# Evolving land models: representing grass functional diversity with lineage-based functional types (LFTs)


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***NESCent Working Group: Evolutionary History of C3 and C4 Grasslands:***

**Biogeochemistry Science Friday**

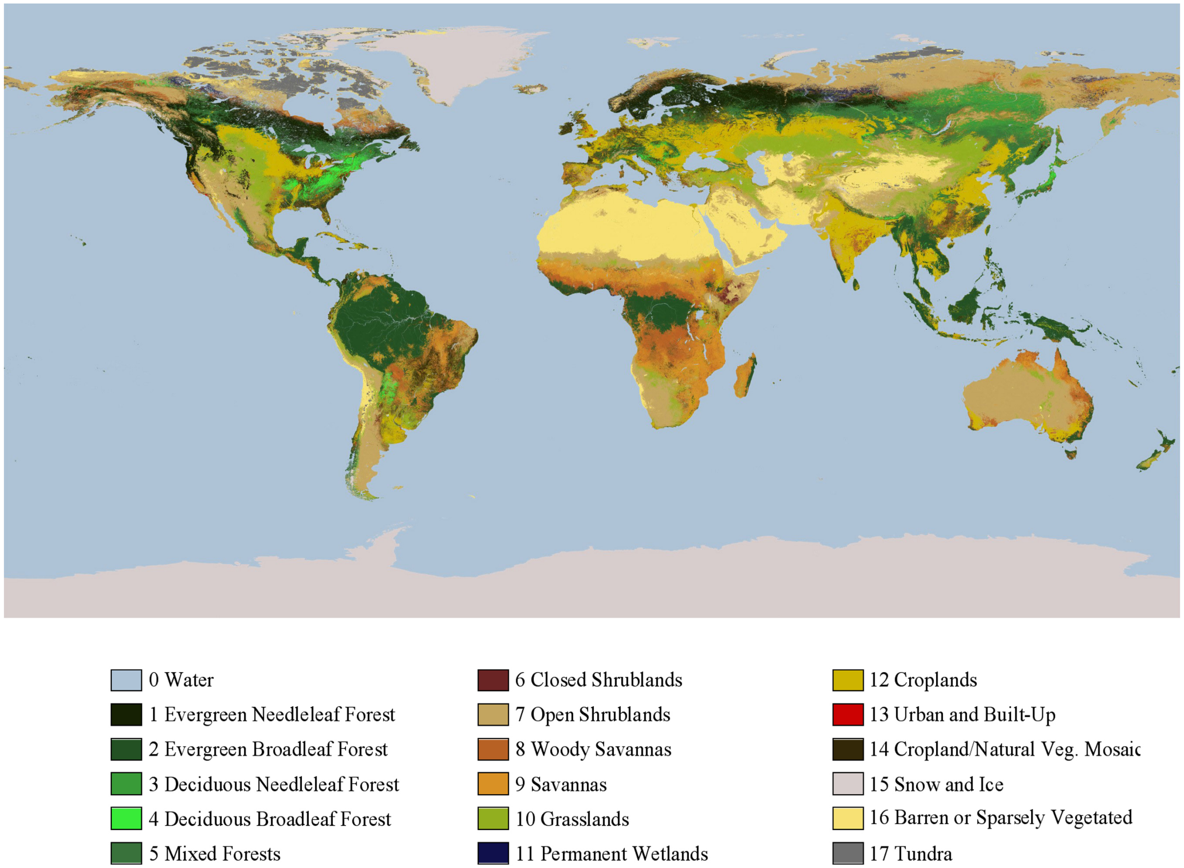
**15 May 2020**

# Acknowledgements

**National Evolutionary Synthesis Center**
**Evolutionary History of C3 and C4 Grasslands: a New Integrative Framework**

**Colin Osborne** (University of Sheffield)
Christopher Still (Oregon State University)
**Caroline Stromberg** (University of Washington)
**Erika Edwards** (Brown University)
**Caroline Lehmann** (University of Edinburgh)
Dan Griffiths (Wake Forest University)
Beth Forrestel (Yale University)
Beth Spriggs (Yale University)
Melinda Smith (Colorado State University)
Michael Anderson (Wake Forest University)
William Bond (University of Cape Town)
Bill Hoffmann (North Caroline State University)
Stephanie Pau (Florida State University)

National Evolutionary Synthesis Center
NESCent




# Plant Functional Types (PFTs)

Development of PFTs for models in 1990s was driven partly by the need to represent fast-response processes like biophysics, hydrology, and physiology in climate models.

The PFT concept is largely based on physiognomy/structure and similarity in responses to environmental perturbations; it is implicitly non-phylogenetic in nature (i.e., evolutionary history and relatedness are ignored or obscured).

# And yet we know that plant species exist within historical, evolutionary, ecological, and environmental contexts

**Evolutionary relatedness and biogeographic history (phylogeny)**

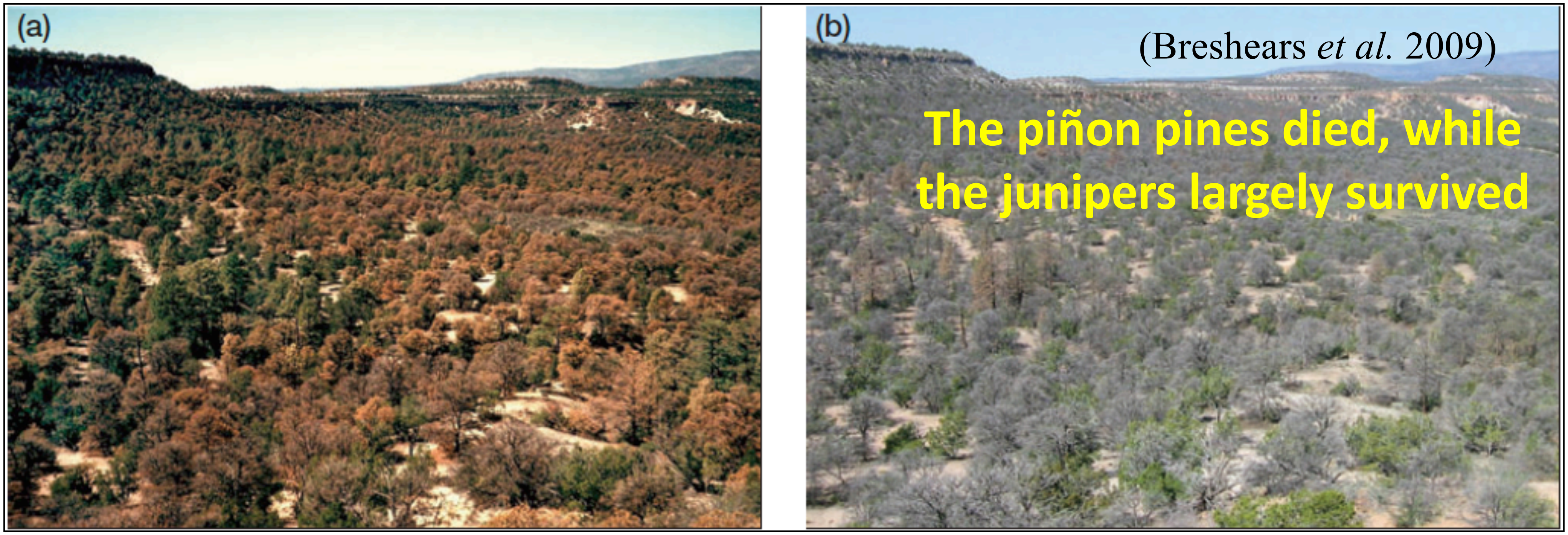
Ecological interactions, specialization

Life history

Environmental responses

Allocation of resources, response to disturbance

# Differential response of Piñon Pine and Juniper to extreme drought. Does a PFT approach work?

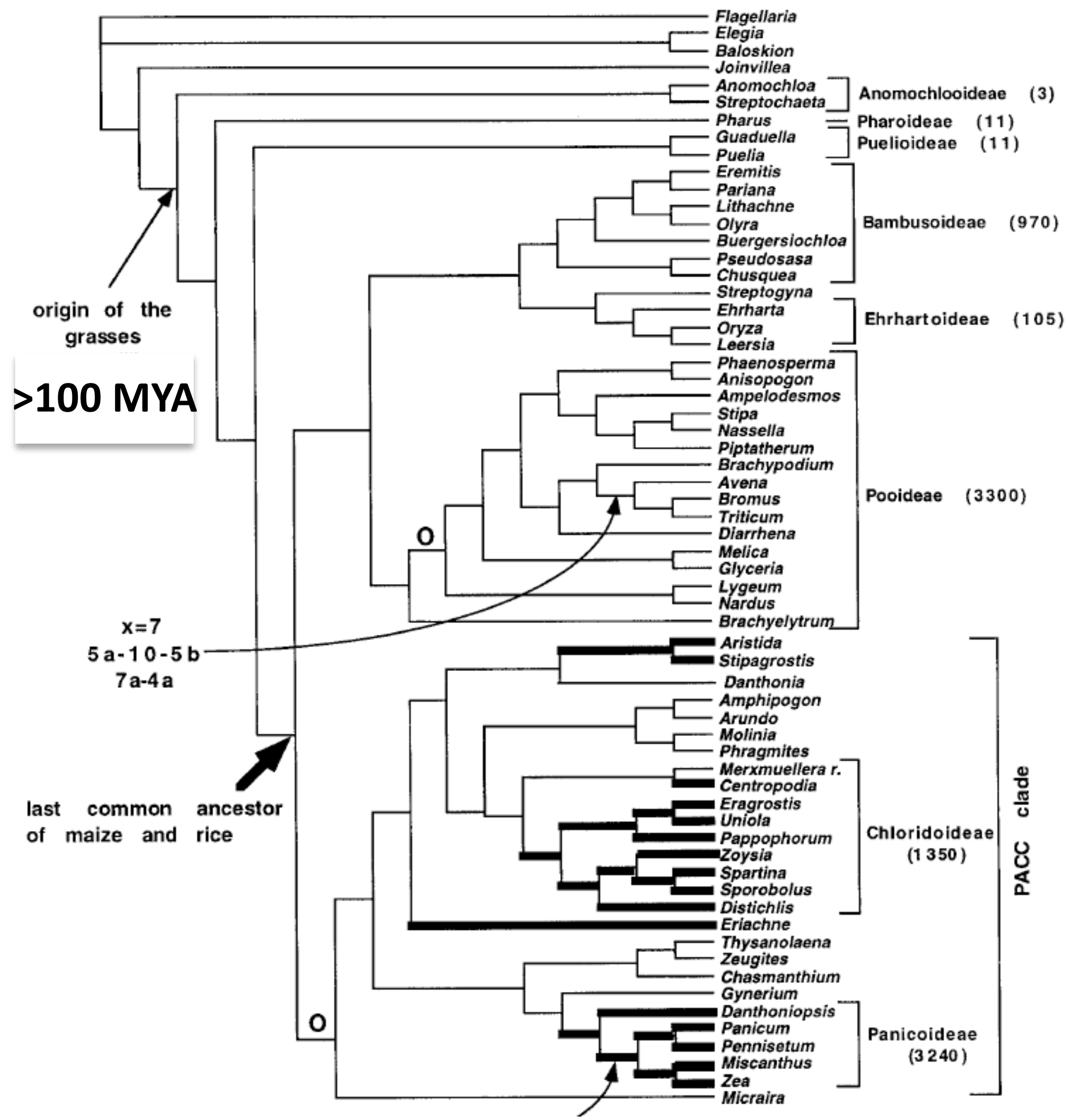



October 2002 October 2004

These pine and juniper species have fundamentally different water and carbon strategies. Hydraulic traits (differences in stomatal regulation, leaf water potential, wood density, iso versus anisohydry stomatal control) played a large role in the differential responses to extreme drought.

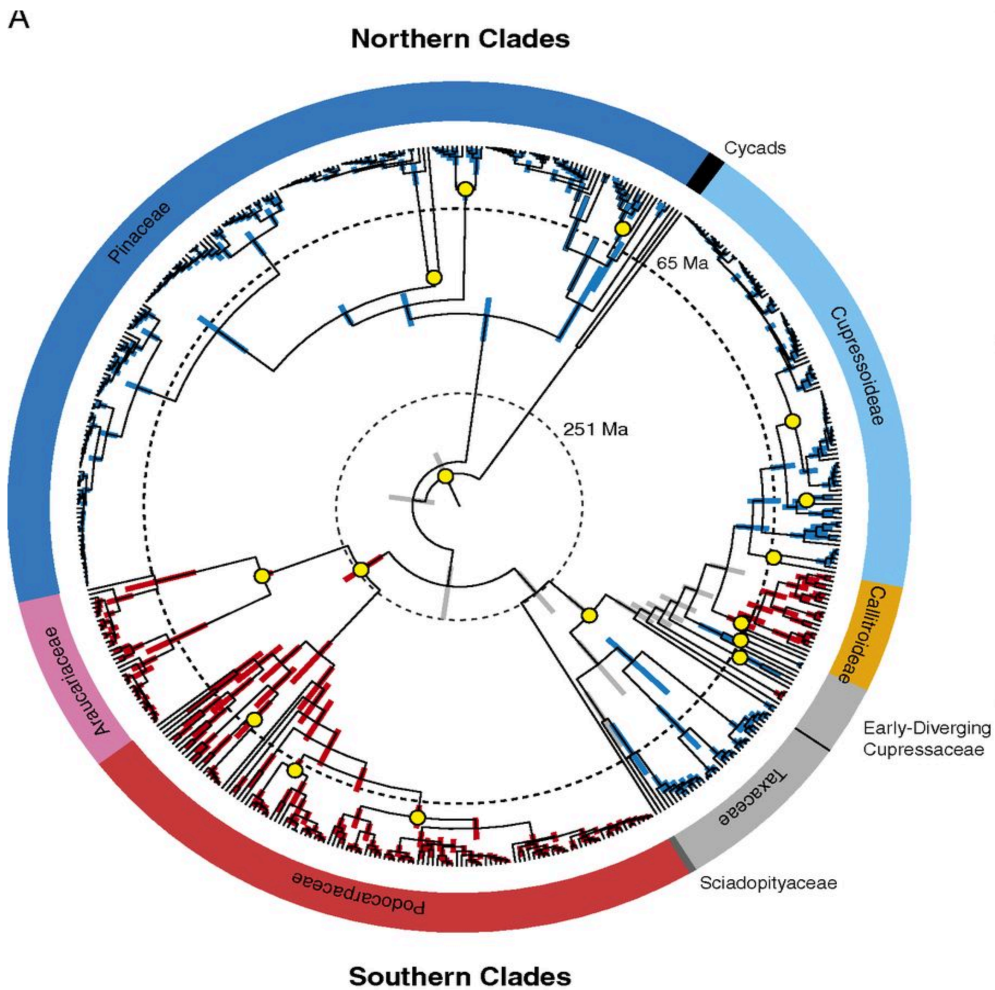
An evolutionary, lineage-based perspective helps explain the differences, which would not be captured by the PFT approach.

