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COMMENTARY
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Key Points:
- A new study shows that woody shrub invasions are reversible if grazing is completely eliminated from a grassland for several years
- This study adds to evidence against alternative stable states in semiarid grasslands

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Evidence Is Growing That Alternative Stable States in Semiarid Grasslands Are the Exception, Not the Rule

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Abstract Woody shrubs have increased in abundance in arid and semiarid grasslands around the globe. This can have negative consequences for communities dependent on grasses for grazing and other ecosystem services. A study by Zheng et al. (2020, https://doi.org/10.1029/2019JG005439) shows that grasslands in Inner Mongolia, China, which have long been invaded by shrubs, may naturally return to a grass-dominated state when grazing is eliminated. This result emphasizes the primary importance of grazing in driving vegetation change in grasslands and argues against the existence of critical thresholds and alternative stable states in semiarid ecosystems.

Plain Language Summary Over the past 100 years, woody shrubs have increased in abundance in many semiarid grasslands around the world, replacing the grasses that are the most valuable forage for livestock. Ecologists have long sought to understand if overgrazing is responsible for shrub invasion and if shrub-invaded areas can be restored back to grasslands. A new study by Zheng et al. (2020, https://doi.org/10.1029/2019JG005439) shows that reversing shrub invasion may be possible. Over a 20-year period, the authors compared areas where grazing was completely stopped to areas where grazing was continued in a shrub-invaded grassland in Inner Mongolia, China. In areas without grazing, grasses gradually increased and shrubs decreased over the study period; in contrast, shrubs remained dominant where grazing continued. As grasses increased, soil texture became finer and less water seeped into the deeper soil layers. This likely benefitted further growth of the shallow rooted grasses over the more deeply rooted shrubs. The result adds to a small number of studies showing that shrub invasion may be less permanent than originally thought

Over the past century, woody shrubs have invaded arid and semiarid grasslands worldwide (D'Odorico et al., 2012). Shrub invasions are viewed negatively by land managers and conservationists because shrubs can reduce the value of rangelands for grazing by livestock, lead to soil erosion and loss of soil fertility and may reduce habitat for grassland-dependent wildlife (Eldridge et al., 2011). While hundreds of studies have examined the ecology of shrub invasion, there are few cases of shrub-invaded grasslands being restored (Bestelmeyer et al., 2013; Zhang et al., 2005). The persistence of shrubs for many decades in areas where grazing is reduced or even eliminated has led to the assumption that shrub invasions may be irreversible (D'Odorico et al., 2012; Laycock, 1991; Van Auken, 2000). A new study by Zheng et al. (2020), however, challenges this assumption. After eliminating grazing for 20 years, the authors document a shrub-invaded grassland returning back to a nearly shrub-free, grass-dominated state. This dramatic vegetation change aboveground was accompanied belowground by a redistribution of soil moisture that likely reinforced grassland recovery (Figure 1).

Overgrazing of arid grasslands can set off a number of positive feedbacks that promote shrub invasion and further loss of grass (D'Odorico et al., 2012). In the classical model of this process, overgrazing by livestock reduces the cover of grasses and increases the exposure of bare soil, leading to soil erosion and a loss of soil fertility. Rainwater infiltration is reduced in bare soil compared to grass patches (Bhark & Small, 2003); thus, as grass cover is lost, there is also more runoff, and the loss of soil moisture further reduces grass growth and survival. These changes benefit woody shrubs, which are more defended from livestock grazing. Their deeper roots also allow them to access more stable sources of moisture deeper in the soil (Li et al., 2013; Walker et al., 1981), and infiltration under shrub canopies may be higher than in grass or in bare soil, preferentially delivering rainwater to the roots of shrubs (Li et al., 2013).

