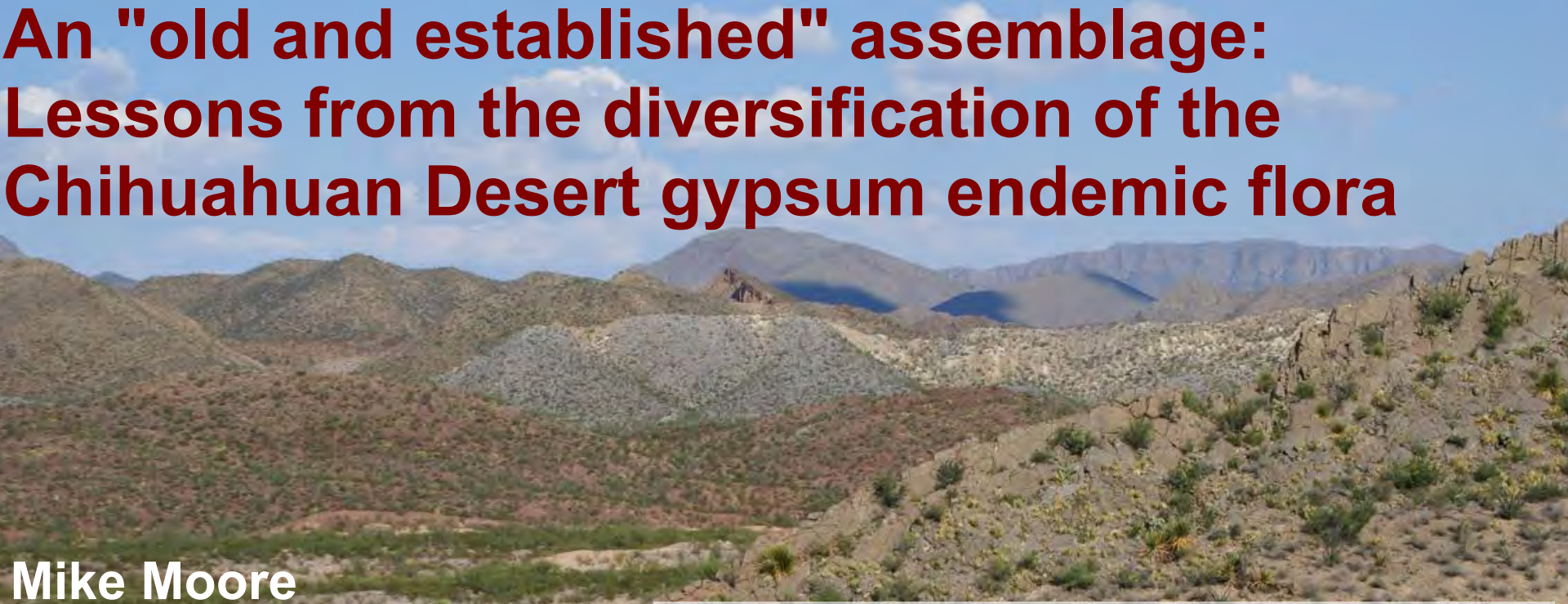
An "old and established" assemblage: Lessons from the diversification of the Chihuahuan Desert gypsum endemic flora



Mike Moore
Clare Muller
Rebecca Drenovsky
Nathaniel Heiden
Zoë Feder
Helene Tiley
Norm Douglas
Hilda Flores Olvera
Helga Ochoterena
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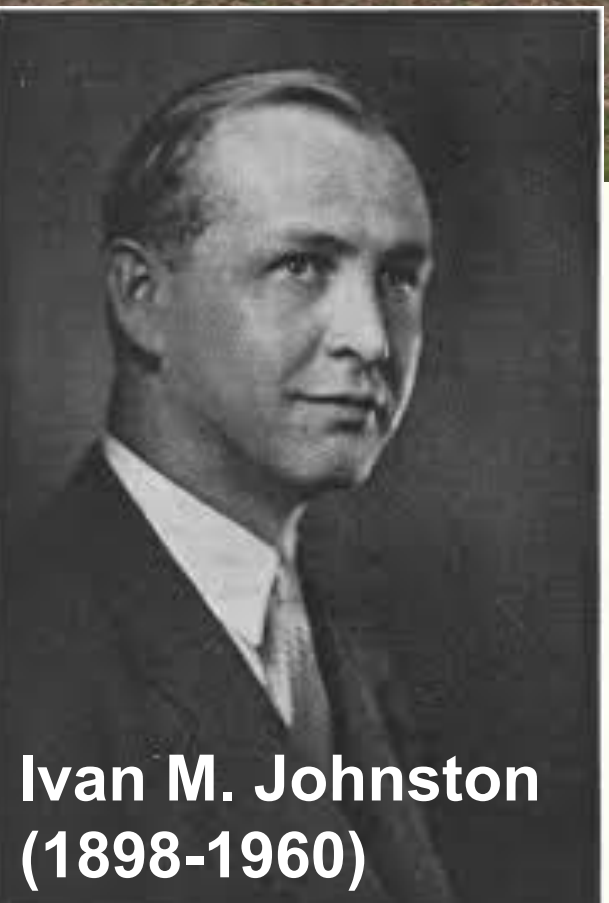
An "old and established" assemblage: Lessons from the diversification of the Chihuahuan Desert gypsum endemic flora



Ivan M. Johnston (1898-1960)

JOURNAL

OF THE

ARNOLD ARBORETUM

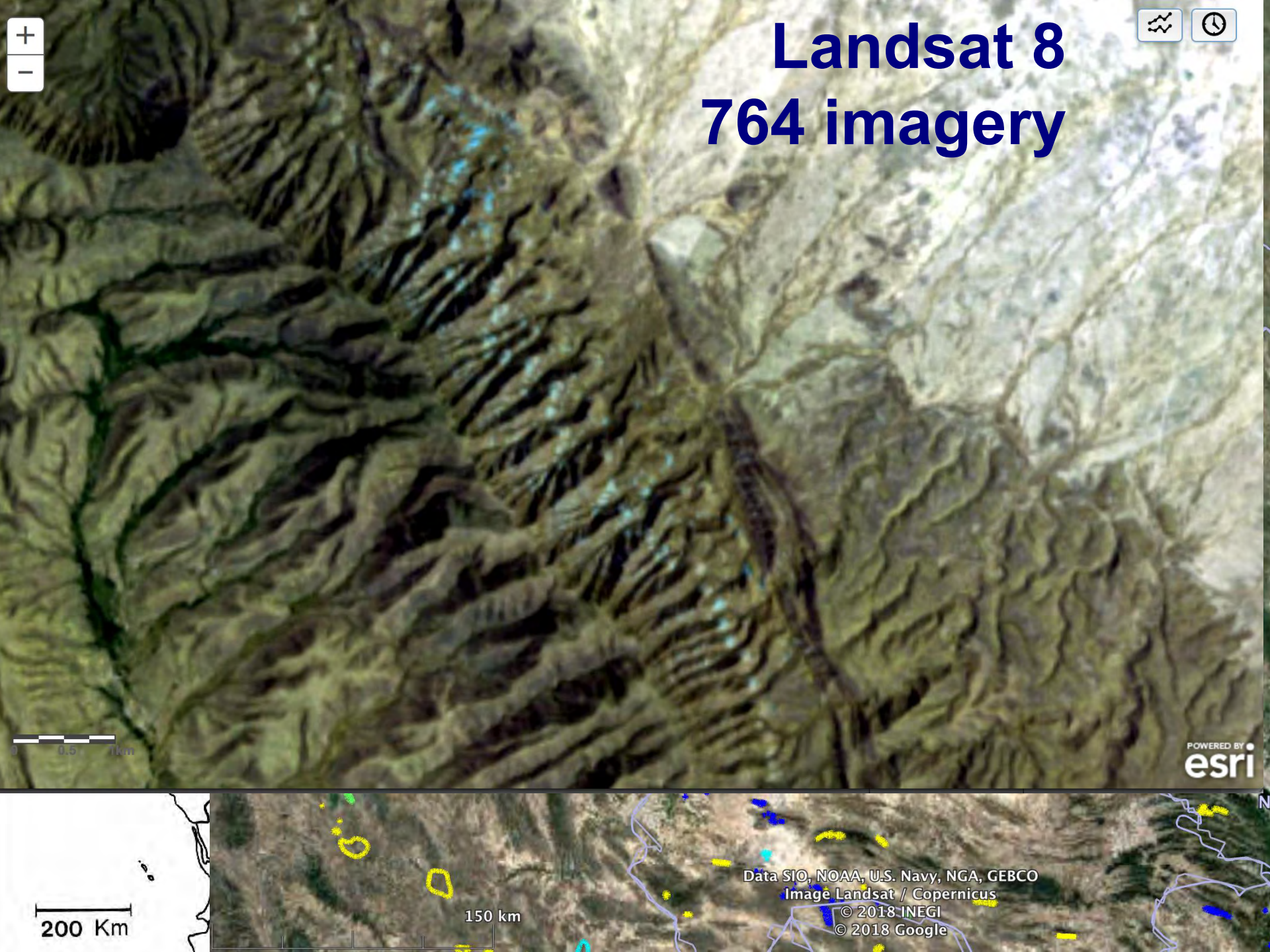
VOL. XXII APRIL, 1941 NUMBER 2

GYPSOPHILY AMONG MEXICAN DESERT PLANTS

IVAN M. JOHNSTON

10+ years of work on Chihuahuan Desert gypsum endemics
Mostly phylogenetics & phylogeography
I'm very interested in historical community assembly
Edaphic endemic floras make excellent case studies

First, an introduction to the flora


Landsat 8
764 imagery
POWERED BY esri
200 Km
150 km
Data SIO, NOAA, U.S. Navy, NGA, GEBCO
Image Landsat / Copernicus
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The Chihuahuan Desert gypsum endemic flora is highly diverse

Including the entire “archipelago”:
240+ species in 41 families

The Chihuahuan Desert g
endemic flora is highly di

52 genera with ≥ 2 gypsum endemic
28 genera with ≥ 3 gypsum endemic

Marshalljohnstonia

Sartwellia

Nerisyrenia

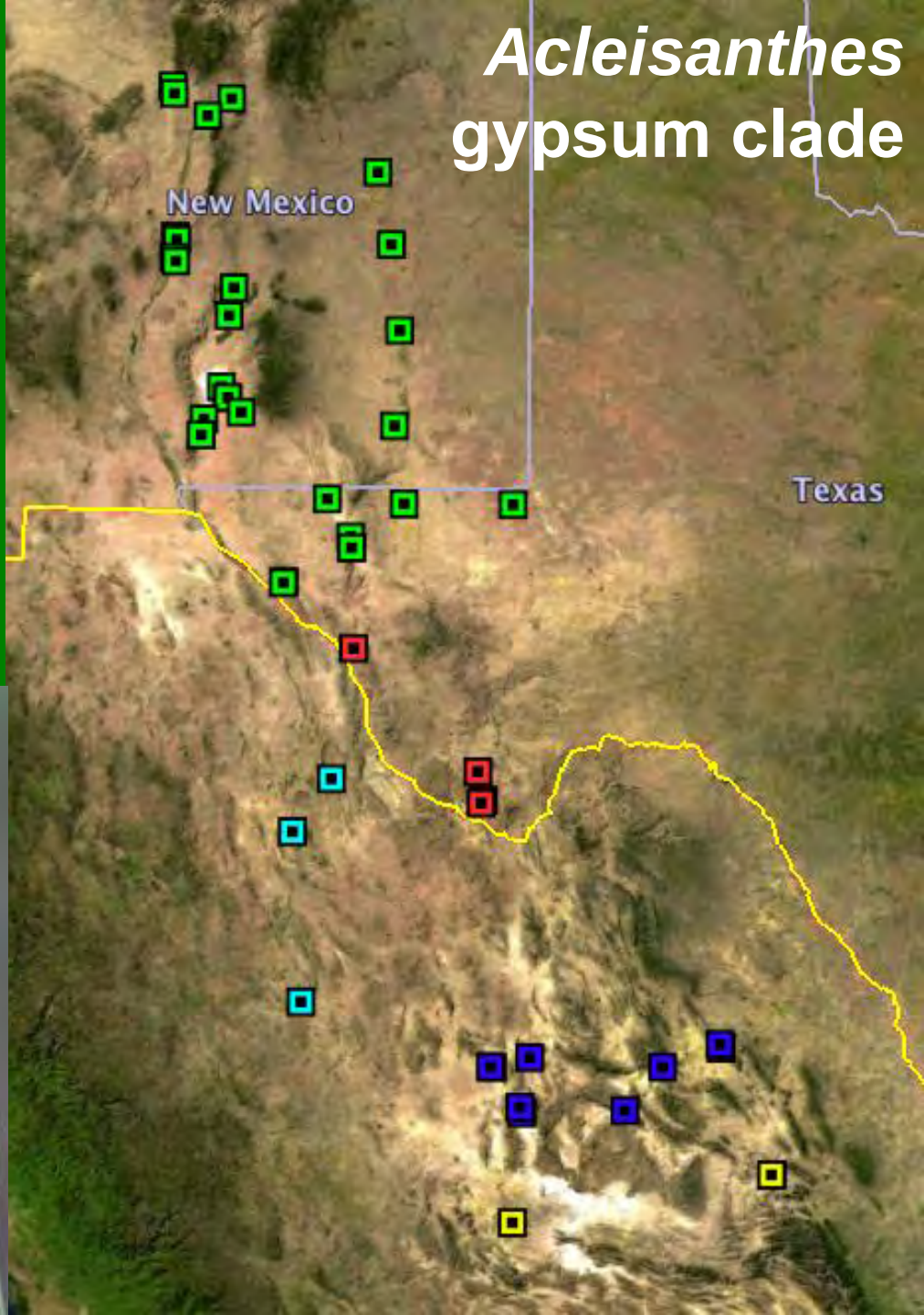
The Chihuahuan Desert gypsum endemic flora is highly diverse

At least 114 origins of gypsum endemism
At least 30 clades of gypsum endemic taxa

Some of these gypsum endemics are very distinctive morphologically

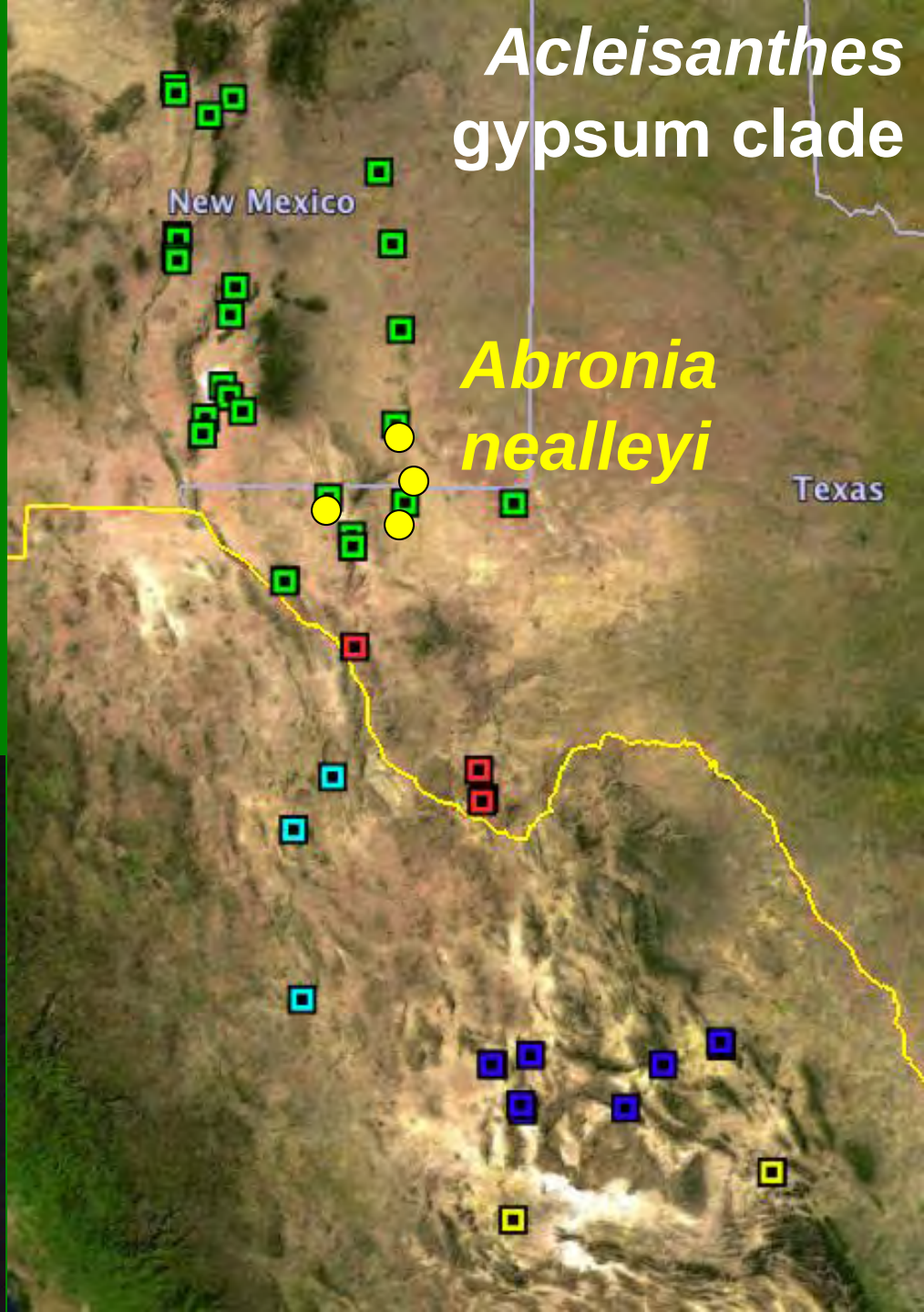
Others are much less distinctive morphologically

Some Chihuahuan Desert gypsum endemics are widely distributed…



Some Chihuahuan Desert gypsum endemics are widely distributed…
…others are not

Morphology & distribution are correlated with lineage age



Nyctaginaceae
tribe
Nyctagineae

matK,
ndhF,
ycf1

Anulocaulis gypsum clade (6 taxa)

Mirabilis nesomii

Abronia nealleyi

Abronia bigelovii

Acleisanthes gypsum clade (6 taxa)

Wide gypsum endemics are in clades & are morphologically distinctive from congeners

Nyctaginaceae
tribe
Nyctagineae

When did these taxa diversify?

