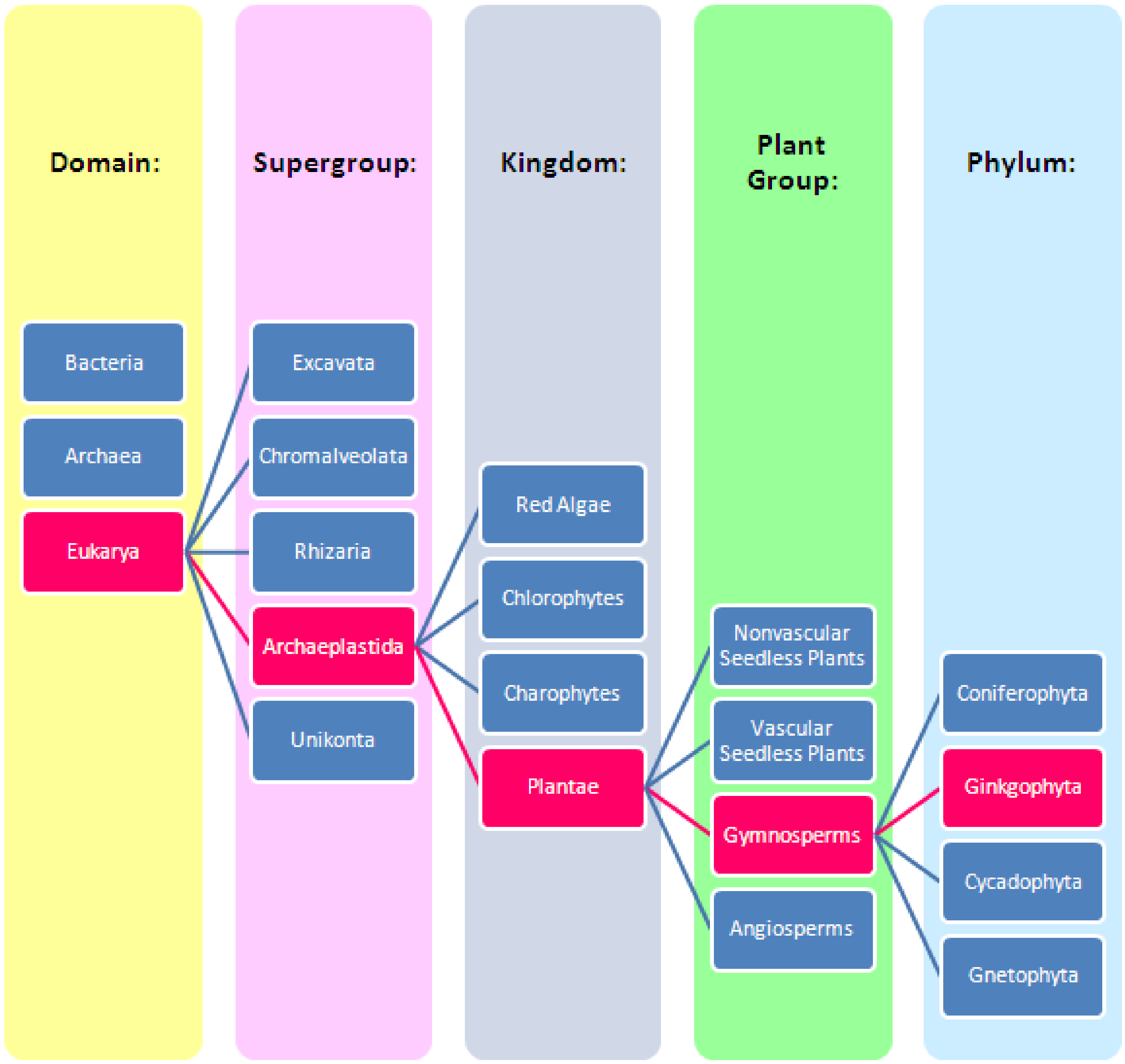
Ginkgo biloba’s footprint of dynamic Pleistocene history dates back only 390,000 years ago

Adedayo Adeleke

Ginkgo biloba is a large shade tree native to China, having fan-shaped leaves and fleshy seeds w ith
edible kernels: the sole surviving species of the gymnosperm famil y Ginkgo-aceae, which thrived in the Jurassic Period, and exists almost exclusively in cultivation.



Previous studies

- The Genus *Ginkgo* first appeared around 170 mya (middle Jurassic period)
- *Ginkgo* went extinct all over the world at the end of the Pliocene to the beginning of Pleistocene glaciation and deglaciation cycles: Only a few relict populations remained in china
- The status of these Chinese regions was just proven about 10 years ago
- There are 2 major geographical regions in China that served as refuge areas

  1) Warm temperate deciduous (to evergreen) forest (WTDF)

  2) Subtropical broadleaved evergreen forest (SBEF)

These therefore make one question whether a) Constituent species populations underwent glacial admixture or b) They remained isolated over the last glacial maximum.

