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The diversity and biomass of savanna ungulates respond differently to land use, resources gradients and drought

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Environmental concerns in the Kenyan Mara

- human population growth[1]
- climate change[1, 2]

Maasai Mara National Reserve, Kenya

[1]Ogutu et al. 2016, [2]Bartzke et al. 2018

Environmental concerns in the Kenyan Mara

Human use

- settlements[1] and livestock[2, 3]
- fences[4], tourism and infrastructure[5]
- agriculture[6]

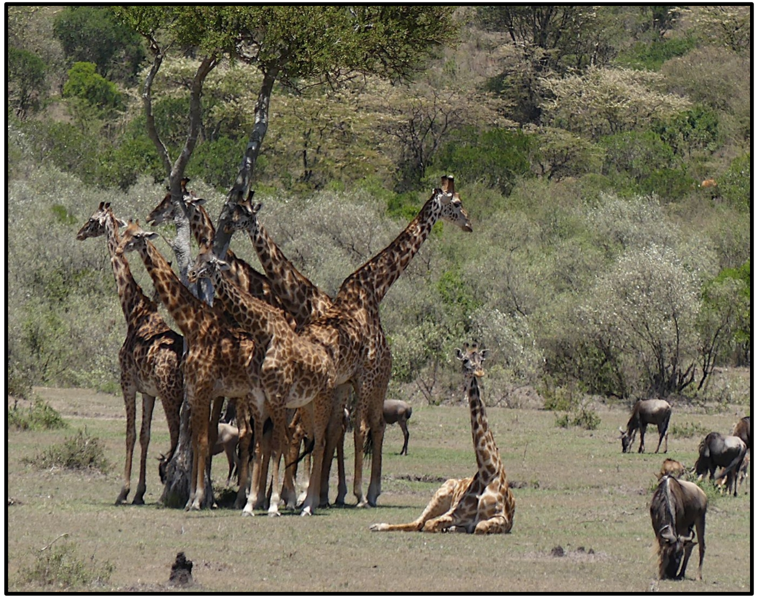
Boma in Maasai Mara, Kenya, 2017

1Lamprey & Reid 2004, [2]Ogutu et al. 2016, [3]Bhola et al. 2012, [4]Løvschal et al. 2022, [5]Green et al. 2019, [6]Veldhuis et al. 2016

Environmental concerns in the Kenyan Mara

Climate change

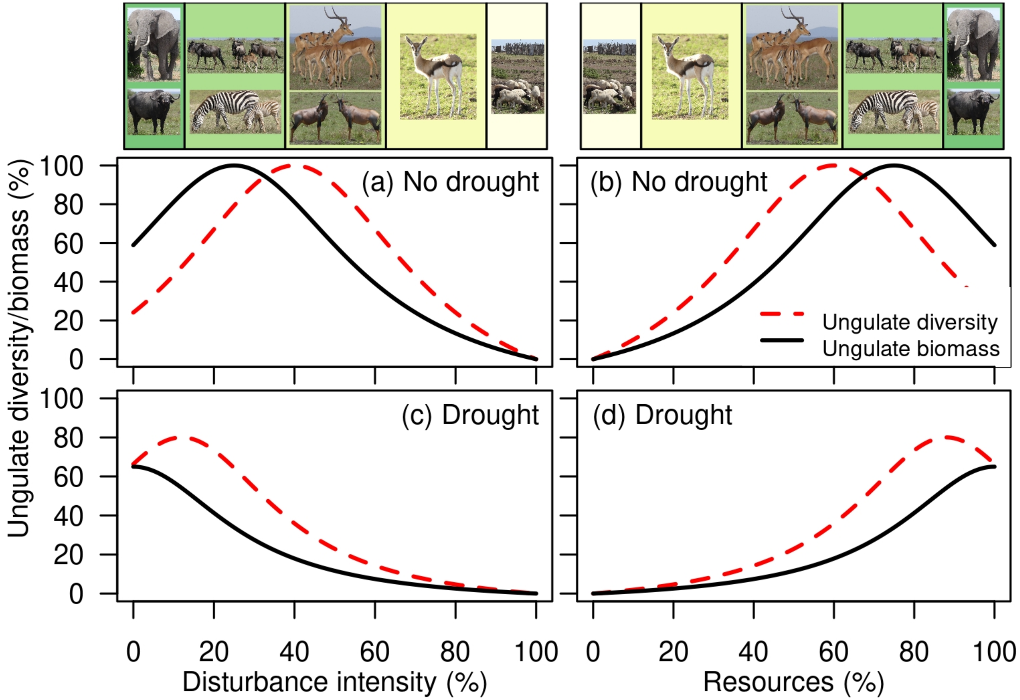
- increasing temperatures, droughts and floods[1, 2]
- changes in environmental resources[3]



