The Plateau Pika: A Keystone Engineer on the Tibetan Plateau

by

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ABSTRACT

The highly-social plateau pika (Lagomorpha: *Ochotona curzoniae*) excavates vast burrow complexes in alpine meadows on the Tibetan Plateau. Colonies of over 300 individuals/ha have been reported. As an ecosystem engineer, their burrowing may positively impact ecosystem health by increasing plant species diversity, enhancing soil mixing, and boosting water infiltration. However, pikas are commonly regarded as pests, and are heavily poisoned throughout their range. The underlying assumption of eradication programs is that eliminating pikas will improve rangeland quality and decrease soil erosion.

This dissertation explores the link between plateau pikas and the alpine meadow ecosystem in Qinghai Province, PRC. This research uses both comparative field studies and theoretical modeling to clarify the role of pika disturbance. Specifically, these studies quantify the impact of pikas on nutrient cycling (via nutrient concentrations of vegetation and soil), hydrology (via water infiltration), local landscape properties (via spatial pattern description), and vascular plant communities (via species richness and composition). The competitive relationship between livestock and pikas is examined with a mathematical model.

Results of this research indicate that pika colonies have both local and community level effects on water infiltration and plant species richness. A major contribution of pika disturbance is increased spatial heterogeneity, which likely underlies differences in the plant community. These findings suggest that the positive impact of plateau pikas on rangeland resources has been undervalued. In concurrence with other studies, this work concludes that plateau pikas provide valuable ecosystem services on the Tibetan Plateau.

DEDICATION

To my friends and family.

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INTRODUCTION

Conflict between natural resource users is common in most rangeland systems. In many areas, humans and their domestic livestock must share a limited forage resource with native herbivores. Typically, native species that compete with livestock are regarded as pests. For example, in the United States the prairie dog has been exterminated over 95% of its former range (Forrest 2005) because of allegations linking it to rangeland degradation (Lybecker et al. 2002). On the other hand, mounting evidence points to the status of the prairie dog as a keystone species (Kotliar et al. 1999), which plays an important role in maintaining the short-grass prairie ecosystem (Kotliar 2000, Miller et al. 2007).

The research outlined below examines an analogous issue in China's far west: the control (poisoning) of plateau pikas (*Ochotona curzoniae*), a species endemic to Tibetan plateau rangelands. While increasingly large sums[1] have been spent on pika eradication (Ma 2006), more and more evidence points to the critical importance of these animals to their native habitat. The plateau pika may in fact function as both as a keystone species (Smith and Foggin 1999) and habitat (allogenic) engineer (Lai and Smith 2003). My work builds on previous research detailing this animal's significance to terrestrial and avian predators (Smith and Foggin 1999, Lai and Smith 2003). However, I focus on the influence of plateau pikas on the plant community and surrounding environment. Goals of this work are to clarify the keystone role of pikas in respect to the plant community and to evaluate the consequences of pika poisoning on this alpine ecosystem. Specifically, I quantify the impact of pikas on nutrient cycling (via

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[1] US $925 million

nutrient concentrations of vegetation and soil), hydrology (via water infiltration rates), local landscape properties (via spatial pattern description), and vascular plant communities (via species richness and composition). Finally, I explore the competitive relationship between livestock and pikas using mathematical models. Each of these topics is discussed in detail in the subsequent chapters.

The purpose of this chapter is to provide a contextual framework by presenting background on the study system and a review of relevant research. The first section begins with a brief physical description of the plateau pika, followed by an account of its phylogeny, historical range, and relationship within the small mammal community. I also present the plateau pika's habitat—the Tibetan plateau—including its geologic history and biogeographic features. Afterwards, I give an account of historical and present-day interactions between pikas and humans. In the second major section, I discuss the biological importance of plateau pikas. I review the keystone species concept and present research on North American prairie dogs as a framework for investigating the plateau pika's ecological impact. Lastly, I place my research in context with other ecological studies on burrowing mammals.

STUDY SYSTEM

The plateau pika

The plateau pika, *Ochotona curzoniae* (Hodgson, 1858), also called the black-lipped pika, is a small (130 – 195 g) mammal that naturally occurs in large colonies on the alpine grasslands[2] of the Tibetan plateau (Smith and Xie 2008)

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[2] I use alpine grasslands to refer broadly to mountain meadow, prairie and steppe. The biomes of the Tibetan plateau are discussed in detail in the next section.

(Figure 1.1). All pikas belong to Order Lagomorpha[3], a group that includes rabbits and hares, but not rodents (Hoffmann and Smith 2005). A distinct difference between plateau pikas and North American pikas is that the latter are rock-dwelling, while the former excavate extensive underground burrow systems in open grassland. Although fossorial, pikas remain above-ground most of the day to feed (Smith and Wang 1991).

Plateau pikas live in highly social family groups, averaging three adults and 11 juveniles (Dobson et al. 1998, 2000). They can exist in a variety of mating systems, including polygynous, polyandrous, promiscuous and monogamous (Smith and Wang 1991, Dobson et al. 2000). Females give birth to three to five litters of two to eight young in the summer months (Smith and Xie 2008), and males provide relatively high levels of parental care (Smith and Wang 1991, Dobson et al. 1998). At the end of the summer, colonies have known to accumulate 300 individuals/ha (Smith and Wang 1991). However, over-winter mortality is high, with as low as 5% (Wang and Smith 1988) to 23% (Dobson et al. 1998) survival. In spring during a brief window before the mating season, approximately 40% of individuals (both male and female) disperse (Smith and Wang 1991, Dobson et al. 1998). However, dispersers typically travel only one to two family ranges from their birth site (Dobson et al. 1998, 2000).

All living pikas belong to the genus *Ochotona* and are found in the northern hemisphere (Smith et al. 1990). Only two species inhabit North America (Table 1.1). Within China, the diversity of pikas is relatively high – 24 out of the 30 extant species are indigenous, and 12 are endemic (Smith and Xie 2008).

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[3] In spite of this, plateau pikas are frequently referred to as rodents, even in the scientific literature (e. g. Wang and Fu 2004).

However, the phylogeny of pikas is far from clear. Order Lagomorpha has been alternatively placed with such diverse groups as rodents (Liu and Miyamoto 1999, Douzery and Huchon 2004), primates (Graur et al. 1996), tree shrews (Schmitz et al. 2000) and elephant shrews (McKenna 1975), among others. Most frequently lagomorphs are paired with rodents in the Superorder Glires (Douzery and Huchon 2004, Hoffmann and Smith 2005).

Within Lagomorpha, the families Ochotonidae and Leporidae diverged as early as the Oligocene (Smith et al. 1990). Pikas evolved in high latitudes and / or altitudes and likely invaded the plateau region multiple times (Yu et al. 2000, Niu et al. 2004). It is widely accepted that pikas appeared first in Asia and later dispersed to North America, probably in the late Pliocene (Mead 1987, Chapman and Flux 2008). The Pliocene is also the time in which the various pika subgroups diverged (Yu et al. 2000, Niu et al. 2004). The diversification of pikas was originally thought to coincide with the Tibetan plateau uplift (Yu et al. 1992). However, due to recent reevaluation of the rising of the plateau (Rowley and Currie 2006, Wang et al. 2008a; see next section), this conclusion should be reevaluated.

The evolutionary relationship between individual species is also a subject of debate (Hoffmann and Smith 2005). Ecologically, pikas fall into one of two types: a long-lived and asocial type with low density and fecundity that lives in talus or rocky slopes, and a short-lived and highly social type that inhabits open grassland and has fluctuating density and fecundity (Smith et al. 1990). However, this ecological division may not reflect evolutionary history.

Molecular analyses have divided genus *Ochotona* into two to five groups, or subgenera (Smith et al. 1990, Yu et al. 1992, Yu et al. 2000, Niu et al. 2004), which are not yet recognized in the current taxonomy (Hoffmann and Smith 2005). Yu et al. (1992) described three groups of pikas: the shrub-dwelling group; the rock/talus-dwelling group; and the steppe-dwelling group, which includes *O. curzoniae*. Yu et al. (2000) placed *O. curzoniae* within subgenus *Ochotona*, a shrub-steppe group, which was separate from subgenus *Pika*, the northern group; and subgenus *Conothoa*, the mountain group. Niu et al. (2004) supports five groups: the northern group; the surrounding Qinghai-Tibet plateau group, the central Qinghai-Tibet plateau group (with *O. curzoniae*), the Yellow river group, and the Central Asia group. Thus, *O. curzoniae* has been placed variously in a steppe-dwelling group, a shrub-steppe group, and a central Qinghai-Tibet plateau group. Due to their similar ecologies, *O. curzoniae* and *O. dauurica*[4] are usually grouped together. They were once thought to belong to the same species, but are now regarded as separate (Yu et al. 2000).

Aside from pikas, only two other lagomorphs are currently found on the Tibetan plateau – the woolly hare, *Lepus oiostolus* (Hodgson, 1840) and the less common Yunnan hare, *Lepus comus* (Allen, 1927), in the far east (Smith and Xie 2008). Neither of these animals forms large colonies. In addition, several species of burrowing rodents have ranges that overlap the plateau pika. The Chinese zokor, *Eospalax fontanierii* (Milne-Edwards, 1867), is a strictly fossorial endemic rodent (Smith and Xie 2008). Both Himalayan marmots, *Marmota himalayana* (Hodgson, 1841), and lacustrine voles, *Microtus limnophilus*[5] (Büchner, 1889) are widespread, but not colonial (Smith and Xie 2008). Other

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[4] *O. dauurica* is occasionally misspelled *O. daurica*.

[5] This species is often misidentified as the root vole, *Microtus oeconomicus* (Pallas, 1776), found only in northern Xinjiang and Inner Mongolia (2008).

small mammals of note include Przewalski's steppe vole, *Eolagurus przewalskii* (Büchner, 1889), Blyth's mountain vole, *Phaiomys leucurus* (Blyth, 1863) and six species of hamster (Smith and Xie 2008).

While the Tibetan plateau clearly supports a diversity of small mammals, the plateau pika is by far the most abundant. Their colonies can reach densities of 300 individuals/ha (Smith and Xie 2008). Indeed, early European explorers described these regions as "Ochotona-steppe" due to the predominance of pika burrows on the landscape (Schäfer 1938). Thus, despite their small size, plateau pikas can collectively exert a large influence over their community and habitat. This relationship will be discussed further with pika ecology.

The Tibetan plateau

The range of the plateau pika is nearly synonymous with the extent of the Tibetan plateau[6] (Figure 1.2). The Tibetan plateau covers much of western China as well as parts of Nepal, India and Bhutan. Within China the plateau extends primarily over Qinghai and Tibet, but also includes areas in southern Xinjiang, western Sichuan and northern Yunnan[7].

The Tibetan plateau covers 2.5 million km^2, or approximately one quarter of China's land area (Ekvall 1968, Miller 1995, Miller and Craig 1997). With an average height close to 4500 m and multiple peaks above 6000 m (Yang 1992), most of the plateau is considered alpine (Aldenderfer and Zhang 2004). However, according to According to Miehe's (2008) hypothesis, much of the *Kobresia pygmaea* meadow typical of this region was once open forest. If

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[6] Also called the Qinghai-Xizang (Tibet) plateau.

[7] The full names of these administrative units in the People's Republic of China are Qinghai Province, Tibet Autonomous Region, Xinjiang Uyghur Autonomous Region, Sichuan Province and Yunnan Province, respectively.

correct, and the current grasslands are the result of anthropogenic livestock grazing, they would not fit a strict interpretation of “alpine” defined as regions above the natural treeline (Körner 2003). I follow Aldenderfer and Zhang’s (2004) definition of alpine as regions over 4000 m in altitude.

The plateau is bordered by high mountain ranges on all sides – the Qilian in the northeast, Himalaya in the south, Karakoram in the west, and Kunlun in the north. Additionally, several mountain ranges fall inside the plateau, such as the Nyaingen tanglha, Tanggula, and Anyemaqin. Over 2000 saline lakes are scattered across the plateau; one of these, Qinghai lake, is the largest in China (Aldenderfer and Zhang 2004). Other features of the plateau include the Yarlung Tsangpo valley (3700-3900 m) in the south, the sparsely vegetated Chang Tang desert (4300-5000 m) to the west, and two basins in the northeast (the semi-desert Qaidam basin at 2600-3000 m, and the wetter Qinghai lake basin at 3200 m) (Aldenderfer and Zhang 2004).

Most of these mountain ranges, as well as the plateau, were created during the collision of the Indian subcontinent with Asia in the vicinity of Mount Everest approximately 50 million years ago (mya) (Zhu et al. 2005). However, the timing and nature of the uplift are controversial, and several models of this continental collision have been proposed. Though some authors propose that this crustal thickening occurred as early as 100 – 50 mya (Kapp et al. 2005), even before continental collision, other authors propose a later date. Until recently, the rising of the plateau was placed around 8 – 10 mya (Garzione et al. 2000, Rowley et al. 2001). However, more current evidence points to the plateau reaching its current height 40 – 35 mya (Rowley and Currie 2006, Wang et al. 2008a). Once the initial height was reached, the plateau remained relatively constant (Royden et al. 1997, Spicer et al. 2003, Rowley and Currie 2006). However, a few authors argue that growth was stepwise and occurred in stages (Tapponnier et al. 2001, Wang et al. 2008a).

Aside from the timing of the collision, the nature of the uplift is also controversial. Two theories explain the rise of the plateau (Tapponnier et al. 2001, Rowley and Currie 2006). The first maintains that the Indian subcontinent slipped below the Eurasian plate via simple crustal subduction (Rowley and Currie 2006). According to this view, an extensive portion of the Indian plate lies beneath the Tibetan plateau, buoying up the surface (Molnar 1989). An alternative model contends that the uplift was largely a result of lithosphere thickening in the crust and upper mantle (Molnar et al. 1993, Tapponnier et al. 2001, Molnar et al. 2006). Eventually, the denser lower lithosphere sunk beneath the mantle, whereas the lighter mantle beneath pushed the surface of the plateau upwards (Molnar 1989). Although there is some acknowledgement that these processes may have worked in concert, the extent to which one event dominated the other remains unclear (Royden et al. 2008).

The Tibetan plateau is a major factor shaping regional climate and hydrology. The plateau uplift is speculated to have led to worldwide climate change, including creation of Asian monsoons (An et al. 2001). Due to its importance as a major watershed, the plateau has been called “China’s water tower” (United States Embassy 2003). China’s three largest rivers, the Yellow, the Yangtze and the Mekong[8], originate on the plateau and surrounding mountains, along with many other Asian rivers, including the Indus and Brahmaputra (Immerzeel et al. 2010). These rivers are vital for the agriculture

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[8] Known as the Huang He, Chang Jiang and Lancang Jiang, respectively.

and livelihood of millions of people living downstream (Xu et al. 2009). It has been estimated that 28% of China's water and 34% of water for the Indian subcontinent originates on the plateau (Aldenderfer and Zhang 2004). Thus, factors affecting the Tibetan plateau may influence the lives of nearly 40% of the world's population (Foggin 2008).

Given its distinctive environment, it is not surprising that the Tibetan plateau harbors many endemic species (MacKinnon et al. 1996, Schaller 1998). Although seventy percent of the plateau is grassland (Ekvall 1968, Miller 1995, Miller and Craig 1997), forests are supported by higher rainfall and humidity in the south and east (Aldenderfer and Zhang 2004). As a result, multiple biomes divide the plateau. Ni (2000) describes 10 such regions: temperate conifer forest; temperate deciduous forest; temperate broadleaf evergreen forest; tropical seasonal rainforest; temperate meadow-shrubland; temperate steppe; temperate desert; alpine meadow-shrubland; alpine steppe; and alpine desert. More recently, the World Wide Fund for Nature (WWF) designated fifteen "ecoregions" on the Tibetan plateau in its global assessment (Olson et al. 2001, Plateau Perspectives 2008): the Hengduan mountains subalpine confer forest (PA0509); northeastern Himalayan subalpine confer forest (PA0514); 3) Nujiang Langcang gorge alpine confer and mixed forest (PA0516); Qilian mountains confer forest (PA0517); 5) Qionglai – Minshan conifer forest (PA0518); central Tibetan plateau alpine steppe (PA1002); eastern Himalayan alpine shrub and meadows (PA1003); Karakoram – west Tibetan plateau alpine steppe (PA1006); north Tibetan plateau – Kunlun mountains alpine desert (PA1011); Qilian mountains subalpine meadow (PA1015); southeast Tibet shrub and meadow (PA1017); Tibetan plateau alpine shrubs and meadow (PA1020); western Himalayan alpine shrub and meadow (PA1021); Yarlung Tsangpo arid steppe (PA1022); and Qaidam basin semi-desert (PA1324). Following this classification, the “Global 200” are ecoregions which are priority areas for conservation (Olson and Dinerstein 1998, 2002). The Tibetan plateau steppe (Global Ecoregion 110; an amalgamation of PA1022, PA1020, PA1017, PA1002, and PA1006) is considered a global ecoregion with vulnerable conservation status (Olson and Dinerstein 2002, WWF [World Wide Fund for Nature] 2009). My research was primarily restricted to habitat defined as Tibetan plateau alpine shrub and meadows (PA1020) and the southeast Tibet shrub and meadows (PA1017) (Olson et al. 2001). Both areas are of considerable conservation concern (Carpenter 2001b, 2001a).

Interactions between pikas and humans

The Tibetan plateau was not inhabited by humans until the late Pleistocene, approximately 45,000 – 10,000 years ago (Aldenderfer 2006). No archeological sites dating before the mid-Pleistocene have been found above 40ºN, suggesting that early humans were not capable of colonizing these cold and remote regions (Dennell 2004). It was not until the advent of complex clothing and control of fire that humans were able to survive in at these altitudes (Aldenderfer 2006).

Due to the high elevation and harsh conditions, most of the plateau is not suitable for farming, but only for livestock production. The yak, *Bos grunniens*, was first domesticated 8000 – 10,000 years ago (Guo et al. 2006). Although wild yak still inhabit remote corners of the Tibetan plateau (Schaller 1998), evidence suggests all domestic yak are descendants of a single small wild population (Guo et al. 2006). Livestock production has traditionally taken the form of Tibetan pastoralism, in which animals are rotated between summer and winter pastures (Ekvall 1968, Miller 1995, Miller and Craig 1997). This pastoral system has existed for approximately 4500 (Li et al. 2003) to 8800 years (Miehe et al. 2009).

Dense populations of plateau pikas have long been considered a nuisance to herders. Even though nomads have grazed yak, sheep and horses in coexistence with pikas for thousands of years, many blame pikas for current rangeland degradation (Formozov 1928, Ekvall 1968). Additionally, some research has suggested pikas compete with the local livestock for food and overgraze the natural grasslands (Fan et al. 1999). Their burrows are said to cause soil erosion, rangeland degradation, and biodiversity loss (Xia 1986, Zhang et al. 1998, Fan et al. 1999). Pikas have also been accused of creating black sands, large darkened areas devoid of vegetation (Schaller 1998). However, other research argues that black sands may be a consequence of trail erosion or global warming (Miehe 1988, 1996, Ma et al. 1997, Schaller 1998).