matK*, *ndhF*, *ycf1

***Anulocaulis* gypsum clade (6 taxa)**

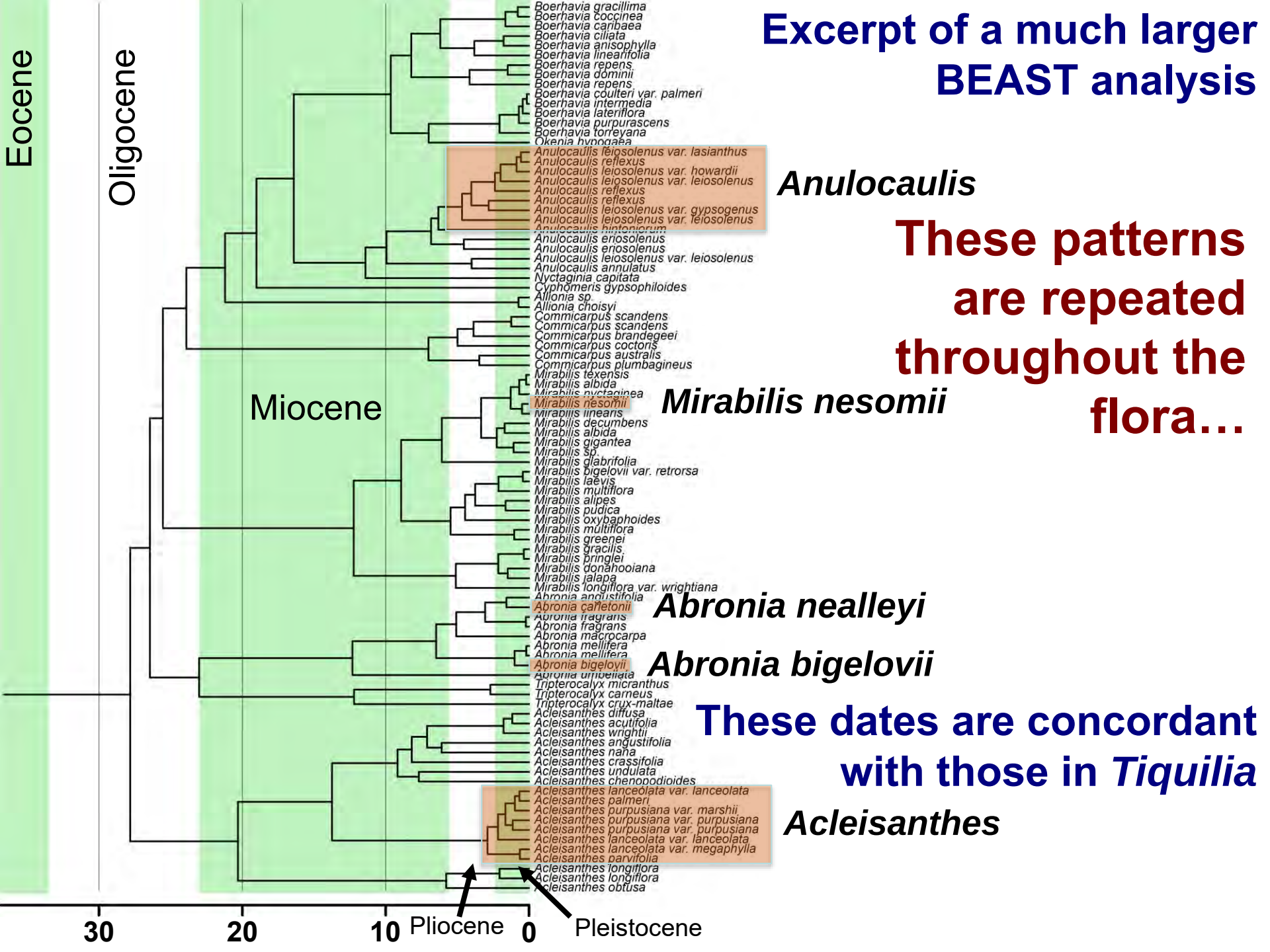
Mirabilis nesomii

Abronia nealleyi

Abronia bigelovii

***Acleisanthes* gypsum clade (6 taxa)**

Morphologically less distinct with narrower geographic ranges



Excerpt of a much larger BEAST analysis

Anulocaulis

These patterns are repeated throughout the flora…

Mirabilis nesomii

Abronia nealleyi

Abronia bigelovii

These dates are concordant with those in *Tiquilia*

Acleisanthes

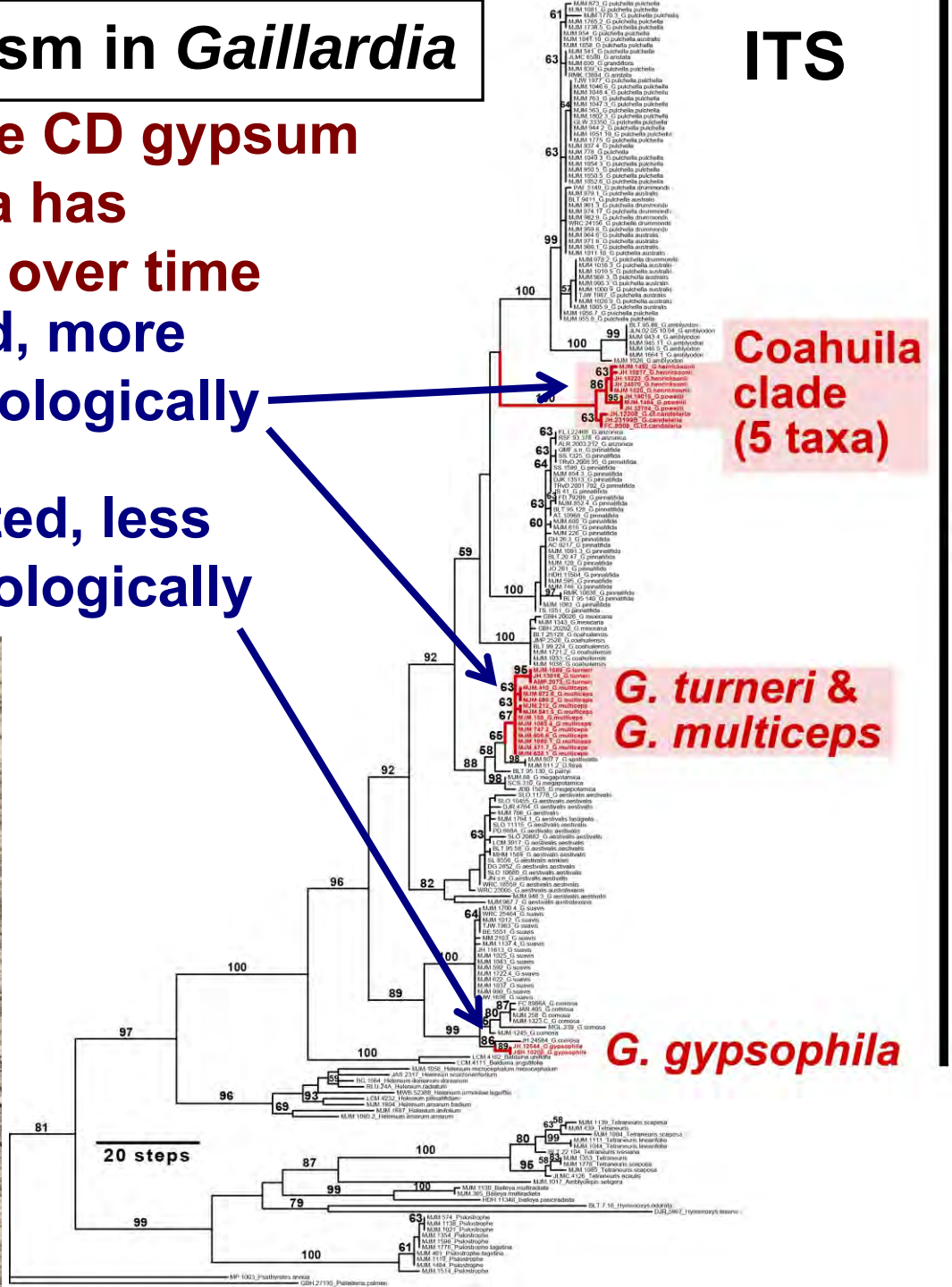
Gypsum endemism in *Gaillardia*

ITS

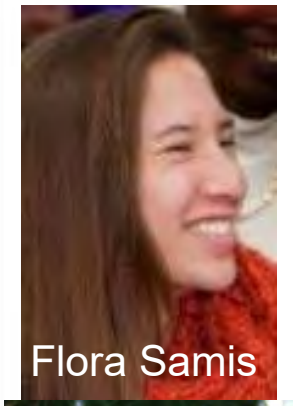
Lesson 1: The CD gypsum endemic flora has accumulated over time

Widely distributed, more distinctive morphologically

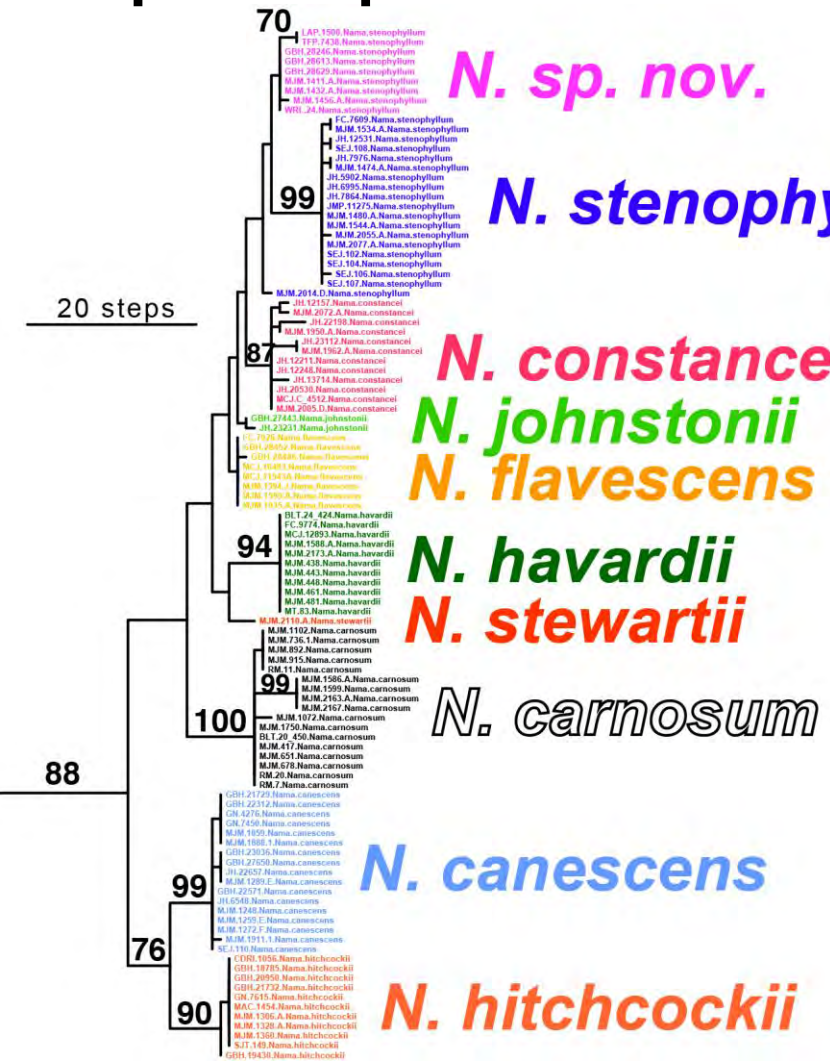
Narrowly distributed, less distinctive morphologically



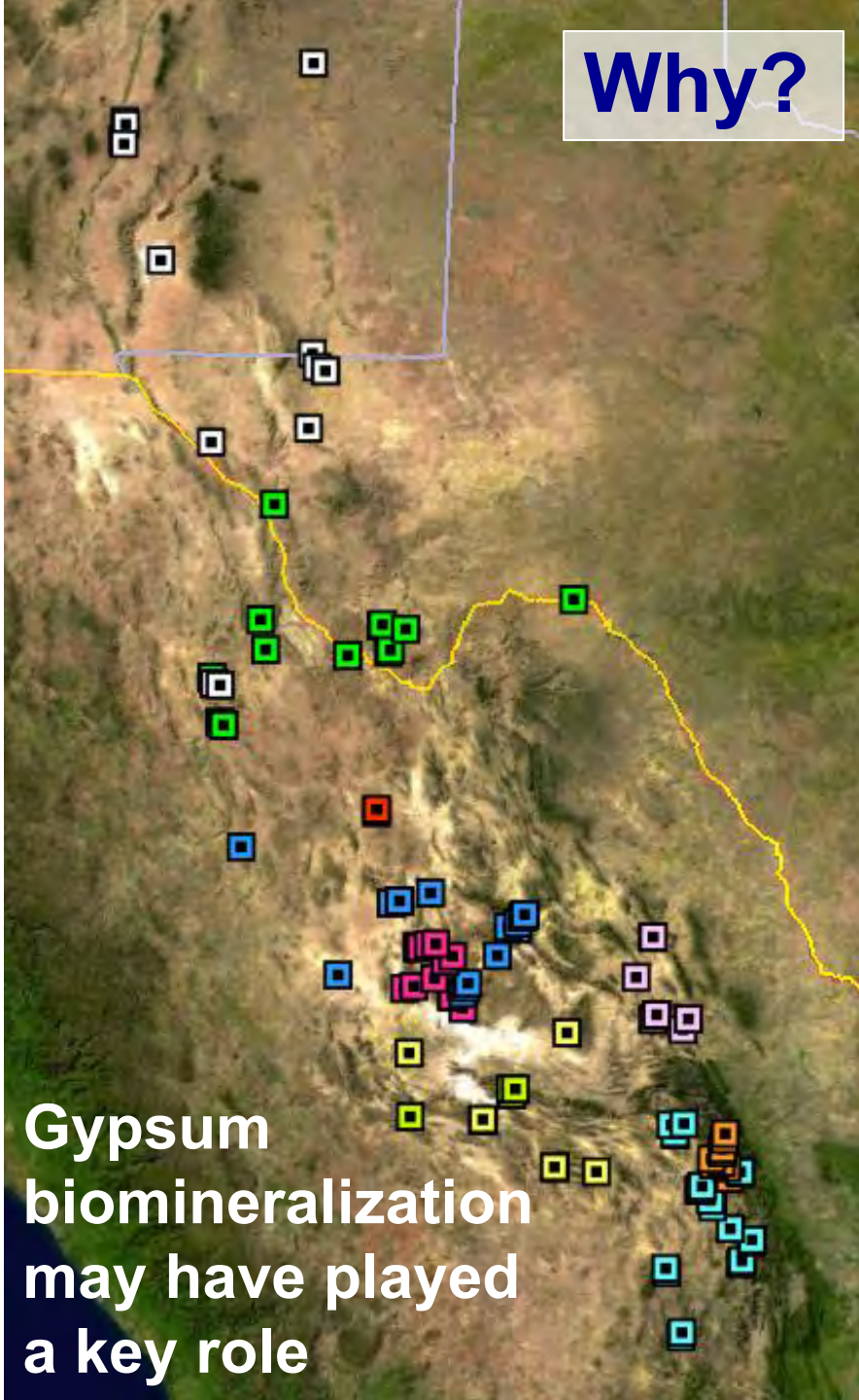
Gaillardia



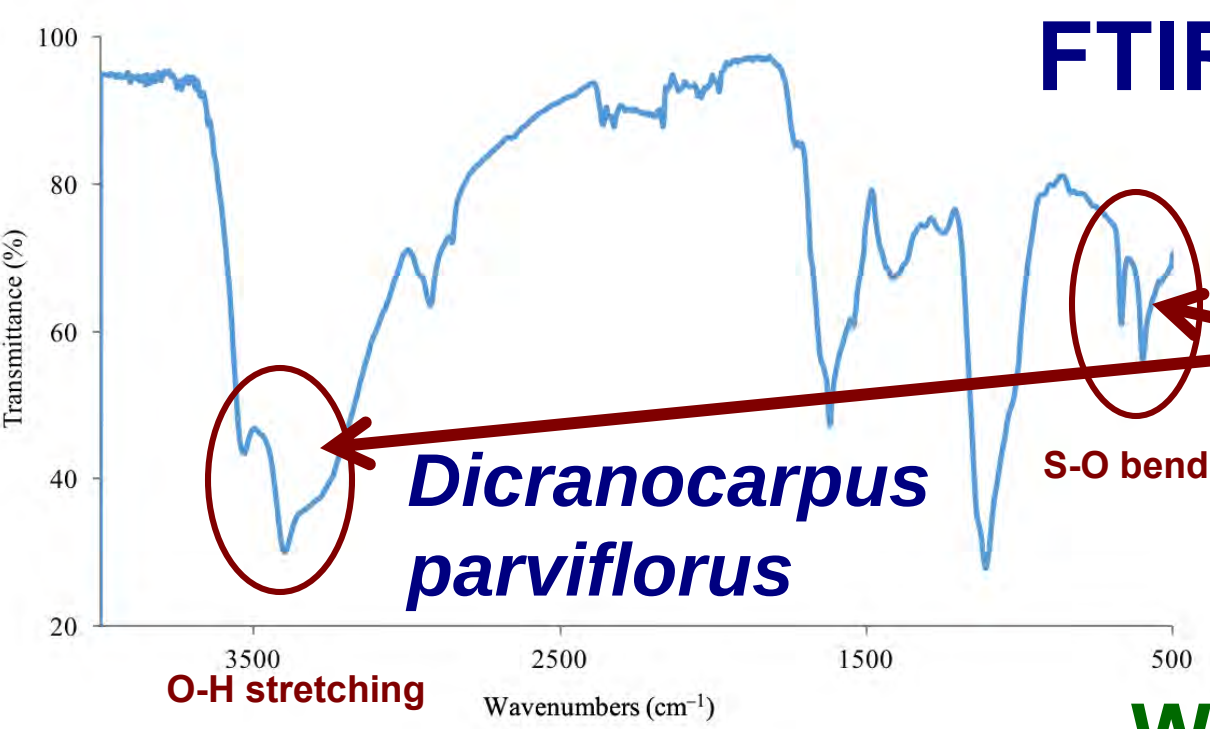
In gypsum endemic clades, allopatric speciation is the norm



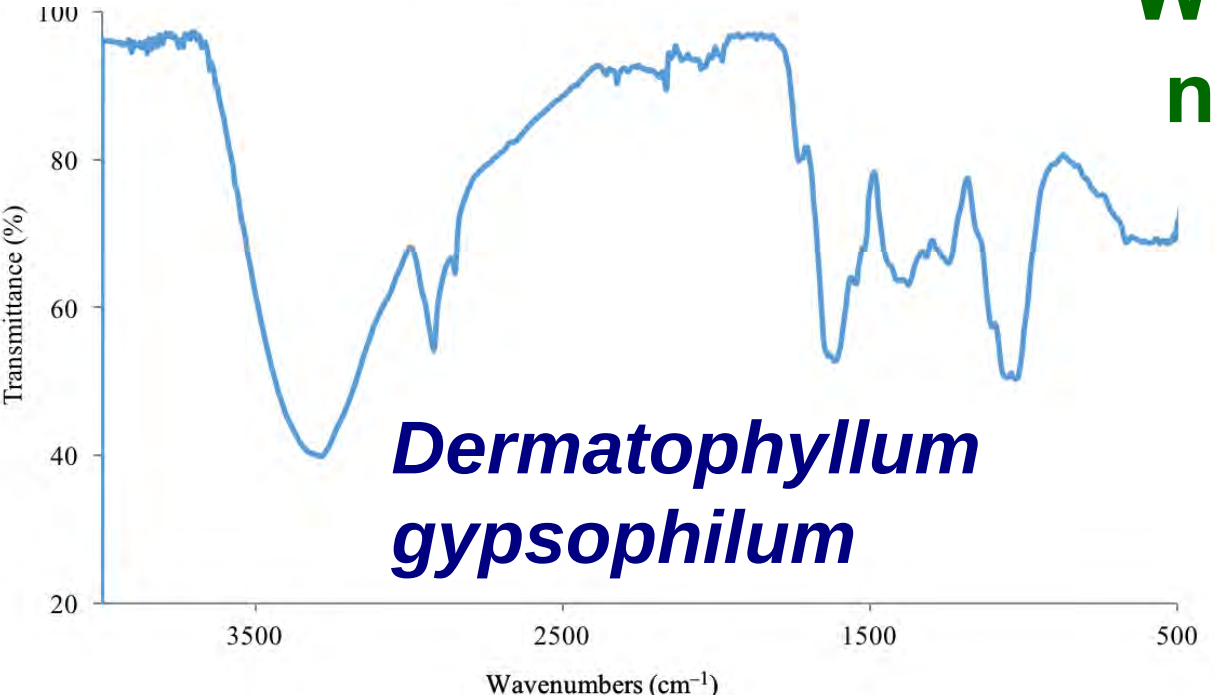
Lesson 2: Widespread gypsum clades appear to be the oldest endemics in the CD



