Life history strategy schemes in consumer-controlled grassy ecosystems

Sally Archibald
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Oxford, June 2018

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ELSEVIER
Review
TRENDS in Ecology and Evolution Vol.20 No.7 July 2005
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Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems

William J. Bond[1] and Jon E. Keeley[2,3]

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[2]U.S. Geological Survey, Western Ecological Research Center, Sequoia-Kings Canyon National Parks, Three Rivers, CA 93271-9651, USA
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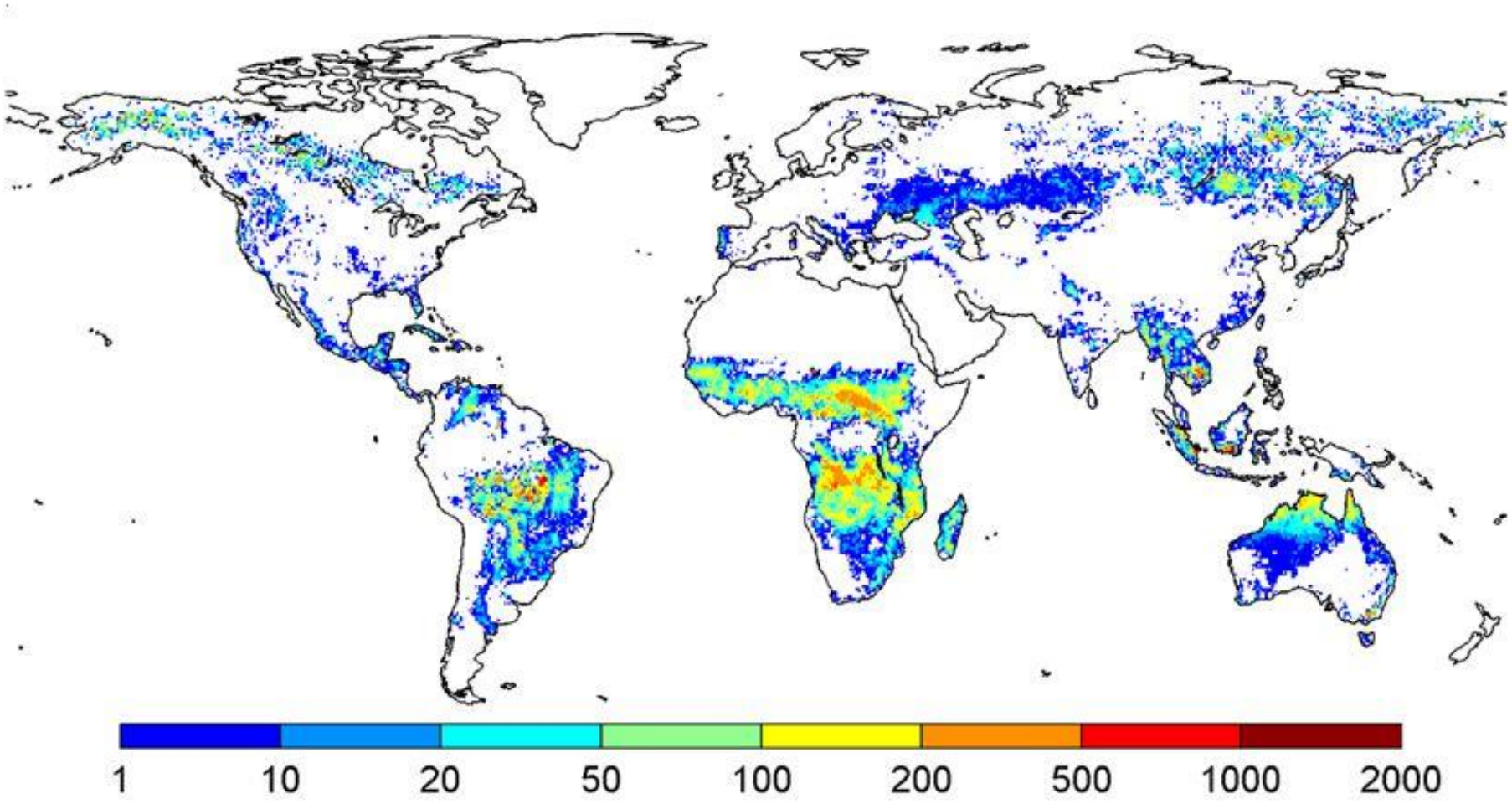
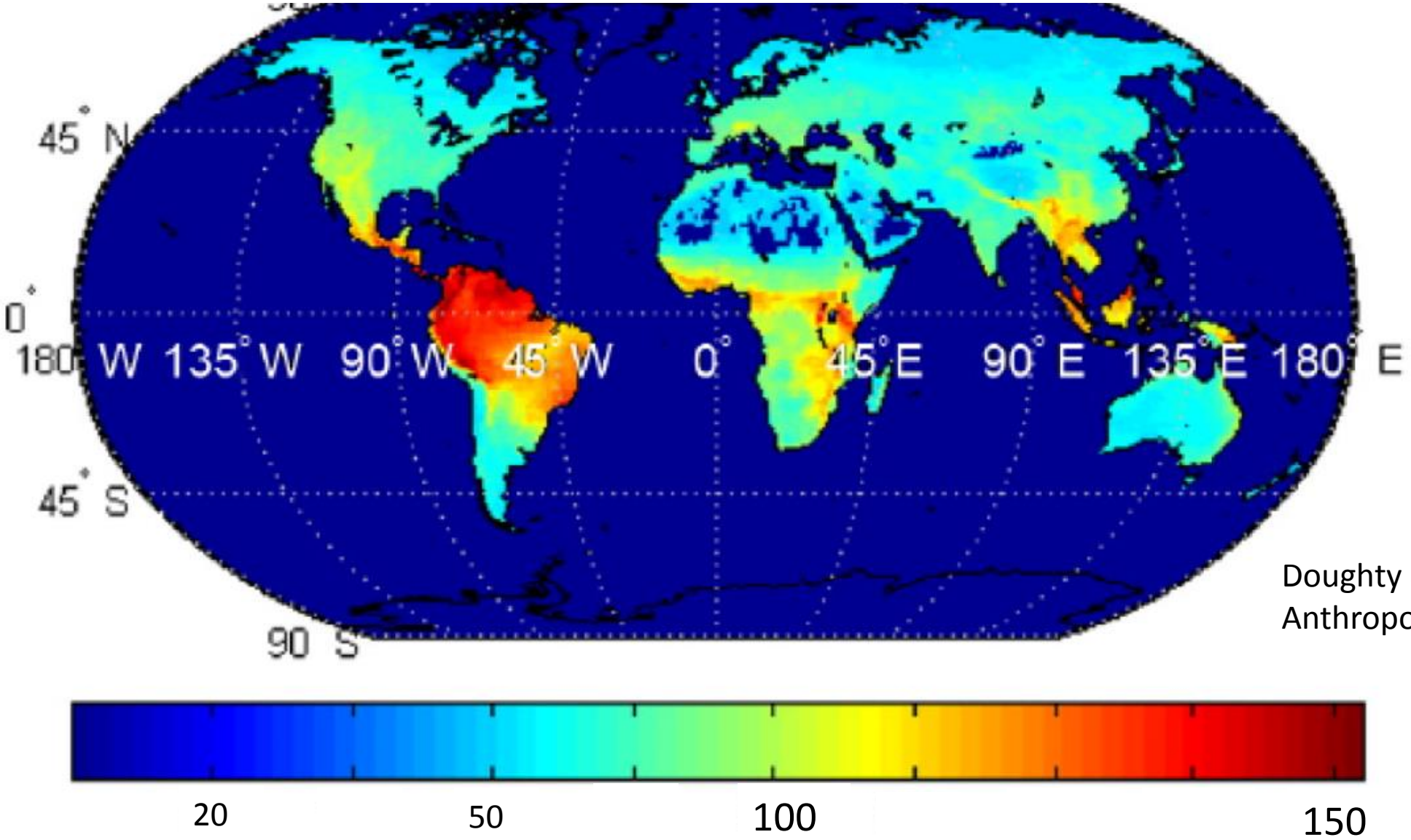
More than 10 years ago Bond and Keeley drew parallels between fire and herbivores as alternative consumers of vegetation. "fire is a globally significant consumer that is analogous to herbivory"

Average carbon losses from wildfires, 1997-2008 (Tonnes km^{-2} $year^{-1}$)



Global Fire and Emissions Database V2 (Guido van der Werf
http://www.falw.vu/~gwerf/GFED/index.html)

Estimated dry matter consumed by mammalian herbivores currently (Tonnes km^{-2} $year^{-1}$)



Doughty *et al* 2016 The Anthropocene review

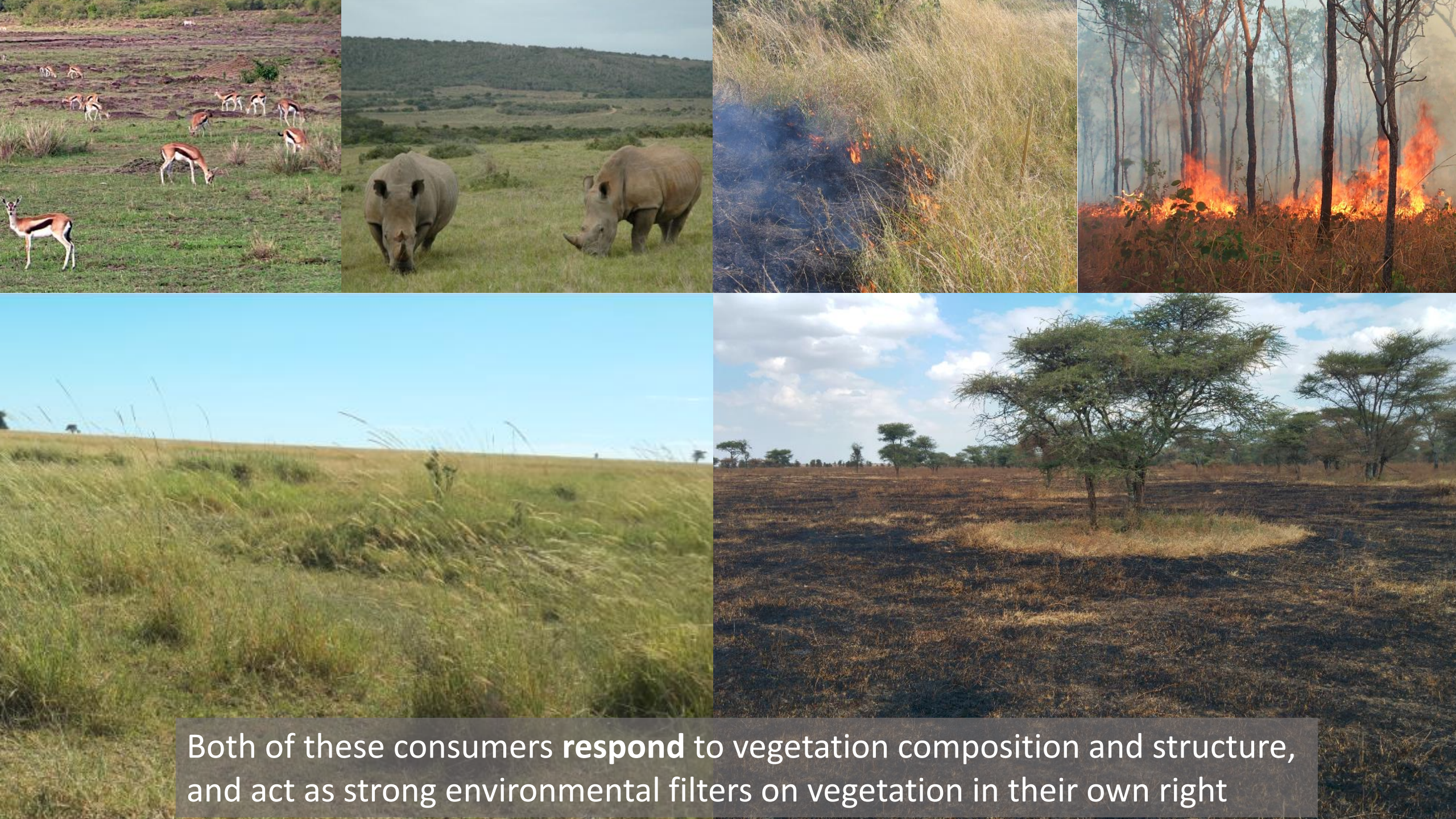
Contrasting fire and herbivory

	Fire	Herbivory
Process	Physical	Biological
Occurrence in time	Stochastic from day to day Strong seasonal dynamics	Persistent from day to day and over the season Annual-decadal dynamics
Occurrence in space	Uniform – removing heterogeneity at landscape scales (depending on the size and intensity of the fire)	Patchy – creating heterogeneity at landscape scales (depending on the size and selectivity of the herbivore)
Selectivity	Selects for dry fuel with a high C:N ratio and a low bulk density	Selects for moist forage with a low C:N ratio and a high bulk density
Key requirements	Continuity in space – without this fires will go out	Continuity in time – without this herbivores will die
Other requirements	An ignition source	A source of drinking water

Archibald and Hempson 2016 Phil Trans

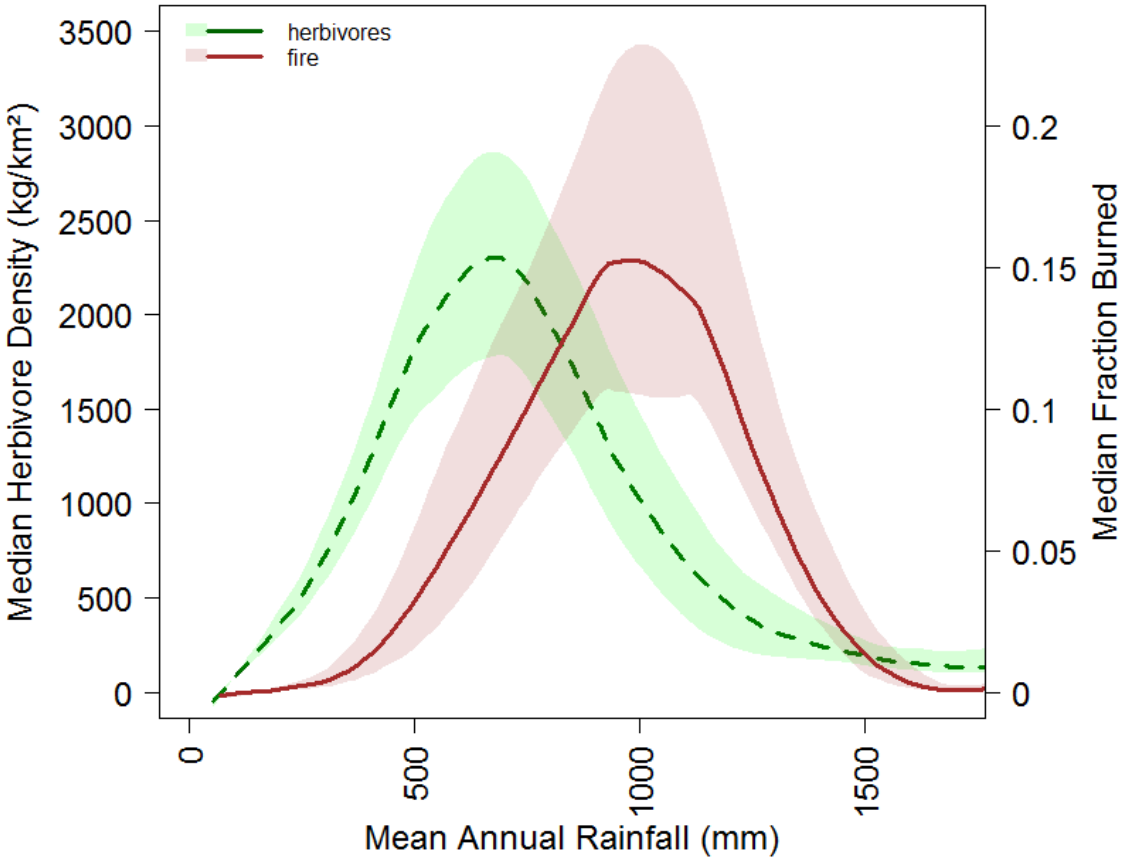




Both of these consumers **respond** to vegetation composition and structure, and act as strong environmental filters on vegetation in their own right