In spite of a lack of evidence that pikas cause rangeland degradation, they have been extensively poisoned throughout their range (Liu et al. 1980, Shen and Chen 1984, Zhong et al. 1985, Fan et al. 1986, Smith et al. 1990, Ma 1995, Zhang et al. 1998, Fan et al. 1999). Even the European Union-funded Qinghai Livestock Development Project listed poisoning of pikas as one of its goals (van Wageningen and Sa 2001). Potent chemicals, such as zinc phosphate, Compound 1080 (fluoroacetate), Fussol, botulin C toxin and various anticoagulants have been used to eradicate the pika, while simultaneously causing widespread environmental pollution (Fan et al. 1999). Over 200,000 km^2, an area roughly the size of Nebraska, were poisoned from 1960 to 1990 (Fan et al. 1999). Use of Compound 1080 and Fussol was abolished in 1978, when they were found to lead to secondary poisoning of predators (Smith et al. 1990). Currently botulin C toxin is used to eradicate pikas (Jing et al. 2006).

New information suggests that large pika populations may be a result of overgrazing, rather than a cause (Cincotta et al. 1992, Smith and Foggin 1999). Pikas tend to favor heavily grazed areas with low cover because there is a wider field of view for spotting predators (Shi 1983, Bian et al. 1994, Zhang et al. 1998). Other literature contends that only when livestock reach high densities are they likely to compete with pikas for food (Xia 1986, Jiang and Xia 1987). This lack of competition occurs because pikas graze selectively, and many of their food sources are avoided by domestic yak and Tibetan sheep (Jiang and Xia 1985, 1987, Schaller 1998). Pikas are also known to eat plants poisonous to livestock (Schaller 1998). Additionally, competition for food between yak and Tibetan sheep is thought to be more intense than the competition between these domesticated animals and pikas (Jiang and Xia 1987). Research on the related Daurian pika also supports this view. Daurian pikas were found to contribute to rangeland degradation only in areas that had already been overgrazed (Zhong et al. 1985). Furthermore, Komonen et al. (2003) concluded that the impact of Daurian pikas on overgrazing is light.

Recent government policy has been to settle Tibetan nomads and to fence rangelands (Goldstein et al. 1990, Williams 1996, Wu and Richard 1999, Foggin 2000, Miller 2000, Banks 2003, Yeh 2003, Yeh 2005, Foggin 2008). Though these polices have been enacted, in part, to reduce rangeland degradation, the nature and extent of this degradation is far from clear (Harris 2010). Fan et al. (1999) estimated that recent grazing practices have resulted in serious degeneration of 50% of the natural grassland habitat. In contrast, Harris's review (2010) of degradation on the Tibetan plateau concluded that government policy (privatization, sedentarization and fencing), in addition to climate change and the conversion to cropland, were the only major drivers. He found little evidence that damage by plateau pikas or burrowing rodents lead to rangeland degradation (Harris 2010).

BIOLOGICAL IMPORTANCE

A great variety of vertebrates are commonly associated with pika colonies (Table 1.2). These animals fall into two broad groups: those that rely on pika burrows for shelter, and those that depend on the pika as a food source. Other animals may benefit indirectly from the presence of pikas through commensal or mutualistic interactions that decrease predation risk or increase feeding efficiency (Dickman 1992); however, this scenario has not been explicitly investigated.

Pika burrows provide much-needed shelter on the open treeless grasslands. Burrows offer not only refuge from predators, but also protection from precipitation and temperature extremes. Hume's groundpecker, *Pseudopodoces humilis*, and six species of snowfinch (*Montifringilla* spp. and *Pyrgilauda* spp.) all nest primarily in plateau pika burrows (Feng et al. 1986, Ma 1995, Schaller 1998, MacKinnon and Phillipps 2000, Lai and Smith 2003). Both the small snowfinch (*Pyrgilauda davidiana*) and Isabelline wheatear (*Oenanthe isabellina*) nest in the burrows of Daurian pikas (*O. dauurica*), an ecologically similar species (Smith et al. 1990). Additionally, two species of lizards (*Phrynocephalus vlangalii* and *Eremias multiocellata*) live and breed in pika burrows (Li 1989).

To this list, I can add two species not previously associated with plateau pika colonies. I observed two species of Anuran inhabit pika burrows at a field location (34^{o}24'05"N 100^{o}23'44"E) near Dawu Township in Golog Prefecture, Qinghai Province. The locality was relatively flat, high alpine (3900m) pastureland dominated by *Kobresia* sedges. This area was wetter than nearby regions due to an actively-flowing stream which lead to small, possibly ephemeral, pond. Plateau pikas were common, and had dug burrows up to the water's edge (Figure 1.3a). Burrows were occasionally flooded after heavy rains (Figure 1.3b), presumably when the stream over-flowed its banks. In August 2005, August 2006 and June 2007, I observed multiple cases when individual frogs (belonging to two distinct anuran species) hopped into a pika burrow when approached. These burrows were moist, but not flooded, and still in active use by the pika, as evidenced by fresh feces near the entranceway. In 2007, one frog species was observed swimming into a submerged pika burrow. These species were later captured and identified as *Bufo raddei* (Figure 1.3c) and *Nanorana pleskei* (Figure 1.3d).

Due to their abundance, plateau pikas are an important food source for most native carnivores (Table 1.3). The steppe polecat, *Mustela eversmanii*, may be a specialist predator of the plateau pika (Smith and Foggin 1999). Other predators include the mountain weasel (*Mustela altaica*), Tibetan fox (*Vulpes ferrilata*), red fox (*V. vulpes*), Pallas' cat (*Felis manul*), wolf (*Canis lupis*), and brown bear (*Ursus arctos*) (Smith et al. 1990, Schaller 1998, Smith and Foggin 1999, Xu et al. 2006, Liu et al. 2010a). Snow leopards (*Uncia uncia*) occasionally prey on pikas as well (Schaller 1998). Aside from mammalian carnivores, the Tibetan plateau is also home to a highly diverse assemblage of raptors. The golden eagle (*Aquila chrysaetos*), upland buzzard (*Buteo hemilasius*), saker falcon (*Falco cherrug*), northern goshawk (*Accipiter gentilis*), black kite (*Milvus migrans*), and little owl (*Athene noctua*) all rely on pikas for a significant portion of their diet (Peshkov 1967, Schaller 1998, Lai and Smith 2003, Li et al. 2004b, Cui et al. 2008).

The importance of plateau pikas both as a food source and a habitat modifier is has led to its label as a keystone species (Smith and Foggin 1999). Smith and Foggin (1999) justify the keystone status of plateau pikas with four different lines of evidence: their burrows house many small vertebrates; they generate microhabitats that lead to increased plant species richness; most predators on the plateau rely on them for prey; and they improve ecosystem-level dynamics. However, use of the keystone designation has fallen into some disfavor (Mills et al. 1993, Hurlbert 1997). In addition, new definitions, such as Power et al.'s (1996), seem to exclude species that are abundant, thus questioning the inclusion of animals such as prairie dogs (Kotliar 2000). I address this debate, as well as the specific designation of plateau pikas, in detail below.

The species formerly known as keystone

The keystone species concept was first introduced by Paine (1966, 1969). His original definition referred to an animal high in the food chain, such as a predator, that was critical to “the integrity of the community and its unaltered persistence through time” (Paine 1969). However, the idea that certain species disproportionately influence community structure developed multiple times. For instance, MacArthur (1972) was fundamental in drawing attention to strong and weak interactors in a community. The same year, Dayton (1972) referred to important species in a community as key or foundation species. Later Wells et al. (1986) applied the term transformer species to organisms that “change the character, condition, form or nature of a natural ecosystem over a substantial area." Though several individuals converged on the same concept, Paine's definition has remained at the forefront; as of October 28, 2010, his 1966 paper had been cited over 2000 times (Thomson Reuters 2010).

In spite of the popularity of Paine's idea, the keystone concept developed far beyond his original description (Appendix A, Table A-1). Holt (1977) was first to broaden Paine's definition to include prey species, citing the snowshoe hare as an example. According to his view, a keystone prey's high reproductive rate supports a predator, which in turn, keeps other prey in check (Holt 1977). Noy-Meir (1981) later redefined the term to avoid an unintended consequence of Holt's definition, which led to an increase in diversity when the keystone prey was removed.

The keystone concept expanded from there. Gilbert (1980) added the term "keystone mutualist" for those organisms "which provide critical support to large complexes of mobile links." Mobile links are foraging species "of mutual concern to the reproduction of many different unrelated plants which, in turn, support otherwise independent food webs" (Gilbert 1980). Brown and Heske (1990) included kangaroo rats as a keystone guild because "they have major effects on biological diversity and biogeochemical processes." Terborgh (1986) cited palm nuts, figs, and nectar as keystone plant resources because of their "prominent roles in sustaining frugivores through periods of general food scarcity." Folke et al. (1996) declared that the group of species controlling the most vital ecosystem processes should be termed "keystone process species." Soon, summaries of these different classification schemes began to appear. Lamont (1992) offered a highly detailed organizational plan which included first-, second- and third-order keystone species. Bond (1993) grouped keystones into eight types, consisting of predators, herbivores, pathogens or parasites, competitors, mutualists, earth-movers, system processors, and abiotic agents.

The keystone concept also came to include animals critical as ecosystem engineers (Redford 1984, Naiman et al. 1986). Ecosystem engineers are organisms that “modify, maintain and create habitats” (Jones et al. 1994). Jones et al. (1994) highlighted the similarities between keystones and engineers, and suggested that many, but not all, keystone species control their environment through ecosystem engineering. Reichman and Seabloom (2002) used the term “keystone ecoengineer” to emphasize that changes wrought by ecosystem engineers “should be distinctive from processes that are strictly abiotic … and large relative to the purely physical processes operating in the system”. However, others argued against conflating the concepts of ecosystem engineer and keystone species (Wilby 2002).

Even as these neologisms developed, another movement emerged to challenge the inclusiveness of the keystone concept. Paine’s (1969) original definition was broad in the sense that it included both an abundant trophic generalist as well as a rare food specialist. For Estes and Palmisano (1974), it was enough for a species to be “important … in determining structures and dynamic relations within nearshore communities” to be considered keystone. Indeed, Wells et al.’s (1986) concept was not limited to positive alterations, but also included the negative effects of invasive organisms. Bond (1993) went so far as to include humans as “the most important keystone species in most ecosystems.” This trend culminated with Holling’s (1992) extended keystone hypothesis, in which all terrestrial ecosystems were controlled by key organisms and processes. Jones et al. (1994) added that keystones were common to all habitats, not merely terrestrial ones.

Perhaps in reaction to this broad application, other authors sought to limit the keystone concept. Dayton's (1972) definition was the first to exclude common organisms, explaining that key species include only those that "have roles in the maintenance of the community disproportionate to the abundance or biomass of the species." Piraino and Fanelli (1999) argued that though there may be many *key* species influencing communities, there were few keystones. In Menge et al.'s (1994) reinvestigation of rocky intertidal communities, they discovered that *Piaster* acted as a keystone only under certain contexts. This led the authors to contend that keystone species were "not universal" (Menge et al. 1994). Mills et al. (1993) also found little evidence for the type of community structure dominated by keystones.

Mills et al. (1993) were the first to broadly endorse abandonment of the keystone species concept. They claimed the keystone concept was "broadly applied, poorly defined, and nonspecific in meaning" (Mills et al. 1993). Likewise, Hurlbert (1997) argued that the term has been so indistinctly applied that it "now means little more than 'important for something.'" However, both Hurlbert (1997) and Mills (1993) acknowledged that all species are not equally important in an ecosystem. Instead, Mills (1993) recommended refocusing on strong and weak interactors. Hurlbert (1997), on the other hand, advocated using functional importance, which he defined in Hurlbert (1971) as, "the sum over all species, of the changes (sign ignored) in productivity which would occur on removal of the particular species from the community."

Despite these salient points, not all authors considered the keystone concept as irreparable. Power et al. (1996) provided the most direct rejoinder to Mills et al. (1993), but they were not the first to speak in its defense. Demaynadier and Hunter (1994) , Menge et al. (1994) and Paine (1995) gave rebuttals to the abandonment of keystone idea. One common objection was that the “strong interactors” and “functionally important species” advocated by Mills (1993) and Hurlbert (1997) did not distinguish between ecological dominants and species with effects disproportional to their abundance (Piraino and Fanelli 1999, Vanclay 1999, Davic 2000). Other views in favor of the keystone concept can be summarized as follows: 1) it is already widely used by scientists (Demaynadier and Hunter 1994); 2) other terms used by ecologists are just as vague (e.g. biodiversity (Hodges 2008), ecosystem (Demaynadier and Hunter 1994) or niche (Godsoe 2009)); 3) it draws attention to the disproportionate influence of species in an ecosystem (Demaynadier and Hunter 1994, Paine 1995); 4) it is supported by many well-documented examples (Demaynadier and Hunter 1994, Menge et al. 1994, Power et al. 1996); 5) it is easily communicated to the public (Demaynadier and Hunter 1994, Paine 1995); and 6) it is useful for setting management and conservation priorities (Demaynadier and Hunter 1994, Paine 1995, Simberloff 1998).

Power et al. (1996) sought to reestablish the keystone concept by explicitly defining keystone species as “one whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance.” Rather than ending the debate, this description instead re-ignited earlier controversy over the inclusiveness of the keystone concept (Menge et al. 1994, Davic 2000, 2002, Higdon 2002). Davic (2003) modified Power et al.’s (1996) definition so that the effect of keystone need only be large relative to its biomass dominance in a functional group. Although the debate is not settled, most acknowledge that keystone status is context dependent; that is, a species may be a keystone in some areas, and not in others (Menge et al. 1994, Power et al. 1996, Christianou and Ebenman 2005).

More recently, publications have shifted from defining keystones to solving a different problem – the need for *a priori* keystone identification (Appendix B, Table A-2). Holt (1977) provided the first quantification of a keystone species as one with a high reproductive to predation rate. Many alternative metrics have now been proposed to delineate keystones, including position in the food web; the performance of ecological services not carried out by other organisms, i.e. a lack of redundancy (Walker 1992, 1995, Kotliar 2000); the number of secondary extinctions resulting from its loss (Christianou and Ebenman 2005, Ebenman and Jonsson 2005); control of energy or matter flow (Jordán et al. 1999, Jordán et al. 2006, Libralato et al. 2006); alteration of the dominant ecosystem vegetation (Khanina 1998); control of important ecosystem processes (Folke et al. 1996); and community importance (Mills et al. 1993, Power et al. 1996).

While many studies mention the effects of keystone species loss, few studies can make predictions that can be tested in the field. Some go as far to say that any species found to be biomass-dominant should be considered a potential keystone until proven otherwise (Davic 2003). Network analysis of food webs has been suggested as a method to identify keystones (Jordán et al. 1999, Solé and Montoya 2001, Christianou and Ebenman 2005, Jordán et al. 2006). Furthermore, a variety of indexes to measure the “keystoneness” of a species have been developed (Jordán et al. 1999, Okey et al. 2004, Libralato et al. 2006, Estrada 2007, Jordán et al. 2008). Interestingly, Christianou and Ebenman's (2005) study found that even weakly interacting species can be keystones if their cumulative interactions are strong enough.

Application of the keystone concept

One species whose keystone status has been substantially debated is the North American prairie dog, *Cynomys* spp. (Kotliar et al. 1999). This debate is of particular relevance because the plateau pika plays an ecological role similar to that of the black-tailed prairie dog, *Cynomys ludovicianus*. Like plateau pikas, prairie dogs are said to cause rangeland degradation and have been poisoned over much of their range. Yet prairie dogs have also been shown to increase local plant primary productivity, augment soil mixing, boost soil oxygenation, and enhance water infiltration (Table 1.4; reviewed in Miller et al. 1994, Ceballos et al. 1999)

Although there has been substantial research on prairie dogs, there is considerable disagreement in the literature as to how much, and to what extent, these animals influence community and plant diversity. The prairie dogs' elimination is thought to be a key factor in the decline of other prairie endemics, such as the black-footed ferret, *Mustela nigripes* (Sharps and Uresk 1990). However, other researchers report lower or equivalent diversity between species found on and off prairie dog colonies (e.g. harvester ants (Kretzer and Cully 2001); nocturnal rodents and lagomorphs (Mellink and Madrigal 1993); small rodents (Agnew et al. 1986); amphibians and reptiles (Kretzer and Cully 2001); carnivores (Ceballos et al. 1999); and multiple species (Lomolino and Smith 2003)). Frequently, authors report differences in species composition, while not finding significant differences in abundance or diversity (Ceballos et al. 1999, Kretzer and Cully 2001, Lomolino and Smith 2003, Russell and Detling 2003).

These conflicting results, in addition to Power et al.'s (1996) reclassification of the keystone concept, led Stapp (1998) to challenge the keystone role of the prairie dogs. Opponents of Stapp's view citied the significant effect of prairie dogs on ecosystem structure, function, and composition (Ceballos et al. 1999, Miller et al. 2000). They regard equivocal results as differences in methodology, rather than differences in local conditions (Miller et al. 2000). Kotliar (2000) concluded that prairie dogs could satisfy Power et al.'s definition when the extent of their disturbance is great.

Somewhat fittingly, the keystone species concept was described in theory (Paine 1966) several years before it was named (Paine 1969). This sequence of events highlights the disjunction between the general concept of keystone and its precise delineation. To call an organism keystone begs the question, whose keystone. In particular, the plateau pika, fits the definitions conceptualized by Noy-Meir's (1981) keystone prey and Naiman et al.'s (1986) keystone modifier. While at first glance, pikas seem excluded from Power et al.'s (1996) keystone criteria due to their high abundance, following Kotliar's (1999) reasoning, plateau pikas may in fact fit this definition when their disturbance is widespread. Additionally, by considering importance relative to dominance within a functional group (Kotliar 2000, Davic 2003), rather than absolute dominance (Power et al. 1996), plateau pikas could easily fit the keystone criteria. Thus, multiple lines of evidence (including Smith and Foggin (1999)) support the use of the keystone concept with plateau pikas.

Environmental impact of fossorial herbivores

The term ecosystem engineer has generated considerably less controversy, though it also identifies ‘key’ organisms. Ecosystem engineers “directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials” (Jones et al. 1994). Burrowing mammals are classic examples due to their importance in soil formation (Grinnell 1923, Reichman and Smith 1990, Whitford and Kay 1999). Both plateau pikas and prairie dogs have been considered habitat engineers due to their extensive burrow systems.

Bioturbation, or soil mixing by organisms, has a variety of physical impacts. The process of digging a hole generates both underground voids as well as surface mounds of excavated soil. These microhabitats contribute to the spatial heterogeneity of the landscape. For example, depressions collect seeds and plant debris, which may encourage plant growth over these areas. These openings alter the drainage of water in the watershed (Hole 1981). During tunnel construction, subsoil mixes with topsoil, holes are backfilled with soil, and soil clumps are broken up. These actions can change soil bulk density and increase soil oxygenation.

The impact of burrowing mammals on ecosystem processes has been well documented (Whicker and Detling 1988). Local levels of plant available nutrients may vary between burrows and inter-burrow spaces. Coppock et al. (1983a) and Aho et al. (1998) both reported higher nitrogen concentrations and increased plant available nitrogen near prairie dog towns. In nitrogen limited systems, increased nitrogen availability may increase plant biomass and consequently forage availability. Ayarbe and Kieft (2000) identified increased total organic carbon and microbial respiration on mounds of kangaroo rats, indicating high levels of easily metabolized organic carbon. Increased levels of plant available nitrogen and phosphorus have been documented on zokor mounds (Wang et al. 1993, Zhang and Liu 2003). Previous studies have also shown burrowing animals can increase soil water infiltration and decrease water repellency (Leprun 1976, Ursic and Esher 1988, Garkaklis et al. 1998).