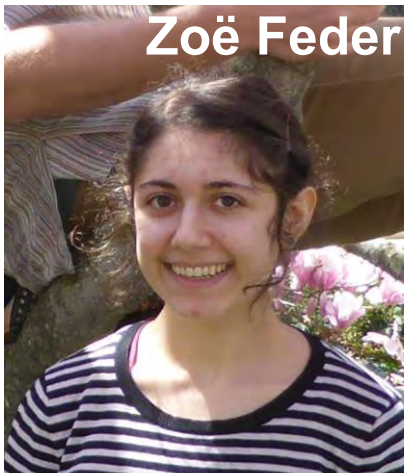
FTIR spectrometry of leaves



Peaks indicative of gypsum

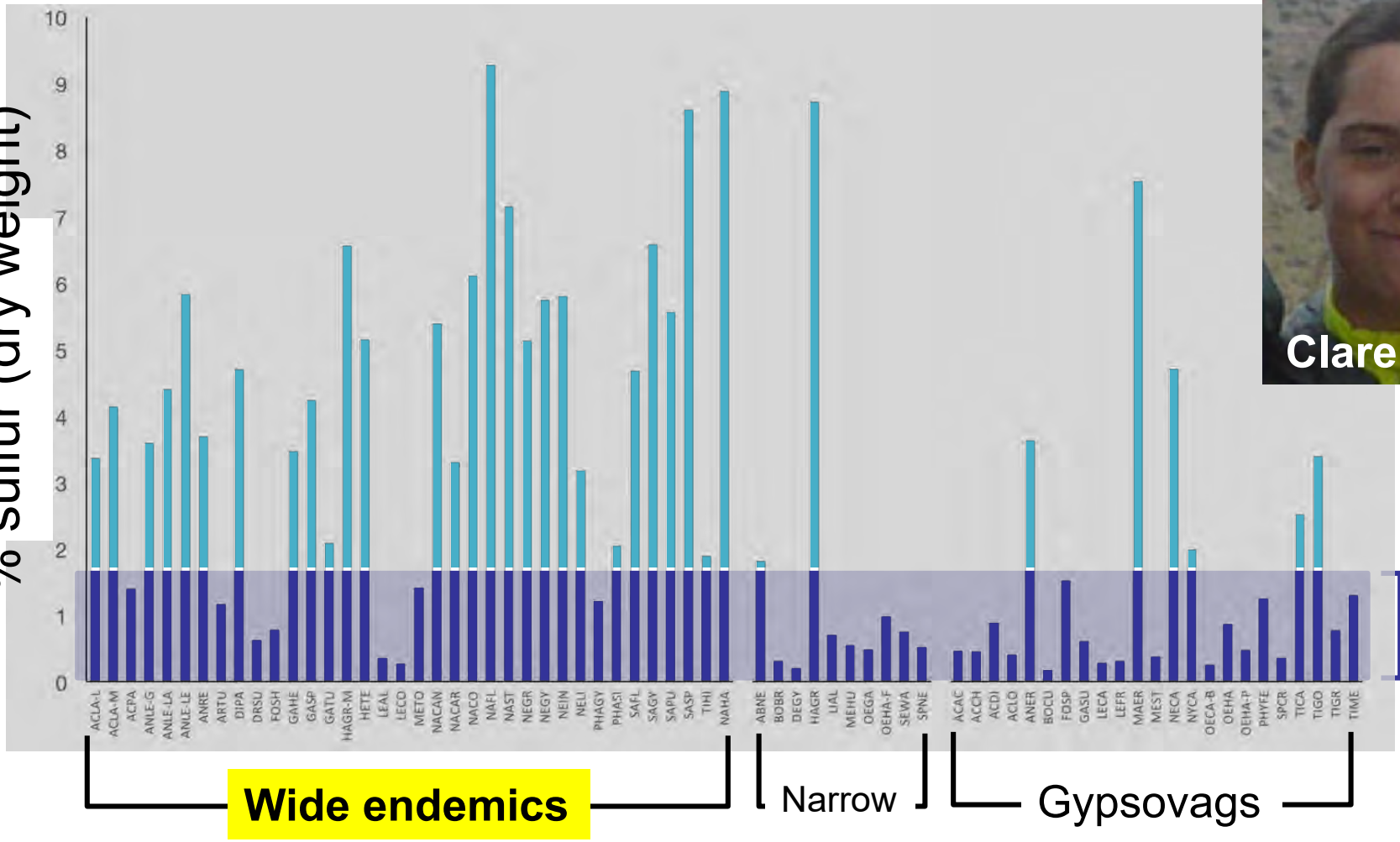


What about foliar nutrient levels?



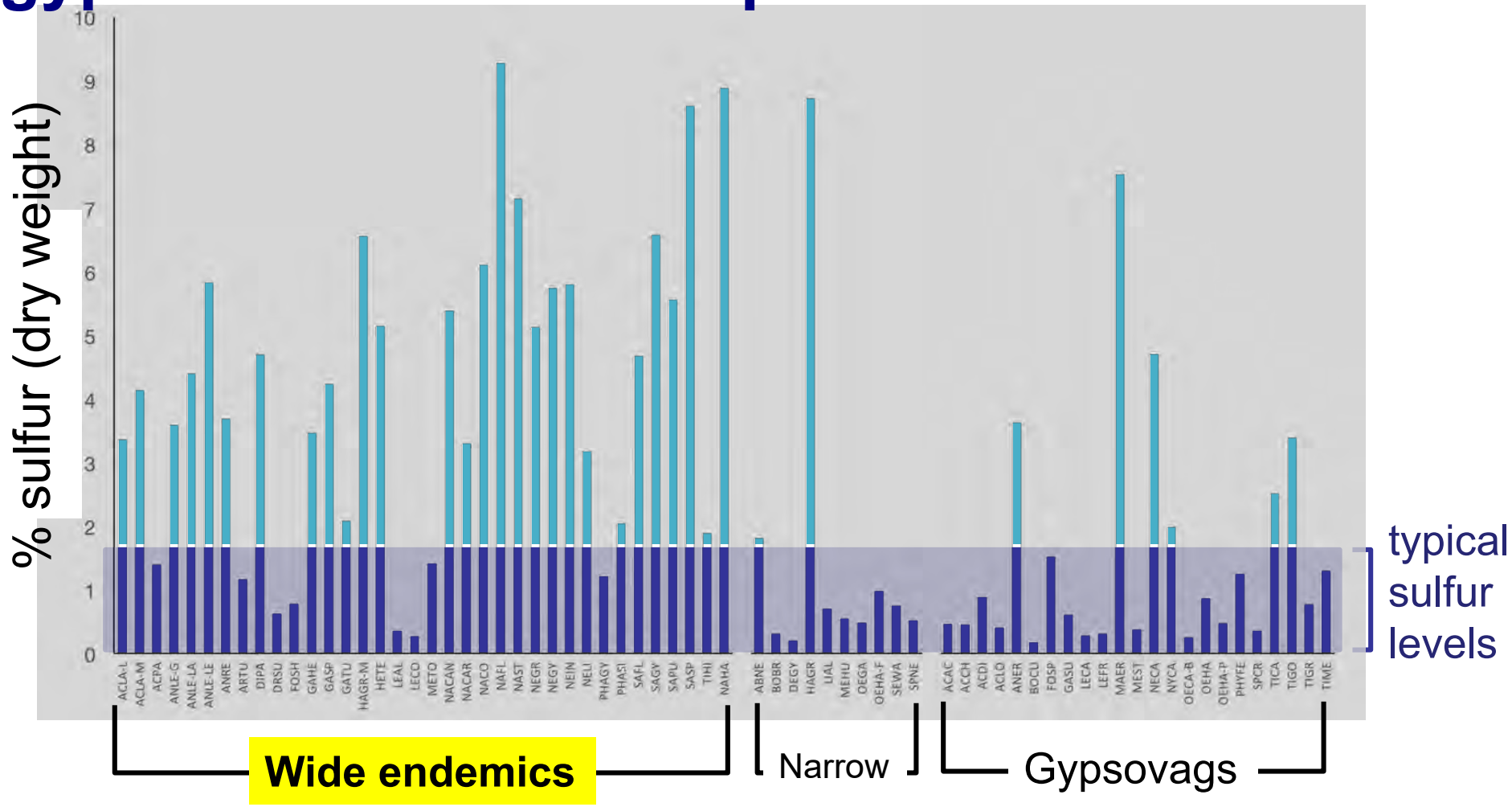
Ellie Tiley
Keyi Feng

Gypsum detected in all samples with ≥1.8% sulfur

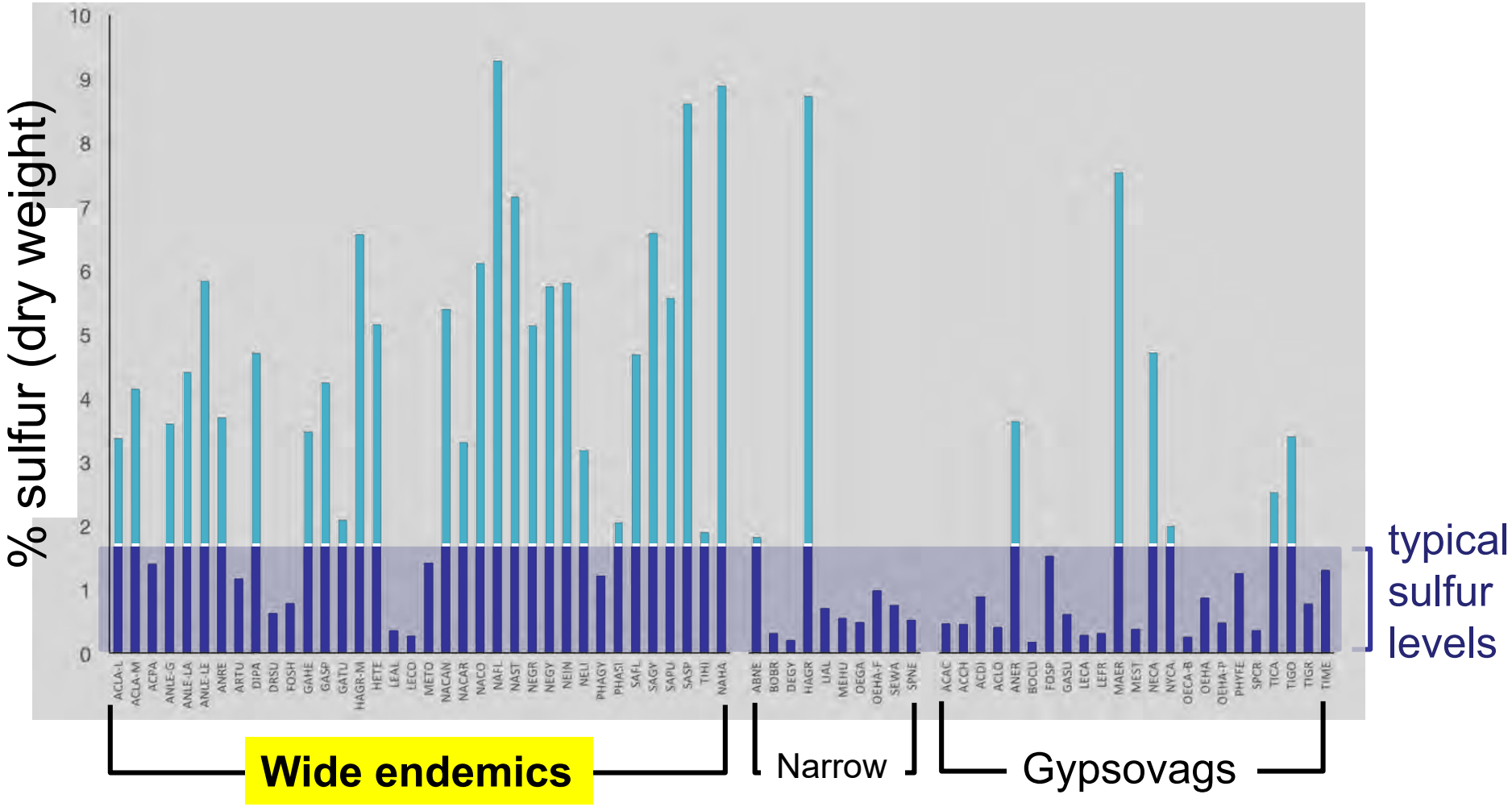


But is gypsum biomineralization an adaptive response or a preadaptation?

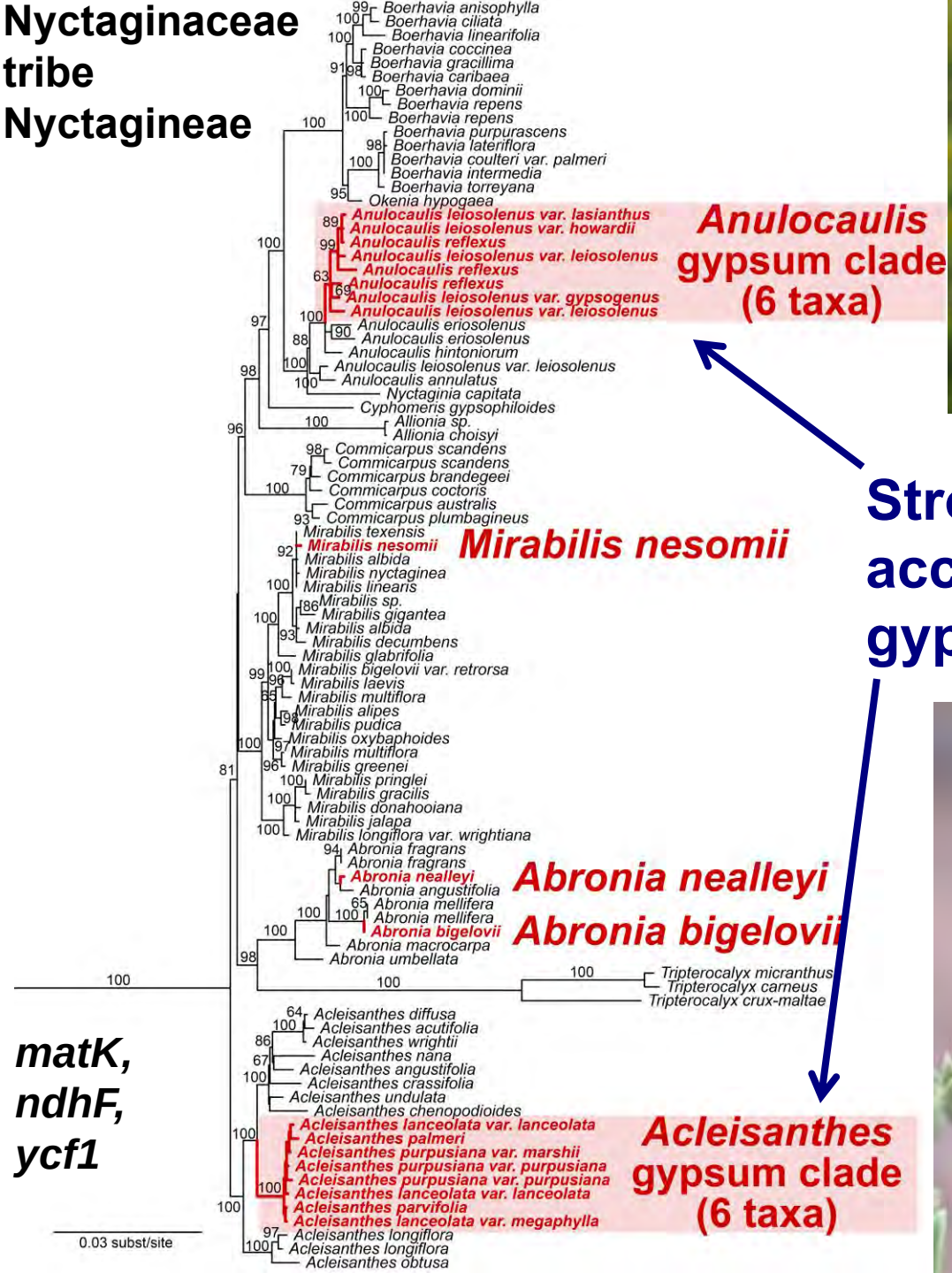
One way to test preadaptation hypothesis: is gypsum accumulation present in relatives?



No evidence of S or gypsum accumulation in most gypsovags and narrow endemics



Nyctaginaceae
tribe
Nyctagineae



matK,
ndhF,
ycf1

Anulocaulis gypsum clade (6 taxa)

Mirabilis nesomii

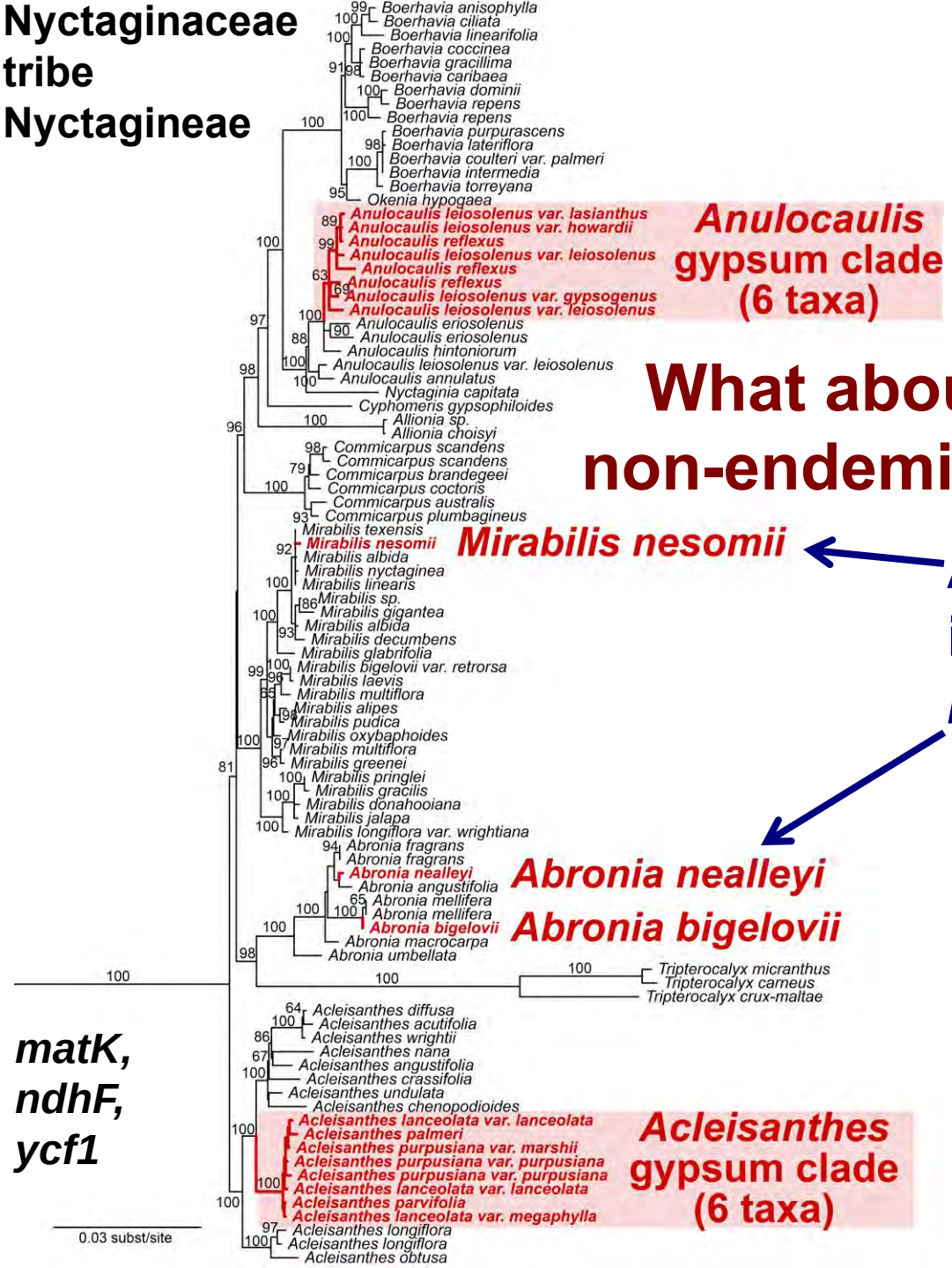
Abronia nealleyi

Abronia bigelovii

Acleisanthes gypsum clade (6 taxa)

Strong evidence for gypsum accumulation in widespread gypsum endemic clades

Nyctaginaceae
tribe
Nyctagineae



***Anulocaulis* gypsum clade (6 taxa)**

What about non-endemics?