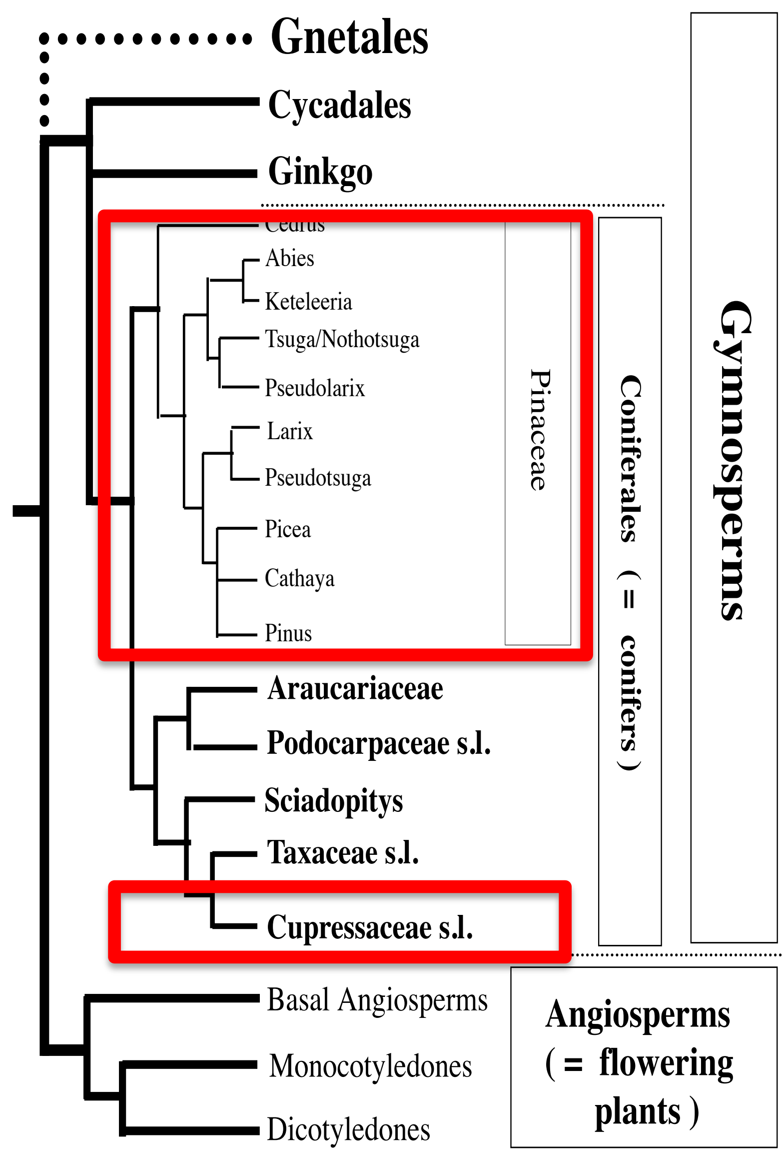
**Lineage** - closely related species connected to a common ancestor - in this example below, sorghum and maize are sister taxa, as are barley and wheat, with each pair separated by one node or branch point (speciation event).

# Phylogeny of Coniferales

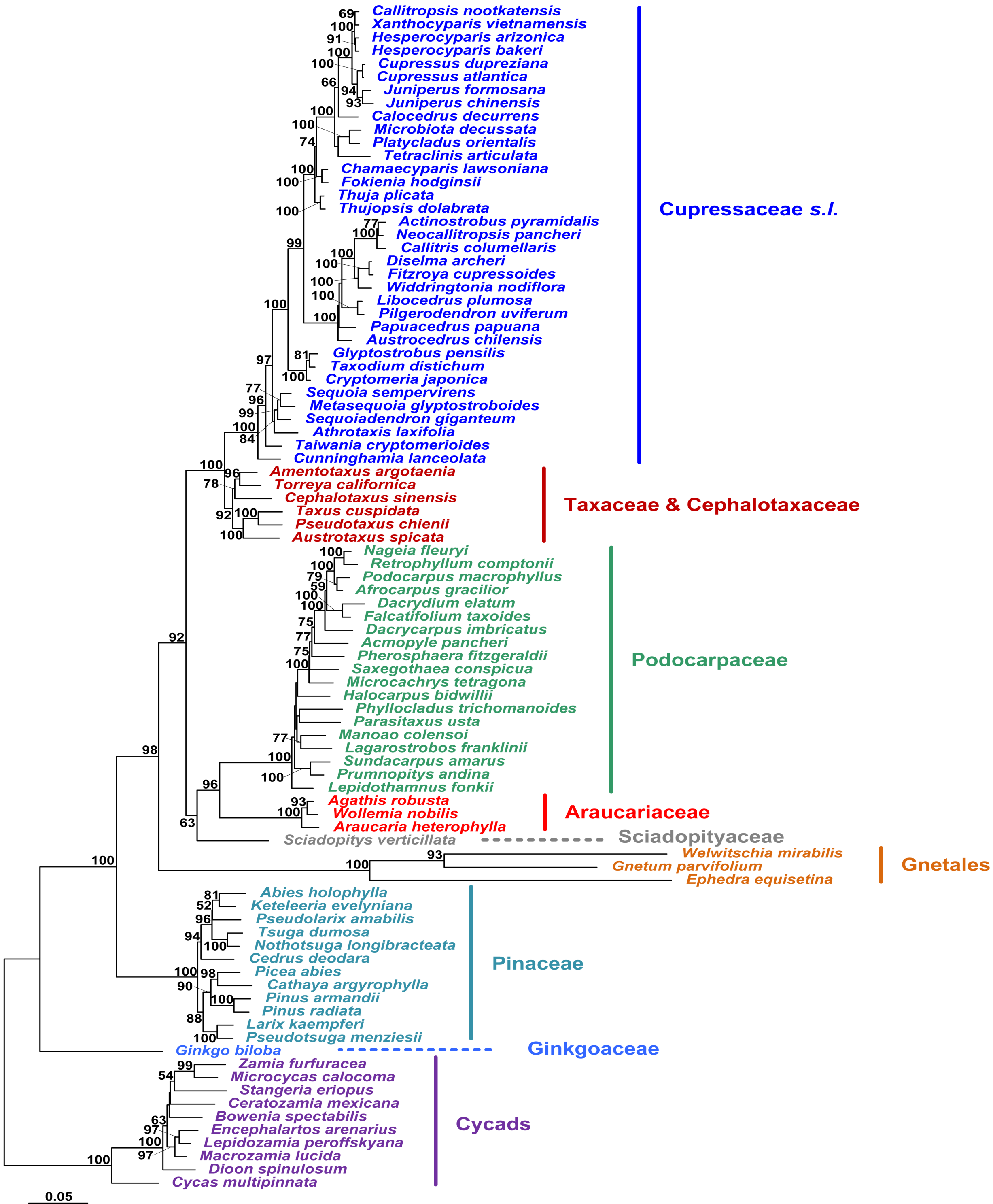
Leslie A B et al. PNAS 2012;109:16217-16221




The conifer families that pine and juniper species sit within diverged from each other at least 251 million years ago! Representing all conifers with 1 or 2 PFTs (evergreen and deciduous needleleaf trees) completely ignores this evolutionary history

http://www.conifers.dk

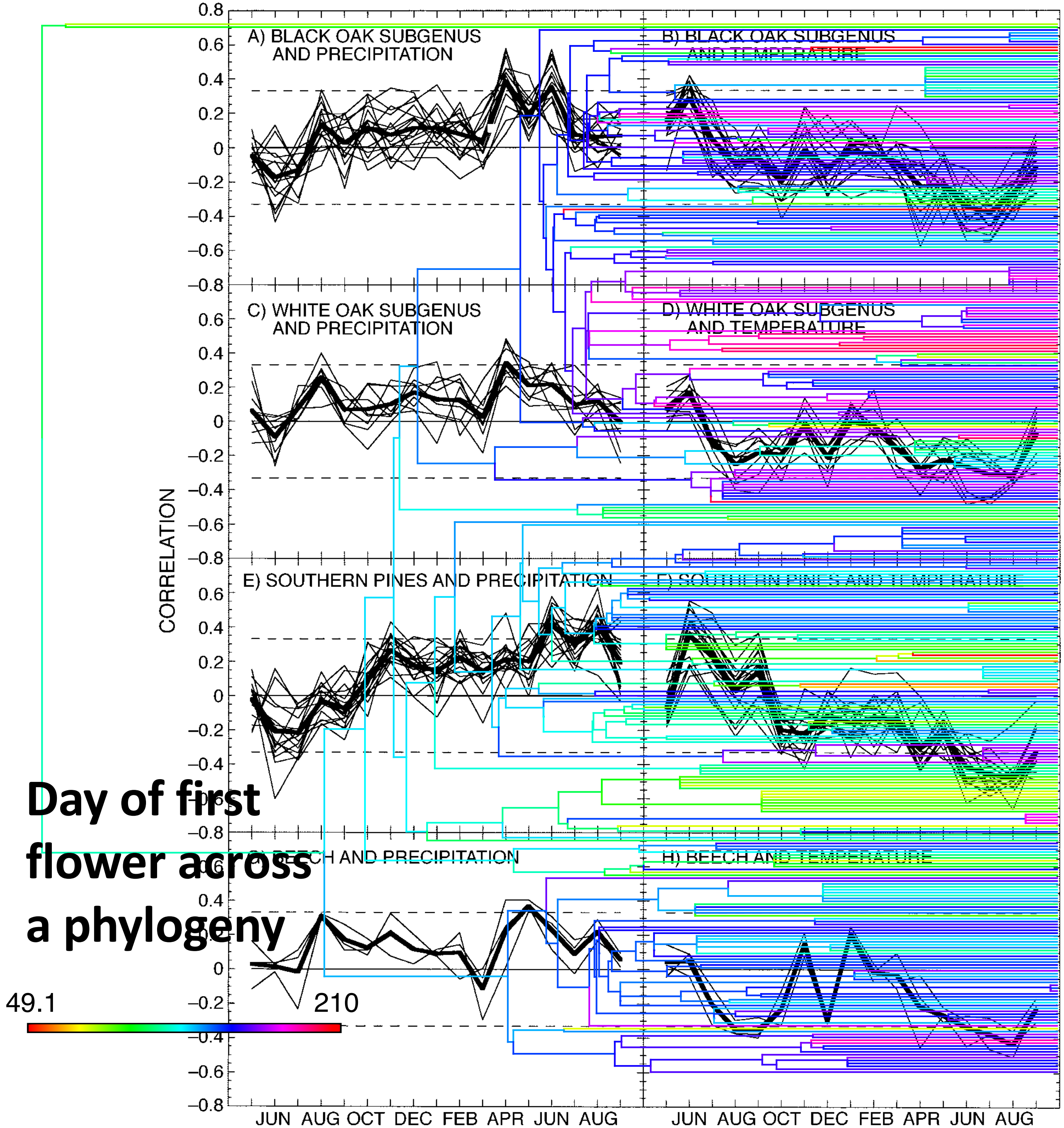



Existing PFT classifications would essentially classify all of these conifer families as evergreen needleleaf or deciduous needleleaf

