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Small mammalian herbivores as mediators of plant community dynamics in the high-altitude arid rangelands of Trans-Himalaya

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A B S T R A C T

The high-altitude rangelands of the Trans-Himalaya represent a grazing ecosystem which has supported an indigenous pastoral community for millennia alongside a diverse assemblage of wild herbivores including burrowing mammals (pikas and voles). Pastoralists consider the small mammals to cause rangeland degradation and as competitors for their livestock, and actively eradicate them at many places. We present data on the ways in which small herbivores like pikas and voles mediate plant community dynamics. Vegetation cover and plant species richness were compared on and off both active and abandoned small mammal colonies. Plant species richness was higher inside colonies (about 4–5 species/plot) than outside (about 3 species/plot) whereas vegetation cover was only marginally lower (52% compared to 60%). Soil disturbance due to small mammals is seen to be associated with higher plant diversity without causing dramatic decline in overall vegetation cover. Such disturbance-mediated dynamics and vegetation mosaics produce a rich array of testable hypotheses that can highlight how small mammals influence assembly processes, succession, and dominance hierarchies in plant communities in this arid ecosystem. So, eradicating small mammals may lead to declining levels of diversity in this ecosystem, and compromise ecosystem-functioning. Changes in traditional pastoral practices and overstocking are more likely to be responsible for degradation. We emphasize that eradicating small mammals can lead to loss of diversity in this ecosystem and it is not a solution for the degradation problems.

1. Introduction

The current rate of biodiversity loss threatens to disrupt the normal functioning of many ecosystems around the world (Chapin et al., 2000). In fact, much of human endeavor hinges upon ecosystem functions (like productivity, biogeochemical cycling) that are known to have a positive relation with species richness (Kinzig et al., 2001; Loreau et al., 2002). Since a majority of the Earth's surface is managed for wild and domestic herbivores, understanding the mechanisms that mediate diversity in grazing ecosystems is of key importance (Olff and Ritchie, 1998). Small burrowing herbivorous mammals are known to play a major role mediating plant diversity in many grazing ecosystems. They influence plant diversity and dominance hierarchies (Brown and Heske, 1990) directly via defoliation (Detling and Painter, 1983) as well as through

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indirect effects on plant–soil interactions (Aho et al., 1998). While their importance has been recognized in the rangelands of North America (Reichman and Seabloom, 2002), small mammals continue to be actively eradicated from central Asian highlands (like the Trans-Himalaya encompassing the Tibetan plateau and marginal mountains in China, India and Nepal), in the name of pest control (Jing et al., 1991; Zhong et al., 1991).

This negative attitude towards small herbivorous mammals is largely due to the varied perceptions of local pastoralists on rangeland degradation. This region has supported livestock alongside a diverse assemblage of wild herbivores for millennia, and pastoralism continues to be the mainstay of the local economy and chief land-use (Handa, 1994; Mishra et al., 2003). However, most traditional pastoral societies in the world have changed drastically over the last few decades, as traditional practices (like rotational grazing, seasonal movements, etc.) have broken down (Leneman and Reid, 2001). Coexistence of wild and domestic herbivores is no longer harmonious in many parts of the world (Prins, 1992), including the Trans-Himalayas (Mishra et al., 2003, 2004; Bagchi et al., 2004). Pasture degradation is a major conservation concern in central Asian highlands as many regions are now unsuitable for sustaining livestock and conserving native wildlife (Tong et al., 2004). Such degradation is attributed largely to breakdown of traditional grazing practices and overstocking (Mishra et al., 2001; Holzner and Kriechbaum, 2001a,b). These impose forage limitations on wild species (Bagchi et al., 2004) and lead to their local extinctions (Mishra et al., 2002). Nevertheless, local pastoralists attribute pasture degradation to wild herbivores, especially small burrowing mammals and this has culminated in widespread eradication schemes targeted at rodents and lagomorphs (Jing et al., 1991; Zhang et al., 1998; Smith and Foggin, 1999; Holzner and Kriechbaum, 2001b). Eradication continues in many places as data to evaluate the conservation implications of these programs remain scarce.