Mirabilis nesomii

Also evidence of gypsum in *Abronia nealleyi* & *Mirabilis nesomii*

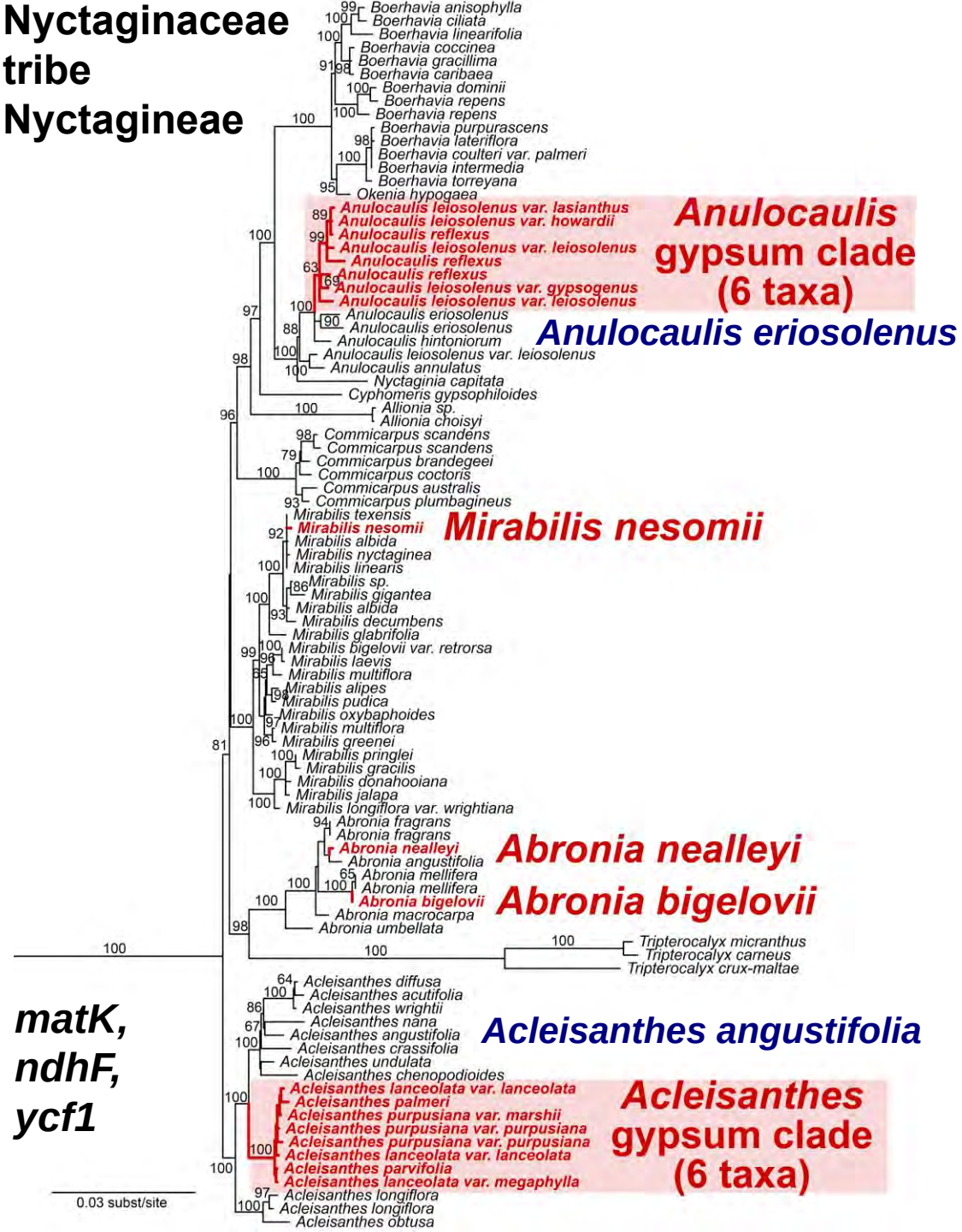
Abronia nealleyi

Abronia bigelovii

***Acleisanthes* gypsum clade (6 taxa)**

matK, ndhF, ycf1

Nyctaginaceae
tribe
Nyctagineae



Anulocaulis gypsum clade (6 taxa)

Anulocaulis eriosolenus

Mirabilis nesomii

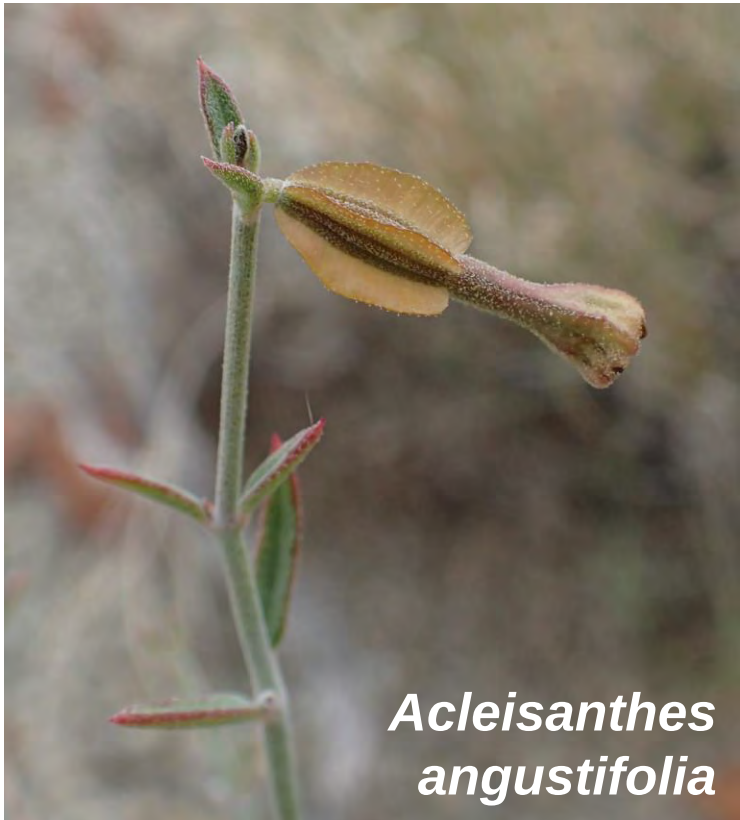
Abronia nealleyi

Abronia bigelovii

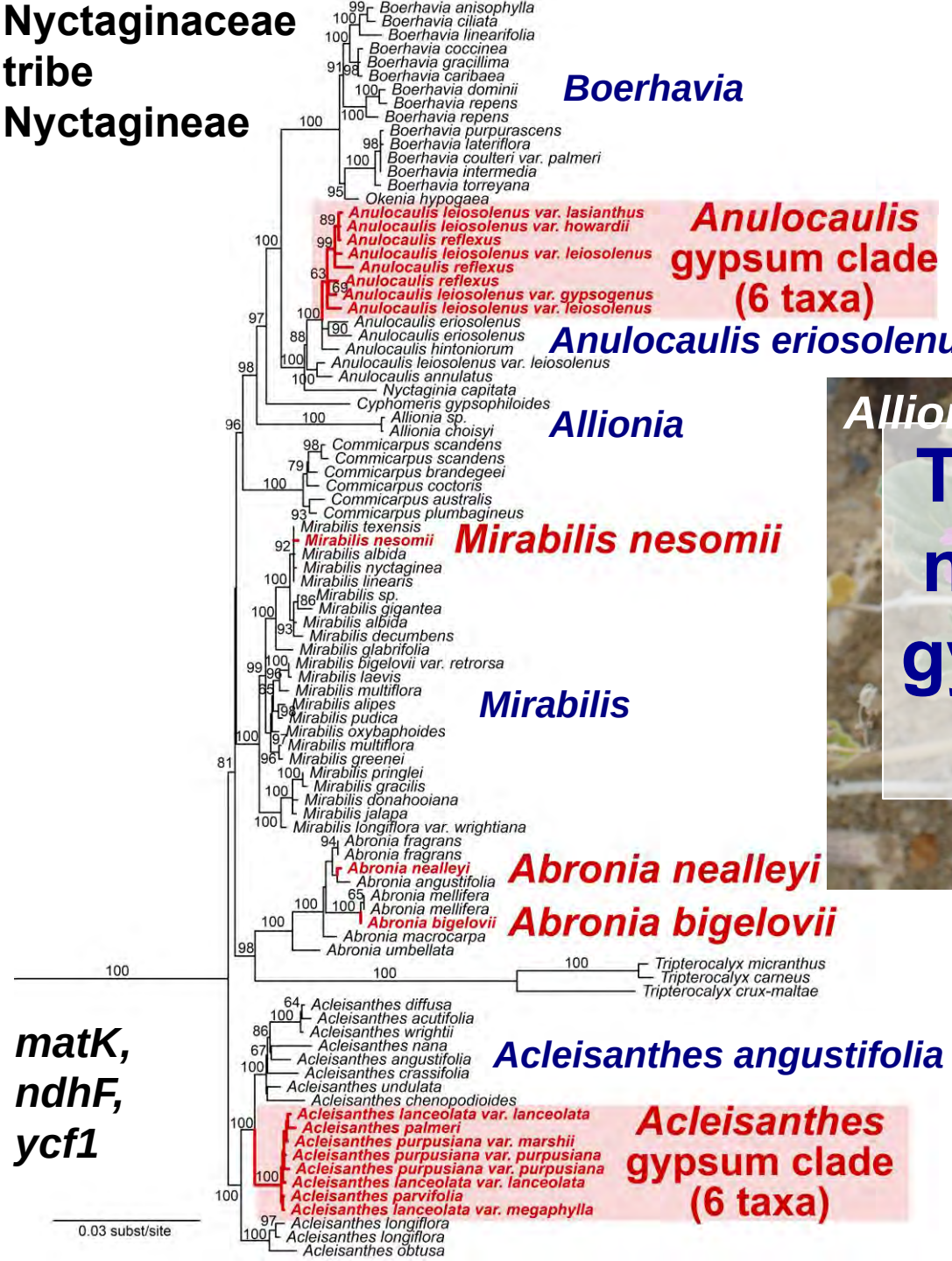
Acleisanthes angustifolia

Acleisanthes gypsum clade (6 taxa)

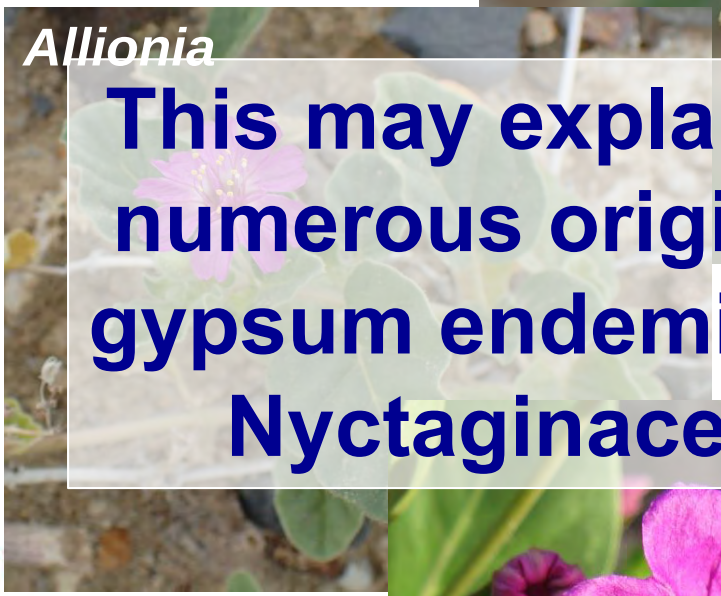
matK, ndhF, ycf1



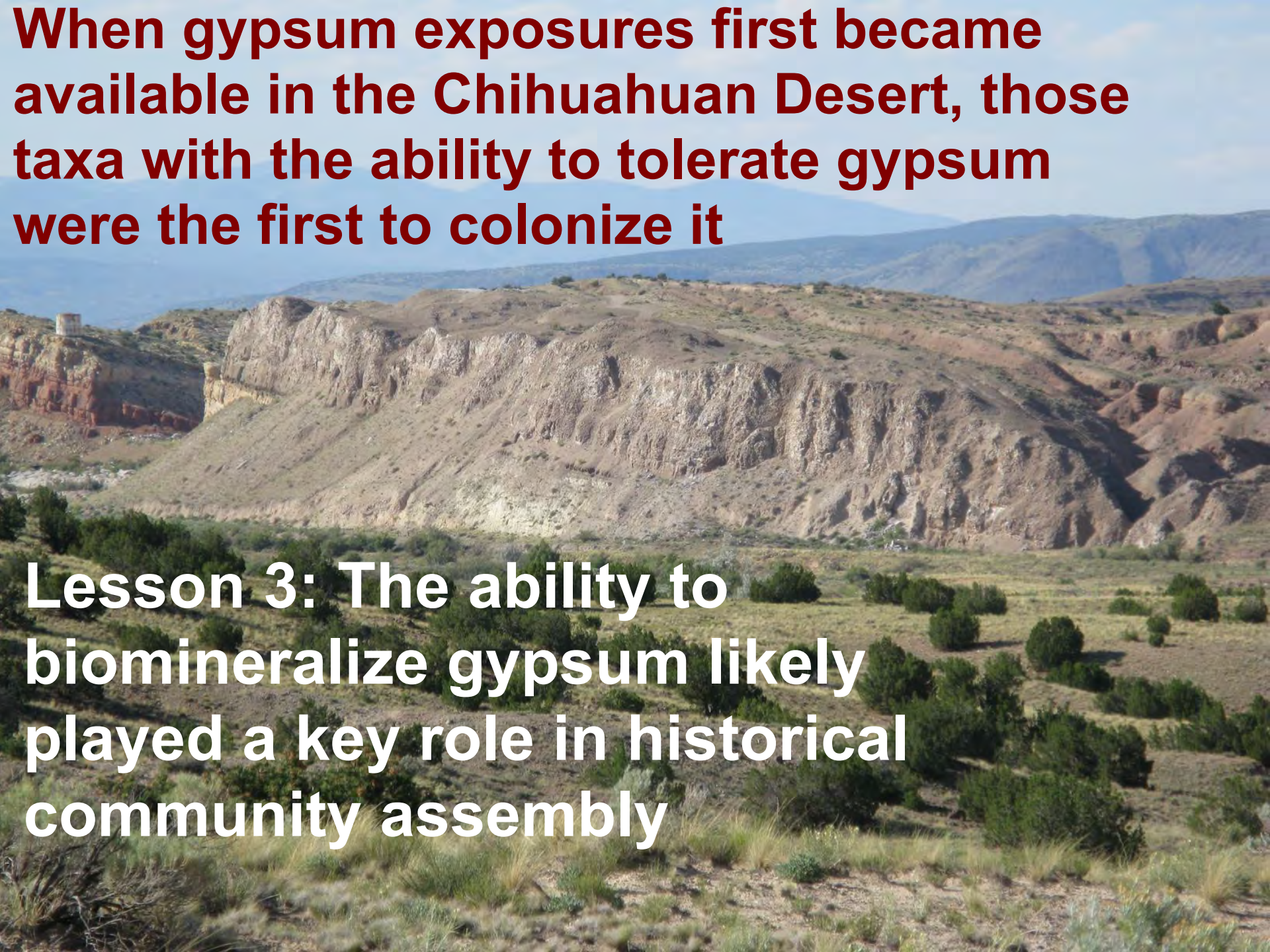
Nyctaginaceae
tribe
Nyctagineae



matK,
ndhF,
ycf1

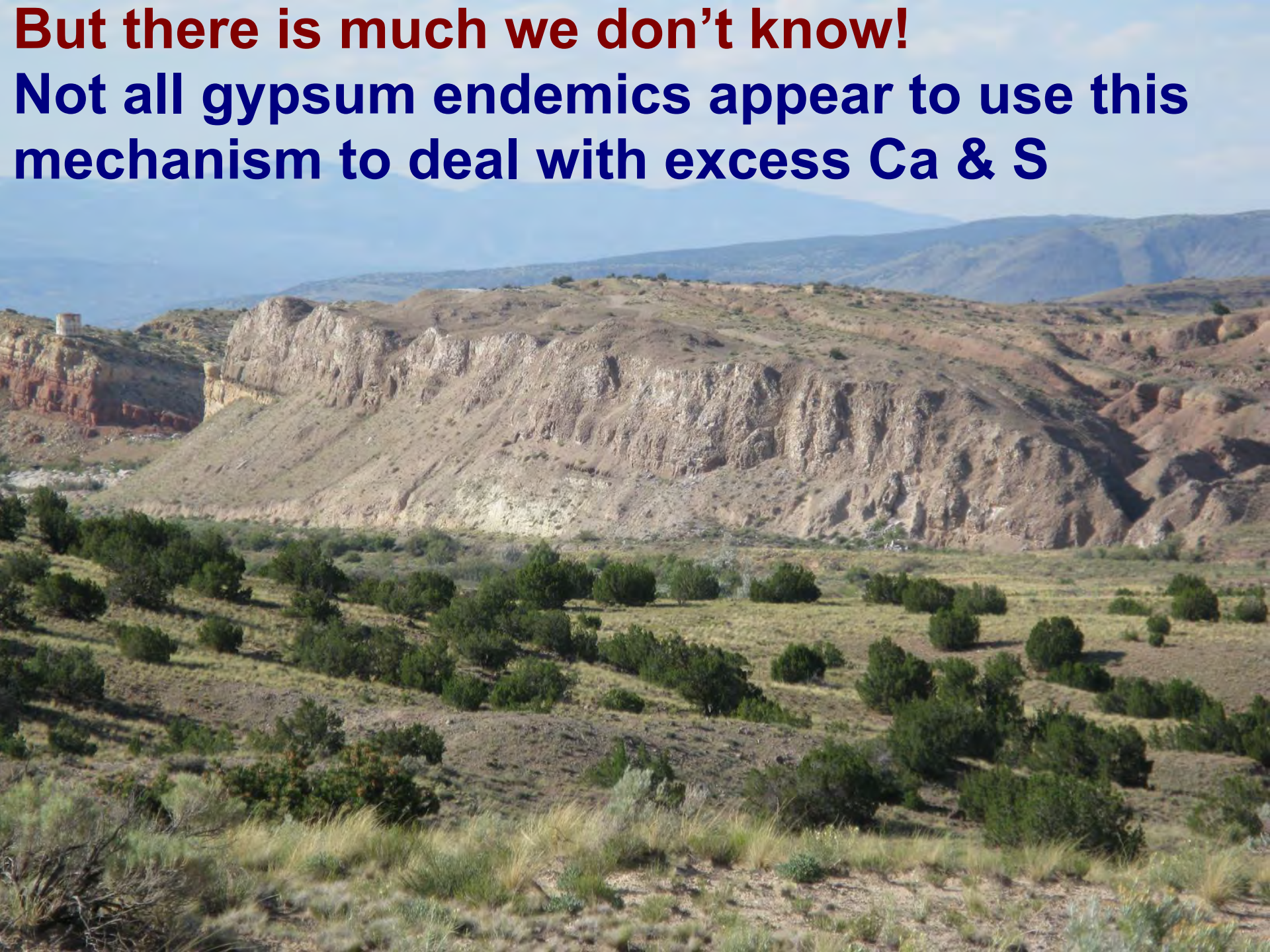


This may explain the numerous origins of gypsum endemism in Nyctaginaceae



When gypsum exposures first became available in the Chihuahuan Desert, those taxa with the ability to tolerate gypsum were the first to colonize it

Lesson 3: The ability to biomineralize gypsum likely played a key role in historical community assembly


But there is much we don't know!
Not all gypsum endemics appear to use this mechanism to deal with excess Ca & S

Leucophyllum alejandrae

Mentzelia perennis

What are the mechanisms enabling survival on gypsum in these lineages?

