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A spatial simulation model to assess controls upon grassland degradation on the Qinghai-Tibet Plateau, China

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ABSTRACT

Large areas of alpine meadow across the Qinghai-Tibet Plateau (QTP), western China, are undergoing degradation. Drawing upon field and remotely sensed data we develop a spatially explicit grid-based simulation model to explore the long-term dynamics of alpine meadow communities in this area. Our model represents the spatial dynamics of four plant functional types (PFTs) – sedges, grasses, forbs and weeds – together with disturbance from livestock grazing and small mammal activity. The model is most sensitive to parameters related to the reproductive rate and lifespan of the three plant functional types. Comparisons between model outcomes and field observations of vegetation composition suggest that the model produces plausible predictions of community dynamics. Simulation experiments indicate that grazing intensity is a fundamental control of plant community dynamics in these ecosystems. As grazing intensity increases there is a shift from a community dominated by grasses and forbs (very low grazing level) to grasses and sedges (low and moderate grazing levels) to degraded ground (high grazing levels). Severely degraded alpine meadows (locally termed 'Heitutan' or 'black beach') emerge after 370 simulation years under high levels of grazing pressure, but after only two decades under extreme grazing pressure. Under low to moderate intensity grazing regimes small mammals play an important role in maintaining meadow ecosystems. However, our model suggests that small mammal activity is no longer beneficial to the grassland ecosystem under high grazing pressures, increasing the rate of Heitutan formation. The time frame for a return to a sedge-dominated community is shortest under a moderate intensity grazing regime, but even in this instance it may take several hundred years.

1. Introduction

Herbivores play an important role in grassland ecosystems (Huntly, 1991; Milchunas, Sala, & Lauenroth, 1998). At high densities, however, grazing animals can change the floristic and structural characteristics of vegetation, reduce species richness, enhance soil erosion and potentially drive grasslands into undesirable alternative stable states (van Knoppel et al., 1997). In extreme situations, grazing may eliminate much of the vegetation cover, reducing soil fertility and the economic productivity of the land. Recent reviews by Harris (2010), Li et al. (2013) Lu et al. (2017) and Miehe et al. (2017) highlight the web of multi-scalar and interactive factors implicated in degradation atop the Qinghai-Tibet Plateau (QTP) in Western China. However, the ecological dynamics that drive degradation in relation to grazing and other environmental pressures remain uncertain and contested. Field-based studies of degraded grasslands, while valuable, are inevitably local and short-term, and so may fail to reveal the long-term temporal dynamics of these plant communities. The sparse and often non-representative nature of scientific observation and measurement, and the patchy (unknowingly incomplete) record of past changes limits our ability to interpret and explain how these ecosystems may change in the future (Dearing et al., 2012).

Uncertainties around the temporal dynamics of the formation and recovery of degraded areas make active intervention (restoration) challenging. Suding, Gross, and Houseman (2004) and Hobbs and Cramer (2008) argue that for restoration programs to be effective they must: (i) focus on the underlying causes and processes of degradation (rather than the symptoms) and (ii) be grounded in an understanding of the feedbacks and constraints operating in the degraded system. Successful restoration of grasslands on the QTP is likely to require changes in land management (e.g. reduced grazing pressure) alongside active intervention. In some parts of the Sanjiangyuan region, traditional

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agricultural skills have been used in an effort to speed up recovery of severely degraded alpine meadow (locally termed 'Heitutan' and 'black (soil) beach'; Li et al., 2014; Dong, Zhao, Wu, Shi, & Ren, 2013). In some instances, this effort includes resowing of native grasses (e.g. Li et al., 2016).

Grid-based models have been used to simulate plant community dynamics in a range of ecosystems (e.g., Komac, Kefi, Nuche, Escós, & Alados, 2013; Paruelo et al., 2008; Weber, Jeltsch, van Rooyen, & Milton, 1998). Because spatially-explicit grid-based models can blend qualitative rules and mathematical equations (Wissel, 2000), they can be used to explore ecological problems in instances where quantitative data are limited or there are scale constraints. Here we develop and test a fine-grained and small extent (1 ha, $1 \times 10^4\,m^2$), spatially explicit simulation model representing the community dynamics of meadows on the QTP. We use the model to evaluate how community dynamics might respond to changes in the grazing regime. Specifically, we ask:

1. How do different levels of grazing pressure influence plant community dynamics in alpine meadows on the QTP?
2. Over what time frames does degradation (the Heitutan condition) emerge under different grazing regimes?
3. What is the role of small mammal population irruptions in these plant communities? Do these irruptions interact with grazing intensity to drive grassland degradation?
4. What is the time frame for restoration of Heitutan under different grazing scenarios? Is resowing of grasses a potentially effective restoration strategy?

2. Regional setting

The QTP ranges in elevation from 3000 to 5000 m a.s.l. and covers an area of about 2.6 million km^2 (Brierley, Li, Cullum, & Gao, 2016). The region has a cold and dry alpine climate, with a mean annual temperature below zero, but more than 2500 sunshine hours per year. Mean annual precipitation is less than 500 mm, with about 70–75% of the annual precipitation falling during the rainy season (summer) from June to September.

