
Does mega-herbivory limit tree recruitment?

Results and implications of a herbivore
exclusion experiment in Hluhluwe iMfolozi

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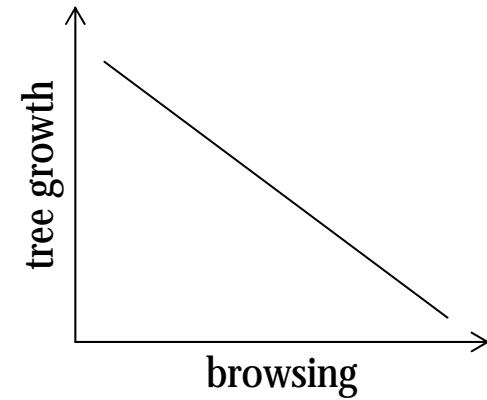
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Introduction

- What prevents the emergence of new large trees into a savanna system?
 - Basic limitations of fire on recruitment of trees from juvenile (small) to adult (large) life stages
 - e.g. Higgins *et al.* 2001
 - What about herbivory?
 - Especially in an African context, where native herbivores are still a part of the system
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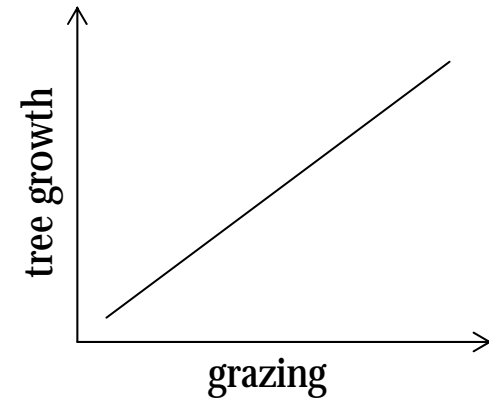
Browsing?

- Browsing acts directly on the tree layer
 - Particularly on small trees (Roques *et al.* 2001)
 - Browsers may regulate shrub and tree dynamics in savanna landscapes (Augustine & McNaughton 2004, Prins & van der Jeugd 1993)



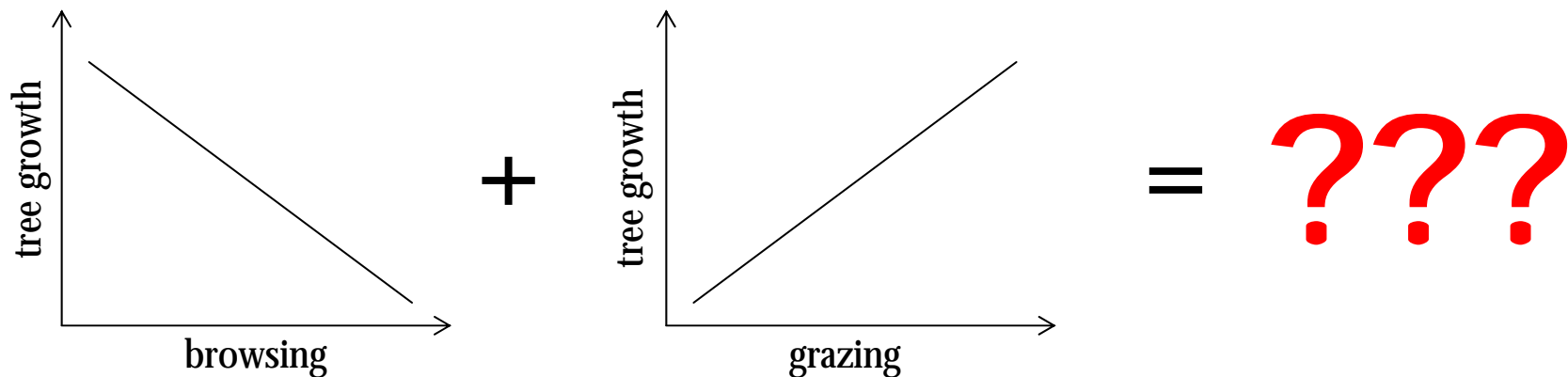
Grazing?