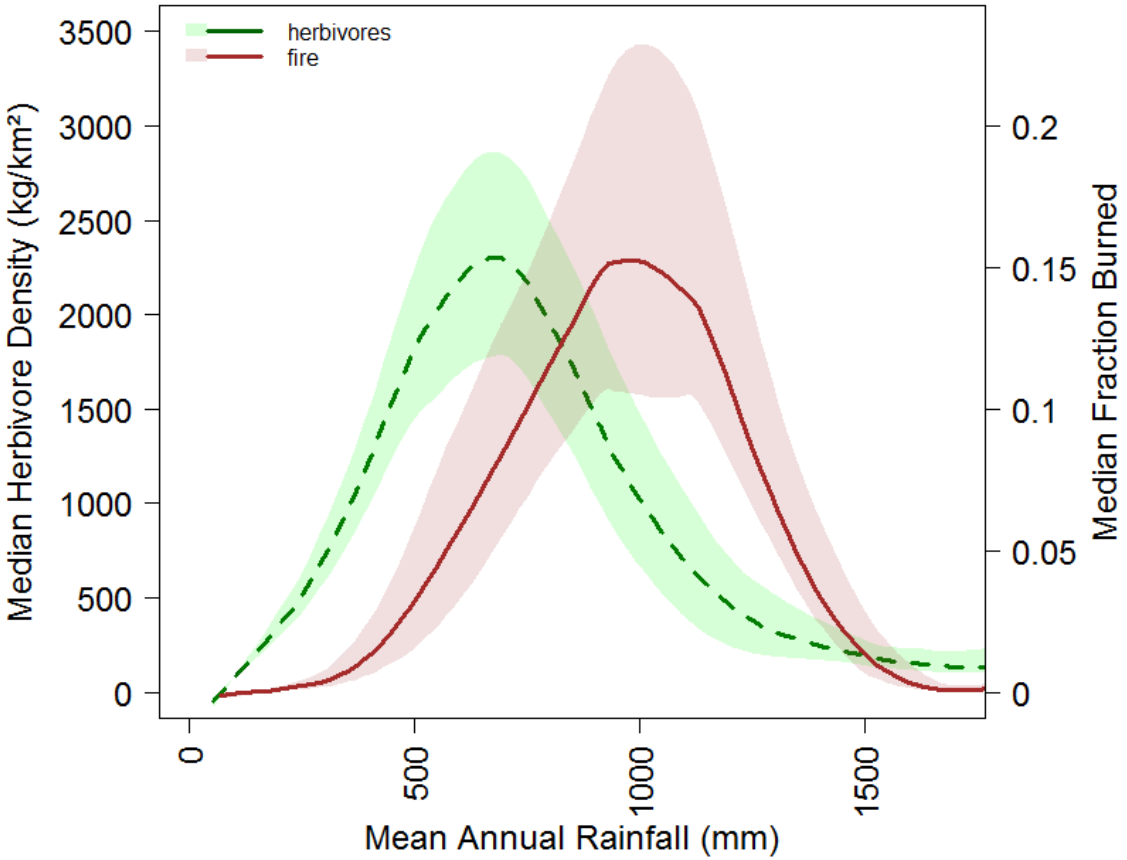
Environmental limits in Africa

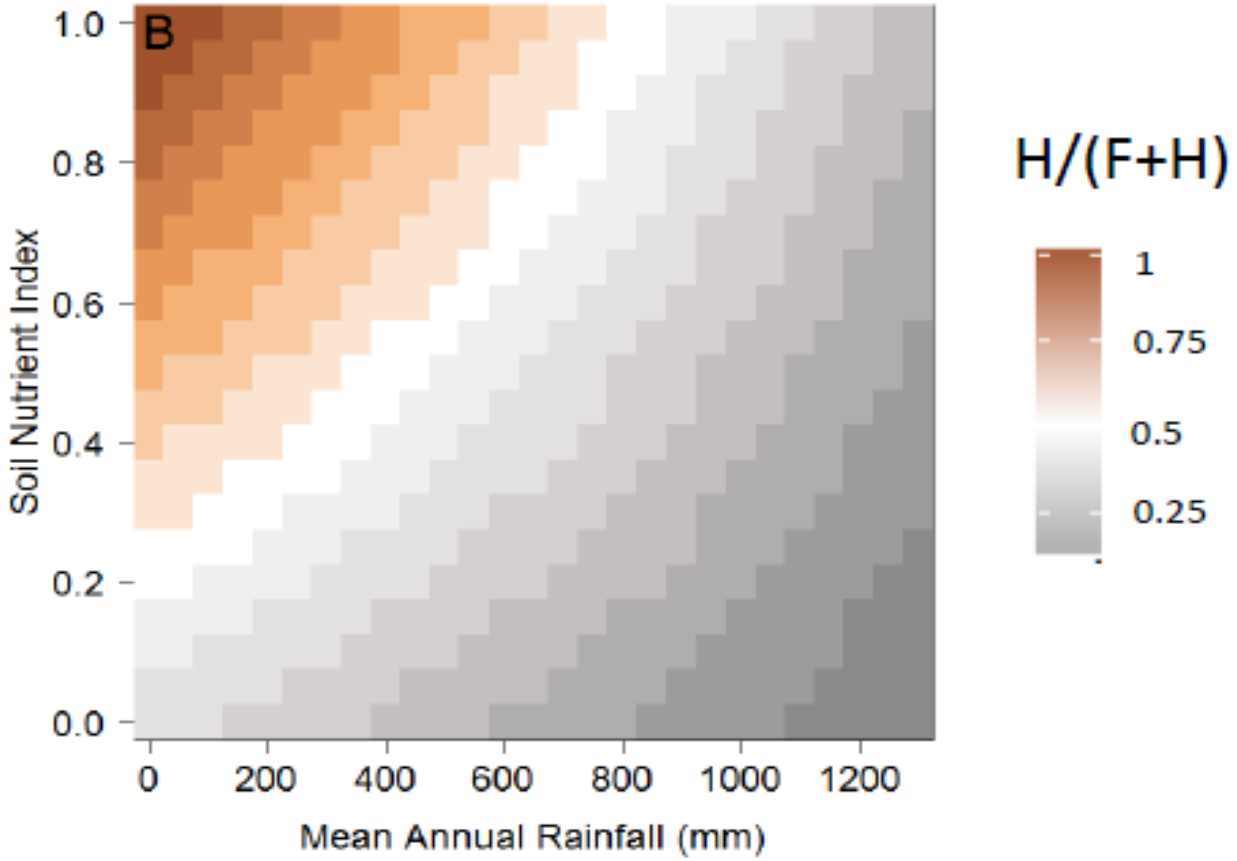


Herbivores dominate as consumers at low rainfalls (forage relatively more palatable, less flammable)

Archibald and Hempson Phil Trans 2016

Environmental limits in Africa

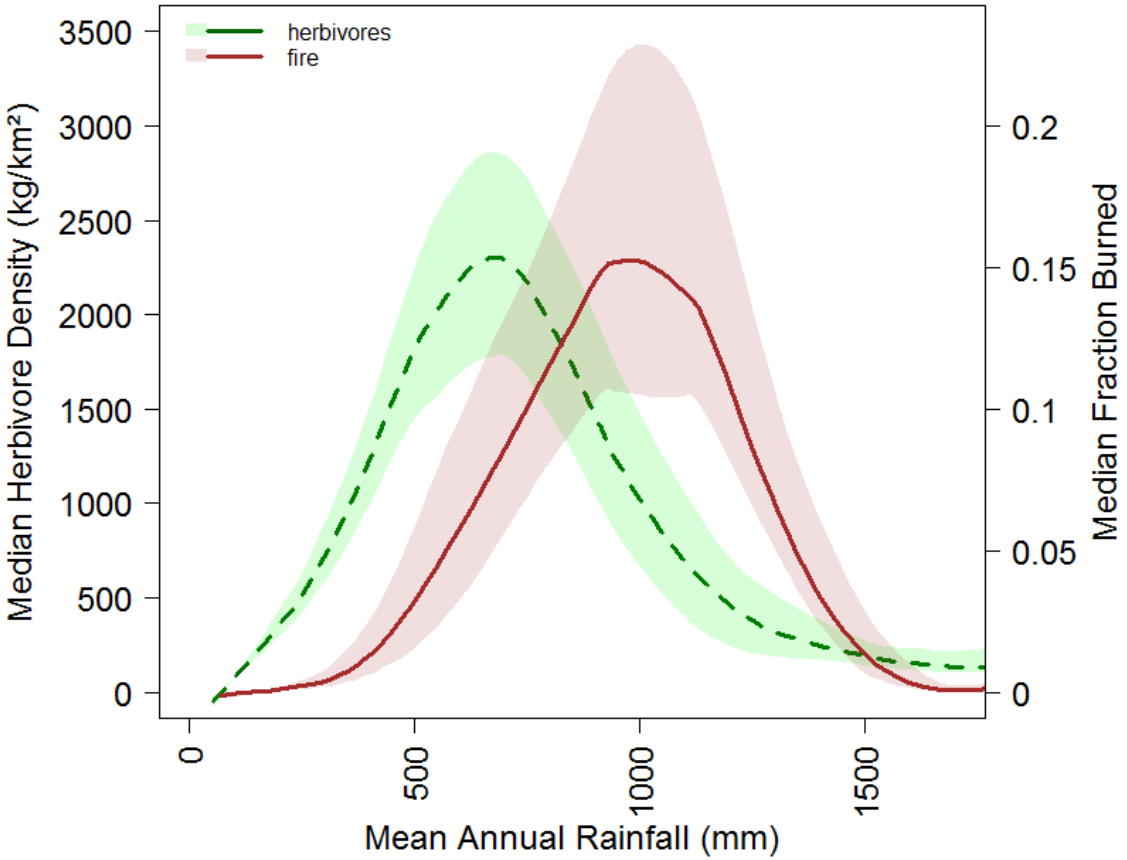


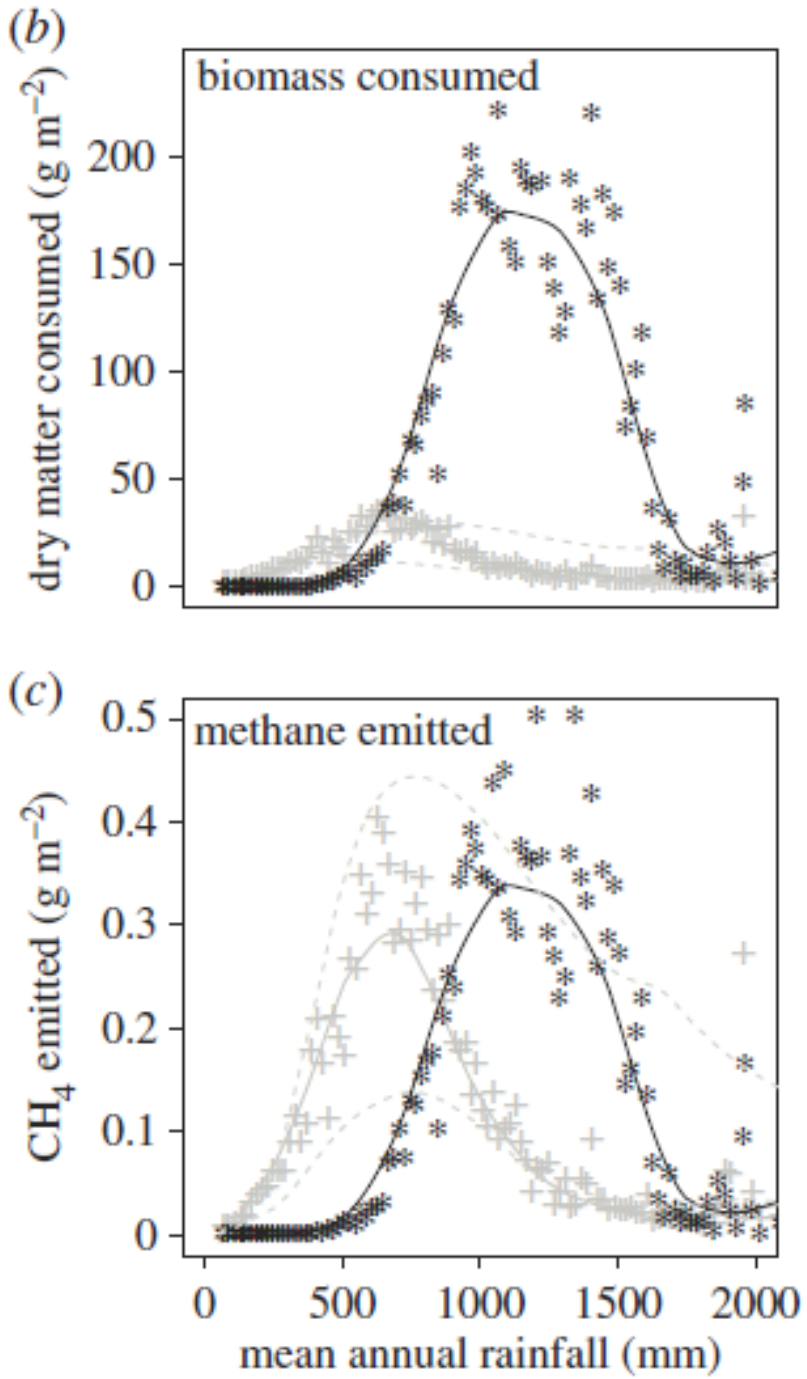


Herbivores dominate as consumers at low rainfalls (forage relatively more palatable, less flammable)

