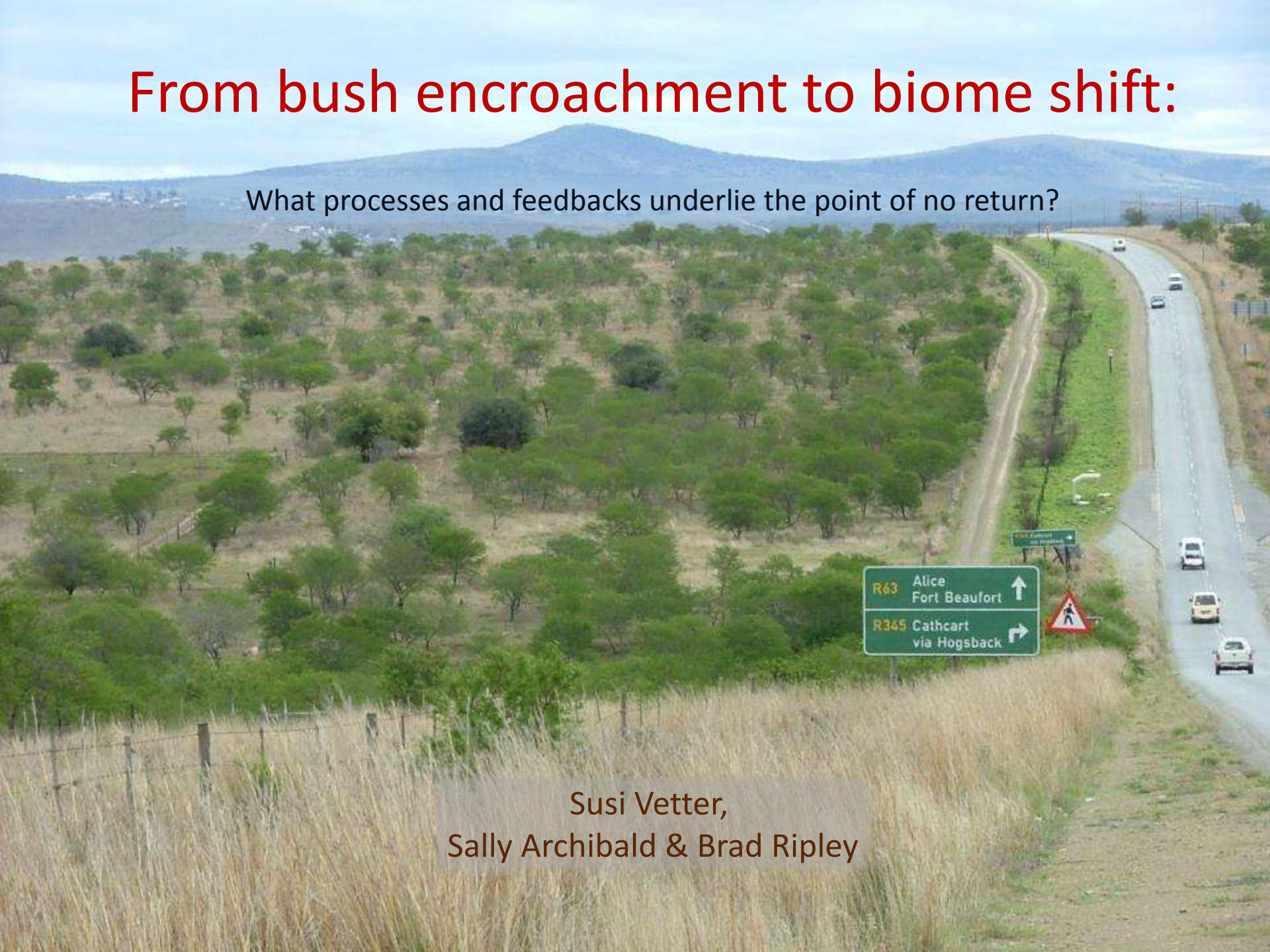
From bush encroachment to biome shift:

What processes and feedbacks underlie the point of no return?



Susi Vetter,
Sally Archibald & Brad Ripley

Overview

- Savanna and forest: alternative stable states

- When does bush encroachment represent a biome shift?

- Are there points in the sequence of events that represent critical thresholds?
  - how do we recognise them?
  - what are the management options?

A key threshold is likely to be the loss of a flammable C4 grass layer – this is associated with particular woody plant and grass traits.

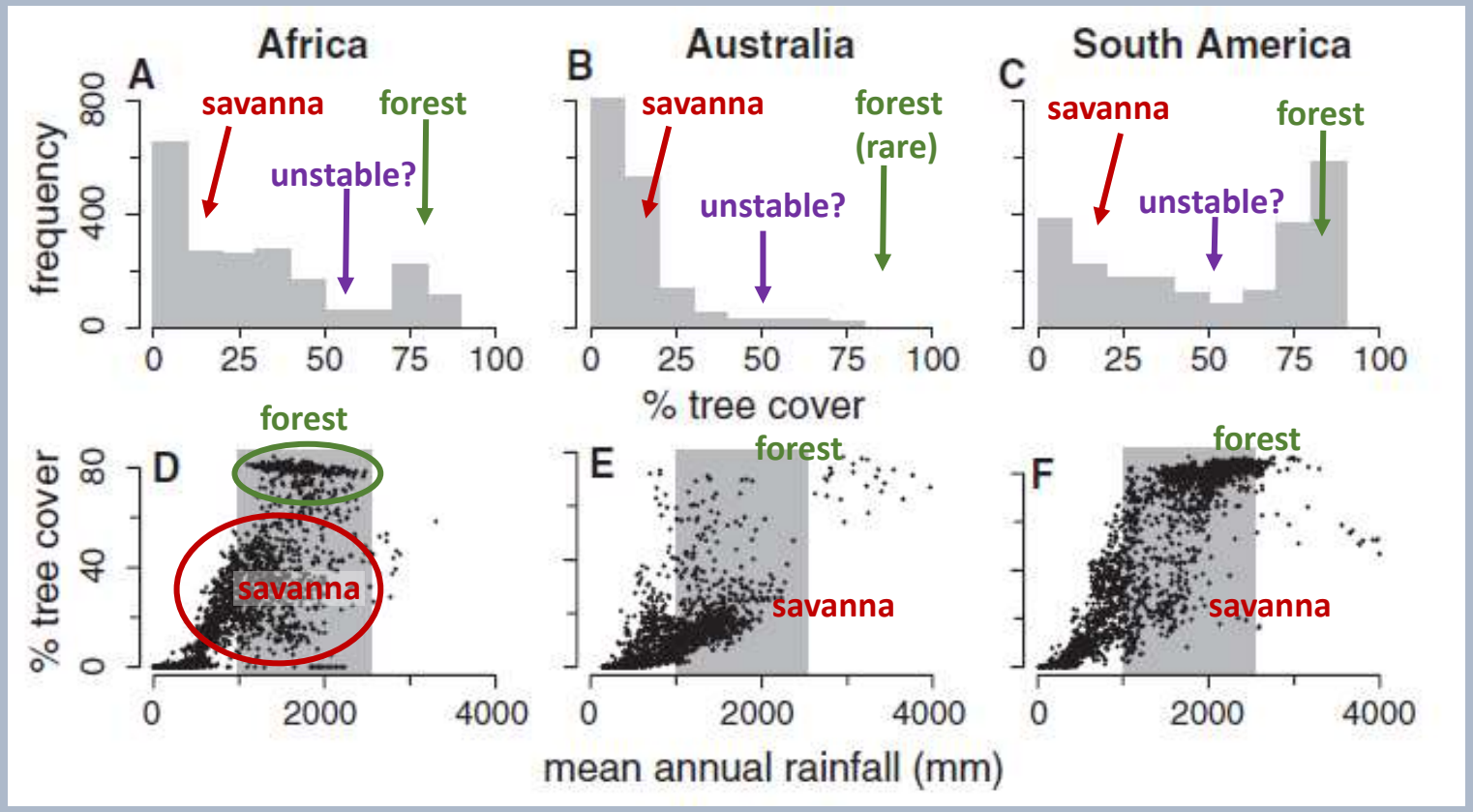
Savanna and forest:

Alternative stable states in mesic, seasonal tropics.