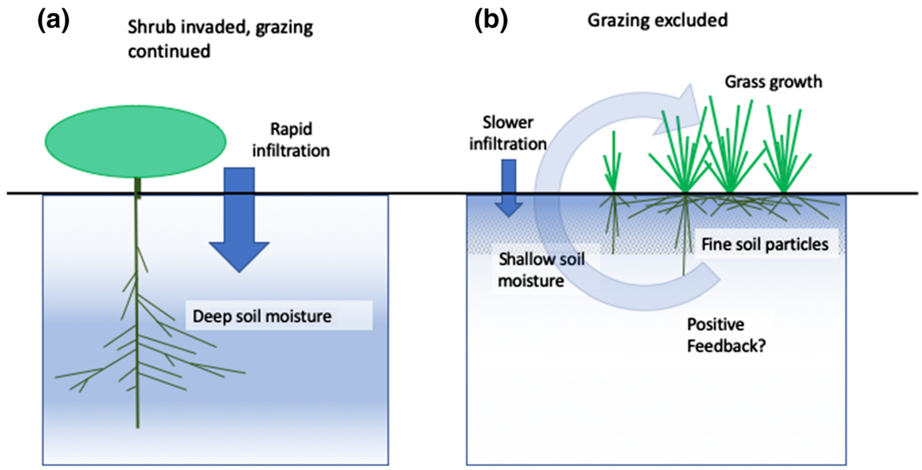

Figure 1. Zheng et al. (2020) document vegetation and ecosystem changes that occur when grazing is eliminated from a shrub-invaded rangeland for 20 years. (b) In the grazed state, shrub biomass was high, infiltration into the soil was rapid, and there were more roots and soil moisture in deeper soil layers. (a) When grazing was eliminated, grasses recolonized, and fine soil particles built up in the upper soil layers, followed by increases in soil moisture and roots in the upper soil layers. These changes may have driven a positive feedback that further decreased shrub growth and increased grass growth.

If these positive feedbacks are strong enough, grazing can push a grassland beyond a tipping point, initiating a vicious cycle of grass loss and shrub invasion. The stability of such an ecosystem is often likened to a ball resting in a pair of valleys (Figure 2a, D'Odorico et al., 2012; Laycock, 1991). When the ball is in the valley on the left, the system is grassland; when the ball is in the valley on the right, the system has few grasses and becomes shrub invaded. Positive feedbacks between vegetation and the environment mean that if the ball is nudged left or right, it naturally rolls back to its original resting place. However, a period of grazing that dramatically reduces grass cover can push the ball past a critical threshold toward a shrub invaded state. In a model with multiple stable states, simply eliminating grazing would not restore the ecosystem back to a grass-dominated state—the shrub invasion would be irreversible.

While conceivable in theory, there is limited empirical support for the idea that positive feedbacks are strong enough to maintain the shrub-invaded state indefinitely in the absence of grazing (Bestelmeyer et al., 2013; Scheffer, 2009). Complicating matters, other environmental changes, reduced fire frequency, climate change, and increased atmospheric carbon dioxide, have been hypothesized to contribute to shrub invasion (D'Odorico et al., 2012). Ultimately, studies that experimentally control grazing in shrub-invaded grasslands and then measure the long-term effects on vegetation and the environment are critical for deciding whether shrub invasion is reversible (Bestelmeyer et al., 2013; Mata-González et al., 2007). The new paper by Zheng et al. (2020) documents such an experiment, and their data give us an unprecedent look at long-term recovery of a shrub-invaded grassland. The authors excluded livestock from a semiarid grassland that had been grazed for centuries and invaded by woody shrubs in Inner Mongolia, China (Figure 1a). Over the course of 20 years, they measured vegetation and soil changes in the areas where they stopped grazing and compared them to pastures where grazing continued. After 8 years, shrub biomass began to decline and grass biomass increased, while in the grazed pastures, shrub biomass remained high and grass biomass low (Figure 1). As the vegetation changed, there were dramatic changes belowground as well: fine soil and root biomass, and soil moisture increased in upper soil layers, while soil moisture and root biomass decreased in the deeper soil layers (Figure 1b). Such changes in the physical environment likely benefited grass establishment and limited shrub growth—perhaps representing a virtuous cycle of grassland recovery. By contrast, the environment where grazing continued remained stable during the entire study period (Figure 1a).