- Grazing by mega-herbivores is a major consumer of grass biomass
 - “Competes” directly with fire for fuel
 - Contributes to patchiness in the fuel layer → fires spread less easily
 - Less competition from grasses?
- From rangelands, cattle grazing often leads to bush encroachment (e.g. Roques *et al.* 2001)



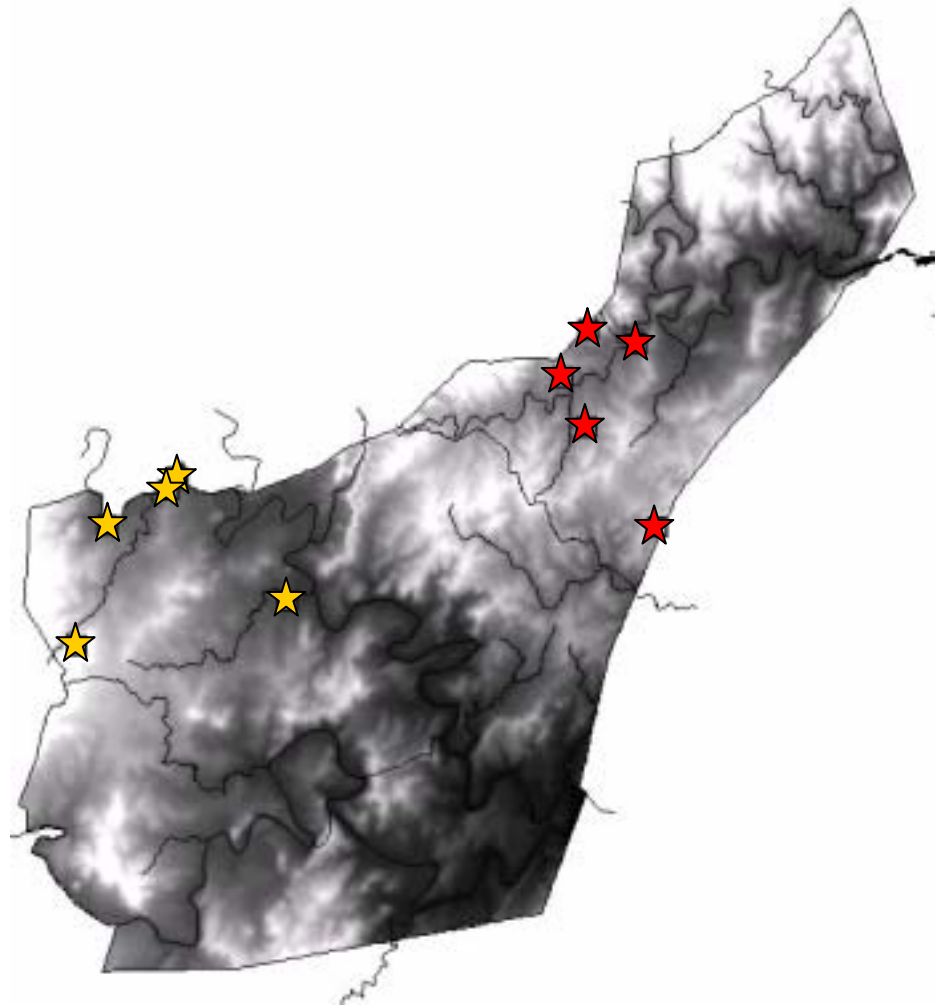
Browsing v. grazing

- Both grazers and browsers present in native assemblages of African herbivores
- How does mega-herbivory affect tree growth in African savannas?
 - In which circumstances is browsing the major driver?
 - In which circumstances does grazing and its effect on grass?