Sporobolus nealleyi

Oenothera hartwegii subsp. *filifolia*

Acknowledgments

- Melissa Moore
- All members of the Moore lab, past & present
- NSF DEB-1050539 & National Geographic Society
- Oberlin College Office of Sponsored Programs
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- Tom Wendt, Bob Jansen, Billie Turner, Jim Henrickson, & Plant Resources Center, UT
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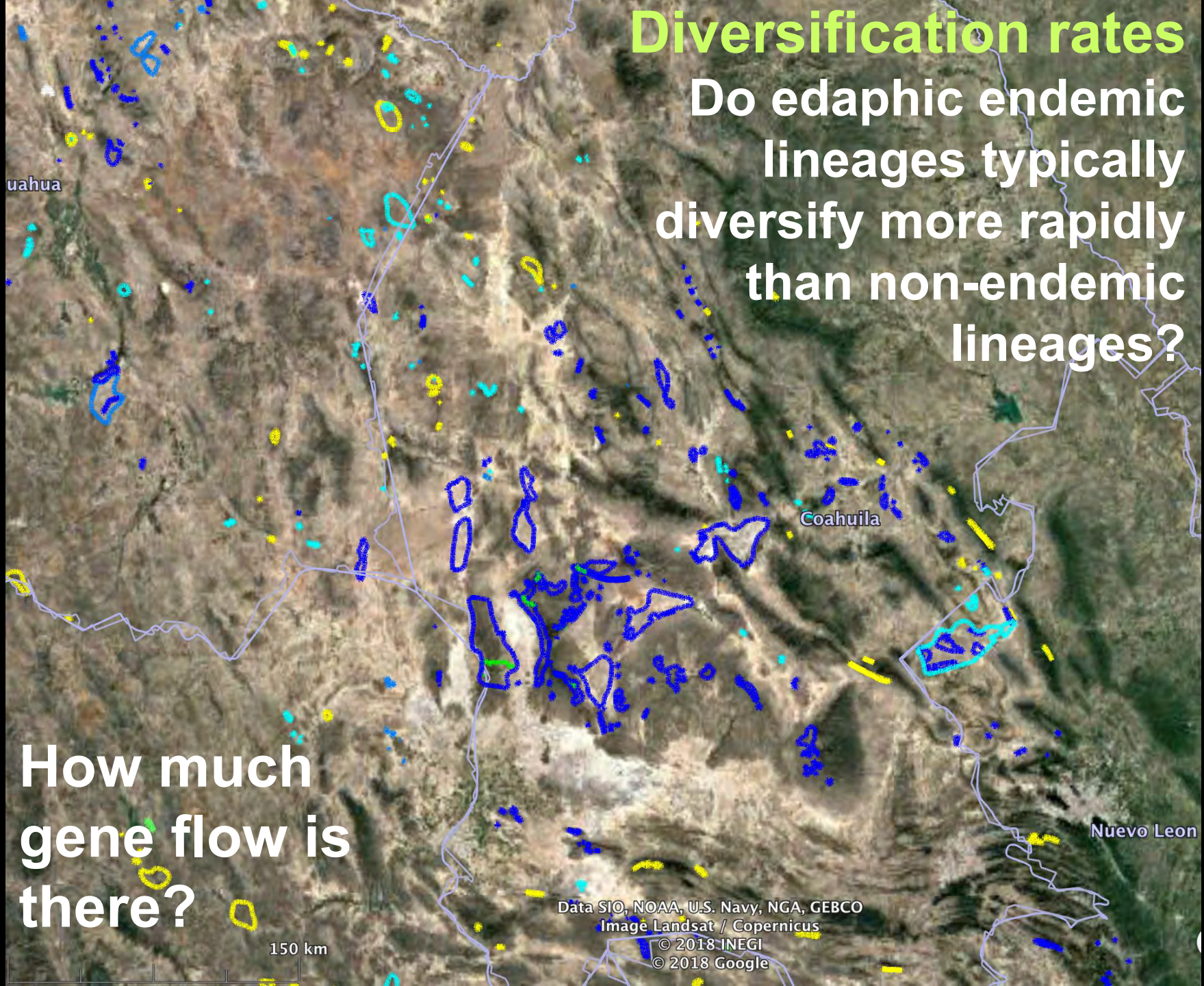
- Rich Spellenberg, Donovan Bailey, Patrick Alexander, NMSU
- Mike Howard, BLM; Mike & Shirley Powell, Sul Ross State University
- Dave Anderson, WSMR; Tim Lowrey, UNM; Jon Erz, Sevilleta NWR
- George Hinton
- SEMARNAT, Desuvalle A.C.
- Richard Worthington, UTEP; Bob and Debby Merkel
- Chemistry Department, Oberlin College


Diversification rates
Do edaphic endemic lineages typically diversify more rapidly than non-endemic lineages?
How much gene flow is there?
uahua
Coahuila
Nuevo Leon
150 km
Data SIO, NOAA, U.S. Navy, NGA, GEBCO
Image Landsat / Copernicus
© 2018 INEGI
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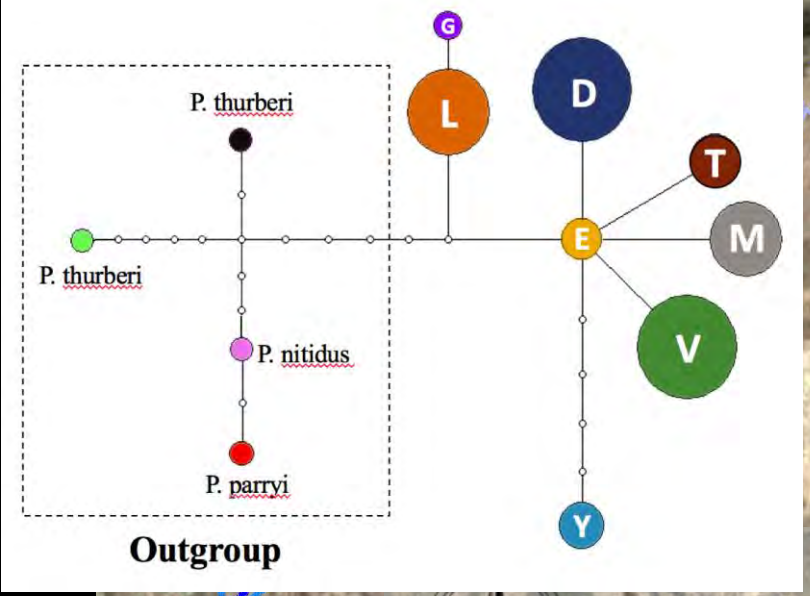
Diversification rates

Do edaphic endemic lineages typically diversify more rapidly than non-endemic lineages?

Example:
Petalonyx crenatus
(Loasaceae)

Plastid phylogeography

plastid ndhF/rpl32 & rpl32/trnL haplotypes



Apparently little seed movement!

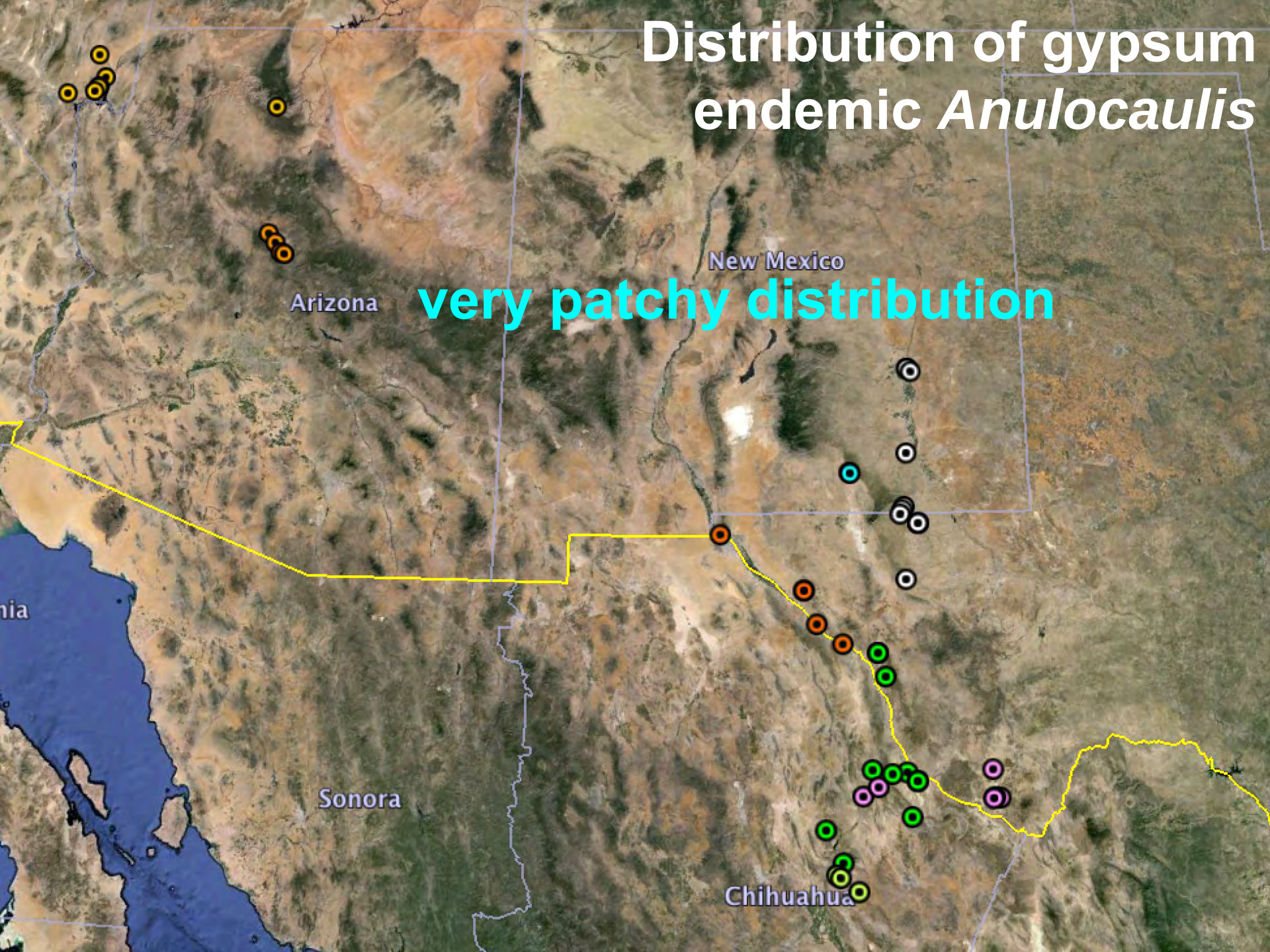
Plastome insights into gene flow in *Anulocaulis* (Nyctaginaceae)

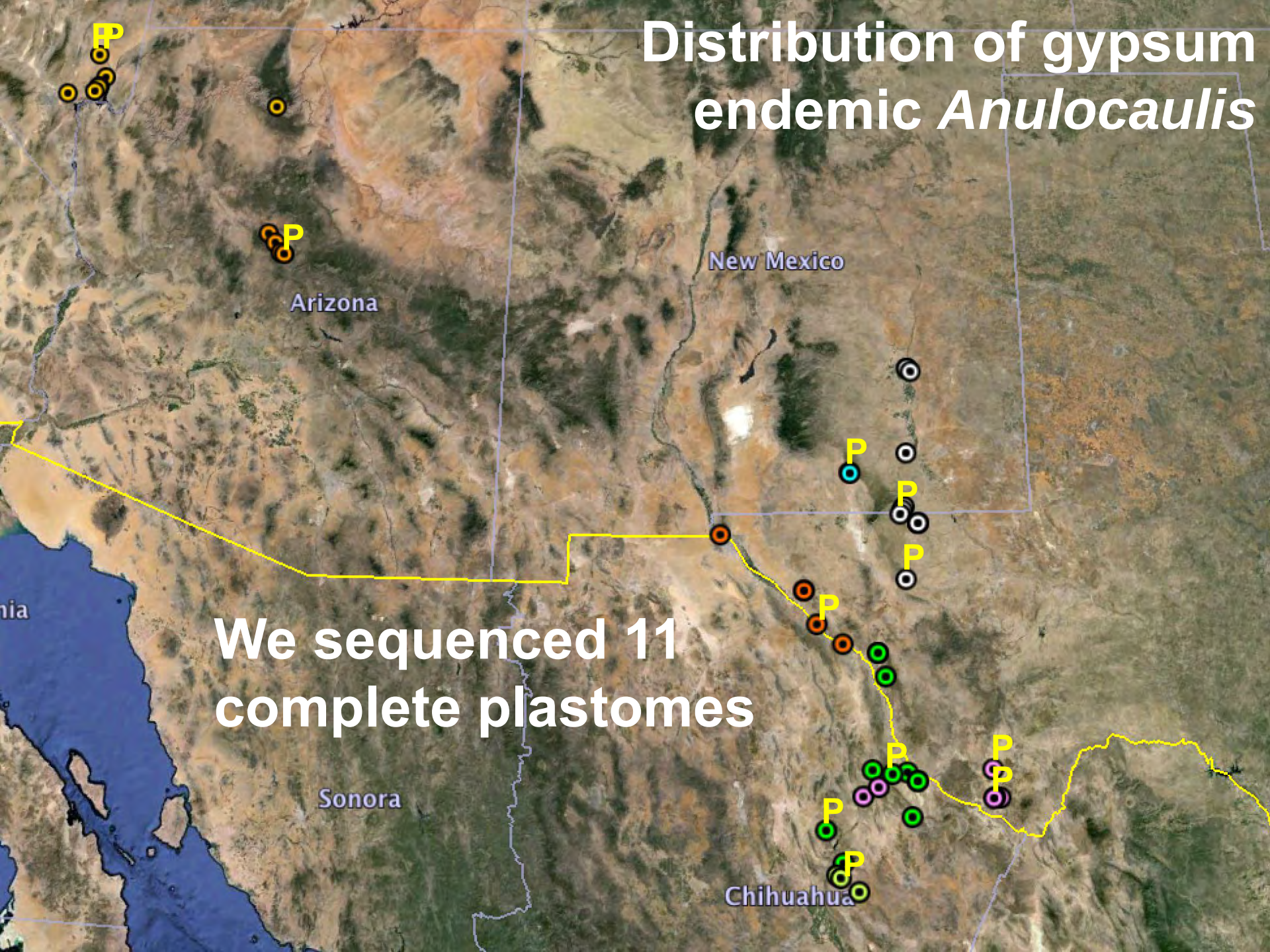
long-lived perennials

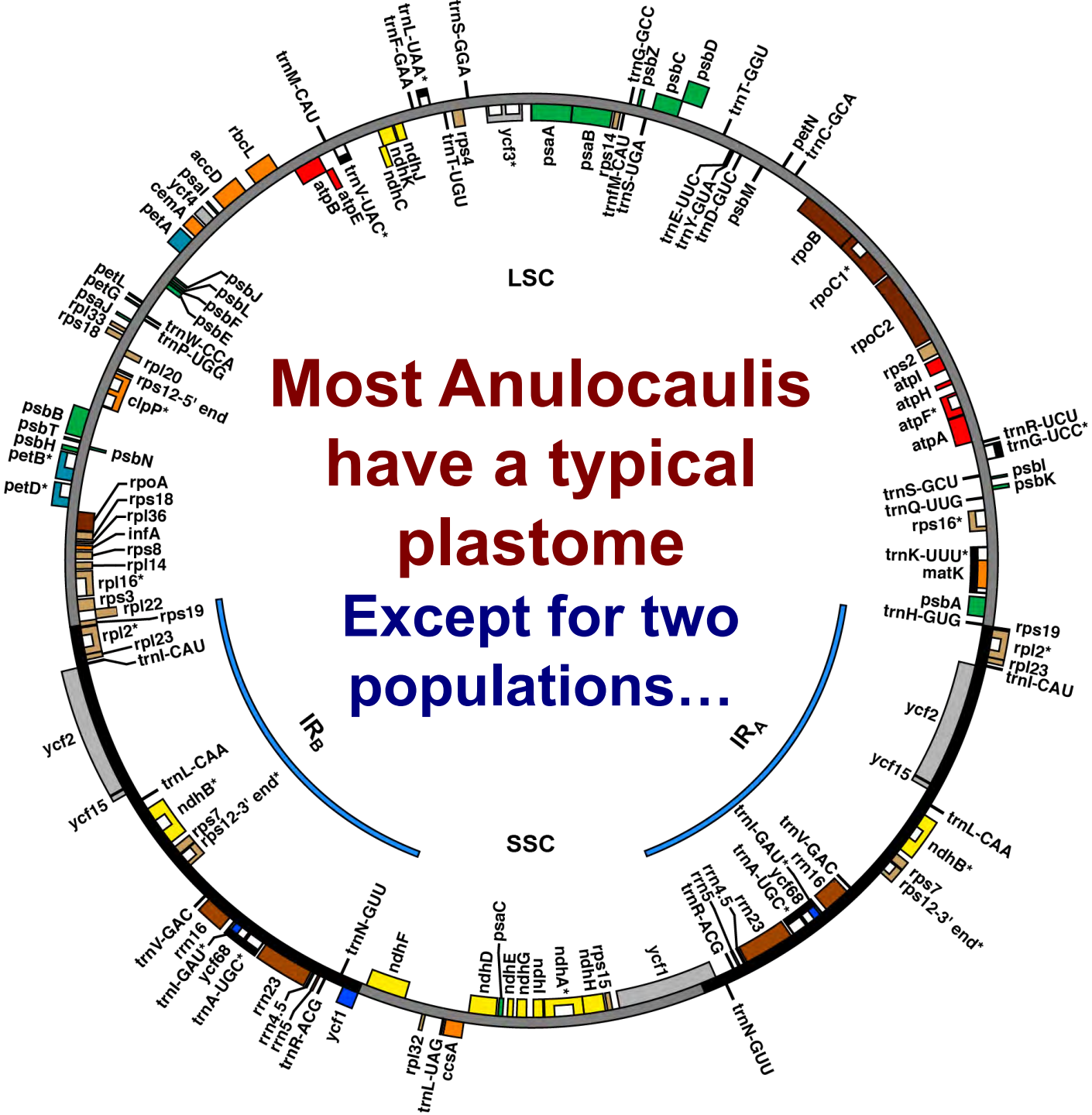
9 taxa, 6 of which are endemic to gypsum

Anulocaulis (Nyctaginaceae)

9 taxa, 6 of which are endemic to gypsum


Distribution of gypsum endemic *Anulocaulis*
New Mexico
Arizona
very patchy distribution
Sonora
Chihuahua

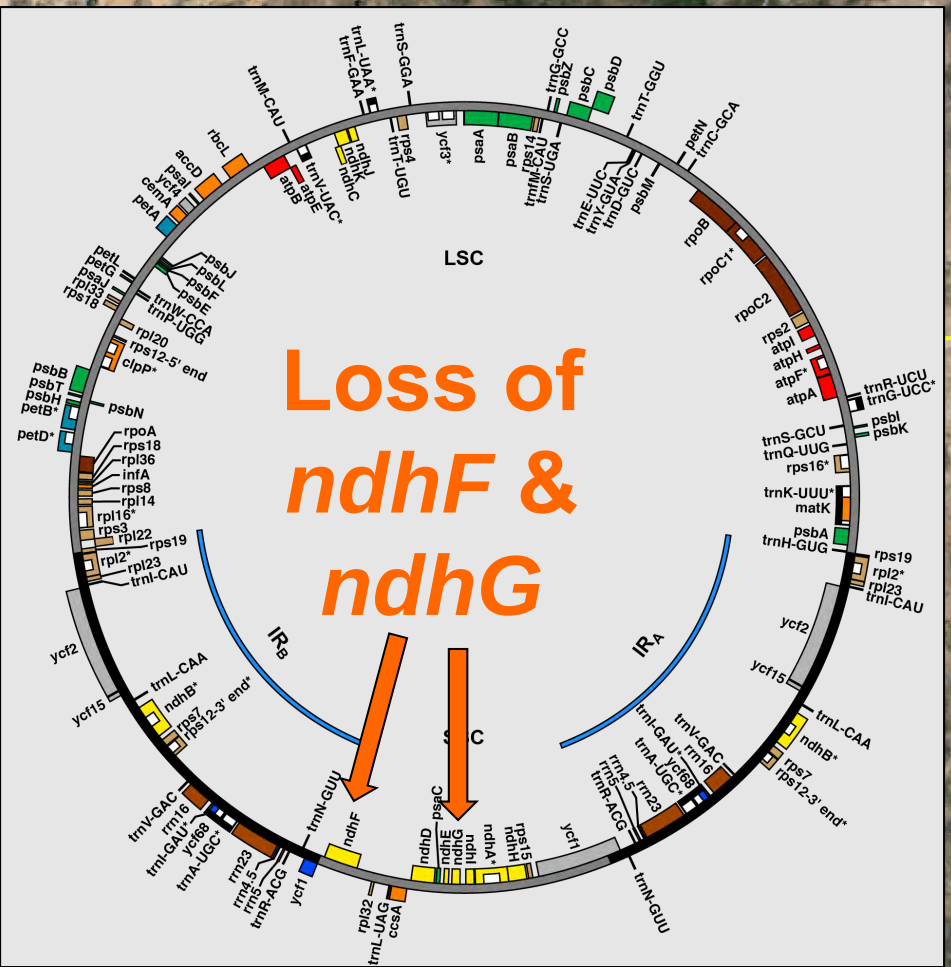

Distribution of gypsum endemic *Anulocaulis*
New Mexico
Arizona
Sonora
Chihuahua
We sequenced 11 complete plastomes