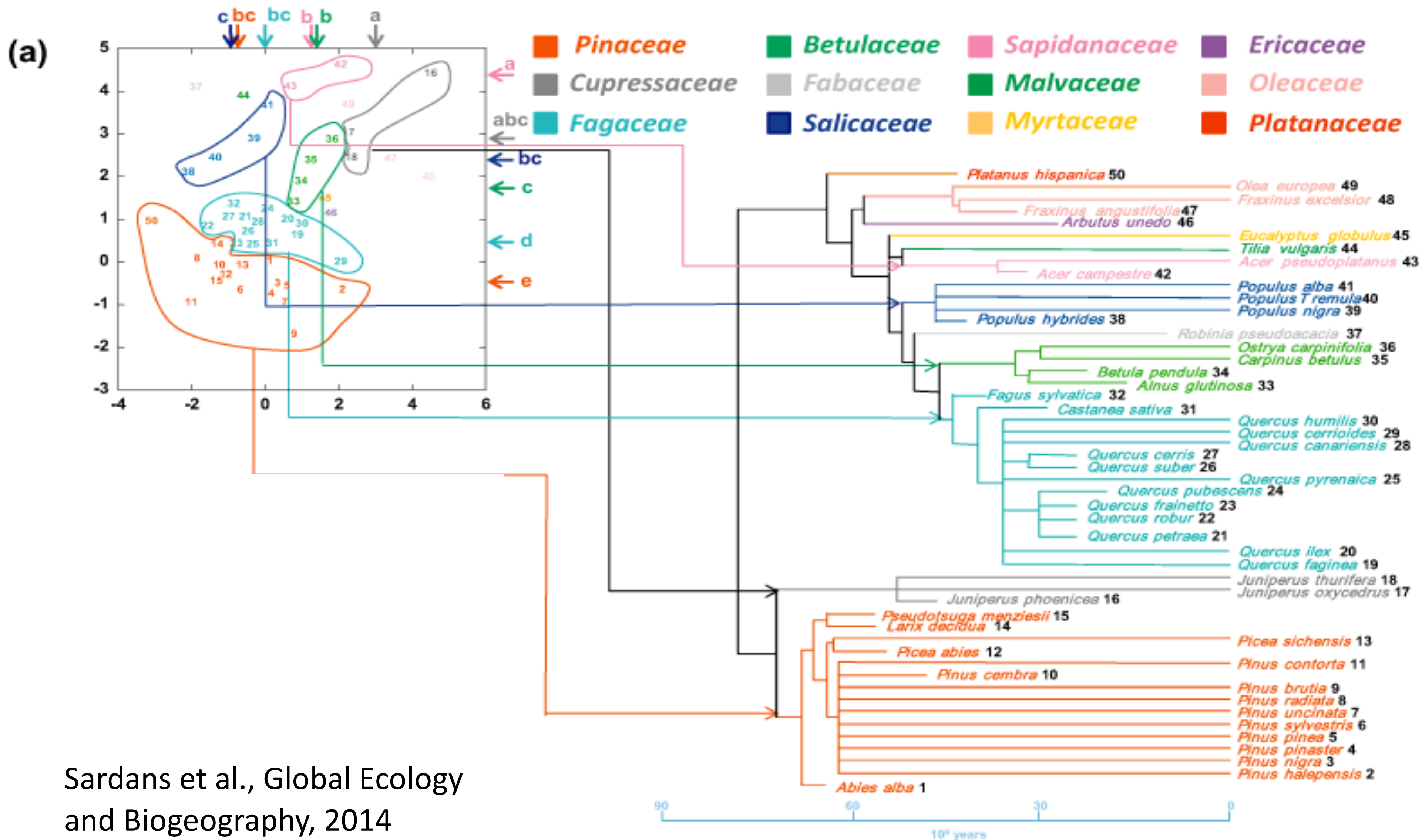
Phylogeny shown to be increasingly important for ecological structure and function

Tree growth responses to climate variation (Cook et al., Oecologia, 2001)

Phenology (Davies et al. J. Ecology 2013)



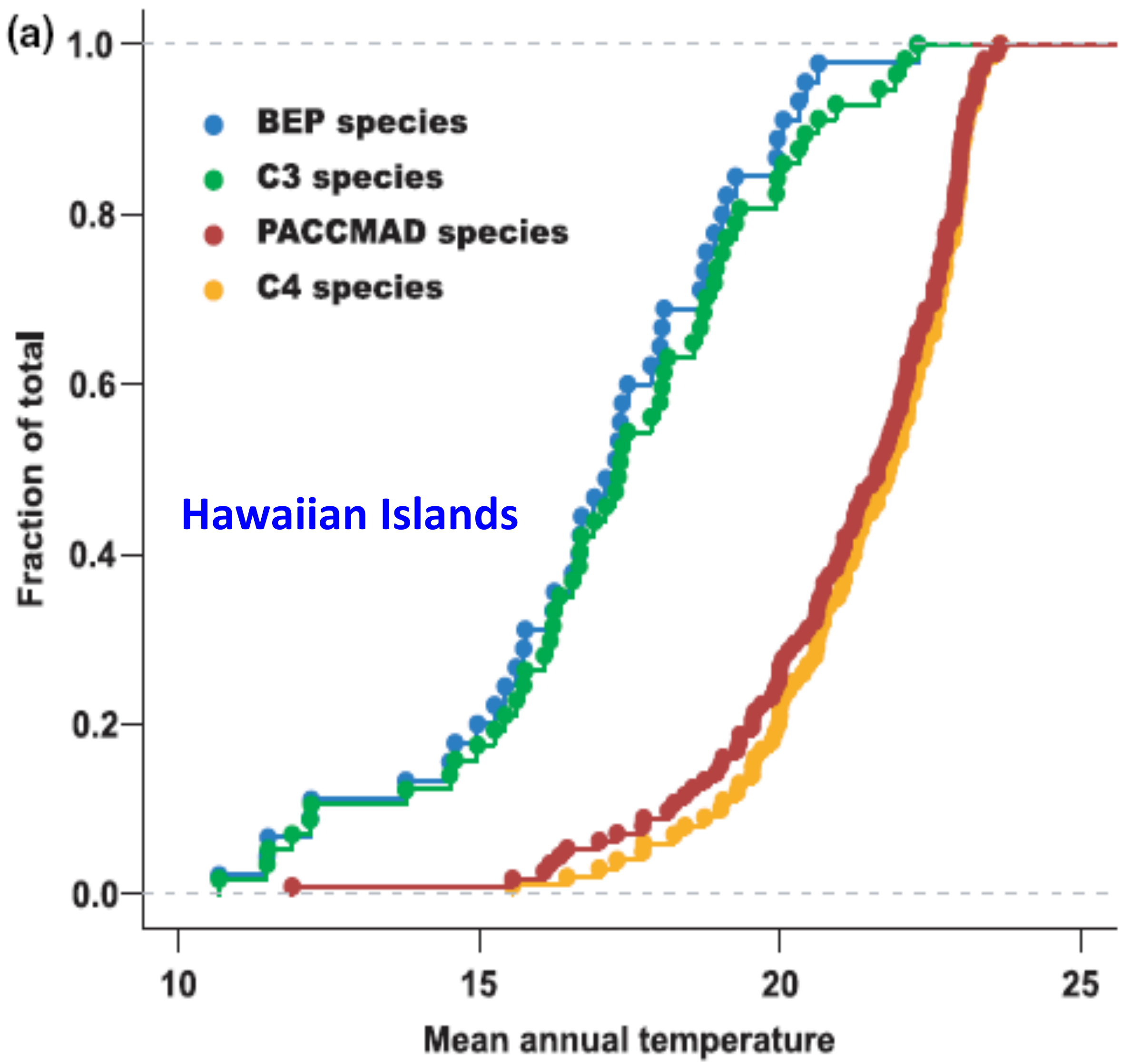
# Foliar elemental composition of European forest tree species associated with evolutionary traits and environmental and competitive conditions




Sardans et al., Global Ecology and Biogeography, 2014

**Phylogenetic signal statistics of PC scores**
**PC1 ($K$ = 0.544, $P$ = 0.01)**
**PC2 ($K$ = 0.340, $P$ = 0.002)**

# In a sense the same problem has occurred with grass diversity and $C_3$ and $C_4$ PFTs




BEP - clade with primarily temperate and boreal cool-climate $C_3$ grasses (no $C_4$ grasses)

PACCMAD - clade with tropical and subtropical $C_4$ grasses and some $C_3$ grasses (including *Arundo, Cortaderia, Phragmites*)

**Edwards and Still, *Ecol. Ltrs*., 2008**

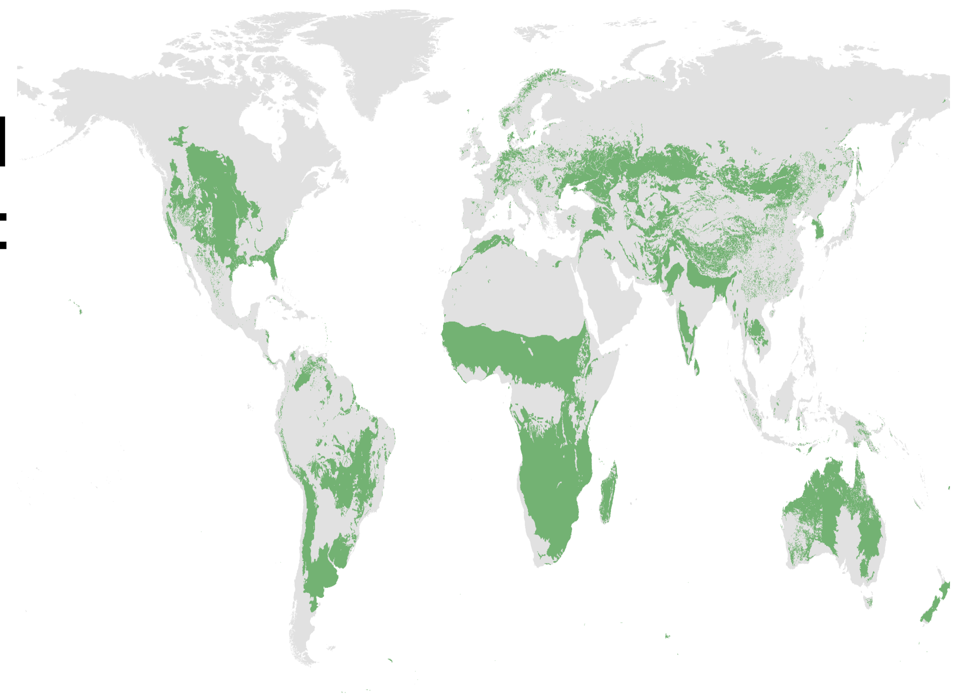
“..due to the complexity of temperature effects on physiology, it must be determined whether the low temperature response is a result of the presence of the $C_4$ photosynthetic pathway, or if it is due to other factors related to the apparent tropical origin of these taxa.”
(Teeri and Stowe, Oecologia, 1976)

**Put another way, is the ecological sorting of C3 and C4 grasses along temperature gradients due primarily to physiological differences related to the pathways, or is it due to ecological characters related to tropical origins compared to the temperate origins of most C3 grasses?**

# Grasses in a tree-centric world

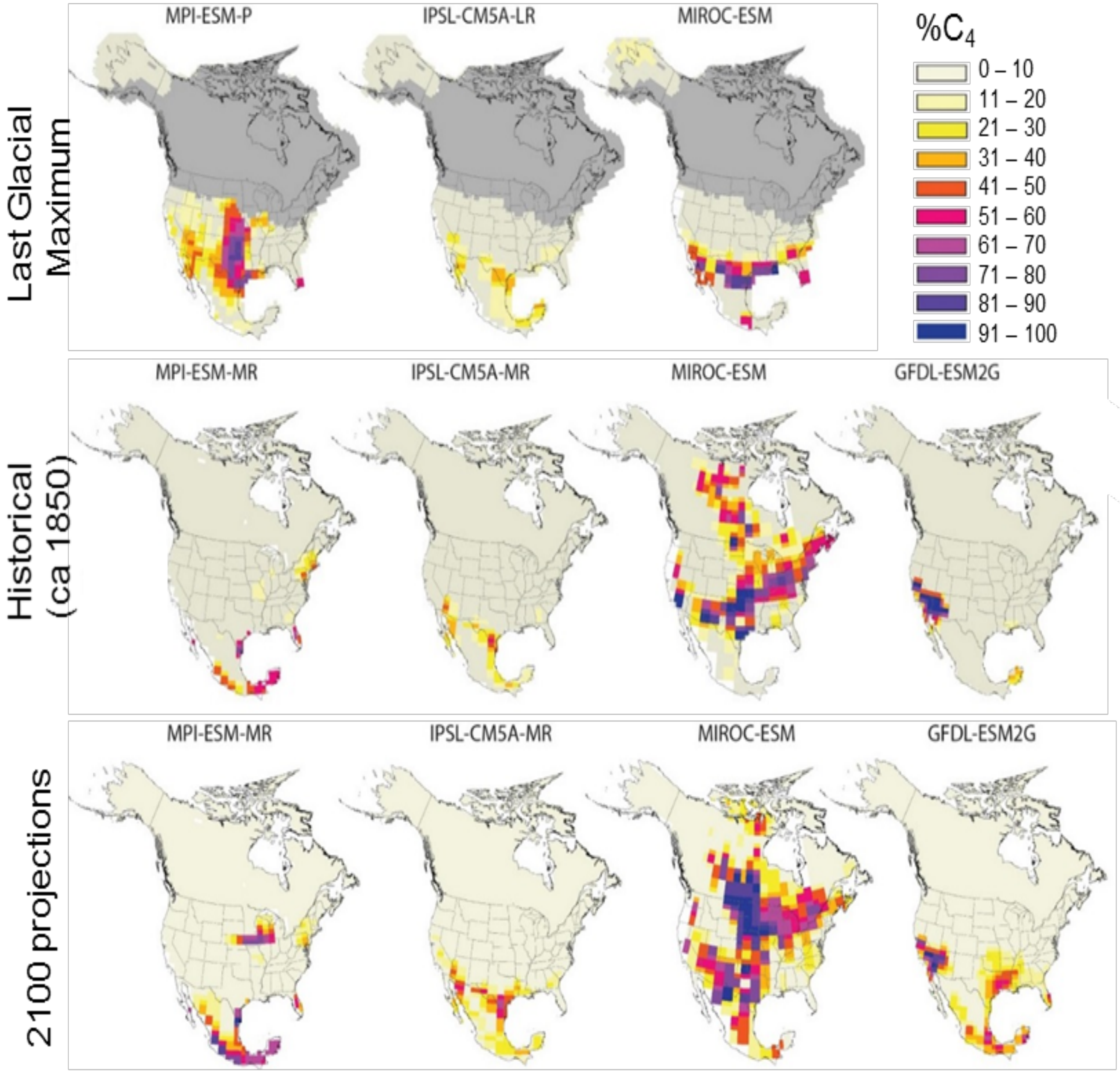
Most of the food we eat is derived from grasses (i.e., most C in your bodies was processed by a grass); C4 grasses alone are estimated to account for ~25% of terrestrial GPP (Still et al. 2003)