Drought in Mara Reserve, Kenya, 2017

[1]Ogutu et al. 2016, [2]Bartzke et al. 2018, [3]Li et al. 2020

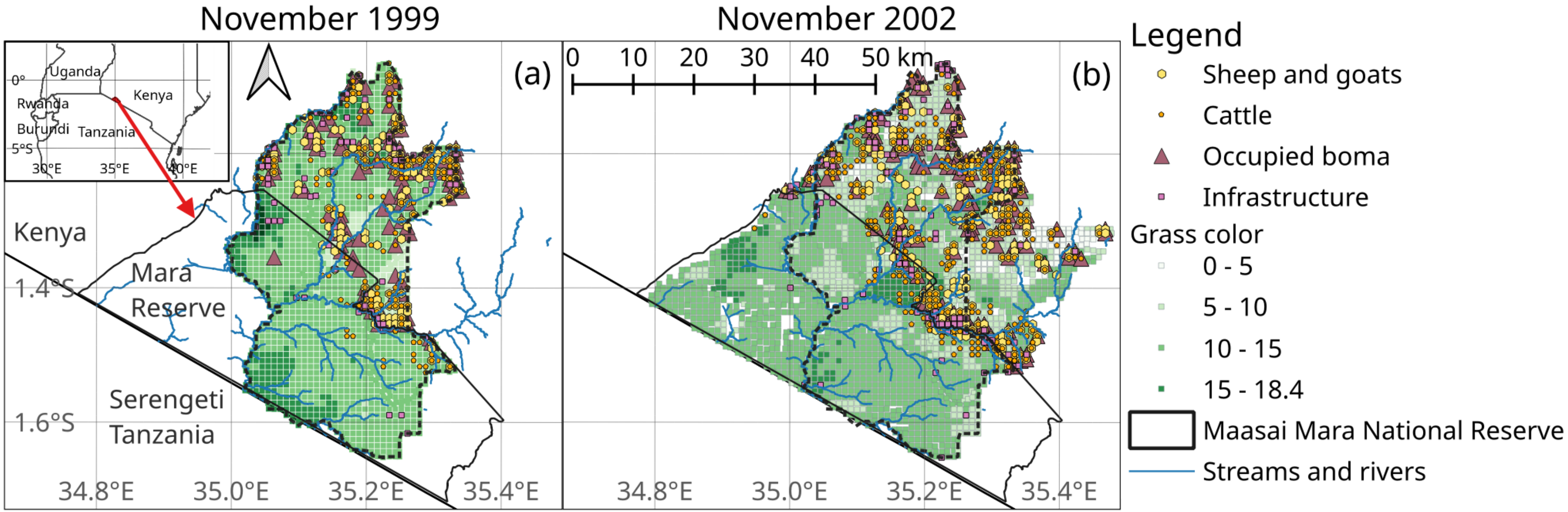
Conceptual framework



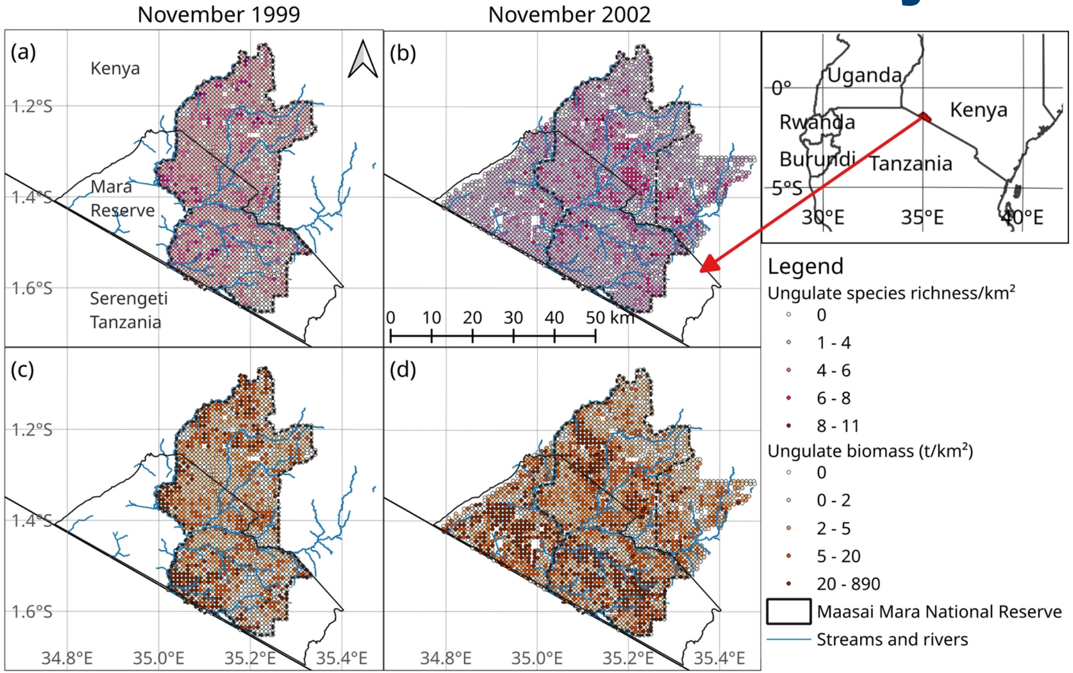
Hypothetical change in the peak diversity (red dotted lines) and peak biomass (black lines) of African savanna ungulates during normal rainfall (a, b) versus