# Ant diversification, biogeography, and trait evolution


Photograph C.S. Moreau

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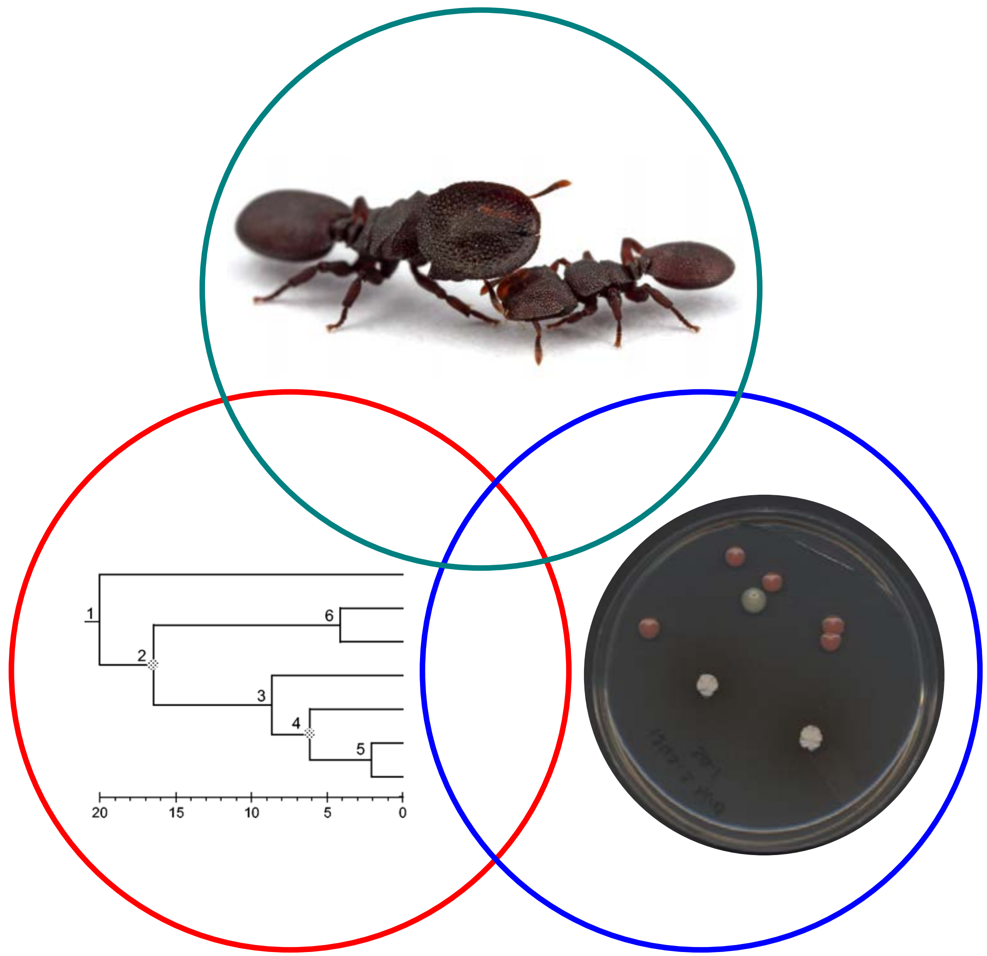
# Major themes of my research program

Ant Ecology and Evolution




Macroevolution

Microbiomes

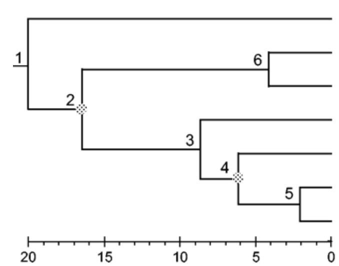
Ant photograph © Alex Wild; Bacteria photograph Stefanie Kautz

# 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

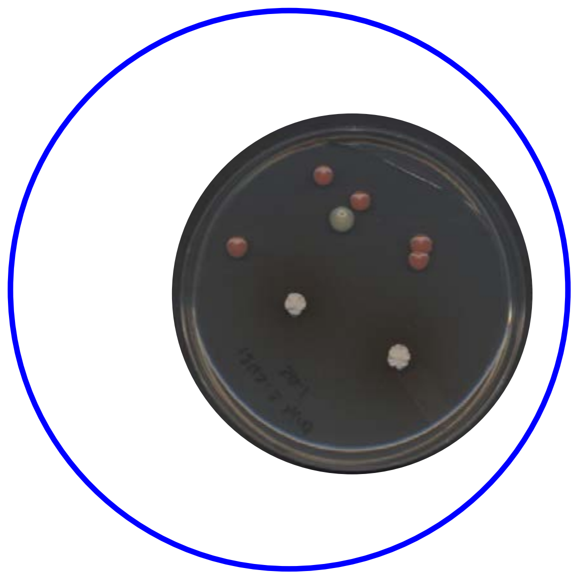



- Phylogenetics
- Divergent dating
- Biogeography
- Trait evolution
- Natural History
- Molecular evolution

Macroevolution

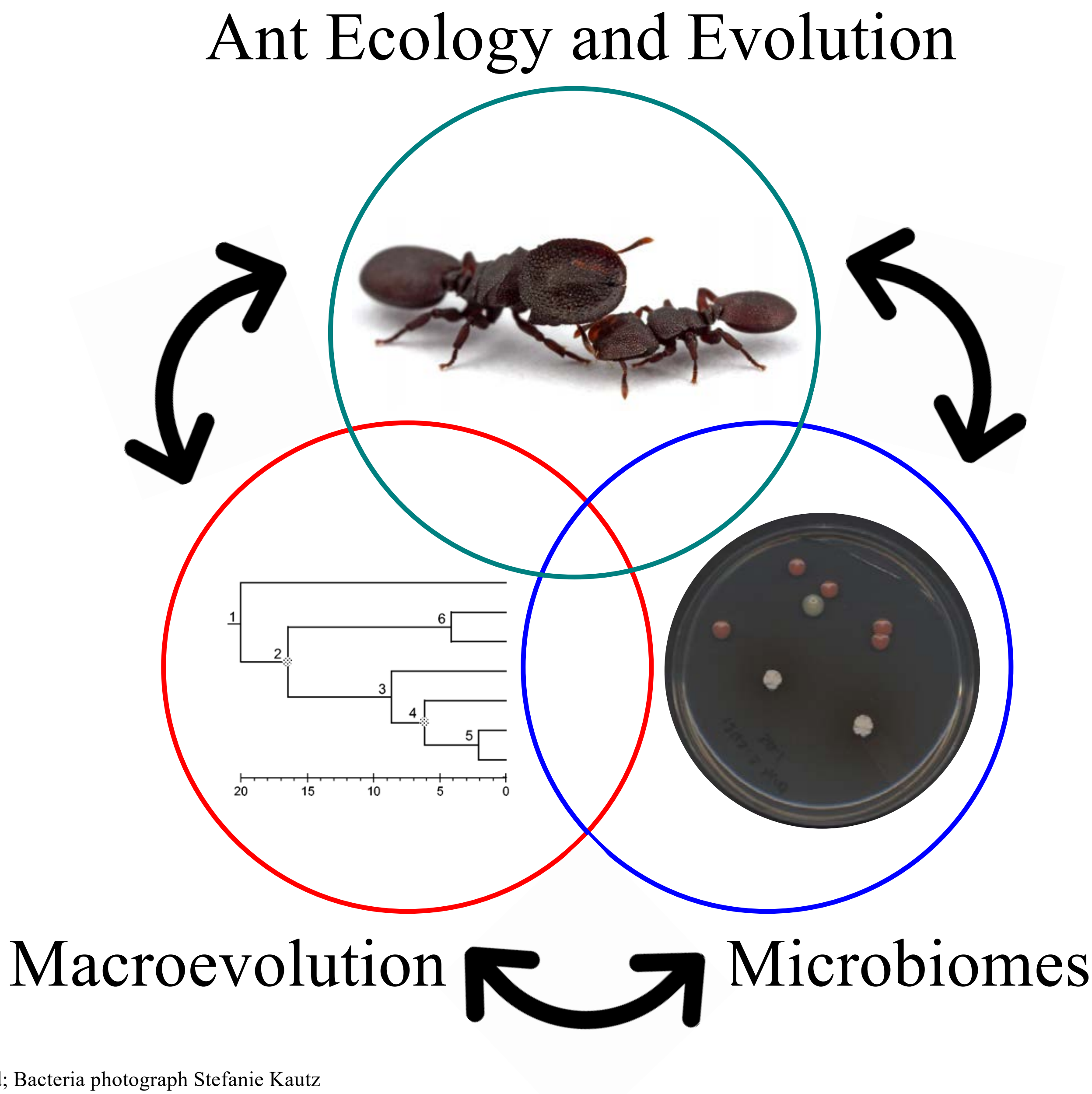
# Major themes of my research program

- 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 photograph © Alex Wild; Bacteria photograph Stefanie Kautz

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

DIVERSIFICATION BIOGEOGRAPHY SILK WEAVING NECTARIES SPECIATION

# Feedback with angiosperms driving ant evolution?

PNAS

## The rise of the ants: A phylogenetic and ecological explanation

Edward O. Wilson*† and Bert Hölldobler‡§

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

Contributed by Edward O. Wilson, March 18, 2005


## 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. Gove[3], Andrew M. Latimer[4], Jonathan D. Majer[3], Robert R. Dunn[1,3]

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


## Plant point of view:

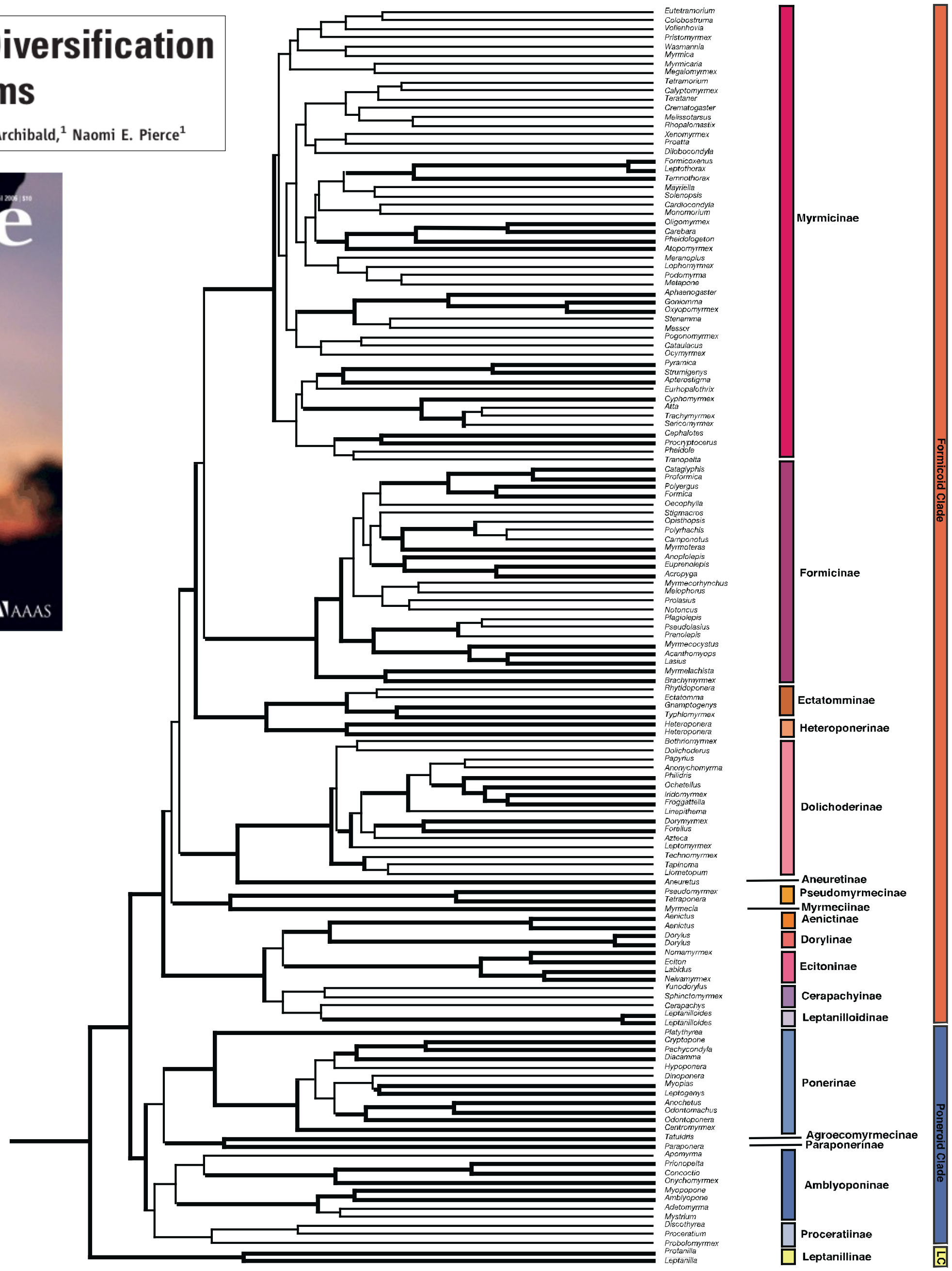
1) Seed dispersal by ants (myrmecochory) evolved independently at least 100 times (present in at least 77 families and 11,000 plant species).

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.

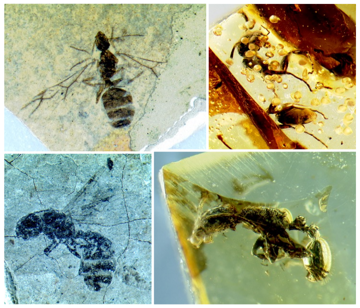
## Phylogeny of the Ants: Diversification in the Age of Angiosperms

Corrie S. Moreau,[1*] Charles D. Bell,[2] Roger Vila,[1] S. Bruce Archibald,[1] Naomi E. Pierce[1]

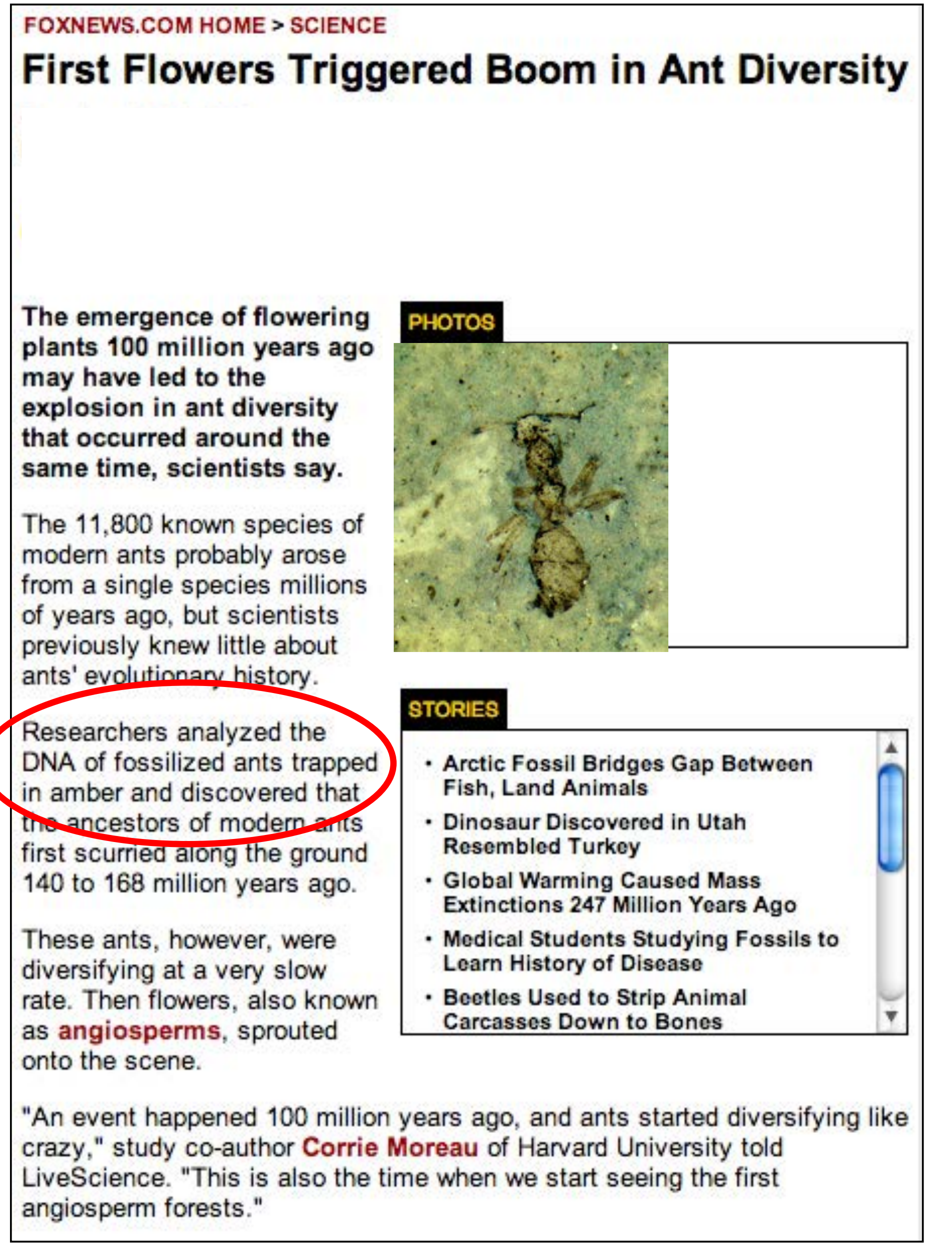

Moreau *et al.* (2006)
*Science* 312: 101-104.