The Experiment

- Two parks
 - Hluhluwe GR
 - cooler in summer
 - wetter
 - fire more frequent
 - fewer herbivores
 - iMfolozi GR
 - hotter
 - drier
 - fire less frequent
 - more herbivores



The Experiment

**Highest
herbivory**



**Lowest
herbivory**

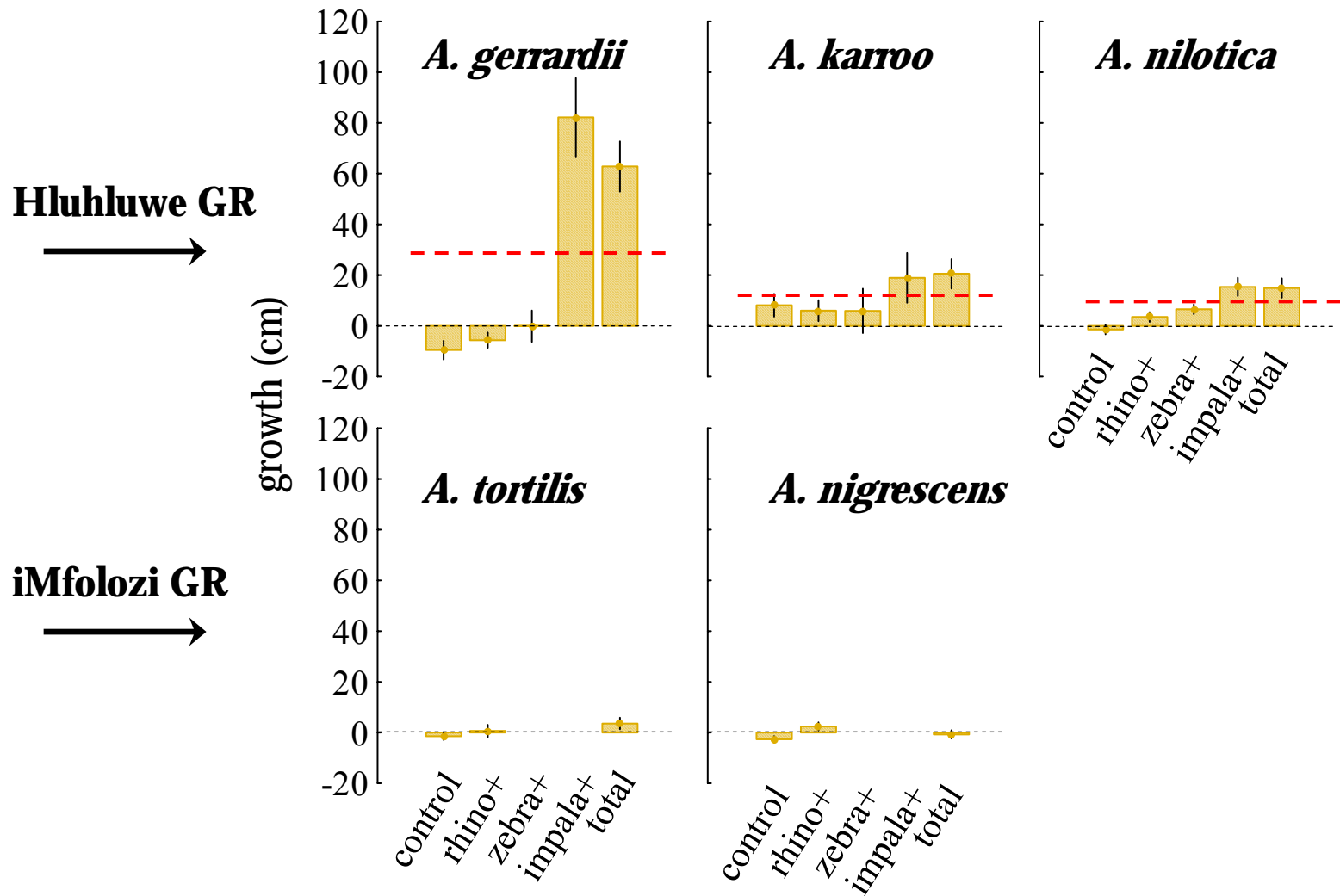


**None =
Control (Co)**

**Rhino and
larger (Rh+)**

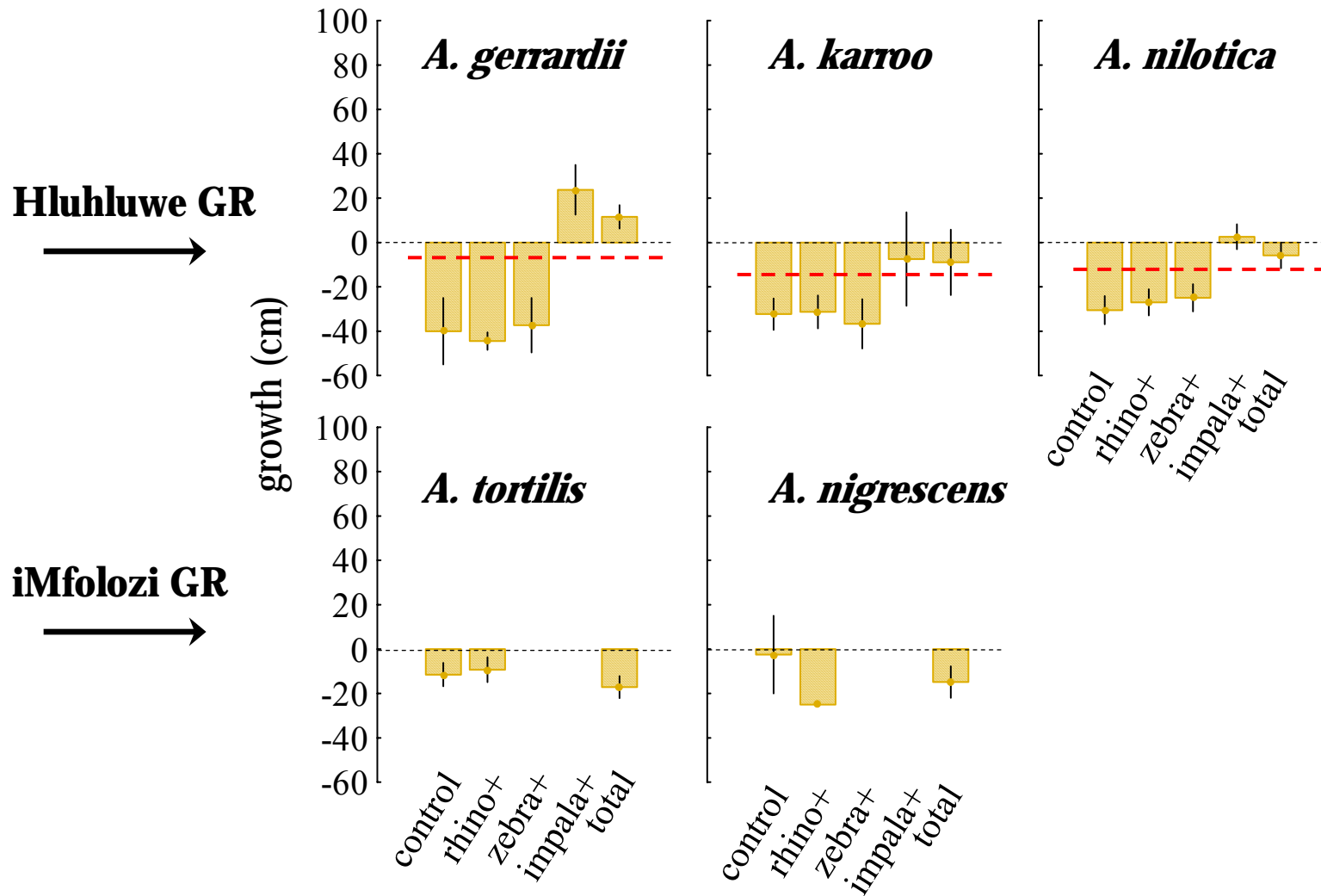
**All = Exclosure
(Ex)**

Height growth of small trees (ht<50cm)