(Warman & Moles 2009, Staver et al. 2011, Hirota et al. 2011, Dantas et al. 2016)

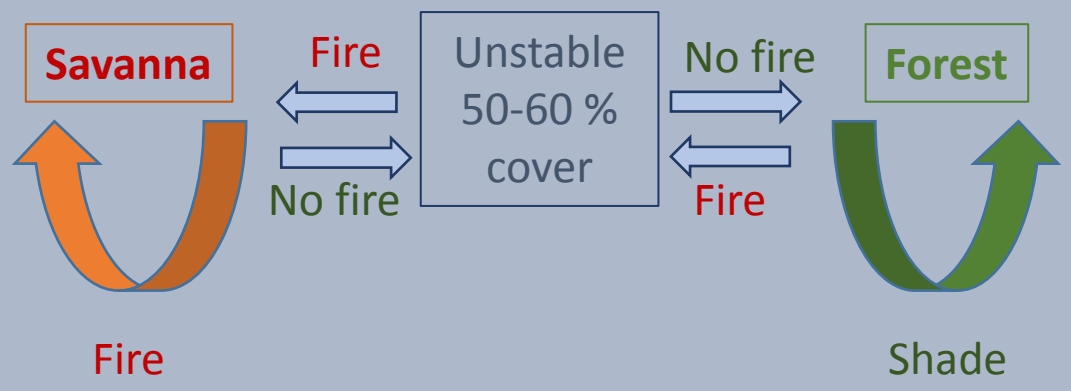
A-C: Frequency distribution of tree cover – sites with ~ 50-60 % tree cover rare

D-F: Tree cover vs. mean annual rainfall



Staver et al. (2011)

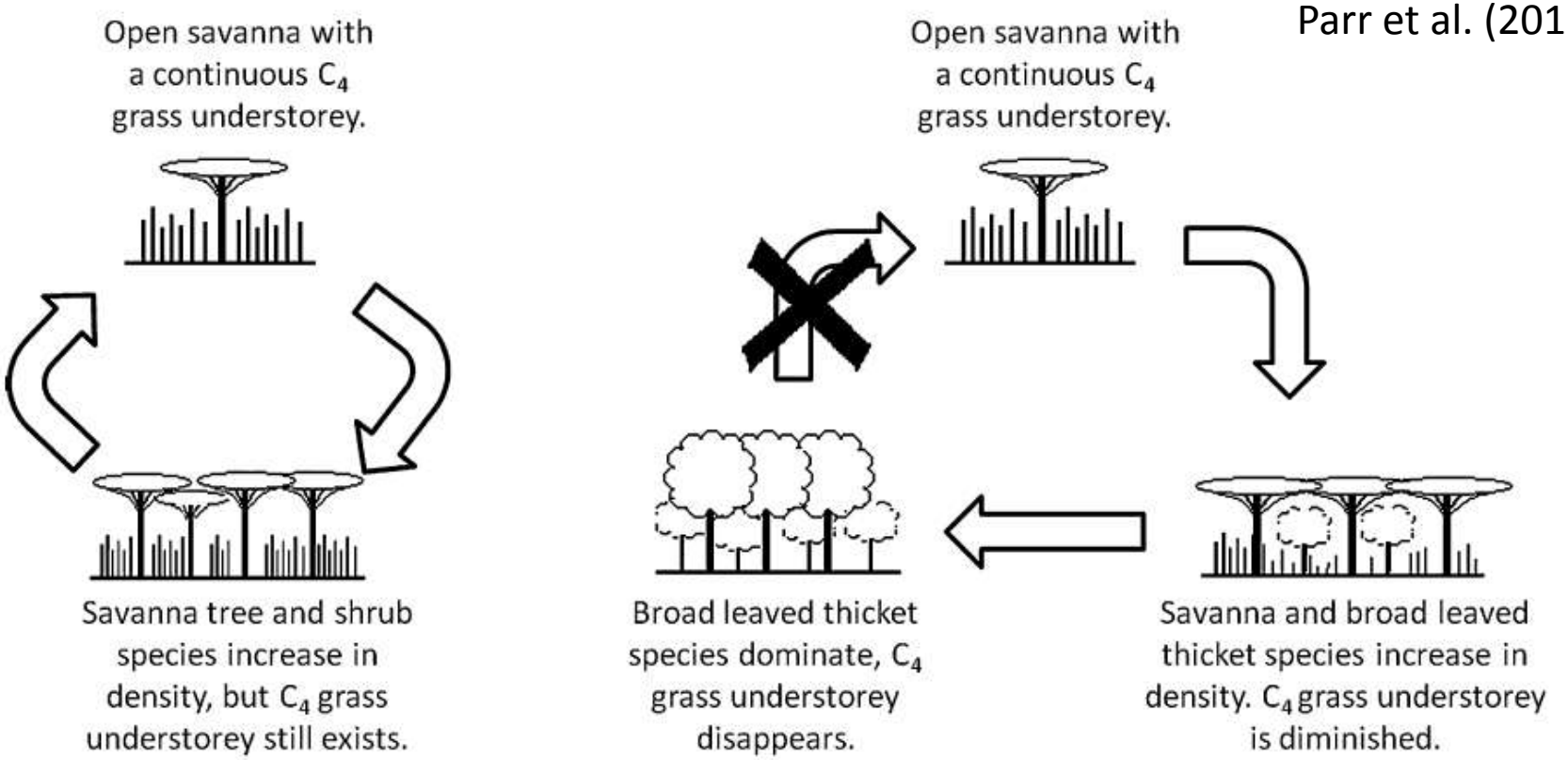
Savanna, forest states maintained by different feedbacks



Transition between stable states can be rapid and hard to reverse (“regime shift”)

Bush encroachment – what is the end point?

Parr et al. (2012)



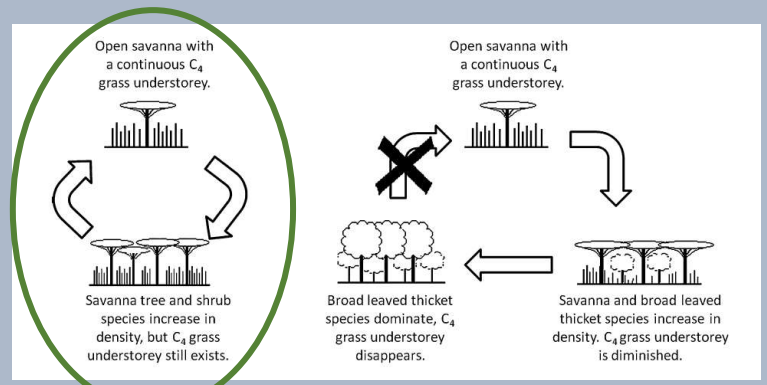
(a) Savanna thickening

Part of a cyclical process. Encroached savanna ecologically similar to open savanna, and able to revert back to open savanna.

(b) Thicket expansion

Thicket expands into savanna, eventually causing a biome switch to forest. Not part of a cyclical process, and unlikely to switch back to open savanna

Savanna thickening



Open savanna, scattered mature trees

Savanna with many small acacia seedlings

Savanna with dense immature acacias (gullivers)

Savanna with dense mature acacias, low grass biomass

Savanna with many broadleaf seedlings

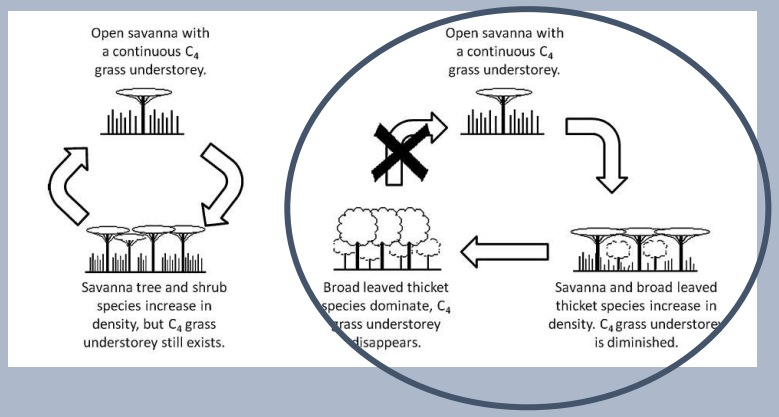
Thicket clumps

Thicket or Forest

When/where does this process occur?

In arid savannas, where savanna trees recruit in discrete cohorts, self-thin and eventually die?

Succession: from savanna to thicket to forest



Open savanna, scattered mature trees

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Savanna with dense immature acacias (gullivers)

Savanna with dense mature acacias, low grass biomass

Thicket or Forest

?

Savanna with broadleaf seedlings

Thicket clumps
Loss of flammable C4 grass layer

Where does this process occur?

- key stages and feedbacks
- key species involved - what are their traits?
- what processes can prevent, control or reverse key transitions?

