)
Emmett Collins-Sussman (Undergraduate intern)
Adya Crispino (Undergraduate intern)
Asha Gandreti (Undergraduate intern)
Tatsuya Inagaki (Postdoctoral researcher)
Ren Kondo (Undergraduate intern)
Ryan Mo (Undergraduate intern)
Leo Navarro (Undergraduate intern)
Morgan Purefoy (Undergraduate intern)
Sylvana Ross (Ph.D. student)
Cheyenne Reuben-Thomas (Ph.D. student)
Patrick Salinas (Undergraduate intern)
Jaden Thomas (Undergraduate intern)
Alex Wong (Undergraduate intern)
Brandon Yoon (Undergraduate intern)

Funding Sources:

U.S. National Science Foundation
National Geographic Society
Cornell University



... and thank you!