Modified by soil nutrients: more herbivory on higher nutrient soils

Consumption and emission patterns





Archibald and Hempson Phil Trans 2016

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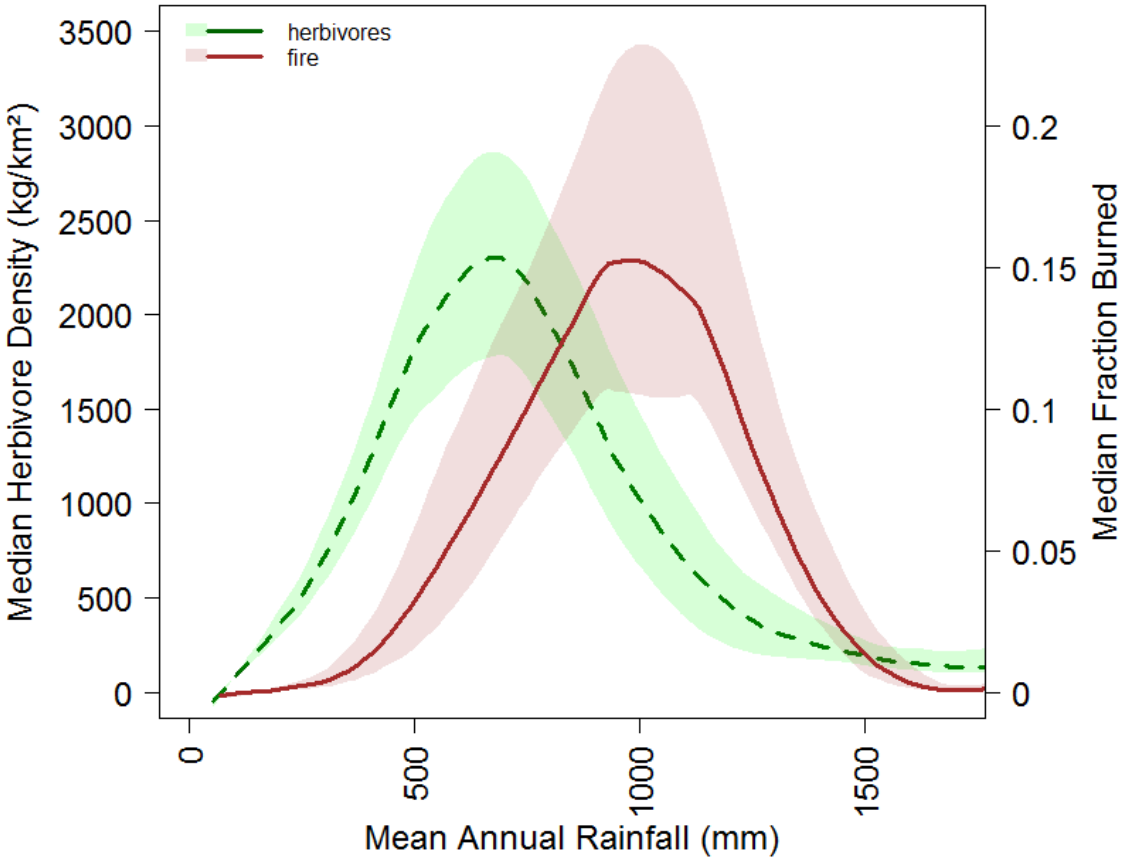
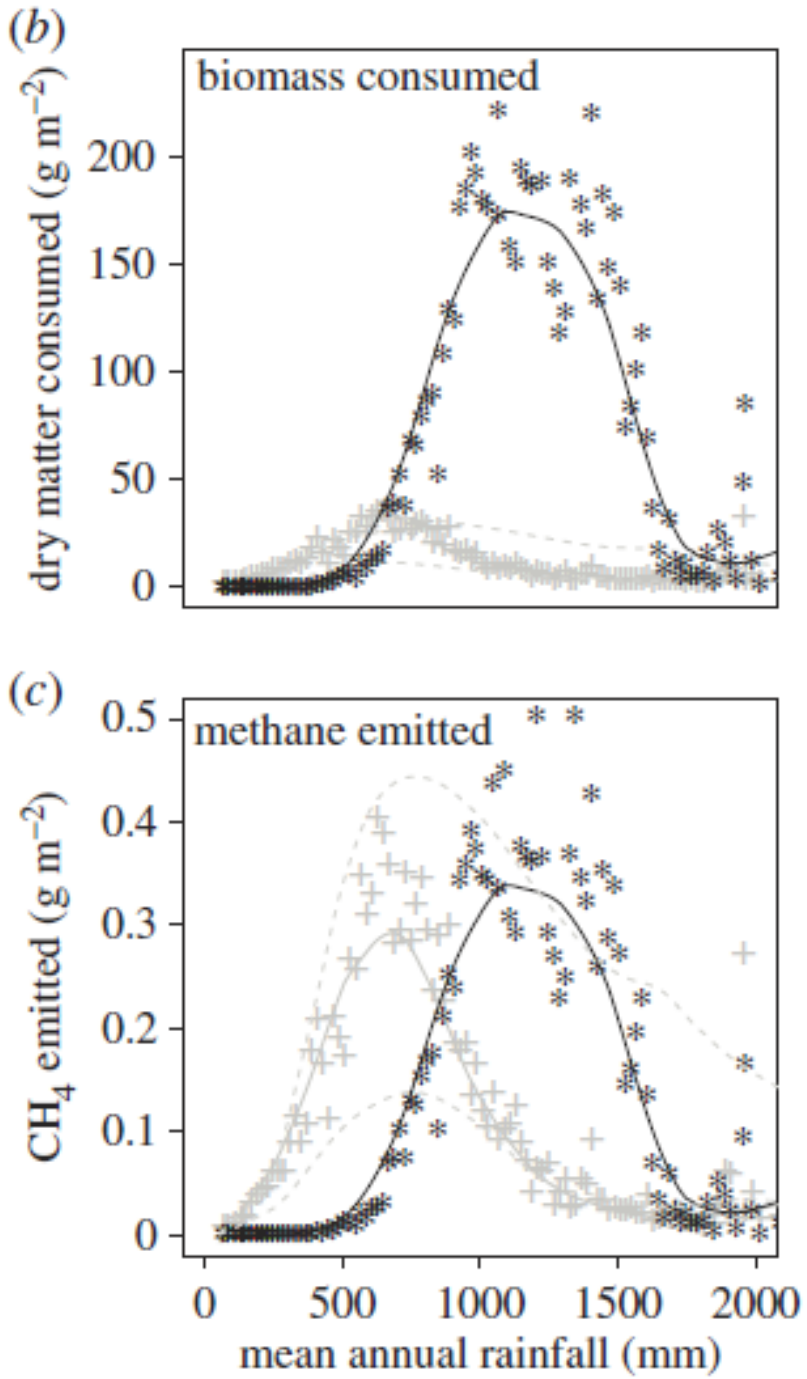




Currently herbivores emit ~4.1 Tg Methane/yr.
In the past, herbivores probably emitted more methane than fire (~5.9 Tg/yr compared with ~5.1Tg/yr)

Archibald and Hempson Phil Trans 2016

FIRE

HERBIVORES

INTERACT

Fire affects the type and degree of herbivory, and herbivory affects the type and degree of fire: it is impossible to understand these consumers in isolation.

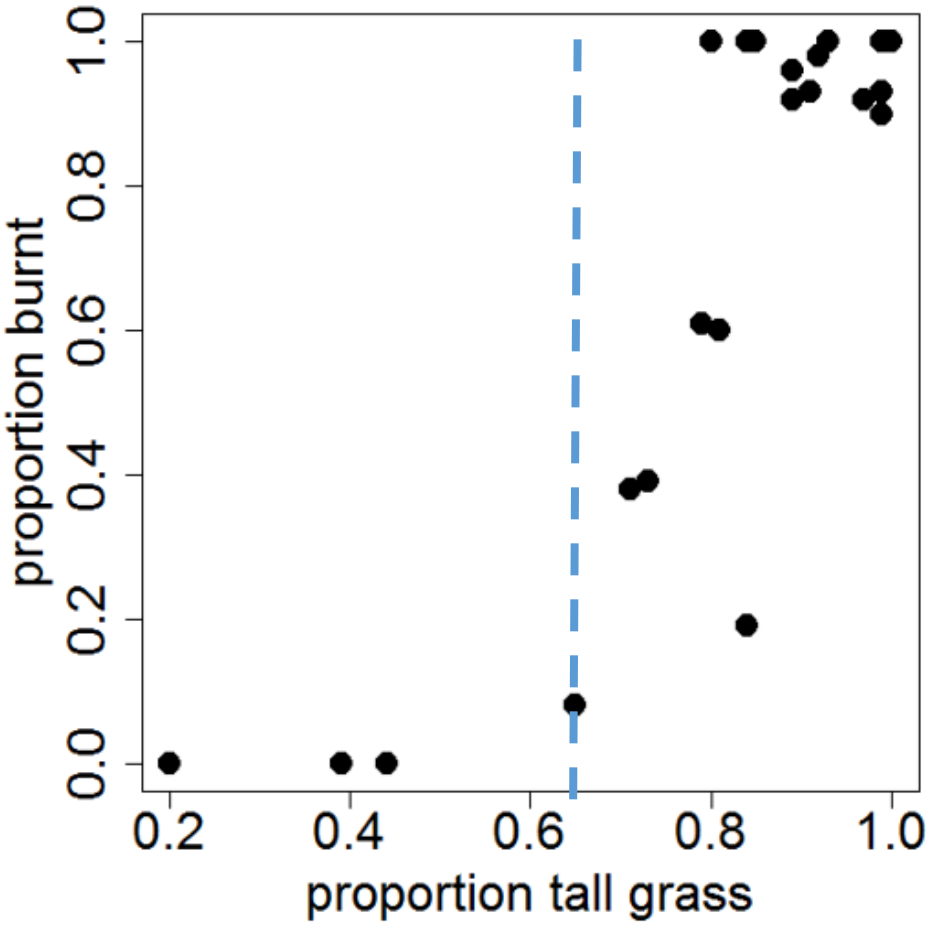
Interactions between fire and herbivory: enabling or antagonistic?

1. Browsers enable fire by keeping systems open
   - Elephants can open closed systems to release grass and fire (Beuchner 1961)
   - Meso-browsers prevent canopies from closing (Staver 2011, Trollope 1984)

2. Fire enables browsers by maintaining forage within browse height

3. What about grazers and fire?

Grazing impact on fire

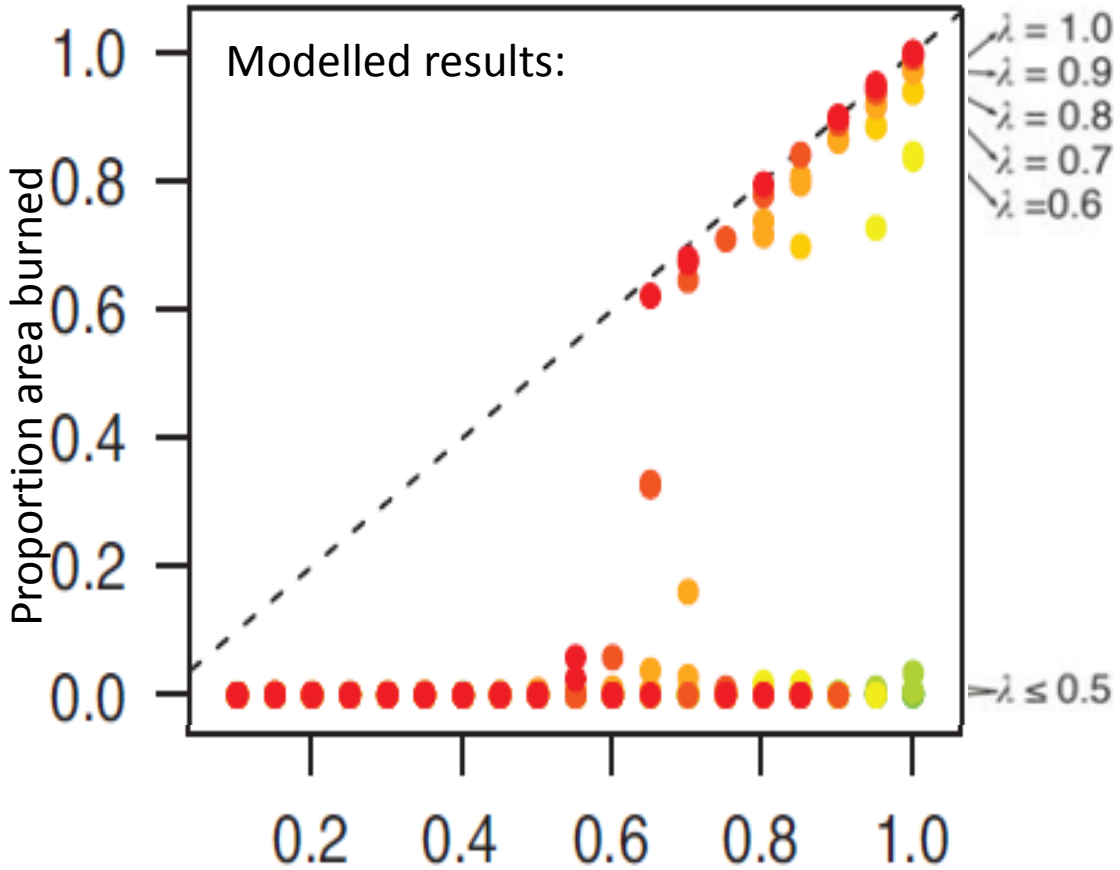


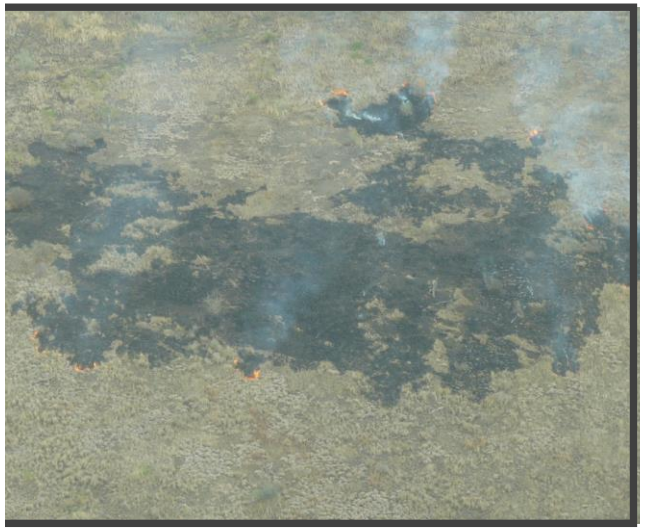
If grazers can keep grass short enough, then fire can not spread

- Threshold dynamics due to percolation

Archibald 2017 “Conserving Africa’s Megadiversity in the Anthropocene”

Grazing impact on fire





If grazers can keep grass short enough, then fire can not spread

- Threshold dynamics due to percolation

Archibald 2017 “Conserving Africa’s Megadiversity in the Anthropocene”

Grazers consume fuel and prevent fire spread. Evidence:

Over time: Norton-Griffiths Serengeti 1979. Increased Wildebeest numbers reduced fire

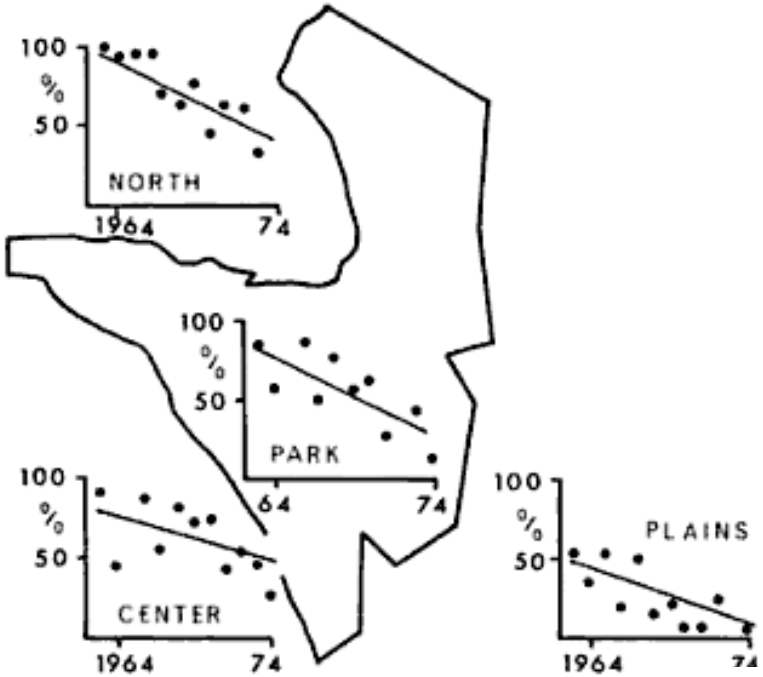
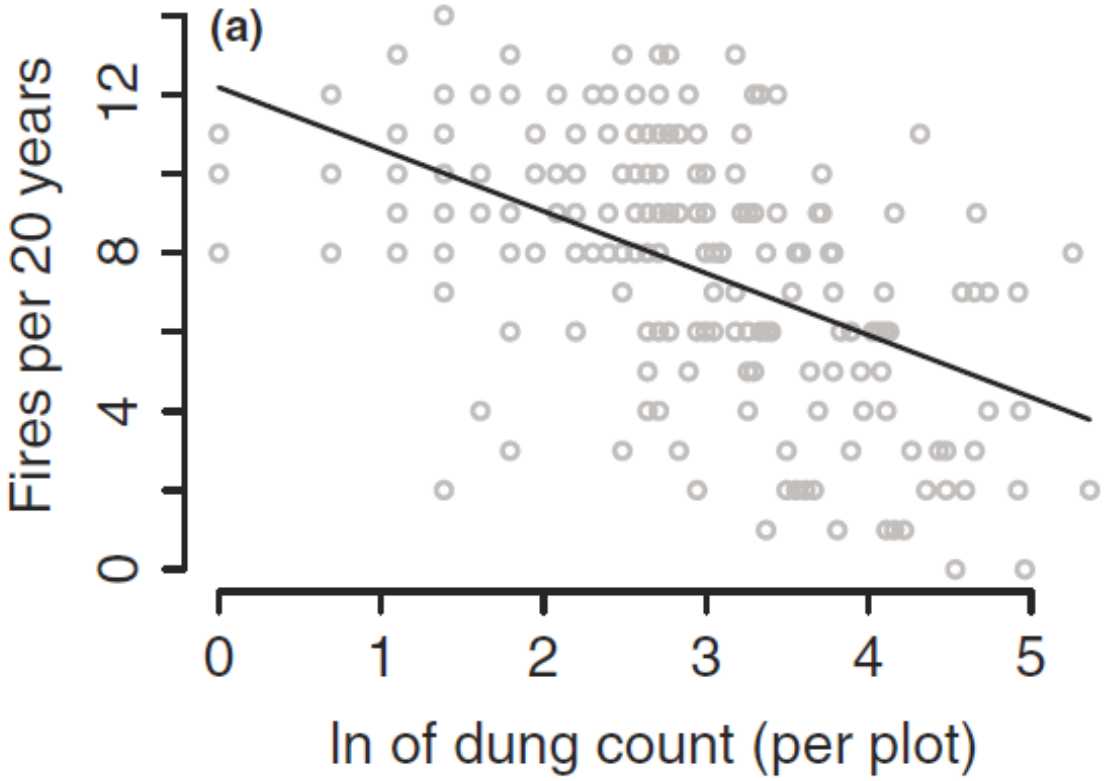
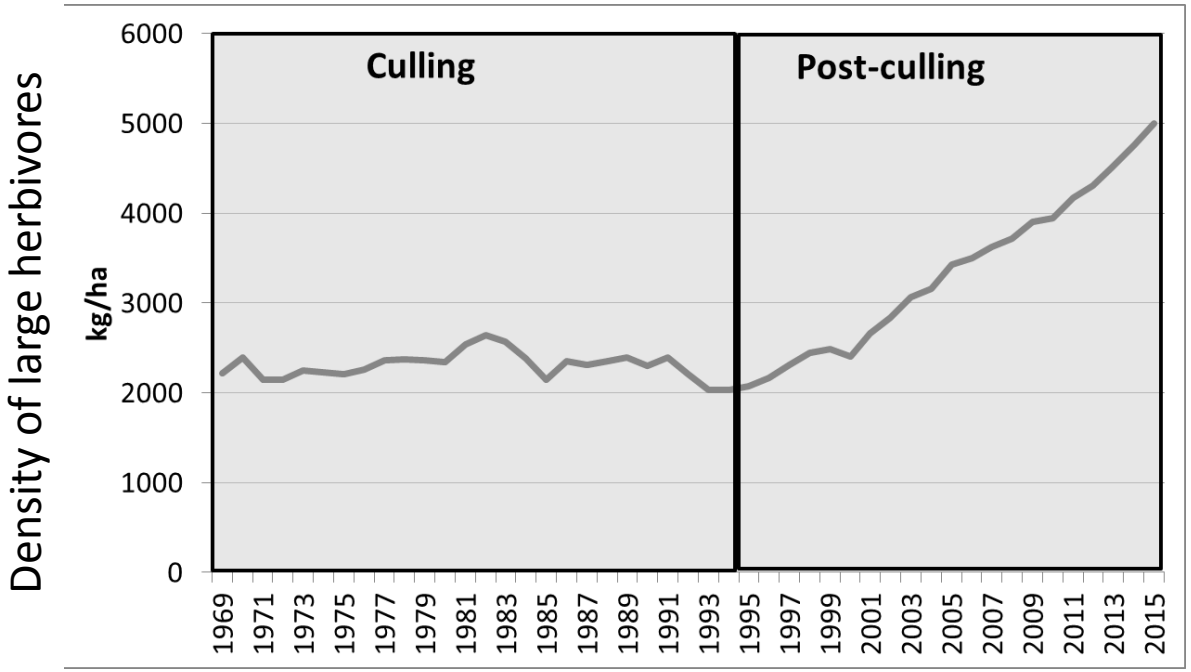