- 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



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## 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

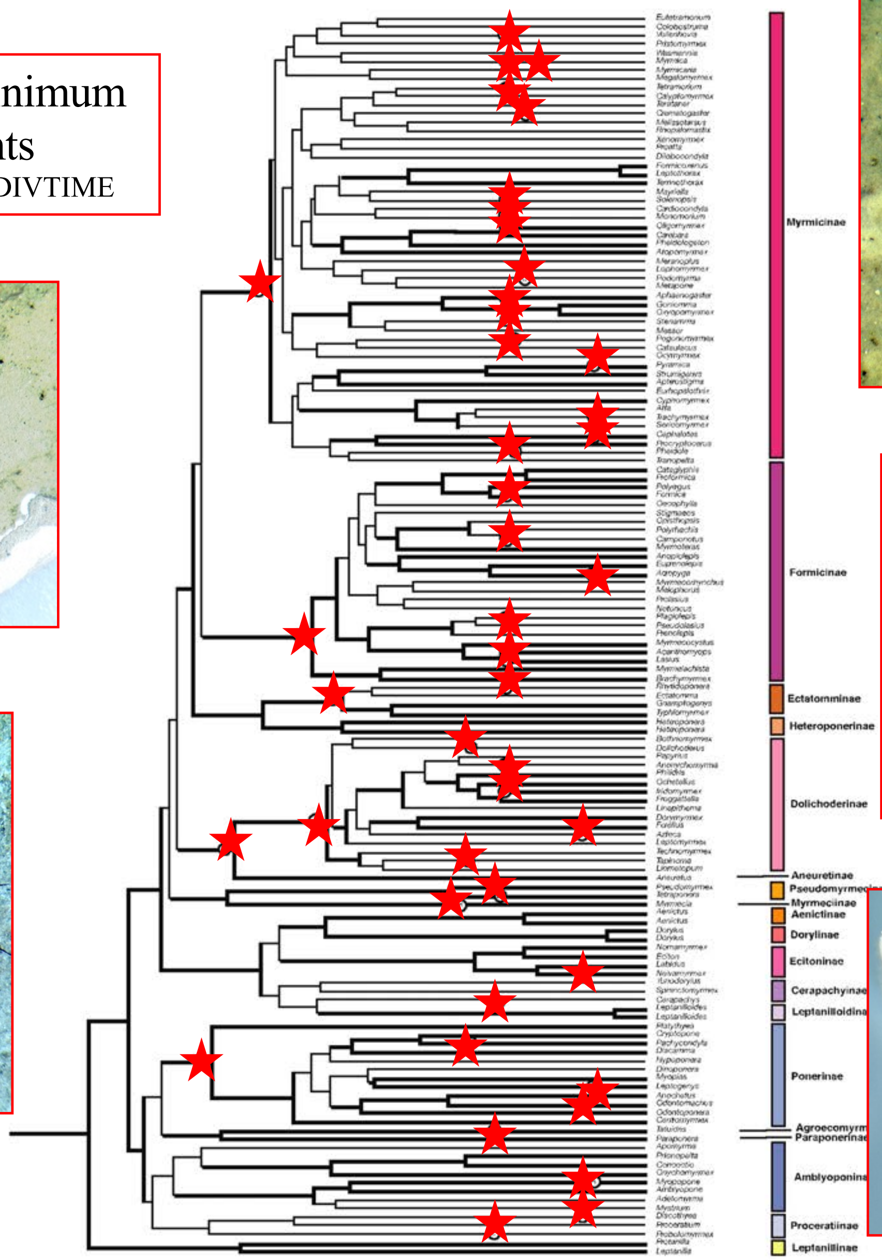
http://www.foxnews.com/story/0,2933,190884,00.html

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

DIVERSIFICATION BIOGEOGRAPHY SILK WEAVING NECTARIES SPECIATION

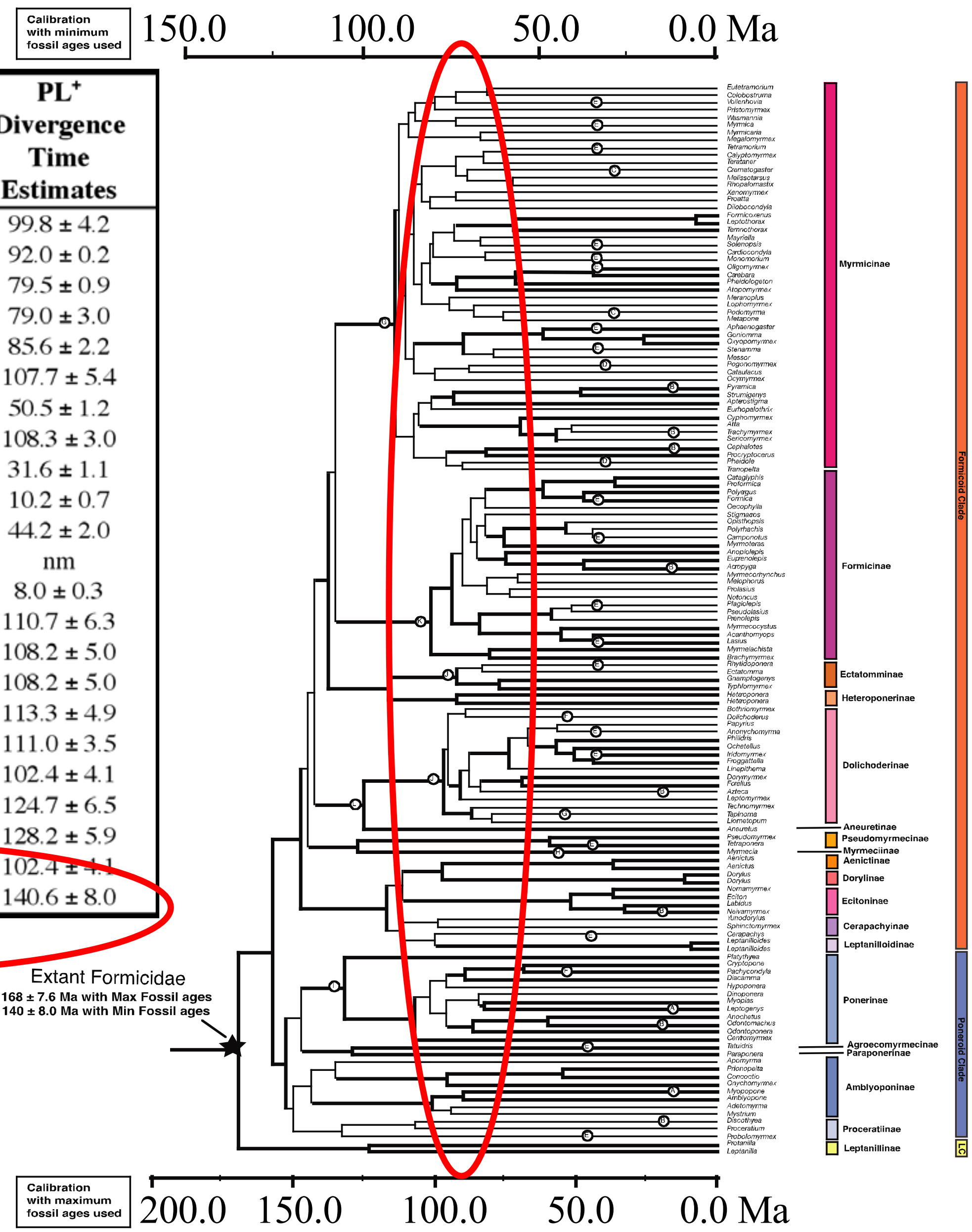
43 fossils used as minimum calibration points

Analyzed with r8s & MULTIDIVTIME




Photographs S.B. Archibald

| Clade | PL Divergence Time Estimates | PL+ Divergence Time Estimates |
|---|---|---|
| Myrmicinae | 114.0 ± 4.5 | 99.8 ± 4.2 |
| Formicinae | 101.4 ± 3.8 | 92.0 ± 0.2 |
| Ectatomminae | 92.3 ± 0.6 | 79.5 ± 0.9 |
| Heteroponerinae | 91.8 ± 2.7 | 79.0 ± 3.0 |
| Dolichoderinae | 96.6 ± 1.9 | 85.6 ± 2.2 |
| Aneuretinae | 124.6 ± 4.8 | 107.7 ± 5.4 |
| Pseudomyrmecinae | 59.2 ± 0.9 | 50.5 ± 1.2 |
| Myrmeciinae | 127.2 ± 2.2 | 108.3 ± 3.0 |
| Aenictinae | 37.3 ± 0.8 | 31.6 ± 1.1 |
| Dorylinae | 12.0 ± 0.4 | 10.2 ± 0.7 |
| Ecitoninae | 52.1 ± 1.0 | 44.2 ± 2.0 |
| Cerapachyinae | nm | nm |
| Leptanilloidinae | 9.7 ± 0.4 | 8.0 ± 0.3 |
| Ponerinae | 131.5 ± 5.9 | 110.7 ± 6.3 |
| Agroecomyrmecinae | 128.7 ± 4.5 | 108.2 ± 5.0 |
| Paraponerinae | 128.7 ± 4.5 | 108.2 ± 5.0 |
| Amblyoponinae | 143.1 ± 5.2 | 113.3 ± 4.9 |
| Proceratiinae | 131.9 ± 3.9 | 111.0 ± 3.5 |
| Leptanillinae | 123.0 ± 3.4 | 102.4 ± 4.1 |
| Formicoid Clade | 147.0 ± 8.2 | 124.7 ± 6.5 |
| Poneroid Clade | 152.4 ± 6.2 | 128.2 ± 5.9 |
| Leptanilloid Clade | 123.0 ± 3.4 | 102.4 ± 4.1 |
| Formicidae | 168.8 ± 7.6 | 140.6 ± 8.0 |




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

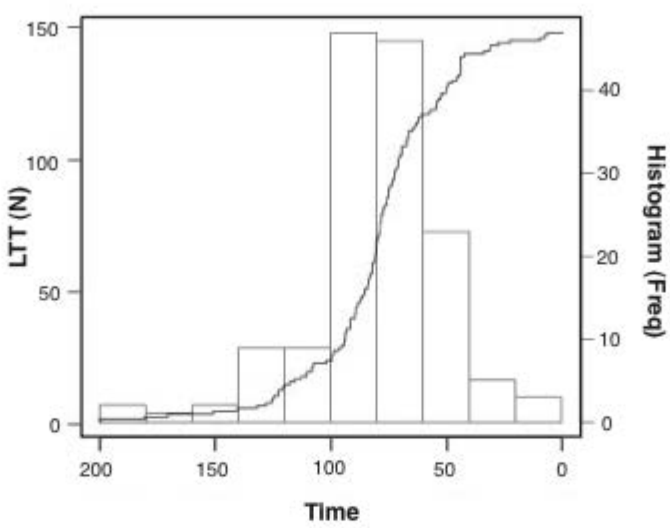



**Table S5.** Results of fitting three models to ant data. logL=Likelihood, p = parameter. AIC = Akaike information criterion. Comparison of diversification rate models to model A performed with APE v1.4. (see text).

| Model | Description | | logL | $X^2$ | *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)

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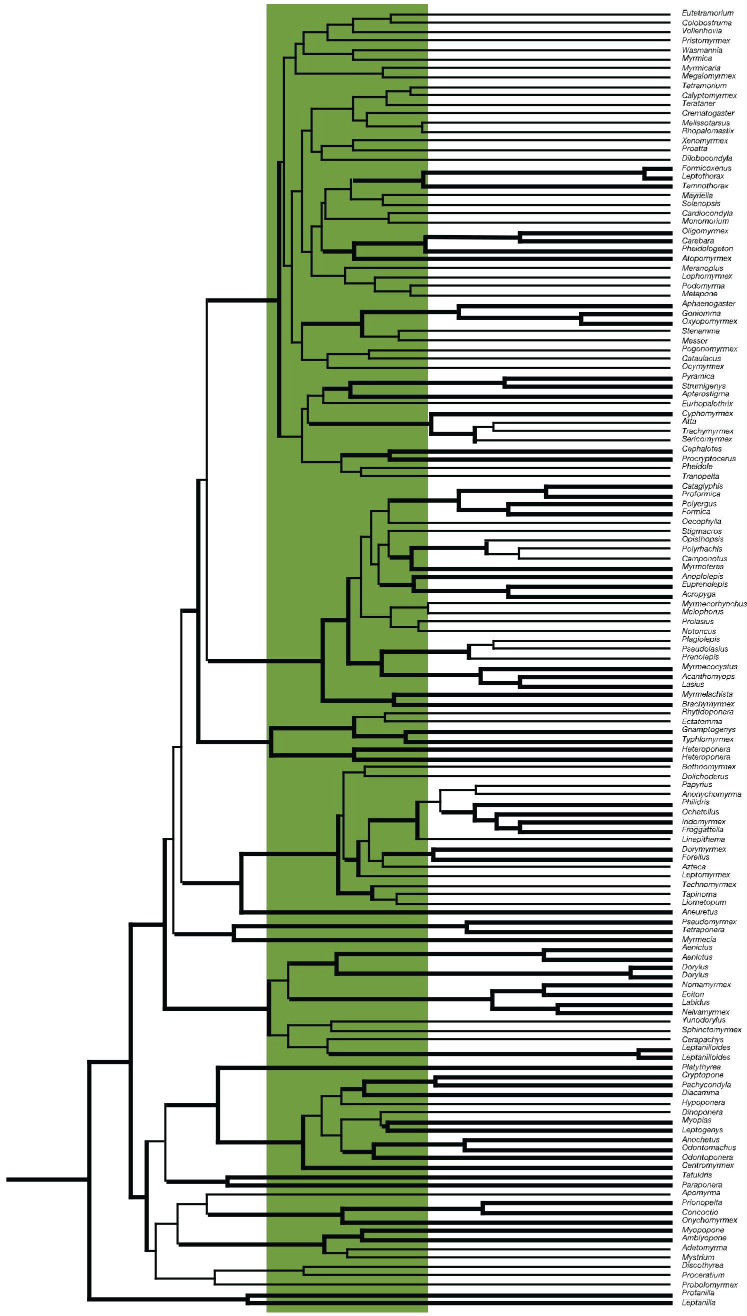
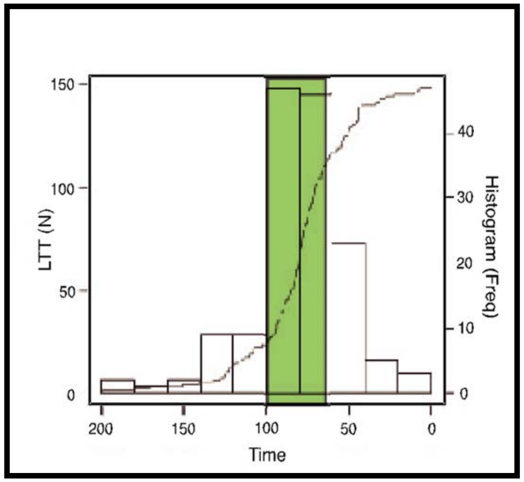
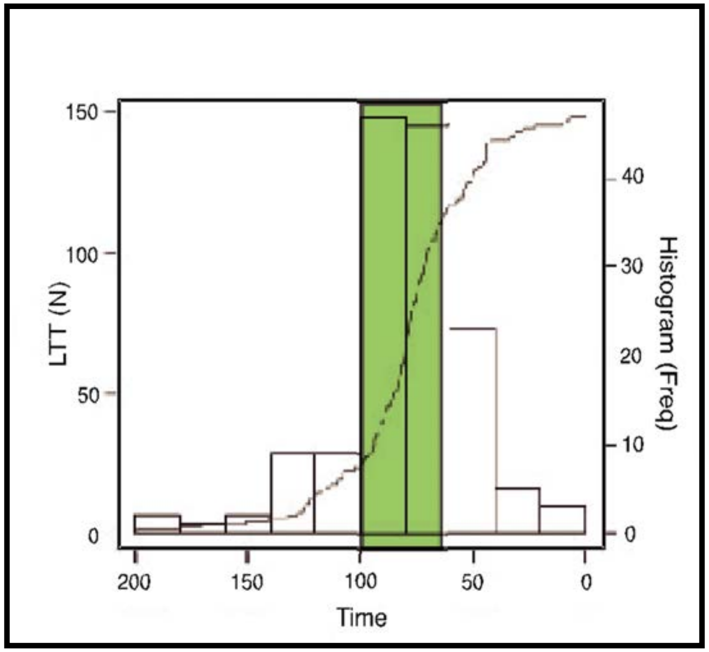



Moreau *et al*. (2006)
*Science* 312: 101-104.