drought (c, d) in relation to disturbance intensity (a, c) and resources (b, d).

Connell 1978, Grime and S. Pierce 2012a, b

Human use in the drought year of 1999 and in the normal rainfall year of 2002



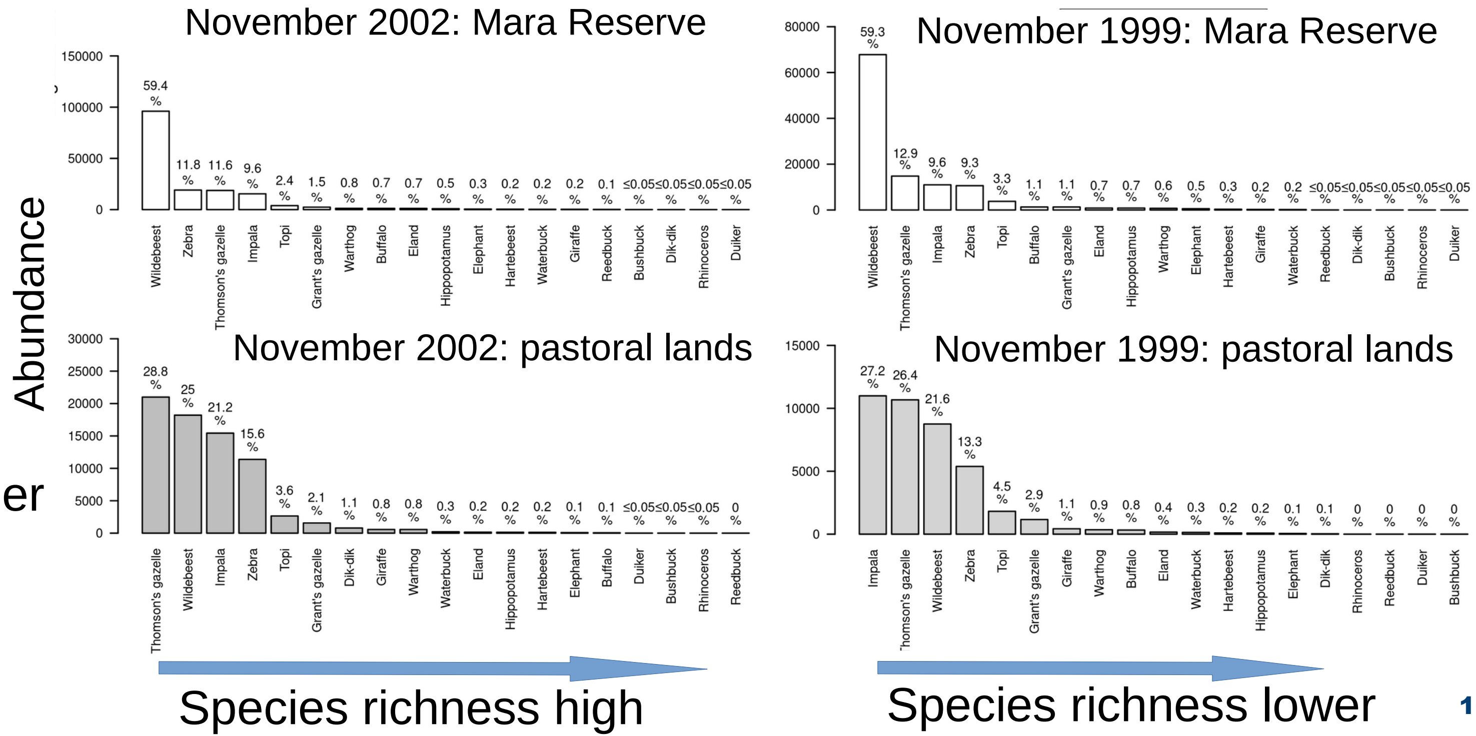
Ungulate species richness and biomass in the drought year of 1999 and in the normal rainfall year of 2002