Grasses cover some 40% of earth's land surface and dominate the herbaceous surface layer in many ecosystems not traditionally thought of as grassy



And yet, grasses are often ignored or underrepresented in databases:

For example, of the 2,548 plant species in the Glopnet leaf trait database analyzed in (Wright et al., 2004 Nature), only 16 were $C_4$ grasses (0.6%)

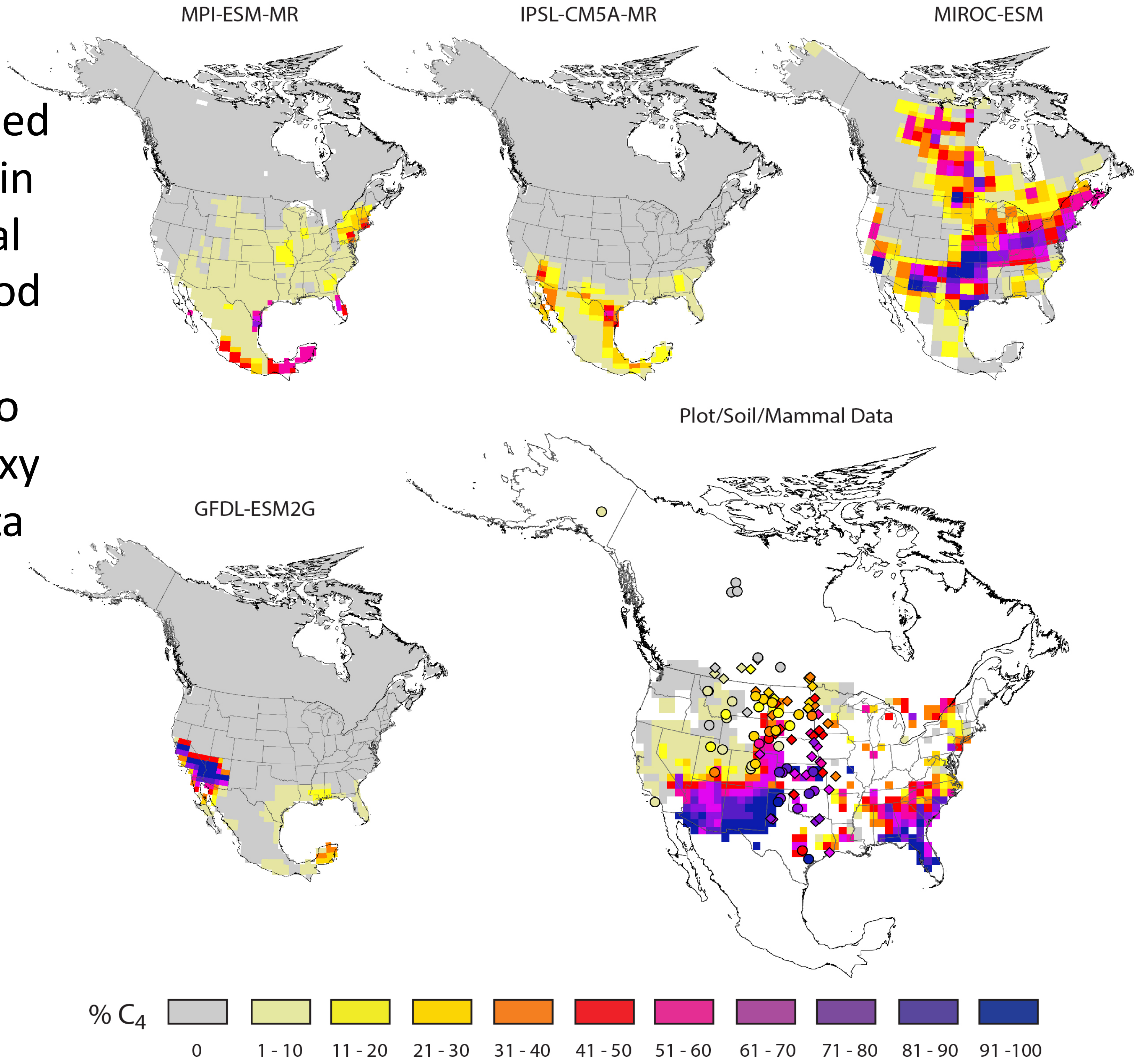



**Still, Cotton & Griffith, et al. *Glob. Ecol. Biogeog. 2018***

Model Simulations of C4 PFT cover at the LGM, historical, and future:

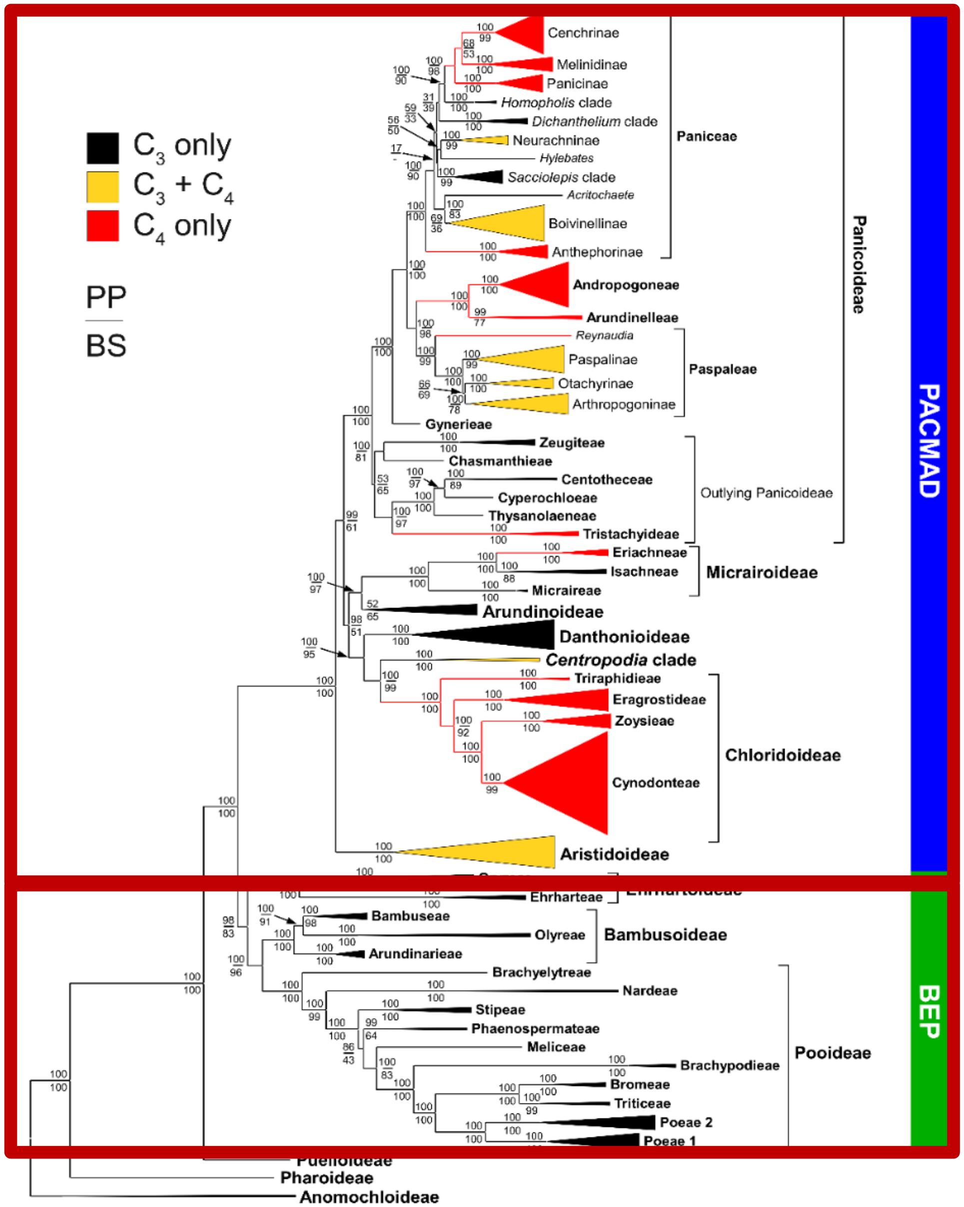
Of the 40+ individual CMIP5 models, only 6 provided a $C_4$ PFT cover fraction. The contributing models disagree with one another and largely fail to match proxy data on C4 and C3 grass cover or biomass across time scales

# CMIP5 modeled $C_4$ grass PFT in the historical modern period (~1850 CE) compared to available proxy and plot data




**Still, Cotton & Griffith, et al. *Glob. Ecol. Biogeog. 2018***

# 11,000+ grass species
# 23 $C_4$ grass lineages that differ greatly in their functional traits



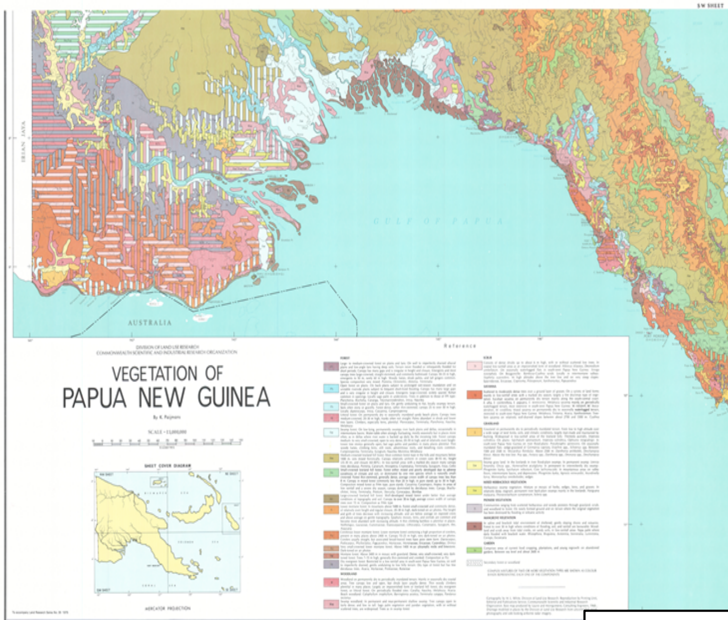

Slide courtesy of Dan Griffith

**GPWG II 2011**

Most ESMs have only a single C4 grass and one or two C3 grass PFTs, so many functional differences (traits) are not captured. But it's not necessarily the number of PFTs that is the issue, but rather how they capture functional diversity in traits and biogeographic history.

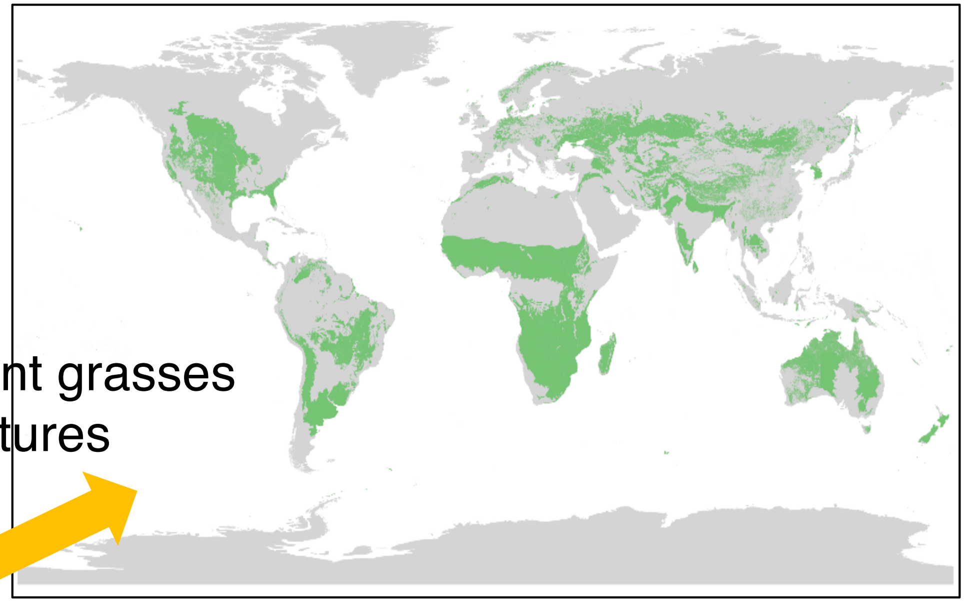
How to create lineage functional types (LFTs) which would better capture grass diversity?