The present study adds to a small list of others showing that grasslands can recover if grazing is completely eliminated for a long period of time (Castellano & Valone, 2007; Mata-González et al., 2007; Zhang et al., 2005). These results should cause us to reconsider the simple model of alternative stable

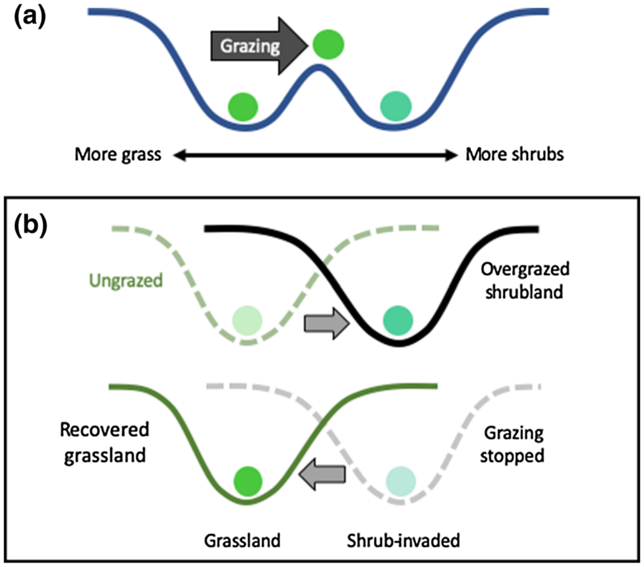

Figure 2. (a) The classical model of vegetation change in arid grasslands involves multiple stable states separated by critical thresholds. When the ecosystem is dominated by grasses, the ball is in the left-hand valley. Positive feedbacks maintain the grassland state. However, a period of heavy grazing, black arrow, can push the ecosystem to the right by removing grass cover. If grazing pushes grass cover beyond a critical threshold, the ecosystem moves into an alternative shrub invaded state. Once in this valley, positive feedbacks prevent the grassland recovering, even if grazing is stopped. (b) An alternative model for feedbacks in arid grasslands does not involve positive feedbacks driven solely by the amount of grass cover in the system. In this model, the ungrazed ecosystem (dashed green line) has only a single grass-dominated equilibrium state. Long-term livestock grazing, however, fundamentally alters the ecosystem stability (thick black line). The grazed ecosystem is stable only in the shrub-invaded state. Once grazing is stopped, feedbacks in the ungrazed system (solid green line) push it back toward a grass-dominated state.

states (Figure 2a). In this model, whether positive feedbacks push the system toward grassland or shrub invasion fundamentally depends on the current amount of grass in the system (Bestelmeyer et al., 2013). Grazing is seen as an external force that pushes the system toward shrub invasion primarily by reducing grass cover or biomass. However, the experiment in Zheng et al. (2020) shows that even a system with extremely reduced grass cover may not be locked into an irreversible shrub-invaded state.

Perhaps a better model involves two separate stability surfaces, one for an ungrazed system and another for a grazed system (Figure 2b). Reduced grass cover and grazing interact to push the system toward further grass loss and shrub invasion. When grazing is stopped, however, the system naturally moves back toward a grass-dominated state. The difference from the classical model of alternative stable states is that it is not simply the amount of grass in the system that determines whether it moves toward shrubs or grass but rather the interaction between grazing and grass cover. This has both positive and negative implications for land management. On the one hand, results that show grasslands can recover naturally after shrub-invasion means that expensive restoration measures such as shrub removal may not be required (Mata-González et al., 2007). This is a good thing where semiarid grasslands are restored for the sake of ecosystem services other than grazing (Eldridge et al., 2011). Unfortunately, completely eliminating grazing for decades, not just years, would not be viable for many communities that depend on livestock (Easdale, 2016). If reducing grazing is critical to recovery of semiarid grasslands, restoration efforts may need to be coupled with economic development programs that create alternative sources of income for pastoral communities (Safriel & Adeel, 2008).

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