3 hypotheses

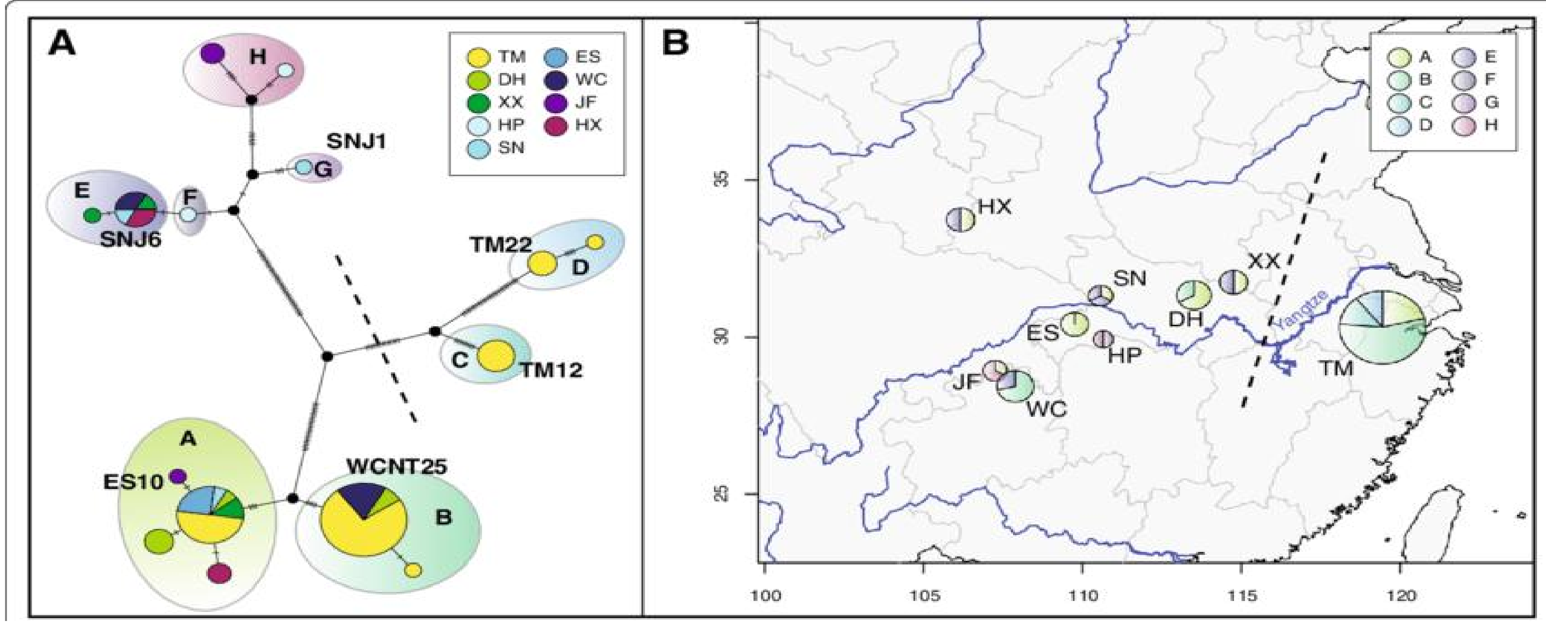
1. During the glacial periods, populations merged and admixed at lower elevations (isolation with admixture)
2. Populations remained isolated during the glacial as well as interglacial periods (continual isolation)
3. Life history traits can impose restrictions on the range dynamics and population genetic structure of temperate plants