# Assembling an observational global grass layer map using botanical records, expert knowledge, and plot data

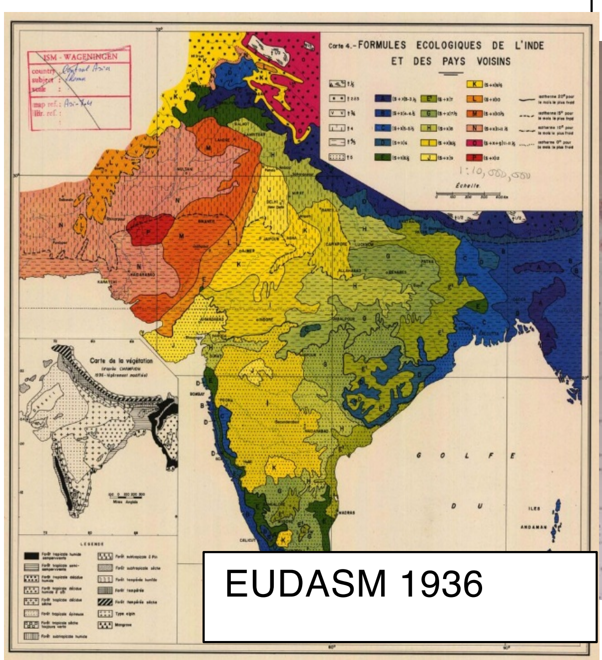



Paijmans 1975

Classified:
- dominant grasses
- key features



- **Validated against plots**
- **Gridded data**
  - **Climate**
  - **Lineages**
  - **$C_3/C_4$**

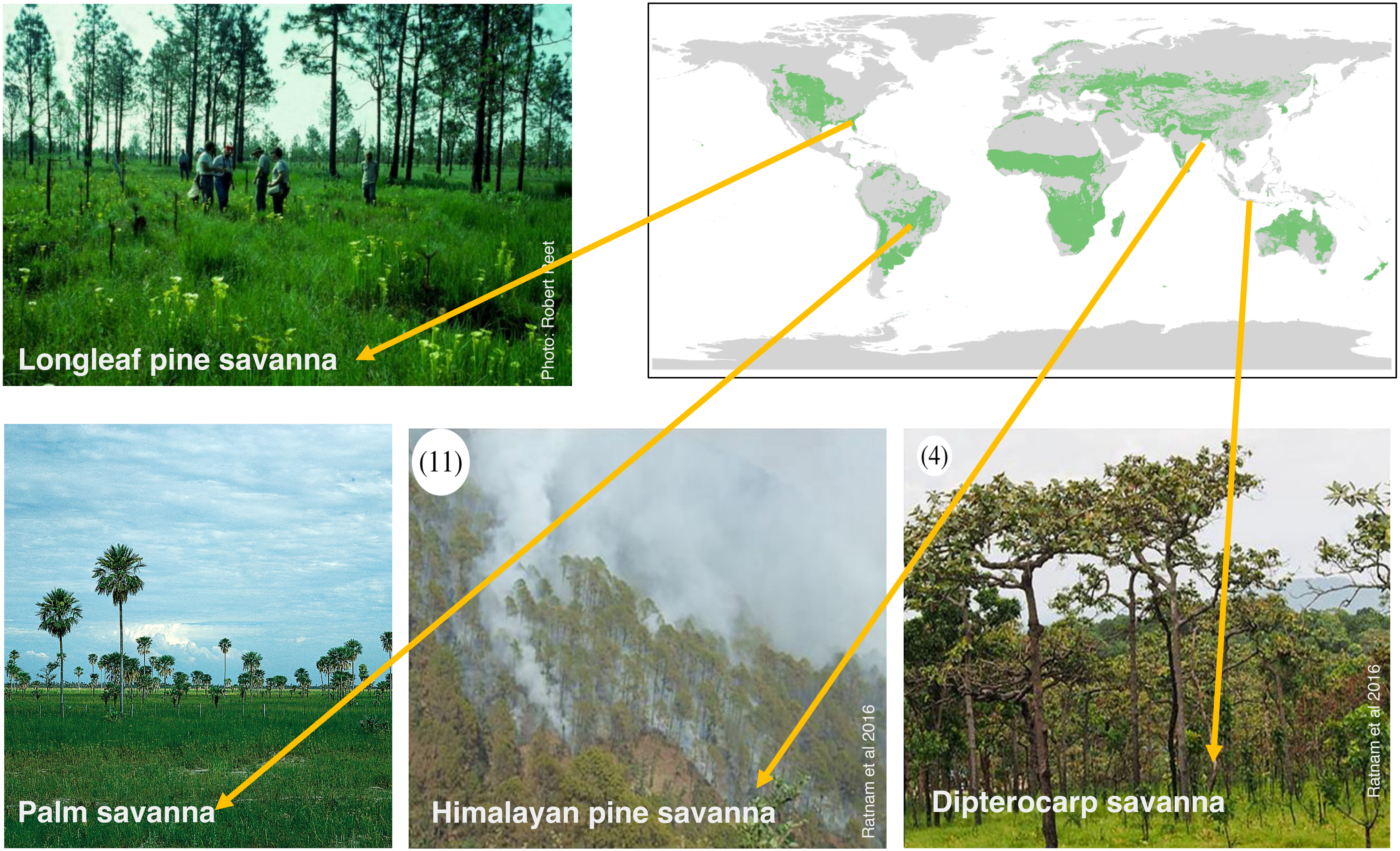



EUDASM 1936

**Vegetation map of the People's Republic of China 2007**

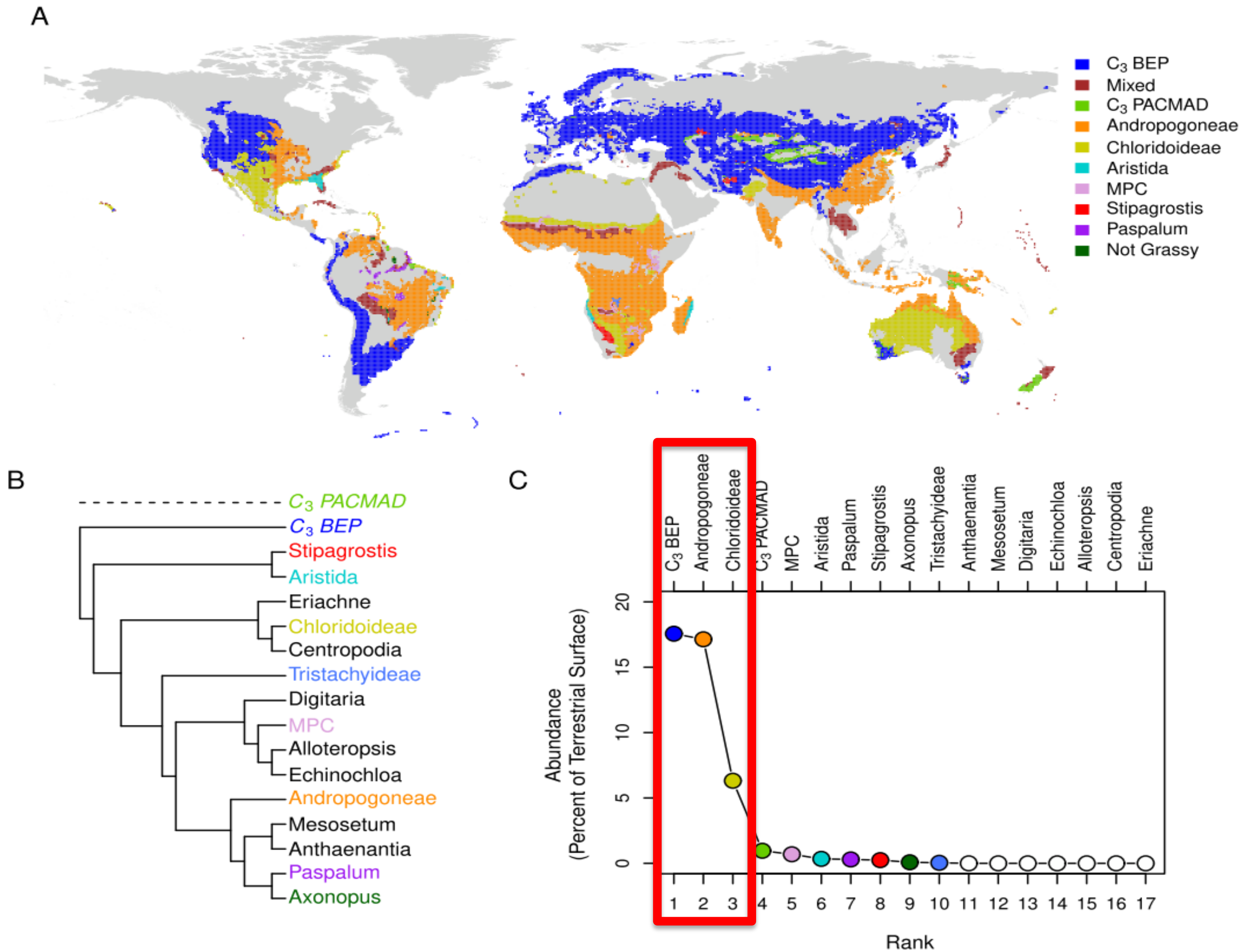
Slide courtesy of Dan Griffith

# Examples of grass-dominated herbaceous vegetation layers



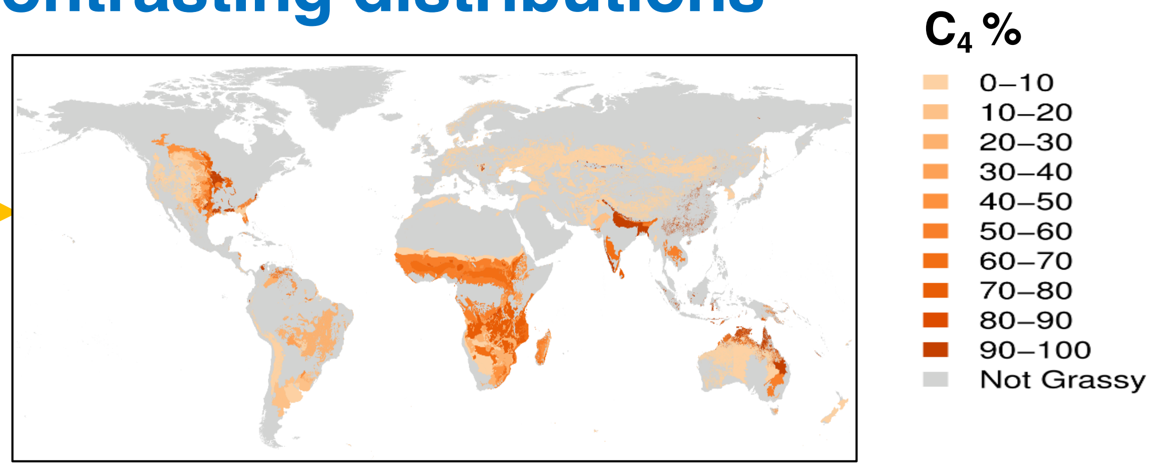

Slide courtesy of Dan Griffith

# Modern distribution of the grass lineages

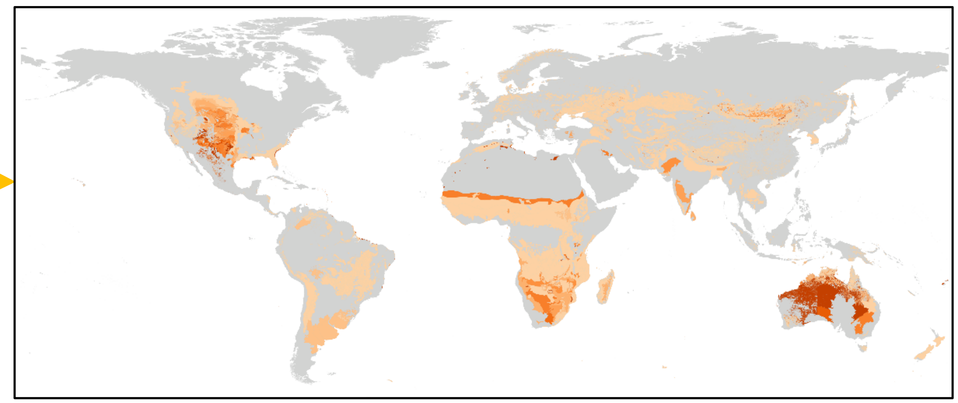


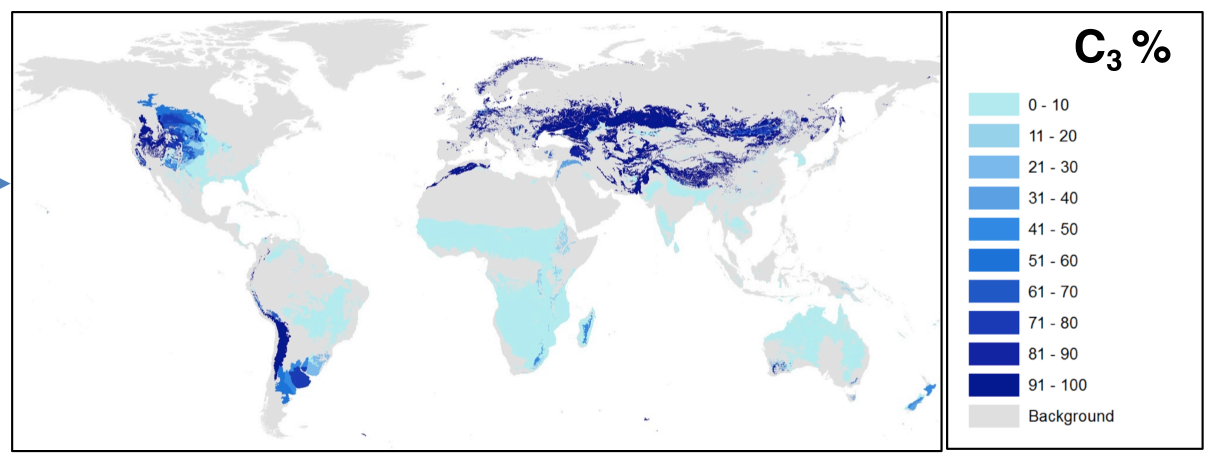

Lehmann, Griffith, et al. (in press, ***Nature Plants***)

