INTRODUCTION

• Many arid and semi-arid rangelands exhibit distinct spatial patterning of vegetated and bare-soil-dominated patches.
• The latter potentially represent a grazing-induced, degraded ecosystem state, but could also arise via mechanisms related to feedbacks between vegetation cover and soil moisture availability that are unrelated to grazing.
• The degree to which grazing contributes to the formation or maintenance of degraded patches has been widely discussed and modelled, but empirical studies of the role of grazing in their formation, persistence, and reversibility are limited.
• We report on a long-term (17 yr) grazing removal experiment in a semi-arid savanna where vegetated patches composed of perennial grasses were interspersed within large (>10 m²) patches of bare soil.
Following herbivore removal, cover increased only slightly in the short-term (to 7% in 2002), but increased dramatically to 24% in 2016 (Treatment contrast for bare patches: $F_{1,20} = 11.01, P = 0.003$). Ascending bunchgrasses showed similar trends in relation to patch type and herbivore treatment as the tufted bunchgrasses, but patterns were more variable among sites.

Low-forage-value graminoids were unique in being the only functional group for which herbivore removal significantly affected cover in vegetated but not bare patches.

Non-graminoid functional groups (forbs and dwarf shrubs) varied in abundance among years and between patch types (with greater cover in 2002 and in vegetated patches), but neither were affected by herbivore removal ($P > 0.15$).

CONCLUSION

Removal of large herbivores from a semi-arid savanna allowed bare-soil-dominated patches to become revegetated to a more homogenous distribution of herbaceous vegetation cover compared to the grazed savanna.

This shift from a two-phase mosaic to a continuous herbaceous layer occurred only with long-term herbivore removal. Short-term removal of herbivores for 1 – 3 years was insufficient to allow bare patches to become revegetated.

This indicates that simply restoring a savanna landscape from livestock grazing for one or two growing seasons will be insufficient to restore bare patches.

The study provides important insights to the concept of alternative stable states in rangeland ecosystems. Bare patches often develop physical surface crusts that reduce water infiltration and increase surface runoff.

These processes are thought to generate positive feedbacks that prevent vegetation reestablishment and thus could potentially result in an alternative stable state that cannot be reversed via a reduction in grazing pressure alone. Our results show that in the short term, bare patches are indeed relatively stable even in the absence of grazing. However, they do not represent alternative stable states because long-term removal of herbivores results in grass reestablishment.

The functional groups that responded significantly to herbivore removal were the tufted bunchgrasses, that increased and the low-forage-value graminoids that declined in vegetated patches inside but not outside exclosures. The two most abundant species in the tufted bunchgrass functional group, *Enteropogon macrostachyus* and *Thameda triandra*, are particularly sensitive to grazing because they exhibit minimal inflorescence production where they are accessible to grazers.

Given that we detected long-term (17 yr) but not short-term (3-yr) increases in tufted bunchgrass cover in bare patches inside exclosures, we suggest that tufted bunchgrasses require multiple years of protection from grazers in order to establish via seedlings and grow successfully in bare patches, potentially facilitated by the establishment of stoloniferous grasses that helped to reduce water loss to runoff.

Large herbivores fundamentally shaped the composition and spatial pattern of the herbaceous layer by maintaining a two-phase herbaceous mosaic, but bare patches within this mosaic can recover given herbivore removal over sufficiently long time scales, and hence do not represent an alternative stable ecosystem state.

**SUMMARY**

- Bare soil exposure in bare patches declined more rapidly in exclosures relative to controls (Figure 2). The effect of herbivore removal was marginally evident after 3 years (Treatment contrast for bare patches in 2002: $F_{1,20} = 3.99, P = 0.059$), and highly significant after 17 years (Treatment contrast for bare patches in 2016: $F_{1,20} = 14.60, P = 0.001$).

- Stoloniferous grasses cover increased over time throughout the experiment (Year: $F_{2,20} = 16.68, P < 0.001$), but that herbivore exclusion did not influence the rate of increase either in bare patches (Treatment contrast for bare patches in 2002 and 2016: $F_{1,20} < 1.43, P > 0.25$) or in vegetated patches (Treatment contrast for vegetated patches in 2002 and 2016: $F_{1,20} < 0.85, P > 0.37$; Figure 3a).

- Tufted bunchgrasses responded positively to herbivore removal, but this response was contingent on patch type, was low in bare patches at the start of the experiment (1 - 3% Figure 3b) and in the presence of herbivores, remained low after 3 years (1%) and 17 years (6%; Figure 3b).