The actions of pikas are not restricted to bioturbation. Direct foraging on plants may lead to a variety of community impacts. Although grazing causes an immediate reduction of plant biomass, plants may exceed levels of growth needed to compensate for defoliation in the process known as overcompensation (Owen and Wiegert 1976, Owen 1980, Owen and Wiegert 1981). Following this topic, the “herbivore optimization hypothesis” argues that grazing leads to increased community productivity (McNaughton 1979). Though the of validity of this process was initially challenged (Belsky 1986, Bartolome 1993, Painter and Belsky 1993, Patten 1993), recent work has focused on the prevelance and extent of overcompensation. Some authors have found higher levels of plant productivity in grazed areas (Varnamkhasti et al. 1995, Frank et al. 2002), while others have reported a trend of lower above-ground biomass in response to grazing (Milchunas and Lauenroth 1993). Other recent evidence indicates this overcompensation may be short term and not persist over multiple seasons (de Mazancourt et al. 2005). In the case of prairie dogs, several studies have shown grazing may lead to an increase, rather than reduction, of plant species biomass by stimulating plant growth (Clements 1920, McNaughton 1979, Strauss and Agrawal 1999, Agrawal 2000). Specifically, studies have found that prairie dogs exhibit positive effects on intraseasonal aboveground plant biomass (Coppock et al. 1983a) and root biomass (Ingham and Detling 1986). Ingham and Detling (1984) have even argued that by constantly grazing foliage, prairie dogs may keep grasses in a young vegetative state preferred by ungulate grazers. Though grazing may be less influential on plant productivity than moisture availability and shared evolutionary history (Milchunas and Lauenroth 1993), grazing by herbivores can play a large role in community-level dynamics.

In addition to plant biomass, prairie dogs also influence vegetation composition and structure (Bonham and Lerwick 1976, Agnew et al. 1986, Whicker and Detling 1988, Weltzin et al. 1997a, Weltzin et al. 1997b). Archer et al. (1987) found increased rates of vegetation change on prairie dog colonies, which could lead to higher species turnover. Considerable influence on soil seed banks has been reported (Fahnestock et al. 2003). Furthermore, Coppock et al. (1983a) found increased live-to-dead ratios and greater digestibility of remaining species in regions inhabited by prairie dogs. Several studies have shown a link between increased habitat heterogeneity caused by prairie dogs and an increase in plant species diversity (Coppock et al. 1983a, Whicker and Detling 1988, Stapp 1998, Ceballos et al. 1999, Kotliar et al. 1999)

Several lines of evidence suggest that the Tibetan plateau flora may respond similarly to that of the North American temperate grasslands. Increased aboveground plant biomass has been reported on zokor mounds compared to surrounding meadow (Wang et al. 1993, Zhang and Liu 2003). Both Pallas' pika and Daurian pikas have also been found to increase plant species diversity in areas they inhabit (Smith et al. 1990).

CONCLUSION

The plateau pika is a transformative agent on the Tibetan plateau. As both a keystone species and ecosystem engineer, its presence is predicted to have a large impact on the ecosystem. When pikas are eradicated, burrows collapse and local bird populations decline (Lai and Smith 2003). Carnivores such as the steppe polecat could be eliminated if plateau pika densities drop too low (Smith and Foggin 1999). Additionally, factors affecting the pika habitat have the potential to influence the lives of millions of people living within the watershed. In light of negative historical interactions with humans and a continuing poisoning campaign, the ecological impacts of plateau pikas demand careful attention. My research examines the influence of plateau pikas on the plant community and ecosystem processes. Results of this study will have broad implications for the management of both livestock and small mammals on the Tibetan plateau.

Table 1.1. The distribution of extant pikas. For Chinese endemics, only province or autonomous region names are listed. Abbreviations are: GS, Gansu; HA, Henan; HB, Hubei; NX, Ningxia; QH, Qinghai; SN, Shaanxi; SX, Shanxi; SC, Sichuan; XJ, Xinjiang; XZ, Xizang; and YN, Yunnan. Country abbreviations are AFG , Afghanistan; BTN, Bhutan; CAN, Canada; CHN, China; IND, India; IRN, Iran; JPN, Japan; KAZ, Kazakhstan; KGZ, Kyrgyzstan; KOR, Republic of Korea; MMR, Myanmar; MNG, Mongolia; NPL, Nepal; PAK, Pakistan; RUS, Russian Federation; TJK, Tajikistan; TKM, Turkmenistan; USA, United States; and UZB, Uzbekistan. Conservation status, C, is identified as LC, least concern; EN, endangered; CR, critically endangered; or DD, data deficient (IUCN [International Union for Conservation of Nature] 2008).

Scientific Name	Common Name	C	Distribution
Palearctic			
Endemic to China			
O. argentata	silver pika	CR	NX
O. cansus	Gansu pika	LC	GS, QH, SN, SX, SC, XZ
O. erythrotis	Chinese red pika	LC	GS, QH, SC, YN
O. gaoligongensis	Gaoligong pika	DD	YN
O. gloveri	Glover's pika	LC	QH, SC, XZ, YN
O. himalayana	Himalayan pika	LC	XZ
O. huangensis	Tsing-ling pika	LC	GS, HA, HB, QH, SN, SX, SC
O. iliensis	Ili pika	EN	XJ
O. koslowi	Kozlov's pika	EN	QH, XJ
O. muliensis	Muli pika	DD	SC
O. nigritia	black pika	DD	YN
O. thomasi	Thomas's pika	LC	GS, QH, SC
Indigenous to China			
O. alpina	Altai pika	LC	CHN, KAZ, MNG, RUS
O. curzoniae	plateau pika	LC	CHN, IND, NPL
O. dauurica	Daurian pika	LC	CHN, MNG, RUS
O. forresti	Forrest's pika	LC	BTN, CHN, IND, MMR
O. hyperborea	Siberian pika	LC	CHN, JPN, MNG, RUS,KOR
O. ladacensis	Ladak pika	LC	CHN, IND, PAK
O. macrotis	large-eared pika	LC	AFG, BTN, CHN, IND, KAZ, KGZ, NPL, PAK, TJK
O. nubrica	Nubra pika	LC	CHN, IND
O. pallasi	Pallas's pika	LC	CHN, KAZ, MNG, RUS
O. roylei	Royle's pika	LC	CHN, IND, NPL, PAK
O. rutila	Turkestan red pika	LC	CHN, KAZ, KBZ, TJK, UZB
O. thibetana	Moupin pika	LC	BTN, CHN, IND, MMR
Absent from China			
O. hoffmanni	Hoffmann's pika	EN	MNG, RUS
O. pusilla	steppe pika	LC	KAZ, RUS
O. rufescens	Afghan pika	LC	AFG, IRN, PAK, TKM
O. turuchanensis	Turuchan pika	LC	RUS
Nearctic			
O. collaris	collared pika	LC	CAN, USA
O. princeps	American pika	LC	CAN, USA

Table 1.2. Native vertebrates associated with plateau pika colonies on Tibetan plateau grasslands.

Scientific Name	Common Name	Source
Amphibia		
Bufo raddei	Mongolian toad	this research
Nanorana pleskei	plateau frog	this research
Aves		
Accipiter gentilis	northern goshawk	Smith and Wang (1991), Smith and Foggin (1999)
Aquila chrysaetos	golden eagle	Prejevalsky (1876), Smith and Foggin (1999)
Athene noctua	little owl	Smith and Wang (1991), Smith and Foggin (1999)
Buteo hemilasius	upland buzzard	Prejevalsky (1876), Schäfer (1938), Schaller (1998), Smith and Foggin (1999), Lai and Smith (2003), Li et al. (2004c), Li et al. (2004b)
Falco cherrug	saker falcon	Schäfer (1938), Schaller (1998), Smith and Foggin (1999)
Milvus migrans[1]	black kite	Schäfer (1938), Smith and Foggin (1999), Lai and Smith (2003)
Montifringilla adamsi	Tibetan snowfinch	Schaller (1998), Lai and Smith (2003)
Montifringilla nivalis	white-winged snowfinch	Lai and Smith (2003)
Pseudopodoces humilis	Hume's groundpecker	Prejevalsky (1876), Meyer de Schauensee (1984), Schaller (1998), Lai and Smith (2003), Zhang et al. (2006)
Pyrgilauda blanfordi	plain-backed snowfinch	Schaller (1998), MacKinnon and Phillipps (2000)
Pyrgilauda davidiana	small snowfinch	Meyer de Schauensee (1984), MacKinnon and Phillipps (2000), Lai and Smith (2003)
Pyrgilauda ruficollis	rufous-necked snowfinch	Prejevalsky (1876), Schäfer (1938), Schaller (1998), MacKinnon and Phillipps (2000), Lai and Smith (2003), Zhang et al. (2006)
Pyrgilauda taczanowskii	white-rumped snowfinch	Schäfer (1938), Meyer de Schauensee (1984), MacKinnon and Phillipps (2000), Lai and Smith (2003), Zhang et al. (2006)

Table 1.2. Continued.

Mammalia		
Canis lupis	wolf	Smith et al. (1990), Schaller (1998), Smith and Foggin (1999)
Felis manul	Pallas' cat	Prejevalsky (1876), Schaller (1998), Smith and Foggin (1999)
Mustela altaica	mountain weasel	Smith et al. (1990), Smith and Foggin (1999), Yang et al. (2007)
Mustela eversmanii	steppe polecat	Schaller (1985), Smith et al. (1990), Schaller (1998), Smith and Foggin (1999), Yang et al. (2007)
Ursus arctos	brown bear	Prejevalsky (1876), Schäfer (1938), Smith et al. (1990), Schaller (1998), Smith and Foggin (1999), Xu et al. (2006)
Vulpes ferrilata	Tibetan fox	Prejevalsky (1876), Schaller (1998), Smith and Foggin (1999), Liu et al. (2010a)
Vulpes vulpes	red fox	Prejevalsky (1876), Schaller (1998), Smith and Foggin (1999), Yang et al. (2007)
Reptilia		
Eremias multiocellata	multi-ocellated racerunner	Smith and Foggin (1999)
Phrynocephalus vlangalii	Qinghai toad-headed lizard	Smith and Foggin (1999)

[1] Although the black kite, *Milvus migrans,* has been considered a separate species on the Tibetan plateau – namely *M. lineatus,* the black-eared kite (MacKinnon and Phillips 2000) – current classification lumps them with *M. migrans* (Johnson et al. 2005).

Table 1.3. Pikas in the diet composition of major plateau predators. Pika species, SP, are given as *Ochotona curzoniae*, OC; *O. dauurica*, OD, an ecologically similar species; OS, not identified to species by the source; and SM, combined data for pikas and small rodents. Method describes the way in which percent of diet was calculated.

Name	SP	Diet	Method	Source
Aves				
Aquila nipalensis, steppe eagle	OD	11–17%	percent occurrence in pellet and nest remnants	Peshkov (1957)
	SM	97–99%	percent content of pellet and nest remnants	Peshkov (1957)
Bubo bubo, Eurasian eagle-owl	OD	73%	percent occurrence in pellet and nest remnants	Peshkov (1957)
	SM	100%	percent content of pellet and nest remnants	Peshkov (1957)
Buteo hemilasius, upland buzzard	OD	24%	percent occurrence in nest remnants	Peshkov (1967)
	OS	100%	percent occurrence in food pellets	Schaller (1998)
	OC	75%	percent of diet (stable isotope)	Li et al. (2004b)
	OC	28%	percent occurrence in stomach contents	Li et al. (2004c)
	OC	59%	percent of stomach contents	Li et al. (2004c)
	OC	70%	percent occurrence food in pellets	Li et al. (2004c)
	OC	89%	percent content of food pellets	Li et al. (2004c)
Falco cherrug, saker falcon	OS	90%	percent occurrence in food pellets	Schaller (1998)
	OD	22%	percent occurrence in pellet and nest remnants	Peshkov (1957)
	SM	96%	percent content of pellet and nest remnants	Peshkov (1957)
Mammalia				
Canis lupis, wolf	OS	6–53%	percent of diet from scat analysis	Schaller (1998)
	OS	5–19%	frequency of occurrence in scat	Schaller (1998)

Table 1.3. Continued

Felis manul, Pallas' cat	OD	40%	percent occurrence in scat	Ross et al. (2010)
	OD	71%	frequency of occurrence in scat	Ross et al. (2010)
Mustela altaica, mountain weasel	SM[§]	27%	percent of diet (stable isotope)	Yi (2005)
	OC	100%	percent occurrence in scat	Yang et al. (2007)
Mustela eversmanii, steppe polecat	SM[§]	27%	percent of diet (stable isotope)	Yi (2005)
	OC	96%	percent occurrence in scat	Yang et al. (2007)
Uncia uncia, snow leopard	SM	0–2%	percent content in scat	Schaller (1998)
Ursus arctos, brown bear	OS	59%	percent content in scat	Schaller (1998)
	OC	78%	percent occurrence in scat	Xu et al. (2006)
	OC	46%	percent content in scat	Xu et al. (2006)
Vulpes ferrilata, Tibetan fox	SM[‡]	94%	percent content in scat	Schaller (1998)
	OC	84%	percent occurrence in scat	Liu et al. (2010a)
Vulpes vulpes, red fox	SM	51–67%	percent content in scat	Schaller (1998)
	OC	100%	percent occurrence in scat	Yang et al. (2007)

[‡] Author notes that these are mostly pika remains.
[§] Author notes that small mammals were previously poisoned in study area.

Table 1.4. Ecosystem services associated with prairie dog colonies.

Ecosystem service	Source
Soil mixing, oxygenation	Grinnell (1923), Whicker and Detling (1988), Huntly and Reichman (1994), Kotliar et al. (1999)
Water infiltration	Grinnell (1923), Whicker and Detling (1988), Huntly and Reichman (1994), Kotliar et al. (1999)
Plant species diversity	Coppock et al. (1983a), Whicker and Detling (1988), Stapp (1998), Ceballos et al. (1999), Kotliar et al. (1999), Fahnestock and Detling (2002)
Plant species turnover	Archer et al. (1987)
Seed bank	Fahnestock et al. (2003)
Plant growth/ biomass	Coppock et al. (1983a), Ingham and Detling (1984), Uresk (1985)
Forage quality (digestibility, live-dead ratio, N concentration)	Coppock et al. (1983a), Aho et al. (1998)

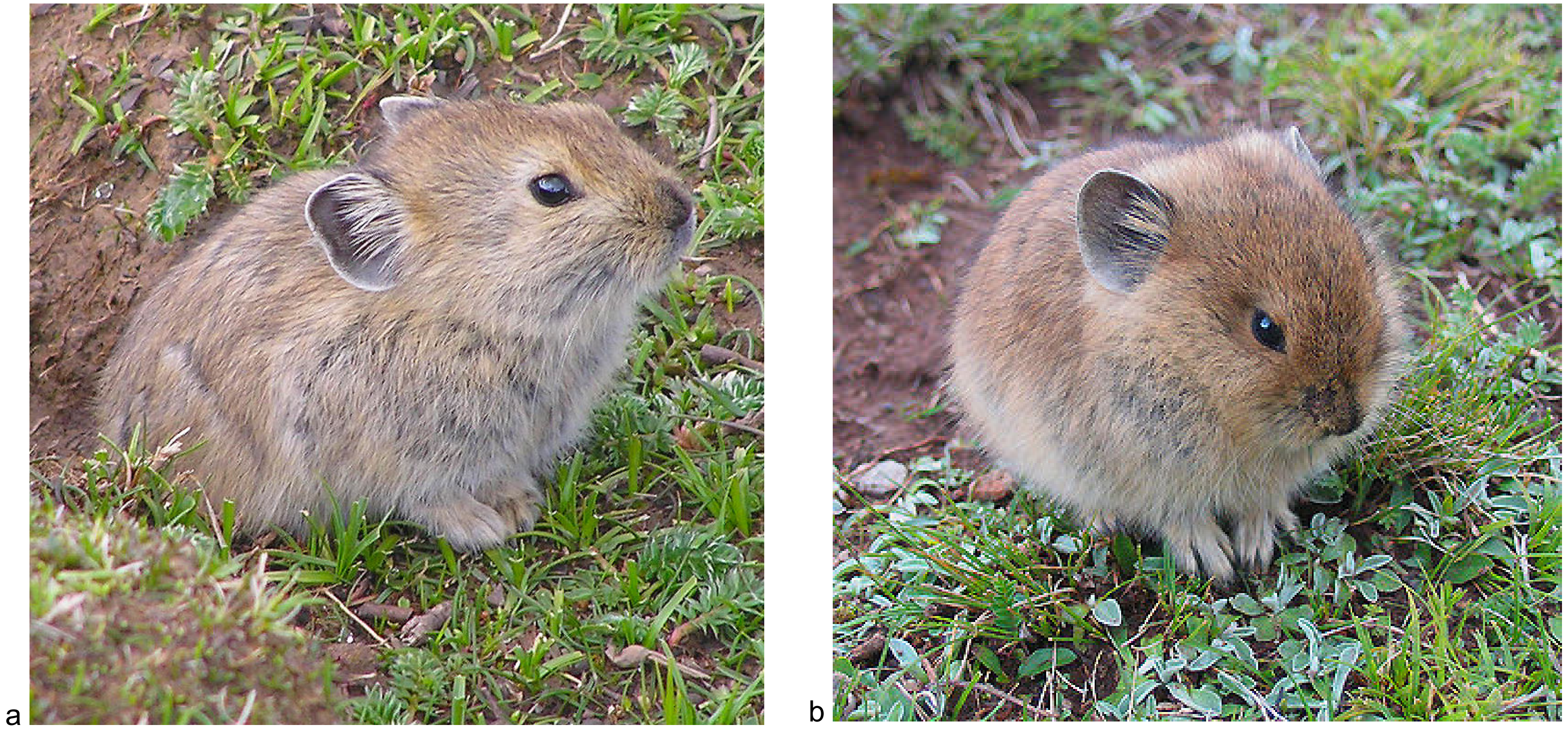

Figure 1.1. An adult (a) and juvenile (b) plateau pika near Dawu Township, summer 2006. Images were cropped, sharpened and filtered in Photoshop CS4. Photographs were taken by Brigitte Hogan (a) and Lee Anne Schaffer (b).