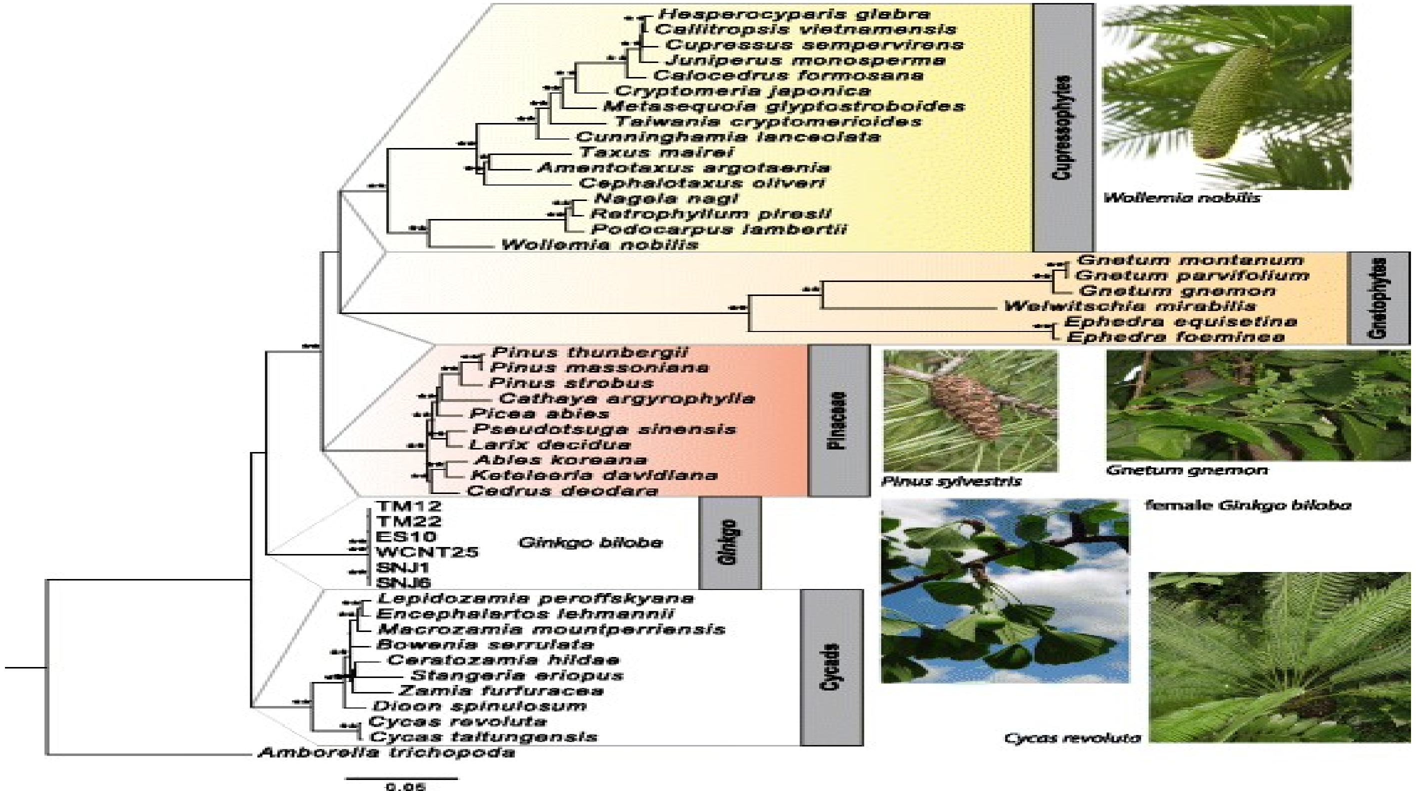
Main goals of Paper

- To reconstruct a reliable phylogenetic tree to define phylogenetic positions among clades found within *G. biloba*
- To estimate split times for internal nodes among *Ginkgo* genotypes
- Elaborate on the hypothesis that *G. biloba* expanded repeatedly during cooling periods throughout the late