# Grassy biomes are dominated by just 3 evolutionary lineages which have contrasting distributions

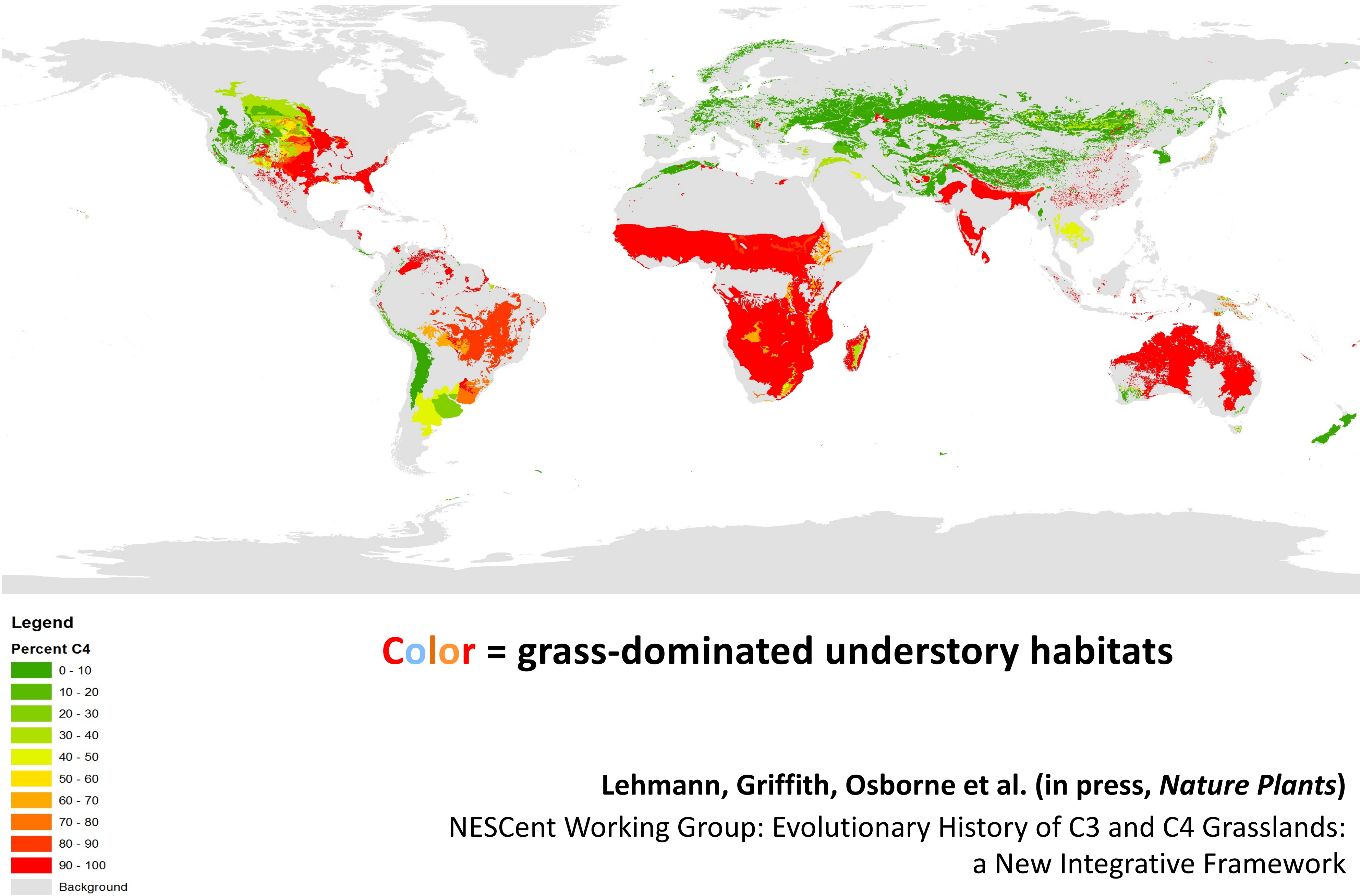







# Modern distribution of the grassy understory and $C_3$ and $C_4$ species relative dominance based on the lineage map

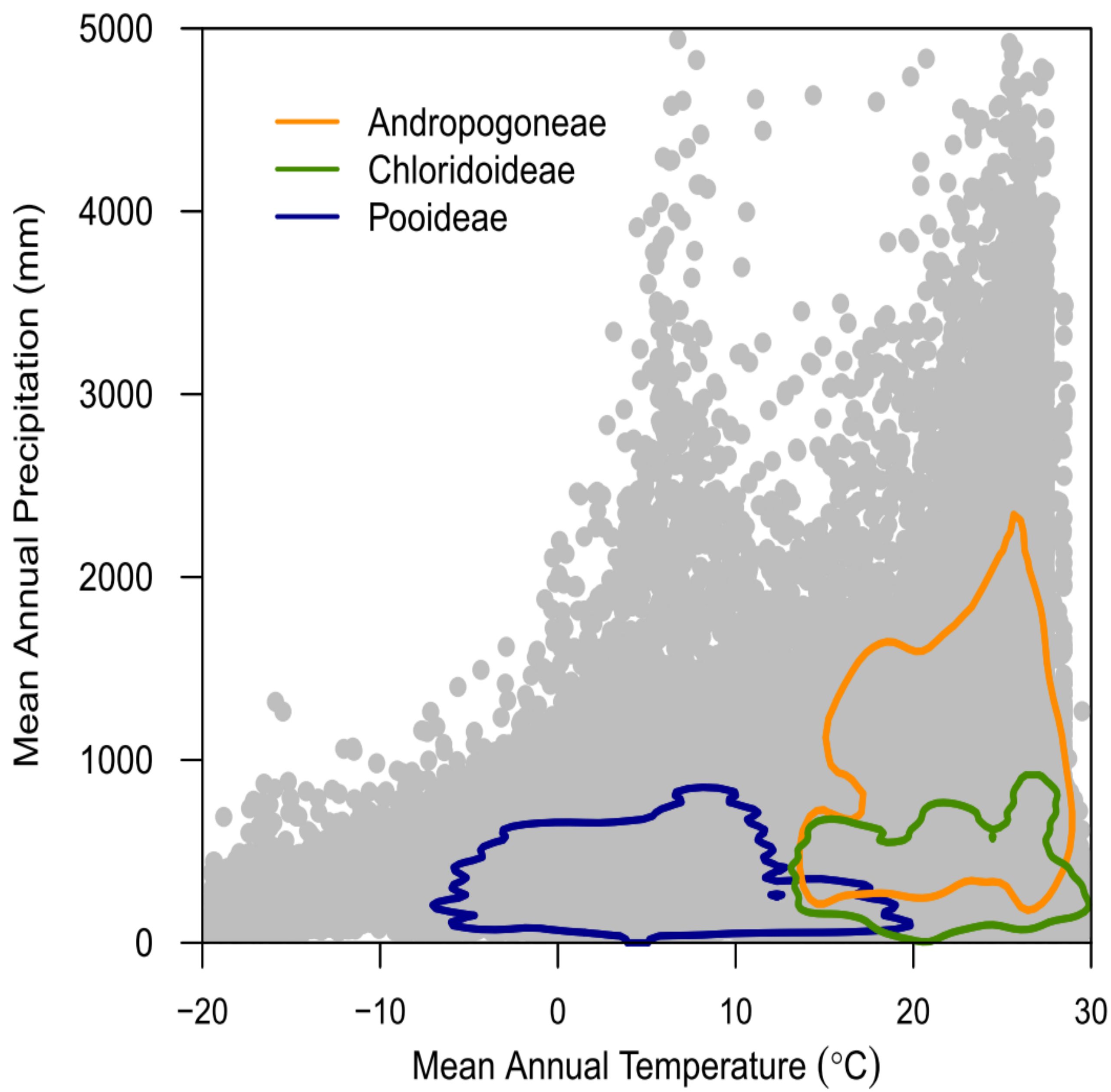



**Color = grass-dominated understory habitats**

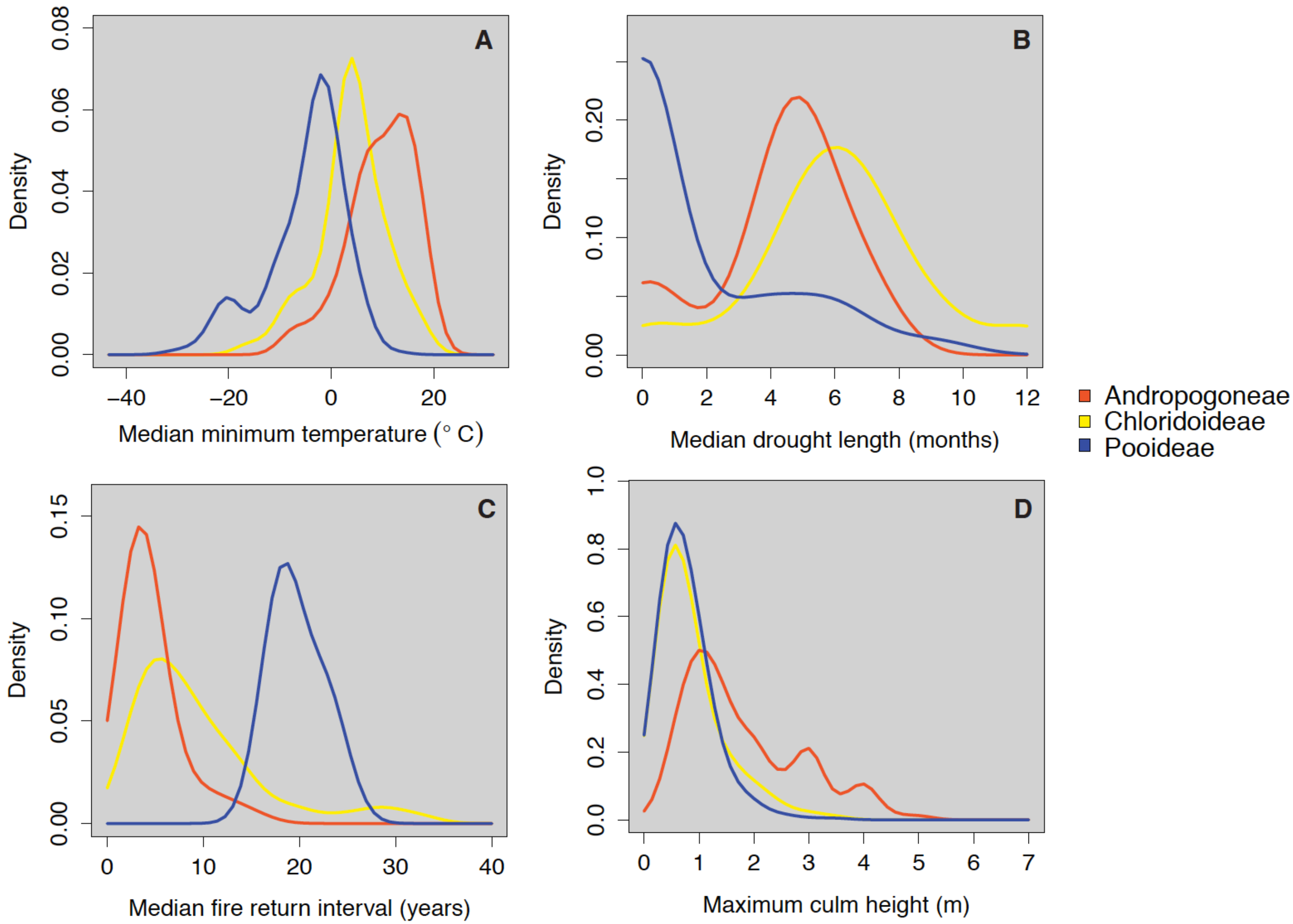
**Lehmann, Griffith, Osborne et al. (in press, *Nature Plants*)**

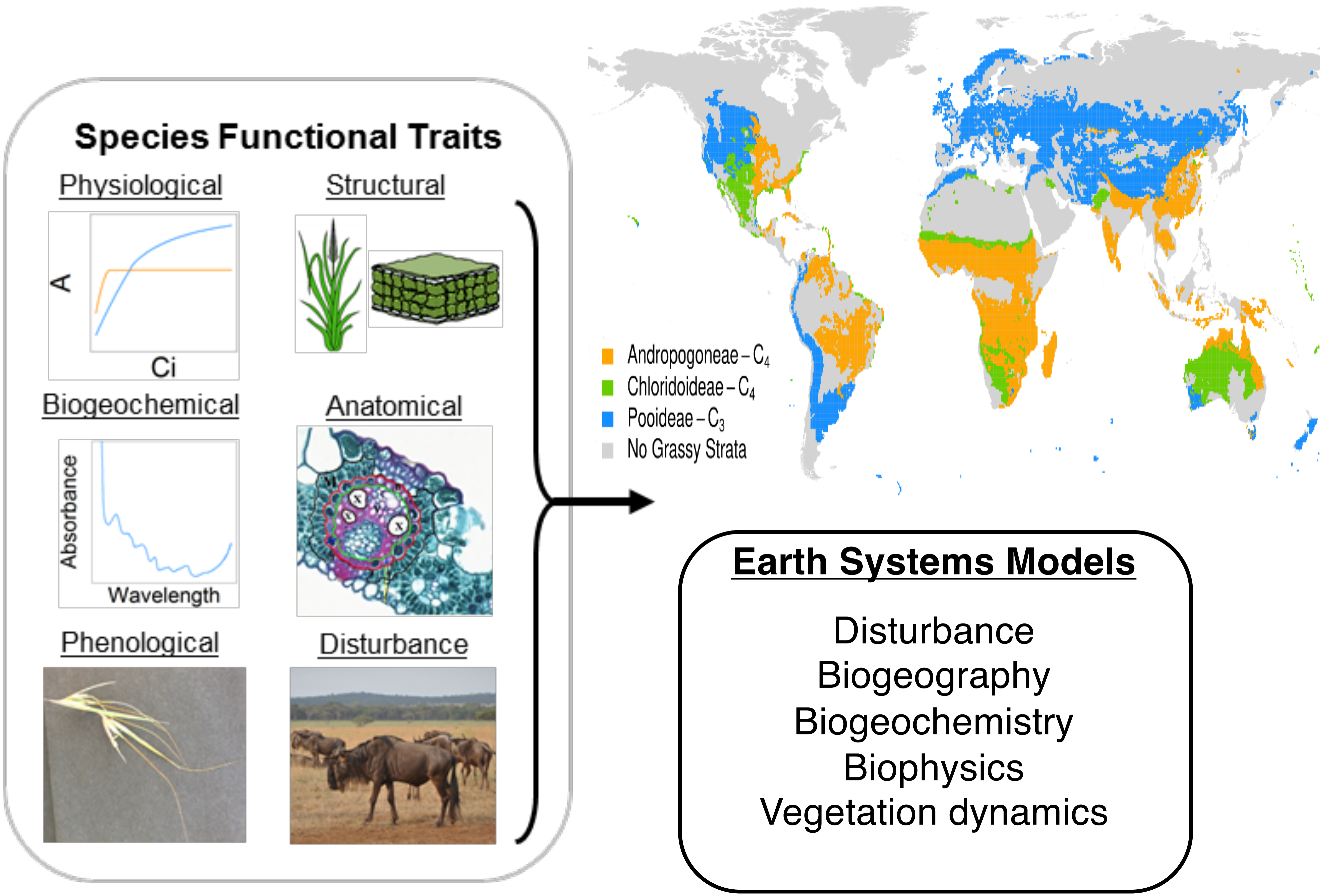
NESCent Working Group: Evolutionary History of C3 and C4 Grasslands: a New Integrative Framework