Small mammalian herbivores constitute a species rich group in the Trans-Himalaya, representing a unique biogeographical guild of high-altitude fauna with high conservation importance (Chapman and Flux, 1990). So, it becomes important to evaluate their role in mediating plant community dynamics of high-altitude rangelands in the light of the current, widespread eradication schemes. However as mentioned earlier, unlike other parts of the world such as North America; there is a lack of field data to evaluate these aspects for central Asian rangelands. In a brief review, Smith and Foggin (1999) addressed the plateau pikas (*Ochotona curzoniae*: Ochotonidae) as keystone species for the Tibetan plateau and highlighted their importance as prey for many canids and mustelids. While emphasizing many different roles that these small mammals can potentially play, they recognized the paucity of data to evaluate the eradication programs. Recently, there is some evidence on how zokors (*Myospalax fontanierii*: Cricetidae) may influence vegetation patterns (Zhang and Liu, 2003). The Changthang region of Indian Trans-Himalaya remains one of the few relatively undisturbed places where pastoralists have not taken to persecuting small mammals, and where their ecological role can be properly evaluated. In this paper, we provide data that establish plateau pikas and Stoliczka's voles (*Alticola stoliczkanus*: Muridae), as mediators of plant community dynamics such as North American pocket gophers (Geomyidae) and praire dogs (Sciuridae). We also address pertinent conservation issues that arise from programs that sponsor their eradication. Specifically we ask the following questions for an intensive study area in Changthang, northern India: (i) Do pikas and voles have an impact on the spatial patterns of plant species diversity in the Trans-Himalayan rangelands? (ii) Do they reduce vegetation cover? This was done by comparing data on species richness and vegetation cover from plots inside small mammal colonies with random off-colony plots. From this we infer the likely consequences of small herbivore extermination for the biodiversity of grazing ecosystems like the Trans-Himalaya.

2. Materials and methods

2.1. Study area

Trans-Himalaya, comprising the Tibetan plateau and the Tibetan marginal mountains lies in the rain-shadow of the Himalayas and covers more than 2.5 million km^2. in central Asia (China, India and Nepal). The study was carried out in Changthang High-altitude Cold-desert Wildlife Sanctuary (33°N, 79°E) where the Tibetan plateau extends into Ladakh, northern India. By Miocene, most of Changthang was uplifted to an average altitude of 4500 m. asl, and a unique high- altitude grazing ecosystem evolved following the Pleistocene radiations (Schaller, 1977). The vegetation is dry alpine steppe formed by grasses, sedges, forbs and shrubs adapted to a cold-arid environment. Chamaephytes and hemicryptophytyes are the common life-forms while the tree layer is absent. Climate is cold and arid with temperatures dropping below −30 °C between November and March, allowing a short growth season for plants (May–August). The area is grazed by many livestock including yaks, yak–cattle hybrids, horses, goats and sheep. The extant wild herbivores are kiang (*Equus kiang*), Tibetan gazelle (*Procapra picticaudata*), Bharal (*Pseudois nayaur*), Himalayan marmot (*Marmota bobak*), Tibetan woolly hare (*Lepus oitolus*) along with pikas and voles. Together, these constitute the natural prey for predators like the Snow leopard (*Uncia uncia*), Tibetan wolf (*Canis lupus chanko*), Eurasian lynx (*Lynx l. isabellina*) and several mustelids.

2.2. Sampling and analyses

We collected data on plant diversity (species richness) from colonies of Stoliczka's voles (30 g) and the plateau pikas (170 g) during June–July 2004 (peak standing plant biomass) within a study area of about 150 km^2. (altitude between 4750 and 5000 m. asl). These form colonies with numerous burrows (spread over about 1 ha). The small mammals remain in the same area for 2–5 years and then move away to form new colonies. This provides a natural experiment where we can compare the influence of soil disturbance on plant communities in active colonies with abandoned ones as well as random undisturbed sites. With the help of local herders, we located 11 pika and vole colonies that were active and 5 colonies that had been abandoned in the last 3–4 years. We ascertained plot size (2 × 2 m. quadrats) by progressively doubling sampled area from 0.25 to 32 m^2 and noting species accumulation. As species accumulation reached an asymptote at 2 × 2 m., we randomly laid 4 such quadrats inside each colony to estimate plant species richness (i.e., local-diversity). Vegetation cover was determined by the line-intercept method (Muller-Dumbois and Ellenberg, 1974) with 20 points along a 10 m. rope laid randomly inside and outside the colonies. Literature suggests that small herbivores are central-place foragers and their influence extends 9–10 m. outwards from their colonies (Huntly, 1987). So, we collected the same data from locations 50–100 m. away from the colony to represent random undisturbed sites. This amounts to 2 treatments – 'active/abandoned colony' and 'inside/outside colony' which can evaluate the effect of soil disturbance on species richness and vegetation cover.