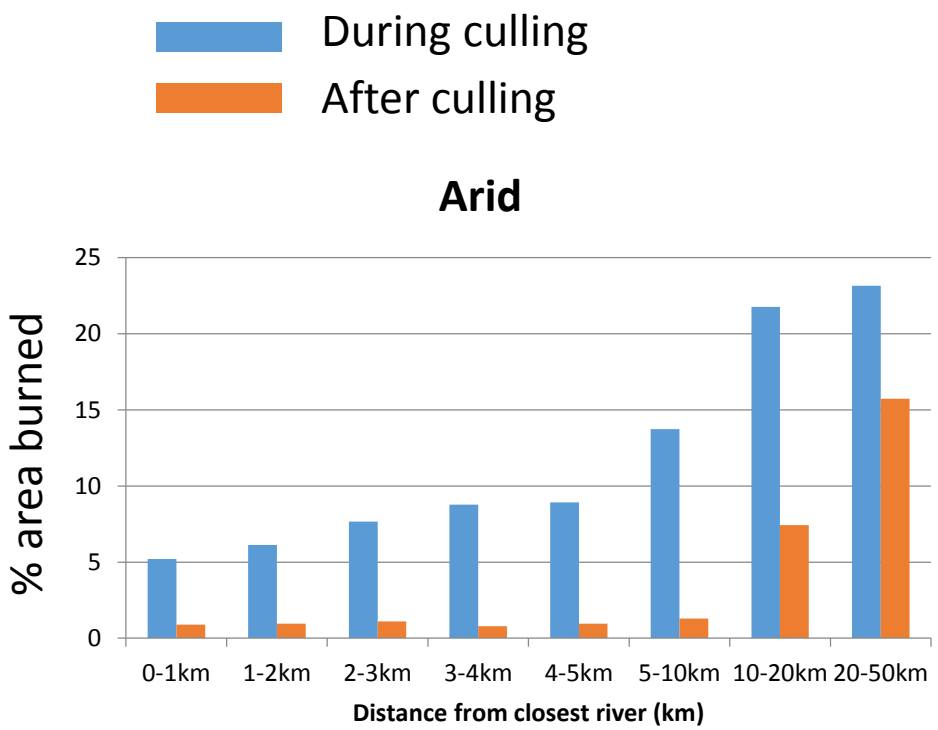
Figure 13.9 The decrease in the a each year between 19

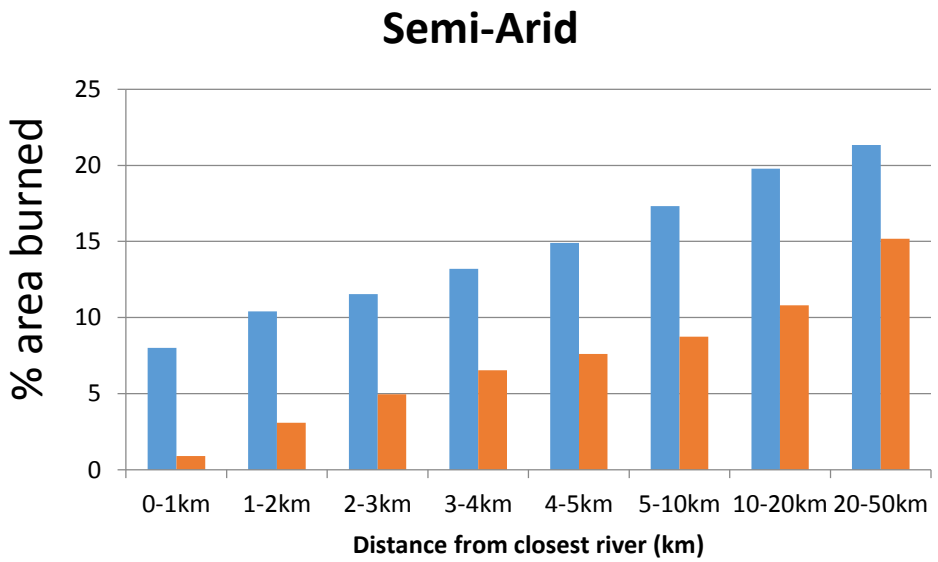
In space: Staver 2012 Ecol Let. Areas with many animals have fewer fires.



Other evidence: Kruger National Park







30% reduction in area burned after culling stopped in the 1990s'

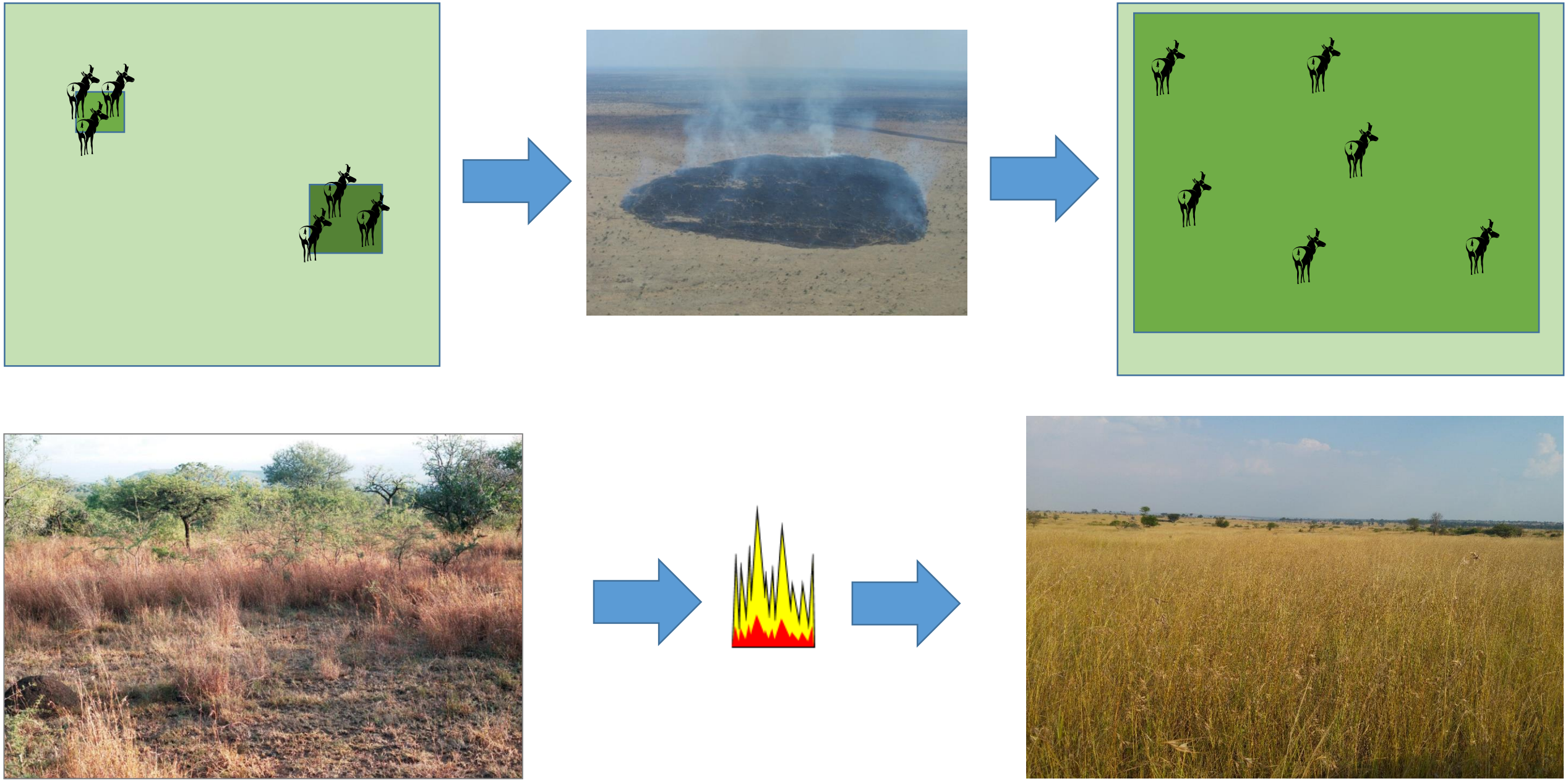
Smit and Archibald in prep

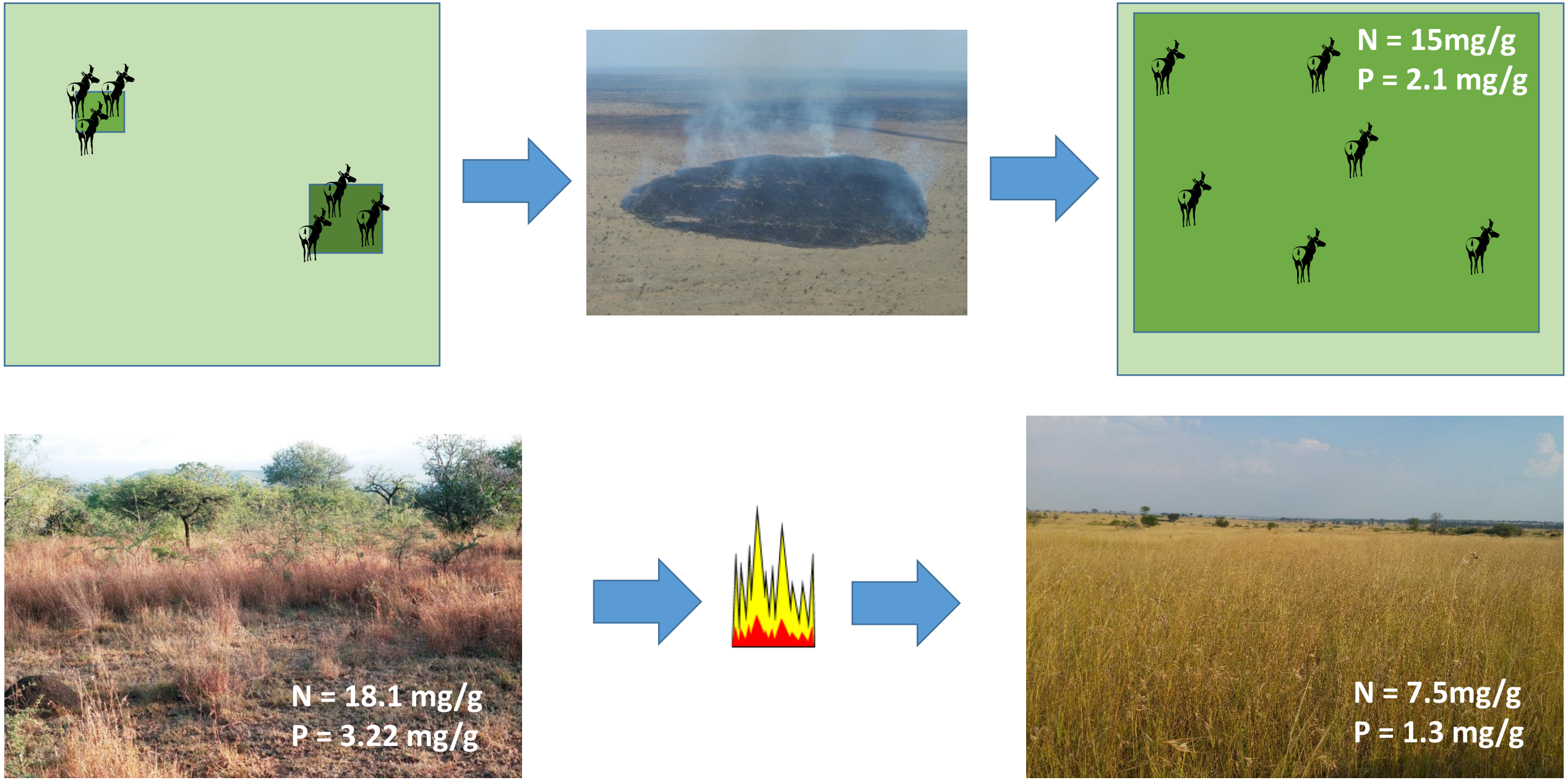
Fire impact on grazers

Immediately after a fire many grazers are attracted to the new, green, nutritious grass.