The primary $C_4$ grass lineages grow in warm and wet conditions with frequent fire (Andropogoneae) and warm and dry conditions (Chloridoideaea). The primary C3 grass lineage (Pooideae) grows in cool, dry conditions

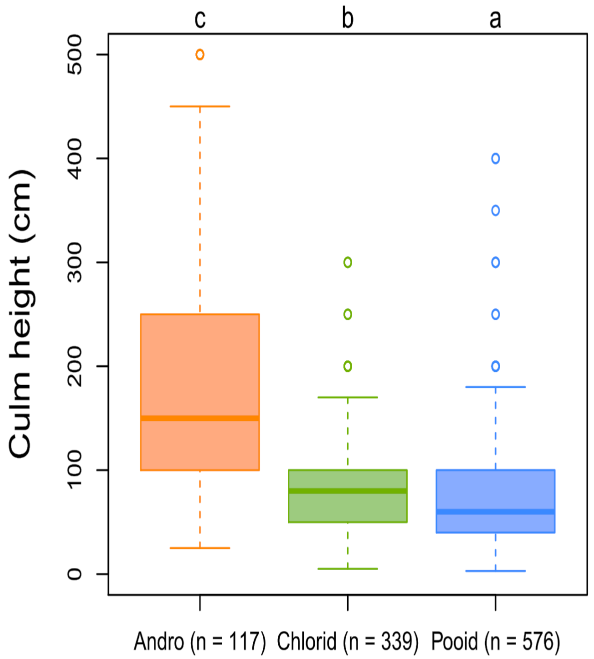


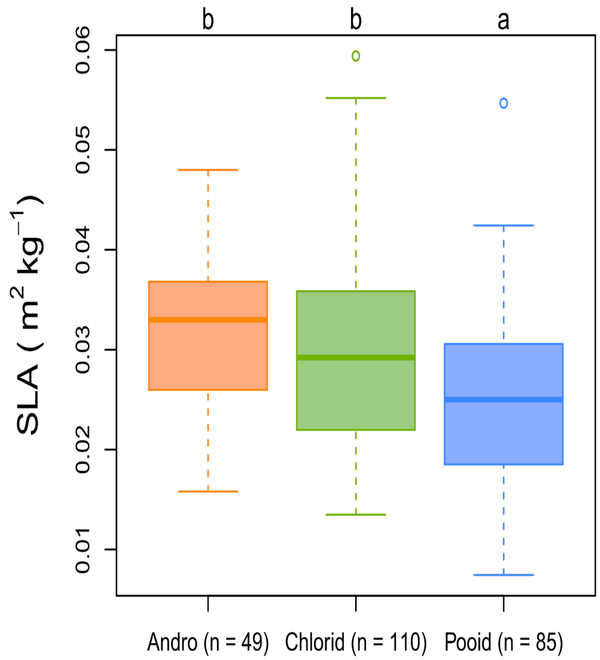

Lehmann, Griffith, Osborne et al. (in press, *Nature Plants*)


A
Density
Median minimum temperature (° C)
B
Median drought length (months)
C
Median fire return interval (years)
D
Maximum culm height (m)
Andropogoneae
Chloridoideae
Pooideae

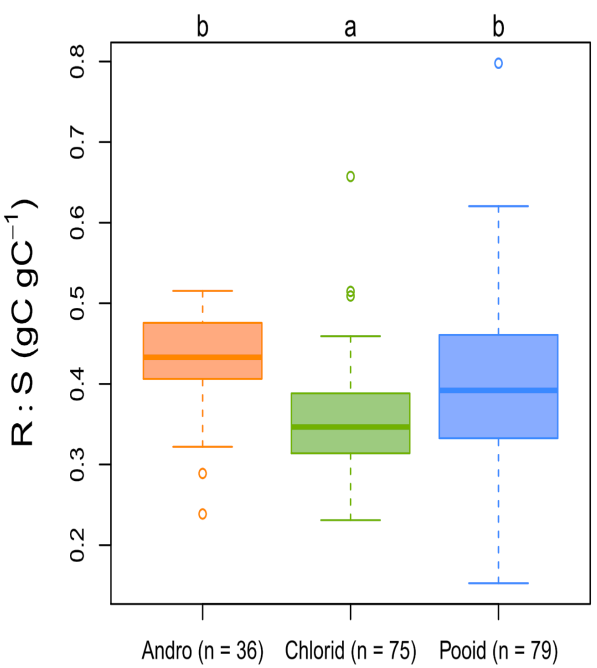

Species Functional Traits
Physiological
A
Ci
Structural
Biogeochemical
Absorbance
Wavelength
Anatomical
Phenological
Disturbance
Andropogoneae – C4
Chloridoideae – C4
Pooideae – C3
No Grassy Strata
Earth Systems Models
Disturbance
Biogeography
Biogeochemistry
Biophysics
Vegetation dynamics