Data were analyzed in an Analysis of Variance (ANOVA) framework with the inside/outside treatment nested within the active/abandoned treatment using SAS v9.0 (SAS Institute, Cary, USA). Two ANOVAs were performed – for species richness and percent vegetation cover. We also noted the number of burrows per quadrat at each active colony as an indicator of soil disturbance to see if species richness varied with extent of soil disturbance (separate one-way ANOVA).

3. Results

A total of 18 plant species were encountered during sampling (regional-diversity). Common plants included *Artimisia, Carex, Dracocephalum, Kobresia, Oxytropis, Potentilla, Salsola,* and *Stipa*. No species was found to occur exclusively in any one of the 4 treatment-combinations. Average species richness (number of species per quadrat), and percent vegetation cover are summarized in Fig. 1.

The ANOVA for species richness (number of species per quadrat) and percent vegetation cover are summarized in Table 1. For species richness, there was a significant interaction effect ($P = 0.019$), as there were more species per quadrat inside abandoned colonies than outside active colonies. Vegetation cover seems marginally lower ($P = 0.064$) inside active colonies (52%) compared to the general landscape (>60%).

The openings of the burrows were between 4 and 8 cm in diameter, and the number of burrows varied between 0 and 6 per quadrat. Mean species richness varied significantly with number of burrows ($F_{6,78} = 3.15$, $P = 0.008$). The unimodal pattern (Fig. 2) suggests that species richness peaks at an intermediate level of disturbance (3–4 burrows per quadrat), and then declines with excessive soil disturbance.

4. Discussion

The data demonstrate a clear pattern: small mammals are associated with higher plant species richness at a local scale. Most of these plant species are important constituents of herbivore diets (Harris and Miller, 1995; Bagchi et al., 2004; Mishra et al., 2004). Since these small mammals establish new colonies every 2–5 years, this localized influence can extend to larger scales over longer durations of time. However, there are many possible mechanisms by which this pattern can arise. Firstly, this pattern could be due to disturbance-mediated vegetation dynamics where intermediate levels of soil disturbance (Fig. 2) may lead to higher levels of diversity (Laska, 2001). Under this scenario, soil disturbance by small mammals would create colonization opportunities and allow propagules of competitively subordinate plants to establish. After this initial phase of disturbance-assisted colonization

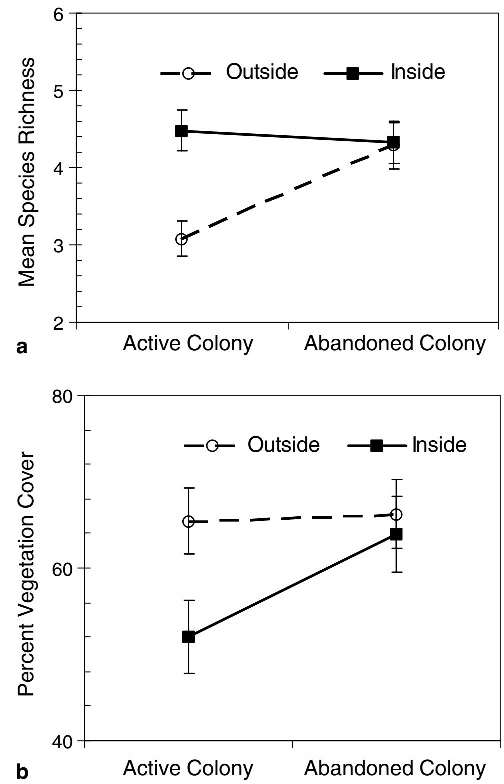

Fig. 1 – Estimated mean (±SE) of species richness (number of species per quadrat), and percent vegetation cover. Data relate to 2 × 2 nested arrangement of treatments (inside/outside colony nested within active/abandoned colony) from 16 colonies of small herbivorous mammals in Ladakh, Trans-Himalaya, northern India.