Hluhluwe: *A. gerrardii* $p < 0.0001$, co=rh+=z+<im+=ex *A. karroo* $p = 0.33$ *A. nilotica* $p = 0.0006$, co<z+=im+=ex
iMfolozi: *A. tortilis* $p = 0.18$ *A. nigrescens* $p = 0.047$, co<rh+

Height growth of saplings (50cm < ht < 150cm)



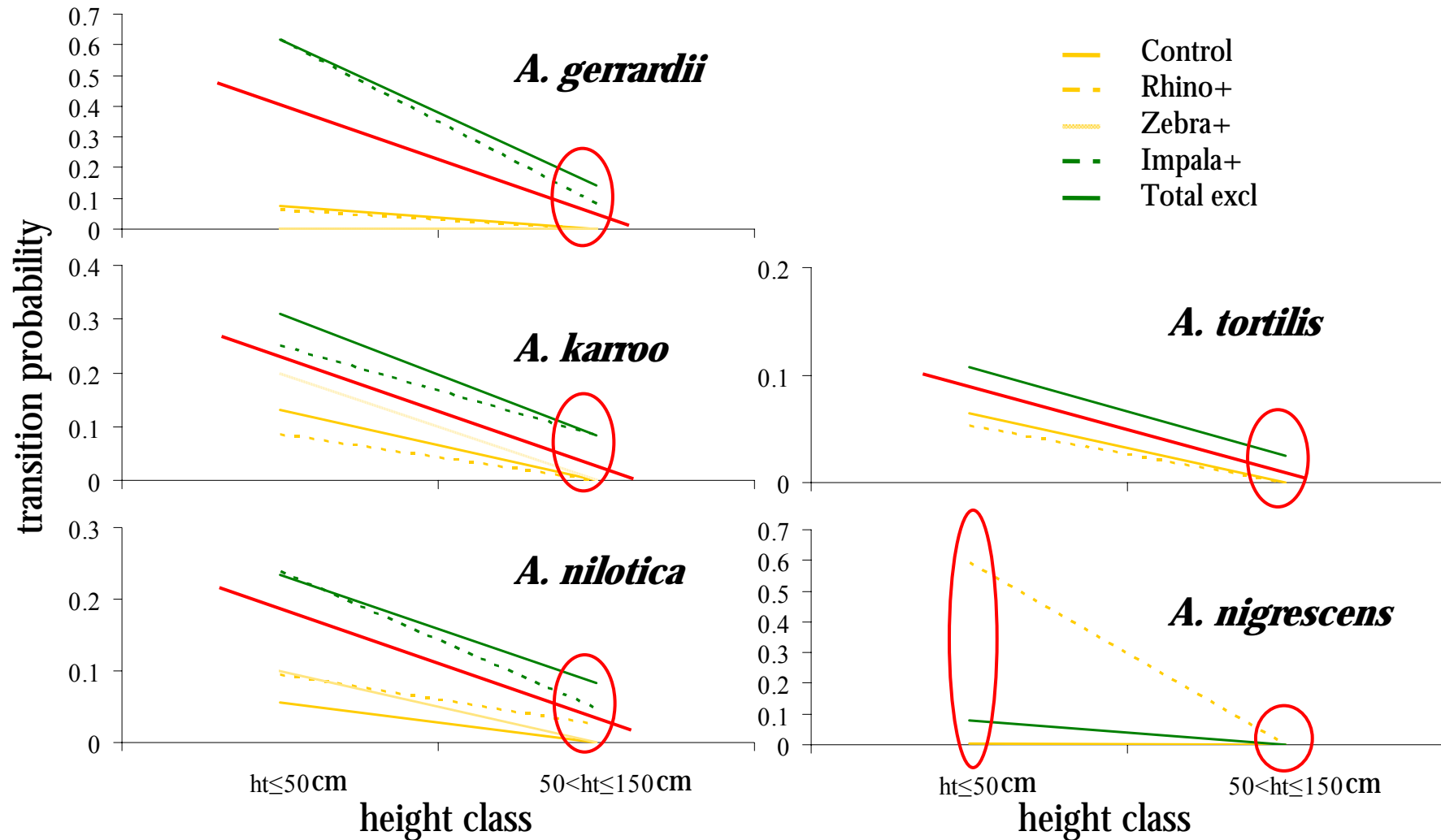
Hluhluwe: *A. gerrardii* $p < 0.0001$, rh+=z+ < im+=ex *A. karroo* $p = 0.60$ *A. nilotica* $p < 0.0001$, co=rh+=z+ < im+=ex
iMfolozi: *A. tortilis* $p = 0.62$ *A. nigrescens* $p = 0.65$