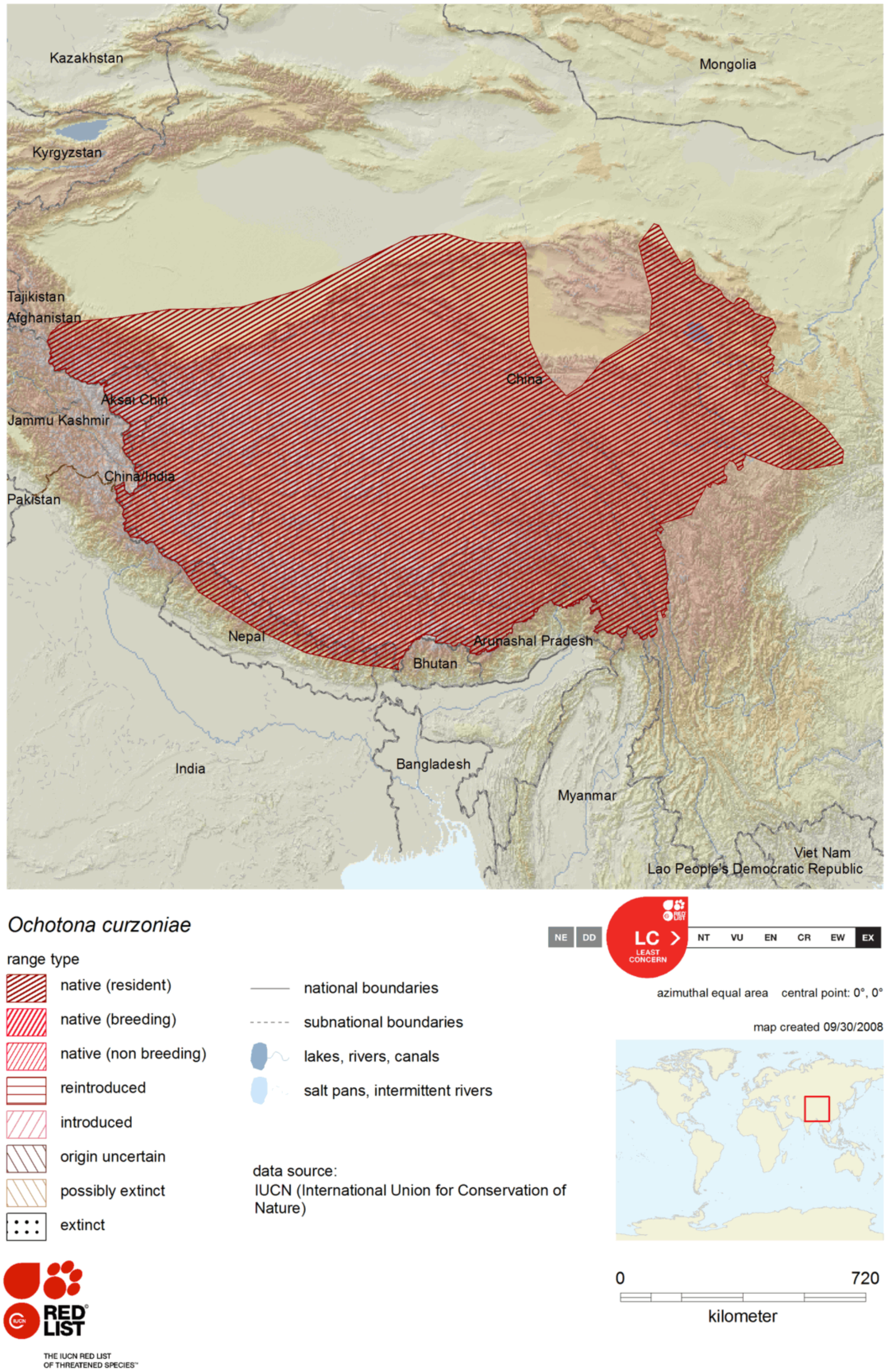

Figure 1.2. The distribution of plateau pikas on the Tibetan plateau (Smith and Johnston 2010).

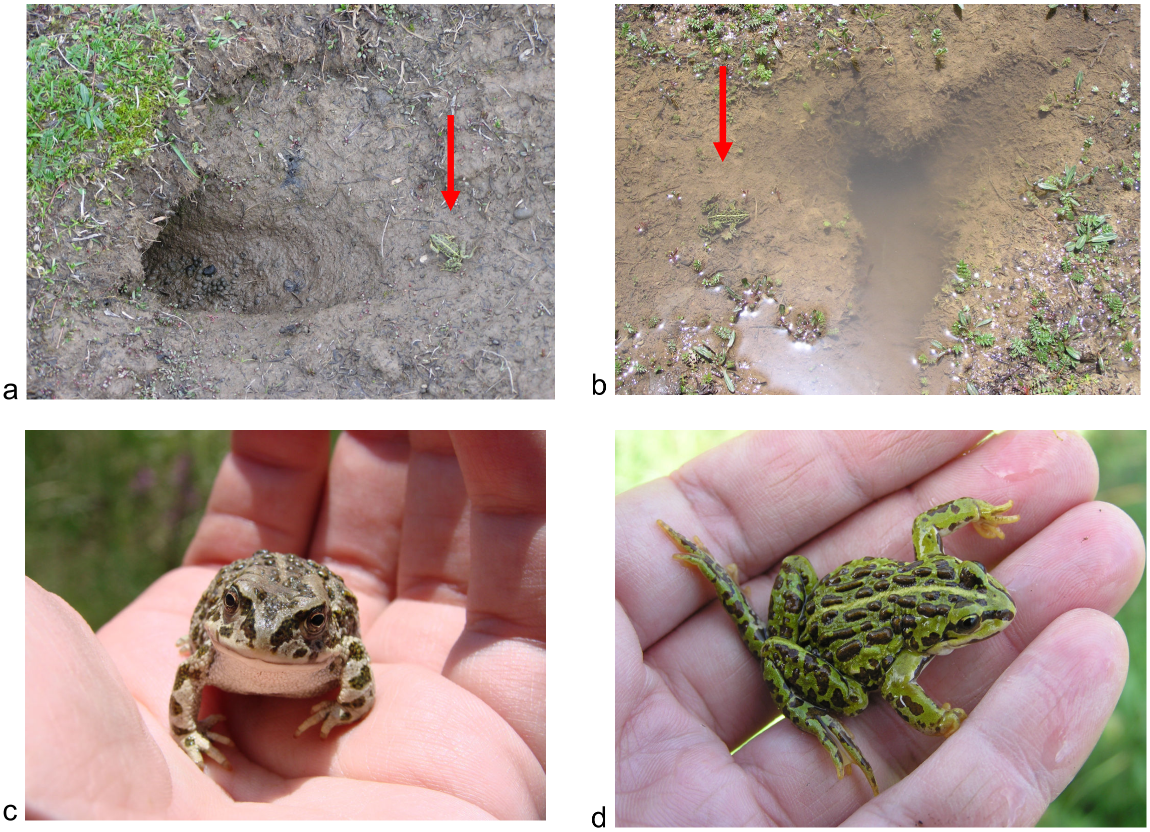

Figure 1.3. Anurans inhabiting plateau pika burrows in a wet *Kobresia* sedge-meadow. Meadow was located at 3900 m near Dawu Township, Qinghai Province. These frogs used both active (a) and submerged burrows (b). Both species were later caught and identified as *Bufo raddei* (c) and *Nanorana pleskei* (d). *Nanorana pleskei* is also shown in (a) and (b), indicated by arrows. Images were cropped, sharpened and filtered in Photoshop CS4. Photographs were taken by Brigitte Hogan (a, b, d) and Rachel Wasser (c).

CHAPTER 2
Ecosystem functioning on the Tibetan plateau: the influence of native pika colonies on nutrient and water flow

INTRODUCTION

Ecosystem functioning is the cumulative effect of living organisms on the environment (Naeem et al. 2004, Millennium Ecosystem Assessment 2005). However, not all species are equally important in influencing community structure. Ecosystem engineers, for example, are considered to be strong interactors because they physically alter the environment and thus control resource availability to other trophic levels (Jones et al. 1994). Ecosystem engineers can alter habitat as a consequence of their own growth (autogenic engineers) or via their physical actions (allogenic engineers) (Jones et al. 1994). One common example of allogenic engineering is animal burrowing, which has wide-ranging environmental effects (Meadows 1991, Dickman 1999).

The importance of one particular burrowing mammal, the plateau pika (Lagomorpha: *Ochotona curzoniae*), has led to its label as both a keystone species (Smith and Foggin 1999) and allogenic engineer (Lai and Smith 2003). Plateau pikas are endemic to the high alpine grasslands of the Tibetan plateau. Unlike their North American relatives (*O. collaris* and *O. princeps*), plateau pikas are highly social mammals that excavate extensive underground burrow systems (Smith and Wang 1991, Dobson et al. 2000). As a result, these pikas share more ecological similarities with the North American prairie dog (*Cynomys* spp.; Smith and Foggin 1999). Both organisms share the title of keystone species (Paine 1969), a rather controversial term (Power et al. 1996) used to label organisms of notable importance to ecosystem functioning (refer to Chapter 1). Kotliar et al. (1999) conclude that prairie dogs fit this definition due to the uniqueness of their role in the ecosystem, and the magnitude of their disturbance compared to other prairie herbivores, such as bison. The plateau pika can be considered a keystone for analogous reasons. For instance, plateau pika burrows provide critical habitat for many small vertebrates (Feng et al. 1986, Li 1989, Ma 1995, Schaller 1998, MacKinnon and Phillipps 2000, Lai and Smith 2003). Additionally, pikas serve as a prey items for many local mammals (Schaller 1998, Smith and Foggin 1999, Xu et al. 2006, Liu et al. 2010a) and raptors (Peshkov 1957, Lai and Smith 2003, Li et al. 2004b, Badingqiuying 2008, Cui et al. 2008).

Another similarity between plateau pikas and prairie dogs is their present-day conflict with humans. An intensive poisoning campaign, resembling the twentieth century eradication of prairie dogs, is currently targeting the plateau pika (Liu et al. 1980, Shen and Chen 1984, Zhong et al. 1985, Fan et al. 1986, Smith et al. 1990, Ma 1995, Zhang et al. 1998, Fan et al. 1999). Since the 1960s, over 200,000 km^2 of high-altitude grasslands have been treated with rodenticides (Fan et al. 1999), a management practice which continues today (Ma 2006). Poisoning continues because pikas are thought to compete with livestock for food (Fan et al. 1999), while their burrows are said to cause soil erosion, rangeland degradation, and biodiversity loss (Xia 1986, Zhang et al. 1998, Fan et al. 1999). Conversely, some evidence suggests that large pika populations may be a result of overgrazing, rather than a cause (Cincotta et al. 1992, Smith and Foggin 1999). Pikas tend to favor heavily grazed areas with low cover because there is a wider field of view for spotting predators (Shi 1983, Bian et al. 1994, Zhang et al. 1998). Other literature suggests that only when livestock reach high densities are they likely to compete with pikas for food (Xia 1986, Jiang and Xia 1987).

The elimination of pikas from this ecosystem may have far-reaching consequences due to the loss of their extensive burrowing and foraging activities. My research investigates the impact of pika colonies on ecosystem properties, specifically nutrient availability and water flow, in their alpine meadow habitat. Before examining these possibilities, I summarize the primary features of their high altitude environment and detail the nature and extent of their environmental engineering.

Tibetan plateau habitat

The Tibetan plateau is the world's largest low-latitude alpine region, spanning 2.5 million km^2 (Schaller 1998) at an average elevation over 4000 m (Wang 1988, Spicer et al. 2003, Qiu 2008). Much of this rugged environment is covered by grassland (Hu and Zhang 2004). These grasslands are critically important at both the local and global levels.

Due to the high elevation and harsh conditions, most of the plateau is not suitable for farming. Instead, the alpine grasslands are primarily used as rangelands by nomadic pastoralists (Ekvall 1968, Miller 1995, Miller and Craig 1997). The Tibetan pastoral system of herders and livestock has existed here for as long as 8800 years (Miehe et al. 2009). Livestock, primarily yak and sheep, closely graze meadows dominated by thick mats of *Kobresia* sedges. Indeed, the anthropogenic grazing of livestock is thought to be the source of this sod turf, some of which dates back as far as 2000 years (Kaiser et al. 2008). Consequently, the breakup of these tightly-knit soils via animal burrowing could have a powerful transformative influence on the local ecosystem.

At the regional scale, the Tibetan plateau is significant as a major watershed. The plateau is known as “China’s water tower” because it forms the headwaters of the Yangtze, Yellow and Mekong rivers[9] (Messerli et al. 2004). As a result, nearly 28% of China’s water and 34% of water for the Indian subcontinent originates on the plateau (Aldenderfer and Zhang 2004). Thus, factors affecting this region’s hydrology, such as grazing and bioturbation, may influence the lives of millions of people living downstream (Xu et al. 2009).

Finally, these high grassland soils are important as storehouses of organic carbon. The Tibetan plateau contains the world’s largest expanse of alpine permafrost (Jin et al. 2007), or soil that has remained below freezing for at least two years (Brady and Weil 2002). The cold environment has gradually accumulated the highest density of organic carbon in China (Zhang et al. 2007), which represents 2.5% of the global carbon pool (Wang et al. 2002). Under climate change, this region is expected to experience higher annual and winter temperatures (Cruz et al. 2007). Therefore environmental engineering within these alpine soils may become of increasing consequence.

Engineering of pika burrows

Plateau pikas are the most abundant small mammal on Tibetan grasslands (alpine meadow, meadow-steppe and desert-steppe) from 3000 to 5000 m (Smith and Xie 2008), with large colonies reaching over 300 individuals/ha (Smith et al. 1990). The primary resource created by burrowing mammals is subterranean living space (Dickman 1999). Bioturbation by pikas affects multiple spatial scales, ranging in extent from an individual entrance hole

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[9] Known as the Chang Jiang, Huang He and Lancang Jiang, respectively.

to a colony of pikas, which may cover many kilometers. Vertical variation is generated in the form of below-ground spaces and above-ground structures.

Beginning at the smallest scale, an entrance hole is approximately 10 cm in diameter and connects a belowground tunnel with the surface (Figure 2.1a). The primary surface structure is a mound of excavated soil (Figure 2.1b). This spoil heap develops as unwanted debris is pushed out of the entrance hole. Mound tailings are deposited to one of the entrance holes, forming an elliptical-shaped pile that buries nearby vegetation and adds relief to the otherwise flat meadow surface. The above-ground territory may also include shallow latrine pits and grazed runways connecting entrance holes (Figure 2.1c).

The mound is a dynamic unit that grows as new soil is added and shrinks as environmental conditions weather the accumulated soil. Plants colonizing the exposed soil eventually cover the mound with vegetative growth, and the mound becomes less distinguishable from the surrounding “undisturbed” meadow. [Older mound soil is especially difficult to distinguish in regions with low vegetative cover resulting from environmental conditions or high grazing pressure]. If an entrance hole is abandoned (due to flooding or anthropogenic disturbance), the surface will collapse, creating a small depression (Wei et al. 2007) that is quickly filled by debris and vegetation. Thus, over the lifetime of a small patch, the area may cycle between burrow hole, mound, and meadow.

Typically two to three pika holes are found in a 4 m^2 area. The complexes of mounds and pits form patches within the colony. Although entrance holes appear as distinct units on the meadow surface, they connect below-ground with the shared family burrow structure (the exception are “duck holes,” vertical tunnels used for temporary refuge (Smith and Wang 1991, Dobson et al. 1998)). Family burrow structures are cooperatively shared and maintained by 1 to 5 adults and can contain as many as 230 entrance holes (Dobson et al. 1998). These are connected by a network of subterranean tunnels 20 to 25 cm below the surface (Wei et al. 2007). The shared below-ground space also includes nest chambers and latrines.

At the local landscape scale, individual family burrow systems merge to form a larger burrow complex that is maintained over multiple generations (Dobson et al. 1998). Though small patches of ground may cycle through patch types, these burrow complexes, or colonies, tend to be stable in spatial extent (Dobson et al. 1998). Thus colonies exist as isolated regions within the surrounding terrain. At high pika densities, the colony edge is often determined by geographic barriers such as lakes, steep slopes or roads, rather than an abrupt transition to uncolonized meadow. Increasingly, uncolonized meadow is the result of anthropogenic poisoning. Poisoning, when effective, quickly eliminates obvious traces of burrowing as abandoned holes collapse and plants re-colonize the exposed soil. Thus, burrow construction generates a variety of micro-habitats which contribute to local landscape heterogeneity at multiple spatial scales.

Influence on ecosystem processes

Pikas cause direct as well as indirect ecosystem effects. Burrowing mammals directly impact other trophic levels through their grazing, foraging, food caching and seed dispersal (Dickman 1999). Herbivores are known to increase nutrient levels in plants through several mechanisms. These include grazing older leaves, which are replaced by nutrient-rich new growth (McNaughton 1979, Coppock et al. 1983a); reducing the height of forage, thereby concentrating nutrients (McNaughton 1979, Coppock et al. 1983a); increasing the quality of plant litter (Knapp et al. 1999); and providing easily available nutrients in the form of feces and urine (McNaughton 1979, Coppock et al. 1983b, Knapp et al. 1999). There is some evidence that plateau pikas preferentially graze on plants high in phosphorus, but not in potassium, calcium, or magnesium (Wang et al. 1992).

Pika burrows also indirectly affect the environment via nutrient cycling. Burrowing moves older lower soil horizons to the surface. The break up of soil clumps during tunnel construction may lower the soil's bulk density, thereby increasing oxygenation in deeper layers (Hole 1981). Burrowing can also increase soil fertility, water infiltration, microbial activity, and soil turnover (Meadows 1991). Higher decomposition rates and carbon levels at the surface may lead to increased plant-available nutrients (Ayarbe and Kieft 2000). As a result of these changes, variability in nutrient cycling is expected across microhabitats within pika colonies.

The impact of other small burrowing mammals, particularly prairie dogs, has been well-documented (Grinnell 1923, Whicker and Detling 1988, Huntly and Reichman 1994, Kotliar et al. 1999). Prairie dogs augment soil mixing and boost soil oxygenation within their colonies (Sharps and Uresk 1990). Both Coppock et al. (1983a) and Aho et al. (1998) both reported higher nitrogen concentrations and increased plant-available nitrogen near prairie dog towns. Ayarbe and Kieft (2000) found increased total organic carbon and microbial respiration on mounds of kangaroo rats (*Dipodomys* spp.). The mounds of another Tibetan plateau mammal, fossorial zokors (Rodentia: *Eospalax fontanierii*), also have higher levels of plant-available nitrogen and phosphorus than surrounding soils (Wang et al. 1993, Zhang and Liu 2003).

As a consequence of variable nutrient availability, plants in varying proximity to pika mounds may also exhibit different nutrient concentrations. Evidence from vegetation composition and structure on prairie dog mounds supports this supposition (Bonham and Lerwick 1976, Agnew et al. 1986, Whicker and Detling 1988, Weltzin et al. 1997b, Fahnestock et al. 2003). Coppock et al. (1983a) documented increased live-to-dead ratios and greater plant digestibility in regions inhabited by prairie dogs. Whicker and Detling (1988) reported higher nitrogen concentrations in plant shoots over prairie dog colonies. Likewise, certain plants growing on old haypiles of the North American pika had significantly higher percentages of nitrogen than the same species growing in surrounding areas (Aho et al. 1998). Increased nitrogen availability may increase plant biomass and consequently forage availability (Aho et al. 1998). An increase in the nitrogen concentration of plants has also been linked with phosphorus co-limitation in nitrogen limited systems (Frank 2008).

Water transport is closely linked with nutrient cycling. Animal burrowing contributes toward many aspects of water movement in soils (Hole 1981). Specifically, the formation of mounds and pits increases the presence of openings that drain water and dissolved organic matter, both of which enhance water infiltration rates (Hole 1981). Previous studies found that the presence of burrowing animals can increase soil water infiltration and decrease water repellency (Leprun 1976, Ursic and Esher 1988, Garkaklis et al. 1998). Prairie dogs have also been shown to increase water availability at colonized sites (Day and Detling 1994). Similarly, pikas are predicted to increase soil water retention in terms of gravitational water (water that readily drains from saturated soil) and plant-available water (water remaining in the soil above the wilting point) by opening voids, mixing soil, and depositing organic matter (Brady and Weil 2002).

Goals of this work are to clarify the total effect of pikas on ecosystem processes, and to evaluate the consequences of small mammal poisoning in an alpine meadow ecosystem. In practice, differences due to burrowing will be difficult to distinguish from differences due to herbivory and selective grazing. Therefore, pika herbivory and bioturbation will be considered concomitantly. Their influence on ecosystem functioning is examined in terms of soil and plant nutrients and water flow.