Most Anulocaulis have a typical plastome

Except for two populations…

Distribution of gypsum endemic *Anulocaulis*



Distribution of gypsum endemic *Anulocaulis*

Verde Valley

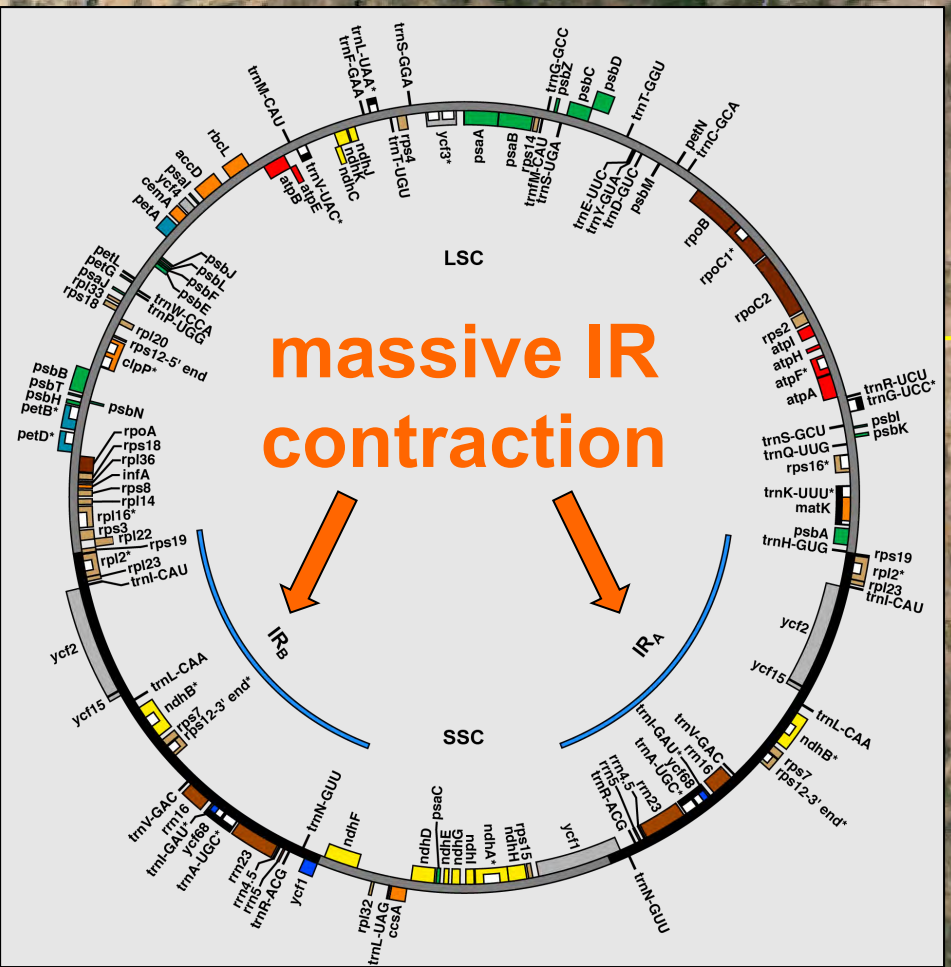
A. leiosolenus

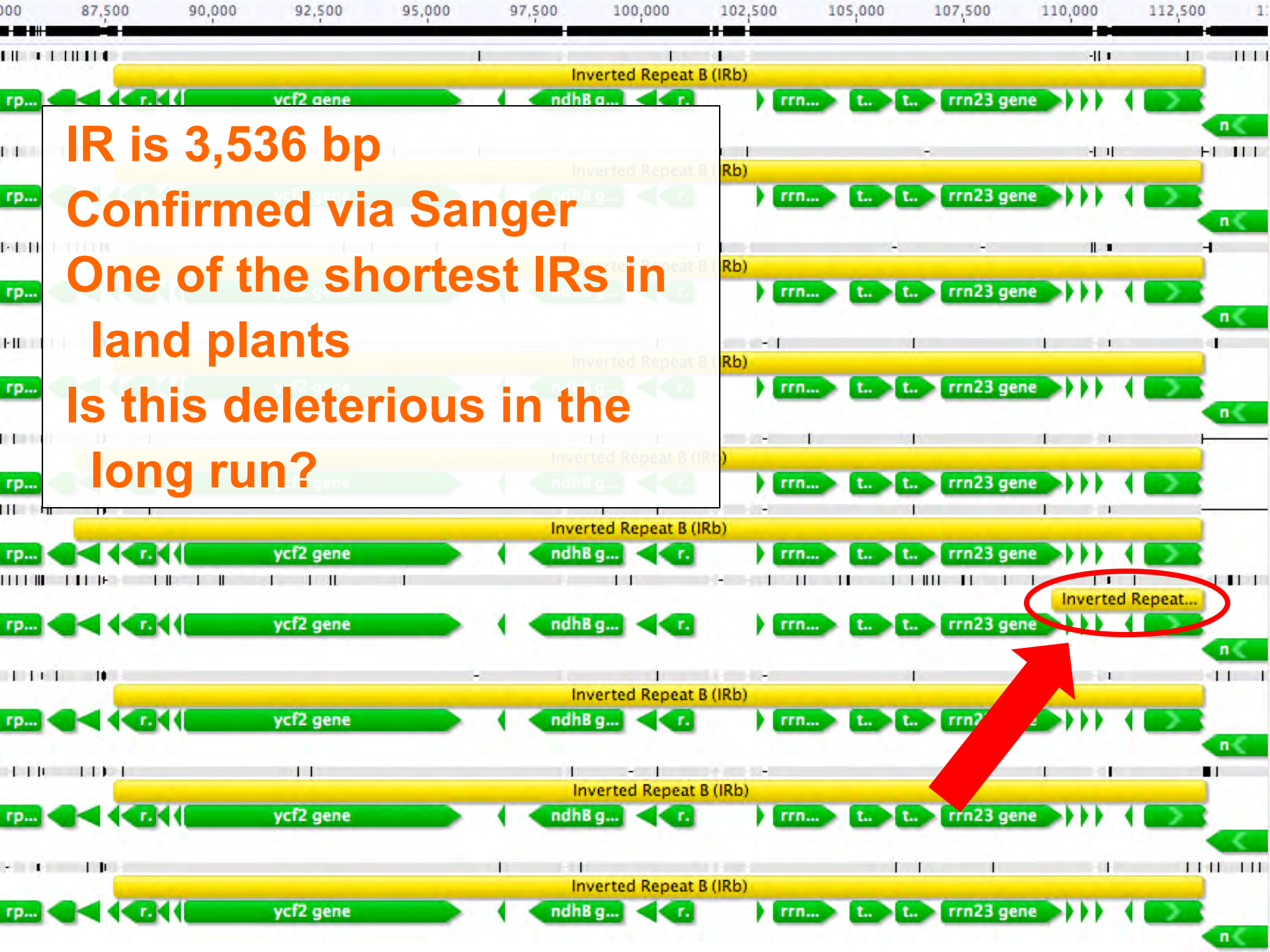
var. *leiosolenus*

Arizona

New Mexico

Chihuahua




IR is 3,536 bp
Confirmed via Sanger
One of the shortest IRs in land plants
Is this deleterious in the long run?
87,500
90,000
92,500
95,000
97,500
100,000
102,500
105,000
107,500
110,000
112,500
Inverted Repeat B (IRb)
ycf2 gene
ndhB g...
rrn...
rrn23 gene
Inverted Repeat...

Distribution of gypsum endemic *Anulocaulis*

Verde Valley

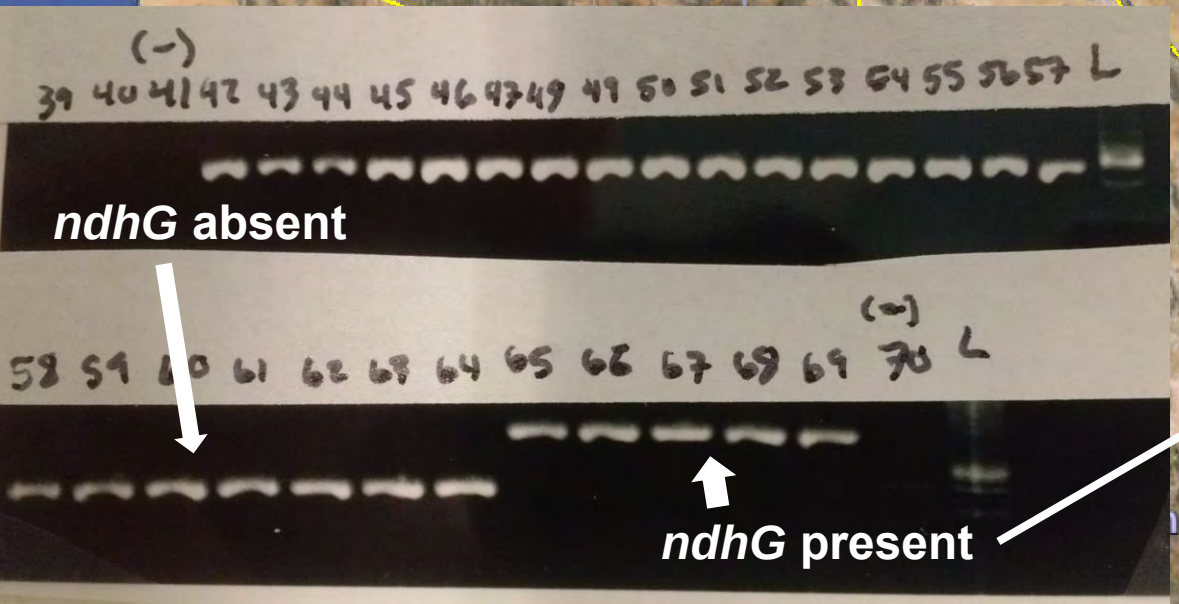
A. leiosolenus var. *leiosolenus*

Arizona

What can we infer from this about demography and gene flow?

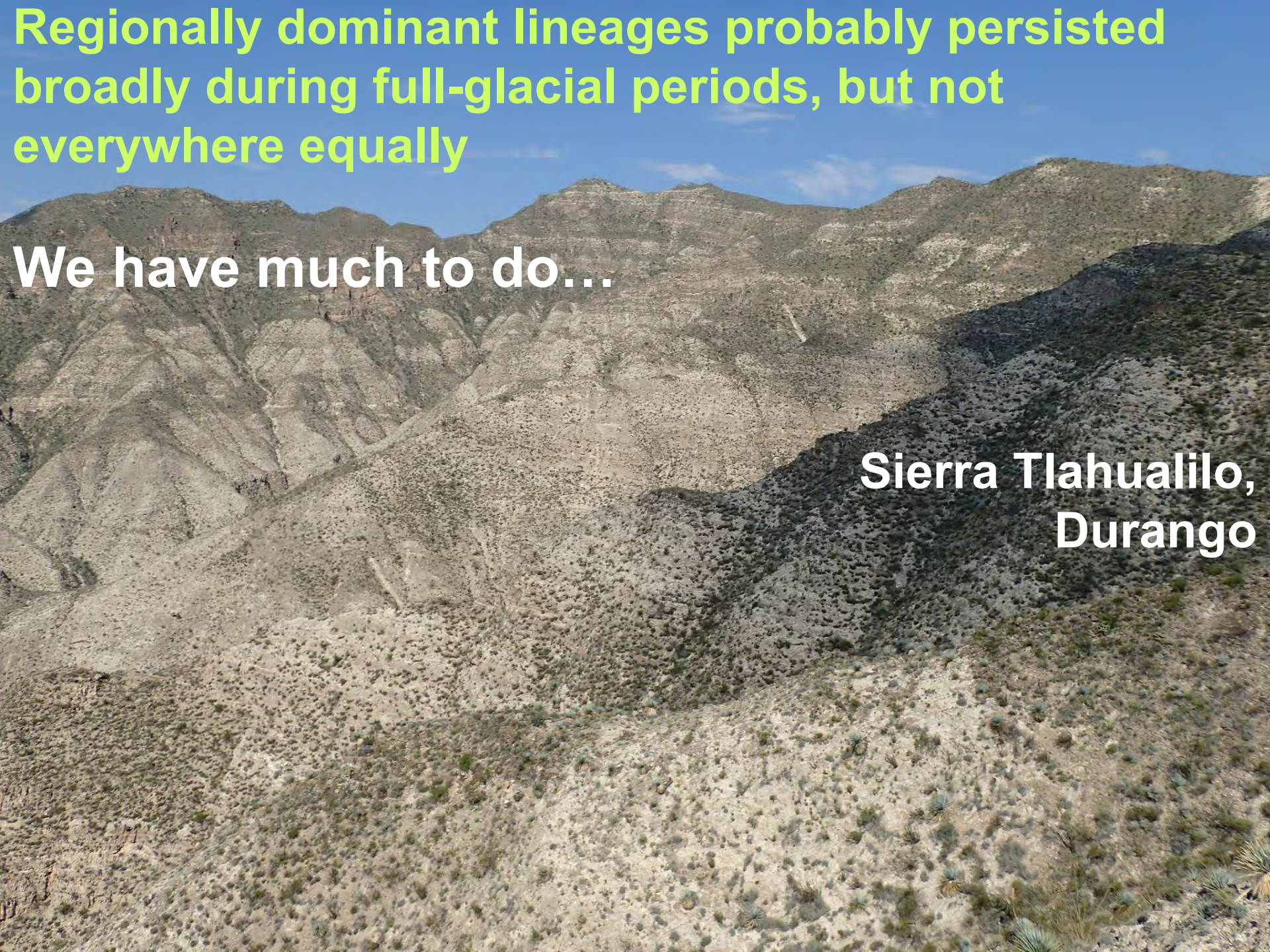
A. leiosolenus var. *lasianthus*

Big Bend

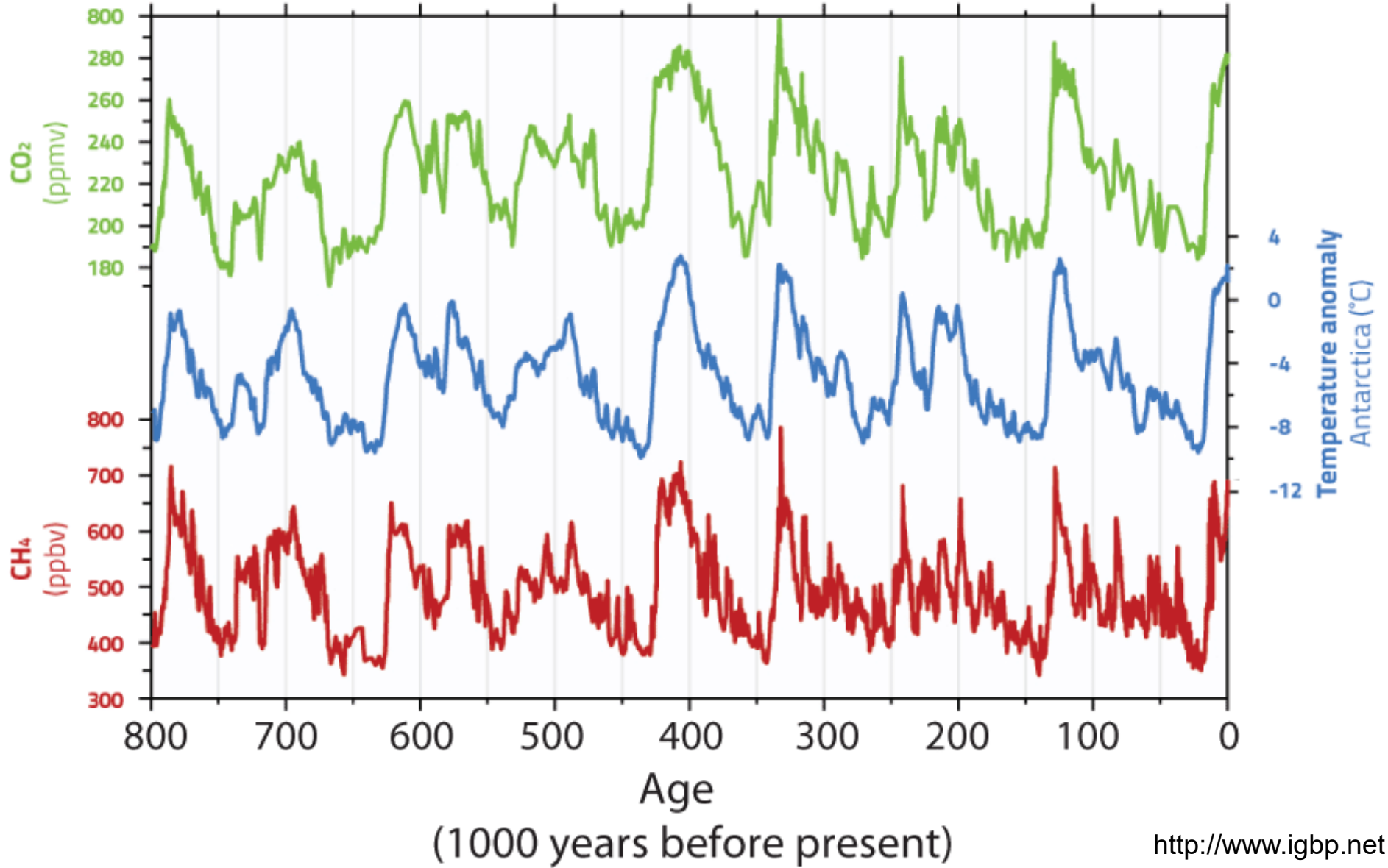


Fixation due to selectio
Most likely due to drift.
…due to small, isolated
Limited geographic ext
very limited gene flo
But does not preclude

Norman Douglas, 2013

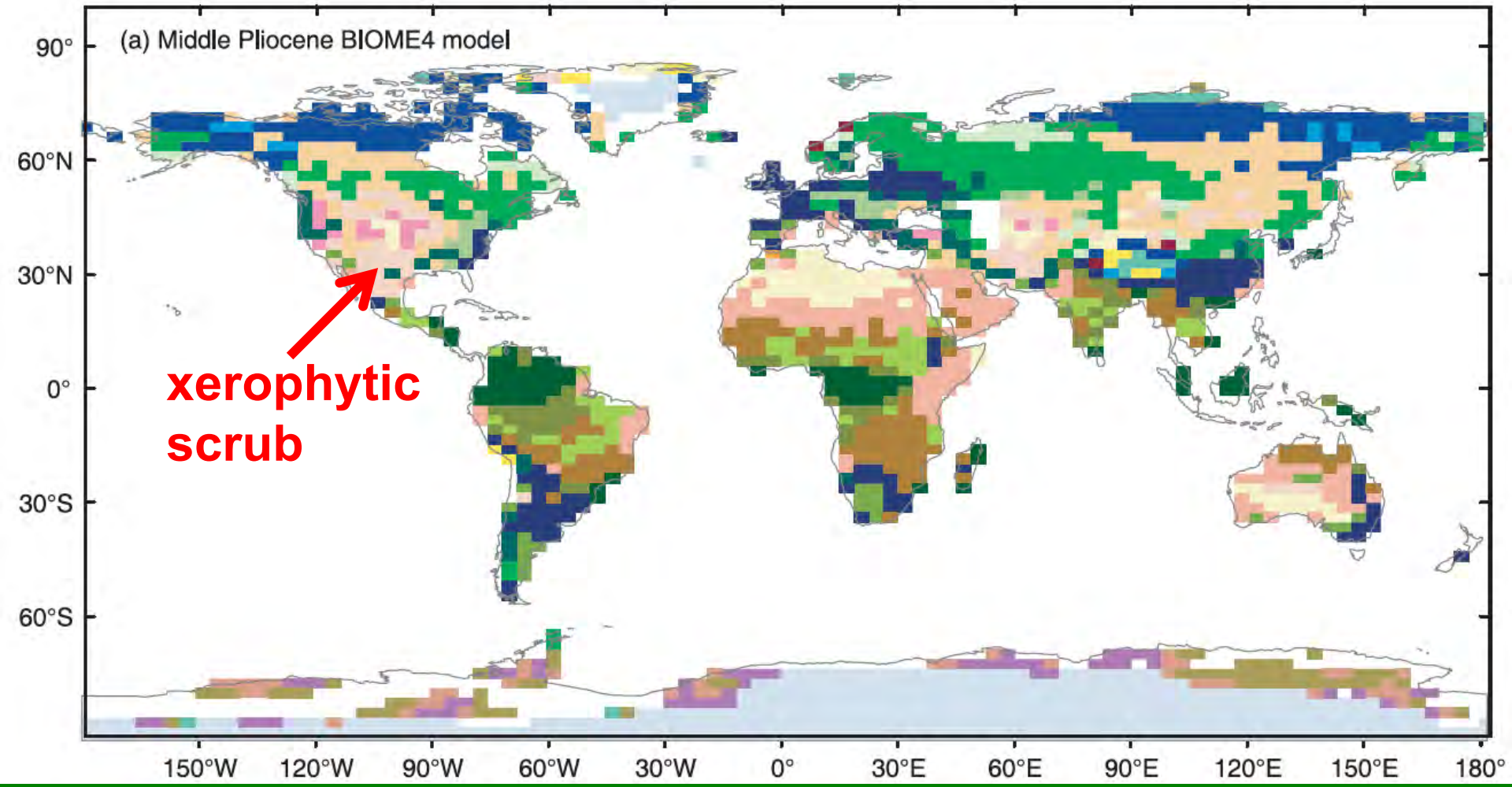

Regionally dominant lineages probably persisted broadly during full-glacial periods, but not everywhere equally
We have much to do…
Sierra Tlahualilo, Durango