Biome shift from savanna to thicket or forest:

Change is — structural

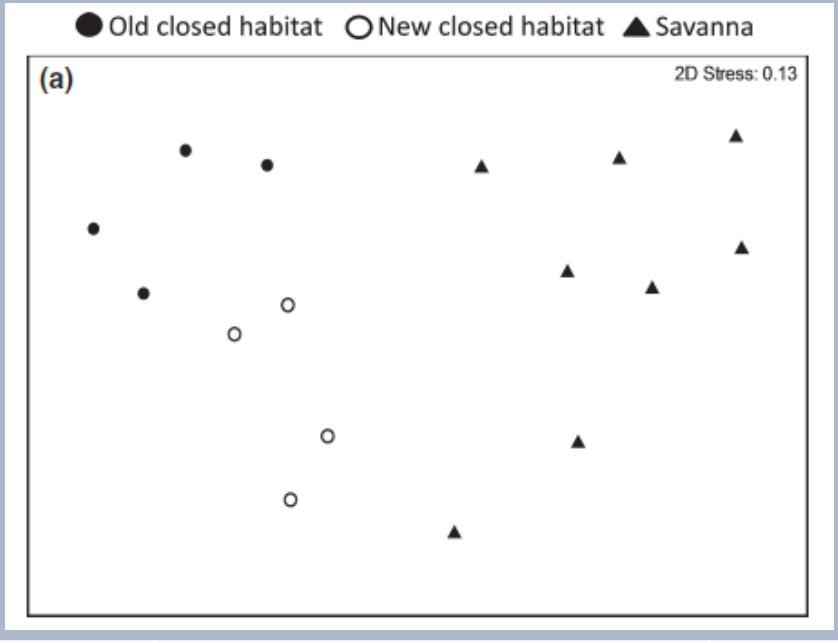
compositional

functional

Hluhluwe-iMfolozi (Parr et al. 2012)

Smaldeel, Eastern Cape

How is this…



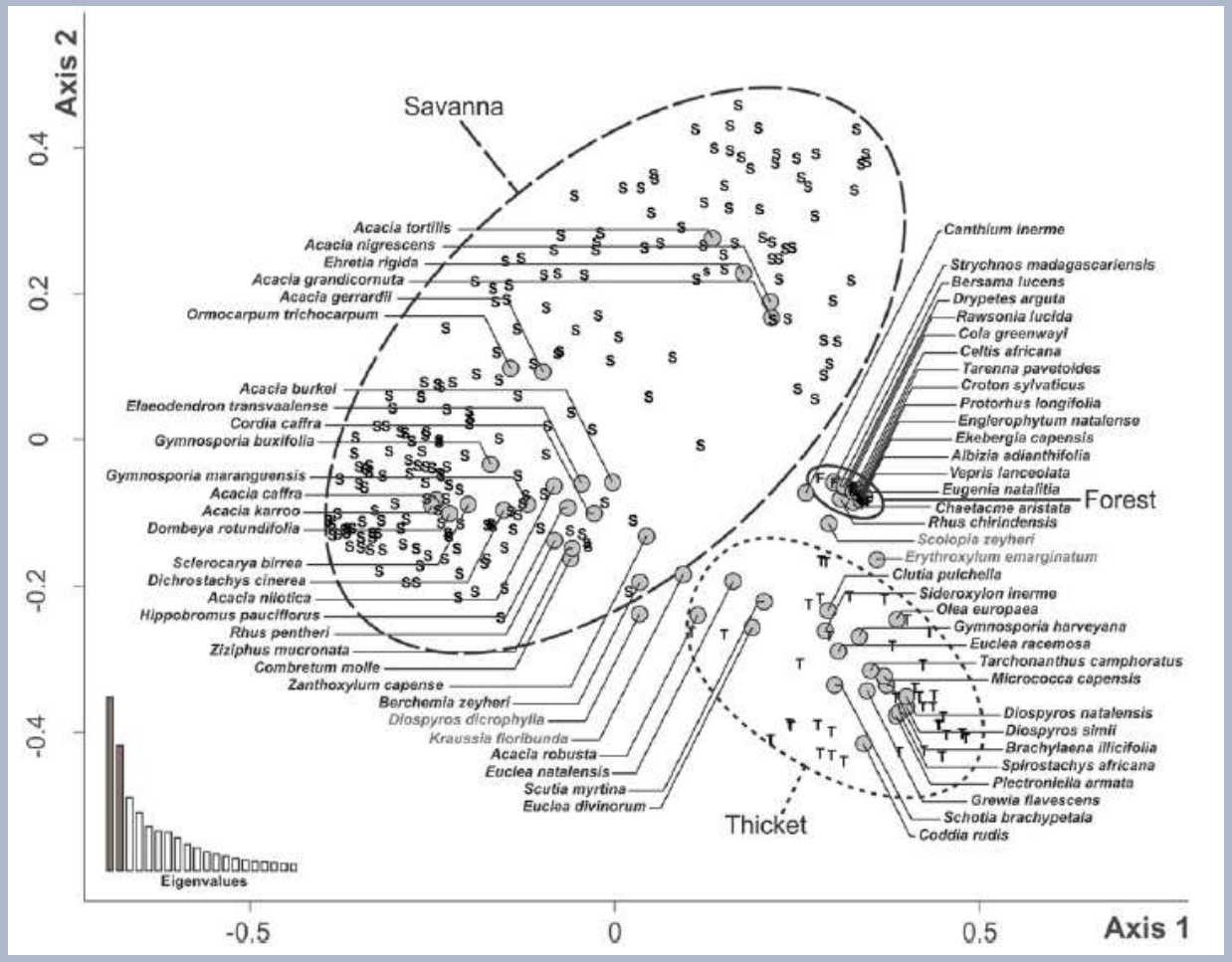
different to this?

	Savanna	Thicket
Woody spp.	*Dichrostachys cinerea* *Acacia karroo*	*Euclea racemosa* *Maytenus heterophylla*
Grasses	*Themeda triandra* *Eragrostis curvula*	*Dactyloctenium australe*

Vegetation composition, Hluhluwe – Parr et al. (2012)

Savanna, thicket and forest:

Found under same soil and climate conditions. Characterised by distinct plant communities:



Charles-Dominique et al. (2015): Hluhluwe

Savanna, thicket and forest:

Characterised and maintained by different processes, feedbacks, and traits:

	Savanna	Thicket	Forest
Light environment	High light	Low light	Low light
Consumer processes	High fire, High grazing	Low fire, High browsing	Fire absent Low herbivory
Grass layer	Continuous, C4 Flammable, Light requiring	Patchy, C3 Not flammable, Shade tolerant	Patchy, C3 Not flammable, Shade tolerant
Woody plants	Fire tolerant, Shade intolerant Many fine-leaved, Low LAI C storage: roots	Fire intolerant, Shade tolerant Broad leaved High LAI C -> growth	Fire intolerant, Shade tolerant Broad leaved High LAI C -> growth

Charles-Dominique et al. (2015): Hluhluwe; Cardoso et al. (2016): Ghana

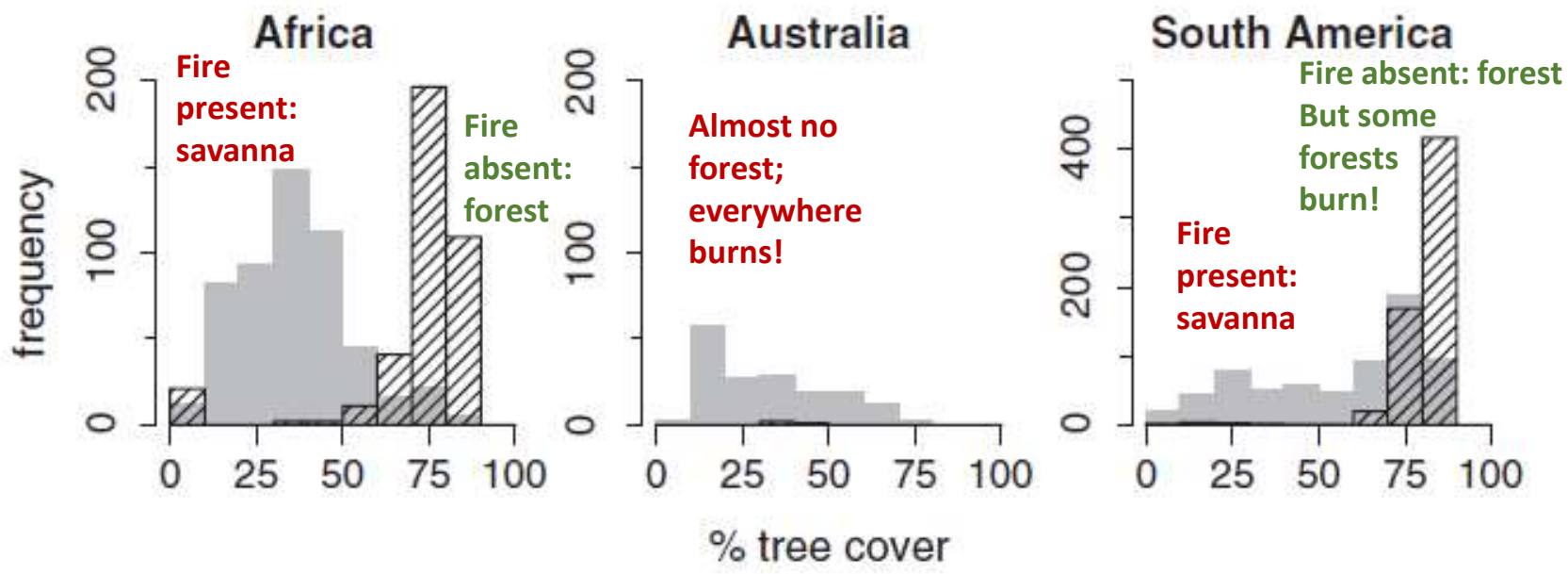
Key process in switch to thicket: loss of a flammable C4 grass layer?