Proportion of trees growing into larger ht classes

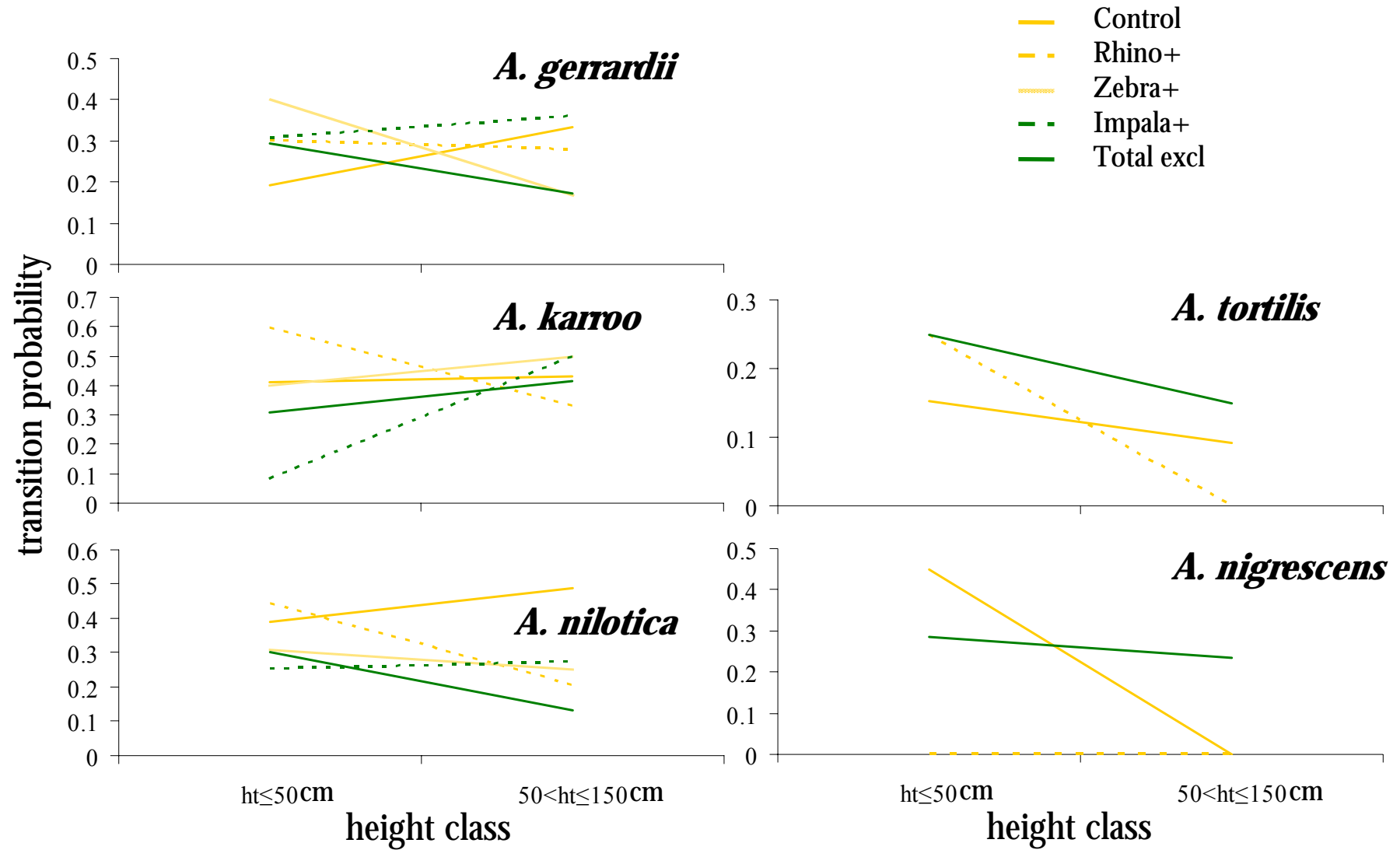
- Do changes in growth translate into population growth?