A Pliocene age implies persistence through Pleistocene glacials



http://www.igbp.net

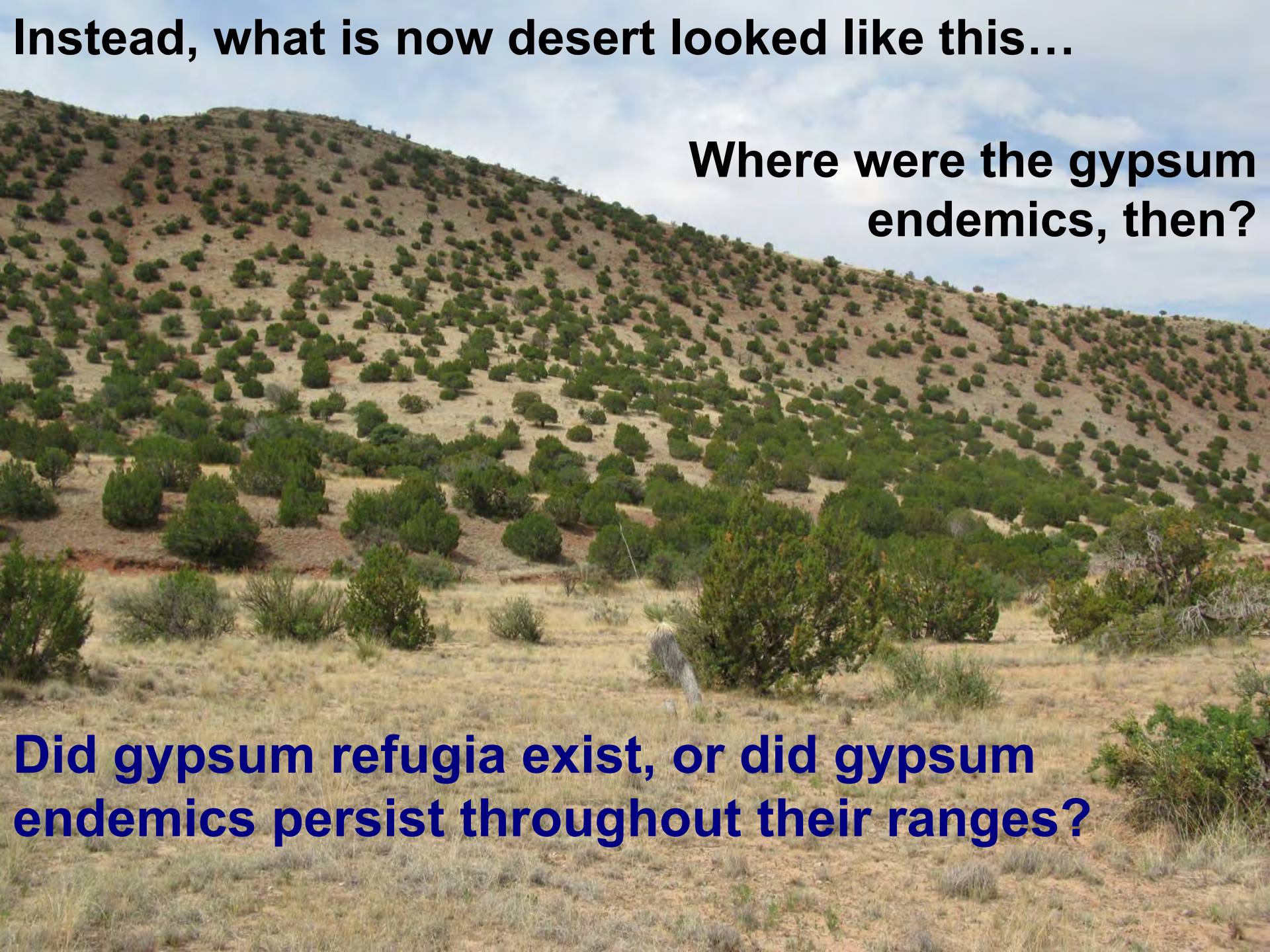
Pliocene climate models imply suitable habitat existed for gypsum endemics



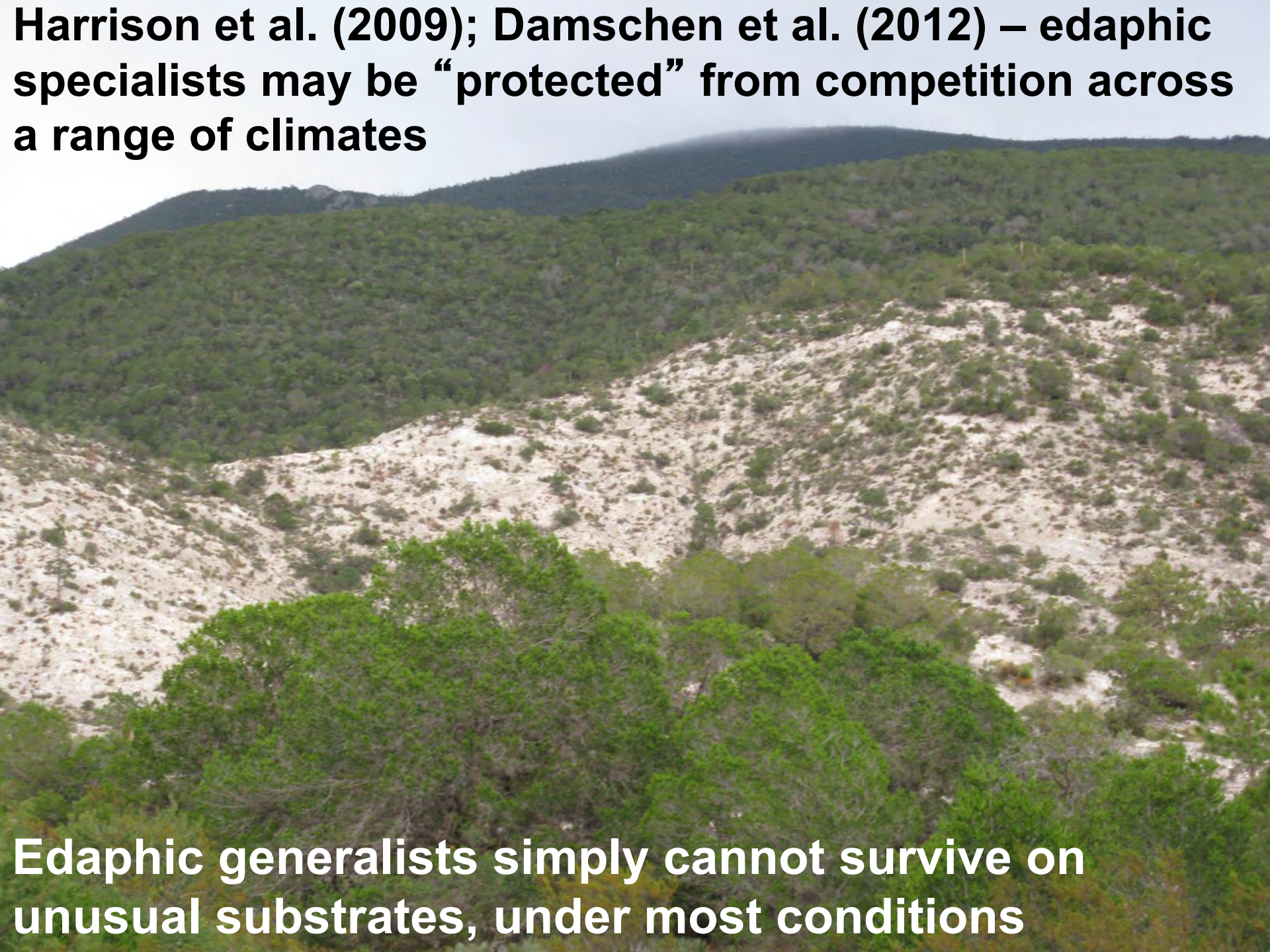
Salzmann et al. (2008) *Global Ecol. Biogeogr.* 17: 432-447

All available fossil evidence suggests that during Pleistocene full-glacial periods, there was no landscape-scale desert

- Pollen cores
- Packrat middens


Instead, what is now desert looked like this…
Where were the gypsum endemics, then?
Did gypsum refugia exist, or did gypsum endemics persist throughout their ranges?

Harrison et al. (2009); Damschen et al. (2012) – edaphic specialists may be “protected” from competition across a range of climates



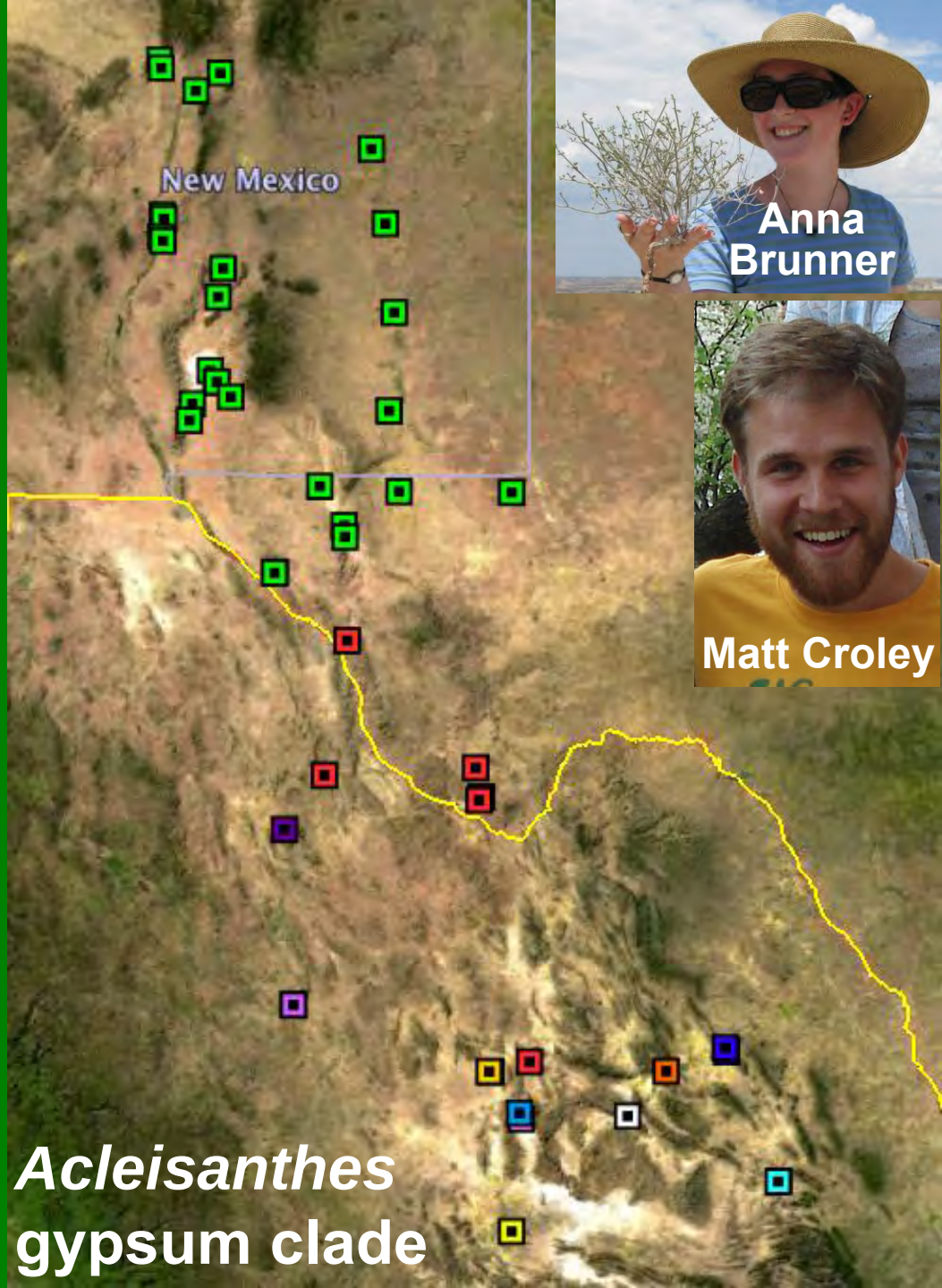
Edaphic generalists simply cannot survive on unusual substrates, under most conditions

This hypothesis can be addressed phylogeographically

If taxa persisted broadly through the Pleistocene, haplotype diversity should be high

Testing this requires broad population sampling

Today: preliminary results



Gypsum endemic clade haplotype map

***A. lanceolata* populations invariant**

The same for ITS & across plastid genome

Plastid haplotype variation is very high in Coahuila and Nuevo León


Rebecca Mostow


Shiva Mandala


Anna Brunner


Matt Croley

New Mexico

A. lanceolata

A. parvifolia

A. megaphylla

A. purpusiana

***Acleisanthes* gypsum clade**

A. palmeri

Gypsum endemic clade haplotype map

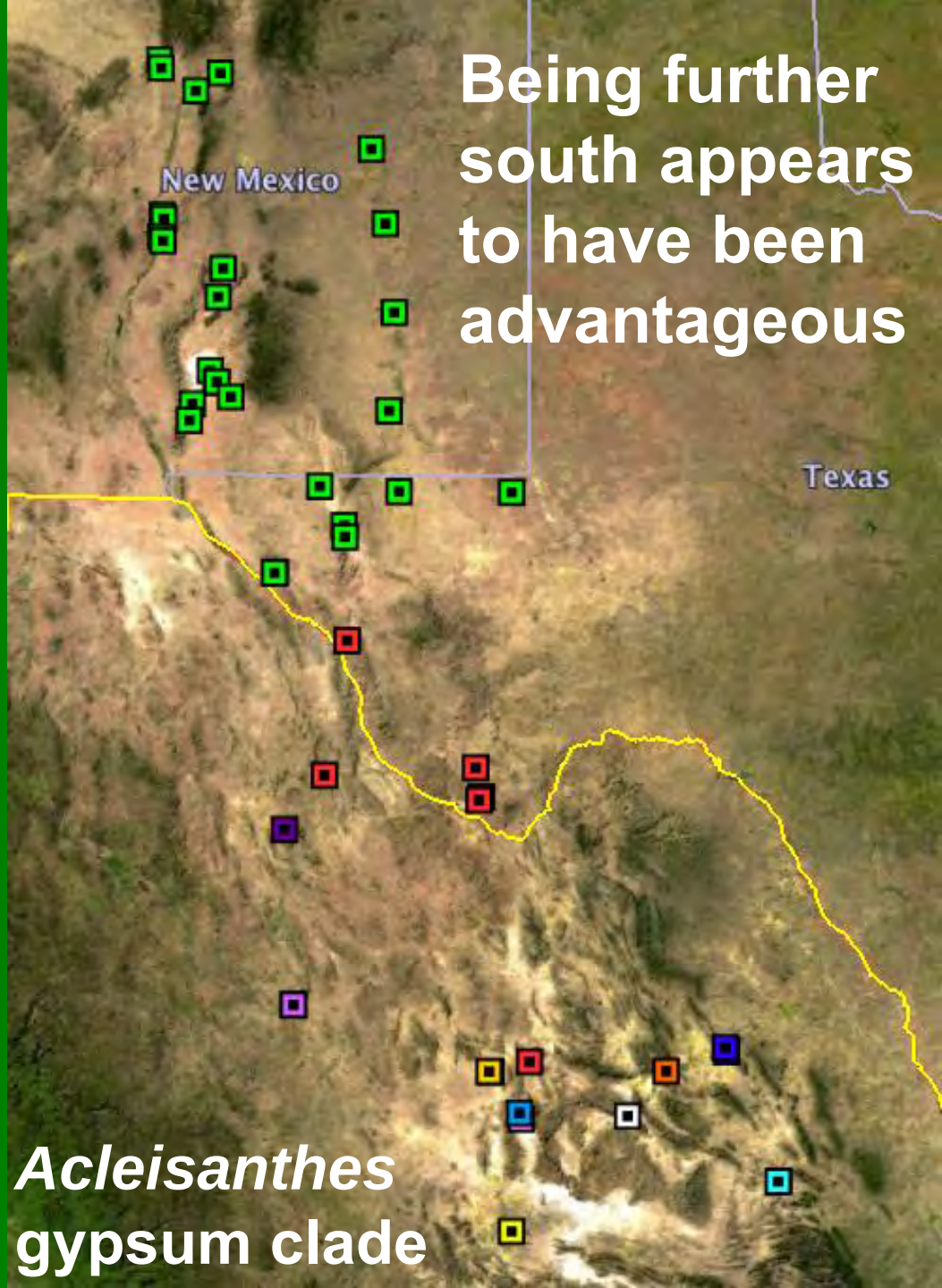
A. lanceolata populations invariant

The same for ITS & across plastid genome

Plastid haplotype variation is very high in Coahuila and Nuevo León


Rebecca Mostow


Shiva Mandala



Being further south appears to have been advantageous

Acleisanthes gypsum clade

Plastid haplotype variation in *Tiquilia hispidissima*

The same pattern as in gypsum endemic *Acleisanthes*

James Medina

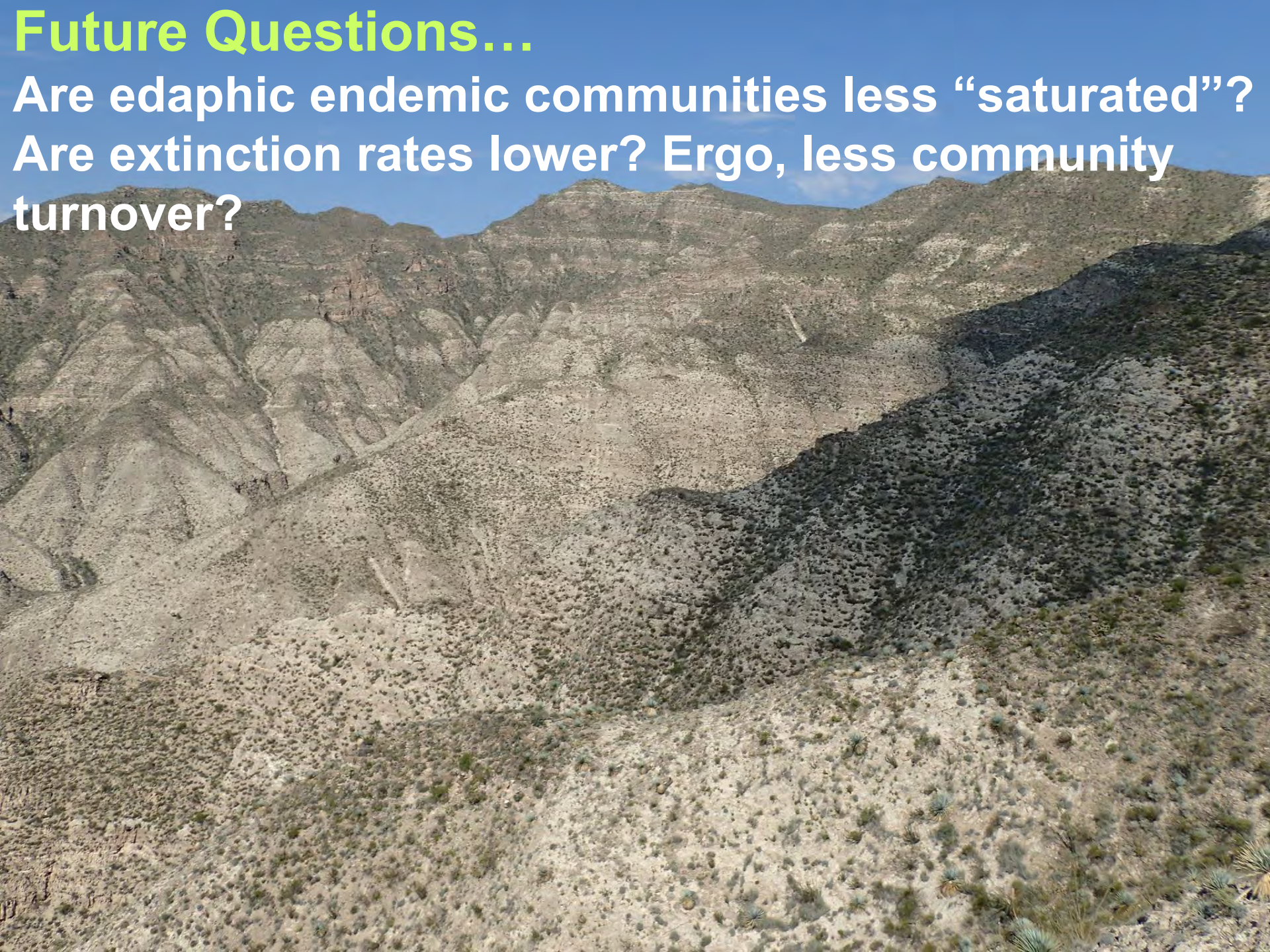
How do we explain this pattern?