Assumes fire is a key process that maintains savanna structure and function.

What is the evidence?

Savanna and forest both occur between 1000 and 2500 mm rainfall with a dry season < 7 months.

Key determinant: Fire



Frequency distribution of tree cover in areas of intermediate rainfall and mild seasonality.
Grey bars: fire present; hatched bars: fire absent (Staver et al. 2011).

Review of bush encroachment in southern Africa (O'Connor et al. 2014):

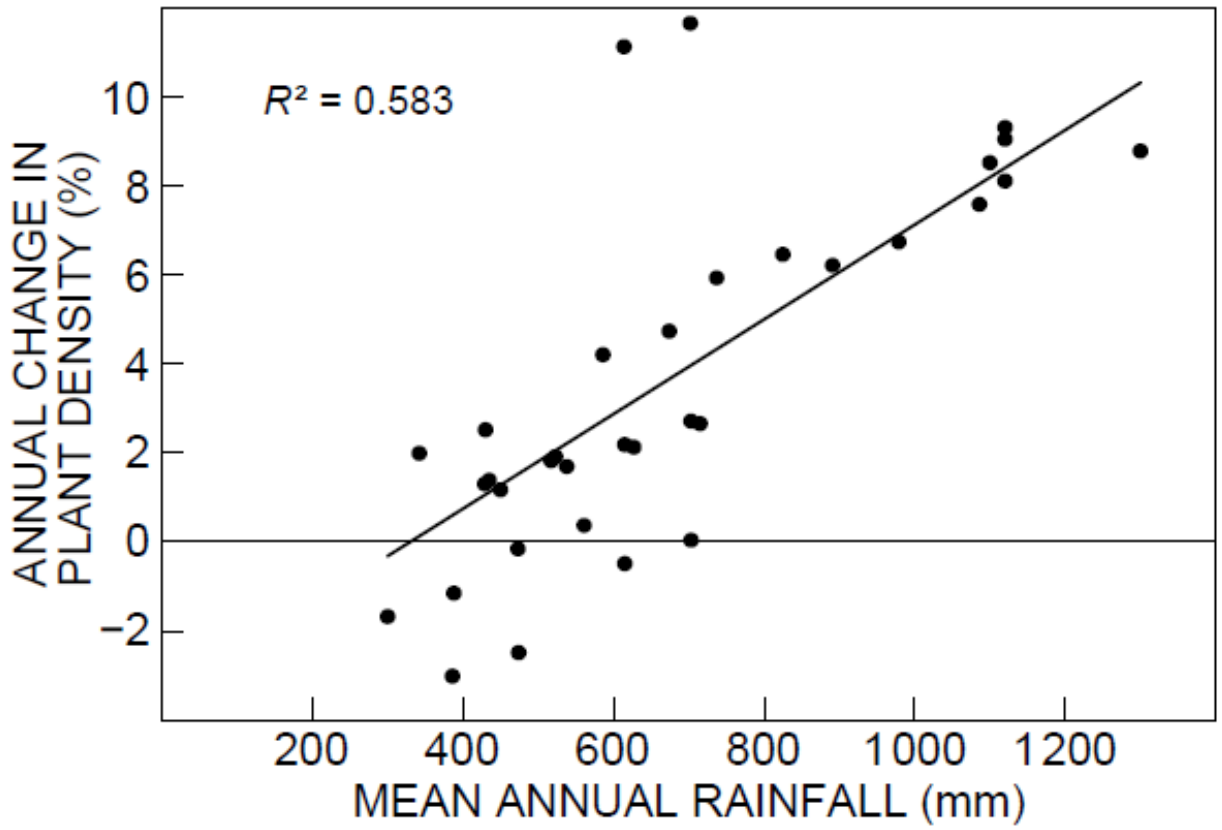
Compared burned and unburned treatments in 28 fire exclusion experiments:

Fire exclusion increased woody density across savanna types ranging from 386 to 1300 mm per annum.

Annual rate of increase in woody density: 6 % greater under fire protection.

Effect of fire suppression increases with rainfall:

Above ~ 700 mm MAP, all unburned sites showed an increase in tree cover!

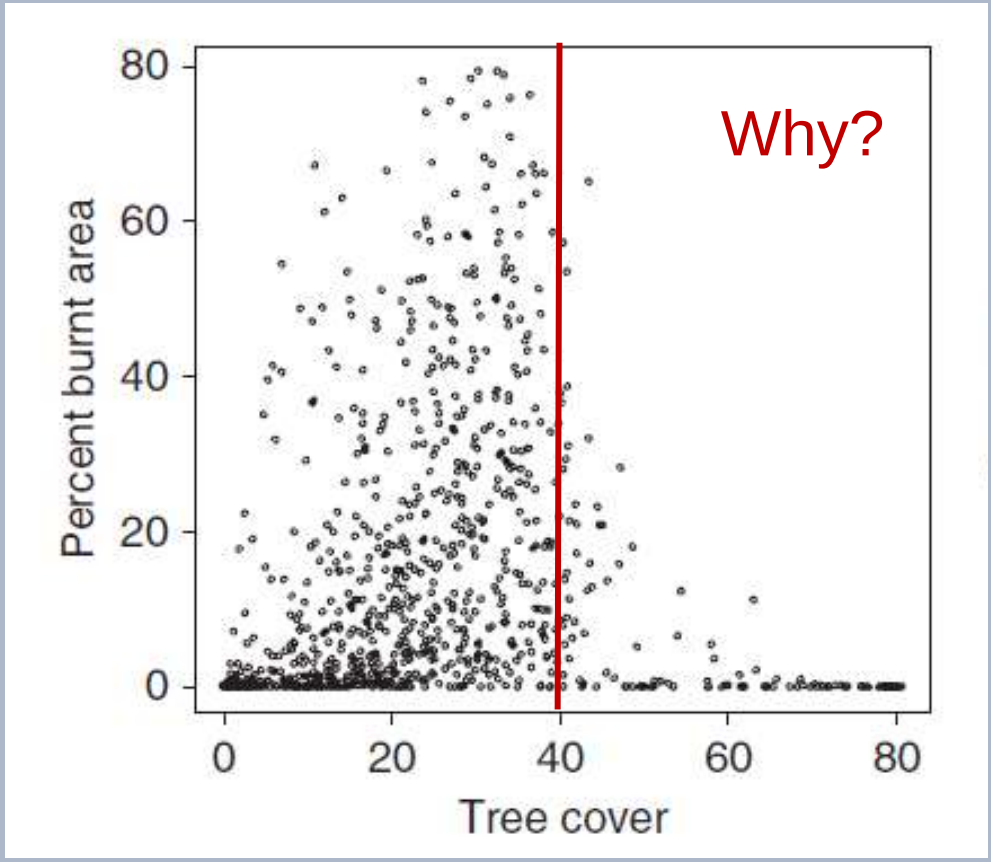


Annual rate of increase in woody plant density on fire-protected plots along a rainfall gradient of the savanna regions of Africa (O'Connor et al. 2014)

Is there a feedback of bush encroachment on probability of burning?