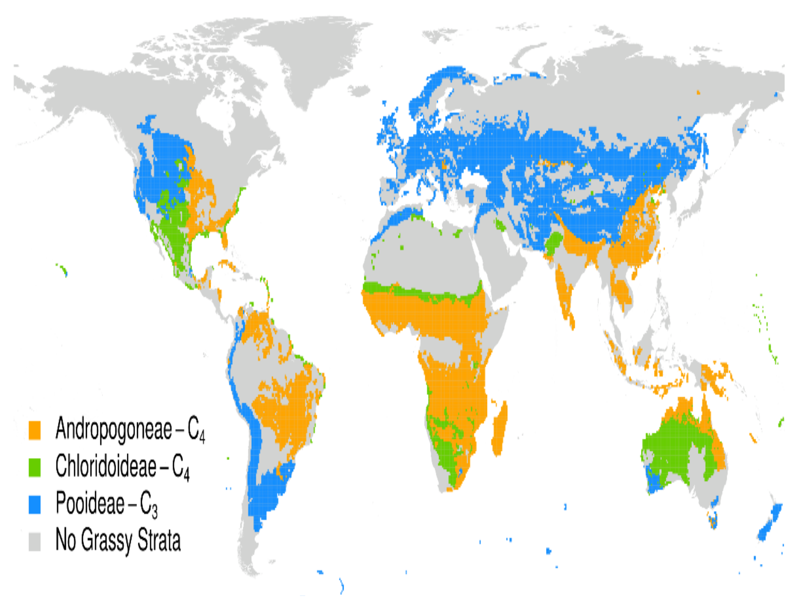
# Structural traits

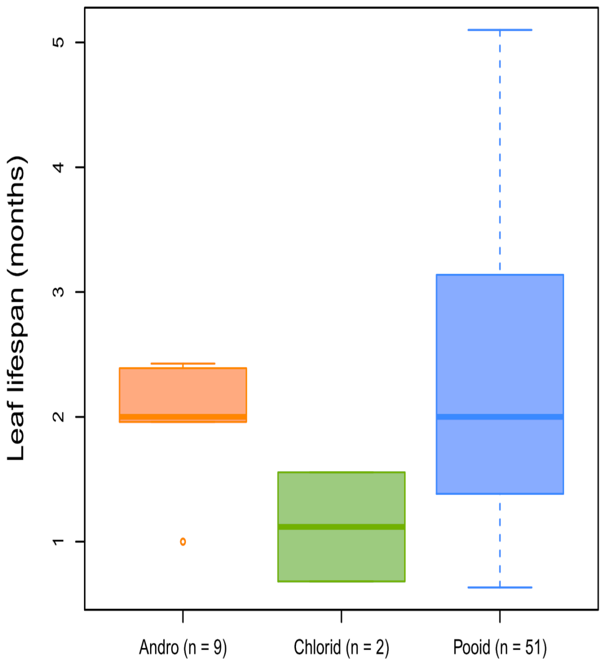


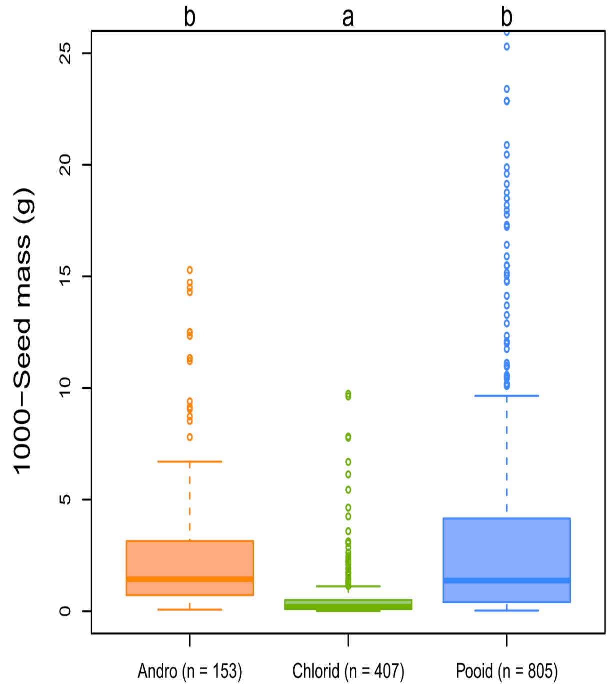




# Physiological traits



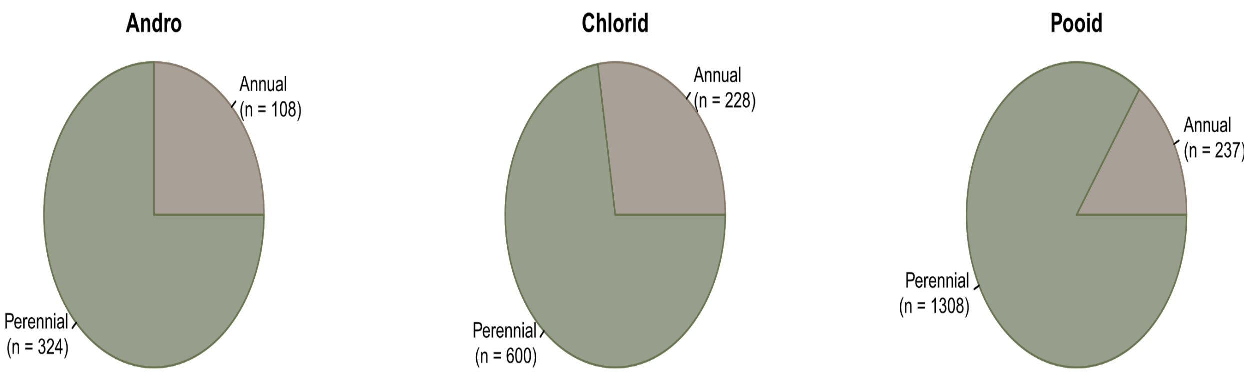


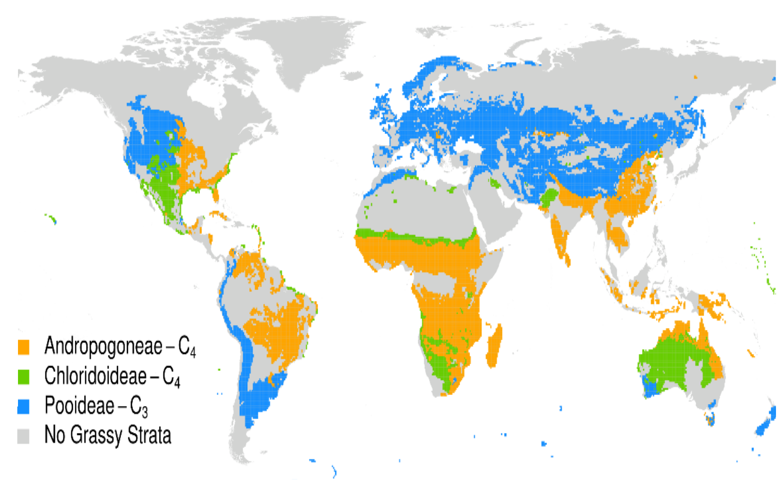




# Biogeochemical traits

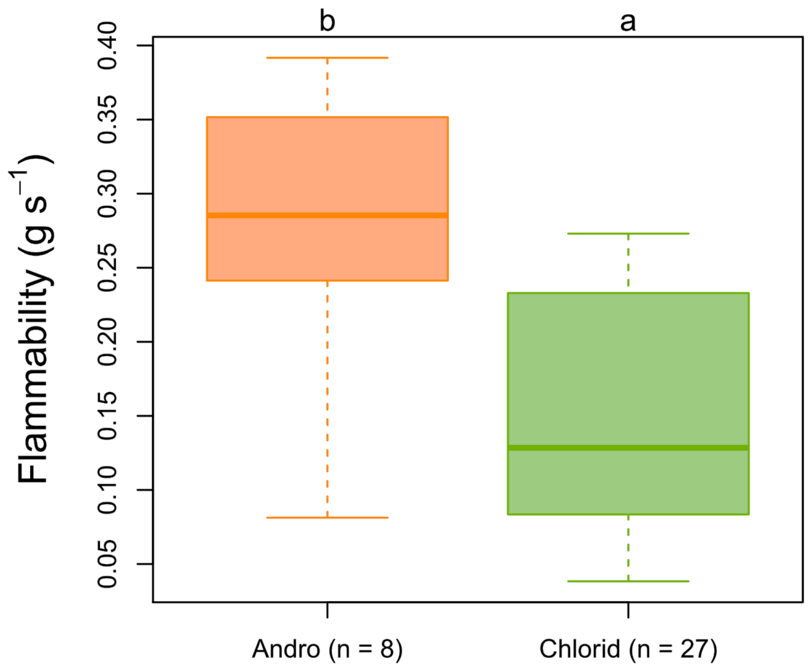
# Phenological and reproductive traits

# Anatomical traits

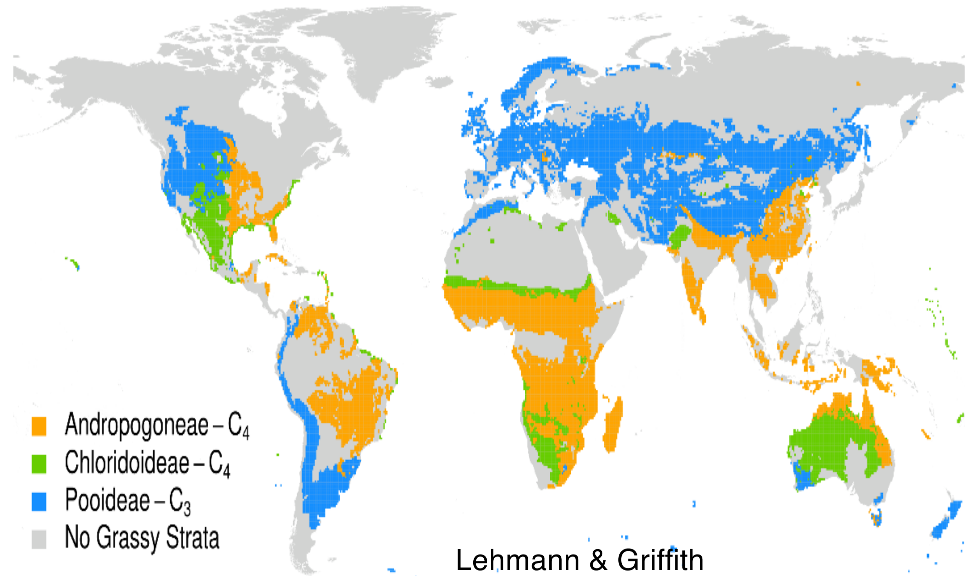


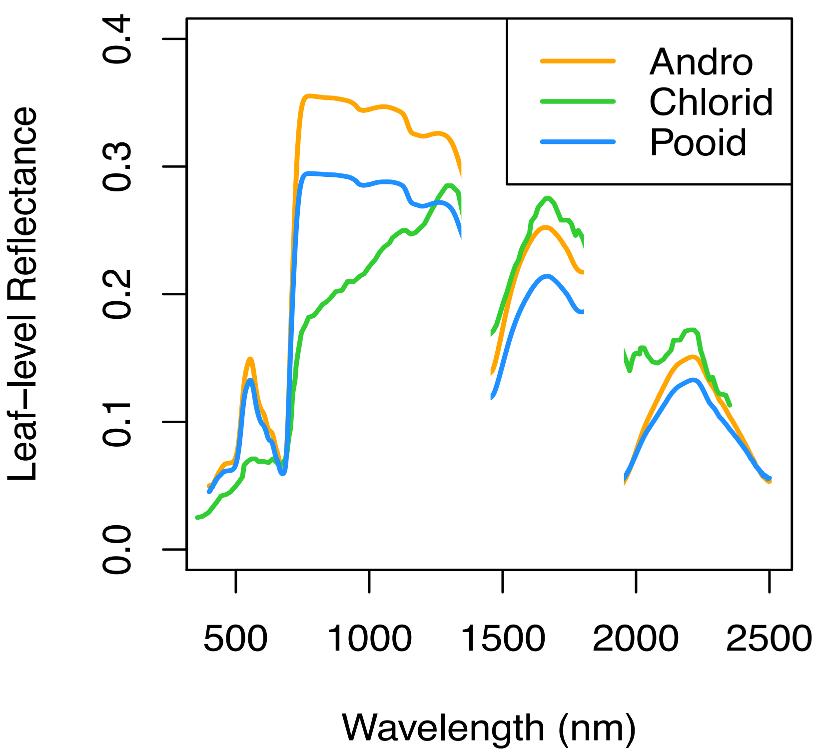

Lehmann et al. in press *New Phytologist*




# Disturbance-related traits




Lehmann & Griffith
et al in press *Nature Plants*



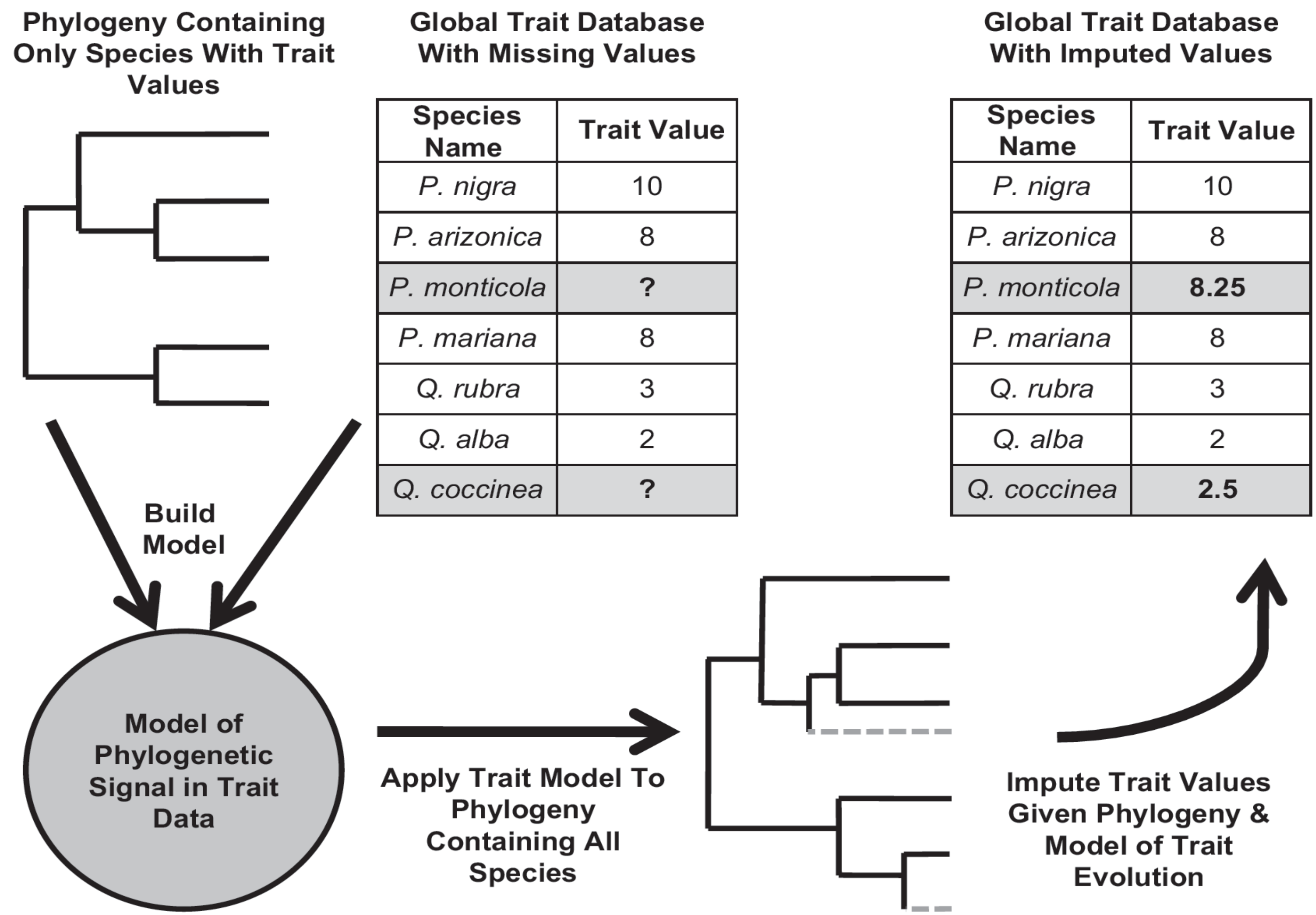

# Spectral traits

**Common PFT parameters from ESMs, and median LFT parameters (IQR; interquartile range) for three dominant grass lineages, taken from the literature and trait databases.**

| | | PFT | | LFT | | |
|---|---|---|---|---|---|---|
| Category | Parameter | C3 | C4 | Andropogoneae | Chloridoideae | Pooideae |
| Physiological | Vmax ($\mu mol\ m^{-2}\ s^{-1}$) | 90 | 39 | 38 | 45.625 (4.438) | 63.64 (27.655) |
| | Jmax ($\mu mol\ m^{-2}\ s^{-1}$) | 100 | 400 | 180 | 108.1 (42.5) | 128.8 (45.293) |
| | Rd ($\mu mol\ m^{-2}\ s^{-1}$) | 1.1 | 0.8 | 0.93a (0.15) | 2a (1.383) | 0.86a (0.69) |
| | Phi ($\mu mol\ \mu mol^{-1}$) | 0.085 | 0.06 | 0.064 | 0.06 | 0.085 |
| | Trange ($^{\circ}C$) | > 15.5 | < 15.5 | > 5 | > - 5 | > -30 and < 5 |
| Structural | SLA ($m^2 kg^{-1}$) | 33 | 16 | 33b (11) | 29b (14) | 25a (12) |
| | Culm Height ($cm$) | | | 150c (150) | 80b (50) | 60a (60) |
| | R:S ($gg^{-1}$) | 2 | 2 | 0.433b (0.066) | 0.347a (0.074) | 0.392b (0.128) |
| Biogeochemical | C:N ($gg^{-1}$) | 17 | 10 | 66.142b (14.7) | 39.98a (22.2) | 55.7ab (9.95) |
| | Nrubisco (*proportion*) | 0.137 | 0.09 | 0.052 (0.005) | 0.081 (0.028) | 0.21 |
| | rNIR (*reflectance*) | 0.35 | 0.35 | 0.38 | 0.49 | 0.35 |
| Anatomical | IVD ($\mu mol$) | - | - | 85.701a (25.2) | 136.785b (40) | 242.117c (58) |
| | Xylem dia. ($\mu mol$) | - | - | 21.36b (12.18) | 16.82a (10.72) | 19.31a (6.67) |
| Phenological | LL (*months*) | 12 | 1.68 | 2 (0.43) | 1.119 | 2 (1.755) |
| | 1000-seed mass ($g$) | - | - | 1.436b (2.416) | 0.2a (0.411) | 1.37b (3.75) |
| | Life History (% *annual*) | - | - | 0.25 | 0.275 | 0.153 |
| Disturbance | Curing rate (%) | 20 | 80 | 80 | 50 | 20 |

Griffith et al. in press *New Phytologist*

# A suggested framework for using phylogeny to guide filling of trait databases…could be used for fleshing out LFT trait databases for non-grasses




Global Trait Database With Missing Values

| Species Name | Trait Value |
|---|---|
| *P. nigra* | 10 |
| *P. arizonica* | 8 |
| *P. monticola* | **?** |
| *P. mariana* | 8 |
| *Q. rubra* | 3 |
| *Q. alba* | 2 |
| *Q. coccinea* | **?** |

Global Trait Database With Imputed Values

| Species Name | Trait Value |
|---|---|
| *P. nigra* | 10 |
| *P. arizonica* | 8 |
| *P. monticola* | **8.25** |
| *P. mariana* | 8 |
| *Q. rubra* | 3 |
| *Q. alba* | 2 |
| *Q. coccinea* | **2.5** |

Swenson, *Ecography* 2013

# Towards lineage-based functional types (LFT)

To represent grasses with C4 photosynthesis as a key functional trait, at least two clade/lineage groupings are needed:

***Andropogoneae*** are typically tall species that dominate wet and seasonally burned ecosystems,

***Chloridoideae*** grasses are typically smaller and associated with semi-arid regions

To represent grasses with C3 photosynthesis as a key functional trait, only one clade/lineage grouping is needed:

***Pooideae***: typically cold and dry adapted, less fire resistant, and smaller in stature

Creation of lineage-based FTs will help guide and constrain inclusion/selection of burgeoning plant trait data. Grasses are a good starting place. Trees will be harder, but new efforts to develop LFTs for conifers in the western US are promising

**Postdoctoral position in Grassland Ecosystem Modeling**

The Still Lab at Oregon State University invites applications for a postdoctoral research working on Earth System Modeling of grassland function and biogeography. The successful applicant will work as part of a large, interdisciplinary team to implement and test a new, evolutionary approach to capturing grass functional diversity and biogeography in Earth System Models. The approach, based on lineage functional types, will be based upon expansion of the grass trait database, additional data mining of existing literature on grass functional traits, and model development of processes important to grass modeling. The modeling work will be done in close collaboration with W.J. Riley at the Lawrence Berkeley National Laboratory and D. Griffith at NASA Ames Research Center.

**Major Duties/Responsibilities:**

Develop and apply models for global grassland processes.

Evaluate biogeochemical and plant physiological interactions and their effects on carbon and energy exchanges with the atmosphere.

Work creatively, independently, and productively.

Work as a member of a large multidisciplinary research team. Author peer-reviewed journal articles

**Please apply at https://jobs.oregonstate.edu/postings/90490**