Packrat middens:

Pleistocene full-glacial climates remained warmer and drier further south in the Chihuahuan Desert

Localized extinction & recolonization further north?

However…
…not all gypsum endemics share this pattern



Future Questions…

Are edaphic endemic communities less “saturated”? Are extinction rates lower? Ergo, less community turnover?

Almost everything we know about gypsum ecophysiology comes from work in Spain


Gypsum soils usually have a surface crust


Ononis tridentata
Many Spanish gypsum endemics have elevated foliar S & Ca…


…whereas others do not
Teucrium turredanum

Strong correlation between geographic extent & levels of foliar S accumulation

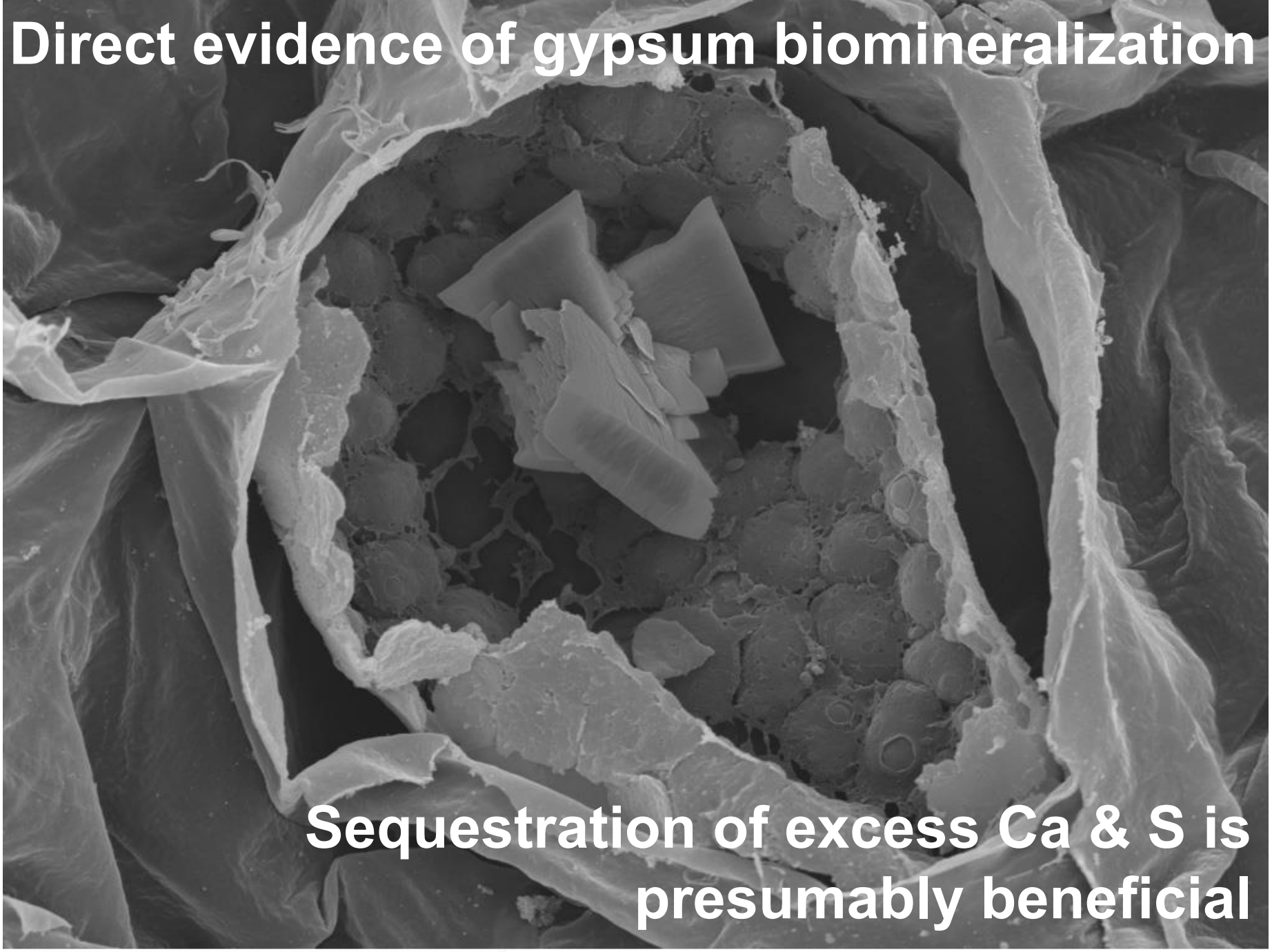
gypsum exposures in Spain

courtesy Juan Mota

Helianthemum squamatum

Sara Palacio

Recent work demonstrates that wide endemics accumulate gypsum


Direct evidence of gypsum biomineralization
Sequestration of excess Ca & S is presumably beneficial
30µm

Do Chihuahuan Desert gypsum endemics display the same patterns?

Yes!

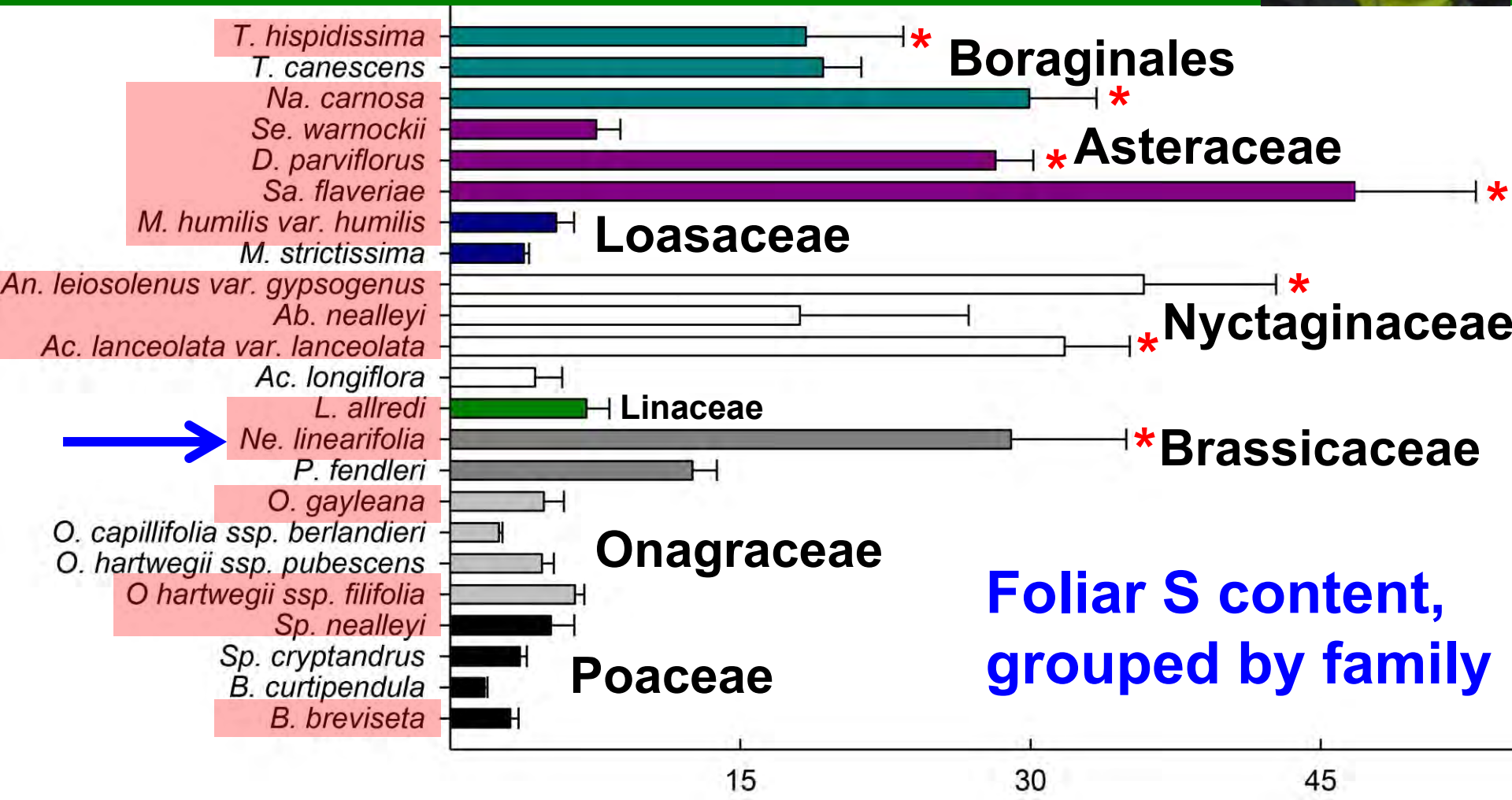
We have the benefit of a phylogenetic context

I would propose that gypsum accumulation may be one key mechanism that has driven historical community assembly on gypsum, perhaps globally

Today: a brief synthesis of ecophysiological and evolutionary evidence for the Chihuahuan Desert

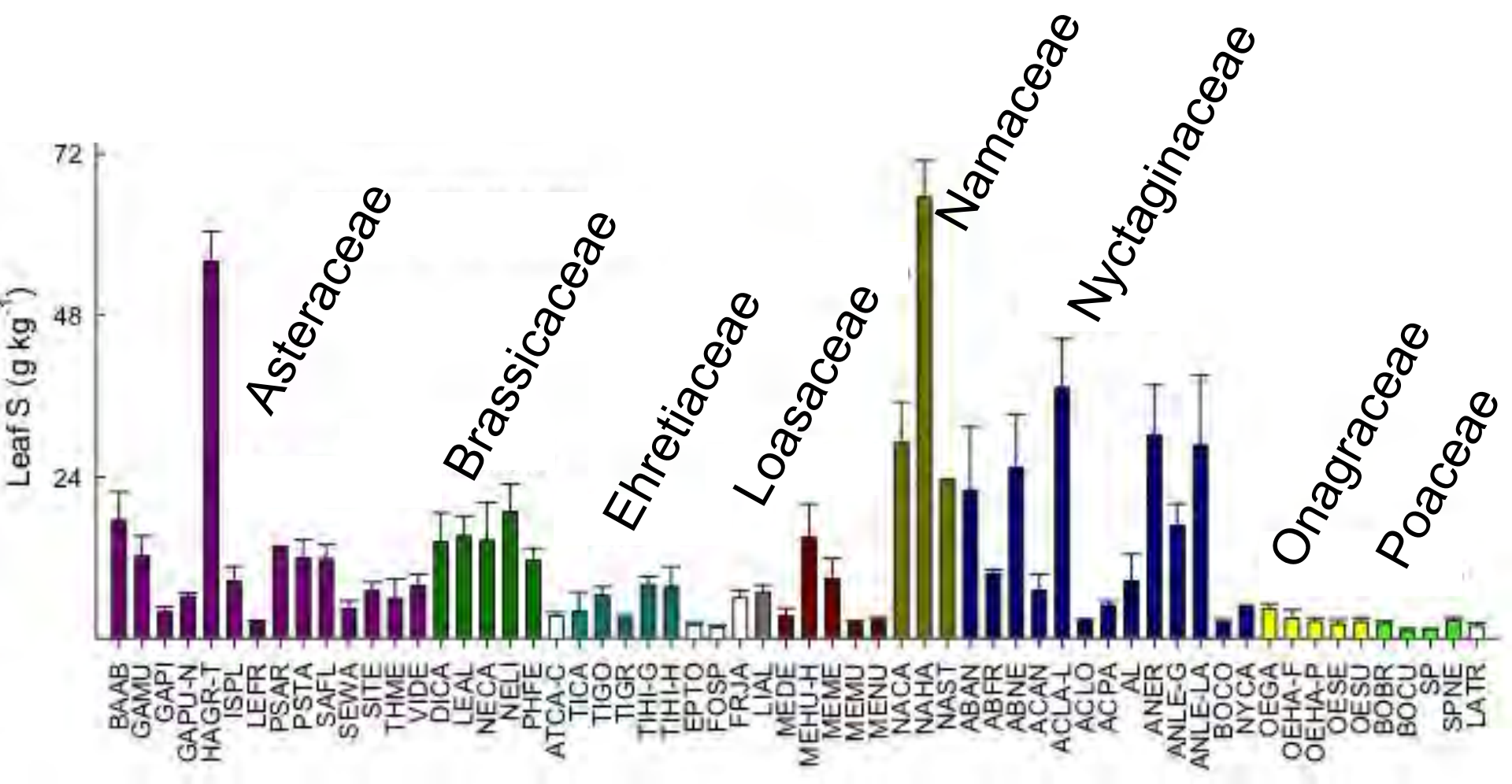
Foliar S levels are elevated in taxa with spectra indicative of gypsum

Except for mustards!

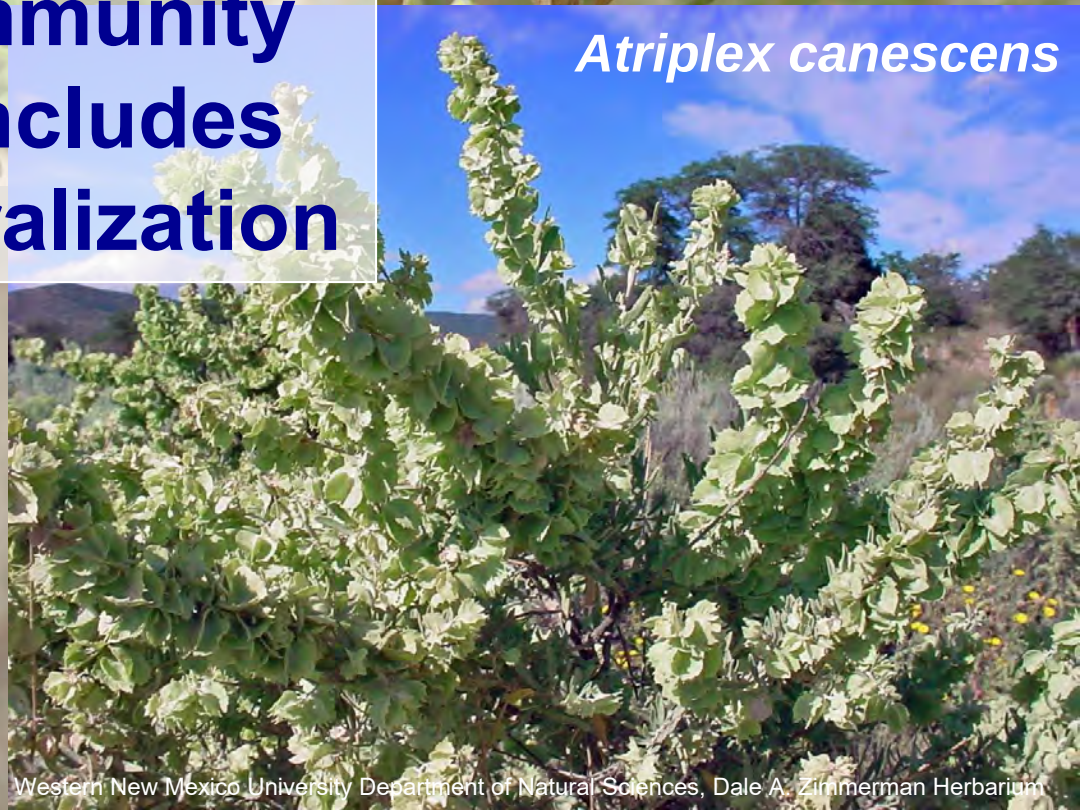


Data from broader study in 2016

Patterns are very similar between Spanish & Chihuahuan Desert gypsum floras



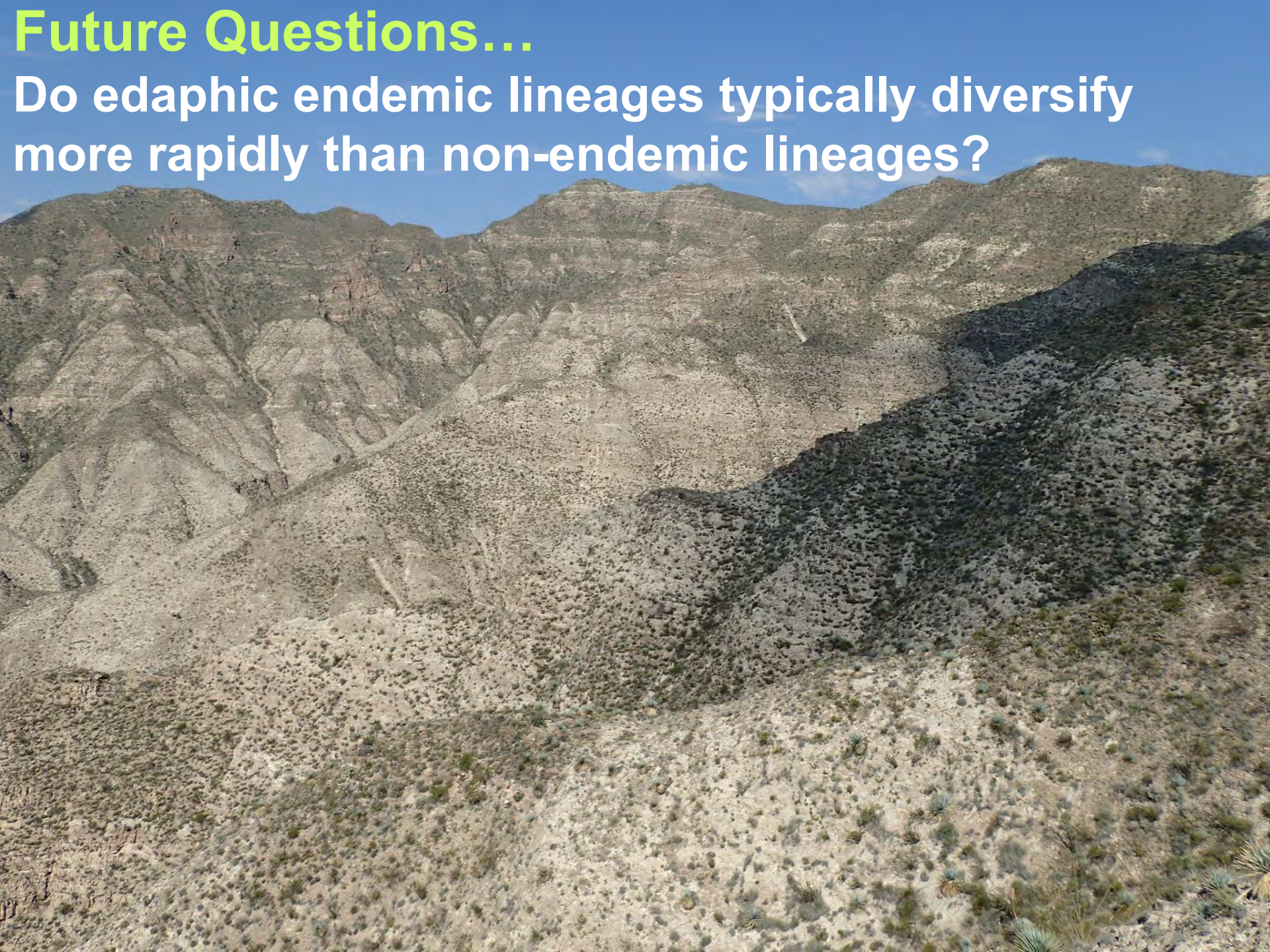
I would propose a model of historical community assembly that includes gypsum biomineralization



A big thanks to these folks!

Part 2: Are gypsum plant communities more stable through periods of climate change?

Or, how old are these communities?



Future Questions…

Do edaphic endemic lineages typically diversify more rapidly than non-endemic lineages?