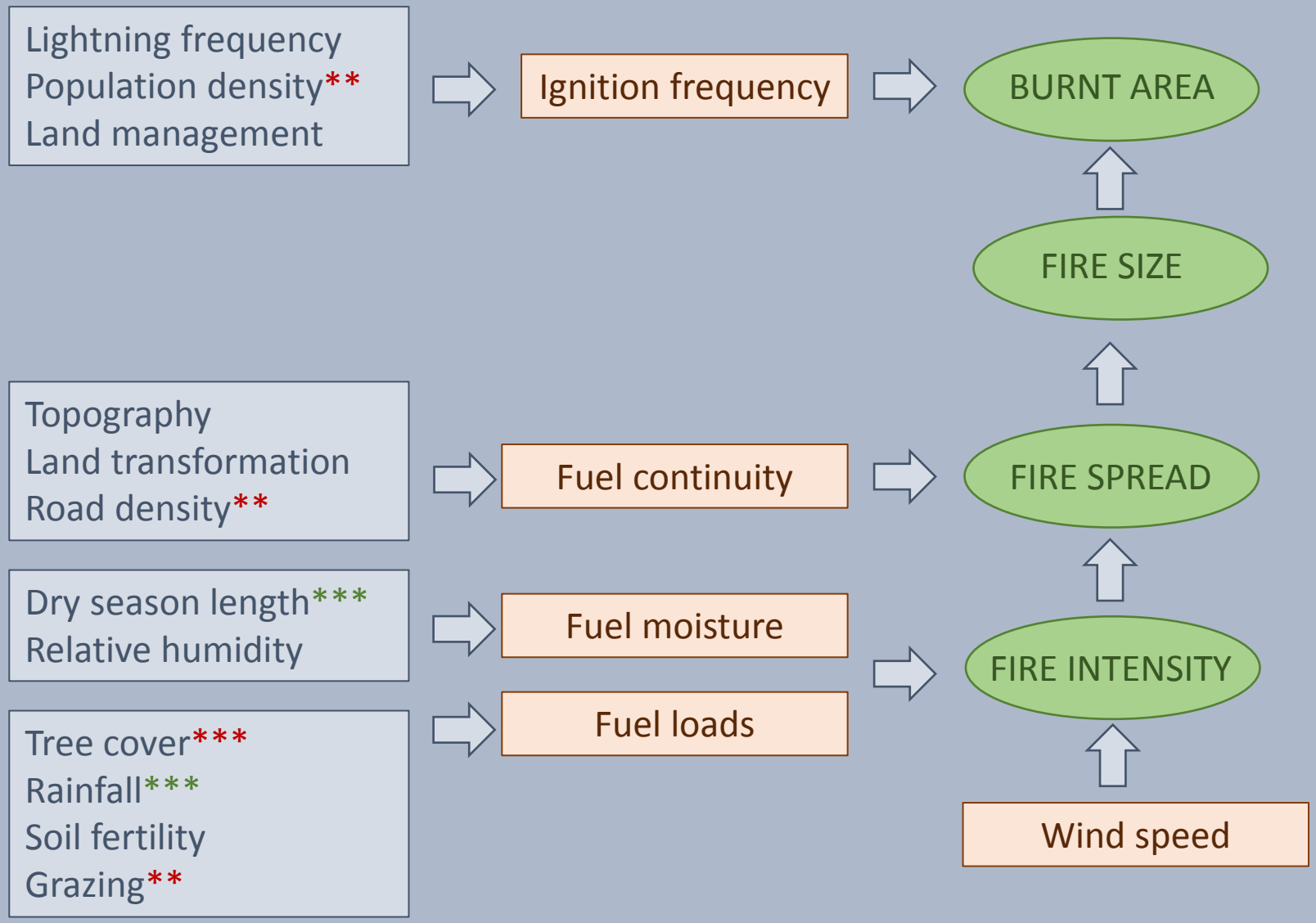
Tree cover suppresses fire spread

Above ~ 40 % tree cover fire no longer spreads.

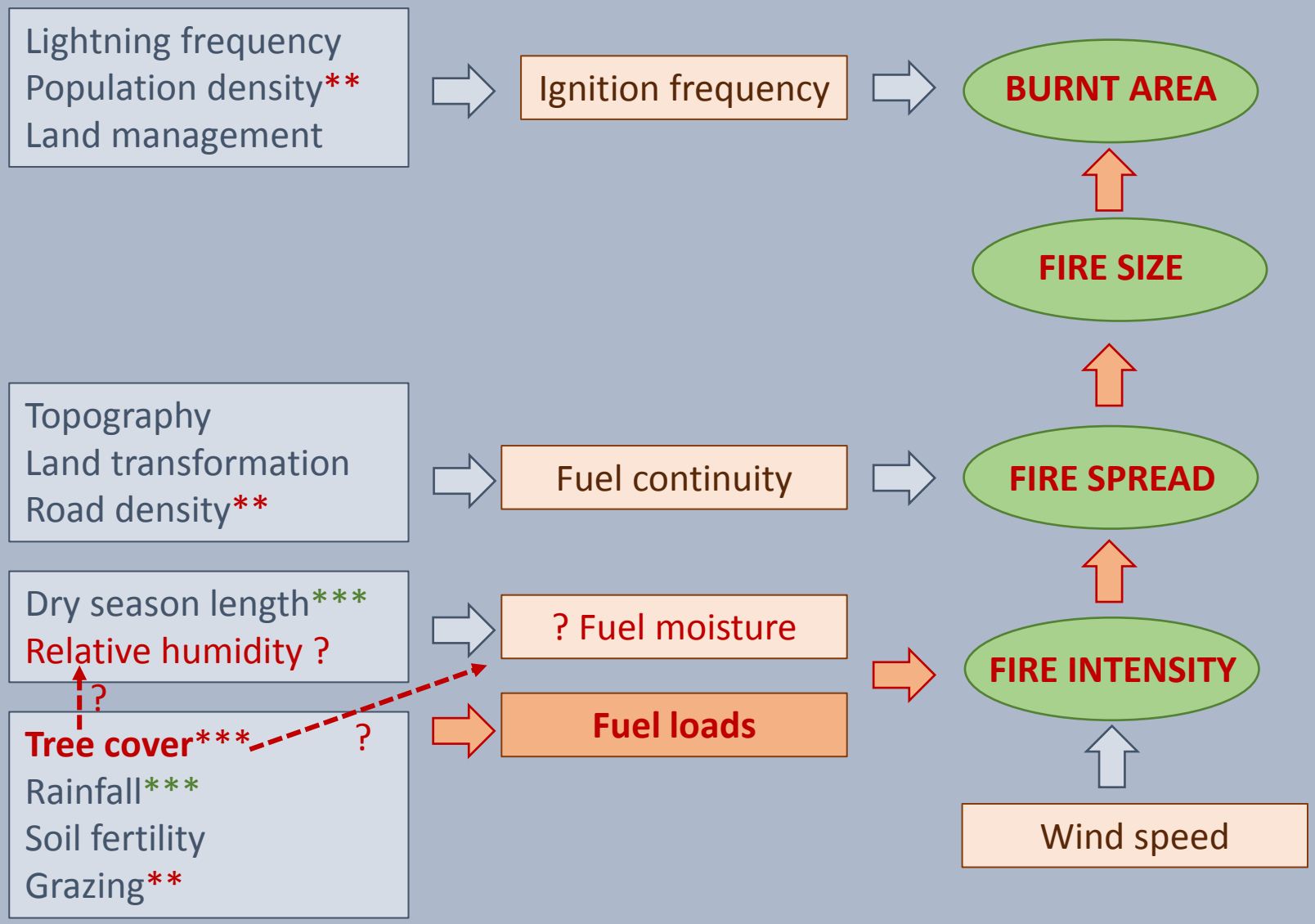


(Archibald et al. 2009)

What limits fire spread? (Archibald et al. 2009)

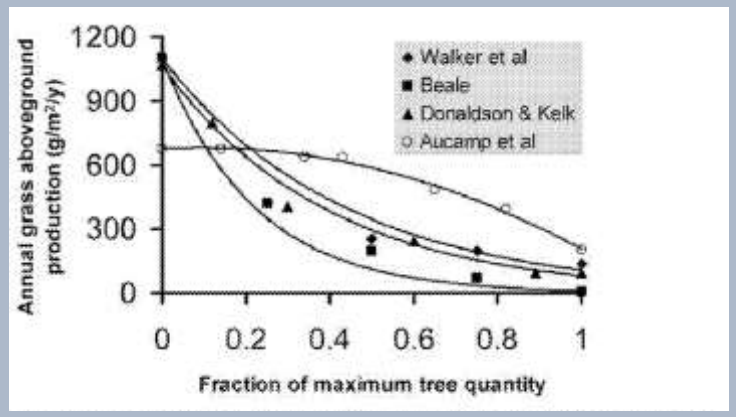


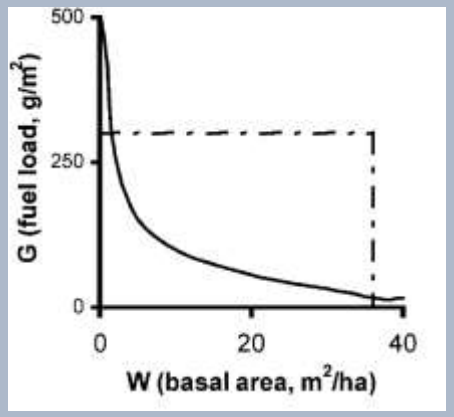
What limits fire spread? (Archibald et al. 2009)



Why does fire stop spreading under dense tree cover?

- reduction in biomass (competition) – Scholes 2003





- change in grass characteristics – less flammable

- altered microclimate – cooler and moister?

- feedbacks with grazing?

Does shade lead to loss of flammable grasses?

Quite a bit of evidence but needs more work!

C4 species have an advantage over C3 grasses under high light (Sage & McKeown 2006, Osborne & Freckleton 2009).