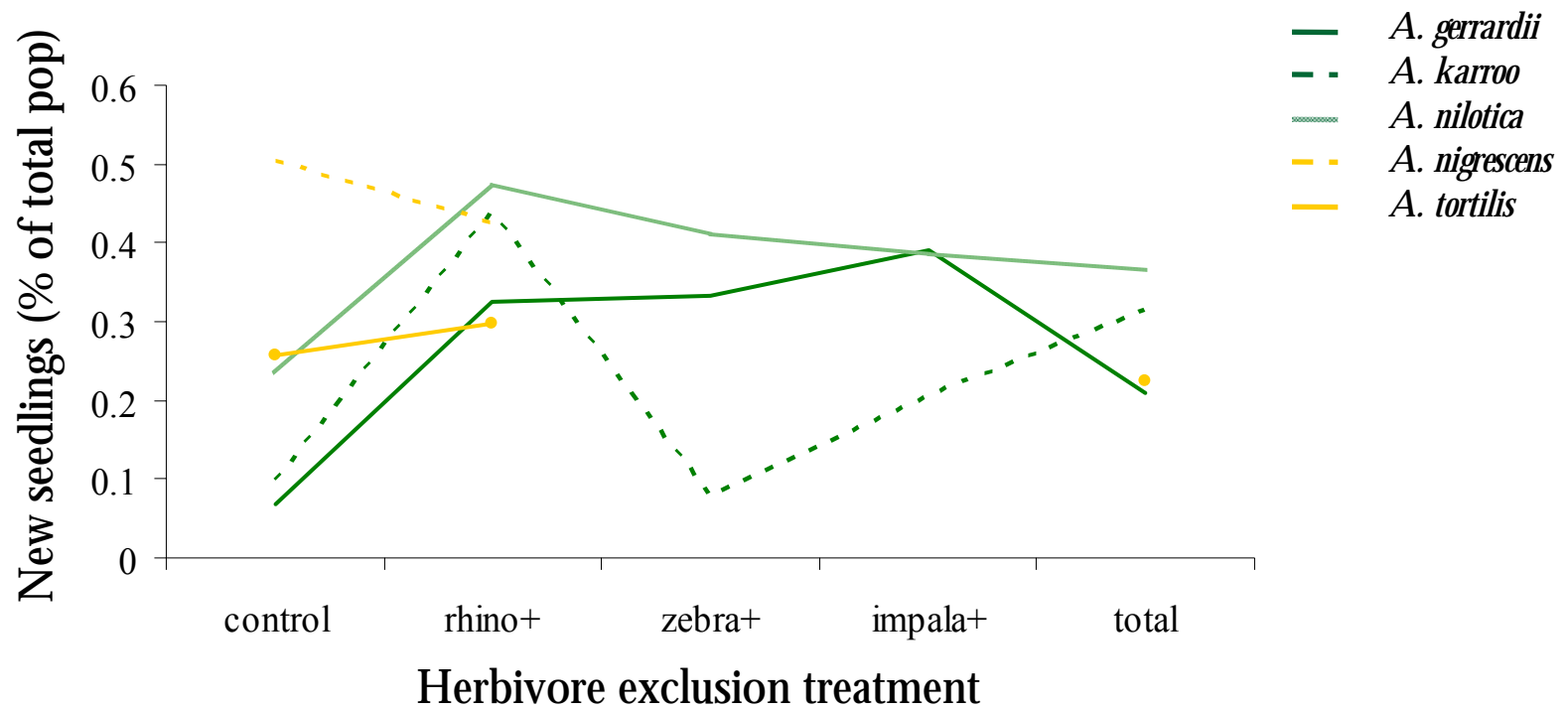
Proportion of trees growing into larger ht classes



Mortality



Seedling recruitment



Conclusions – what type of driver is herbivory?