Alpine grasslands comprised of low-productivity, cold-tolerant perennial plants make up more than 50% of the plateau area. Putting to one side quibbles about terminology, 'alpine meadows' are synonymous with *Kobresia*-dominated pastures, with *Kobresia pygmaea* (syn: *Carex parvula*) the dominant species (Fig. 1; *cf.*, Miehe et al., 2017). Alpine meadow soils are thin (20–50 cm), have a coarse texture (light or sandy loam) and high organic content (Dong et al., 2012; Kaiser et al., 2008; Qiao and Duan, 2016). However, the moist and cool conditions, coupled with nutrients being concentrated in the root material, mean that plants tend to be nutrient limited (Miehe et al., 2017). Multiple lines of evidence suggest that over thousands of years human activities have induced a shift in vegetation across much of the Plateau from forest to grazing-adapted grasslands (Miehe et al., 2009; Qin et al., 2010). The emergence of modern grazing systems around 2200 years ago triggered the establishment of *Kobresia* pastures (Miehe et al., 2009, 2017), and livestock grazing still underpins the regional economy. Under 'traditional' grazing regimes, alpine meadows contain a diversity of palatable annual species that grow during summer, supporting grazing animals (Li et al., 2016). However, overgrazing degrades the root mats, enhancing soil erosion and altering system responses to biogeochemical and hydrological processes (Babel et al., 2014).

Although grassland resources in the region have been grazed for millennia, no evidence has been presented showing notable degradation prior to the 1970s (Li et al., 2013; Miehe et al., 2017). However, beyond this point grazing intensified and degradation is now evident over a range of scales across the QTP (Li et al., 2013; 2018). In some areas this has induced localised declines in ecological condition to desertification and formation of Heitutan (Li et al., 2014; see Fig. 1). The initial stages of degradation are characterised by the fragmentation of the previously continuous turf. Overgrazing results in a reduction in the relative abundance of palatable grasses and a corresponding increase in forbs and poisonous plants. The emergence of cracks in the root mats and bare patches creates ideal conditions for small mammals (Li et al., 2016; Miehe et al., 2017; Zhou, Zhao, Tang, Gu, & Zhou, 2005). Once degradation has advanced to the Heitutan stage, the soil has lost so much of its physio-chemical structure and fertility that little vegetation can persist (Li et al., 2014). At high densities various small mammal species (e.g. plateau pika, *Ochotona curzoniae*) can affect grasslands via their burrowing and gnawing, loosening the turf/sod and killing plant roots (Li et al., 2016; Zhang et al., 2016). The role of these burrowing mammals in grassland degradation is contested. Some researchers see plateau pika as critical ecosystem engineers, while others consider them harmful (cf., Smith & Foggin, 1999; Pech, Arthur, Yanming, & Hui, 2007; Sun et al., 2015; Wilson & Smith, 2015). Li et al. (2016) contend that it is likely that pika (and other small mammals) exacerbate rather than cause rangeland degradation, and so should be viewed as a symptom rather than an underlying cause of degradation.

There has been significant debate over the role of a suite of interdependent factors as causes of grassland degradation atop the QTP, including appraisals of stocking levels, the role of small mammals, management practices and climate change (e.g. Harris, 2010; Lehnert, Wesche, Trachte, Reudenbach, & Bendix, 2016; Li et al., 2013; Liu, Duan, Hao, Ge, & Sun, 2014; Ran, Xie, & Li, 2016; Wang & Wesche, 2016; Wang, Lassoie, Morreale, & Dong, 2015). In some cases these arguments arise from the use of differing methods/approaches of assessment, and variable resolution/extrapolation of data, with notable differences between field-based and remotely-sensed analyses (Miehe et al., 2017). Disentangling the drivers of alpine meadow degradation is important because its outcomes have serious impacts on local pastoralists as productivity declines and soil and water resources are affected. A lack of clarity on the underlying mechanisms of degradation adds to uncertainty as to the most appropriate management responses (see Harris, Wang, Badinqiuying, & Bedunah, 2015; Li et al., 2016; Miehe et al., 2017; Wen et al., 2013).

3. Methods

Details of the spatially explicit simulation model, underlying parameterisation data, rules/procedures followed in the simulation experiments and steps taken to evaluate and iteratively refine the model are presented following the 'Overview Design Concepts and Details' (ODD) protocol (Grimm et al., 2010) in the Supplementary Material.

3.1. Overview of the grid-based model

Our grid-based model is implemented in NetLogo 5.1.0 (Wilensky, 1999). It represents four plant functional types (PFTs; Duckworth, Kent, & Ramsay, 2000) and two kinds of bare ground (degraded and unoccupied) (Fig. 1). The four PFTs are: (i) sedges (representing a suite of three species, mostly *Kobresia* spp.), (ii) grasses (seven species [e.g., *Stipa* and *Poa*]), (iii) forbs (seven species [e.g., *Leontopodium* and *Potentilla*]) and (iv) weeds (five species [e.g., *Oxytropis and Pedicularis*]). The sedge PFT includes all clonal *Kobresia* species. The grass PFT encompasses non-tap-root taxa that provide a food source for animals, the forb PFT represents those tap-root plants with the lowest resistance to grazing, and weeds are tap-root plants that are not grazed by domestic animals. Areas of bare ground can be in one of two states (i) degraded ground (i.e. eroded areas): or (ii) unoccupied ground (i.e. non-degraded areas with recently dead plants).

The model considers an area of one hectare (ha) on a square lattice of 100 by 100 cells (each 1×1 m) and runs on an annual time-step (Fig. SM 1-1). The spatial scaling of the model reflects the grain of the data we use to inform its development, and is representative of the ecological process dynamics that are simulated by the model. We simulate the dynamics of a small generic area of alpine meadow on the

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