At light transmittance < 20 %, most C4 grasses struggle to grow (Sage 2004).

C4 species unable to utilize sunflecks of short duration (Adams & Ripley, unpublished data)

Can explain loss of continuous C4 grass layer.

But much variation in flammability and fire response among C4 species – needs more exploration.

NB influence of phylogeny and selection pressure in habitat (Ripley et al. 2015).

Flammability and fire response are strongly related.

- Highest in grasses from fire-prone habitats
- Highest among C4 Andropogonae (Ripley et al. 2015)

What traits determine flammability? (Simpson et al. 2016)

Flammability comprises ignitability, sustainability and combustibility.

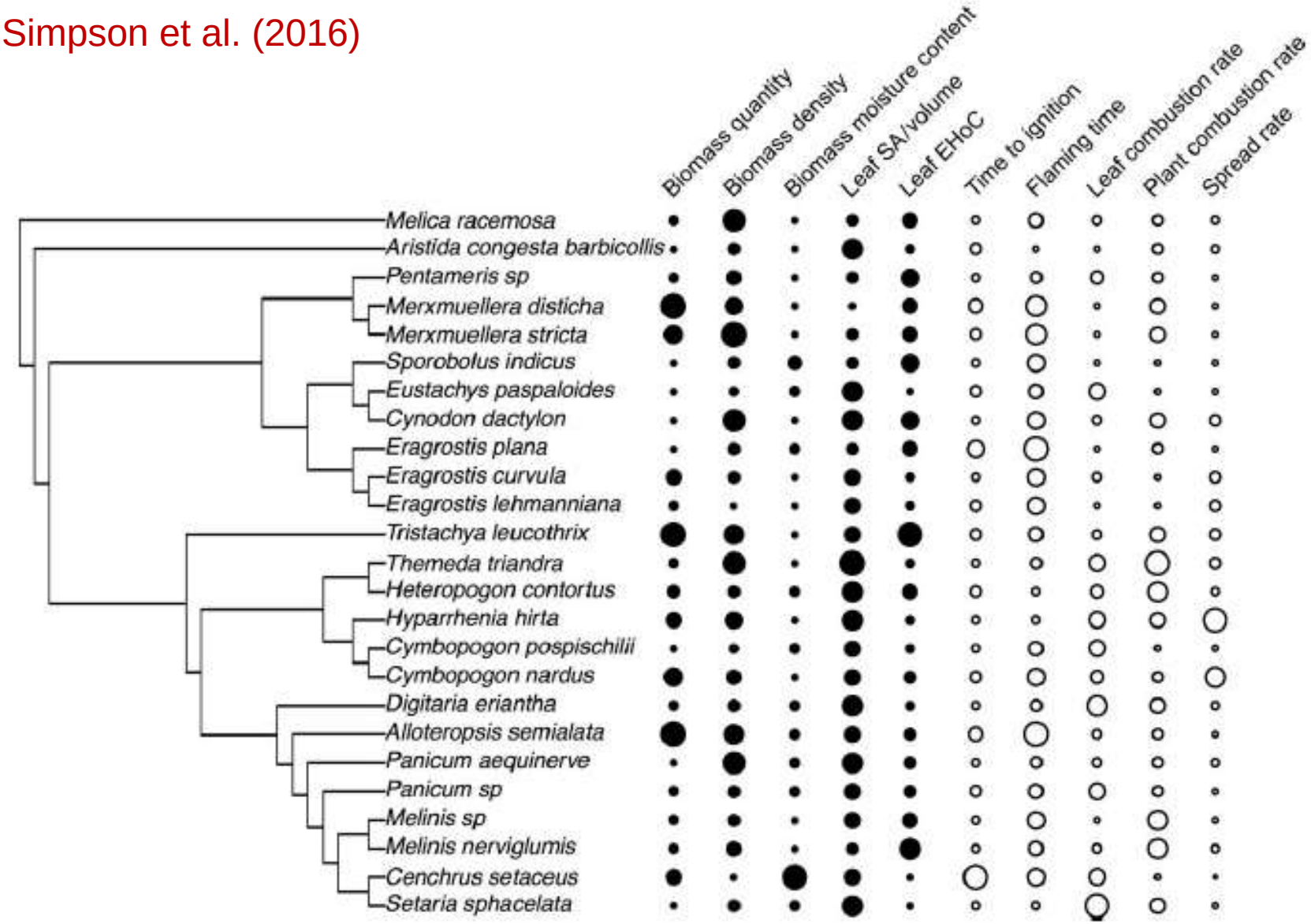
Five traits that were able to predict flammability components:

High total above-ground biomass: burned more intensely and for longer – highest fire spread rates

High moisture content: slower to ignite and burn.

Other predictors of flammability components:
- biomass density
- leaf surface-to-volume ratio
- leaf effective heat of combustion.

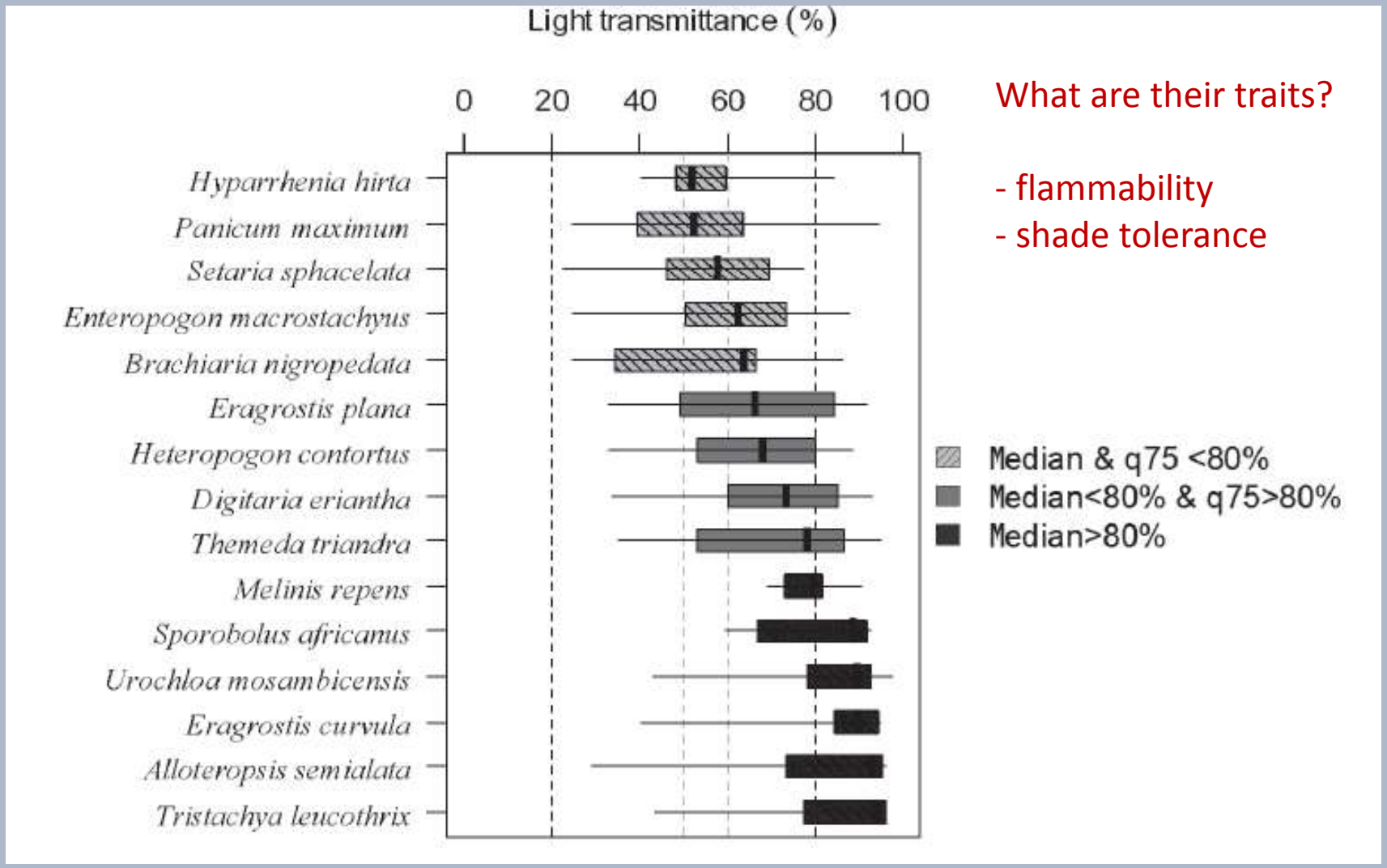
Simpson et al. (2016)



Is there a trade-off between flammability and fire response, and shade tolerance?