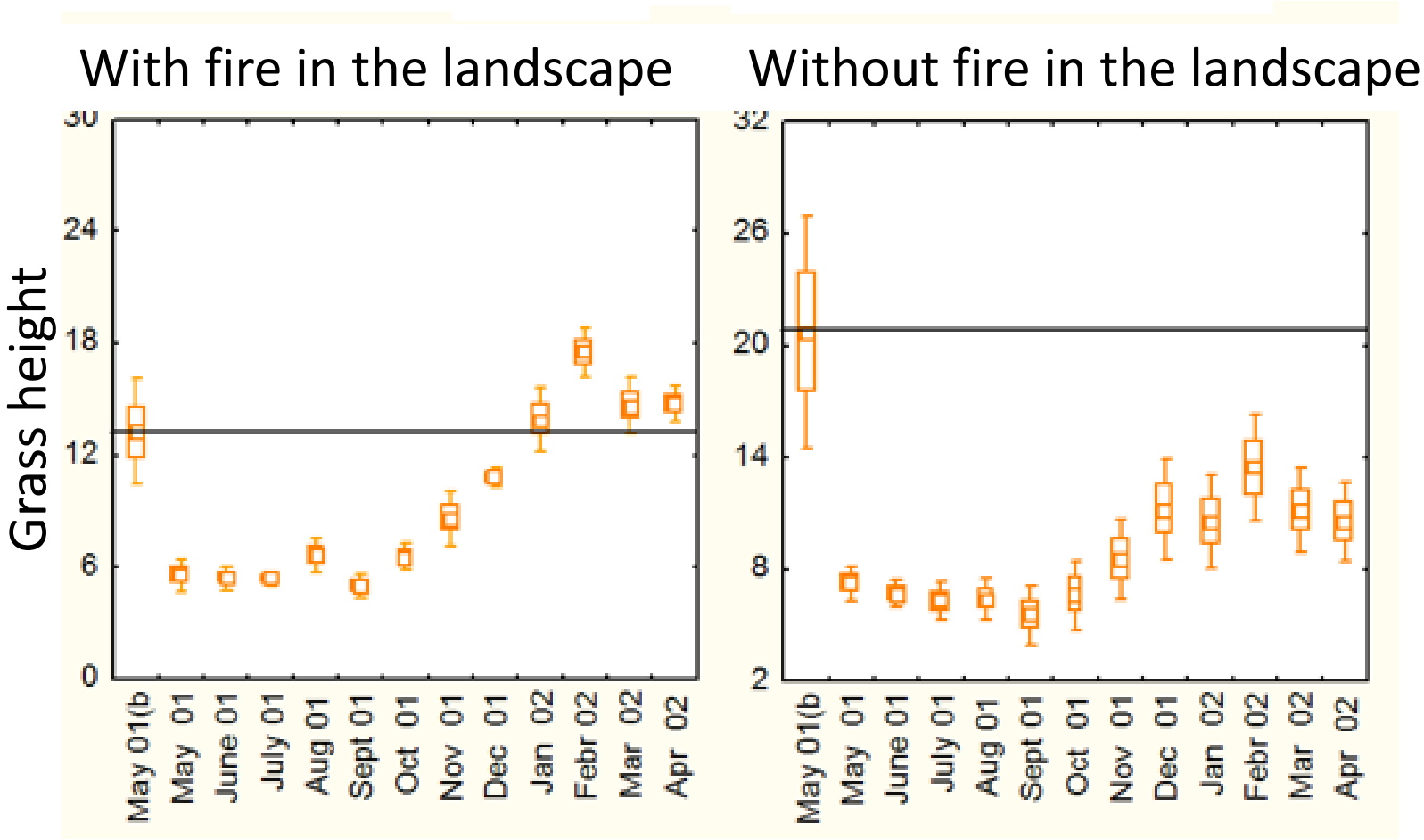
But over longer time-periods, fire's effect can be negative.

This is because it affects the species composition of the grasses.



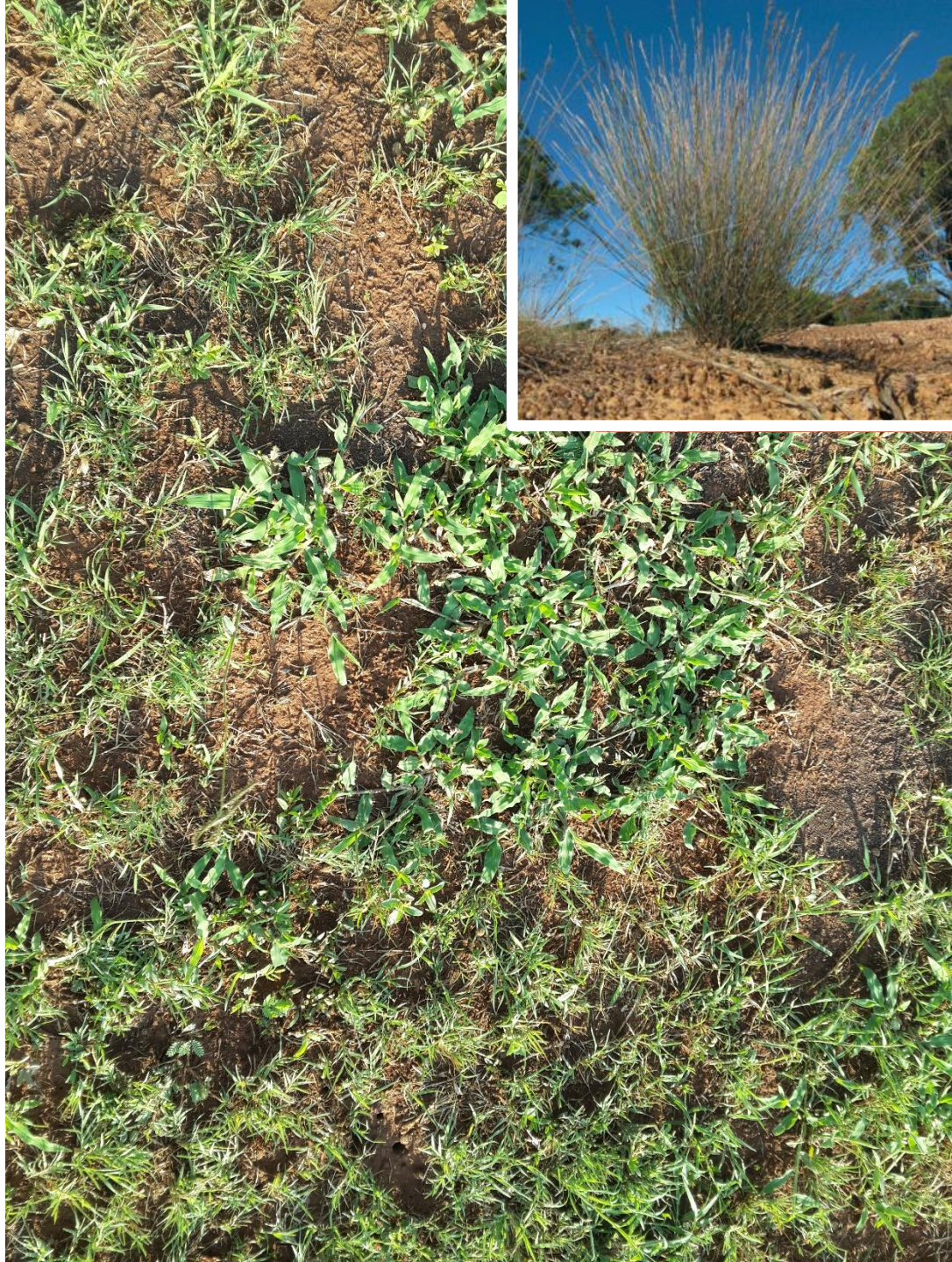

N = 15mg/g
P = 2.1 mg/g
N = 18.1 mg/g
P = 3.22 mg/g
N = 7.5mg/g
P = 1.3 mg/g

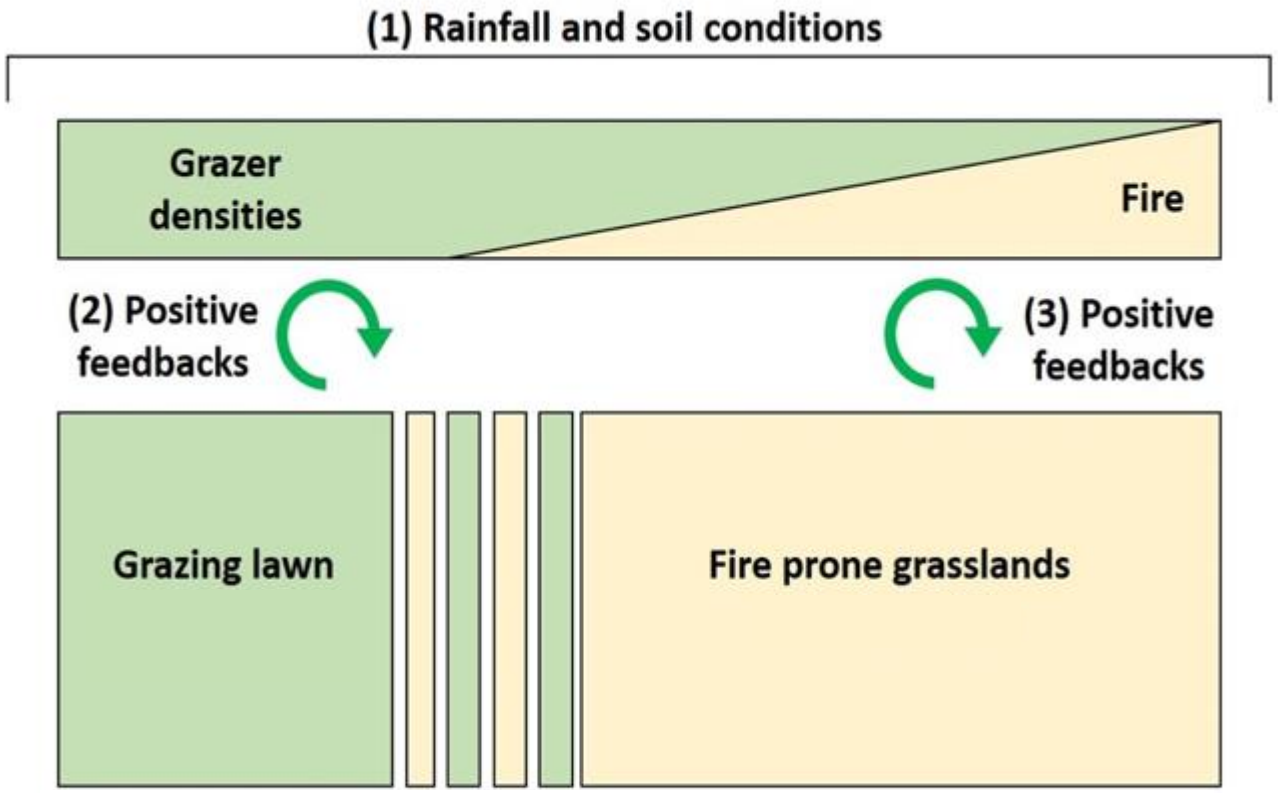
Fire prevents the establishment and spread of short-grass ecosystems



Archibald et al Ecol App 2005

Interactions between fire and grazers are mediated by the grass communities that each consumer creates

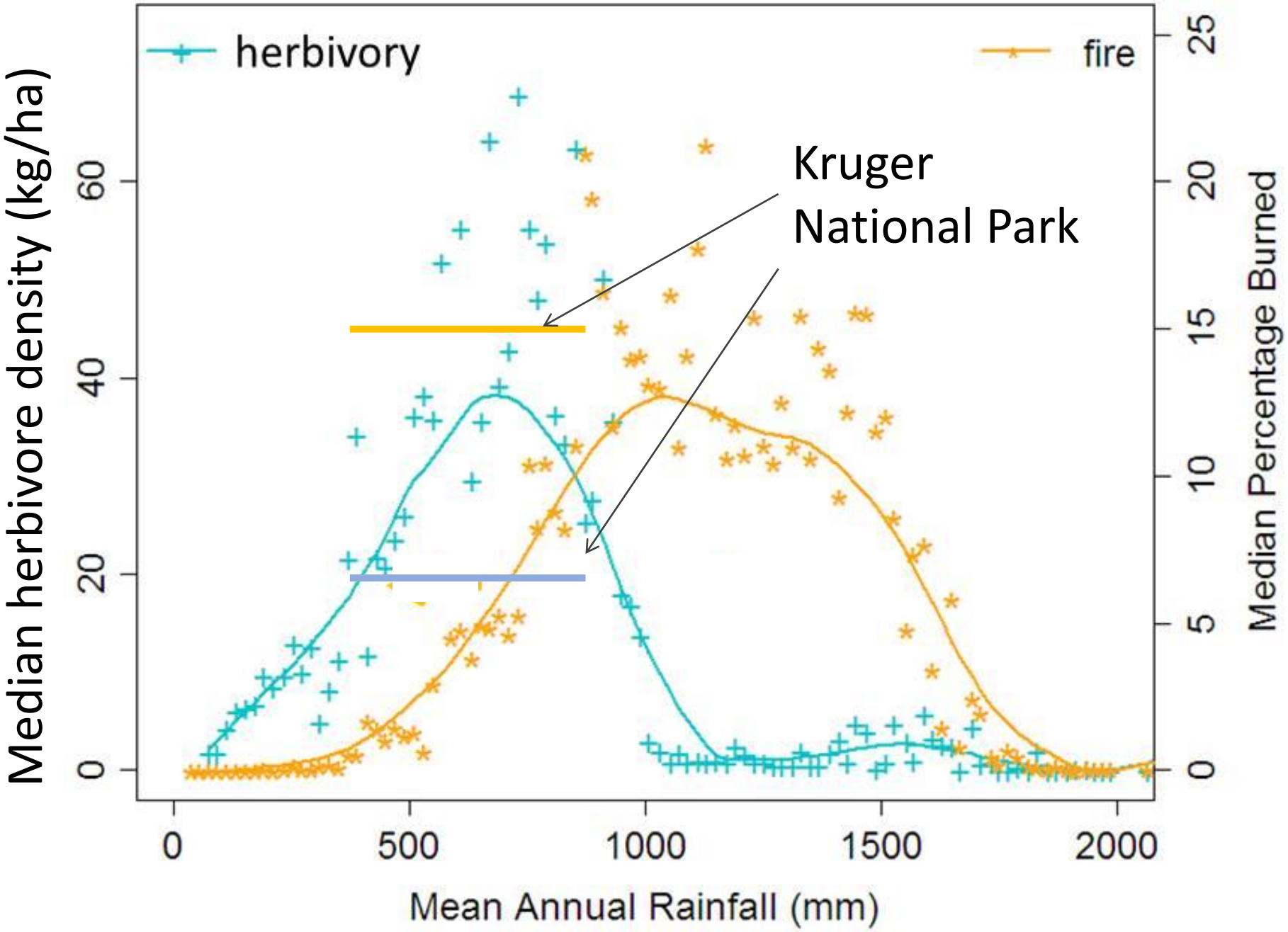




- Antagonistic relationships between herbivory and fire:
- Grazing promotes short-grass ecosystems that restrict fire. Fire promotes tall-grass ecosystems that most grazers avoid.
- Positive feedbacks promote alternate grassland states.

Archibald and Hempson 2016

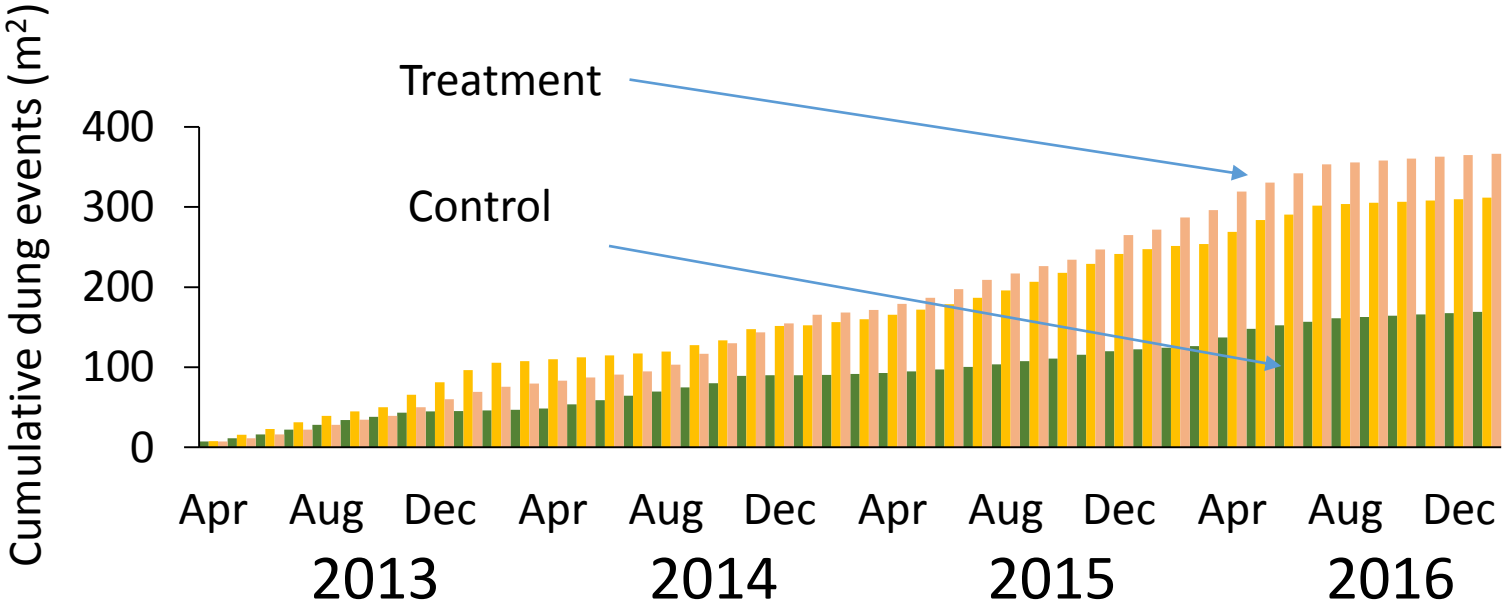
(Figure Jason Donaldson)


herbivory
fire
Kruger
National Park
Median herbivore density (kg/ha)
Median Percentage Burned
Mean Annual Rainfall (mm)
0
20
40
60
0
5
10
15
20
25
0
500
1000
1500
2000

In collaboration with SANPARKS we initiated the fire-grazer program in the Kruger National Park

Aim: to increase wildebeest habitat at Satara through careful fire application

First paper out December 2017: Donaldson et al J Applied Ecology.