MATERIALS AND METHODS

Study site

My research was conducted in Qinghai Province, from June to August in 2006 and 2007 (Figure 2.2). I sampled grassland, specifically alpine meadow, in the eastern Tibetan plateau between 3300 and 3800 m. These meadows were used as winter pastures by yak and sheep, which grazed grasses and sedges to a uniform height. I avoided regions with evidence of other ungulate grazers (horses, goats, wild ungulates etc.) and small herbivores (marmots, zokors, voles etc.).

In general, soils at my site are similar to those of other grassland habitats (USDA mollisol/ FAO-UNESCO phaeozem), with little or no organic horizon and a relatively thick A horizon. However, typical of Tibetan plateau grassland soils is a dense mat of roots in the top 10 to 30 cm of soil, termed the “Afe” horizon (Wang et al. 2003, Kaiser et al. 2008, Wang et al. 2008b). Indeed, higher root to shoot ratios are found in alpine meadow and steppe (16.0 to 66.2 and 6.8 to 12.1, respectively) than any other plateau habitat (Luo et al. 2005). The collective depth of upper soil layers (topsoil and subsoil) in this area is relatively low, with layers in Qinghai and Tibet grasslands ranging between 0.2 and 1 m thick (Wang et al. 2002). While much of the ground in this region is seasonally frozen, permafrost is primarily restricted to mountain-top “islands” and slopes with a northerly aspect (Qiu et al. 2002). The most recent interpretation of soils under similar *Kobresia* meadows is as a humic cambisol (Kaiser et al. 2008), or more generally as alpine meadow soil (Hu and Zhang 2003, Wang et al. 2003).

Meteorological measurements were not available at all study localities, but values for Dawu Township (see below) have been reported in the literature, and are considered typical for this habitat. Annual precipitation is 420 – 560 mm (Liu et al. 2010b), most of which falls as rain from May to September (Dong et al. 2004b). Soil surface layers are generally dry aside from late summer monsoonal rains (Yang et al. 2003). The average annual temperature is below freezing, and ranges from below -32 ºC in January to just above 25ºC in the warmest summer days (Dong et al. 2004b). However, the daily temperature difference can be large and there is no absolutely frost-free period (Liu et al. 2010b). The growing period is from late May to mid-September with biomass peaks in July (maximum sedge growth) and September (maximum grass growth) (Long et al. 1999).

Experimental design

Sampling was conducted at two distinct spatial scales: the local landscape/ colony level, which investigated localities across eastern Qinghai Province (Figure 2.2), and the patch/ burrow level, which focused within one Township (not shown). This design allowed for inferences to be made about pika colonies at both the colony and patch level. Broad sampling was conducted at six primary localities, often near a city or township: Dawu, Daotang He, Henan, Huashixia, Qinghai Hu and Senduo (Table 2.1). Two sites were selected at each locality: a pika colony ("on-colony site") and a nearby, but uninhabited area ("off-colony site"). Sites were chosen with similar plant communities and livestock densities. Off-colony sites had no visible evidence of pika burrows, which was often the result of poisoning. Thus I cannot rule out the presence of residual effects from prior pika colonization in these off-colony sites. Across Qinghai Province, effort was made to keep differences between localities to a minimum; however, differences between localities sometimes occurred. For instance, low-growing *Kobresia* sedges were the dominant vegetation in all localities except Daotang He and Qinghai Hu, which were drier and dominated by grasses. The majority of this work, and the most intensive sampling, took place at Dawu.

At the patch scale, sampling was conducted within multiple on-colony sites near Dawu Township. At the each site, a 100 m transect line was laid through the densest area of the colony. Along this transect 10 random points at least 2 m apart were selected. At each point, two types of microhabitat (patches) were sampled. Microhabitat was classified as either pika "disturbed" or "undisturbed." Disturbed habitat was centered on the spoil heap adjacent to burrow entrance. Active burrows were easily identifiable by moist fecal matter, freshly excavated soil, and an entrance unobstructed by debris. Undisturbed habitat consisted of meadow without evidence of pika activity and at least 1 m from a burrow entrance (established by a blind stone toss). Due to the dynamic nature of burrowing on the terrain, I cannot rule out the possibility that "undisturbed" regions within a pika colony were once similar to the present "disturbed" regions. For inferences at the patch level, this sampling procedure was repeated at four distinct pika colonies, each separated by 3 km, near the city of Dawu in Golog County.

Soil sampling

At each on-colony site, 20 total soil cores were taken – 10 over disturbed patches and 10 over undisturbed patches. At each off-colony site, 10 total soil cores were collected (all undisturbed patches). Soil cores 15.3 cm (6 inches) deep and 4.8 cm (1.9 inches) in diameter were retrieved at the surface using an AMS soil core sampler with hammer attachment. Average field weight of soils was approximately 330 g. Soils cores were sieved through a 2 mm screen, and fine soil was saved for analysis. Gravel and rocks were weighed and volume was measured by water displacement in a graduated cylinder. Bulk density was used to scale nutrient concentrations to the colony level. Soils were taken to the Soil Nutrition Institute of the Chinese Academy of Sciences in Beijing for chemical analysis. Total nitrogen (N) was determined by the semi-micro Kjeldahl procedure (Zhou and Shao 1987). This method uses concentrated sulfuric acid to convert sample nitrogen to ammonium. While it can detect N in the form of non-resistant organic compounds and ammonium (NH_4^+), it does not account for inorganic N in the form of N-N, N-O or heterocyclic linkages found in nitrates and nitrites (Mulvaney 2008). Organic nitrogen was determined by alkaline hydrolysis distillation (Neyroud and Schnitzer 1975), which recovers forms of non-resistant organic nitrogen. Finally, organic carbon content was determined by digestion with potassium bichromate sulfuric acid solution (Li et al. 1988). Values have been multiplied by the Van Bemmelen factor, 1.724, are reported as total soil organic matter, SOM (Allison 1965). Due to financial constraints, soil samples were only analyzed for the summer of 2006 for pika colonies near Dawu.

Water sampling

Water infiltration rates were measured using a 7.7 cm (3 inch) diameter PVC ring. Infiltrometer rings were placed on level ground and pushed into the soil so that water leakage was minimized from the edges. In disturbed patches, rings were situated at the nearest level ground next to the burrow entrance. The period it took for the falling head to travel between two marked vertical points (separated by 7 cm) was timed with a stop watch. In cases when the recording time exceeded two hours, the experiment was stopped, and time and distance traveled were recorded. Total times were converted into infiltration rates (cm/h) based on dimensions of the PVC ring.

Plant sampling

Plant samples were collected during the summers of 2006 and 2007 for nutrient analyses. Due to the remoteness of the field locations and lack of laboratory space, I clipped only the dominant species, *Kobresia humilis*. This species is grazed by both pikas and livestock. Samples of *K. humilis* could not be located at Daotang He and Qinghai Hu; therefore no plants were collected there. Clippings of green sedge blades were gathered in plastic whirl-pack bags and allowed to air dry. They were later oven-dried at 60º C in the laboratory before analysis. Dry samples were ground using a ball mill (Spex 8000D), and approximately 2 mg of the homogenized powder was used for nutrient analyses. Total plant C and N were determined using a Perkin-Elmer 2400 Series II CHNS/O Analyzer.

Statistical analyses

Statistical significance was set at $p < 0.05$. When data values fit parametric assumptions, differences between burrow and undisturbed soil and colony and off-colony were analyzed with a single-factor ANOVA blocked for site (pika colony or city) (SPSS 2008). Distributions strongly different from normal were evaluated with Friedman's Test. I tested for an effect of water infiltration across sites with an rmANOVA with sampling repeated in space (SAS 2005). Non-significant results were evaluated with a power analysis.

RESULTS

Soil bulk density ranged from 0.80 to 0.93 g/cm^3 (Table 2.2). Total nitrogen varied from 0.32 to 0.43% (Figure 2.3a). Organic matter constituted 5.8 to 7.8% of soil (Figure 2.3b). Plant-available organic soil nitrogen ranged from 265 to 349 mg/kg (Figure 2.3c). Values of soil nutrients were not significantly different between disturbed and undisturbed soil patches within a pika colony.

Foliar nutrient levels in disturbed patches had lower percentages of carbon and higher percentages of nitrogen compared to nearby undisturbed patches (Figure 2.4a, b). The C:N ratio was also lower over disturbed versus undisturbed patches (Figure 2.4c). I did not detect any significant differences between these foliar nutrient levels within pika colonies. At the colony scale, there was no consistent trend in foliar nutrients between on-colony and off-colony sites. The Huashixia site showed consistently opposite results from the other sites, in terms of having higher plant nutrient levels off-colony than on-colony.

The infiltration rate of water ranged from an average of 0.90 cm/h at an off-colony site in Huashixia to 50.46 cm/h at disturbed soil on a pika colony in Dawu (Figure 2.5). One point value at the Henan colony (145.66 cm/h) was discarded because it fell far outside even the highest infiltration rates. The extreme rapidity with which water infiltrated at this particular point was could have been due the location of a pika tunnel immediately under the surface. This discrepancy was remarked in the field, and a supplementary data value was collected from an adjacent sampling point. For all localities but two (Daotang He and Henan), the infiltration rate over disturbed patches was significantly faster than infiltration rates at undisturbed patches within the pika colony. Excepting the Daotang He locality, rates of infiltration in off-colony patches were significantly lower than rates at either disturbed or undisturbed patches within pika colonies.

DISCUSSION

Soil nutrients

My percentages of SOM fell well within the range (2.4 to 9.1%) reported by Kaiser et al. (2008) for *Kobresia pygmaea* meadows (Appendix B, Table B-1). Percentages of total nitrogen and plant-available organic nitrogen levels were also within reported values (Appendix B, Table B-2, Table B-3). Adjusted bulk density tended to be at the lower end of recorded levels (from 0.69 to 1.04 g/cm^3 for non-degraded soils according to Wang et al. (2003)). Soil density is not only affected by animal burrowing. Another influencing factor is plant cover, which is strongly related to livestock density and grazing intensity. Wang et al. (2003) found both increasing bulk density and gravel content as plant cover decreased, resulting in coarser soils with less pore space. Additionally, they reported a decrease in soil hardness from 4.03 kg/cm^2 to 0.38 kg/cm^2 in undisturbed soil versus soil with low vegetative cover (Wang et al. 2003). Variations in plant cover may mask changes in soil characteristics within pika colonies.

Wang et al. (2005) report soil carbon and nitrogen levels of 11.307 kg/m^2 and 0.846 g/m^2, respectively, in alpine *Kobresia* meadows. Research from nitrogen addition experiments by Dong et al. (2004c) suggest that Tibetan plateau soils are nitrogen limited. Low levels of total nitrogen are probably the result of slow decomposition rates (Dong et al. 2004c).

Data concerning the influence of burrowing mammals on soil carbon and nitrogen is conflicting. Increased levels of soil carbon have been reported in soils underneath old haypiles of North American pikas (Aho et al. 1998). Li and Zhang (2006) compared a site with moderate pika density (50/ha) with one poisoned for nearly two decades, and recorded increased SOM at 0 to10 cm and 31 to 50 cm depths in the pika colony. However, Sherrod and Seastedt (2001) found significantly lower levels of soil carbon over areas disturbed by pocket gophers (*Thomomys talpoides*). Zhang and Liu (2003) also found no consistent differences in SOM between occupied, abandoned, and unoccupied zokor colonies. However, they did observe a trend for decreasing SOM in the top 10 cm of soil with long-term zokor occupation (Zhang and Liu 2003).

As with carbon levels, nitrogen levels of soil disturbed by burrowing mammals has been reported at both higher (Wang et al. 1993, Aho et al. 1998) and lower levels (Sherrod and Seastedt 2001) than surrounding areas. Total nitrogen levels may differ from the amount of nitrogen available to plants in the form of nitrate and ammonium. Significantly higher levels of plant-available nitrogen have been reported on zokor (Wang et al. 1993) and gopher (Sherrod and Seastedt 2001) mounds. Sherrod and Seastedt (2001) postulated that lower nutrient levels over gopher mounds are due to lower SOM. Gophers may lower SOM in mound soil by filtering out organic matter before discarding soil on the surface (Sherrod and Seastedt 2001).

Several authors propose mechanisms by which burrowing mammals may alter soil nutrient levels. Inouye et al. (1987) proposed that gophers increase nutrient heterogeneity by transporting low-nitrogen soil to the surface. Higher temperatures in the excavated mound lead to increased mineralization rates. Cortinas and Seastedt (1996) reported higher soil temperatures over gopher mounds, while research by Sherrod and Seastedt (2001) showed greater litter decay over gopher mounds. Typically, nutrient availability is inversely proportional to shade (a measure of plant biomass). However, small mammal mounds could provide bare patches of soil that are temporarily high in plant-available nutrients through increased decomposition rates (Zhang et al. 2003). This remains an area for future research.

Plant nutrients

Although I observed higher nitrogen levels in vegetation near pika burrows, overall no general impact of pika burrowing on nutrients in *Kobresia humilis* were found. Unfortunately, few references regarding plant nitrogen levels exist for these Tibetan meadows, particularly for sedges. Li et al. (2004a) reported nitrogen levels in alpine meadow plants ranging from 1.49 to 3.69%. Sedges and forbs tend to have a higher nitrogen content than grasses; however, almost all forage is low in nitrogen (0.42 to 0.98%) starting in October (Long et al. 1999). Indeed, late in the season, degradable nitrogen may become more limiting than metabolizable energy (Long et al. 1999). In North America, plants on prairie dog colonies have been found to be higher nitrogen than plants on uncolonized sites (Coppock et al. 1983a). Furthermore, as time since prairie dog colonization increased, so did above-ground nitrogen levels (Coppock et al. 1983a). A similar trend for plant nitrogen was not found in my experiment for *K. humilis*, but it is possible this trend could exist in other species.

The calculated percentage of carbon in this study was typical for sedges in this region (Appendix B, Table B-4). I found C:N ratios that were generally higher than reported values, due to slightly higher nitrogen levels at most sites. However, reported *K. humilis* C:N ratios tend to be high (averages of 19.3 to 23.5) compared with overall foliar C:N ratios for Tibetan grassland plants (17.0) and for all species across China's grasslands (17.9) as reported in He et al. (2006).

Several factors can influence plant nutrient levels. Species composition plays a critical role in plant stoichiometry at an ecosystem scale. He et al. (2006) determined that species community composition was more important than temperature or precipitation in explaining plant nitrogen content and C:N ratios across China's grasslands. Thus, while no differences in nutrient levels of *K. humilis* were observed, it is possible that other forage species vary in nutrient levels. For example, Aho et al. (1998) found significantly higher percentages of nitrogen in two of the three plant species they found growing in haypiles of the North American pika. They hypothesized that the third species was tolerant to low nitrogen levels, and therefore less likely to reflect differences in soil nitrogen availability (Aho et al. 1998). On the other hand, plateau pikas forage in open grassland rather than gaps, and do not accumulate haypiles. Therefore, results for my study species may differ from North American pikas'.

Plant nutrient levels in alpine meadows are also influenced by livestock grazing (in terms of livestock species, stocking density and grazing intensity). Nitrogen levels decreased with livestock stocking rates (20.80% ungrazed to 18.60% moderate grazing), but were highest in heavily-grazed areas (26.40%) (Li et al. 2004a). Severely degraded *Kobresia* meadow had nitrogen and carbon levels equal to 47% and 38% of control values, respectively (Wang et al. 2005).

It is possible that differences in herbivore stocking levels may have overwhelmed differences between plant nutrients at pika colony and off-colony sites. In other words, differences in other biotic (livestock) or abiotic (environmental variables) could be more important for determining nutrient levels than the presence of pika colonies. However, these differences could not be quantified in this study.

Finally, plant nutrient levels also vary temporally. Growing season for plants on Tibetan plateau alpine meadows is short, from late May to mid-September (Long et al. 1999). Grasses, sedges, and forbs generally decrease in palatability quickly as their growing season progresses (Coppock et al. 1983a, Long et al. 1999, Li et al. 2004a). For example, the percentage of crude protein in yak forage decreases from a maximum of 15.22% in new growth to 4.74% in dead grass (Yan et al. 2002).

Clearly, an investigation of nutrient levels over a wider range of forage species is desirable for future research. Additionally, ranges of plant carbon and nitrogen heterogeneity in the environment would be useful. Limited current data are available. Ni (2002) reports carbon densities of 500 to 4000 g/m^2 for alpine meadows, while Wang et al. (2005) recorded 105.97 g/m^2 above-ground carbon in a *Kobresia* meadow. For the same meadow, Wang et al. (2005) also give plant nitrogen levels of 3.356 g/m^2.

Pika effects on water infiltration

Solifluction, or the movement of waterlogged soil down slope, is a common phenomenon in these environments (Hall et al. 1999). Animal burrowing may have profound impacts on this action as well as other erosional processes. In general, water infiltration rates due to pika disturbance were significantly elevated both at the patch scale (within a colony) and local landscape scale (between a colony and off-colony). The only site for which this trend did not hold was Daotang He. Interestingly, this site was least like the others in terms of species composition and ground cover (unpublished data). The aridity and tall grasses at this site are suggestive of a habitat type closer to alpine prairie than alpine meadow. An area for future research would be to determine whether increased infiltration rates from burrowing are restricted only to alpine meadows, or are common to other plant communities as well.

It is unlikely that plateau pikas simply choose to burrow in regions with greater water infiltration than surrounding regions. If pikas exhibited bias in choosing to burrow in already water-permeable soils, it might also be expected that water infiltration would be greater in on-colony than off-colony areas. However, one would not necessarily expect to find a consistent difference in permeability levels between disturbed and undisturbed ground within a colony. The more probable explanation is that water infiltration is the result of changes to soil texture due to pika burrowing, rather than a correlated variable.

One frequent justification for pika eradication is that pika burrowing behavior leads to erosion and soil loss (Xia 1986, Zhang et al. 1998, Fan et al. 1999). This research is the first to suggest an alternative viewpoint—namely, that plateau pika burrowing leads to decreased water runoff, and consequently, a reduced level of erosion and soil loss compared to uncolonized meadows. This conclusion is supported by research on pocket gophers in North America. Hakonson (1999) compared runoff in bare soil, bare soil with a gopher addition, and a re-vegetated site. Gophers were found to reduce runoff by a greater percentage than the addition of vegetation (Hakonson 1999). Water infiltration was 200% higher on gopher plots compared with non-gopher plots (compared to a 75% improvement with the addition of vegetation). Furthermore, the amount of collected sediment (erosion) was reduced by gophers, though not to a greater extent than lowered by vegetation (Hakonson 1999).

Burrowing mammals have indisputable effects on soil movement. Sediment transport by gophers has been shown to be long in temporal effects (over three years), but short in spatial impact, with most soil moved within 0.5 m of the burrow entrance (Sherrod and Seastedt 2001). Hakonson (1999) proposed that gopher burrowing decreases erosion because water flows more slowly across these heterogeneous soils due to interference from mounds and pits. This reduced rate allows greater time for sediment to filter out (Hakonson 1999). The increased water permeability found by my research, combined with these reduced rates of water flow across the landscape, would likely lead to lower erosion rates at pika colonies. Additionally, more water could be available for plants at pika colonies. Zhang and Liu (2003) also reported greater soil moisture levels at all soil depths from 0 to 50 cm at a site with moderate pika density (50/ha) compared to a site poisoned for 18 years. These predictions have yet to be tested directly, but are a promising area of future research.