Ungulate diversity in the Kenyan Maasai Mara

Species evenness low

Species evenness higher



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Measurements of ungulate diversity

- raw species richness
- bias-adjusted species richness ^{0}D
- Shannon diversity ^{1}D
- Simpson diversity ^{2}D
- species evenness ^{10}D

Wild ungulates in the Maasai Mara National Reserve, Kenya, in 2017

^{q}D: bias-adjusted effective number of ungulate species (Hill numbers; Hill 1973, Marcon and Hérault 2015)

Environmental predictor variables

space, census year, landuse

human use

- distances to the reserve boundary, to occupied or abandoned bomas, and to infrastructure
- sheep and goats, cattle, fire
- vehicles, litter

Cattle (*Bos indicus*) in the Maasai Mara National Reserve, Kenya, in 2017

Reid et al. 2003, Ogutu et al. 2010, 2014

Environmental predictor variables continued

resources

- distance to water
- rainfall
- vegetation: grass, shrub and tree cover, height or color
- slope and elevation
- carnivores

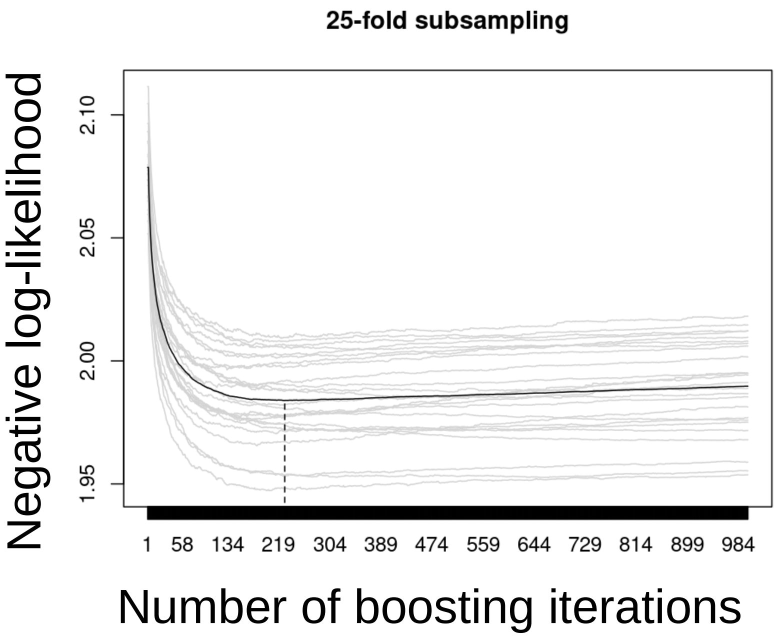
River with *Hippopotamus amphibius* in the Maasai Mara National Reserve, Kenya, in 2017

Hyena (*Crocuta crocuta*) in the Maasai Mara National Reserve, Kenya, in 2017

Reid et al. 2003, Ogutu et al. 2010, 2014

Data analysis: boosted regression models

- machine learning method
- can identify few informative out of many possibly correlated predictors
- simultaneous model fitting and automatic variable selection, tuned by the number of boosting iterations