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

DIVERSIFICATION BIOGEOGRAPHY SILK WEAVING NECTARIES SPECIATION








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?

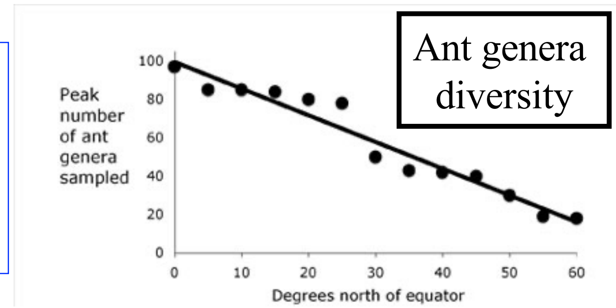
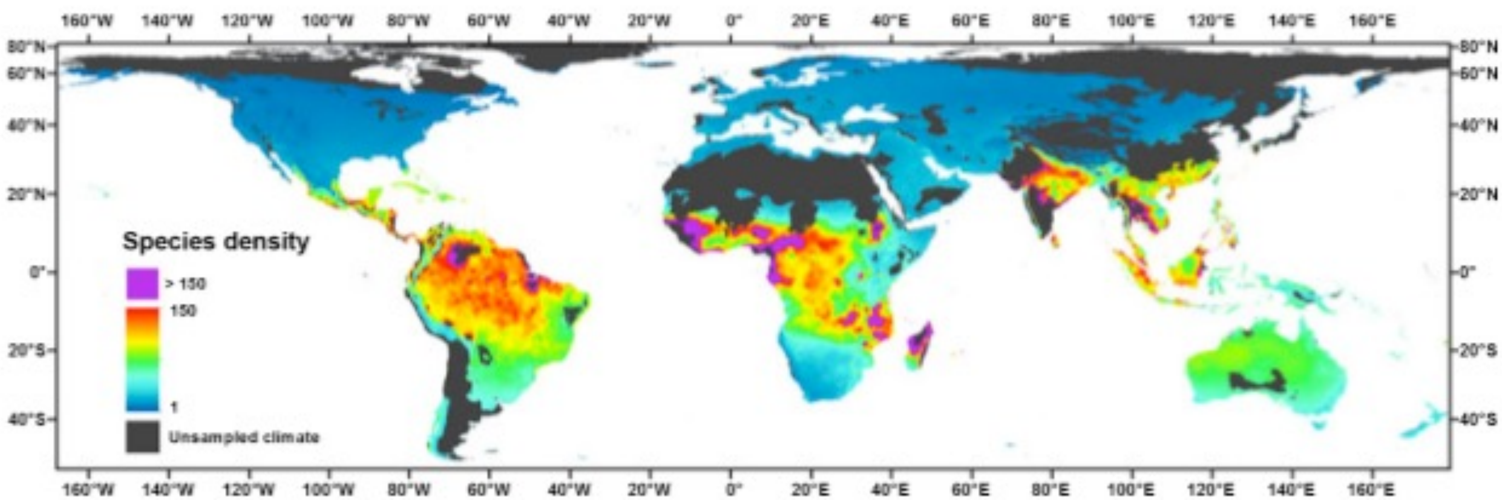



Figure from McGlynn (2010)
*Nature Education Knowledge* 1:32.

Latitudinal gradient in species richness




Ant species diversity

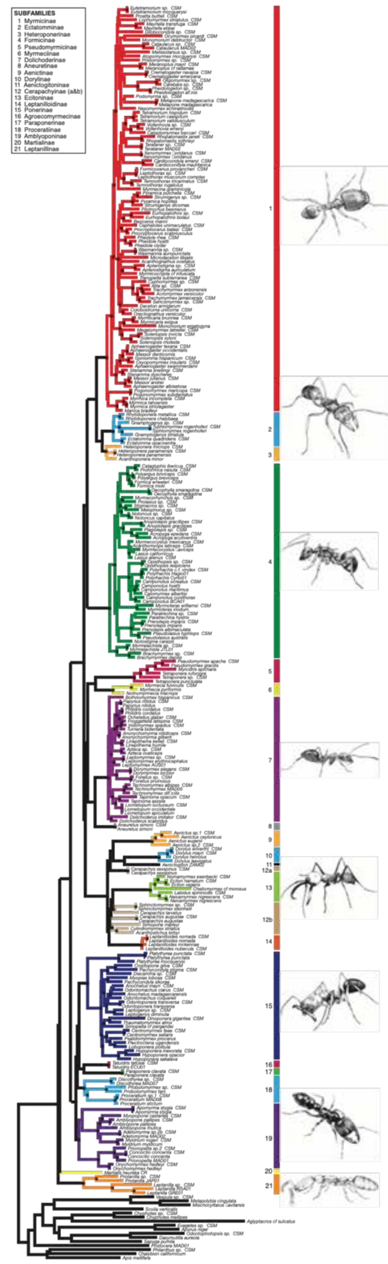
Figure from Jenkins *et al*. (2011)
*Diversity and Distributions* 17:652-662.

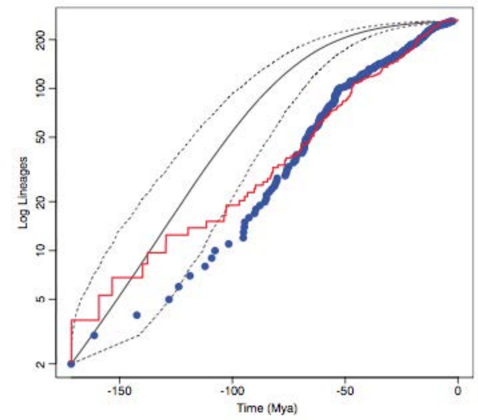
DIVERSIFICATION | **BIOGEOGRAPHY** | SILK WEAVING | NECTARIES | SPECIATION

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

EVOLUTION
INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

Corrie S. Moreau[1,2] and Charles D. Bell[3]






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

Palearctic (gray)
Nearctic (red)
Afrotropic (purple)
Neotropic (green)
Australasia (blue)
Indo-Malaya (yellow)

## Current species distributions

| | Palearctic | Nearctic | Afrotropic | Neotropic | Australasia | Indo-Malaya |
|---|---|---|---|---|---|---|
| Protanilla_sp._CSM | | | | | | ✓ |
| Leptanilla_sp._CSM | ✓ | | ✓ | | ✓ | ✓ |
| Martialis_heureka_CR | | | | ✓ | | |
| Tetraponera_sp._CSM | | | ✓ | | ✓ | ✓ |
| Pseudomyrmex_apache_CSM | | ✓ | | ✓ | | |
| Myrcidris_epicharis | | | | ✓ | | |
| Myrmecia_fulviculis_CSM | | | | | ✓ | |
| Nothomyrmecia_macrops | | | | | ✓ | |
| Bothriomyrmex_hispanicus_CSM | ✓ | | | | | |
| Dolichoderus_imitator_CSM | ✓ | ✓ | | ✓ | ✓ | ✓ |
| Azteca_sp._CSM | | | | ✓ | | |
| Papyrius_nitidus_CSM | | | | | ✓ | |
| Anonychomyrma_nitidiceps_CSM | | | | | ✓ | |
| Froggattella_latispina_CSM | | | | | ✓ | |
| Iridomyrmex_spadius_CSM | | | | | ✓ | ✓ |
| Turneria_bidentata | | | | | ✓ | |
| Ochetellus_glaber_CSM | | | | | ✓ | ✓ |
| Philidris_cordatus_CSM | | | | | ✓ | ✓ |
| Linepithema_keiteli_CSM | | | | ✓ | | |
| Leptomyrmex_sp._CSM | | | | | ✓ | |
| Dorymyrmex_elegans_CSM | | ✓ | | ✓ | | |
| Forelius_sp._CSM | | ✓ | | ✓ | | |
| Tapinoma_opacum_CSM | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Liometopum_luctuosum_CSM | ✓ | ✓ | | | | ✓ |
| Technomyrmex_albipes_CSM | | | ✓ | ✓ | ✓ | ✓ |
| Aneuretus_simoni_CSM | | | | | | ✓ |
| Cerapachys_augustae_CSM | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Sphinctomyrmex_sp._CSM | | | ✓ | ✓ | ✓ | ✓ |
| Cerapachys_larvatus | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Cylindromyrmex_striatus | | | | ✓ | | |
| Acanthostichus_kirbyi | | ✓ | | ✓ | | |
| Simopone_marleyi | | | ✓ | | | ✓ |
| Cerapachys_Yunodorylus_sexspinus_CSM | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Dorylus_mayri_CSM | ✓ | | ✓ | | | ✓ |
| Aenictogiton_ZAM02 | | | ✓ | | | |
| Nomamyrmex_esenbecki_CSM | | ✓ | | ✓ | | |
| Eciton_hamatum_CSM | | | | ✓ | | |
| Cheliomyrmex_cf_morosus | | | | ✓ | | |
| Labidus_spininodis_CSM | | ✓ | | ✓ | | |
| Neivamyrmex_nigrescens_CSM | | ✓ | | ✓ | | |
| Aenictus_sp.1_CSM | | | ✓ | | ✓ | ✓ |
| Leptanilloides_nomada_CSM | | | | ✓ | | |
| Stenamma_snellingi_CSM | ✓ | ✓ | | ✓ | | ✓ |
| Messor_julianus_CSM | ✓ | ✓ | ✓ | | | ✓ |
| Aphaenogaster_albisetosa | ✓ | ✓ | | ✓ | ✓ | ✓ |
| Aphaenogaster_texana_CSM | ✓ | ✓ | | ✓ | ✓ | ✓ |
| Messor_denticornis | ✓ | ✓ | ✓ | | | ✓ |
| Goniomma_hispanicum_CSM | ✓ | | | | | |

## Migration probability between areas over time

Time period 0: from 0 to 50.0

| | Palearctic | Nearctic | Afrotropic | Neotropic | Australasia | Indo-Malaya |
|---|---|---|---|---|---|---|
| Palearctic | -- | 0.5 | 1.0 | 0.1 | 0.1 | 1.0 |
| Nearctic | 0.5 | -- | 0.1 | 1.0 | 0.1 | 0.1 |
| Afrotropic | 1.0 | 0.1 | -- | 0.1 | 0.1 | 1.0 |
| Neotropic | 0.1 | 1.0 | 0.1 | -- | 0.1 | 0.1 |
| Australasia | 0.1 | 0.1 | 0.1 | 0.1 | -- | 1.0 |
| Indo-Malaya | 1.0 | 0.1 | 1.0 | 0.1 | 1.0 | -- |

Time period 1: from 50.0 to 94.0

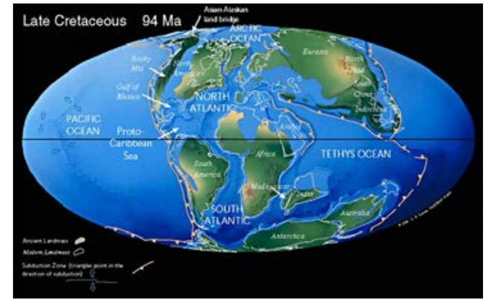
| | Palearctic | Nearctic | Afrotropic | Neotropic | Australasia | Indo-Malaya |
|---|---|---|---|---|---|---|
| Palearctic | -- | 1.0 | 0.5 | 0.1 | 0.1 | 1.0 |
| Nearctic | 1.0 | -- | 0.1 | 0.5 | 0.1 | 0.1 |
| Afrotropic | 0.5 | 0.1 | -- | 0.1 | 0.1 | 0.5 |
| Neotropic | 0.1 | 0.5 | 0.1 | -- | 0.1 | 0.1 |
| Australasia | 0.1 | 0.1 | 0.1 | 0.1 | -- | 0.1 |
| Indo-Malaya | 1.0 | 0.1 | 0.5 | 0.1 | 0.1 | -- |

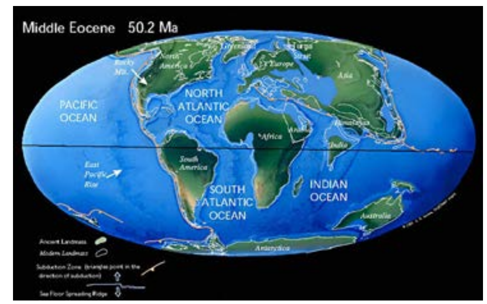
Time period 2: from 94.0 to 150.0

| | Palearctic | Nearctic | Afrotropic | Neotropic | Australasia | Indo-Malaya |
|---|---|---|---|---|---|---|
| Palearctic | -- | 1.0 | 0.1 | 0.1 | 0.1 | 1.0 |
| Nearctic | 1.0 | -- | 0.5 | 0.5 | 0.1 | 0.1 |
| Afrotropic | 0.1 | 0.5 | -- | 1.0 | 0.1 | 0.1 |
| Neotropic | 0.1 | 0.5 | 1.0 | -- | 0.5 | 0.1 |
| Australasia | 0.1 | 0.1 | 0.1 | 0.5 | -- | 0.1 |
| Indo-Malaya | 1.0 | 0.1 | 0.1 | 0.1 | 0.1 | -- |

Time period 3: from 150.0 to 200.0

| | Palearctic | Nearctic | Afrotropic | Neotropic | Australasia | Indo-Malaya |
|---|---|---|---|---|---|---|
| Palearctic | -- | 0.5 | 0.1 | 0.1 | 0.1 | 1.0 |
| Nearctic | 0.5 | -- | 1.0 | 1.0 | 0.1 | 0.1 |
| Afrotropic | 0.1 | 1.0 | -- | 1.0 | 0.1 | 0.1 |
| Neotropic | 0.1 | 1.0 | 1.0 | -- | 0.5 | 0.1 |
| Australasia | 0.1 | 0.1 | 0.1 | 0.5 | -- | 0.1 |
| Indo-Malaya | 1.0 | 0.1 | 0.1 | 0.1 | 0.1 | -- |