- Herbivory does not consistently impact mortality or recruitment
 - Herbivory substantially affects tree growth
 - Herbivory acts to suppress populations of small trees in a persistence life-stage = a demographic bottleneck!
 - In certain circumstances, removal of herbivory results in the release of these individuals
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Keystone species?

- In Hluhluwe, the exclusion of impala from heavily grazed areas seems to make the functional difference for tree growth
- Why would intense grazing result in suppressed tree population growth rather than bush encroachment?



↖ control

total exclusion ↗

Keystone species?

- In native assemblages of African mega-herbivores, some grazers *are* browsers
 - ❑ Mixed feeders are a rare phenomenon
 - ❑ Only impala and nyala in Hluhluwe iMfolozi NP
- Perhaps grazing lawns can occur with their peculiar structure and form because of the proliferation of mixed feeders in African savannas?



Keystone species?

- In iMfolozi, the signal is less clear
 - Only 3 herbivore exclusion treatments: control, rhino ex, total ex
- Even so, pattern not necessarily consistent with that found in the 5 Hluhluwe treatments
- Interaction with increasing grass growth as grazing decreases appears to be more important in regulating tree growth

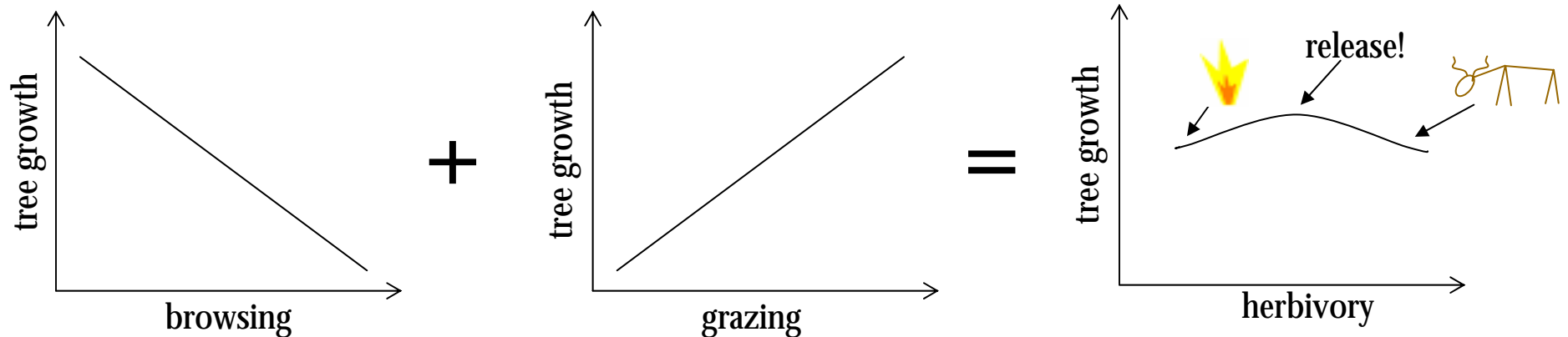


Fire/herbivore interaction

- Release from impala may be sufficient for Hluhluwe *Acacias* to recruit
 - Fire-adapted so fire less of a problem?
 - Release from grazing in iMfolozi results in increased fire intensity
 - Herbivore-adapted so fire more of a problem?
 - Recruitment may only occur when trees are relieved from both herbivory and fire → RAINFALL
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Conclusions

- Influence of herbivory non-linear & interactive
 - ❑ Is the system is herbivore- or fire-dominated?
 - ❑ Species?
 - ❑ Temporal variation?



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