Pleistocene, and that warming periods forced *Ginkgo* into refuge areas

Methods

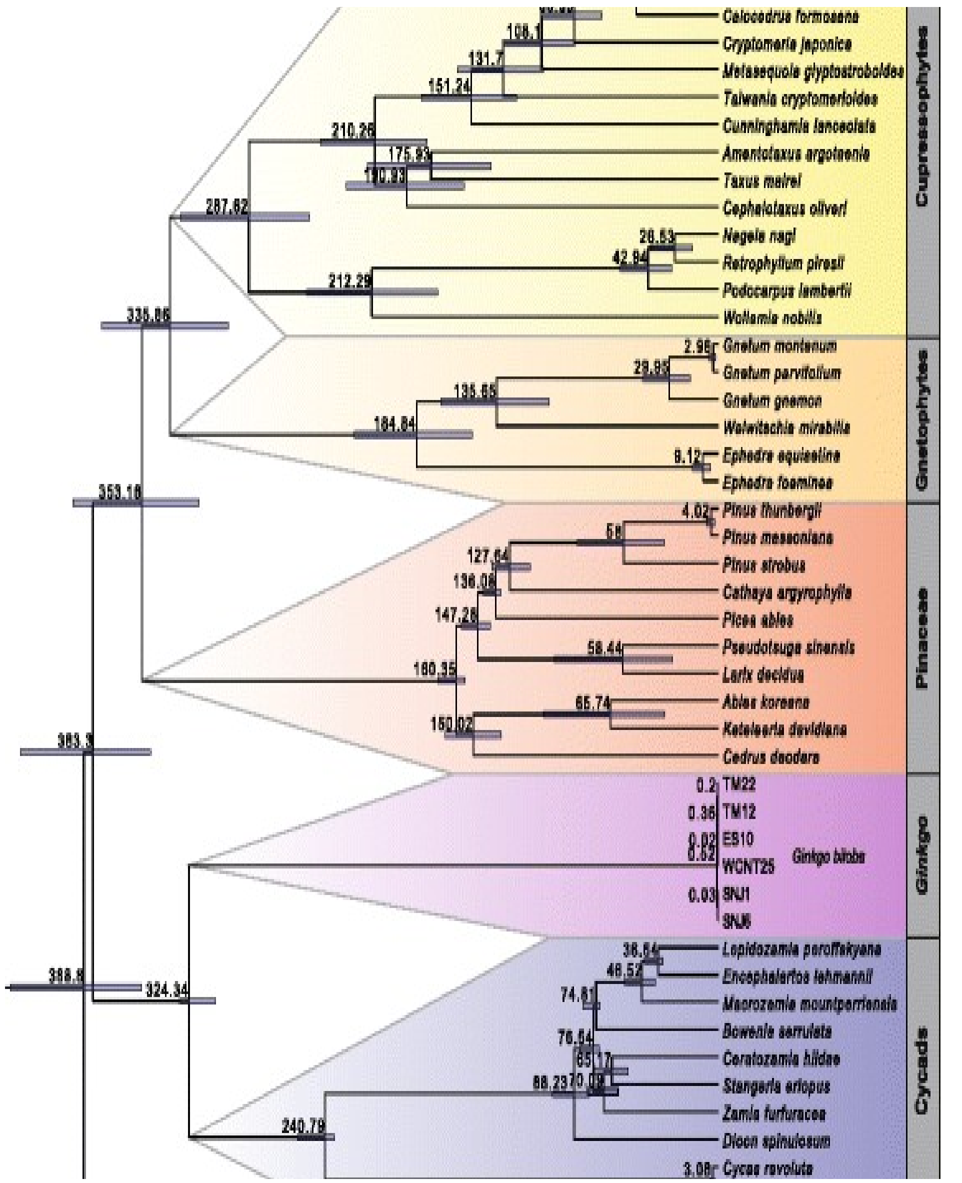
- Entire plastid genome sequencing using a genome skimming approach : to recover plastid genomes for all 71 samples
- Complete plastome alignment of 71 Ginkgo accessions
- Phylogenetic reconstruction and divergence time estimation