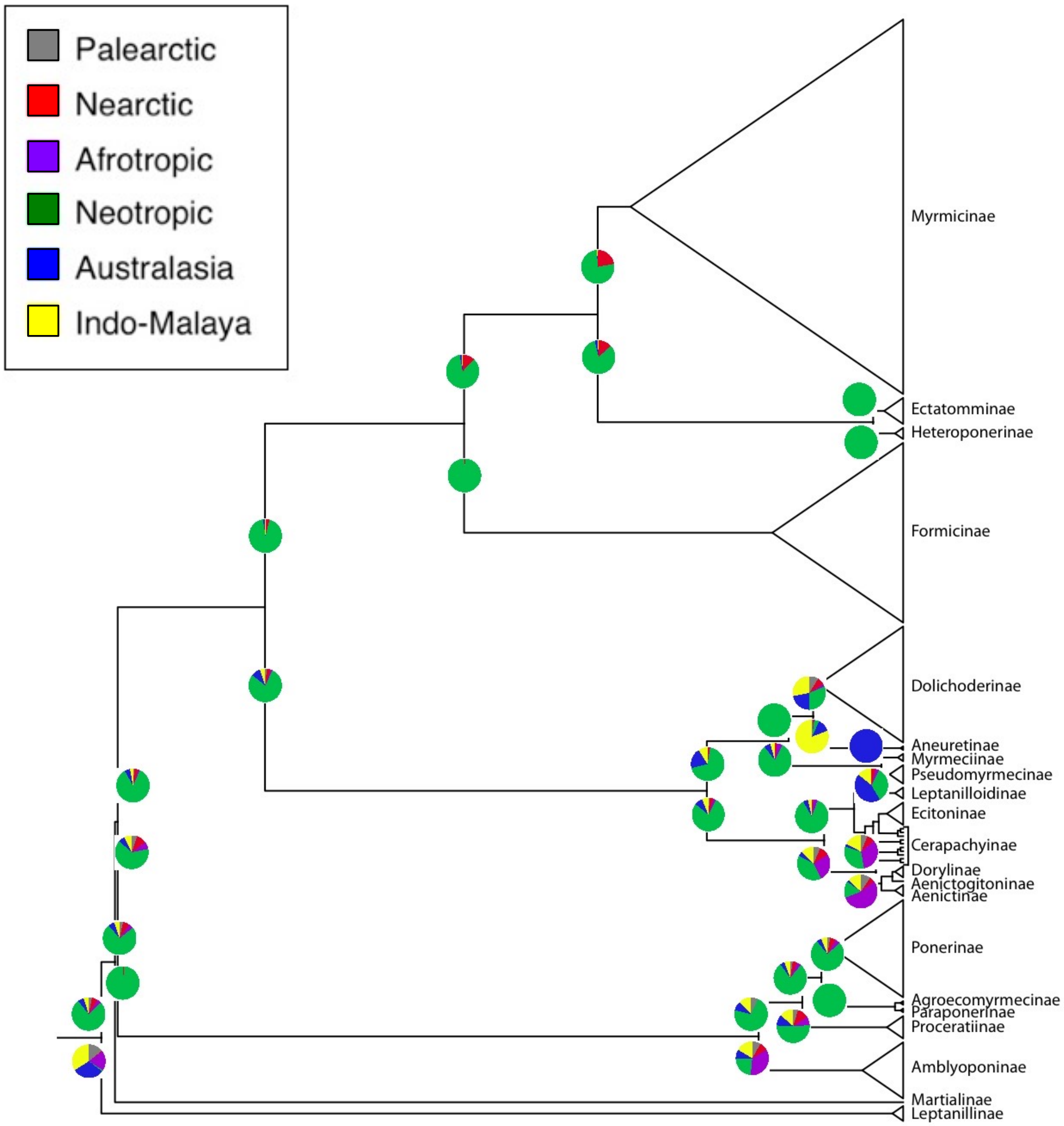





http://www.scotese.com

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

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

# 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


Photograph by C.S. Moreau

Photograph © Alex Wild

Photograph © Alex Wild

# 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

Photographs by C.S. Moreau

# 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** |
|---|---|
| *Dendromyrmex* | No |
| *Camponotus* | Yes |
| *Polyrhachis* | Yes |
| *Oecophylla* | Yes |

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

Photo from Hölldobler & Wilson (1983)

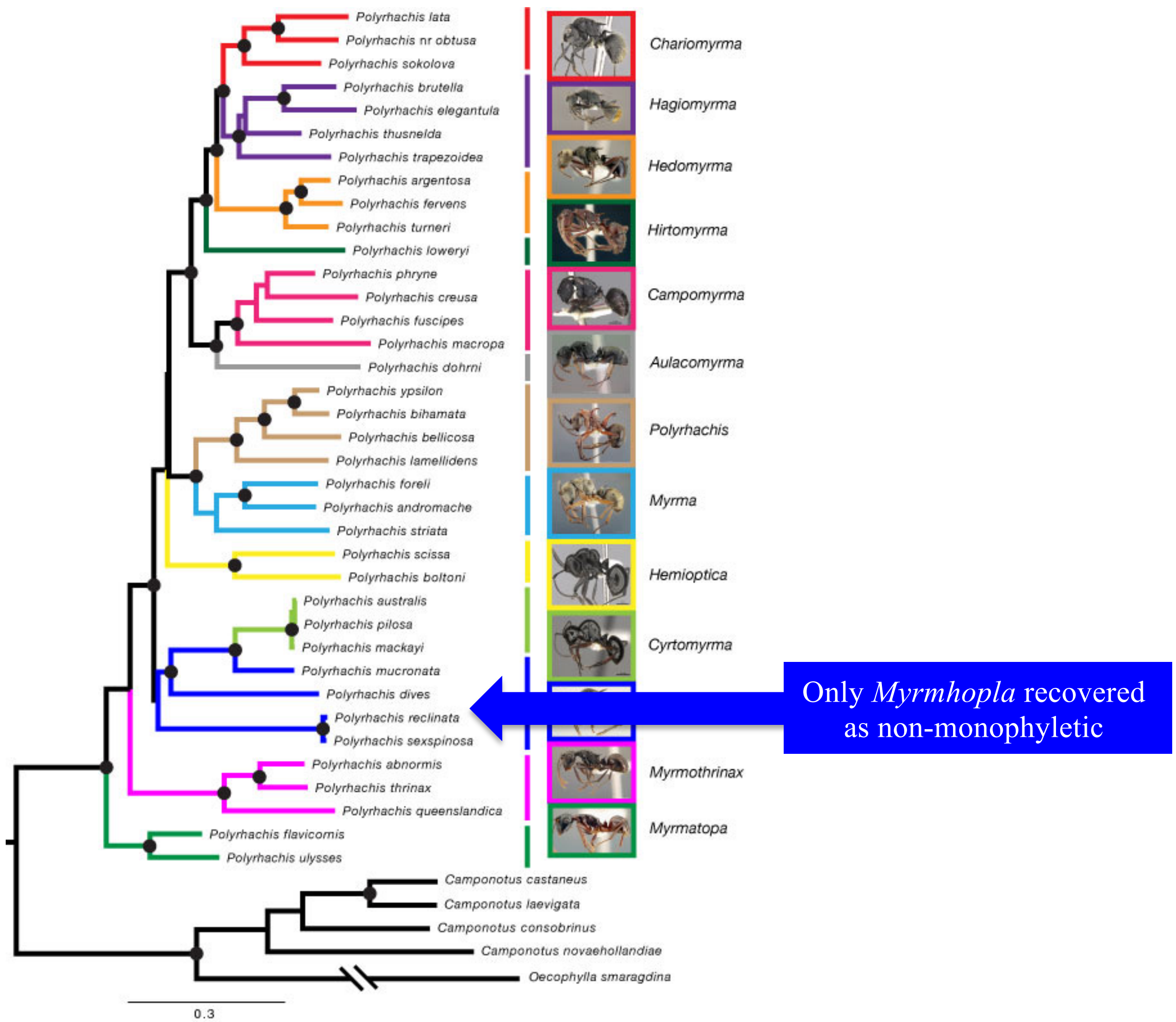
Shift to worker control, cocoon loss, increased silk gland size:

- "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

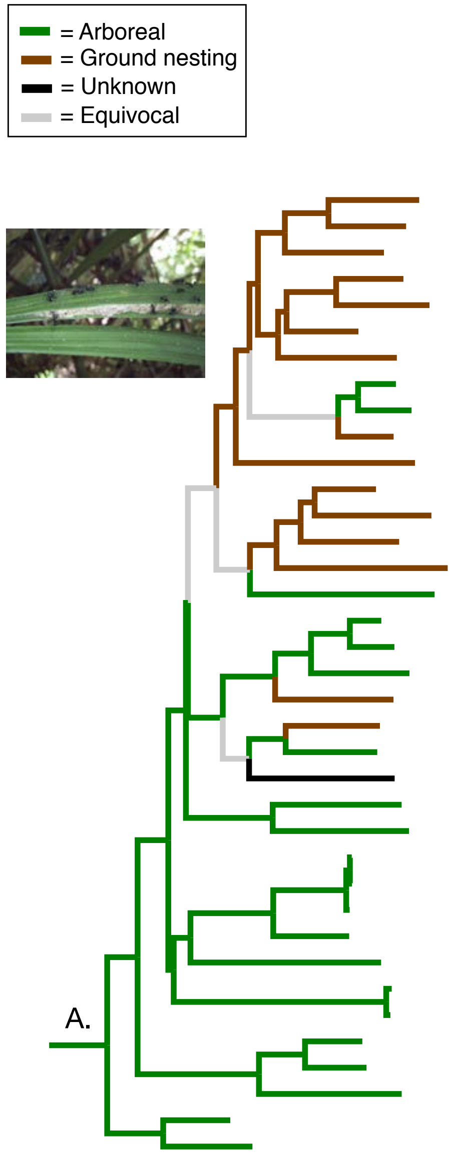



**Inferring the phylogeny of *Polyrhachis***

- 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

Robson, S. K. A., Kohout, R. J., Beckenbach, A. T. & Moreau, C. S. (2015) *Behavioral Ecology and Sociobiology* 69: 449-458.

# Evolution of nest preference



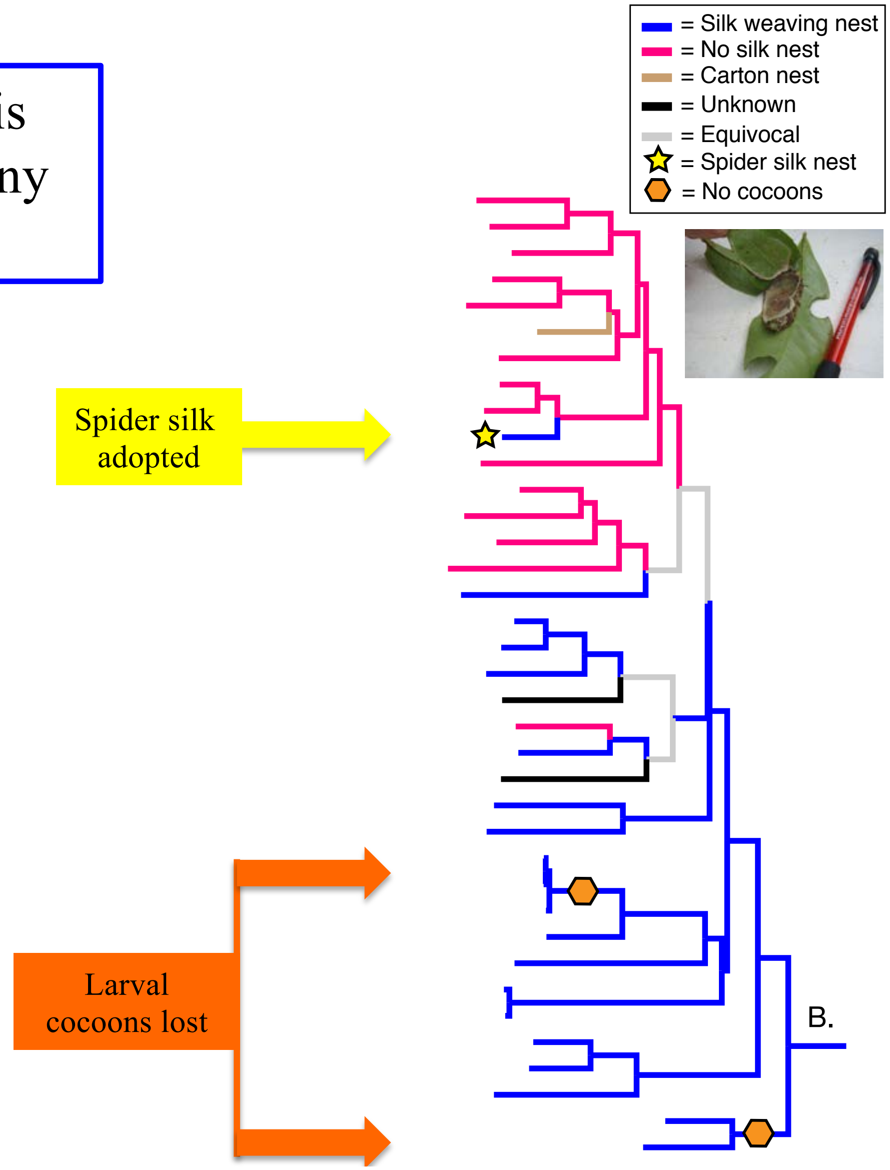

Arboreal nesting is ancestral in spiny ants

**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

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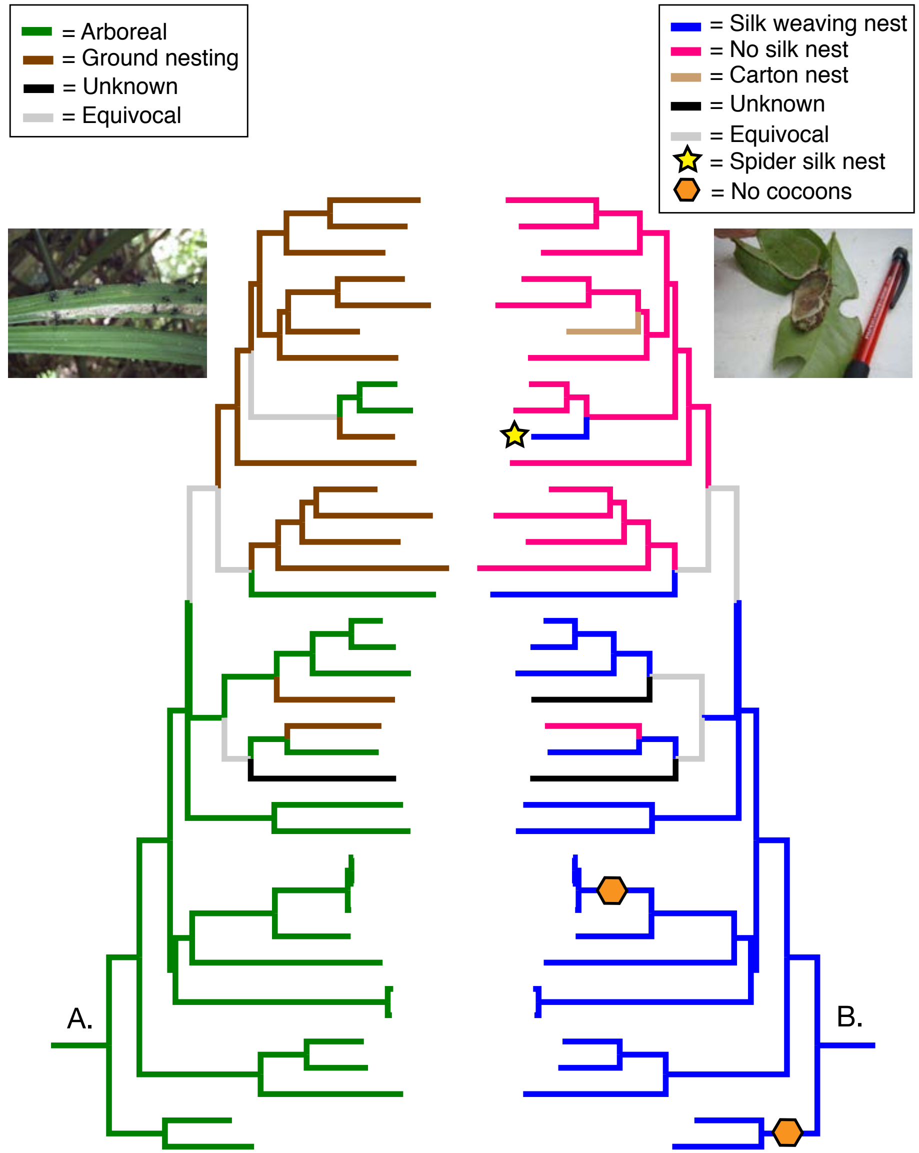
# Correlation of traits




**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

Robson, S. K. A., Kohout, R. J., Beckenbach, A. T. & Moreau, C. S. (2015) *Behavioral Ecology and Sociobiology* 69: 449-458.