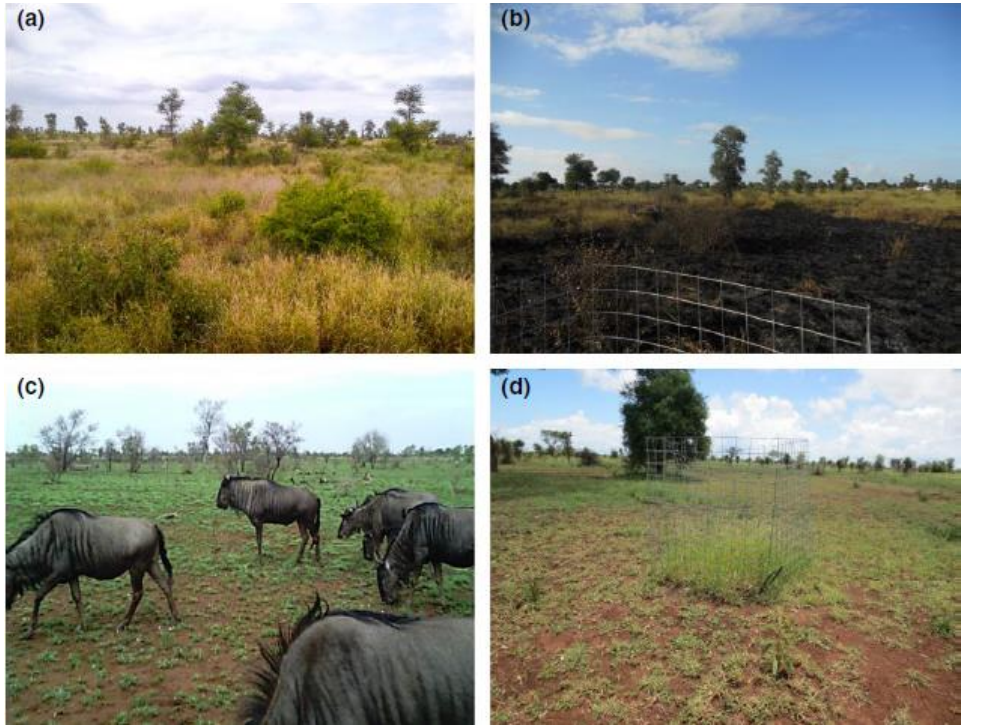
DOI: 10.1111/1365-2664.12956

STANDARD PAPER

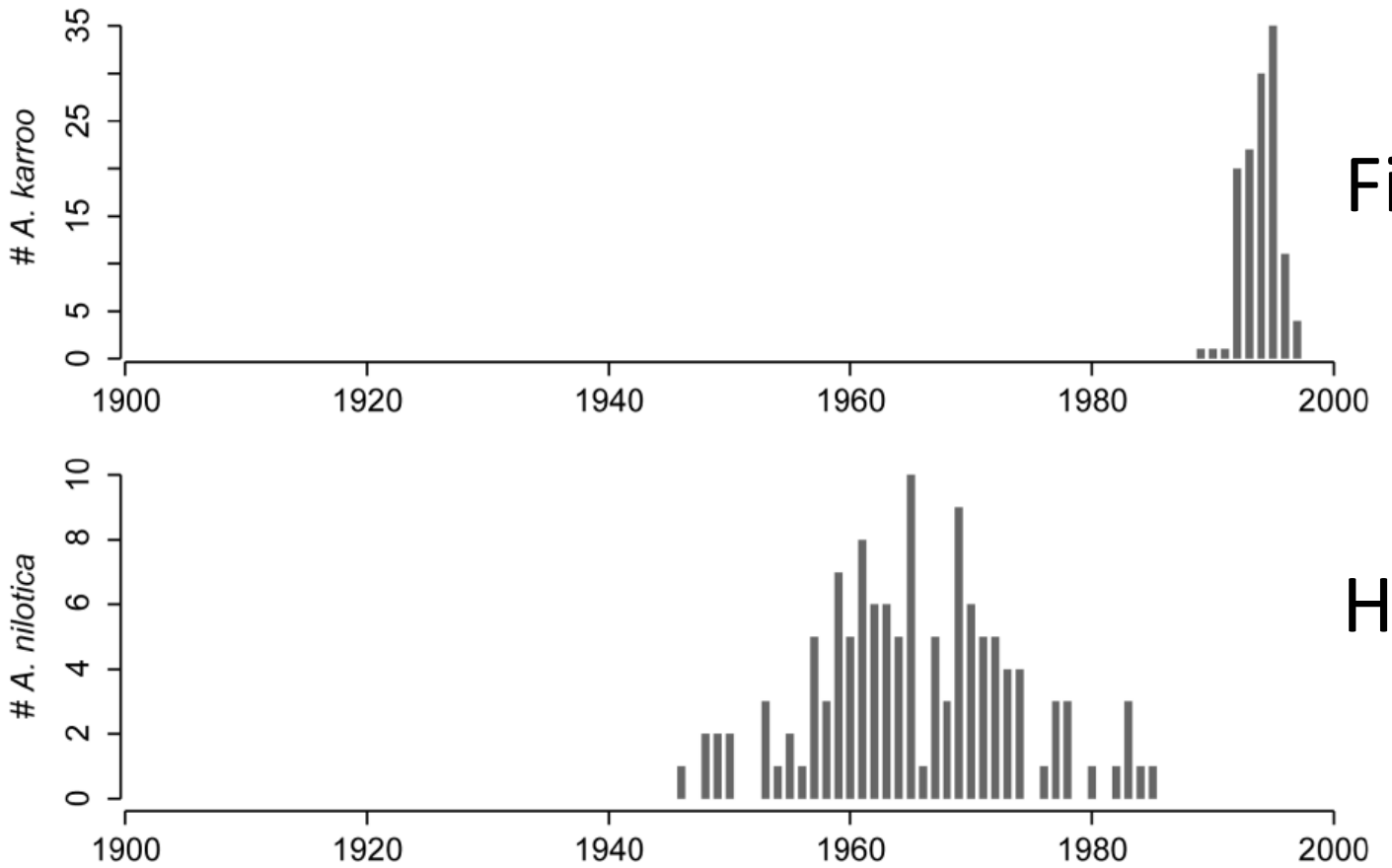
Journal of Applied Ecology

Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns

Jason E. Donaldson[1] | Sally Archibald[1] | Navashni Govender[2] | Drew Pollard[1] | Zoë Luhdo[1] | Catherine L. Parr[1,3]

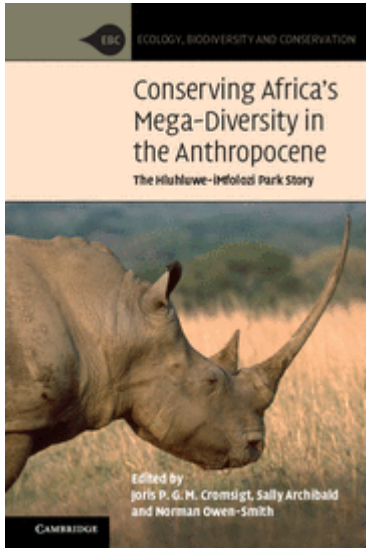


Switches from herbivore to fire-dominated ecosystems in Hluhluwe-iMfolozi Park



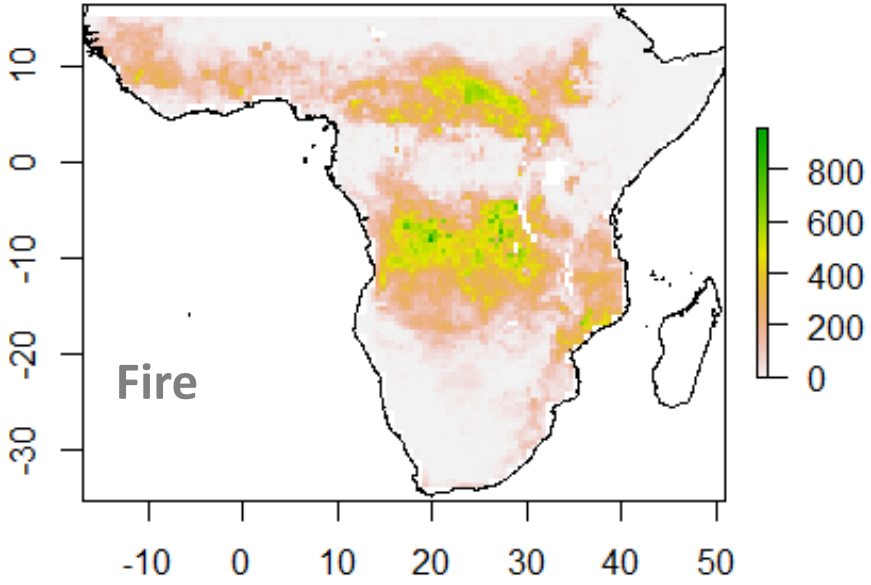
Fire adapted

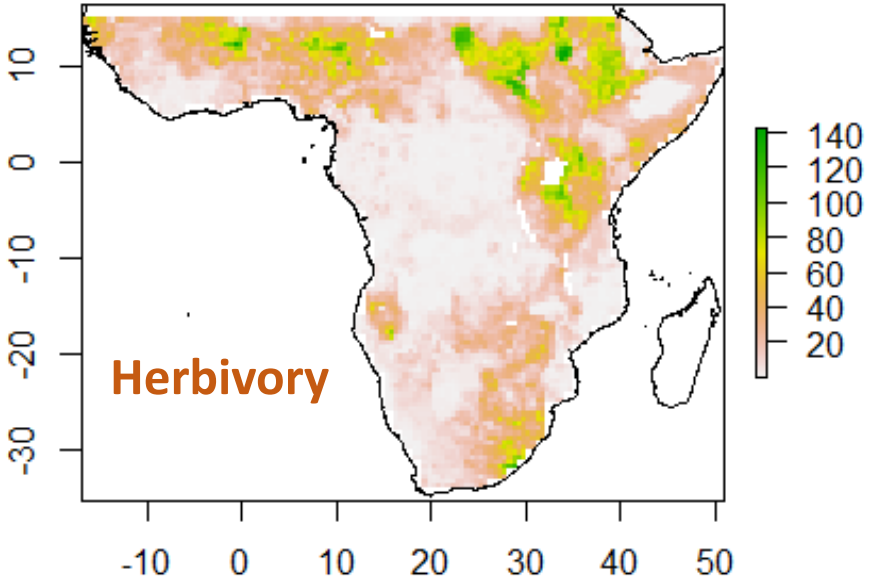
Herbivore adapted

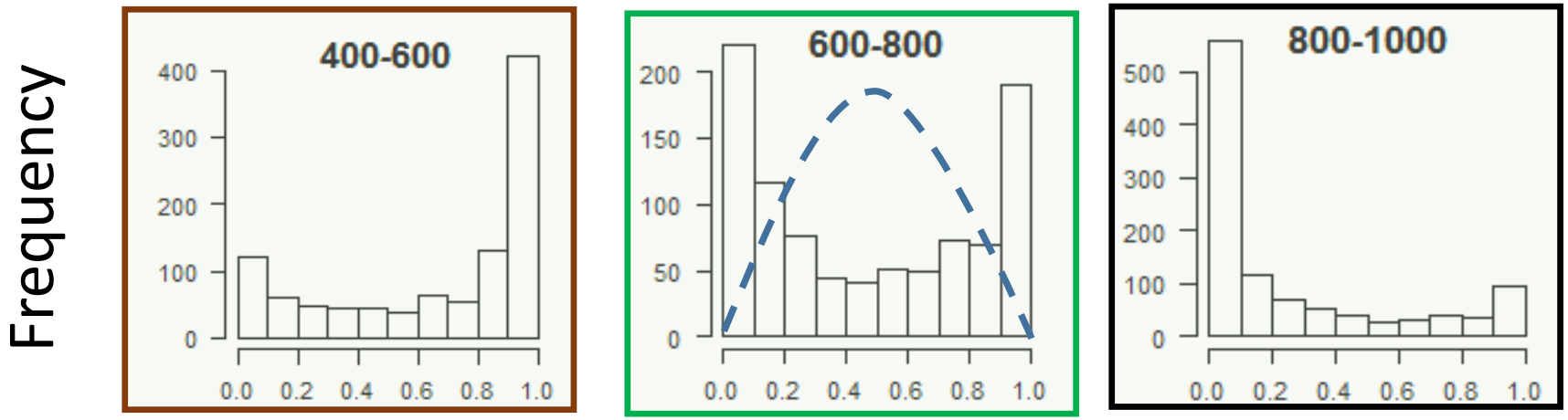


Staver and Bond Ecospheres 2011

Biomass (dry matter) consumed by fire vs herbivory (g/m^2/year)