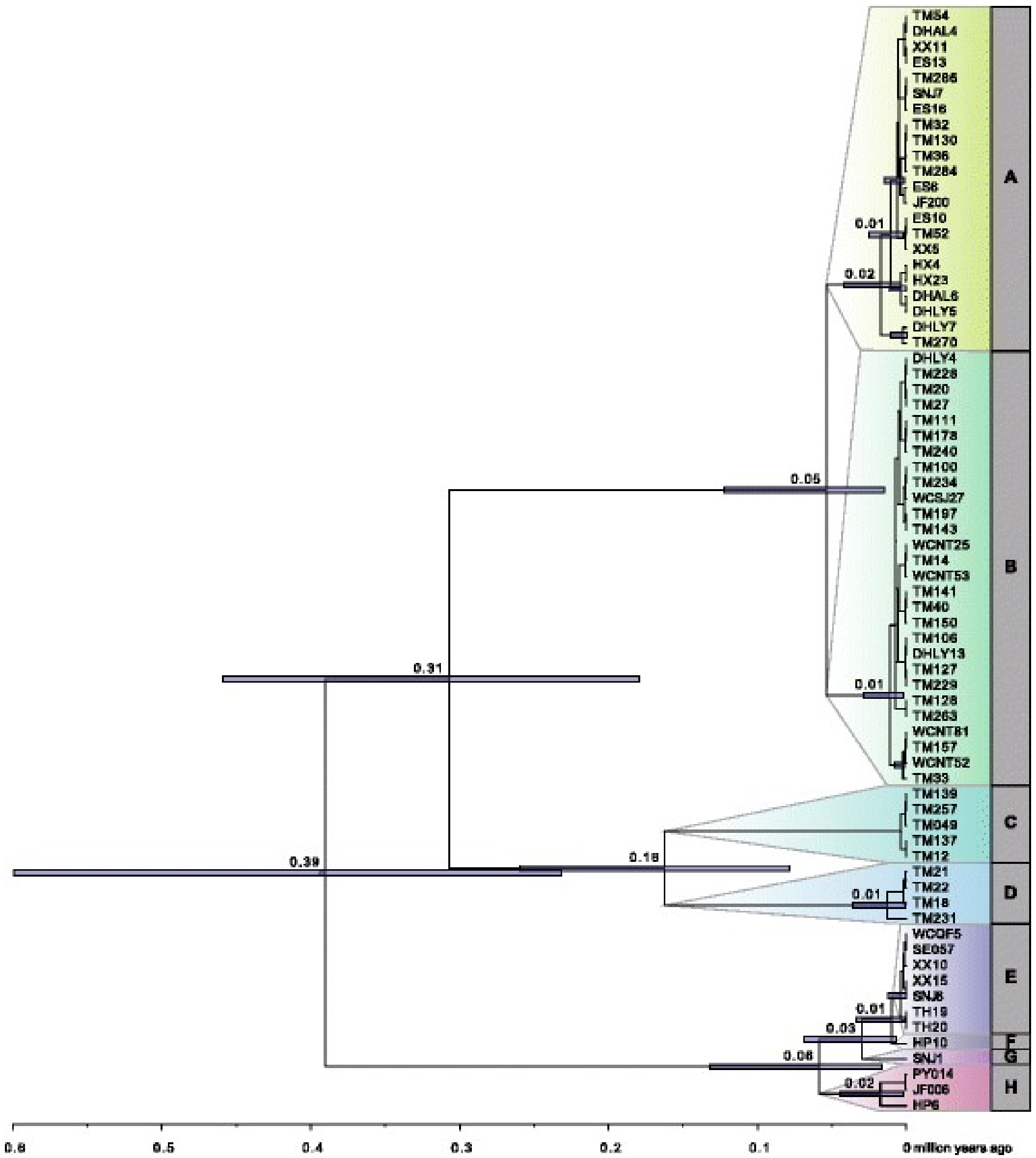


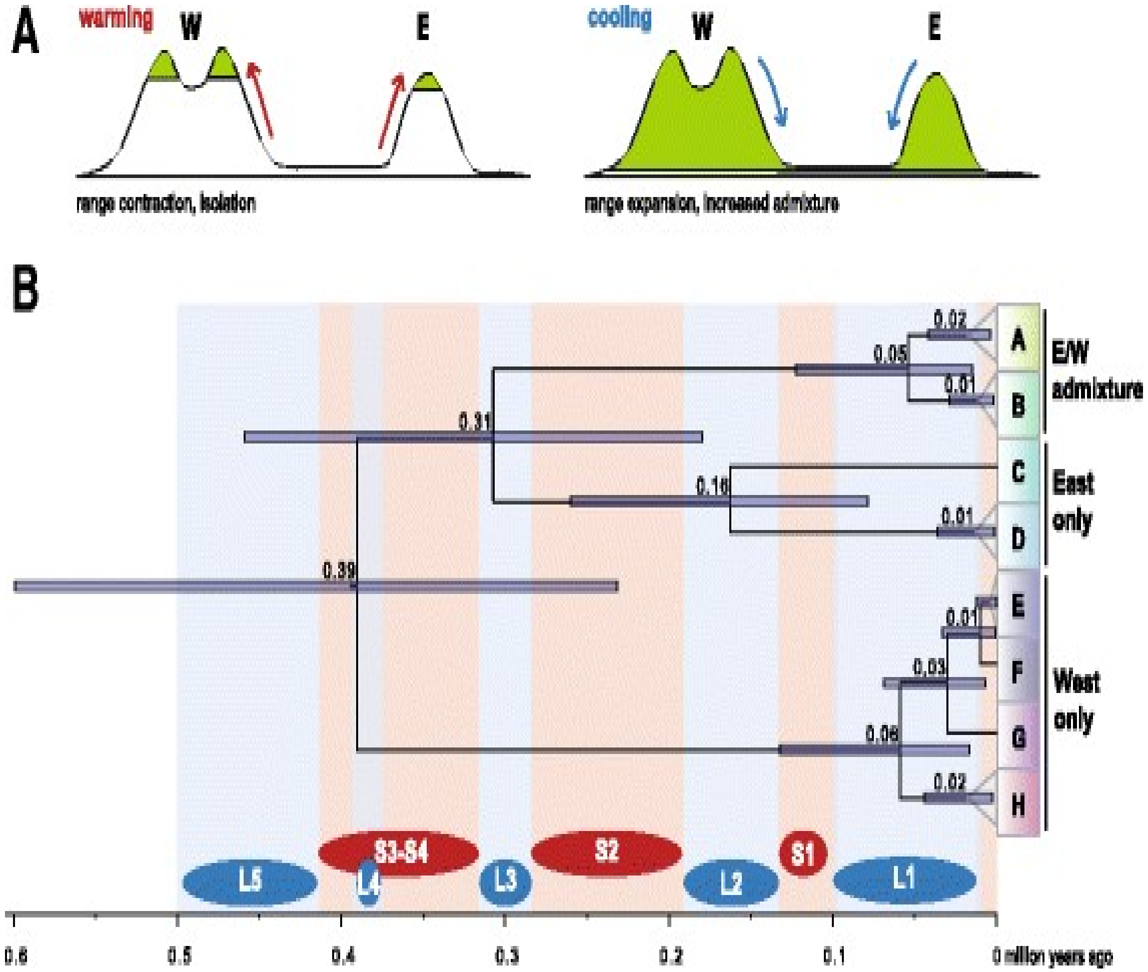


Results

- Network reconstruction reveals eight genetic clusters among extant *Ginkgo*
- Gymnosperm-wide phylogenetic reconstruction and divergence time estimation confirmed the cycad-*Ginkgo* sister relationship and revealed Ginkgoatae stem group age of approximately 325 mya
- Phylogenetic reconstruction and divergence time estimation revealed successive divergence synchronized with Pleistocene cooling phases