# 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

# The evolution of nectaries in non-flowering plants

Jacob Suissa

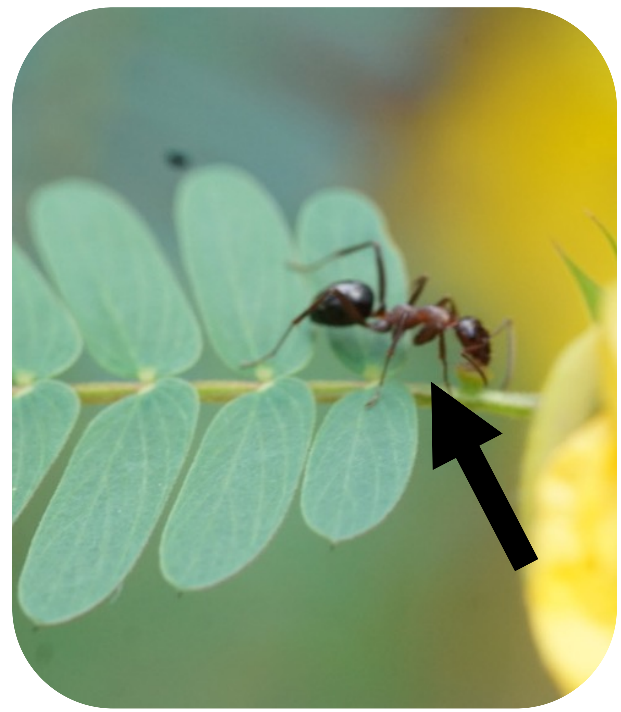
# EFNs as external defense mechanisms

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

*Catalpa*

*Vachellia*

*Chamaecrista*



Photos by Jacob Suissa

Jacob Suissa

# How did we study this?

Ferns

Nitta *et al.,* 2022

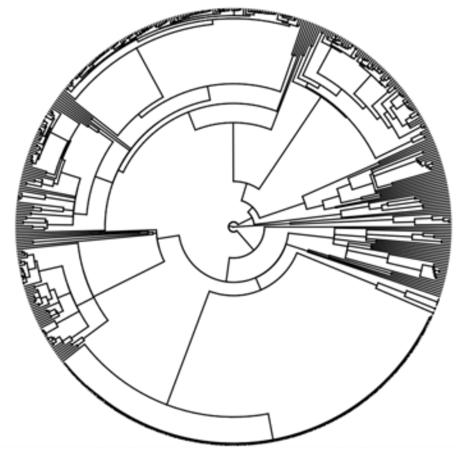
Angiosperms

Smith and Brown *et al.,* 2022

Ants

Nelsen *et al.,* 2018

Fern Herbivores

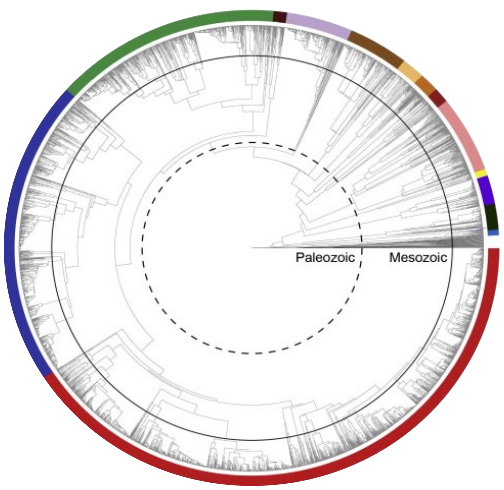


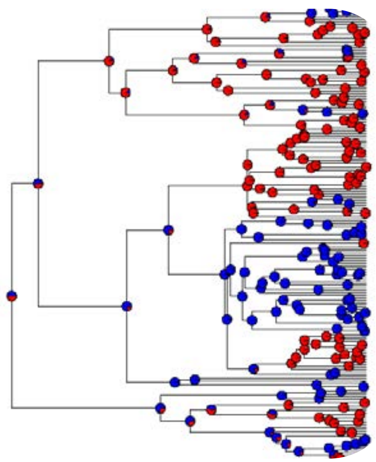
Suissa *et al.,* in review

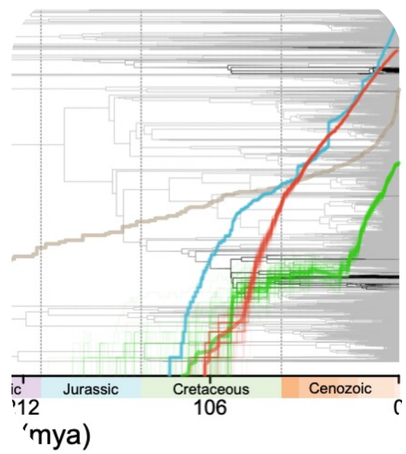
Jacob Suissa

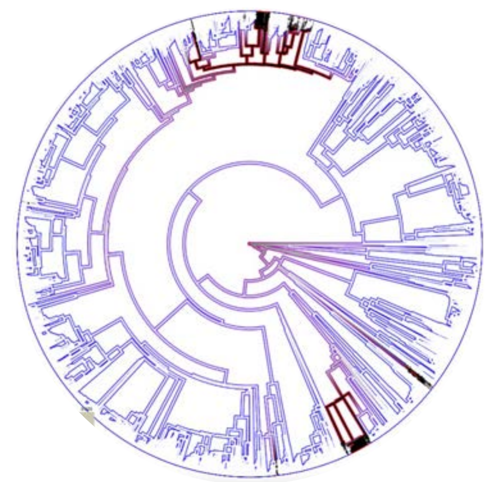
# Methodology

Phylogeny → Stochastic character mapping → Lineage through time plots → Diversification rate analyses





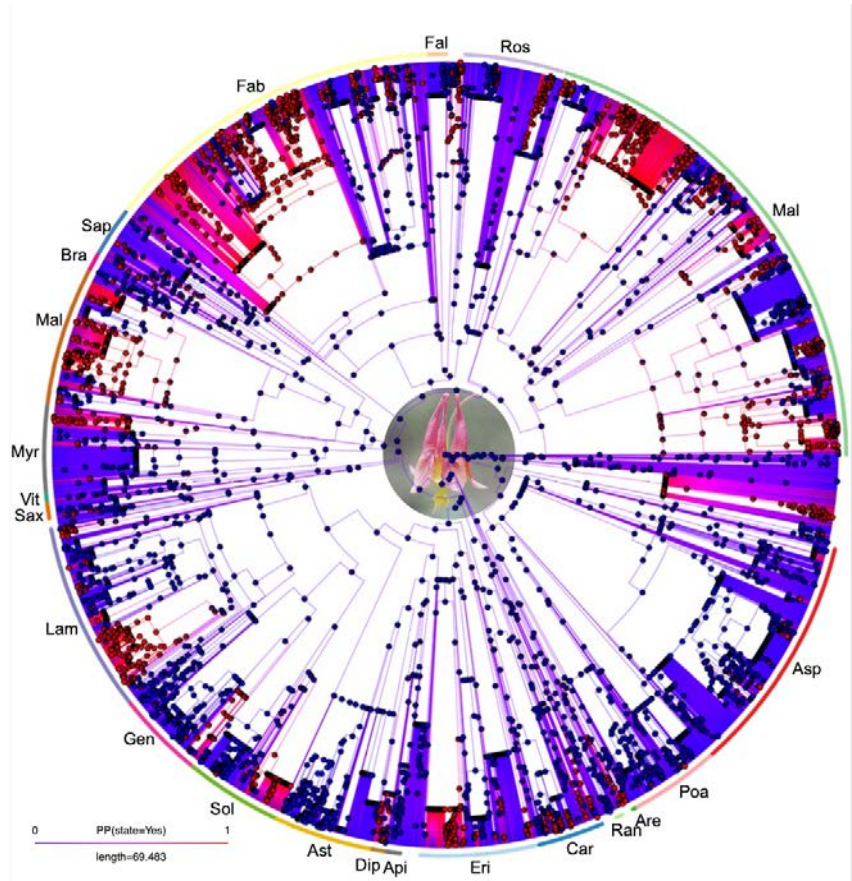
DIVERSIFICATION BIOGEOGRAPHY SILK WEAVING NECTARIES SPECIATION

Jacob Suissa

# Diversity of EFNs in Angiosperms

1555 gains

2318 losses

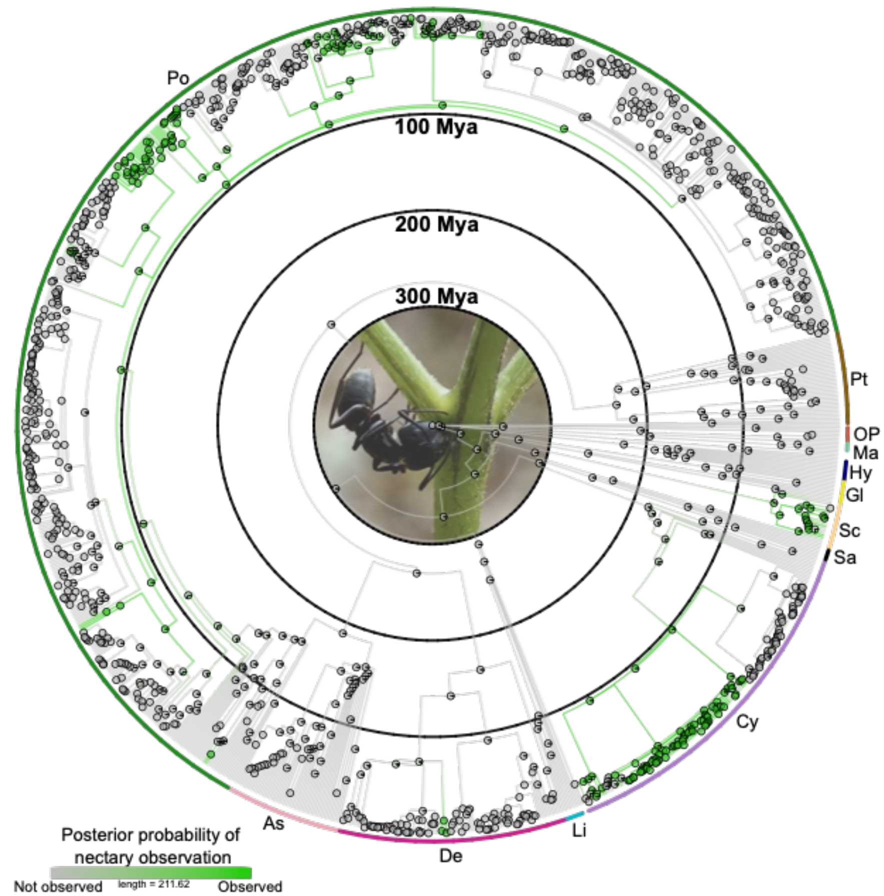


Jacob Suissa

# Diversity of EFNs in Ferns

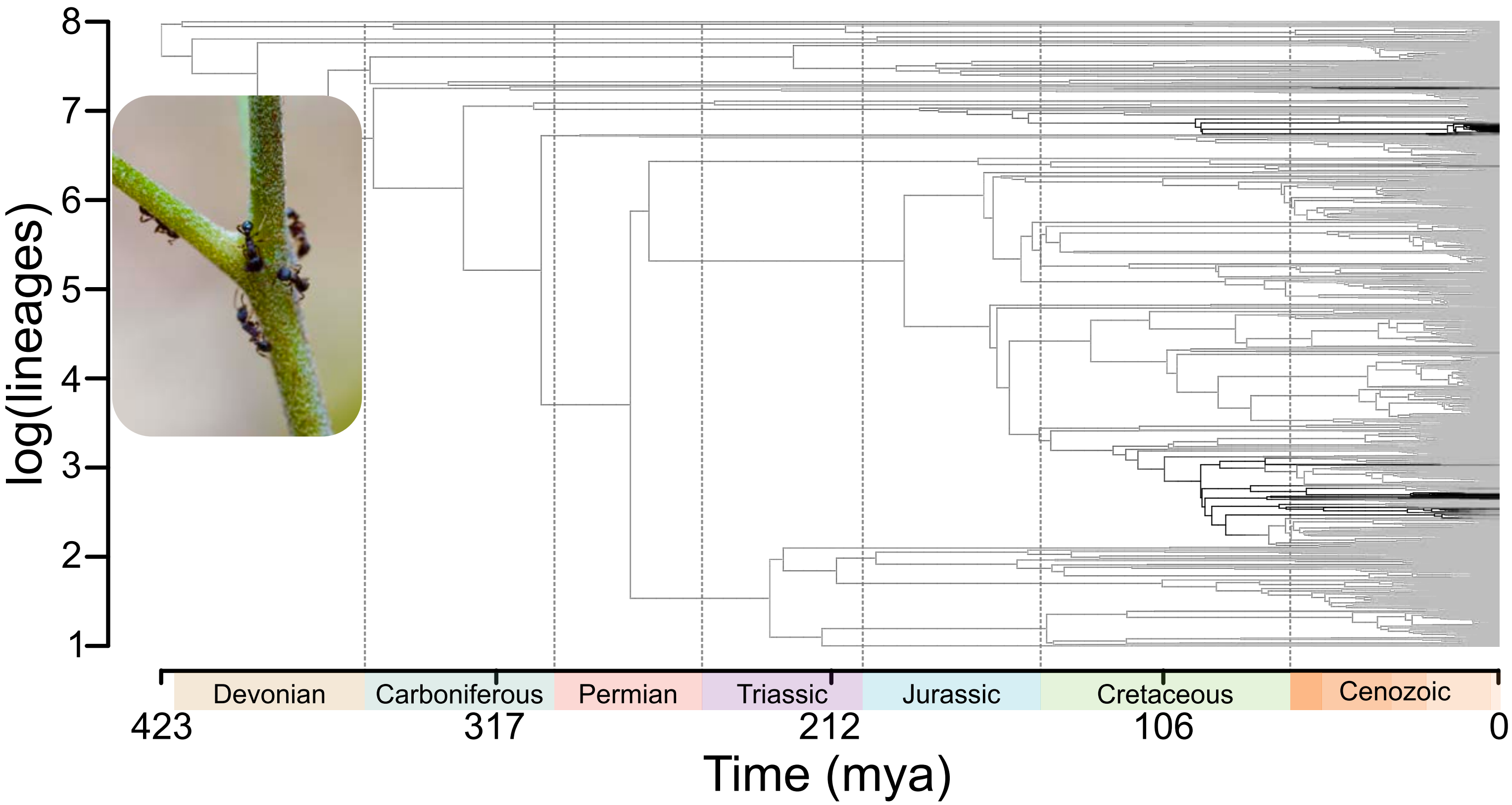
11 gains

2 losses



Jacob Suissa

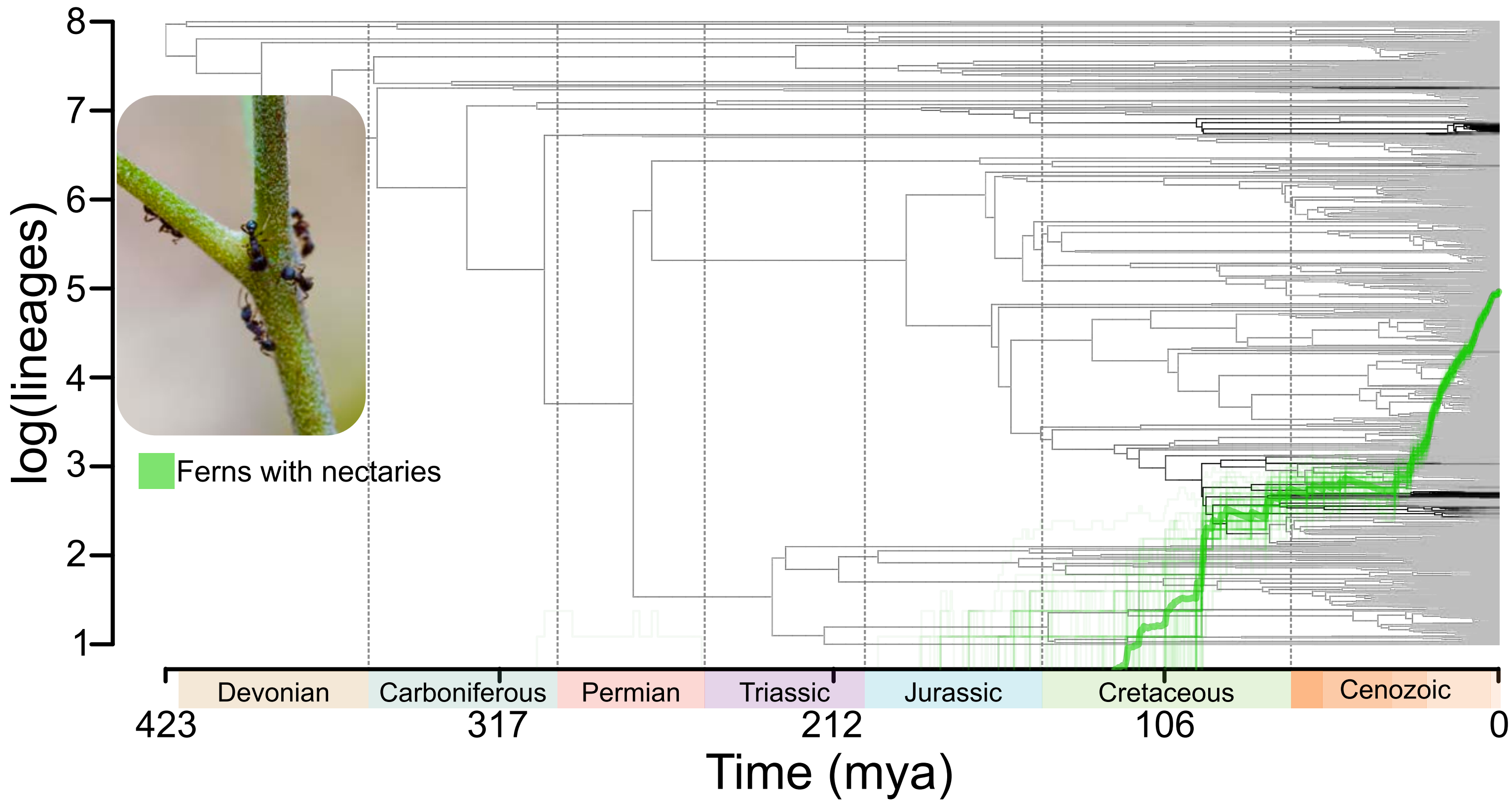
# Tempo and mode of nectary evolution




Suissa, J. S., Li, F.-W. & Moreau, C. S. (2024) *Nature Communications* 15: 4392.