Hothorn et al. 2011, Hofner et al. 2016, Mayr et al. 2012

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Generalized additive models for location, scale and shape

$$f(\mathbf{x}, s, \mathbf{t}, \mathbf{z}, \boldsymbol{\psi}) = \underbrace{\sum_{k \in A \setminus C \cup \{s\}} f_{envt}(x_k, \mathbf{t}, \psi_k)}_{\text{time-varying environmental component}} + \underbrace{\sum_{k \in A \setminus \{s\}, m \in C} f_{envz}(x_{k_m}, \mathbf{z}, \psi_{k_m})}_{\text{time- and location-varying environmental components}} + \underbrace{f_{st}(s, \mathbf{t}, \psi_s)}_{\text{spatio-temporal component}}$$

x predictors
s space
t census years
z locations (Mara Reserve or pastoral lands) in each census year
ψ distribution parameters

- penalized regression spline base learners for continuous predictors and linear base learners for categorical predictors

Mayr et al. 2012

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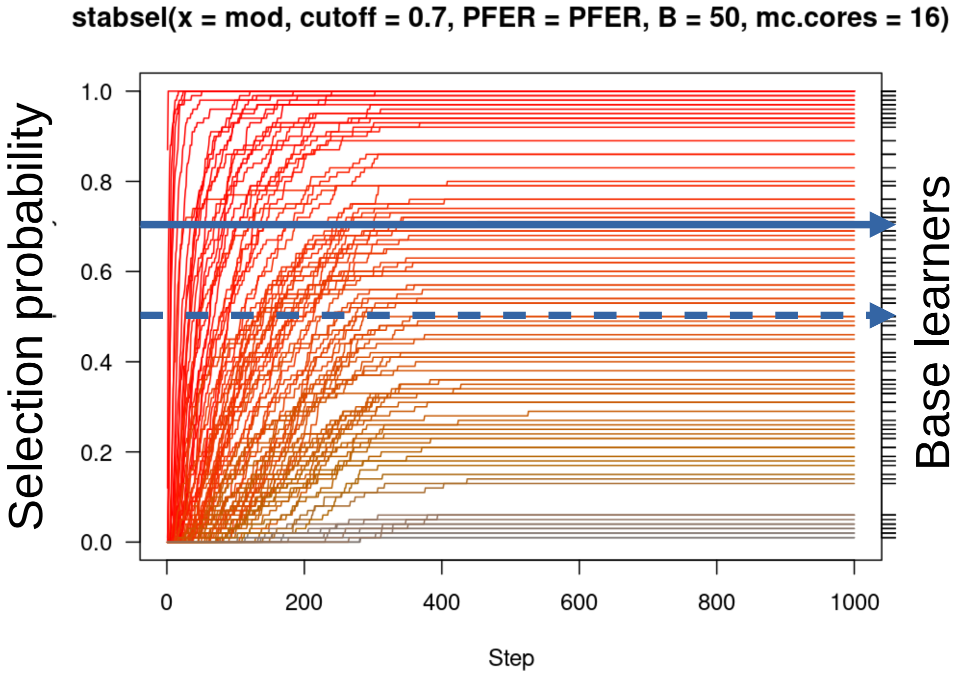
Stability selection