Table 1 – Summary of ANOVA for species richness (number of species per quadrat), and percent vegetation cover

ANOVA	Effect	$F_{1,15}$	P
Species richness	Active/abandoned	3.20	0.094
	Inside/outside	12.84	0.003
	Interaction	6.93	0.019
Cover	Active/abandoned	0.91	0.356
	Inside/outside	3.99	0.064
	Interaction	2.66	0.124

Data relate to 2 × 2 nested arrangements of treatments (inside/outside colony nested within active/abandoned colony) from 16 colonies of small herbivorous mammals in Ladakh, Trans-Himalaya, northern India.

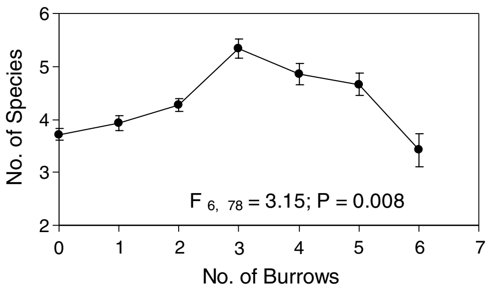

Fig. 2 – Unimodal relationship between soil disturbance and diversity from 16 colonies of small herbivorous mammals in Ladakh, Trans-Himalaya, northern India. Soil disturbance was measured as no. of burrows and diversity as the no. species in (2 × 2 m) quadrats and are shown as mean ±SE. Diversity varies significantly (P = 0.008) with disturbance, but the relationship is unimodal.

(Bakker and Olff, 2003), the colony serves as a 'source' of propagules of otherwise subordinate plant species that can disperse into adjoining areas. As succession ensues following the abandonment of colonies, subordinate species are eventually competitively excluded (Sousa, 1984) causing diversity to decline (from 4.5 to 3 species per quadrat after a colony is abandoned). Thus, small mammal disturbances can potentially reset succession and create transient states of vegetation that contain subordinate species (Bakker and Olff, 2003).

Secondly, a common consequence of small mammal disturbance and herbivory is to increase levels of foliar nutrients (Aho et al., 1998), which can attract livestock and wild ungulates (Coppock et al., 1983). Large grazers might reduce competitively dominant plants and promote coexistence over an area much larger than the small mammal colony, leading to elevated diversity levels both on and off colonies. Under this scenario, we might expect diversity to increase with small mammal activity (as judged by number of burrows), but instead we find that diversity peaks at intermediate burrow densities and declines at the highest small mammal activity (Fig. 2). Furthermore, attraction of large mammals would not explain why plant diversity increases off-colony only after small mammals abandon the colony (Fig. 1).

Thirdly, it is possible that small mammals colonize patches of higher diversity to begin with. This would imply disturbance does not play a role. However, our data suggest that diversity is related to soil disturbance (Fig. 2). Even if small mammals preferentially colonize more diverse patches, such an effect alone is unlikely to explain the patterns we observed.

The relative merits of these alternative mechanisms can be fully evaluated only with manipulative field experiments. However, regardless of the underlying mechanism, small mammals are seen to have a positive association with plant diversity without causing dramatic declines in vegetation cover. So, associating them with rangeland degradation seems to be a misplaced claim. In fact, eradicating them may lead to declining levels of diversity in these rangelands.

As loss of diversity can compromise ecosystem-level processes like productivity and nutrient-cycling (Kinzig et al., 2001; Loreau et al., 2002), the role of small mammals may be critical in maintaining ecosystem function in these rangelands. Observed degradation is more likely due to overstocking of the rangelands and breakdown of traditional herding practices (Mishra et al., 2001). In influencing succession, soil disturbance has a marginally negative impact on vegetation cover. The cover inside active colonies is slightly less than the general landscape, and the visibility of bare patches can portray an apparent 'barren' look to small mammal colonies. Pastoralists' reaction to this reduction in cover may contribute to a negative attitude towards the small mammals.

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