Jacob Suissa

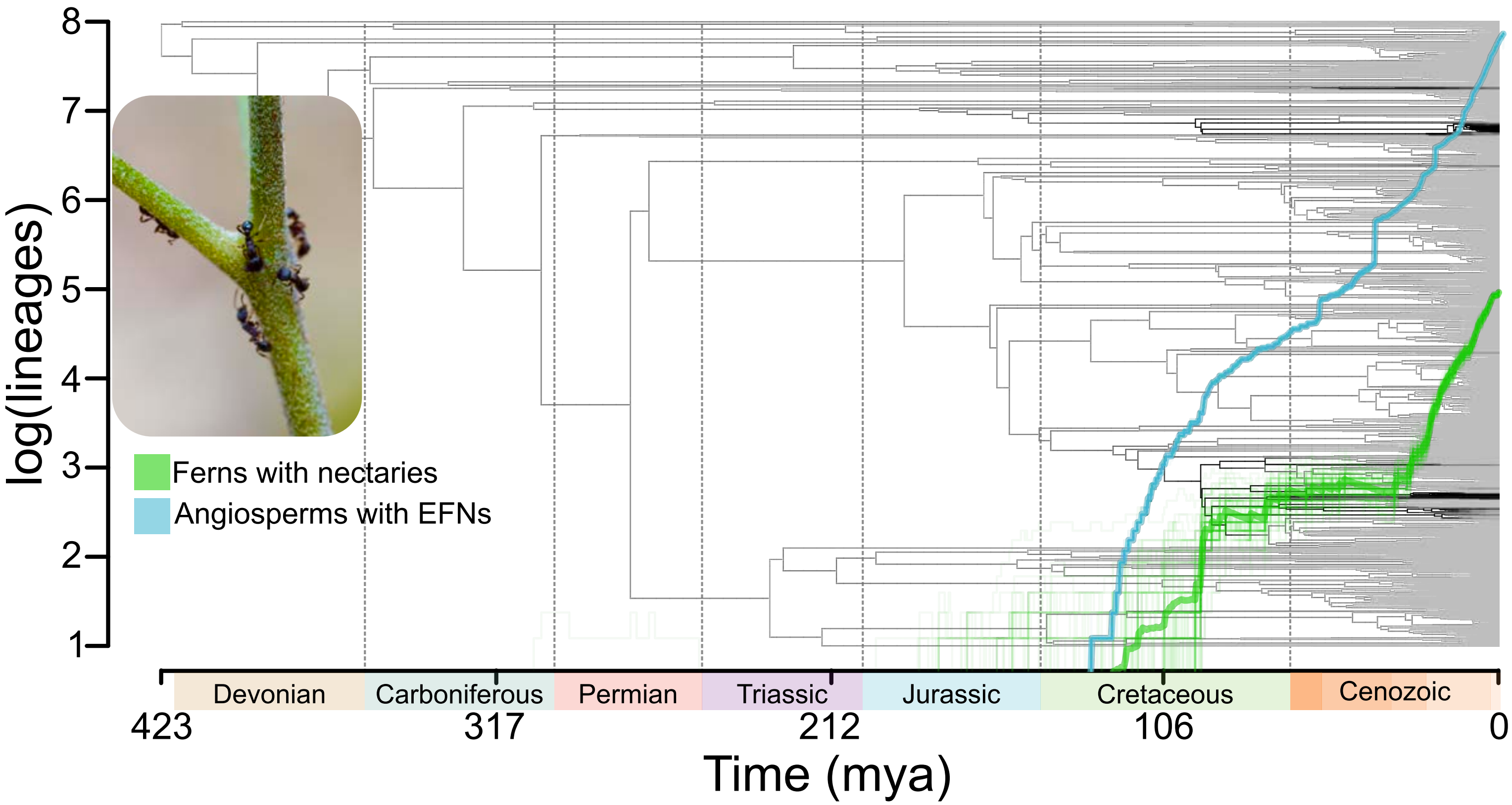
# Cretaceous origin of nectaries in ferns




Suissa, J. S., Li, F.-W. & Moreau, C. S. (2024) *Nature Communications* 15: 4392.

Jacob Suissa

# Cretaceous origin of nectaries in ferns and angiosperms

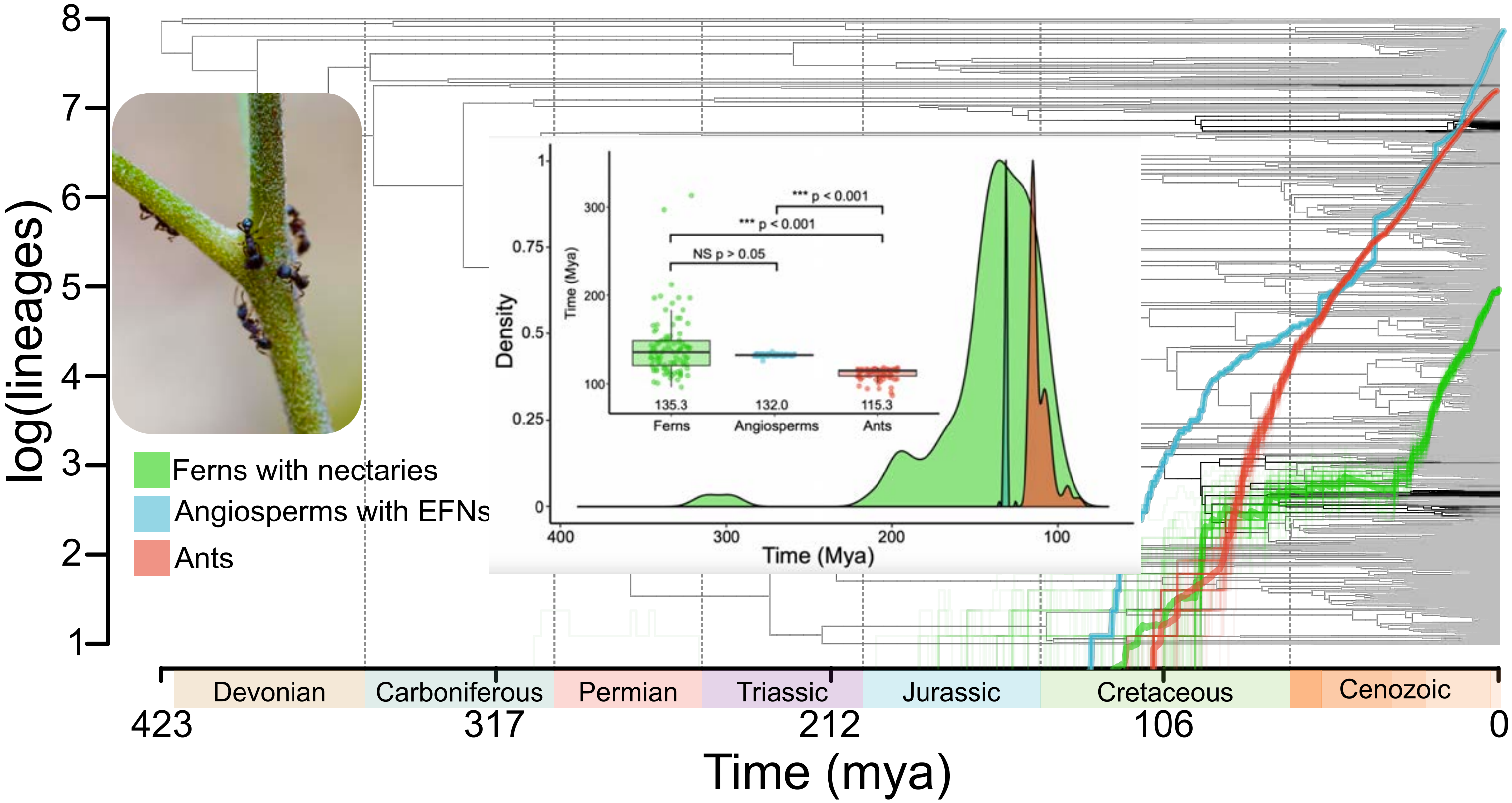



Suissa, J. S., Li, F.-W. & Moreau, C. S. (2024) *Nature Communications* 15: 4392.

DIVERSIFICATION BIOGEOGRAPHY SILK WEAVING **NECTARIES** SPECIATION

Jacob Suissa

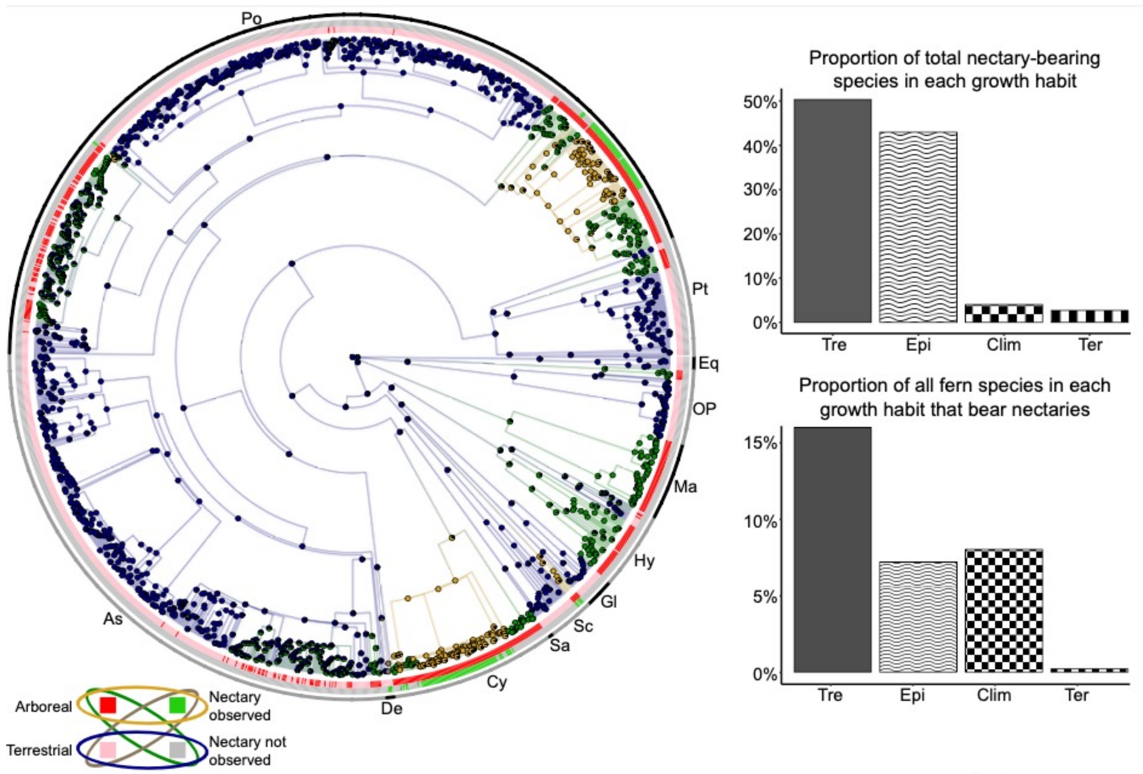
# Origin of nectaries corresponds to the rise of arboreal ants




Suissa, J. S., Li, F.-W. & Moreau, C. S. (2024) *Nature Communications* 15: 4392.

Jacob Suissa

# Proximity is key in fern-nectary evolution




Suissa, J. S., Li, F.-W. & Moreau, C. S. (2024) *Nature Communications* 15: 4392.

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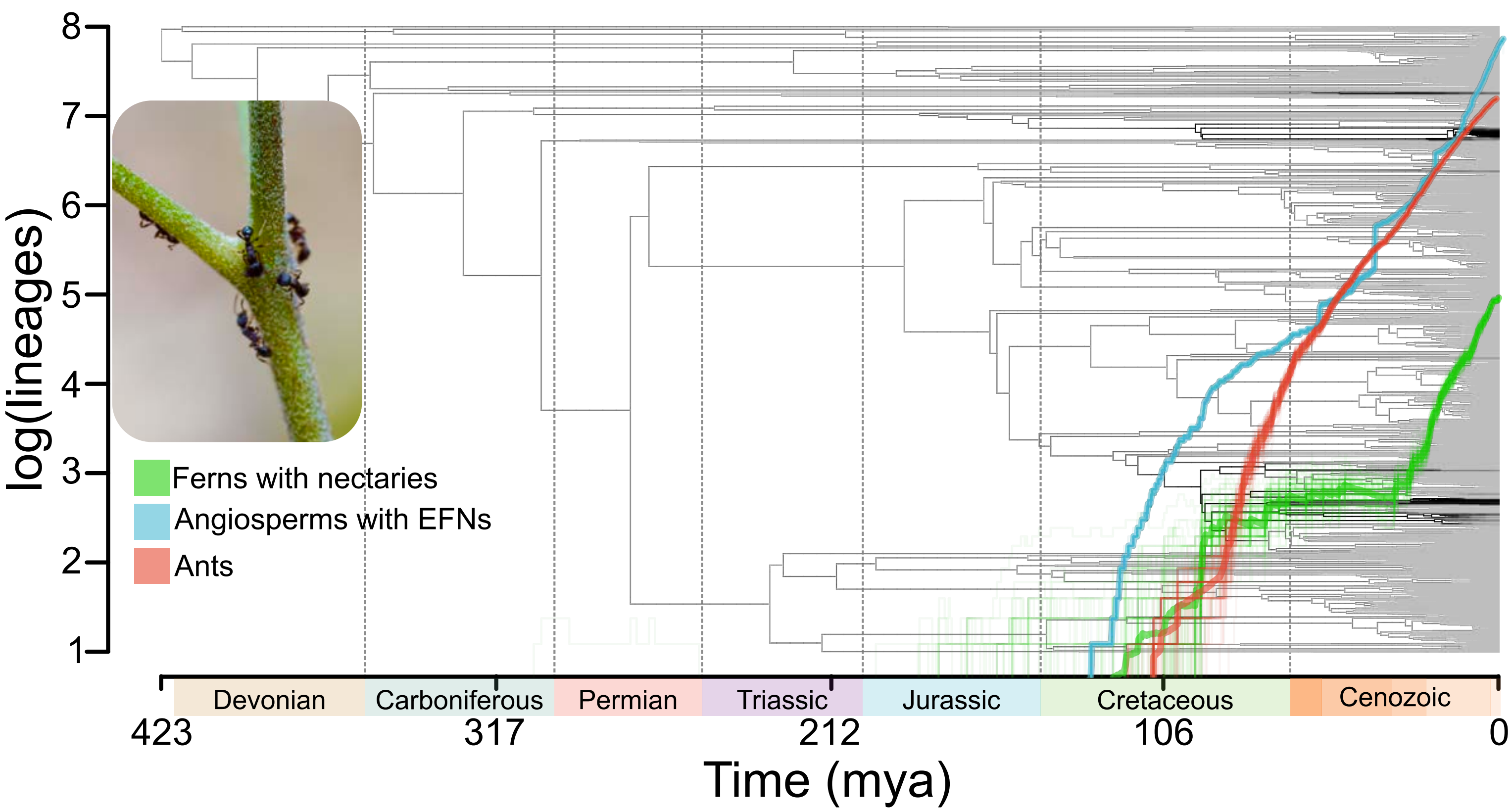
# Lag of nectary diversification in ferns




Suissa, J. S., Li, F.-W. & Moreau, C. S. (2024) *Nature Communications* 15: 4392.