Grass species occurrence vs. light transmittance

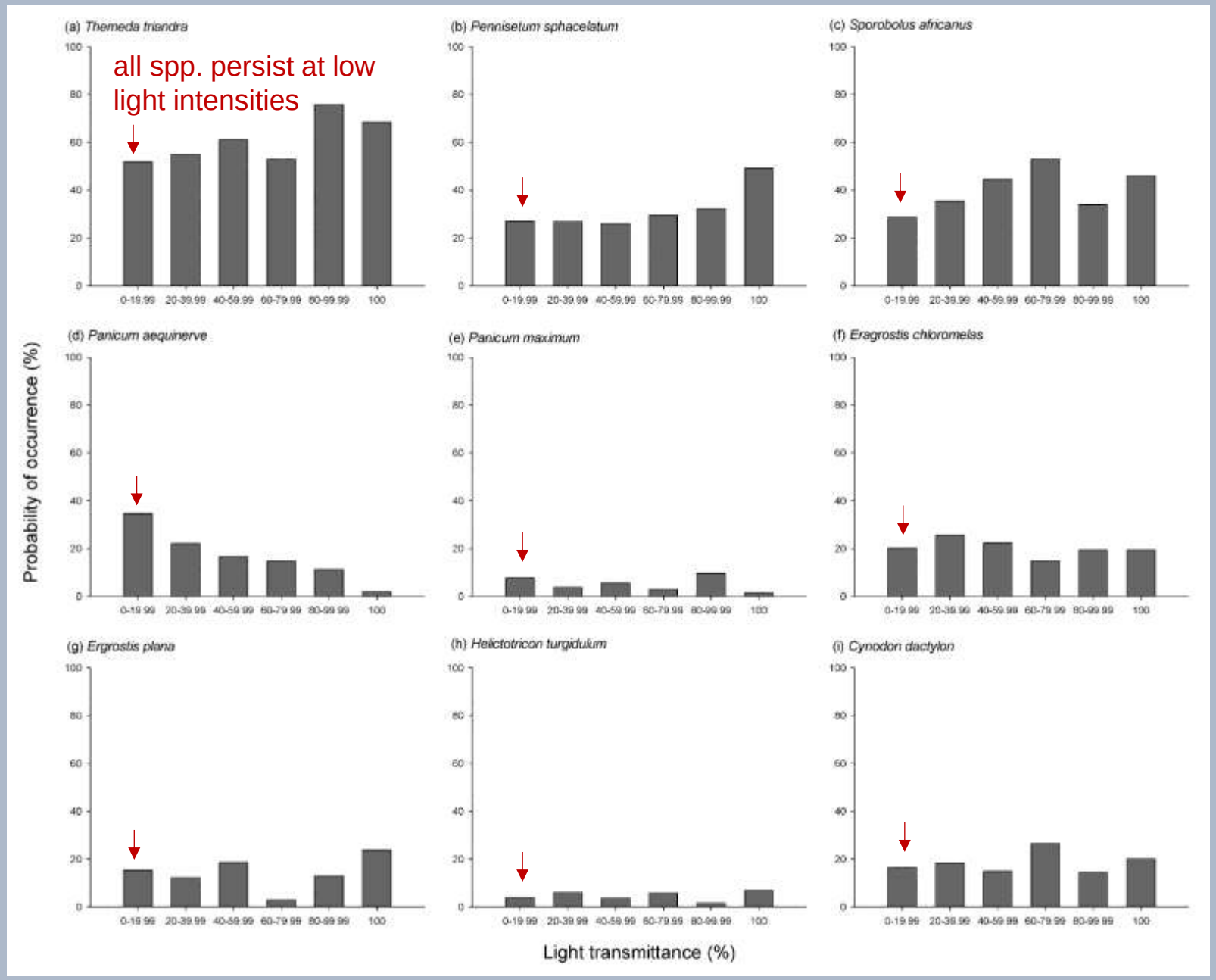
(Nondlazi & Archibald, unpublished data)



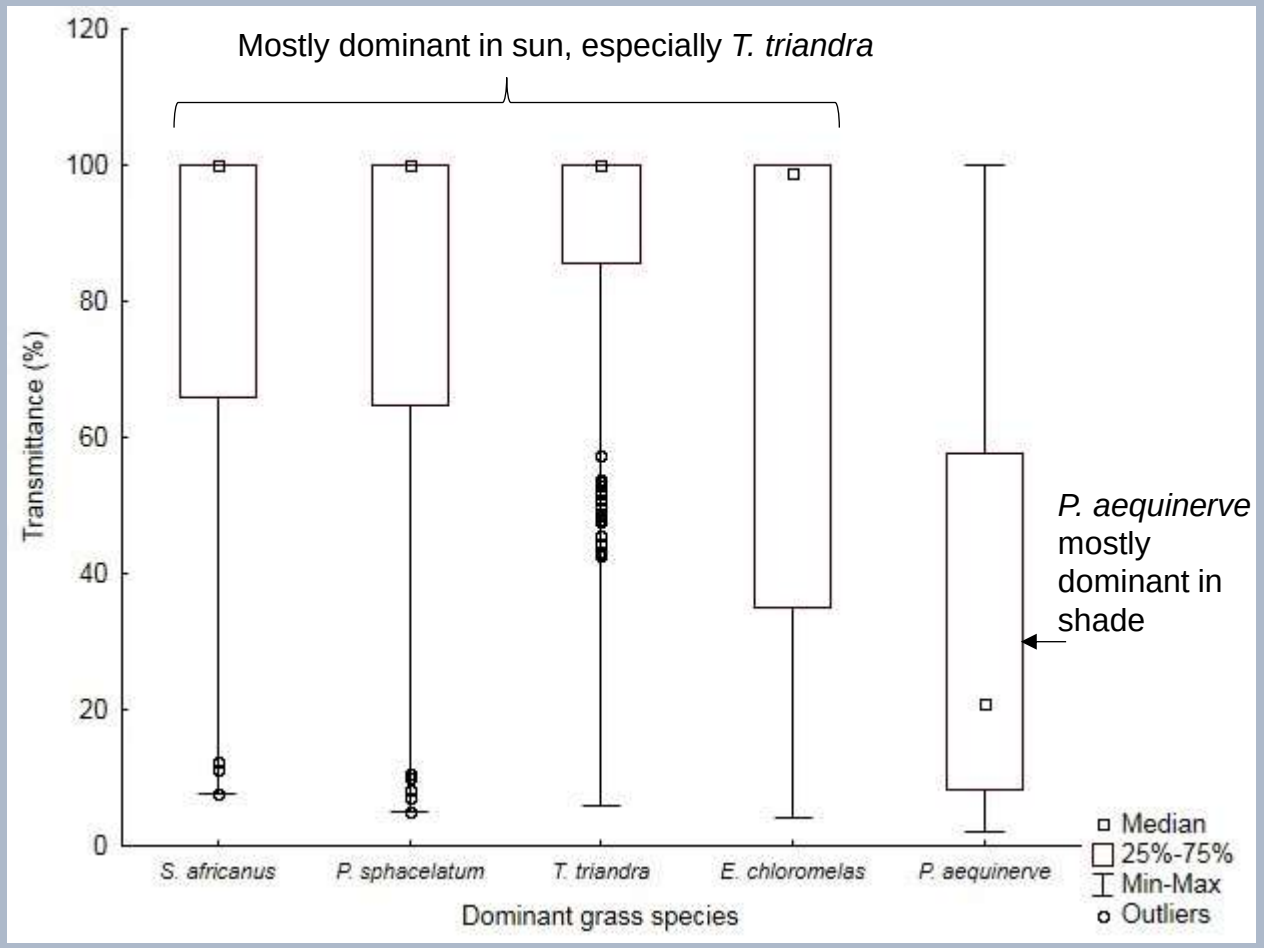
What are their traits?

- flammability
- shade tolerance

Probability of occurrence at different % transmittance (Klopper, unpublished data)



But… at what light transmittance are different grass spp dominant*? (Klopper, unpublished data)



What are their traits?

- flammability
- shade tolerance

* Dominant = most abundant sp. at transect point

Interaction with grazing?

What is the relationship between fire- and grazing tolerance in grasses (and flammability and palatability of the grass sward)?

If a less flammable (and more palatable) grass layer accelerates the loss of fuel and encroachment by trees, what are the implications for land managers?

Many grasses “hang in” under trees if lightly grazed, but this is likely affected by grazing pressure.

Broadleaf thicket pioneers - the woody key players?