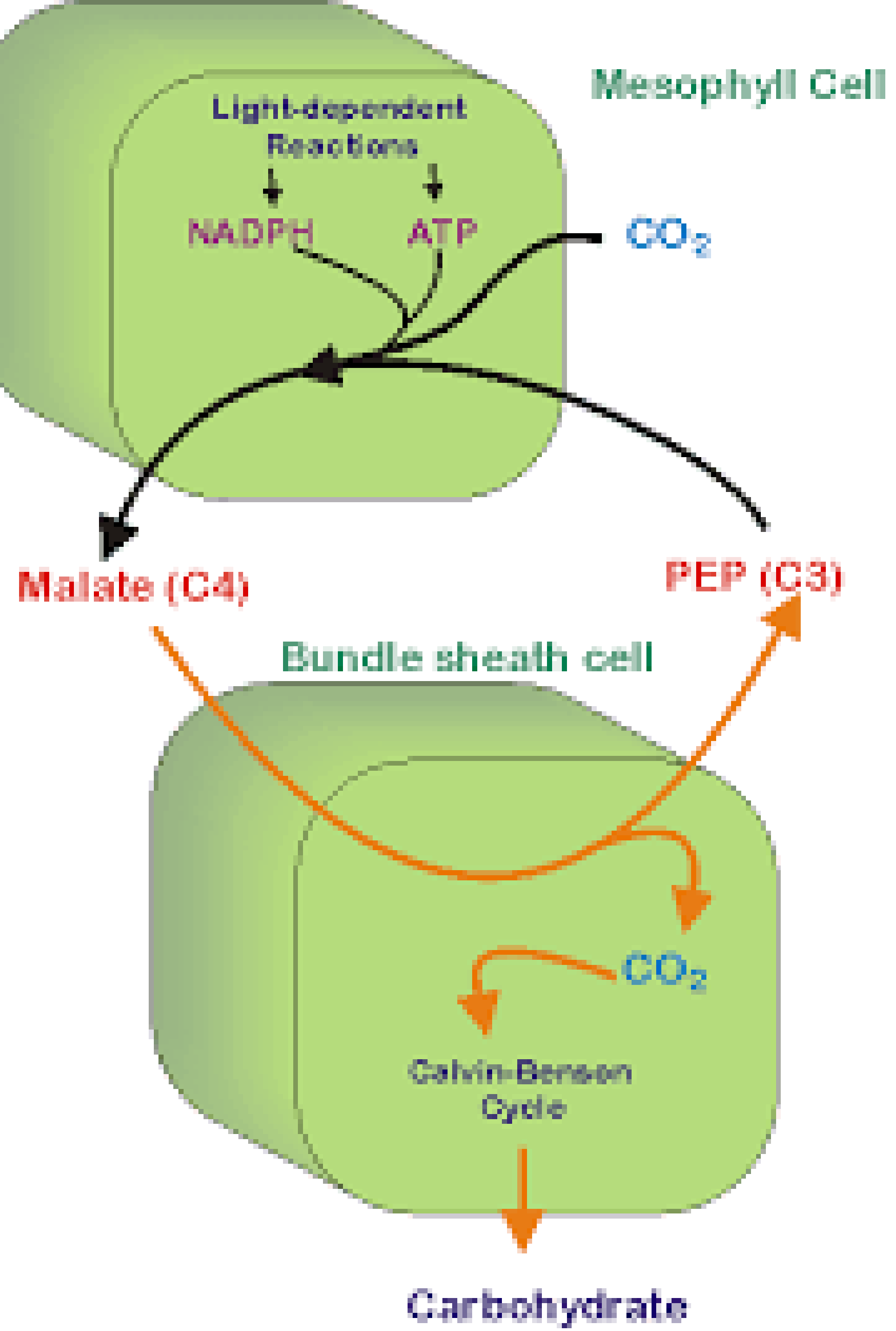

TM54
DHAL4
XX11
ES13
TM286
SNJ7
ES16
TM32
TM130
TM36
TM284
ES6
JF200
ES10
TM52
XX5
HX4
HX23
DHAL6
DHLY5
DHLY7
TM270
DHLY4
TM228
TM20
TM27
TM111
TM178
TM240
TM100
TM234
WCSJ27
TM197
TM143
WCNT25
TM14
WCNT53
TM141
TM40
TM150
TM106
DHLY13
TM127
TM229
TM128
TM263
WCNT81
TM157
WCNT52
TM33
TM139
TM257
TM049
TM137
TM12
TM21
TM22
TM18
TM231
WCQF5
SE057
XX10
XX15
SNJ6
TH19
TH20
HP10
SNJ1
PY014
JF006
HP6
A
B
C
D
E
F
G
H
0.01
0.02
0.05
0.01
0.31
0.39
0.16
0.01
0.01
0.03
0.06
0.02
0.6
0.5
0.4
0.3
0.2
0.1
0 million years ago


A
warming
W
E
cooling
W
E
range contraction, isolation
range expansion, increased admixture
B
0.02
0.05
0.01
0.31
0.16
0.01
0.39
0.01
0.03
0.06
0.02
A
B
C
D
E
F
G
H
E/W admixture
East only
West only
S3-S4
S2
S1
L5
L4
L3
L2
L1
0.6
0.5
0.4
0.3
0.2
0.1
0 million years ago

Conclusions

The deepest footprint of *G. biloba's* living population dates back to approximately 390,00 years ago

The cooling effect during the last glaciation (100 to 200 kya) is largely responsible for the genetic structure among G. biloba's in past refuge areas and present-day directional West-East admixtures.



C4 photosynthesis evolved in warm climates but promoted migration to cooler ones

Introduction

- Some plants evolved ways to concentrate CO2 (like the C4 pathway) in a bid to minimize photorespiration as net photosynthetic gains are reduced at higher temperatures (CO2 fixation by RuBisCo is offset by competition with O2 fixation)
- C3 photosynthesis is the ancestral photosynthetic method and 95% of the earth's plant biomass are C3 plants.
- There is an energy cost associated with C4 photosynthesis, and so it is presumed to become advantageous over C3 photosynthesis only when levels of photorespiration is high e.g. in dry/hot environments

- Grasses (Poaceae) and Sedges (Cyperaceae) account for 80% of C4 species.
- Examples of common C4 plants include

    1) Maize (*Zea mays*)

    2) Sugarcane (*Saccharum officinarum*)

    3) Sorghum (*Sorghum bicolor*)

    4) Switchgrass (*Panicum virganum*)