Another example of ecological degradation often attributed to plateau pikas are so-called “black sands” (not to be confused with the highly fertile “black soil region” of temperate northeastern China (Zeng et al. 1983)). Black sand is a type of heavily degraded alpine soil alternatively translated as black soil, black beach, black shoal or black mountain (Wang et al. 2003, Zhou et al. 2005). It is characterized by low vegetative cover (40 to 50%), soil high in gravel content, and a plant community dominated by poisonous forbs (Schaller 1998, Wang et al. 2003, Xu et al. 2008) Black sand regions are common above 3700 m in the headwaters of the Yangtze and Yellow rivers region (Zhou et al. 2005). Some authors estimate up to 30% of alpine grassland can be considered black sand (Shang et al. 2008). Few studies directly link pikas with black sand formation; rather, many investigate the relationship between livestock overgrazing and degradation. Hall et al. (1999) argue that alpine solifluction is due to slope failure caused by overloading of livestock, rather than frost alone. While pikas are known to dig burrows into the face solifluction lobes, the slope failure itself is linked to the overstocking of yak, which is also implicated in the creation of black soil (Hall et al. 1999). Other researchers argue that black sands may be the result of trail erosion or global warming (Miehe 1988, 1996, Ma et al. 1997, Schaller 1998). Whatever the cause, black soil does not recover easily (Shang et al. 2008).

Erosion is a serious problem in China; it is estimated that 38% of the land has been affected by erosion (Yang and Pang 2006). According to some sources, soil erosion is the most important environmental challenge in northeastern Qinghai (United States Embassy 2003). One contributor to soil loss is reduction in vegetation cover by overgrazing. Wang et al. (2003) estimated a loss of 14890 kg/hm^2 SOM and 1590 kg/hm^2 nitrogen with decreasing alpine meadow vegetation cover from 90 to 70%. The presence of pika burrows on grazed sites could mitigate this effect by increasing topological variation of the land surface, thereby slowing the flow of water and reducing erosion. In their global assessment of water towers, Viviroli et al. (2007) found that mountain water resources in the western and eastern Himalayas could not fully meet downstream water demands.

Another factor influencing alpine soil moisture is climate change. Although precipitation, evaporation and temperature all affect runoff, the most important influence on discharge in this region is permafrost thickness (Chang et al. 2007). The thickness of permafrost at the Yellow river headwaters has been decreasing 10.8 cm per decade (Chang et al. 2007). With the loss of impermeable permafrost, water penetrates more deeply into the soil, leaving less moisture on the surface (Chang et al. 2007). Likewise, a reduction in annually frozen soil could lower available water levels at the surface. On the Tibetan plateau, frozen soil undergoes a cycle of thawing from March to September, freezing at the end of September, and remaining frozen from October to March (Ding et al. 2000). The highest soil moisture levels were reported when ground began to thaw, as the frozen soil releases water (Yang et al. 2003). Thus, soil moisture will be at its lowest during the winter months. If pika burrowing results in enhanced soil water storage, more water could be available during these critical periods. Finally, watersheds originating on the Tibetan plateau account for 66.8% (1879 x 10^9 m^3) of China's available water (Yang and Pang 2006). In a country with a low per capita water supply (Yang and Pang 2006), this potential for increased water availability deserves considerable attention.

CONCLUSION

A broad suite of ecosystem services are provided on the Qinghai-Tibetan plateau, including 1) NPP; 2) carbon storage and O_2 release (via NPP production); 3) water storage; 4) soil conservation; 5) soil fertility; and 6) biodiversity maintenance (Yu et al. 2005). These services have the potential to be strongly impacted by the presence of an endemic keystone species and ecosystem engineer, the plateau pika. Because these services were generally found to decrease in importance along a southeast-northwest gradient (Yu et al. 2005), this study area is a particularly important region of the plateau. The most important economic service (in terms of monetary value) provided by the Tibetan plateau is estimated to be water storage (Yu et al. 2005). Likewise, of the ecosystem properties measured in this study, plateau pikas showed the strongest effects on water infiltration. Plateau pika disturbance was not found to have significant effects on soil or plant nutrient values. Current livestock grazing practices and natural environmental variation likely have greater influence over nutrient cycling in this system than pika burrowing.

Table 2.1. Study localities in Qinghai Province. Six pairs of pika on-colony and off-colony sites were selected for sampling across eastern Qinghai province. Elevation is given in meters.

Location	County	Prefecture	Elevation	Geographical Coordinates
Dawu	Maqen	Golog	3800	34°24'03"N 100°21'38"E
Daotang He	Gonghe	Hainan	3400	36°25'12"N 101°03'18"E
Henan	Henan	Huangnan	3500	34°38'52"N 101°45'31"E
Huashixia	Madoi	Golog	3600	35°05'51"N 98°51'29"E
Qinghai Hu	Gonghe	Hainan	3300	36°36'43"N 100°20'46"E
Senduo	Guinan	Hainan	3500	35°30'35"N 101°13'07"E

Table 2.2. Adjusted bulk density at five sampling sites near Dawu. Mean soil nutrient values and standard deviations scaled to landscape levels by adjusted bulk density at four pika colonies (Dawu 1-4) and one off-colony site (Dawu 5).

	Adjusted Bulk Density (g/ cm^3)	
	Disturbed	Undisturbed
Dawu 1	0.86 ± 0.06	0.88 ± 0.08
Dawu 2	0.80 ± 0.10	0.78 ± 0.10
Dawu 3	0.92 ± 0.17	0.82 ± 0.13
Dawu 4	0.93 ± 0.15	0.92 ± 0.10
Dawu 5	—	0.93 ± 0.07

Figure 2.1. Surface structures created by plateau pikas. These structures include entrance holes (a), mounds of excavated soil (b) and runways (c).

Figure 2.2. Landscape/ colony-level sampling in Qinghai Province. Pairs of pika on-colony and off-colony sites were identified for sampling near Dawu, Daotang He, Huashixia, Qinghai Hu, Tongde (Senduo) and Zekog (Henan).

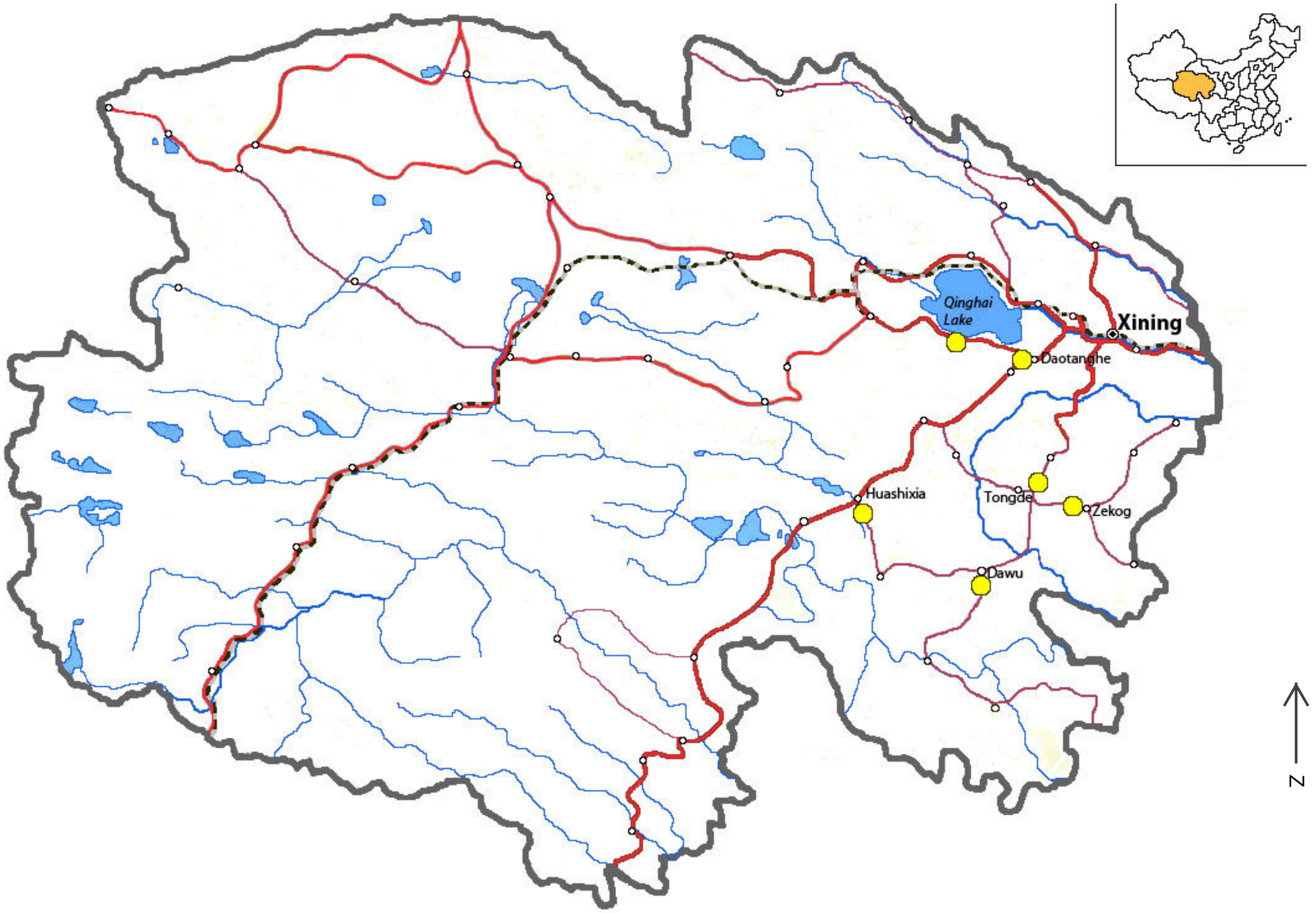


Figure 2.3. Mean soil nitrogen and organic matter (SOM) within four pika colonies in Dawu Township. Standard error bars are shown for total nitrogen and organic matter, while plant-available nitrogen is shown as twice the standard error. White bars show disturbed patches and shaded bars undisturbed patches.

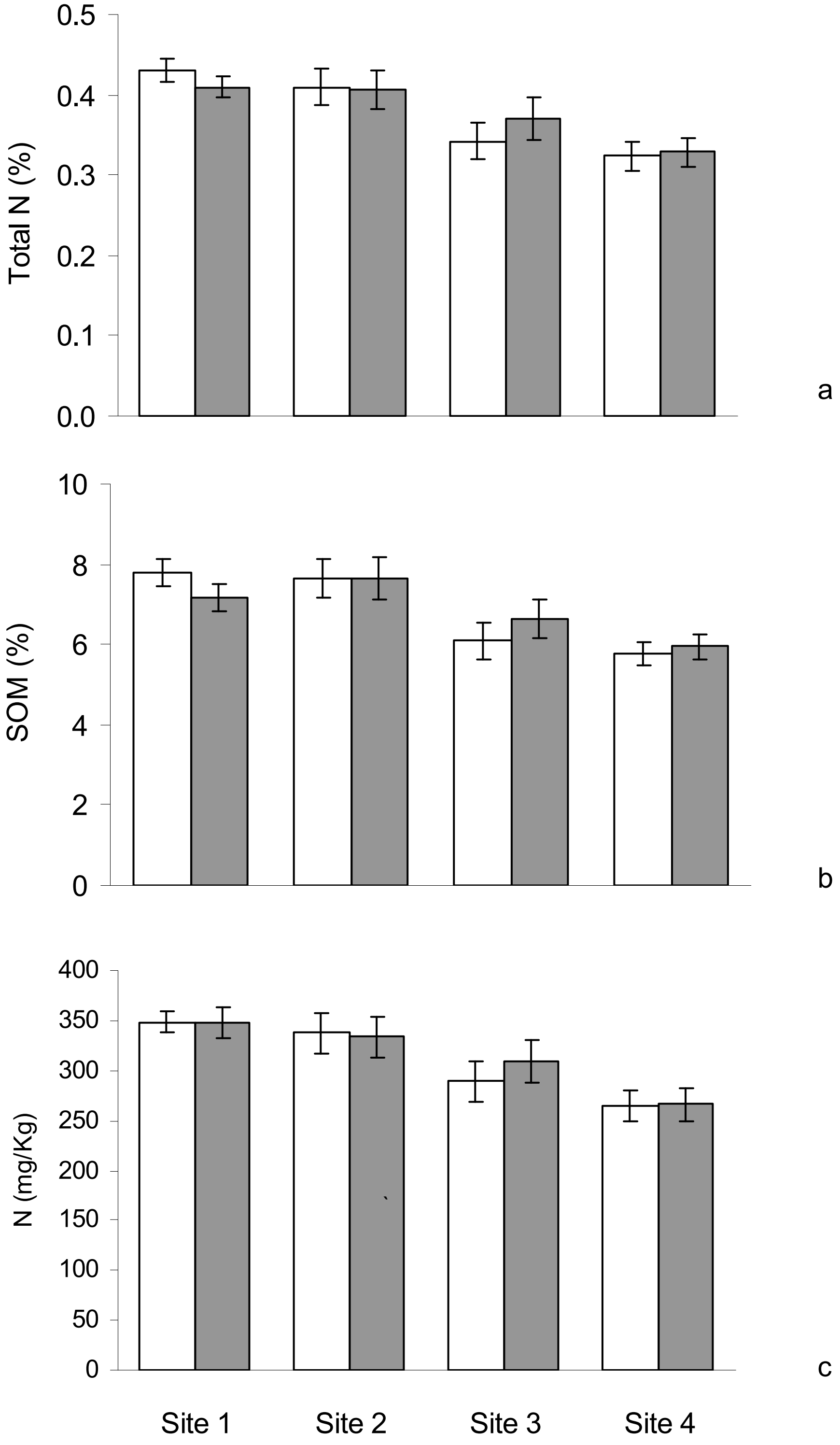


Figure 2.4. Mean nutrient levels in *Kobresia humilis*. Results are shown at two spatial scales—undisturbed areas (gray bars) versus disturbed burrows (white bars) within a pika colony (a - c) as well as on-colony (white and gray bars) versus off-colony (striped bars) across four sites (d – f). Data for the Dawu pika colony (site 3) is repeated, but compared to an off-colony site in d – f. Standard error bars are shown for nitrogen and C:N ratios; twice the standard error is shown for carbon. Values are not shown for Daotang He and Qinghai Hu.

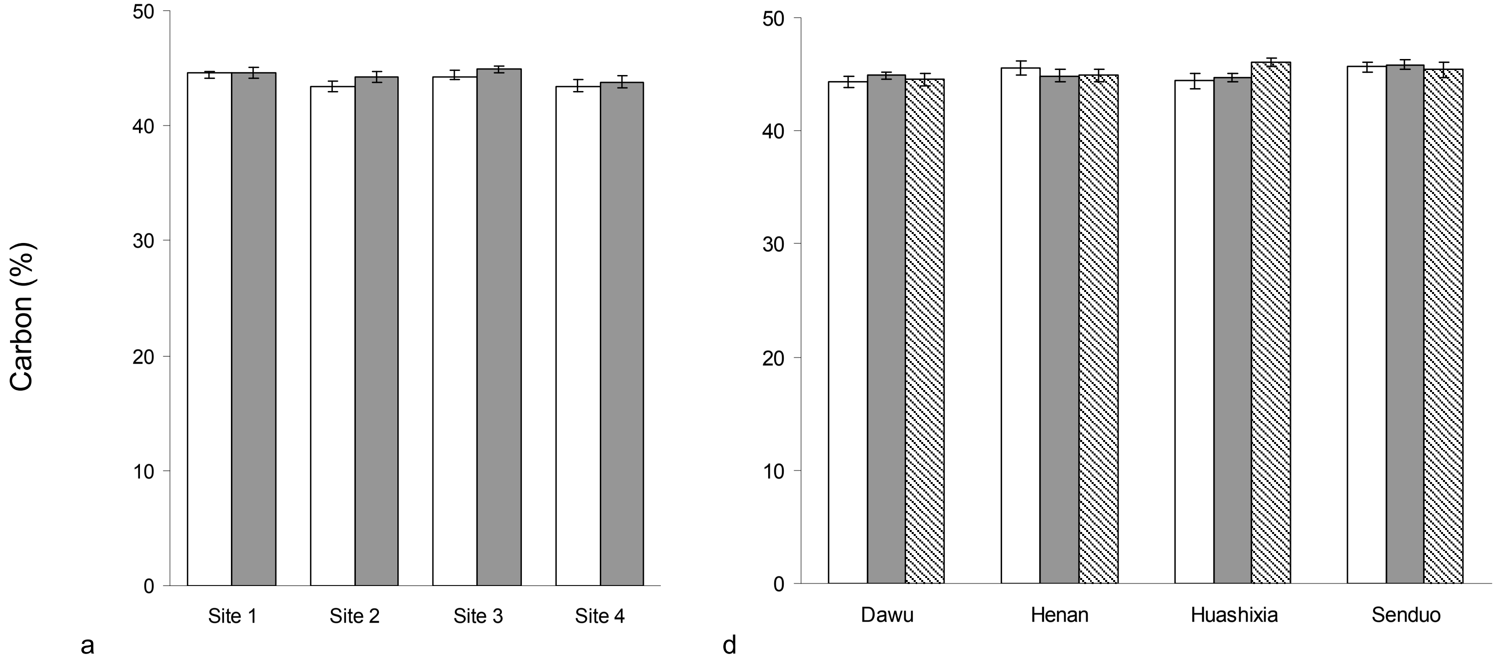


Figure 2.4. Continued.