Particular life history:

- Bird dispersed – colonise areas with some trees, initiate thicket clumps

- Can resprout after fire or browsing – able to push into grass layer*

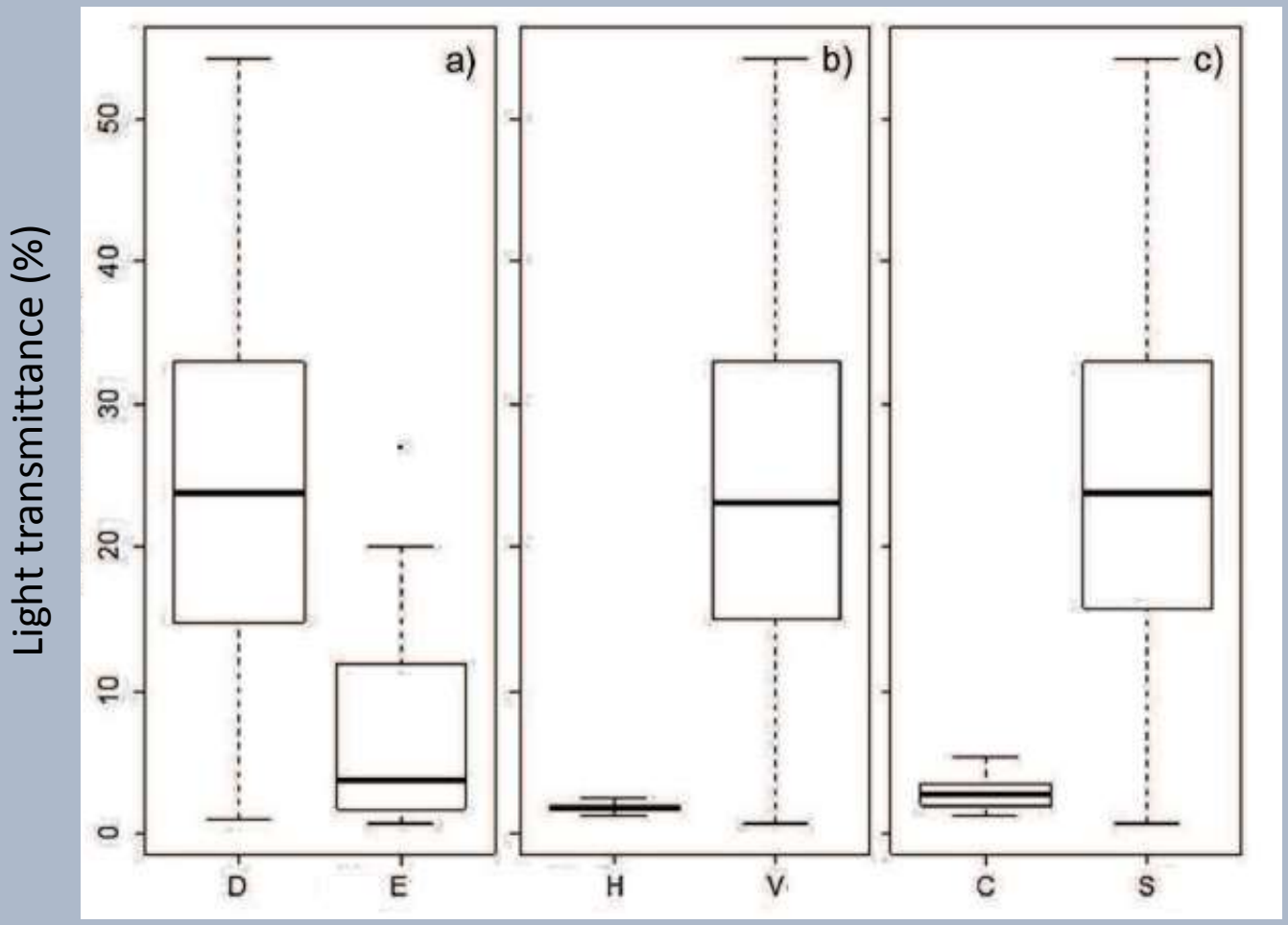
- Transmit less light – form dense canopies and eventually clumps, eliminate C4 grasses

Example: *Euclea* spp. (Smith & Goodman 1987, Skowno et al. 1999 in SA, Sharam et al. 2006 in Serengeti)

* Cardoso et al. (2016) experimentally planted and burned seedlings of 5 pioneer tropical forest tree spp in Ghana. Found that species that invested in starch storage coped best with fire.

Effect of canopy traits on light transmittance

(Nondlazi & Archibald, unpublished data)



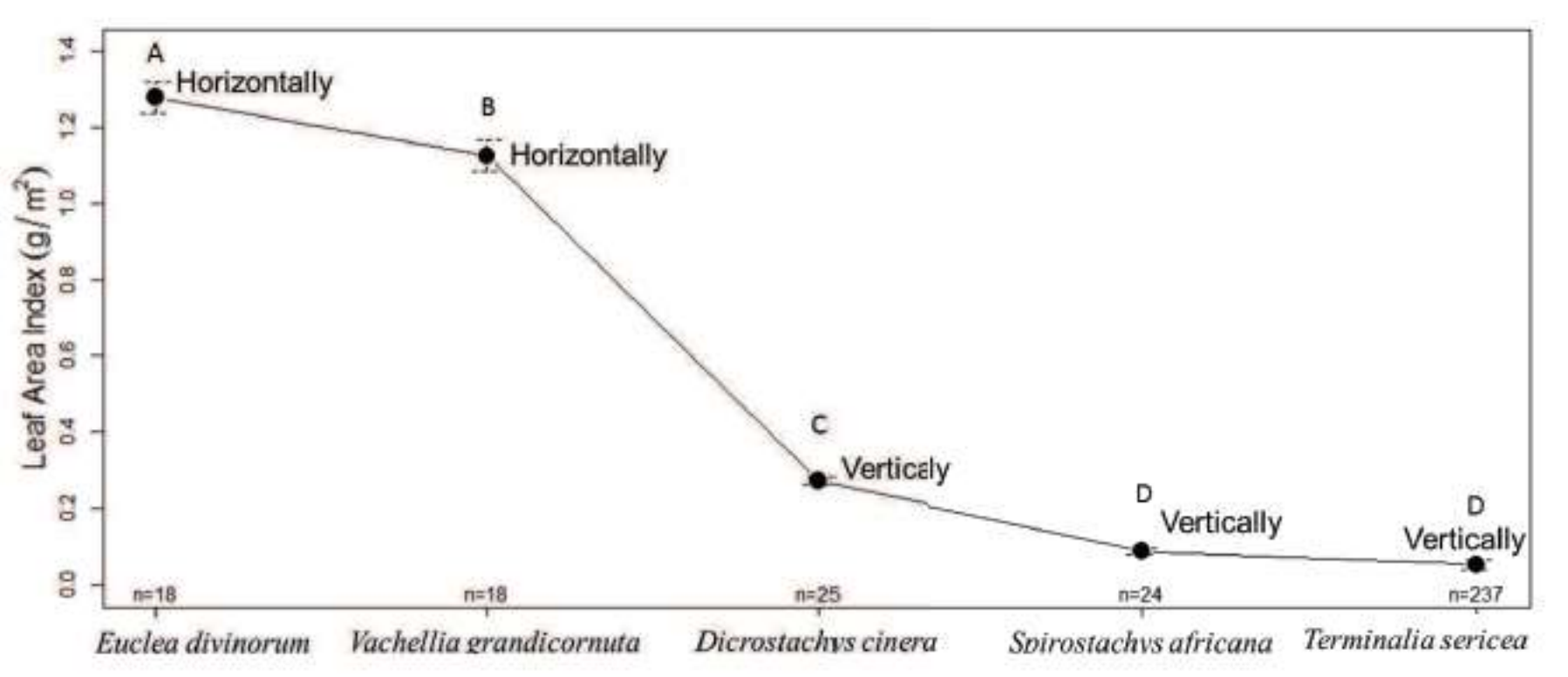
Deciduous > Evergreen

Horizontally << Vertically angled leaves

Compound << Simple leaves

Effect of canopy traits on light transmittance

(Nondlazi & Archibald, unpublished data)



Importance of scale:

Species response to environment, resultant species replacements, recruitment of seedlings: can occur over large areas but process operates at small spatial scales (microhabitat).

Feeding by grazers and browsers – selective at the species-, patch- and area scale.

Fire spread – a landscape scale phenomenon but dependent on emergent properties of grass layer.

Interactions between patches important.

Much work at camp / plot (community) level but need to integrate from ecophysiology of individual plants of different spp. to landscape level processes.

Management – recognise and target crucial transitions?

- Recruitment of savanna tree seedlings

- Establishment of broadleaf seedlings

- Formation of thicket clumps

- Alteration in grass layer – loss of biomass and replacement of flammable with shade tolerant species

Key traits that reduce incidence of fire:

- Woody plants: LAI, tree architecture – traits that shade out grasses

- Grasses: traits associated with low flammability

For different contexts:

- What is the end point of bush encroachment?

- what are the key species or traits that indicate a critical state, but which can still be reversed?

- What is the most effective control?
  - NB fire vs. browsing
  - related to climate, soil fertility, evolutionary history?

Different scenarios for arid, eutrophic, dystrophic savannas?