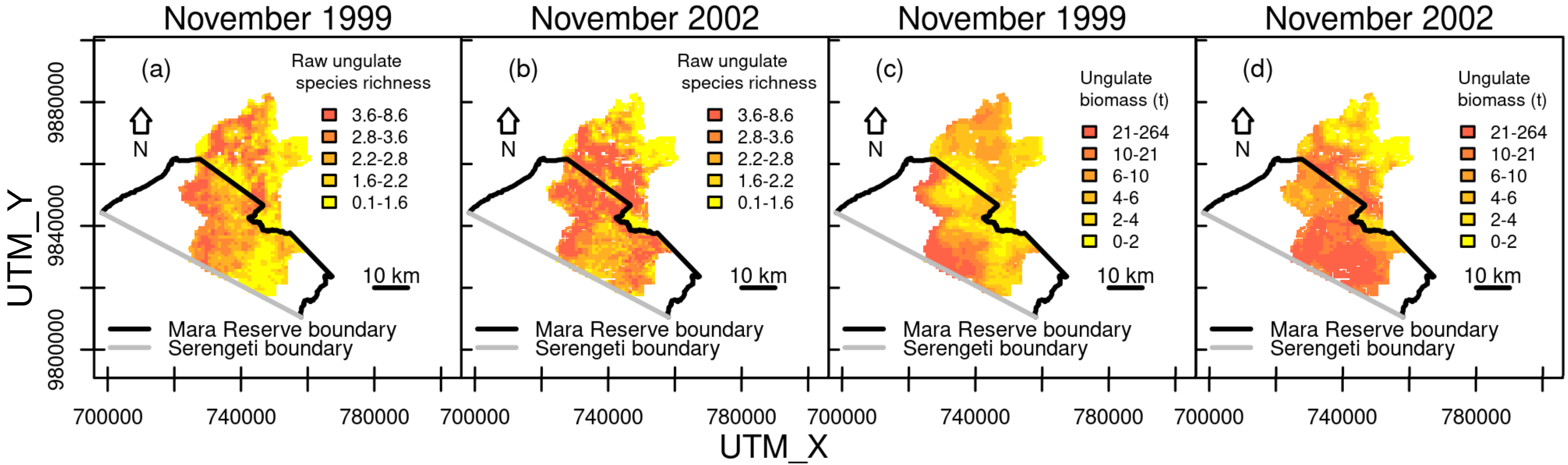
Stable predictors

Less stable predictors

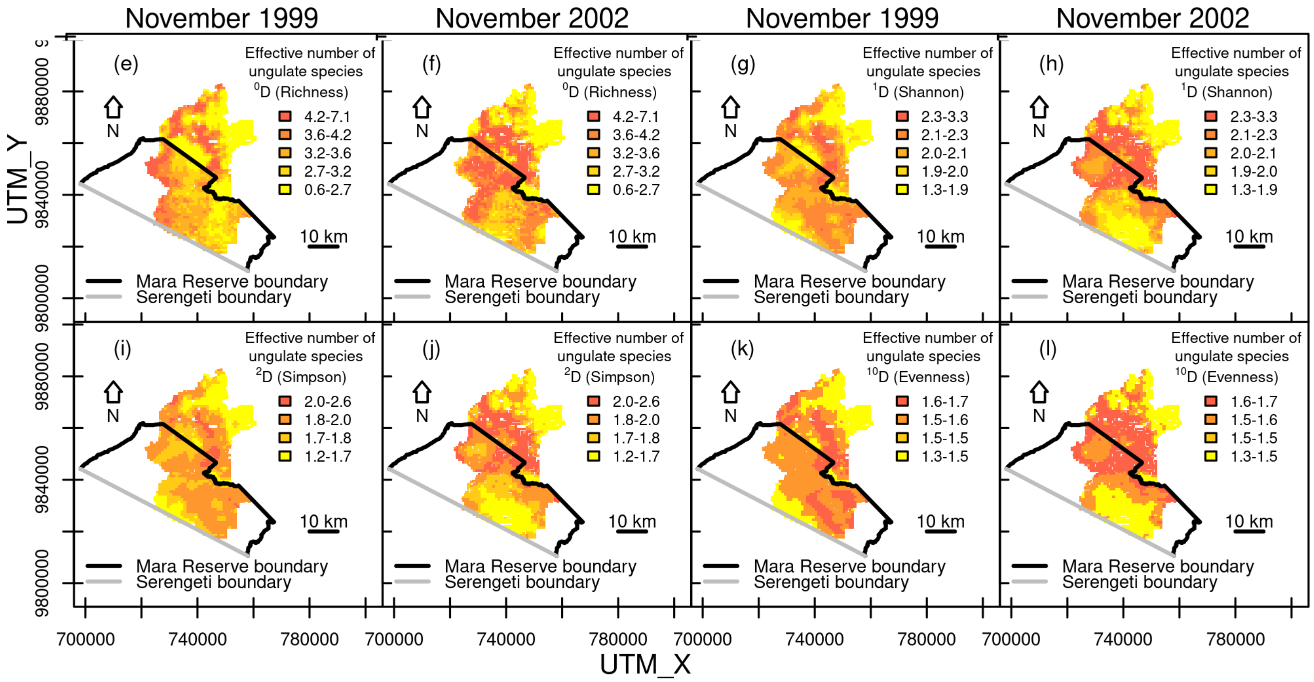
Unstable predictors

Hofner et al. 2015

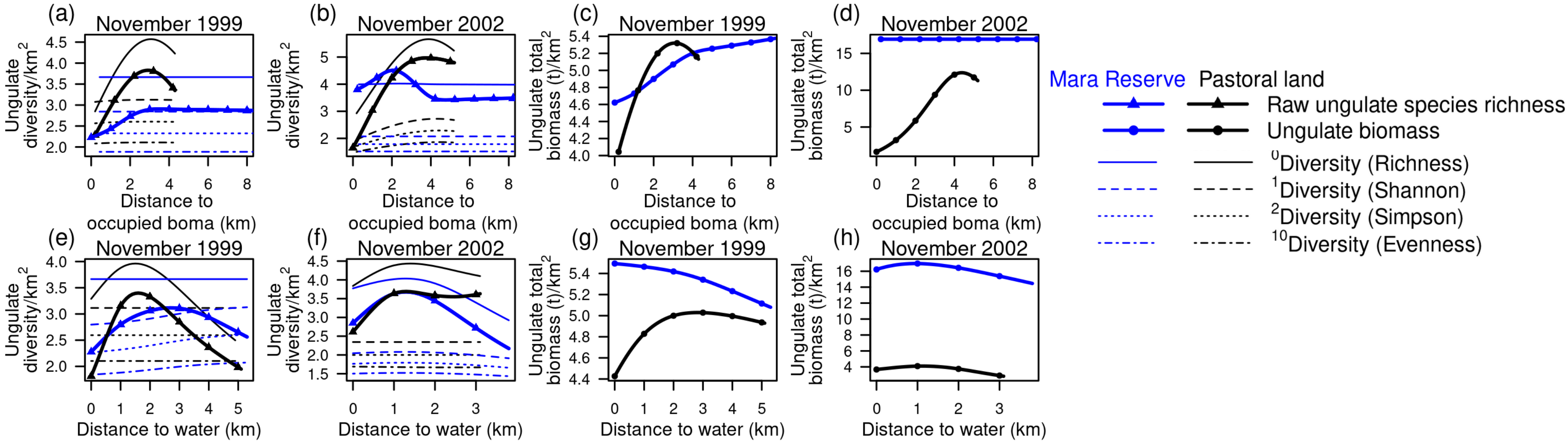
Results: spatio-temporal trends in the raw ungulate species richness and biomass



Spatio-temporal trends in ungulate diversity



Ungulate diversity and biomass in relation to bomas and water



ᵍD: bias-adjusted effective number of ungulate species (Hill numbers; Hill 1973, Marcon and Hérault 2015)