Jacob Suissa

# Increased herbivory during the Cenozoic, a general pattern

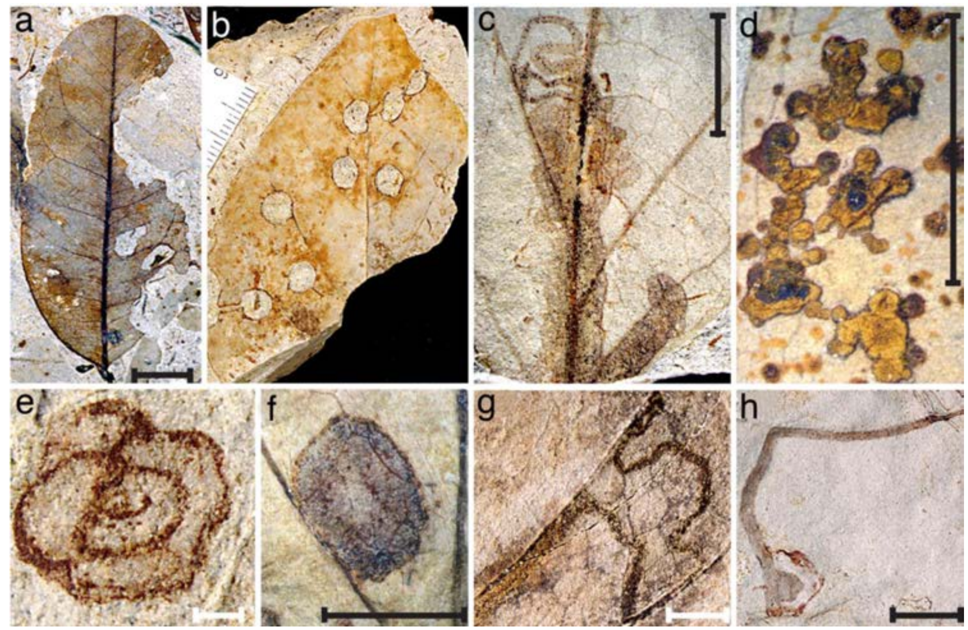
PNAS

## 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[‖]

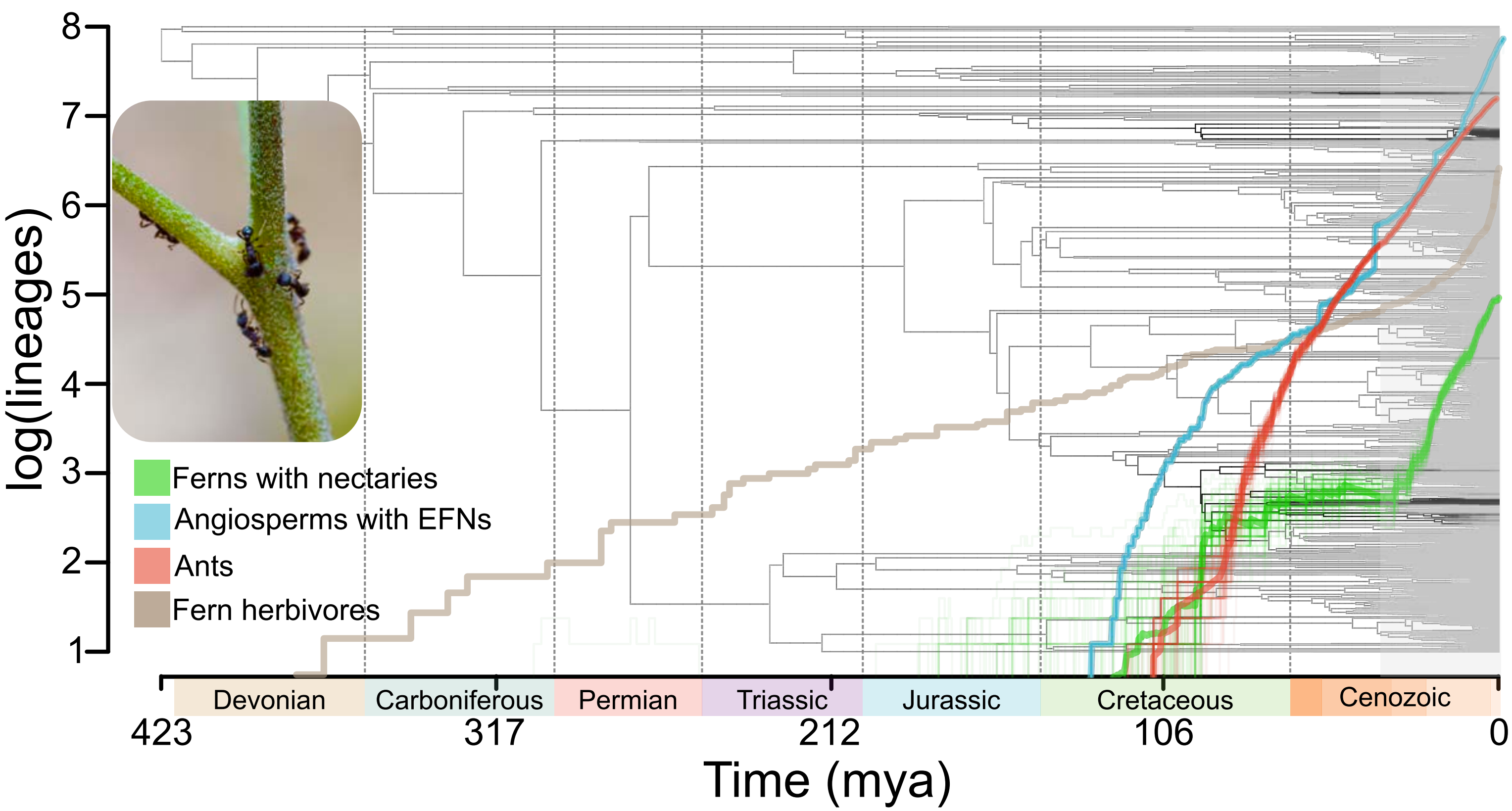
[*]Department of Geosciences, Pennsylvania State University, University Park, PA 16802; [†]Department of Paleobiology, Smithsonian Institution, Washington, DC 20560; [§]Department of Entomology, University of Maryland, College Park, MD 20742; [¶]Department of Earth Science, University of California, 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?




Suissa, J. S., Li, F.-W. & Moreau, C. S. (2024) *Nature Communications* 15: 4392.

# 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)

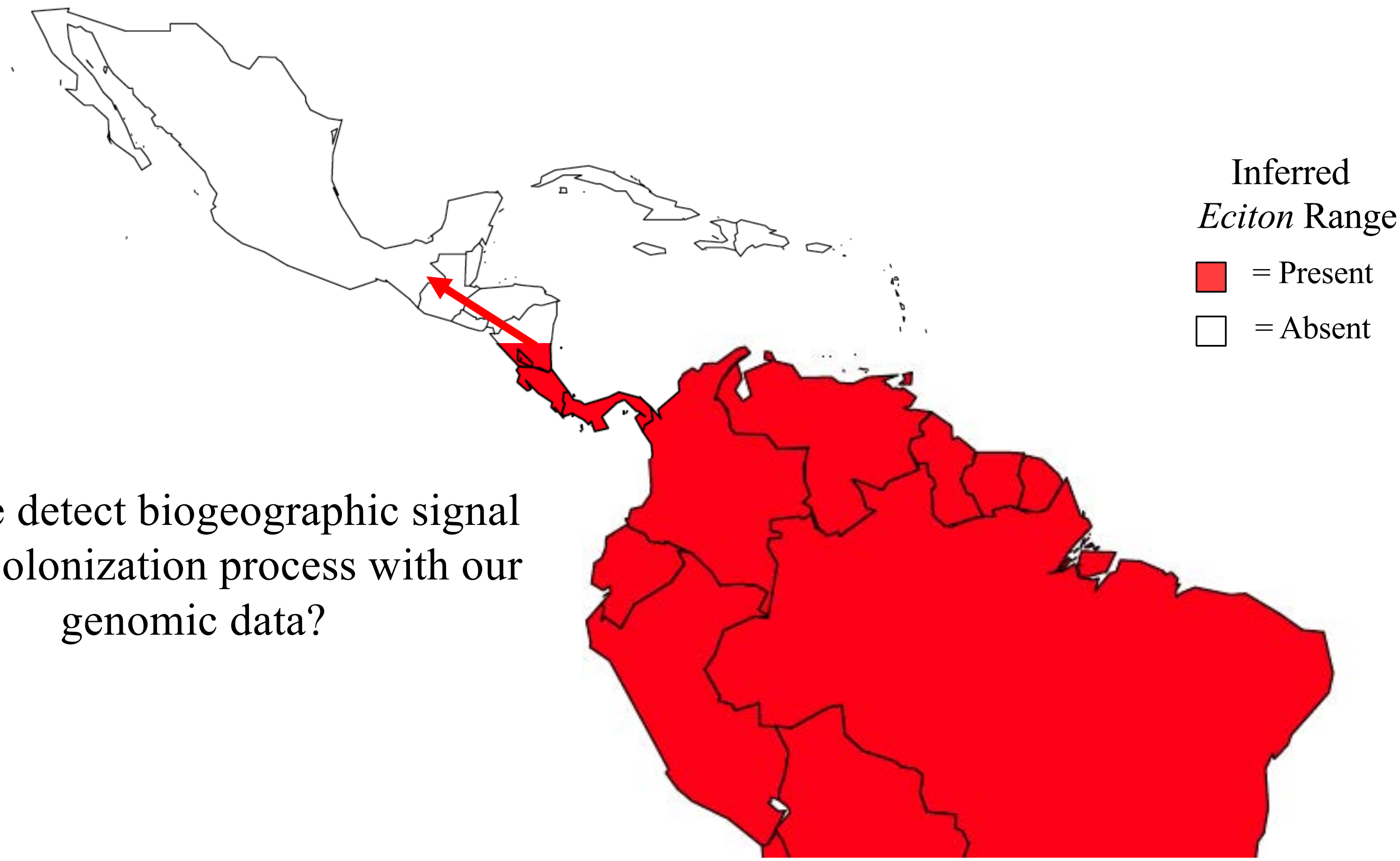
# Panama provides land bridge for Central American colonization [3.0 Ma - Today]


(Brady, 2003; Bagley & Johnson, 2014; Coates et al., 2004)

# Complex emergence of Panama
# [8.0 – 3.0 Ma]


(Brady, 2003; Bagley & Johnson, 2014; Coates et al., 2004)

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




Can we detect biogeographic signal of the colonization process with our genomic data?

(Brady, 2003; Bagley & Johnson, 2014; Coates et al., 2004)

# 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)

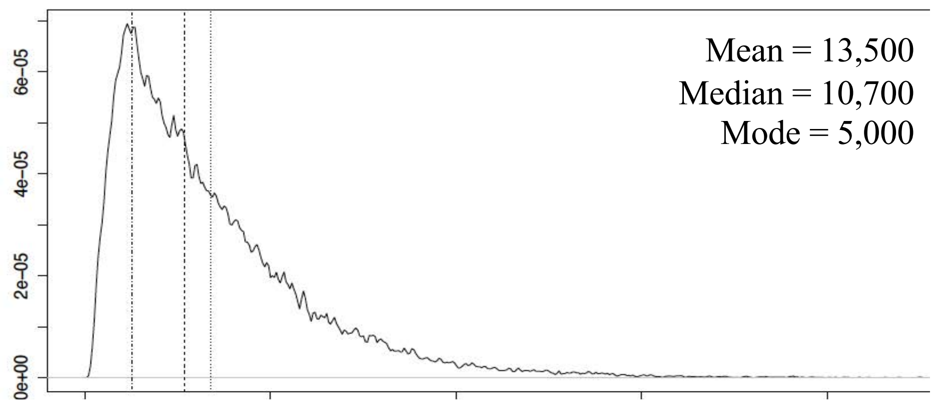
- Colonization across early land bridge (3 – 8 Ma)
- Increase of diversification in CA
- Divergence times between 3 – 8 Ma
- Secondary contact zones potentially coincident

Coates *et al*. (2004); Gutiérrex-García & Vázquez-Dominguez (2013); Winston, Kronauer, & Moreau (2017)

# *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)*




Pairwise Shared Loci (x10,000)

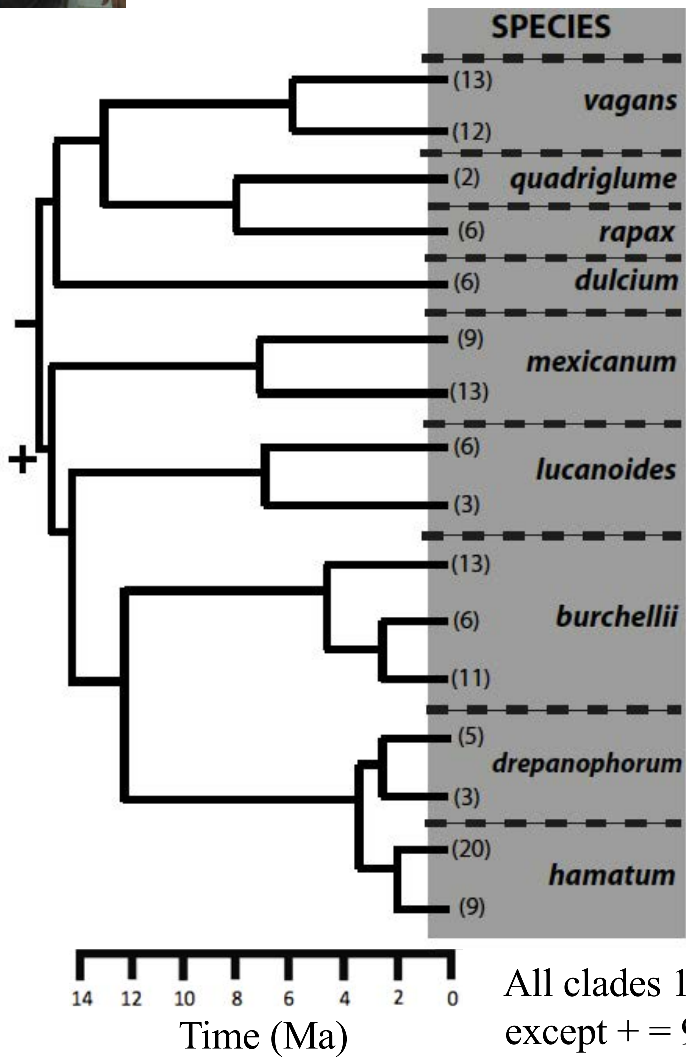
*Loci assembly*: *pyRAD* pipeline
- Employs *vsearch* algorithm
- *De novo* read clustering
- 1-2 weeks split on 40 cores

506,759 parsimony informative loci
- 100bp length
- Shared by at least 4 taxa
- Minimum 10x coverage ($\mu \approx 20$)

Winston, Kronauer, & Moreau (2017); Eaton (2014); Edgar (2010)