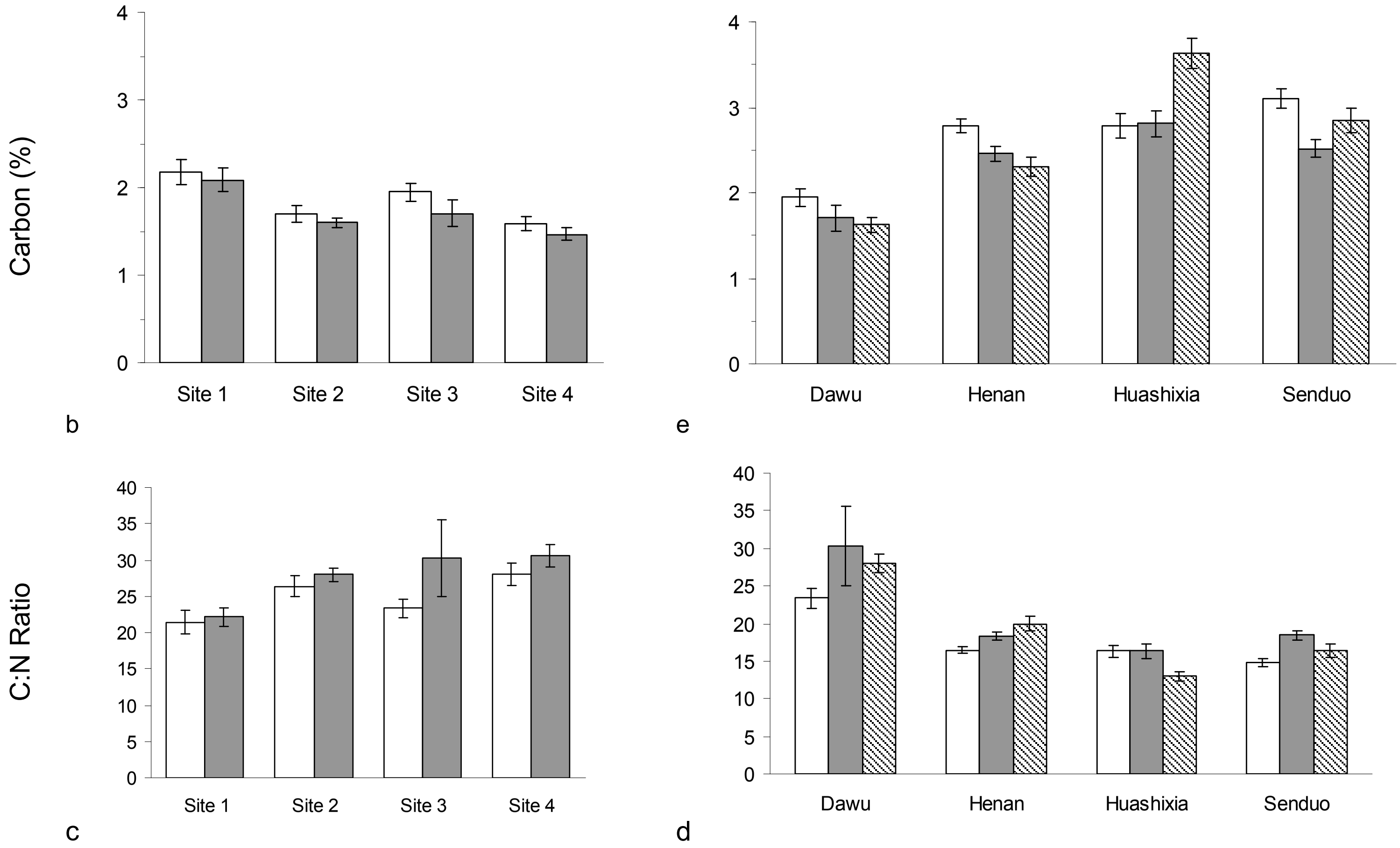
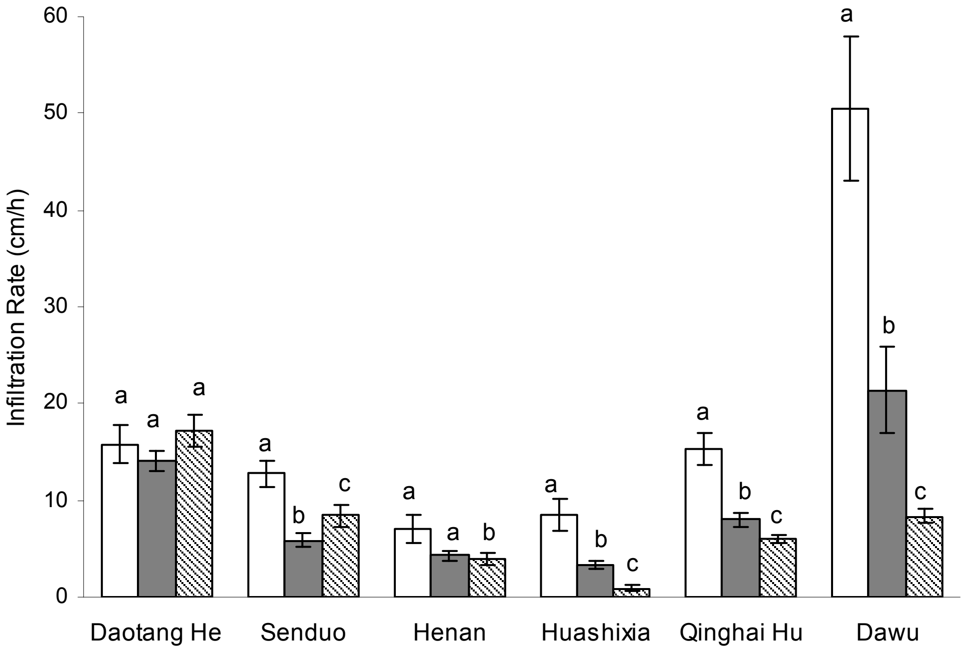


Figure 2.5. Mean infiltration rates across six localities in eastern Qinghai Province. Infiltration is shown in cm/h with standard error bars. White columns represent disturbed patches, gray columns undisturbed patches within a pika colony. Striped columns indicate undisturbed patches from an off-colony site. Different lower case letters within a locality indicate significant difference ($p<0.05$). Each treatment has n=10.



CHAPTER 3

The importance of ecosystem engineers to local landscape heterogeneity: plateau pikas transform alpine meadow communities

INTRODUCTION

Spatial heterogeneity is an important contributor of variation to ecological communities. One source of spatial heterogeneity is natural disturbance from animal burrowing. Burrowing both modifies existing habitat (through physical change and alteration of ecosystem processes) and generates new habitat (through creation of above- and below-ground structures). The resulting patches may provide microhabitat types not found in the undisturbed landscape matrix, thereby increasing habitat diversity. Additionally, burrows function as connective agent between the above-ground and below-ground environments. Their presence may alter nutrient flows and species movement through these habitats. Despite the importance of these functions to the environment, the spatial structure of burrowing animals has received little attention (however, see Reichman and Seabloom's (2002) review of work on pocket gophers and Lacey et al.'s (2000) review of subterranean rodents).

Though all organisms interact with their environment, some species may play larger roles and disproportionately influence community structure (Paine 1969, MacArthur 1972). These species are sometimes referred to as keystones (Paine 1969, Kotliar et al. 1999), and those that physically transform their environment, as ecosystem engineers (Jones et al. 1994, Dickman 1999). One such species is the plateau pika (Lagomorpha: *Ochotona curzoniae*), endemic to the alpine grasslands (specifically alpine meadow, meadow-steppe and desert steppe) of the Tibetan plateau (Smith and Foggin 1999). Plateau pikas are an important food source for most mammalian carnivores in the region (Schaller

1998, Smith and Foggin 1999, Xu et al. 2006, Liu et al. 2010a), as well as a wide variety of raptors (Peshkov 1957, Lai and Smith 2003, Li et al. 2004b, Badingqiuying 2008, Cui et al. 2008). Their range extends over most of the plateau (2.5 million km^2 (Schaller 1998)) at altitudes of 3000 to 5000 m (Smith and Xie 2008). As early as 1938, Schäfer (1938) described these regions as "Ochotona-steppe" due to the predominance of pika burrows on the landscape. The transformative nature of pikas burrows has lead to their description as an allogenic engineer (Lai and Smith 2003), an organism which changes the environment by transforming the existing habitat from one physical state to another (Jones et al. 1994, Dickman 1999). Like other fossorial mammals, plateau pikas can be also be considered keystone engineers with impacts both "distinctive from processes that are strictly abiotic … and large relative to the purely physical processes operating in the system" (Reichman and Seabloom 2002).

In contrast to North American pikas, plateau pikas are highly social mammals that excavate extensive underground burrow systems (Smith and Wang 1991, Dobson et al. 2000). Dense populations of plateau pikas are considered a nuisance by herders (Formozov 1928, Ekvall 1968) and the local government (Ma 2006). Pikas are accused of competing with the local livestock for food (Fan et al. 1999), while their burrows are said to cause soil erosion, rangeland degradation, and biodiversity loss (Xia 1986, Zhang et al. 1998, Fan et al. 1999). Consequently, poisoning of this species continues to be a common management practice and has escalated since 2006 (Ma 2006).

The objectives of this study were to evaluate ecological consequences of spatial heterogeneity caused by pika burrowing on alpine meadow ecosystems.

Specifically, I investigated impacts of these keystone engineers on plant cover and surface structures. Additionally, baseline data on basic burrow system characteristics were collected. By quantifying spatial heterogeneity, it may be possible to account for an important source of variability within grasslands and to assess the overall impact of plateau pikas on their environment.

Spatial structure of pika burrows

The burrowing activity of pikas can be described on multiple spatial scales. Each scale can be considered as a unique accumulation of repeating smaller units. The inherent scale is the patch size, which in this case is the burrow entrance hole. Entrances holes are approximately 10 cm in diameter, slightly larger than the width of a pika. They can be classified as ”burrow holes” connecting to the family burrow structure, and shorter “duck holes” that descend vertically and do not typically connect (Dobson et al. 1998). Duck holes are used as areas for temporary shelter from aerial predators, rather than as continuously inhabited dwellings. Each burrow structure is cooperatively shared by families of 1 to 5 adults and can contain as many as 230 entrance holes (Dobson et al. 1998).

Entrance holes connect the above-ground and below-ground realms. Below the surface the entrance hole leads to a downward sloping tunnel that may level before branching or terminating. The tunnel may be simple, with a single tunnel leading to a nest chamber, or complex, with branching. Branches may lead to other holes (escape routes), nest chambers, storage chambers, or latrines. Most burrow structures consist of a network of subterranean tunnels approximately 20 to 25 cm below the soil surface (Wei et al. 2007). The entrance hole allows transfer of above-ground material, such as water, oxygenated air, and biotic matter, to the subterranean domain. Materials enter the tunnel both passively via wind and gravity and actively via the inhabitants' behavior. The distribution of organic and inorganic material in the tunnel system may thus be spatially heterogeneous, and may be a function of distance from the entrance hole.

The primary above-ground structure associated with plateau pikas is a mound or spoil heap (however, it should be noted that mound formation is not common surrounding duck holes, which are more temporary shelters). The burrow begins as a depression in the ground, which may arise from a natural pit or an intermediate structure, such as a latrine. As excavation is frequently initiated from the surface, new mounds have an elliptical (as opposed to circular) shape resulting from the directional deposition of soil behind the animal. Soil, small rocks and unwanted debris deposited on the surface build an elevated mound on the otherwise even meadow surface. This mound increases in diameter as the below-ground tunnel network expands. As a pit in the surrounding soil surface, the entrance hole naturally collects debris. Daily clearing of the entrance hole removes debris and fecal material, as does seasonal maintenance of underground structures, such as tunnel excavation and wall repair. Over time even the mound of carefully maintained burrows flattens and becomes covered by vegetation.

Other surface structures associated with the burrow system include runways, latrines (regions of accumulated feces) and depressions. Grazed runways are usually only found in environments with particularly dense growth. While the tunnels of some fossorial animals are visible from the surface as raised ridges or lines, plateau pika burrows are not. Abandonment of the burrow structure is rare, but may occur as a result of natural flooding or, more commonly, following anthropogenic poisoning. Neglect of a particular entrance hole is easily detectable by the lack of daily maintenance. In such cases the entrance and tunnels collapse, leaving little physical evidence of the former burrow. Thus, in addition to the spatial heterogeneity created by the expanding burrow structure, temporal heterogeneity is generated as patches cycle between depression, mound and meadow.

At the local landscape level an area of heterogeneous pits and mounds generates relief and variation. The unaltered meadow can be considered the background matrix, and the burrow structures as patches within that matrix. Because pikas are highly social animals, their burrow structures group within families to form an interconnected burrow complex. At the local landscape or colony scale, adjacent groups of these separate family complexes can be considered as the colony unit. The size of this colony depends on the presence of continuous habitat, but is maintained over multiple generations and tends have a relatively stable spatial extent (Dobson et al. 1998). Colony borders are frequently determined by natural barriers, such as mountains, rivers, or wetlands. Large pika colonies have been reported to reach 300 individuals/ha (Smith et al. 1990). At the largest unit of scale, colonies may be separated by meters or hundreds of kilometers, depending on the heterogeneity of the terrain. Pika burrowing therefore generates a variety of micro-habitats which contribute to local landscape heterogeneity at multiple spatial scales.

Increasingly, anthropogenic activity has become a major factor in the distribution of pika colonies at the colony scale. Similar to the eradication of prairie dogs in the western United States, an intensive poisoning campaign is being waged against the plateau pika (Liu et al. 1980, Shen and Chen 1984, Zhong et al. 1985, Fan et al. 1986, Smith et al. 1990, Ma 1995, Zhang et al. 1998, Fan et al. 1999). Aside from directly controlling pika numbers, humans may indirectly influence colony location through grazing practices. Livestock grazing lowers the average plant height (Miehe et al. 2008), thereby increasing the suitability of habitat for pikas (Shi 1983, Bian et al. 1994, Bagchi et al. 2006). Fencing exacerbates this situation by encouraging high livestock densities and an uneven distribution of resources (Bauer 2005). Thus, the heterogeneity generated by plateau pikas must be taken in context with human activity that alters the environment.

MATERIALS AND METHODS

My study site was located at the eastern portion of the Tibetan plateau. The Tibetan plateau is the world's largest low-latitude alpine region, and spans approximately 2.5 million km^2 (Schaller 1998) at an average elevation over 4000 m (Wang 1988, Spicer et al. 2003, Qiu 2008). Although the plateau covers only one quarter of China's land area (Ekvall 1968, Miller 1995, Miller and Craig 1997), it contains 40% of the country's grasslands (Hu and Zhang 2004). These grasslands contribute 2.5% of the global carbon pool and over 20% of China's contribution (Wang et al. 2002). The Tibetan plateau is also regionally significant as a major watershed. Approximately 28% of China's water and 34% of water for the Indian subcontinent originates on the plateau (Aldenderfer and Zhang 2004).

Data were collected in Qinghai Province from June to early August in 2006 and 2007. Four distinct pika colonies approximately 3 km apart were identified near Dawu Township (34°24'03"N, 100°21'38"E) in Golog County. Annual precipitation at this site is 420 – 560 mm (Liu et al. 2010b), most of which falls as rain from May to September (Dong et al. 2004b). The average annual temperature is below freezing (Dong et al. 2004b), and there is no absolutely frost-free period (Liu et al. 2010b). Annual temperature ranges from -32 ºC to 25ºC (Dong et al. 2004b), and daily temperature differences can be large as well (Liu et al. 2010b). The growing period is from late May to mid-September with biomass peaks in July (maximum sedge productivity) and September (maximum grass productivity) (Long et al. 1999).

Alpine meadows at an elevation of 3300 to 3800 m were chosen. Low-growing *Kobresia* sedges were the dominant vegetation in all localities, and they formed thick mats grazed to a uniform height by ungulate and small mammal herbivory. All colonies were also used as winter pastures for yak and sheep. Although stocking rates for domestic animals could not be directly quantified, regions with evidence of other large grazers (horses and wild ungulates) and small mammal herbivores (marmot burrows and zokor mounds) were avoided.

Data were collected in 100 m belt transects, 2 m wide, laid through the densest part of a pika colony. Belt transects were wide enough to encompass two to three pika holes, while still allowing for collection of data at a small spatial scale. Along the transect the region was analyzed in 10 cm^2 blocks. Block size was selected to be approximately equivalent to the size of a burrow entrance. Pika holes were categorized by type (burrow hole or duck hole), age (new, intermediate, or old) and status (active or inactive). Burrow type was distinguished by the characteristics given in the introduction. New burrows were considered to be holes adjacent to fresh deposits of soil covering live plants, and containing few or no colonizing plants. Old burrows were identified by a mound level with the meadow surface, covered by vegetation and with little or no fresh soil visible. Burrows which fit neither category of young or old were identified as intermediate. Status was easily determined as active (versus inactive) by the presence of fresh feces and the absence of debris obscuring the entrance hole.

Statistical analysis

Multiple measures of spatial heterogeneity have been developed to describe spatial distribution of points. I used the R programming environment, R version 2.7.1, (R Development Core Team 2009) with the spatstat package (Baddeley and Turner 2005) to explore distribution of points using the intensity marked point processes.

One statistical assumption of spatial data is spatial homogeneity (stationary). This assumes an even intensity (λ), the mean number of points per unit area, across space. Spatial homogeneity was explored using density plots of kernel-smoothed intensity (Diggle 1985). The kernel (a specific function and bandwidth) calculates density as it moves across the point pattern. I used an isotropic Gaussian kernel with edge correction and explored multiple values for bandwidth by varying the standard deviation, sigma.

To assess if the point pattern was random or non-random, the distribution was compared to the null hypothesis of complete spatial randomness (CSR). CSR was generated from an envelope of 99 randomizations. A pattern that differs from CSR may be clumped (aggregated) or regular. Clustering was assessed by exploring the distance between all points using the mean (first order statistics, such as nearest-neighbor (Liu 2001)) and variance (second order statistics, such as Ripley's K (Ripley 1976)). To account for edge effects, I used appropriate edge corrections for each statistic. Border correction (reduced-sample) estimates were used in all statistics. Kaplan-Meier correction (Baddeley and Gill 1997) was calculated for nearest-neighbor distance statistics. Ripley's isotropic correction and translation corrections (Ohser 1983) were determined for Ripley's K. A theoretical curve was calculated from expected values under complete spatial randomness, corresponding to a homogenous Poisson process.

RESULTS

The number of pika holes in a 200 m^2 area (200 cm x 10000 cm) ranged from 24 to 51; the average hole count ($\overline{x}$ ± SD) across the four sites was 34 ± 11.8 (Table 3.1). The average intensity of holes across all four sites was (0.0017 ± 0.0010). The densest point space occurred at site 1. Marked pika holes (type, relative age, status) were also investigated (Table 3.2). Most holes were classified as burrows (97 ± 4%), and consequently duck-holes were uncommon (Figure 3.3a). New or relatively young burrows were also rare (7 ± 3%) in age-marked points (Figure 3.3b). Approximately equal numbers of burrows were designated medium (49 ± 13%) or old (44 ± 13%) in relative age. However, relative age also showed the highest variance of any burrow classification measure between the colonies. More medium aged burrows than old burrows were found at all sites except site 3. Consistently more burrows were found to be active (74 ± 4%) than inactive (26 ± 4%) (Figure 3.3c). Of the marked points, the highest intensity was reported for burrow-type holes (0.0016 ± 0.0010), followed by active-status holes (0.0012 ± 0.0004).

Further analyses used all points (unmarked) at each site. Exploring multiple bandwidths of the Gaussian kernel indicated that a bandwidth of 10 was sufficient to distinguish clusters of points at all sites (Figure 3.4); thus this bandwidth was used in all subsequent analyses. No gross violations of spatial homogeneity were apparent, though site 3 was somewhat suggestive of a uniform distribution.

Cluster Analysis

Clustering was first explored by visual inspection of the mapped points (Figure 3.2a). Site 1, which also had the highest point intensity, appeared to be the least clustered. The remaining sites had regions without burrows, suggesting potential clusters. Additionally, a Steinen diagram indicated that nearest-neighbor distances were largest at sites 2 and 4 (Figure 3.2b). These clusters were statistically evaluated using summary statistics of distances between unmarked points assuming global spatial homogeneity (Figure 3.6 - Figure 3.9). The estimated edge corrections did not vary widely within test statistics, therefore only the border (reduced-sampled) edge-correction is shown. In all statistics the wide envelope of randomizations was an artifact of experimental design. Because the maximum distance (r) can only be half the length of the shortest side of the plot (Baddeley 2008), only distances up to 1 meter are shown. Distances below 0.1 m are not interpreted as this is the burrow (pixel) width.

The standard nearest-neighbor distance distribution (G function) measures distance between events to generate a cumulative distribution of nearest-neighbor distances (Figure 5). Distributions above the CSR envelope are considered regular, and below CSR are considered clustered. Site 1 shows clustering at small ($r < 3$) and possibly large intervals ($r > 8$). Site 2 displays clustering over much of the small intervals ($r < 7$), and regularity at larger intervals ($r > 8$). Site 3 shows uniform Matern-regularity (observed data at lower envelope) at all distances. Site 4 shows regularity at distances up to 8.

An alternative method, the F function (Figure 6), measures the distance from a reference point to the nearest event rather than recording the distance from event to event. The point-to-event method is used by the empty space function (F function). It is a measure of the minimum distance to the nearest point. Distributions above the CSR envelope are considered regular, and below CSR are considered clustered. All sites suggest clustering at large distances ($r > 9$) with the F function.