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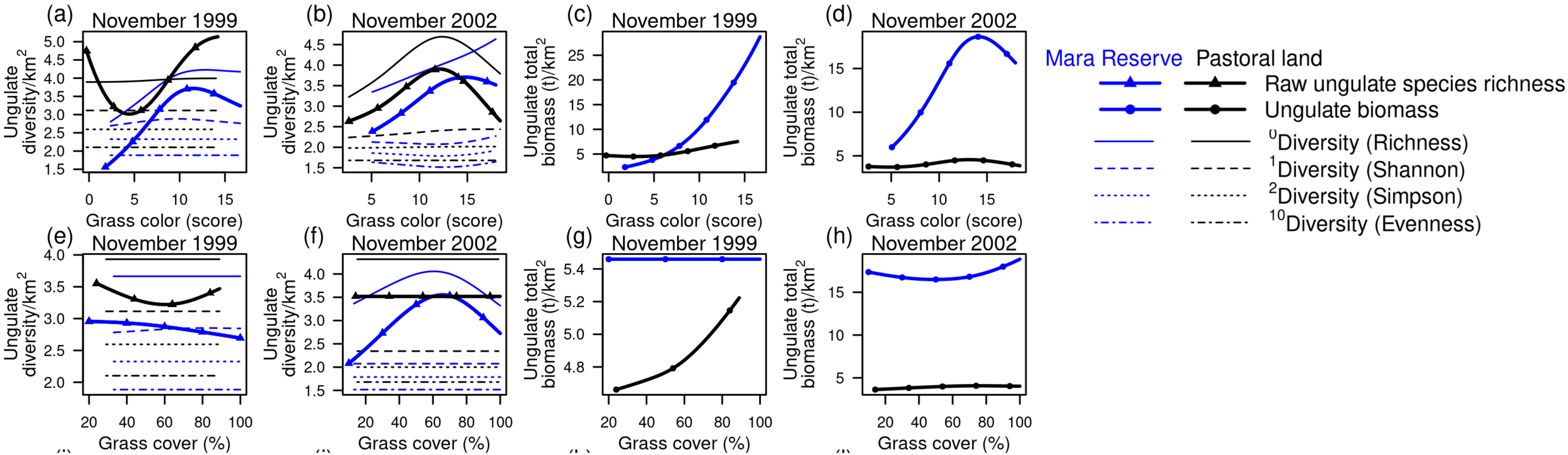
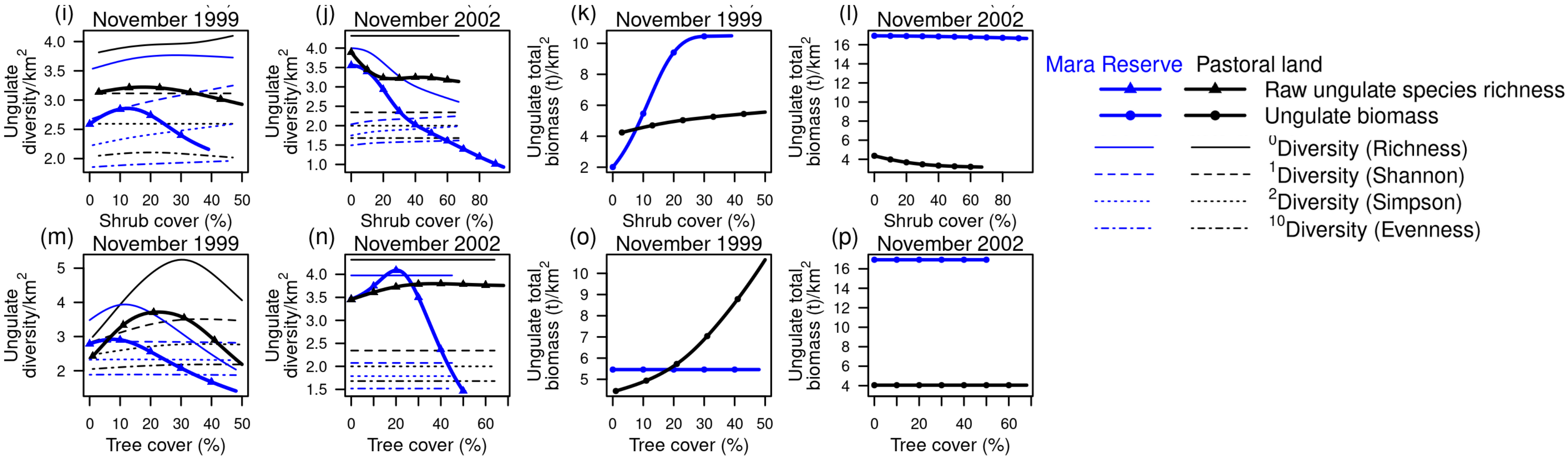
Ungulate diversity and biomass in relation to grass color and grass cover



^qD: bias-adjusted effective number of ungulate species (Hill numbers; Hill 1973, Marcon and Hérault 2015)

Ungulate diversity and biomass in relation to shrub cover and tree cover



^{q}**D: bias-adjusted effective number of ungulate species (Hill numbers; Hill 1973, Marcon and Hérault 2015)**

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Discussion

1) ungulate diversity peaks at intermediate human use
   - intermediate disturbance[1], mass effect[2], habitat diversity[2]
2) ungulate biomass peaks at low human use
   - competition with livestock, resources in protected areas
3) ungulate diversity declines where biomass peaks
   - humped-back model of species richness and biomass production[3]

[1]Connell 1978, [2]Shmida and Wilson 1985, [3]Grime and S. Pierce 2012a

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Discussion continued

3) ungulate biomass depends more strongly on resources than ungulate diversity does
   - resource acquisition by dominant species[1] (wildebeest and zebra)
4) ungulate diversity and biomass peaks partly shift towards less intense human use and more available resources during drought
   - ungulates favoured higher resource areas (but also areas closer to bomas) during drought

[1]Grime and Pierce 2012b

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Conservation implications

- keep boma densities at 0.25 to 0.50 bomas/km^2 and sheep and goats densities low in pastoral landscapes
- let ungulates access green grass and water
- apply fires carefully: shrubs in the reserve and trees on the pastoral lands may reduce ungulate biomass loss during drought

Boma in Maasai Mara, Kenya, 2017

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Conclusions

- intermediate intensity of human use -> higher ungulate diversity with lower ungulate biomass
- low intensity of human use -> critical resources for sustaining ungulate biomass during drought
- buffer zones such as wildlife conservancies around protected areas or habitat corridors should help to maintain ungulate diversity and biomass in savannas

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