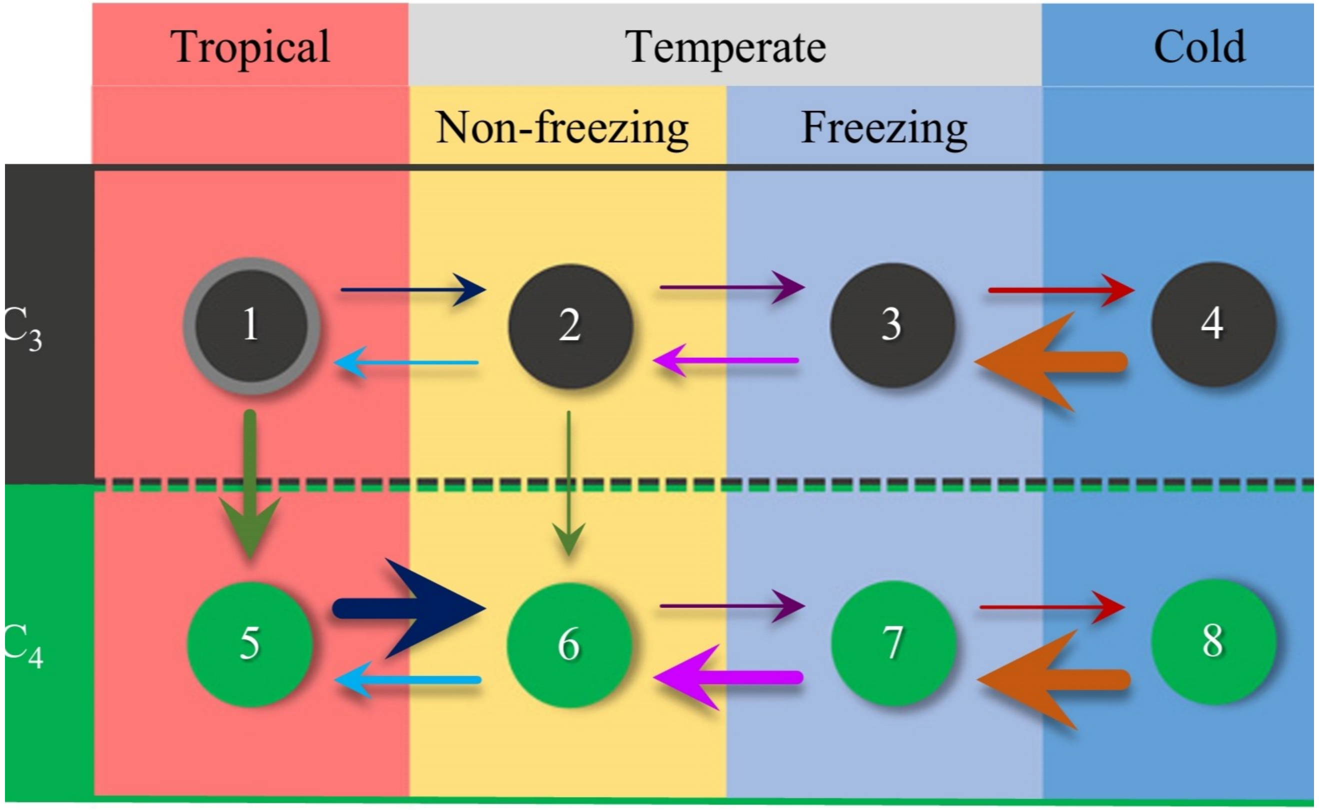
Goal of paper

- To test whether
  1) Temperature influences the rate of C4 origins
  2) Photosynthetic types affect the rate of migration among climatic zones
  3) C4 evolution changes the breadth of the temperature niche

Methods

- Phylogenetic and geographical distribution data for 2133 grass species (a fifth of all C4 grass species) to assess the relationship between photosynthetic types and temperature niches
- Modelled transition rates between photosynthetic and climate types
- Phylogenetic generalized least squares (PGLS) to confirm that photosynthetic type influences thermal maxima and minima as well as the breadth of the temperature niche.

Model of coevolution of photosynthetic types and temperature niches.
Size of arrow indicate transition rates among climates and photosynthetic types



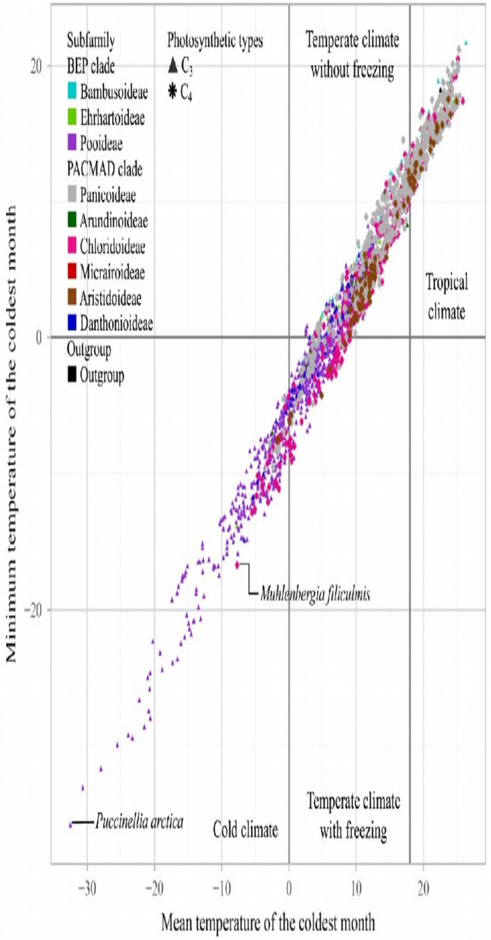
Results

- The percentage of C4 species decreased from tropical to cold climates
- Models supported the hypothesis that C4 origins are more frequent in tropical than temperate climates
- The PGLS analyses show that C4 evolution led to an expansion of the species-level temperate niche