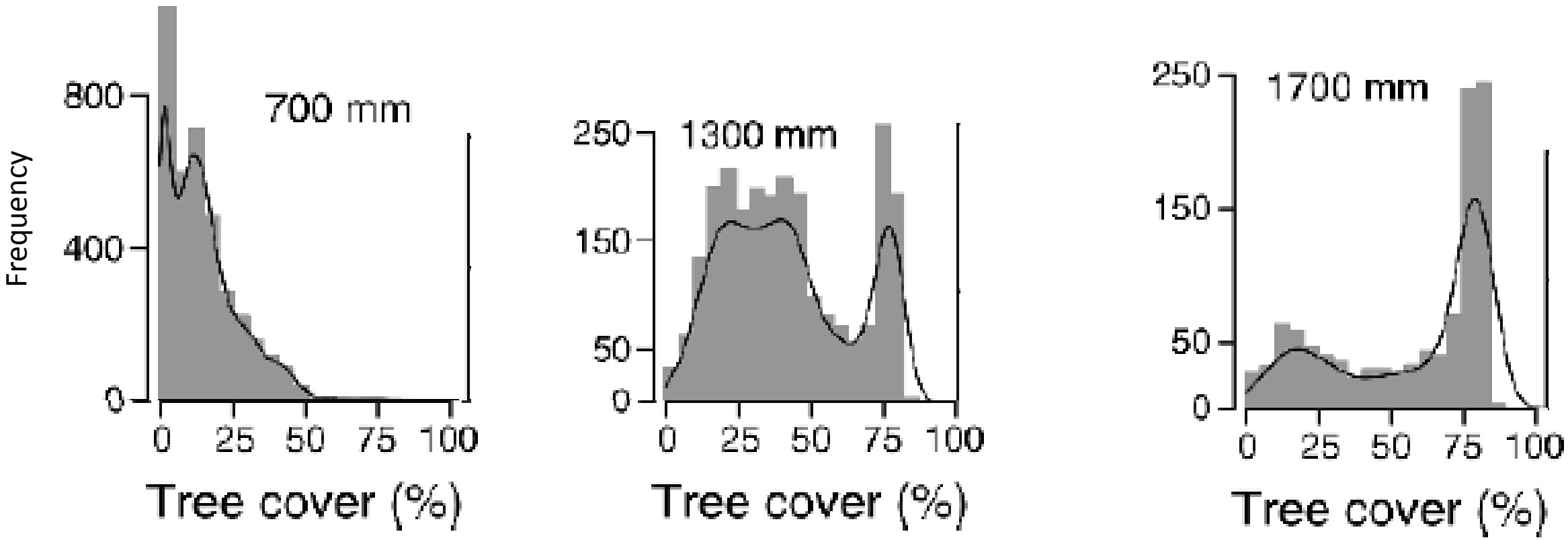


Archibald et al
Phil Trans 2016

Proportion NPP consumed by herbivores across rainfall bands

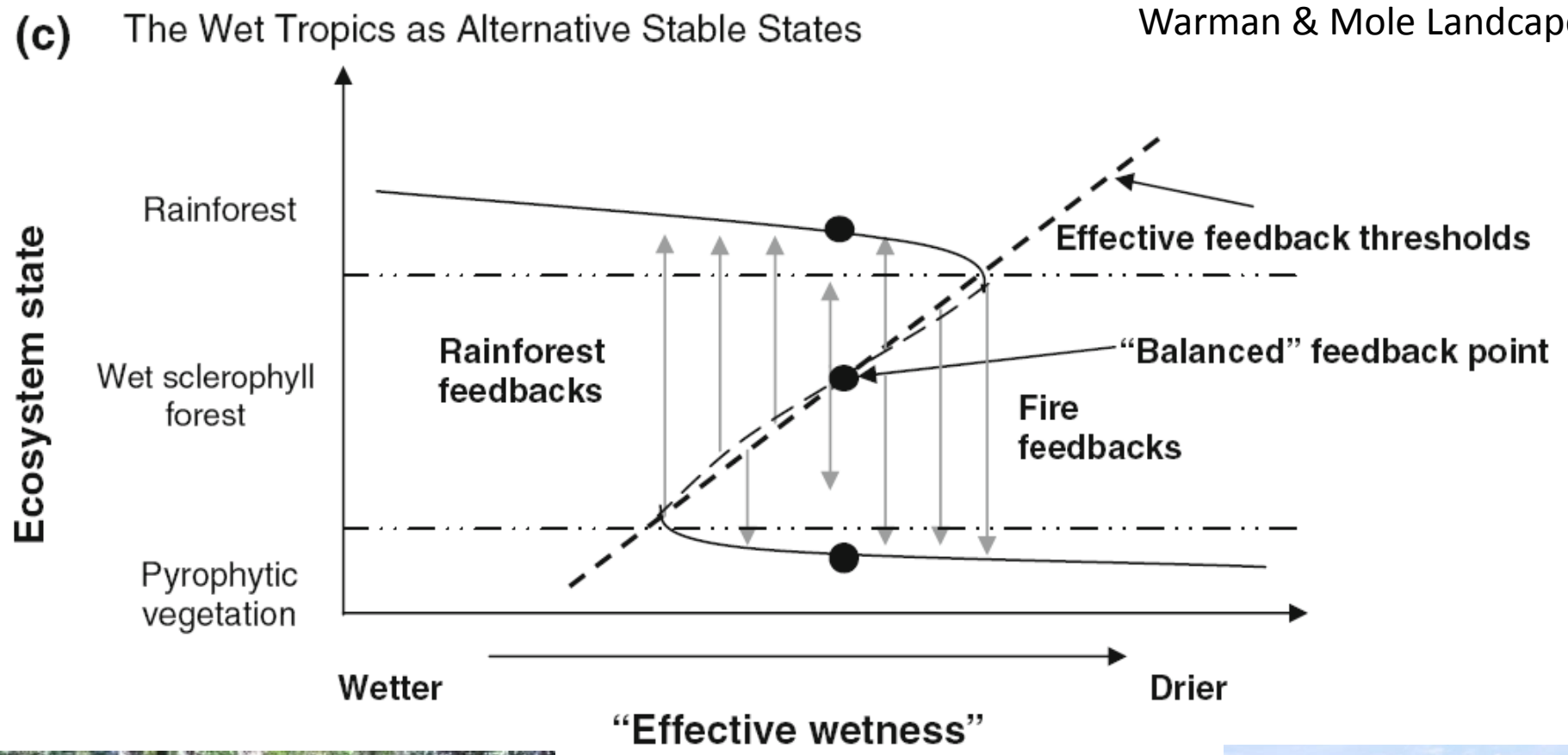
EITHER fire OR herbivory – seldom both together

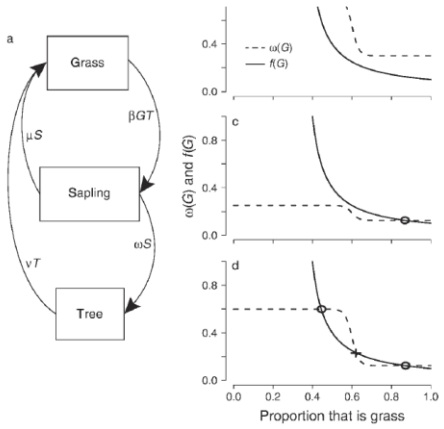
Parallels with evidence for forest-savanna alternative stable states…..



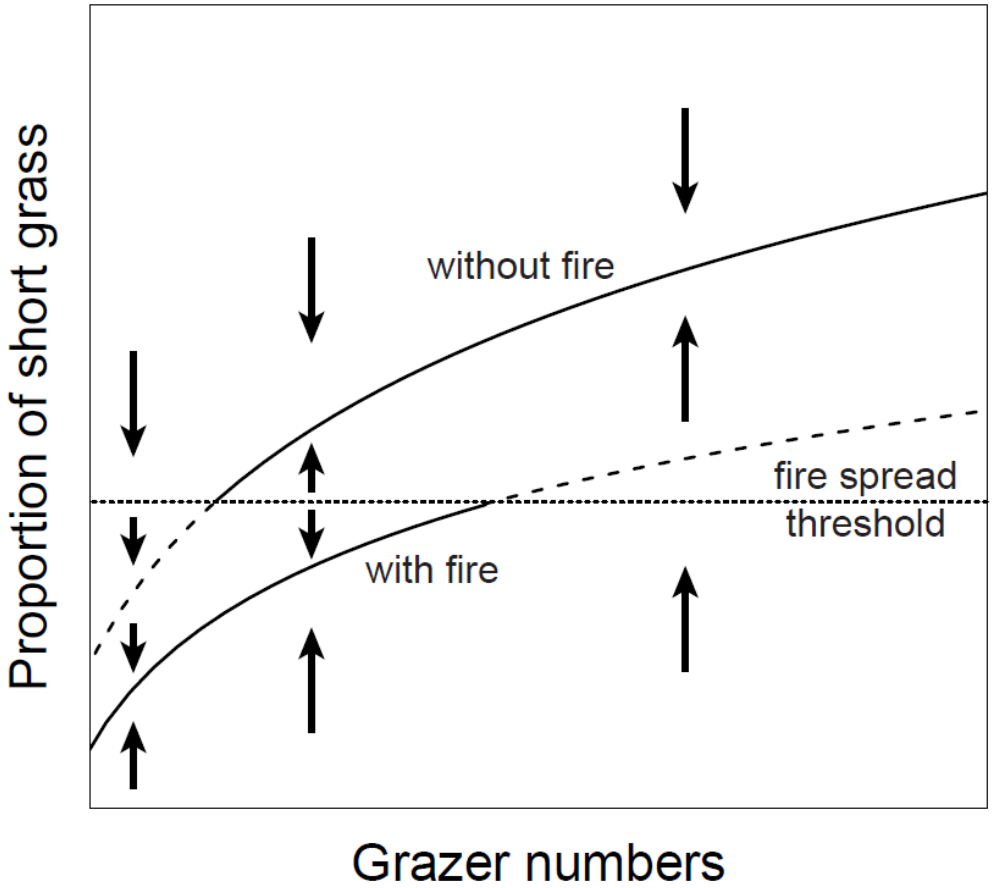
Staver, Archibald, Levin 2011 Ecology Letters

Warman & Mole Landcape Ecol 2009





Staver, et al 2011 Ecol Let

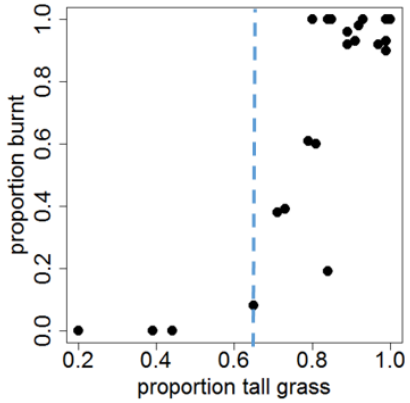


(i) grazing promotes the spread of short-grass patches and bare ground

(ii) fire impedes the spread of short grass

(iii) there is a threshold proportion of short grass where fire is excluded

Therefore one can expect hysteresis in the system



Archibald et al Phil Trans 2016

- Fire and grazing-dominated systems are certainly “alternate states” for a wide range of environmental conditions.
- Whether they are alternative STABLE states remains to be proved.
- Explaining the feedbacks requires understanding life-histories of the grass communities involved.

What traits, and trait syndromes are successful in fire-prone vs herbivore-prone environments?

Why are these two grasslands so distinct?

Traits associated with defoliation

- Attraction/Avoidance:
  - How palatable or flammable is a particular life history (or what are the chances of being consumed in the first place)?
- Tolerance
  - If a plant is consumed, then can it survive the defoliation event, and (over the long term) can this species persist in an environment exposed to frequent fire/herbivory?

Archibald et al Ecology Letters submitted

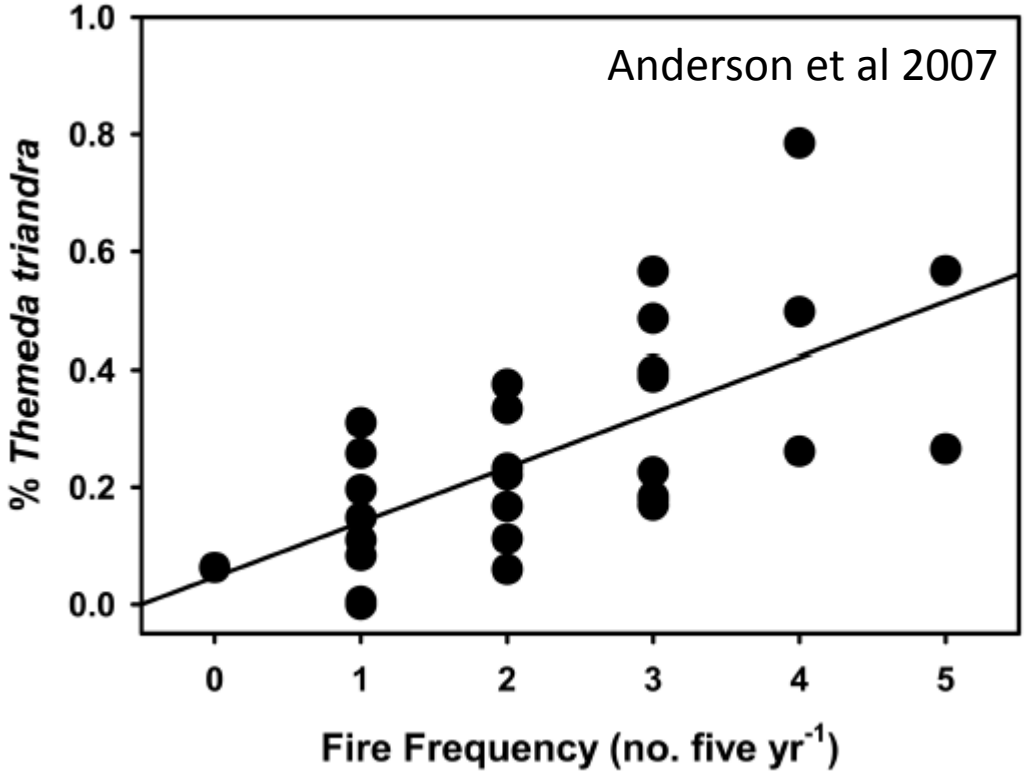
Attraction/Avoidance traits for fire and herbivory

	Fire	Herbivory
Process	Physical	Biological
Occurrence in time	Stochastic from day to day Strong seasonal dynamics	Persistent from day to day and over the season Annual-decadal dynamics
Occurrence in space	Uniform – removing heterogeneity at landscape scales (depending on the size and intensity of the fire)	Patchy – creating heterogeneity at landscape scales (depending on the size and selectivity of the herbivore)
Selectivity	Selects for dry fuel with a high C:N ratio and a low bulk density	Selects for moist forage with a low C:N ratio and a high bulk density
Key requirements	Continuity in space – without this fires will go out	Continuity in time – without this herbivores will die
Other requirements	An ignition source	A source of drinking water

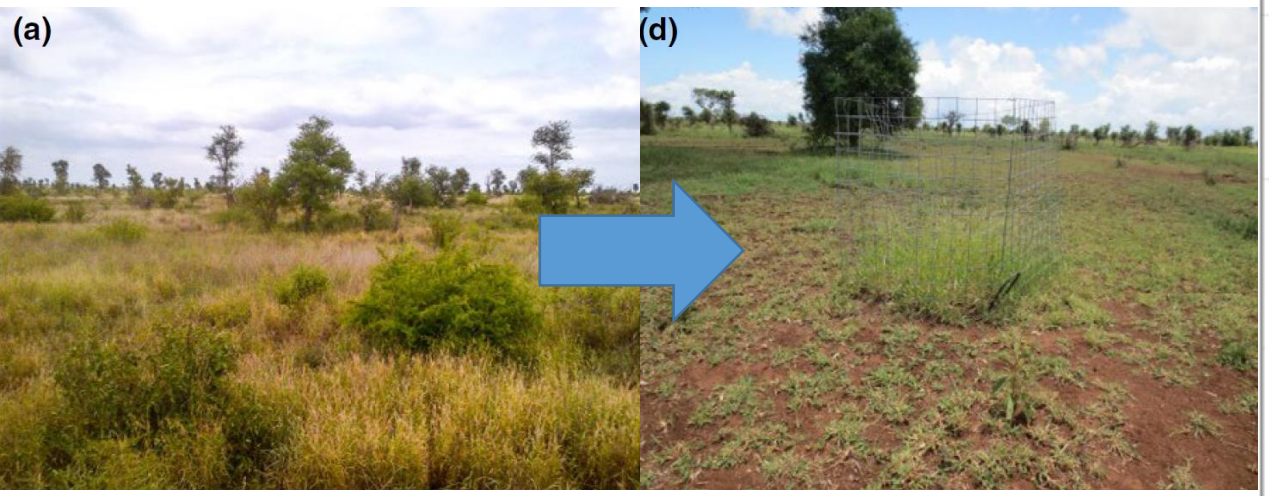
Archibald and Hempson 2016 Phil Trans

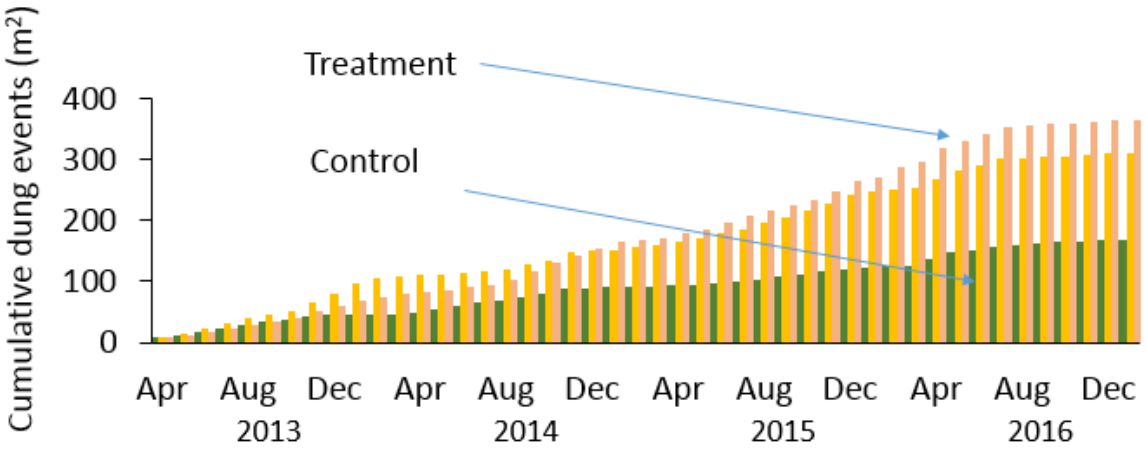
What about tolerance?

