Dating African savannas

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Five things to know about savannas

• C4 GRASSY systems with varying tree cover
• Very extensive in the tropics and sub-tropics
• Occur in climates that also support forests
• Wet/dry growth cycle and grassy fuels produce largest burnt areas in the world
• Support largest remaining remnants of Pleistocene megafauna
The ‘colours’ of the world from space. Vegetation is organised into ‘biomes’ characterised by different major growth forms.
Savannas are the most extensive vegetation in Africa and Madagascar.

What explains the different colours (biomes) of the world?
Africa has the most extensive C4 grasslands in the world

Global distribution of grasslands, including savannas
% legend is of C4 grasses
Woody plants vary from none (grassland biome)
The presence of shade-intolerant grasses defines ‘SAVANNA’. Ecological processes must prevent succession to shade-tolerant forest species.
INDIA: This is a forest
Savannas are defined by the presence of GRASS, not the density of trees. The grasses are typically C4 and very intolerant of shade.
Climate determines world vegetation patterns

Or does it?
Forest/grassland mosaic, Gabon, Africa
Explaining the tropical forest/savanna mosaics

Savannas are anthropogenic, caused by human deforestation
Fires have destroyed forests opening them up to early successional grassy communities.
Savannas burn more frequently than all other biomes
Livestock farming has degraded and destroyed dry forests
Savannas are degraded forests!
Policy implications: The Bonn challenge

- A plan to plant forests (and turn fire off, discourage livestock farming) in the world’s open biomes
- Supported by IUCN, German Government and others
- Science support by World Resources Institute, Washington
- **Goal to ‘reforest’ 1.5 million km$^2$ of ‘degraded’ forests worldwide by 2020**
- **3.5 million km$^2$ by 2030**
- Funding from International donors and Bonn agreement to which countries are signatories
- **COP, Paris. $30 million pledged to 10 African countries for ‘forest restoration’**
The incentive?

- Carbon sequestration to reduce global warming for developed countries
- Funding from rich countries for less developed countries
- Forest restoration of cleared tropical forest areas, especially in South America.
- Plantation forestry and timber products
A map of areas targeted for reforestation
The alternative hypothesis: Savannas are ancient

• Climate misfit is ancient
• Savannas are ‘consumer controlled’
  – Larger vertebrate herbivores are ancient
  – Fires are ancient
Fire and large mammal herbivory maintain African savannas
Testing the antiquity of savannas

• How old are savannas?
  – fossil evidence?
C isotopes of fossil soils and mammals show Mio/Pliocene origin of C4 savannas

The sudden appearance of C4 grassy biomes is unprecedented in earth history

• What drove the grass revolution?

• Are savanna origins driven by
  – Increased fire activity carving into forests?
  – Increased herbivore pressure rolling back forests
How good is the fossil record for fire and herbivore impacts?
Blue dots indicate fossil sites. Most of them are not in modern savanna regions. None in high rainfall savannas of Brazil, Africa, n. Australia.

From Stromberg 2011, AREES, Griffith et al. Science 2017

Africa has the most extensive C4 grasslands in the world.
A clear case for dated molecular phylogenies (from DNA bar-coding sampling)

Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire

Marcelo F. Simon, Rosauro Grathier, Luciano P. de Queiroz, Cynthia Slama, R. Toby Pennington, and Colin E. Hughes

Simon et al. PNAS 2009
How old are fire-dependent savannas in Africa?

• No terrestrial record of charcoal (higher rainfall zones deeply weathered – no fossils)
• Some marine records of charcoal flux
• Phylogenies
  – Estimate dates from phylogenies mapping origins of functional types restricted to frequently burnt savannas
Savanna fire and the origins of the ‘underground forests’ of Africa

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Commentary

The remarkable congruence of New and Old World savanna origins

R. Toby Pennington1* and Colin E. Hughes2

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• ‘Underground trees’ are dwarf trees restricted to frequently burnt savannas and harsh growing conditions
• We used the growth form as an indicator of frequently burnt savannas
• We used a phylogeny to date the divergence of ‘underground trees’ from their taller tree ancestors
Fig. 2 Geoxylic suffrutesces and their tree relatives:
a. *Gardenia subacaulis* (Rubiaceae);
b. *Gardenia ternifolia*;
c. *Protea paludosa* sp. *Secundifolia*;
d. *Protea roupelliae* subsp. *roupelliae*;
e. *Cussonia corbisieri* (Araliaceae);
f. *Cussonia arborea*
An underground tree in the cerrado. One example has been dated to 3800 years old Alves et al. 2013. Anais da Academia Brasileira de Ciências

Geoxyles can be very large and very old – e.g. a Jacaranda species of 50m radius in Brazil has been aged as ~3800 years old!
They ONLY grow in grasslands, not forests.
So grasslands with geoxyles are at least a few 1000 years old!?
Fig. 3 Three habitats rich in geoxylic suffrutices
a. Open woodland in North West Zambia;
b. Seasonally waterlogged grassland in North West Zambia;
c. Highveld habitat, Lydenburg, South Africa
Phylogenetic tests of the age of fire-dependent grasslands are derived from a dated woody plant phylogeny for southern Africa, from DNA bar-coding by Michelle van der Bank et al., UJ.