Table 1 Rates of transitions determined from point estimates of models

State	Rate	Estimated rates
Tropical vs. Temperate climates and C_3 vs. C_4 photosynthesis		
Transition from tropical to temperate climate		
C_3	$Rate_{1\to2}$	0.02200
C_4	$Rate_{5\to6}$	0.11663
C_4–C_3	$Rate_{5\to6}$–$Rate_{1\to2}$	0.09464***
Transition from temperate to tropical climate		
C_3	$Rate_{2\to1}$	0.00004
C_4	$Rate_{6\to5}$	0.04316
C_4–C_3	$Rate_{6\to5}$–$Rate_{2\to1}$	0.04313***
Transition from C_3 to C_4 photosynthesis		
Tropical	$Rate_{1\to5}$	0.00749
Temperate	$Rate_{2\to6}$	0.00016
Tropical – Temperate	$Rate_{1\to5}$–$Rate_{2\to6}$	0.00734***
Temperate = 0	$Rate_{2\to6}$–0	0.00016*
Transition from C_4 to C_3 photosynthesis		
Tropical	$Rate_{5\to1}$	0
Temperate	$Rate_{6\to2}$	0
Tropical = Temperate = 0	$Rate_{5\to1}$ + $Rate_{6\to2}$–0	0^{ns}
Temperate climates without freezing vs. with freezing and C_3 vs. C_4 photosynthesis		
Transition from temperate climate without freezing to with freezing		
C_3	$Rate_{2\to3}$	0.01095
C_4	$Rate_{6\to7}$	0.01356
C_4–C_3	$Rate_{6\to7}$–$Rate_{2\to3}$	0.00262^{ns}
Transition from temperate climates with freezing to without freezing		
C_3	$Rate_{3\to2}$	0.03054
C_4	$Rate_{7\to6}$	0.07954
C_4–C_3	$Rate_{7\to6}$–$Rate_{3\to2}$	0.04900***
Transition from C_3 to C_4 photosynthesis		
Non-freezing	$Rate_{2\to6}$	0.00355
Freezing	$Rate_{3\to7}$	0.00000
Non-freezing – Freezing	$Rate_{2\to6}$–$Rate_{3\to7}$	0.00355***
Freezing = 0	$Rate_{3\to7}$–0	0^{ns}
Transition from C_4 to C_3 photosynthesis		
Non-freezing	$Rate_{6\to2}$	0
Freezing	$Rate_{7\to3}$	0
Non-freezing = Freezing = 0	$Rate_{6\to2}$ + $Rate_{7\to3}$–0	0^{ns}
Temperate vs. Cold climates and C_3 vs. C_4 photosynthesis		
Transition from temperate to cold climates		
C_3	$Rate_{3\to4}$	0.03118
C_4	$Rate_{7\to8}$	0.00421
C_4–C_3	$Rate_{7\to8}$–$Rate_{3\to4}$	−0.02697***
Transition from cold to temperate climates		
C_3	$Rate_{4\to3}$	0.13183
C_4	$Rate_{8\to7}$	0.13628
C_4–C_3	$Rate_{8\to7}$ – $Rate_{4\to3}$	0.00445^{ns}
Transition from C_3 to C_4 photosynthesis		
Temperate	$Rate_{3\to7}$	0.00233
Cold	$Rate_{4\to8}$	0.00000
Temperate – Cold	$Rate_{3\to7}$–$Rate_{4\to8}$	0.00233*
Cold = 0	$Rate_{4\to8}$–0	0^{ns}
Transition from C_4 to C_3 photosynthesis		
Temperate	$Rate_{7\to3}$	0
Cold	$Rate_{8\to4}$	0
Temperate = Cold = 0	$Rate_{7\to3}$ + $Rate_{8\to4}$–0	0^{ns}

Asterisk indicates the differences between rates of transitions, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, ns indicates no differences between rates of transitions.



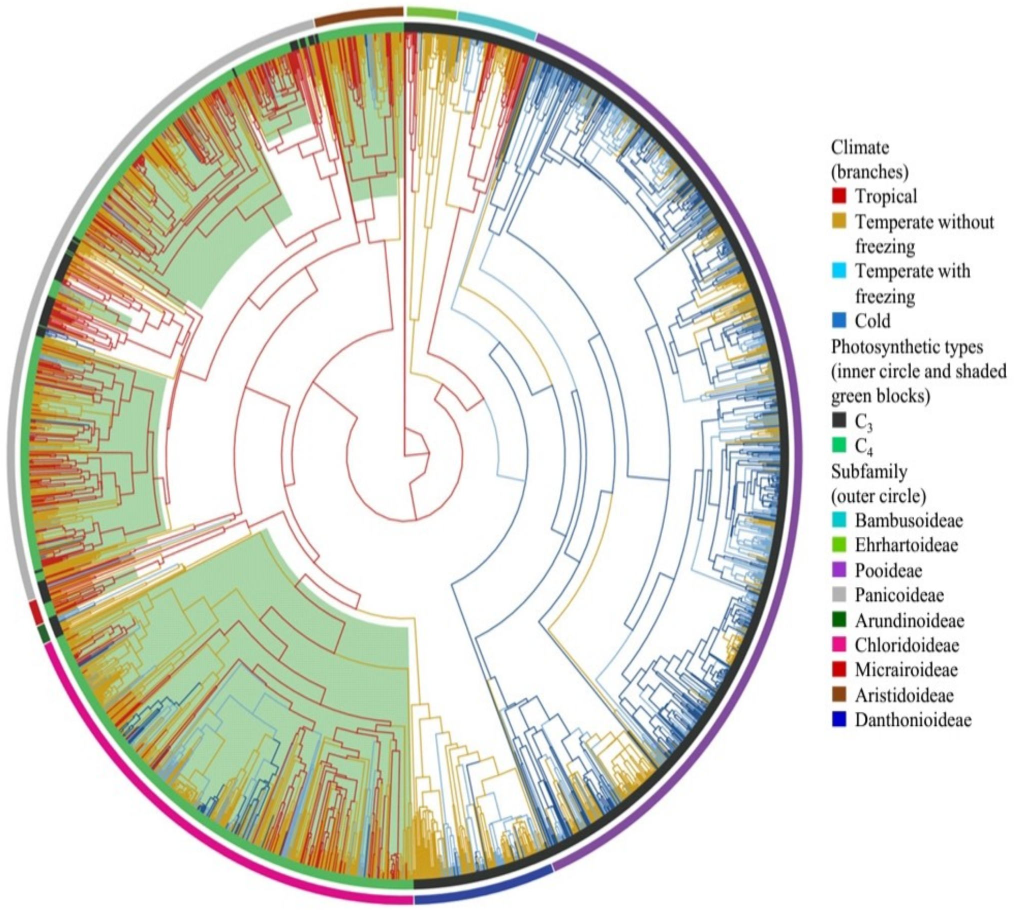


Figure 3 Maximum likelihood reconstruction of the transitions between climatic regions: tropical, temperate without freezing, temperate with freezing a cold climates. Photosynthetic types and subfamilies are indicated.

Conclusion

- C4 plants evolved in tropical climates, expanded to warmer and shifted to cooler environments
- C4 plants are more likely to transition from tropical to temperate climates than C3 species, thus, C4 plants can compete in temperate environments.
- It is possible that advantages of C4 photosynthesis other than reduced photorespiration may compensate for extra energy demand in temperate conditions