Max Winston

# Phylogeny, Divergence Dating, and Biogeographic Inference



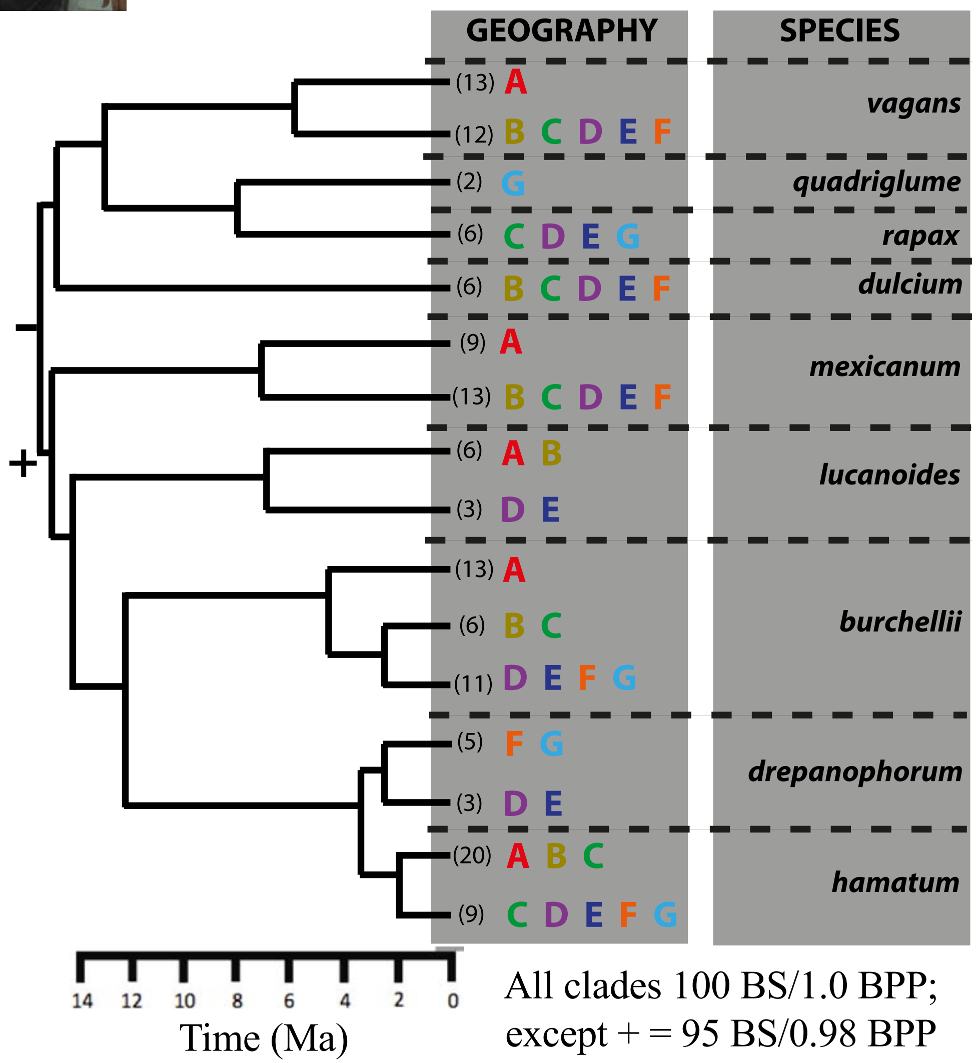

All clades 100 BS/1.0 BPP;
except + = 95 BS/0.98 BPP

- 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

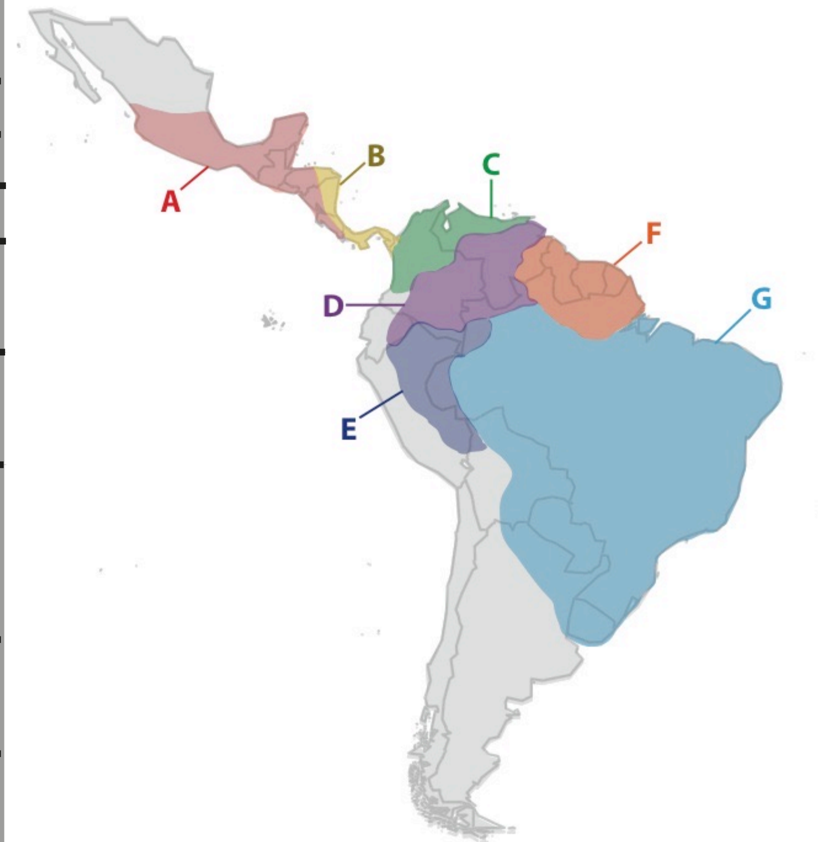
Winston, Kronauer, & Moreau (2017)
*Molecular* Ecology 26: 859-870.

Max Winston

# Phylogeny, Divergence Dating, and Biogeographic Inference




All clades 100 BS/1.0 BPP; except + = 95 BS/0.98 BPP

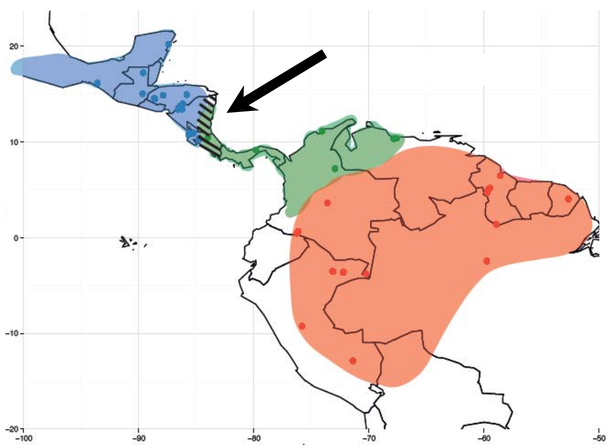



Winston, Kronauer, & Moreau (2017) *Molecular* Ecology 26: 859-870.

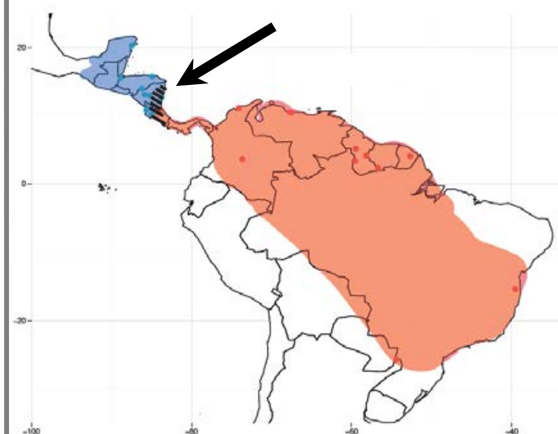
Max Winston

# Coincident Secondary Contact Zones

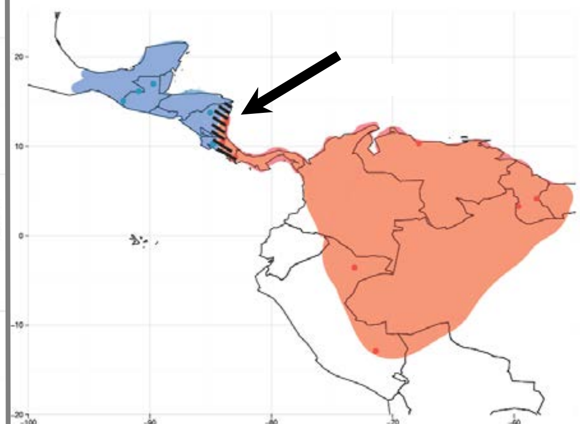
= Secondary Contact Zone



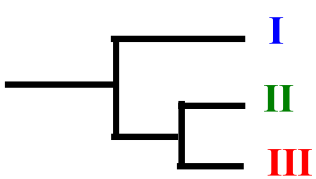
*E. burchellii*

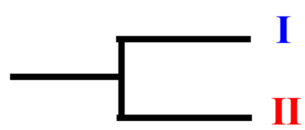


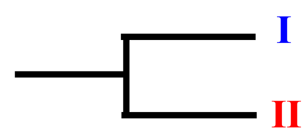
*E. vagans*



*E. mexicanum*




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

Max Winston

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

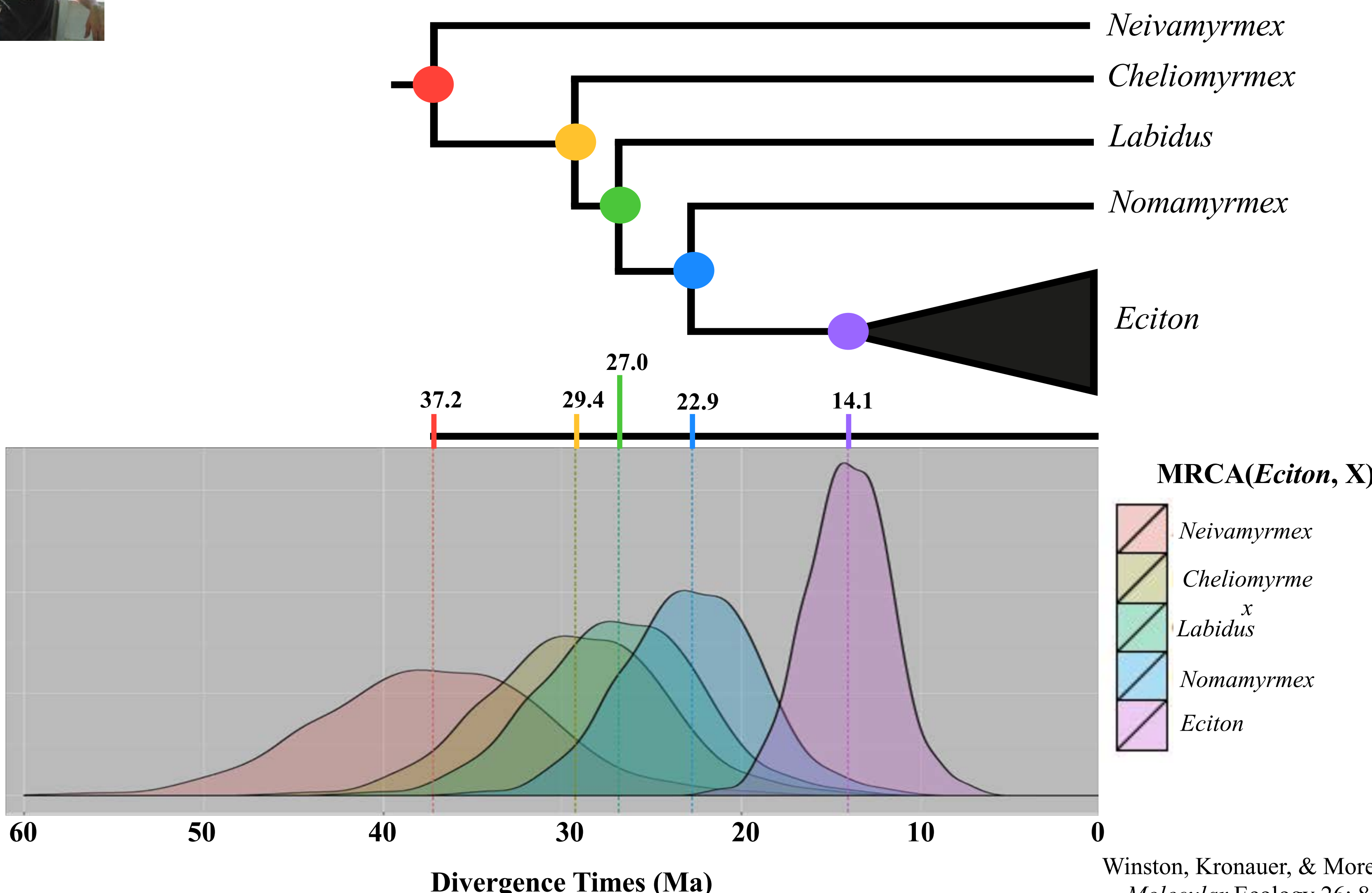
When did this speciation occur?

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

Max Winston

# Divergence Times of Sister Lineages

*Across Central American Isthmus*




Winston, Kronauer, & Moreau (2017)
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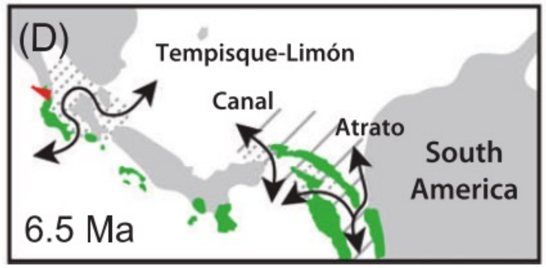
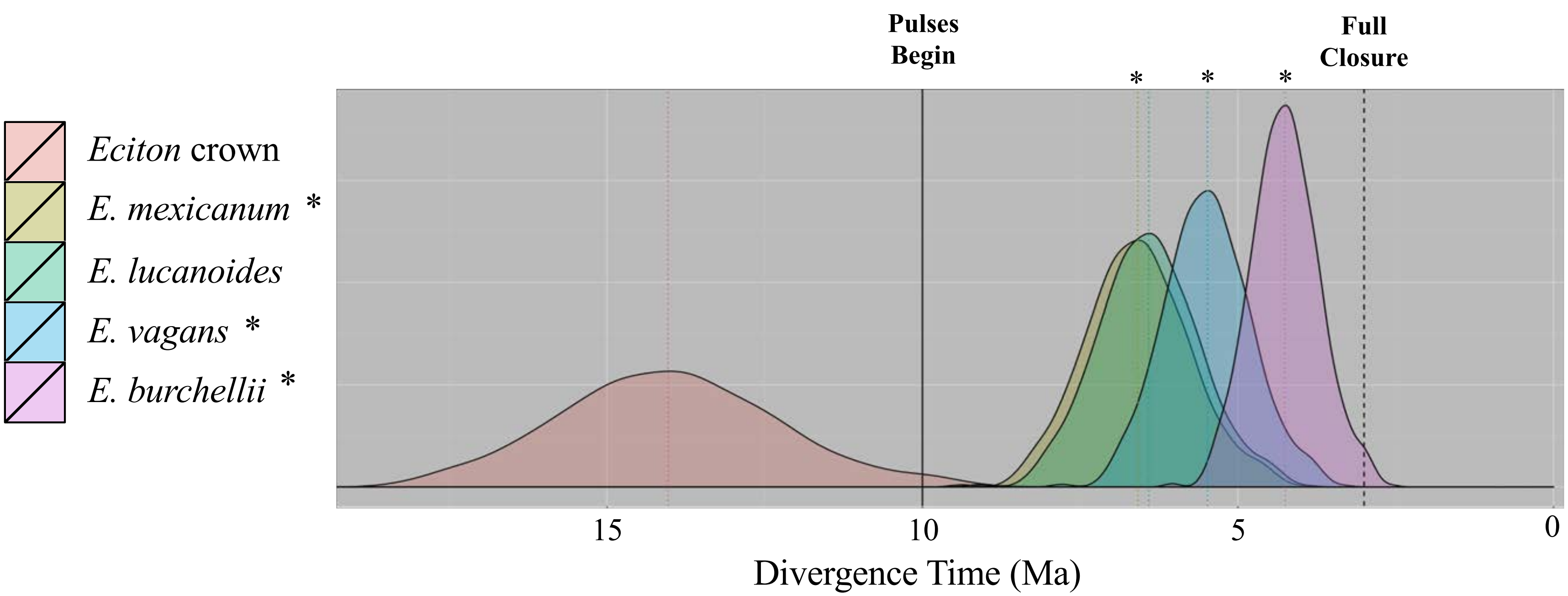
# Divergence Times of Sister Lineages

*Across Central American Isthmus*




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

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

# Which model does the evidence support?

FCC = Full Closure Colonization model

EDC = Early Dynamic Colonization model

| | **FCC** | **EDC** | **Evidence Support** |
|---|---|---|---|
| ***Diversification*** | No effect | Increase | |
| ***Divergence Times*** | Less than 3 Ma | 4 – 8 Ma | |
| ***Parapatry Coincidence*** | Random | Yes | |

Early Dynamic Colonization (EDC)

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

# 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 inform the complex history of the colonization of Central America

# Acknowledgements

**Collaborators on this work:**
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Roger Vila (Universitat Autònoma de Barcelona)
Max Winston (University of Chicago)

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Seyde Delgado (Undergraduate intern)
Mahalia Donaldson (Undergraduate intern)
Leland Graber (Ph.D. student)
Ayress Grinage (Ph.D. student)
Tatsuya Inagaki (Postdoctoral researcher)
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… and thank you!

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