Africa
Dating the origin of fire-dependent savannas

Maurin et al. 2014, New Phytol
Ages of origin of ‘underground tree’ species

Frequency

Age Ma

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15

0 1 2 3 4 5 6 7 8
Testing phylogenetic estimates of origins of flammable savannas with fossil charcoal
CHARCOAL FROM MARINE CORES IN NORTH PACIFIC INCREASES FROM LATE MIOCENE (Herring, 1986)
Ages of origin of ‘underground tree’ species

Frequency

Age Ma

[Bar chart showing the frequency of ages of origin of 'underground tree' species, with ages ranging from 1 to 15 Ma.]
Increased fire activity was general from Late Miocene
What about mammals as creators of savannas?

MAMMALS and CONSUMER-CONTROLLED SAVANNAS. heavily grazed, heavily browsed savannas with grazing-tolerant grasses, browse tolerant trees,

Not enough grass fuel to burn
How old are mammal-dependent savannas in Africa?

- Good fossil record of mammals in rare, dry localities
- Diet inferred from carbon isotopes, scratch marks on teeth
- But would browsing drive back forest?
Spiny plants are a common defence in African savannas.
Spiny plants are usually absent or very rare in forests.
Spiny plants –
A defence against mammalian herbivores

By tracing the evolution of spines we can track changing mammal browse pressure on plants

From: Charles-Dominique et al. 2016. PNAS
B Factors related to spinescence

- Low
- Spinescence
- High

Herbivores

Abiotic environment

Vegetation type

- Rainfall
- Temperature
- Fire
- Nutrient

- Evergreen forest
- Forest-grassland
- Mangrove
- Coastal mosaic
- Succulent karoo
- Halophytic
- Desert
- Grassland shrubland
- Savanna shrubland
- Mixed savanna

- SNSBr
- WDGr
- Total
- LBr
- MSMix
Spiny trees in Africa

• Are most common
  – Where medium-sized grazer/browser antelope, and large antelope browsers are common (*antelope are bovids*)
  – In Savannas and open grassy biomes
  – In drier regions on fertile soils

• So predict evolved in response to
  – New intense browsing pressure from antelope (bovids)?
  – Forest trees unprotected
We could trace appearance of spiny plants from dated phylogeny of 1852 tree species.

We used existing phylogeny of bovids (Bibi, 2015).
AFROTHERIA: HYRACOIDS

Dominant herbivores were Hyracoids and Proboscideans

Extant hyrax (3 genera)
Body mass: 1.3 to 5.5 kg

Extinct *Titanohyrax*
Oligocene (~30 Ma)
Body mass: 500 to 1300 kg
Loxodonta africana an extant Proboscidean, member of Afrotheria
Bovids are the common African herbivores. Antelope Buffalo, wildebeest.
Bovids, the major browsers of spiny plants

- Only arrived in Africa in the mid-Miocene
- Before them, Afrotheria had dominated for tens of millions of years
- Afrotheria browsers were proboscideans and hyracoids
- We suggest bovids, with new style of feeding, exerted heavy browse pressure on juvenile woody plants
- This selected for spines as an effective defence
- But only in sunlit habitats
- So bovids rolled back forests?
From: Charles-Dominique et al. 2016. PNAS
Summary

- Africa’s grasslands and savannas are not at equilibrium with climate
- Savannas are adapted to heavy consumption by fire and/or large herbivores which are ancient
- Removal of these consumers threatens their future
- The C4 grassy biomes pre-date our species, and anthropogenic deforestation, by millions of years
- Forest ‘restoration’ projects are wrongly targeting ancient ecosystems
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Artists impression of an ‘underground tree’ (geoxylic suffrutex)

http://eliap.deviantart.com/art/A-forest-beneath-the-ground-558970642
Herbivore exclusion often leads to striking increases in woody plants.
Tree cover inside and outside an exclosure in semi-arid savannas, KNP. The dominant tree is mopane.

From Asner et al. 2009, PNAS
Bovids are the common African herbivores. Antelope Buffalo, wildebeest.
Mammal herbivory is not evenly distributed across Africa. Both the type of herbivores, and amount consumed vary greatly.
Herbivores in drier savannas frequently consume enough grass to stop fires
Heavily grazed sparse C4 grass in acacia savanna.
Semi-arid 600 mm
Figure 2. Mean annual area burned, expressed as the fraction of each grid cell that burns each year, derived from the July 1996 to August 2012 monthly GFED4 burned area time series.

Fire a ‘necessary evil’ or essential to ‘clean country’?

Where you live influences cultural norms of what is ‘natural’
Among the hotspots of the world, FIRE is a key process in at least SIX
Robinia pseudoacacia  

Robinia hispida  

Geoxyles may also occur in the south-eastern USA  
The ‘ancient’ grasslands of North America
South African montane grasslands are rich in forb species
4000 plant species in South Africa’s grassland biome, with high levels of endemism. Area ~ 350 000 km$^2$
Nick Zaloumis with sod from 10° grassland
Gnidia kraussiana

Raphionacme lucens