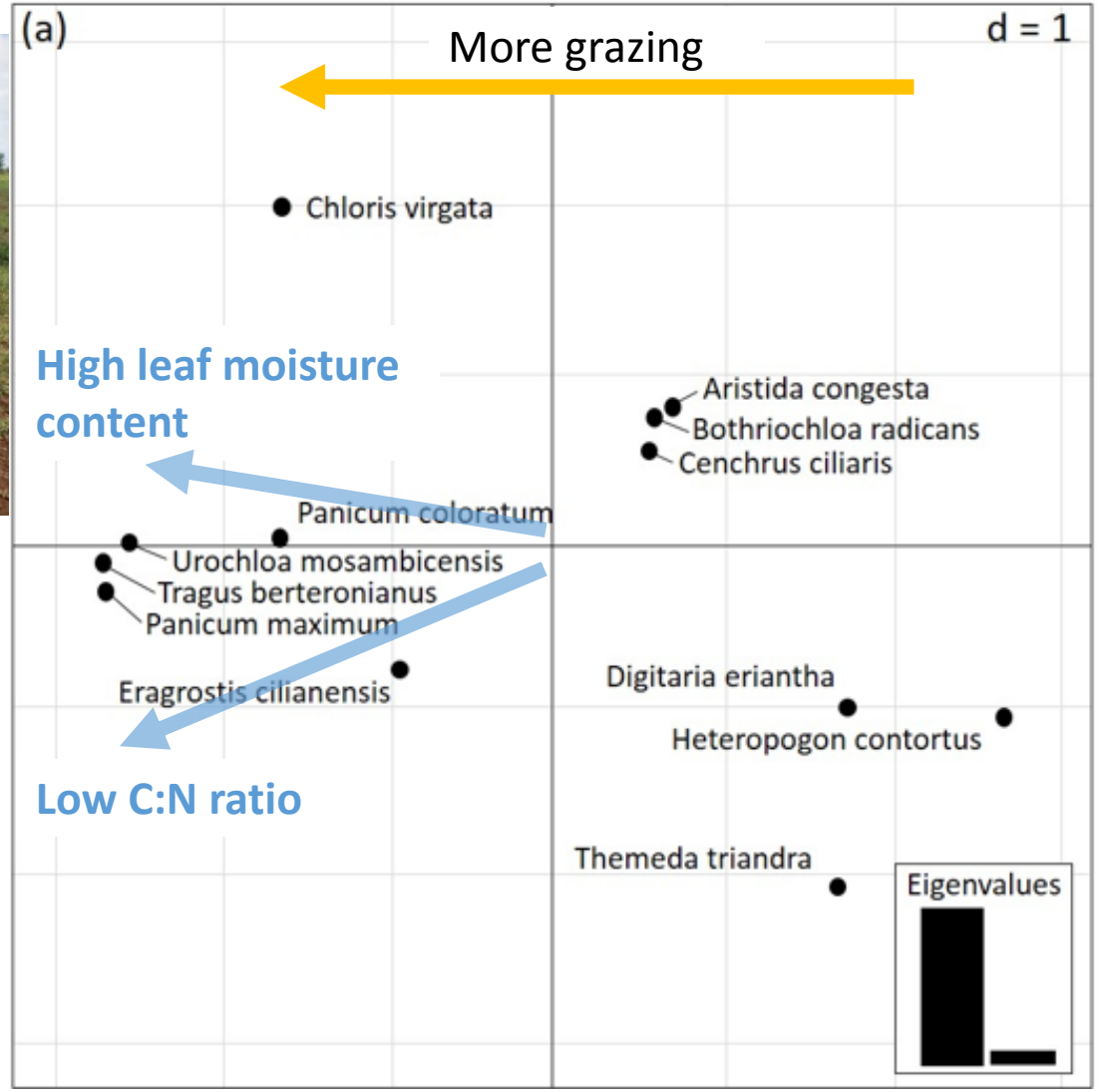
- Fire and herbivory both consume above-ground material.
- Are traits associated with fire tolerance the same as grazing tolerance?
- i.e. do fire and grazing filter grass communities in the same way?



Kruger National Park experiment: evidence that grazing creates more palatable, less flammable grasslands (?more productive?)



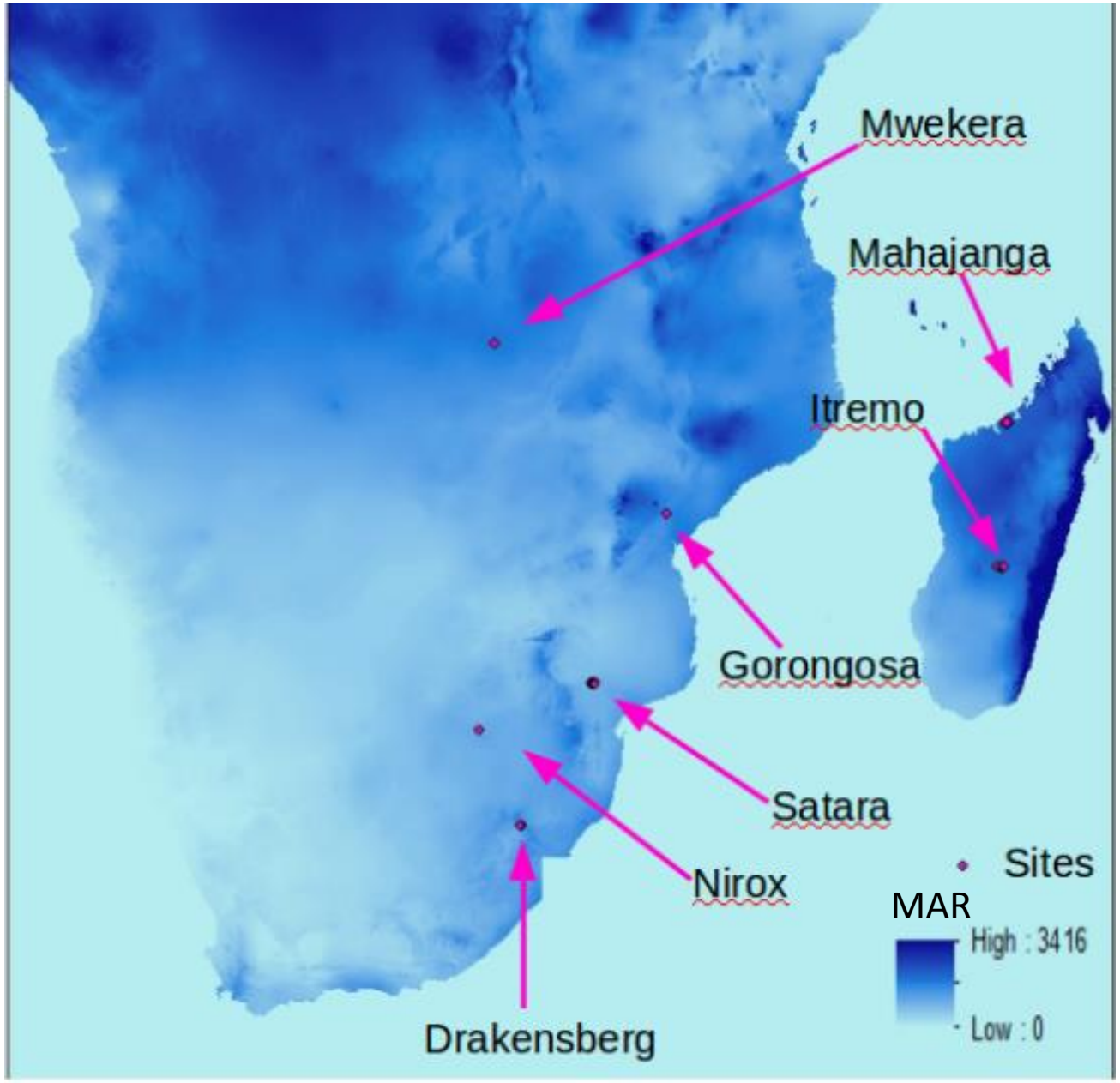




Jason Donaldson PhD – J Applied Ecology 2017

Fire vs grazer functional traits

- Traits that confer flammability and those that confer palatability are very different from each other.
  - Lends support to the alternative stable state ideas presented earlier
- Contrasting fire vs grazing tolerance traits – a work in progress.
  - We expect distinction between species specialised for each consumer (vertical vs lateral growth), but some traits (rapid resprouting) probably shared.
- Why are fire-tolerant grasses intrinsically more flammable?
  - Pausas et al 2017 – flammability as a form of fire tolerance
- Why are grazing-tolerant grasses intrinsically more palatable?



Royal Society grant:

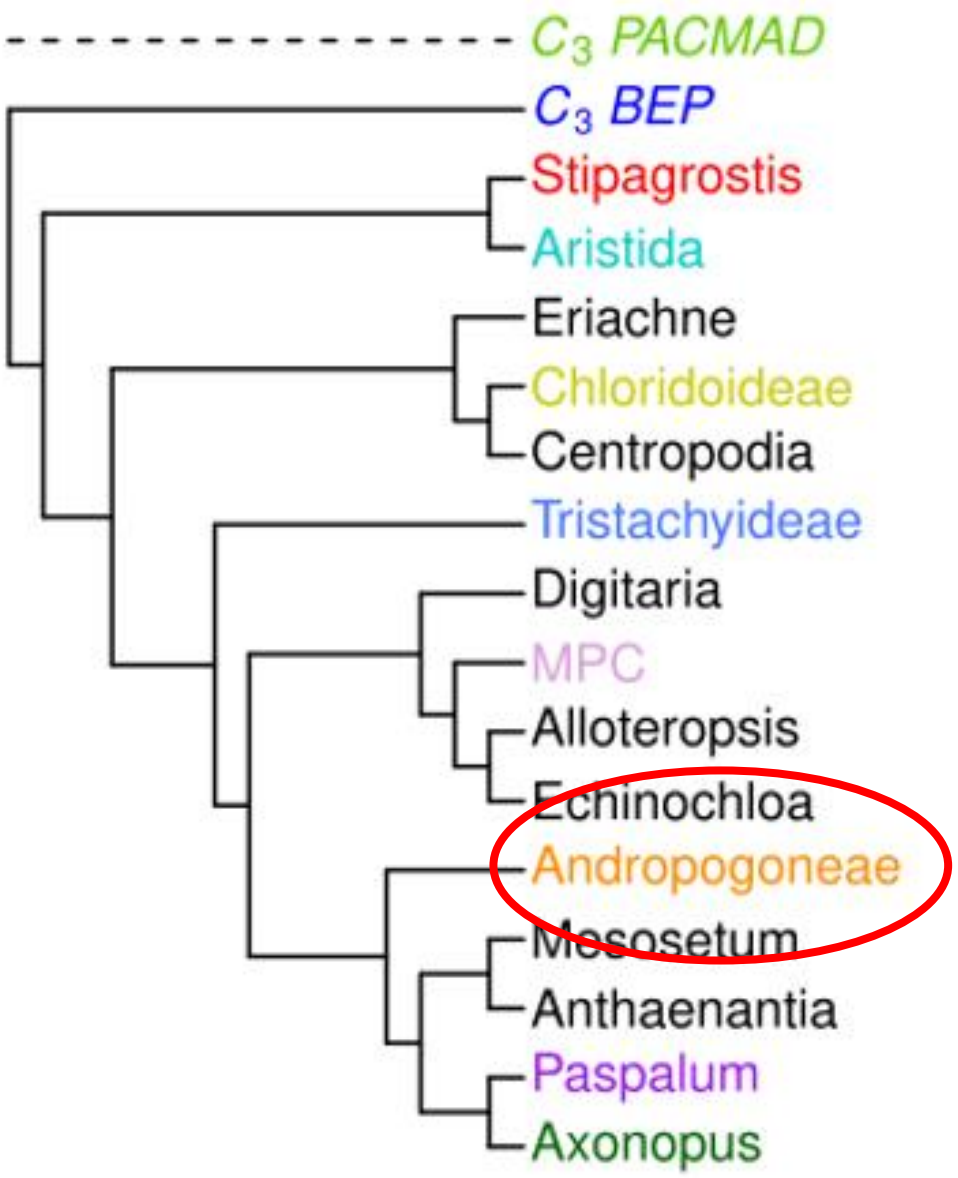
Quantifying changes in traits and community composition across environmental gradients of rainfall, fire and grazing.

Looking for a post-doc and research assistant to work on this project

Collaborations to add more sites - Gabon, DRC, Angola

Broader context

- Fire-adapted grasses are clustered in the grass phylogeny
  - Andropogonoids within Panicoideae
- Grazer-adaptations are probably more widely distributed
  - Grazing occurs in temperate systems too.



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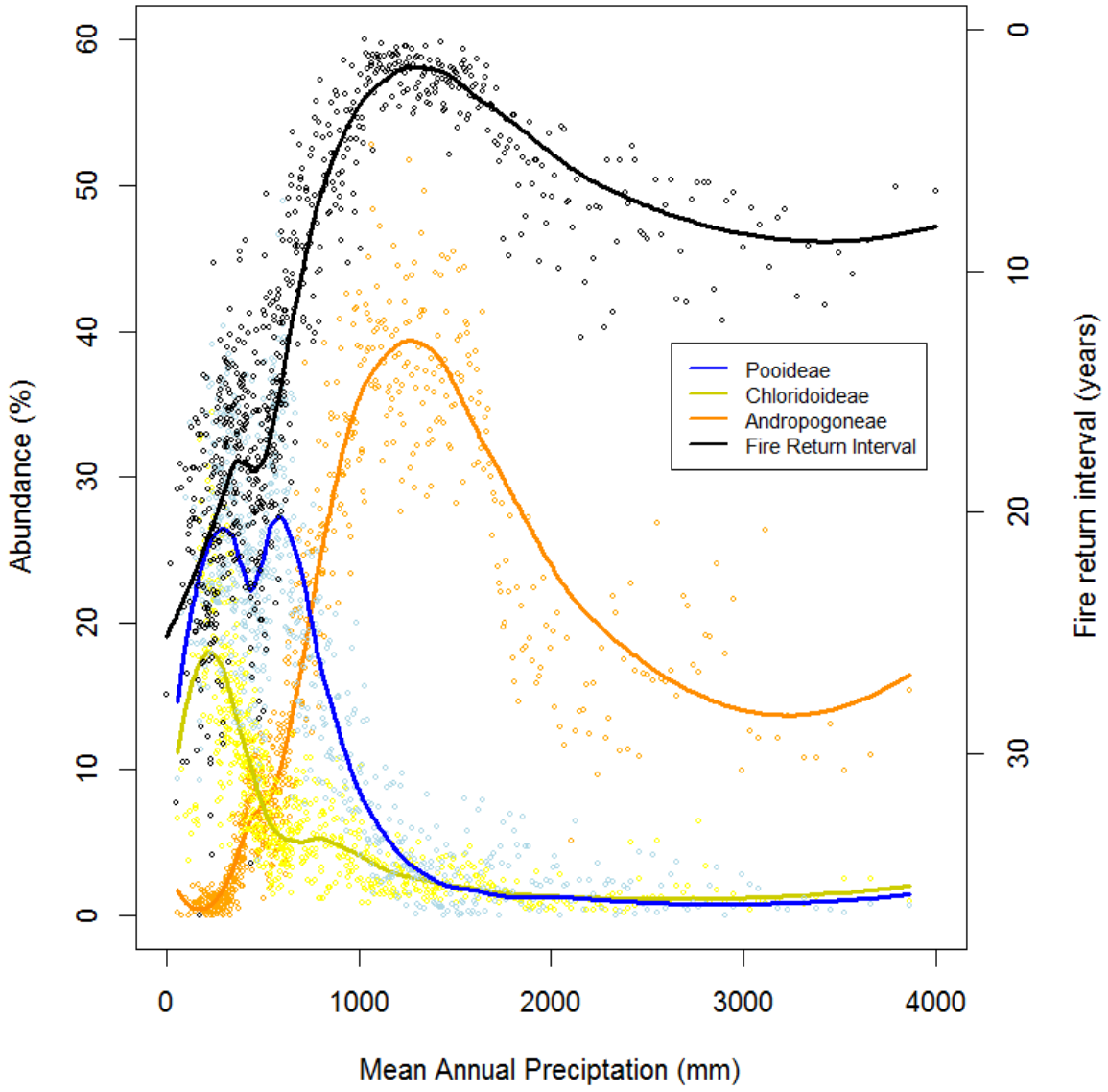
- Grazer-adaptations are probably more widely distributed
  - Grazing occurs in temperate systems too.



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Conclusions

- For a wide range of environmental conditions the dominant consumer is not set, but depends on history of drought, disease, and past management.
- Grass community switches in response to fire/grazing reinforce particular consumer regimes.
- Fire and herbivore functional traits lend support to the idea of alternative stable states between fire vs grazer-dominated grass communities.
- Identifying and quantifying these traits will help to understand the evolutionary pathways by which fire and herbivore adaptations have spread through the grass family.

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