The J function is a combination of the G and F functions: (1 - G)/(1 - F) (Figure 7). Site 1 suggests CSR. Sites 2 and 4 show regularity until a deep dip at $r = 6$ and 8, respectively. For high r-values at site 3, the distribution approaches more regular spacing than expected at random.

The reduced second moment function, Ripley's K, (Figure 8) looks at all pairs of points and gives a variance of interpoint distance by comparing the observed to expected distances. Site 3 and 4 lie on the lower envelope, suggesting a regular distribution. This will be compared with a model of a Matern Inhibition process.

DISCUSSION

I detected less than one pika hole per square meter (0.12 to 0.26 holes/ m^2), even in the sites with the greatest point intensity (0.26 holes/ m^2). An estimate of 1200 to 2250 holes/ ha is reasonable based on constant point intensity; however, spatial extents over 200 m^2 were not directly measured. The most common type of hole encountered was an active burrow of medium to old age. New holes and duck-holes were uncommon.

At each site, the overall point distribution appeared spatially homogeneous. However, nearest-neighbor statistics revealed regions of clustering (more points than expected under complete spatial randomness) and uniformity (fewer points than expected under CSR). Interpretations were limited to small distances (0 to 1 m), which contained the most point-to-point (or event-to-event) distances. The border (reduced-sample) edge-correction was shown for consistency across all statistics, though it represents a highly conservative correction.

At site 1, no nearest-neighbor statistics could reject CSR across most distances. Variance was also as expected under CSR. The only (weak) evidence for clustering is suggested at distances above 0.9 m. Site 2 and 4 indicated regularity (more uniform point distribution) at moderate distances (0.4 x 0.7). Both nearest-neighbor statistics and variance support a uniform point distribution at most distances for site 3.

Location appeared to be an important factor influencing placement of holes over short distances (0 to 1 m). Spatial randomness was most strongly evident at site 1, while sites 3 and 4 showed the most instances of uniformity. Interestingly, site 1 also had a notably higher point count (51) compared to the other sites (29, 32, 24 for sites 2, 3 and 4, respectively). This evidence supports the interpretation that pika holes are randomly distributed at high densities, but perhaps not for lower densities.

The sites with lower point densities (2, 3 and 4) also showed the most evidence for uniform Matern-regularity. Uniform distributions, where points are more widely spaced than would be expected from a random distribution of points, are less common than clustered distributions. This pattern suggests that when pika densities are low, an inhibition process is at work, forcing a wider spacing of holes than would be expected under CSR. This regular spacing was most frequent at moderate distances (0.4 m to 0.7 m). All sites except site 3 suggested clustering at large distances (> 0.9 m). This distance probably indicates clusters of holes within an interconnected family burrow structure.

The mechanisms behind these patterns were not tested directly, but the patterns themselves do suggest several possibilities. One hypothesis is that a biological process, such as territoriality, is at work. Plateau pikas are social mammals, and thus do not defend separate individual territories, though they do form family units. However, the moderate distances over which regular spacing was most often found is too small to fit to family units. Rather, a biological inhibition process at the individual level is more likely, such as inter-sibling competition for space or individual competition for minimum forage requirements. Alternatively, this regular spacing could be a consequence of each family unit expanding its territory to cover a maximum area. Uniform spacing may have consequences at higher pika densities, such as greater chances of invasion by dispersing juveniles.

An alternative hypothesis is that a predominantly abiotic, rather than biotic, process is at work. The distance between holes may be a consequence of soil properties, such as compactness, particle size, and clay content. The slope of the entrance tunnel may dictate a minimum tunnel length, and thus a minimum spacing of burrows. Multiple entrance holes may destabilize the soil surface. Additionally, wider spacing of holes could be an attempt to minimize the infiltration of rain into the tunnel system. Assuming that high pika density is correlated with random hole-spacing, then biotic factors may be stronger than abiotic mechanisms. However, direct evaluation of these hypotheses is necessary to make any formal conclusions about the geometry of burrow spacing.

CONCLUSION

I demonstrate the utility of spatial statistics as a way to evaluate local landscape heterogeneity. While spatial statistics are often exploratory in nature, the process of pattern description can lead to multiple hypotheses that can be directly tested in the field. These methods can motivate future tests that quantitatively evaluate the impacts of ecosystem engineers.

Table 3.1. Frequency and average intensity of unmarked points at four sites. The window rectangle is [0, 20] x [0, 1000] units with a total area of 200 m^2. The control site (not shown) had identical dimensions. It did not contain any pika holes or regions of 100% bare ground. Yak scat at the control site had a frequency of 8 and average intensity of 0.004.

	Site	Pika Holes	Yak Scat	100% Bare Ground
Frequency	1	51	10	451
	2	29	7	209
	3	32	17	102
	4	24	6	190
	$\bar{x}$ ± SD	34 ± 11.8	10 ± 5	238 ± 149.5
Intensity	1	0.00255	0.00050	0.0226
	2	0.00145	0.00035	0.0104
	3	0.00160	0.00085	0.0051
	4	0.00120	0.00030	0.0095
	$\bar{x}$ ± SD	0.0017 ± 0.001	0.0005 ± 0.0002	0.0119 ± 0.0075

Table 3.2. Frequency, proportion, and intensity for marked pika holes. Holes are marked by type (burrow, duck-hole), relative age (new, medium, old) and status (active, inactive) at four sites. The window rectangle is [0, 20] x [0, 1000] units with a total area of 200 m^2.

	Site	Type		Relative Age			Status	
		Burrow	Duck-hole	New	Medium	Old	Active	Inactive
Frequency	1	49	2	2	31	18	37	14
	2	29	0	3	15	10	22	6
	3	29	3	2	10	20	22	10
	4	24	0	2	12	10	18	6
	$\bar{x}$ ± SD	33 ± 11.1	1 ± 1.5	2 ± 0.5	17 ± 9.6	15 ± 5.3	25 ± 8.4	9 ± 3.8
Proportion	1	0.961	0.0392	0.0392	0.6080	0.3530	0.725	0.275
	2	1	0	0.1070	0.5360	0.3570	0.786	0.214
	3	0.906	0.0938	0.0625	0.3120	0.6250	0.688	0.312
	4	1	0	0.0833	0.5000	0.4170	0.750	0.250
	$\bar{x}$ ± SD	0.97 ± 0.04	0.03 ± 0.04	0.07 ± 0.03	0.49 ± 0.13	0.44 ± 0.13	0.74 ± 0.04	0.26 ± 0.04
Intensity	1	0.00245	0.00010	0.00010	0.000155	0.00090	0.00185	0.0007
	2	0.00145	0	0.00015	0.00075	0.00050	0.00110	0.0003
	3	0.00145	0.00015	0.00010	0.00050	0.00100	0.00110	0.0005
	4	0.00120	0	0.00010	0.00060	0.00050	0.00090	0.0003
	$\bar{x}$ ± SD	0.0016 ± 0.001	0.00006 ± 0.0001	0.0001 ± 0.0000	0.0005 ± 0.0003	0.0007 ± 0.0003	0.0012 ± 0.0004	0.0005 ± 0.0002

Figure 3.1. Burrow classification scheme.

(a) Burrow

(b) Duck Hole

(c) New burrow

(d) Medium age burrow

(e) Old burrow

(f) Pika runway

Figure 3.2. Maps of point locations at four pika colonies. Locations displayed for holes (a) and holes and 100% bare ground (c), with x-axis expanded by 10. Corresponding Steinen diagrams with circle radius equal to nearest-neighbor distance, are shown for holes (b) and bare ground (d).

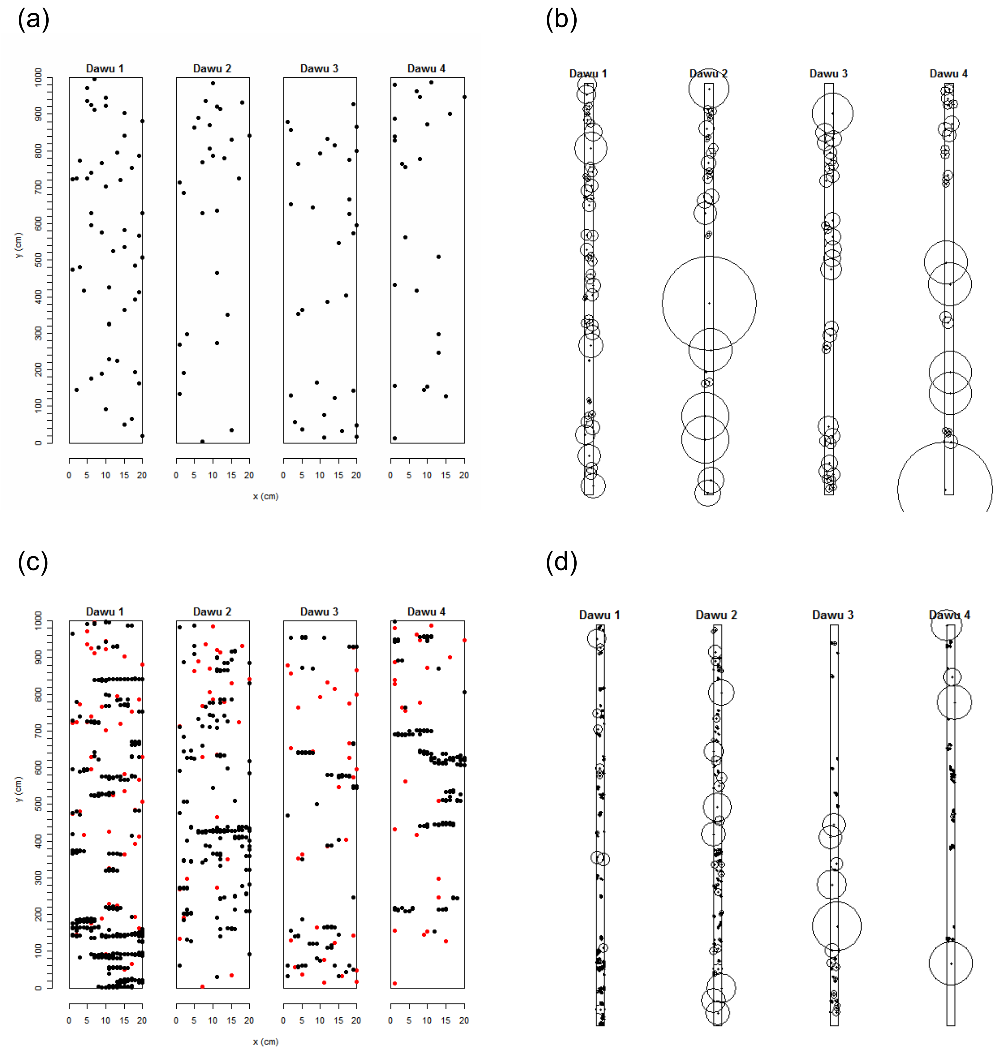
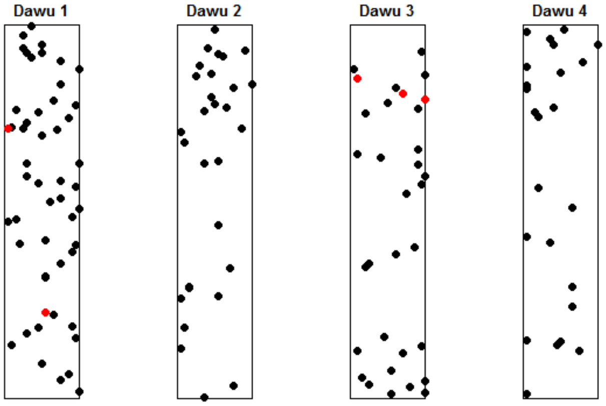
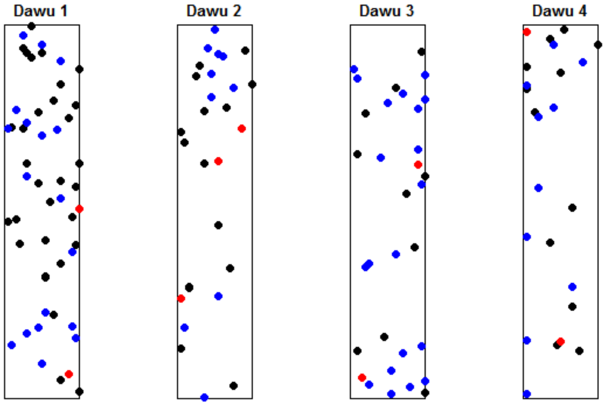


Figure 3.3. Point patterns at four pika colonies. Points are marked by (a) type, (b) relative age and (c) status. The x-axis has been expanded for better visualization.

(a) Type (●burrow, ● duck-hole)



(b) Relative Age (● new, ● medium, ● old)



(c) Status (● active, ● inactive)

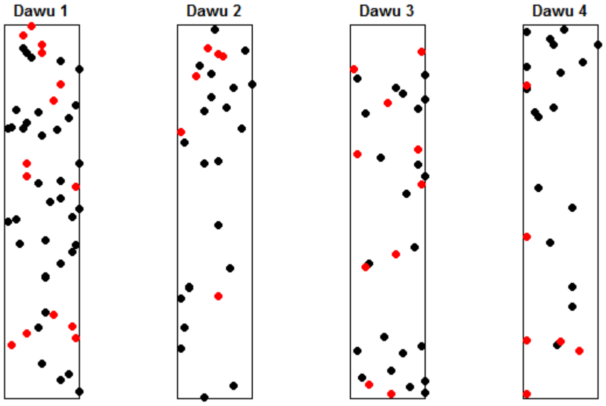


Figure 3.4. Kernel density plot of pika burrows at four colonies. Plots are shown over bandwidth values 5, 10, 15 and 20. Yellow represents a higher intensity of points and blue, a lower intensity.

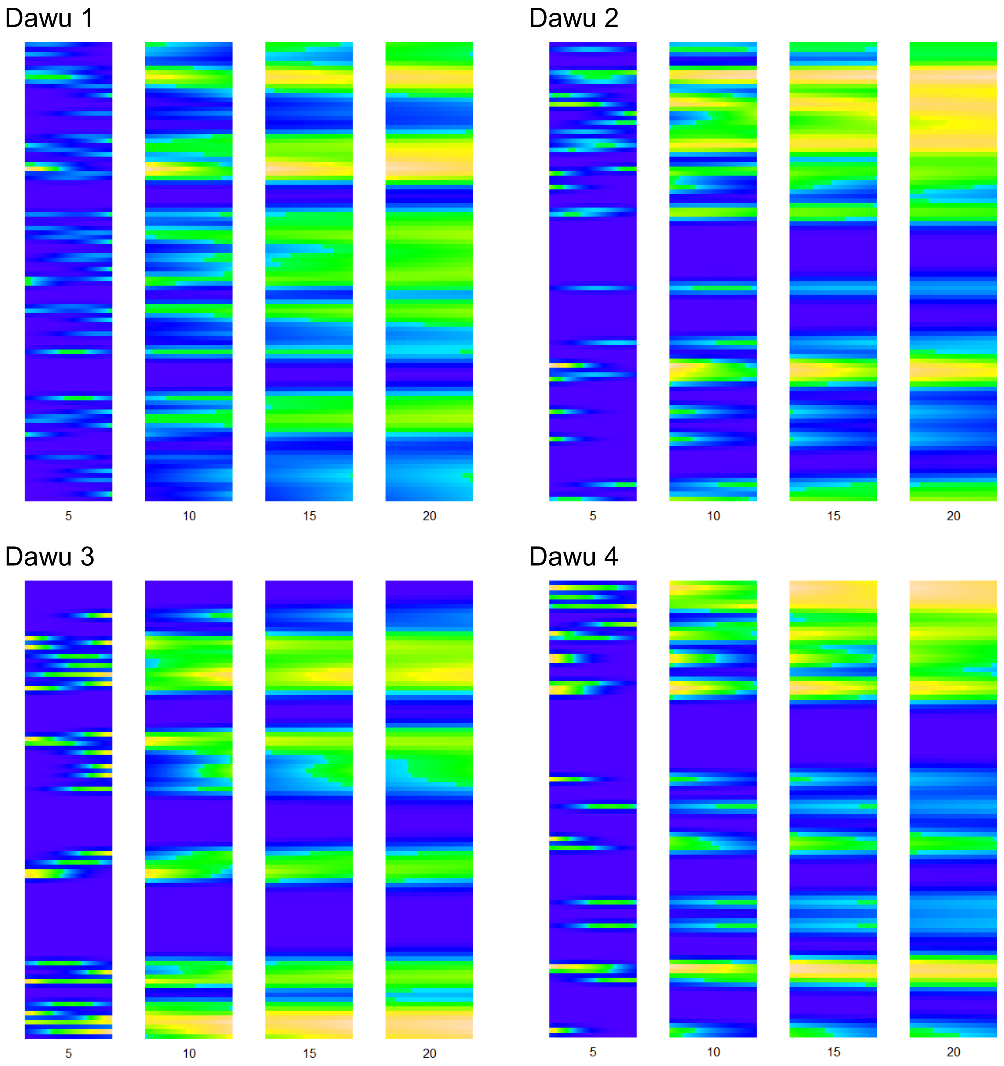
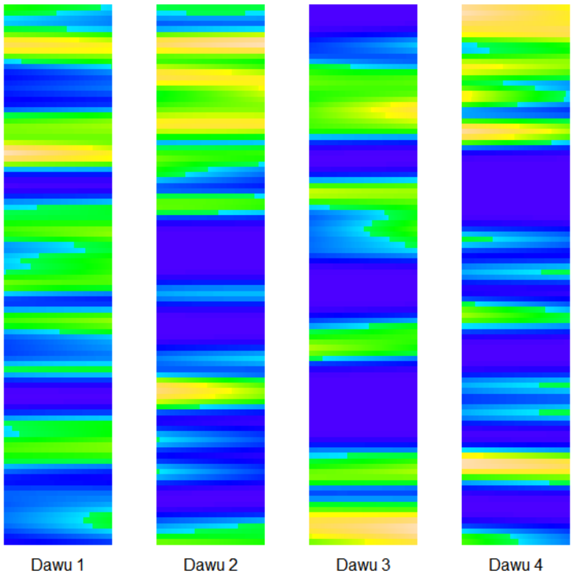


Figure 3.5. Kernel density plot with bandwidth = 15. Plots show pika hole locations (a) and 100% bare ground (b) at four pika colonies. Yellow represents a higher intensity of points and blue, a lower intensity.

(a)



(b)

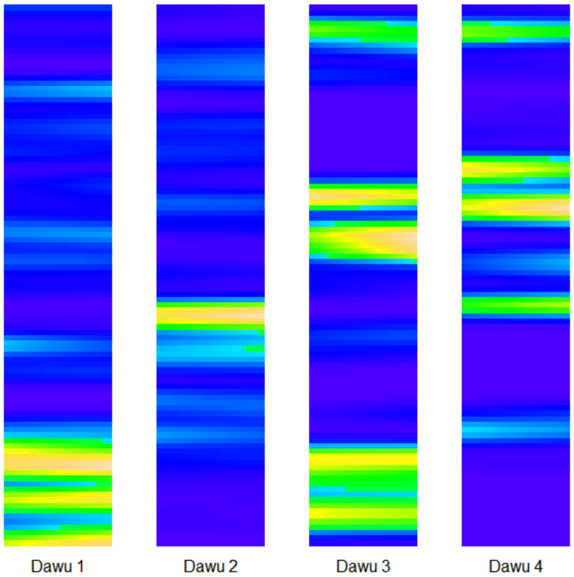
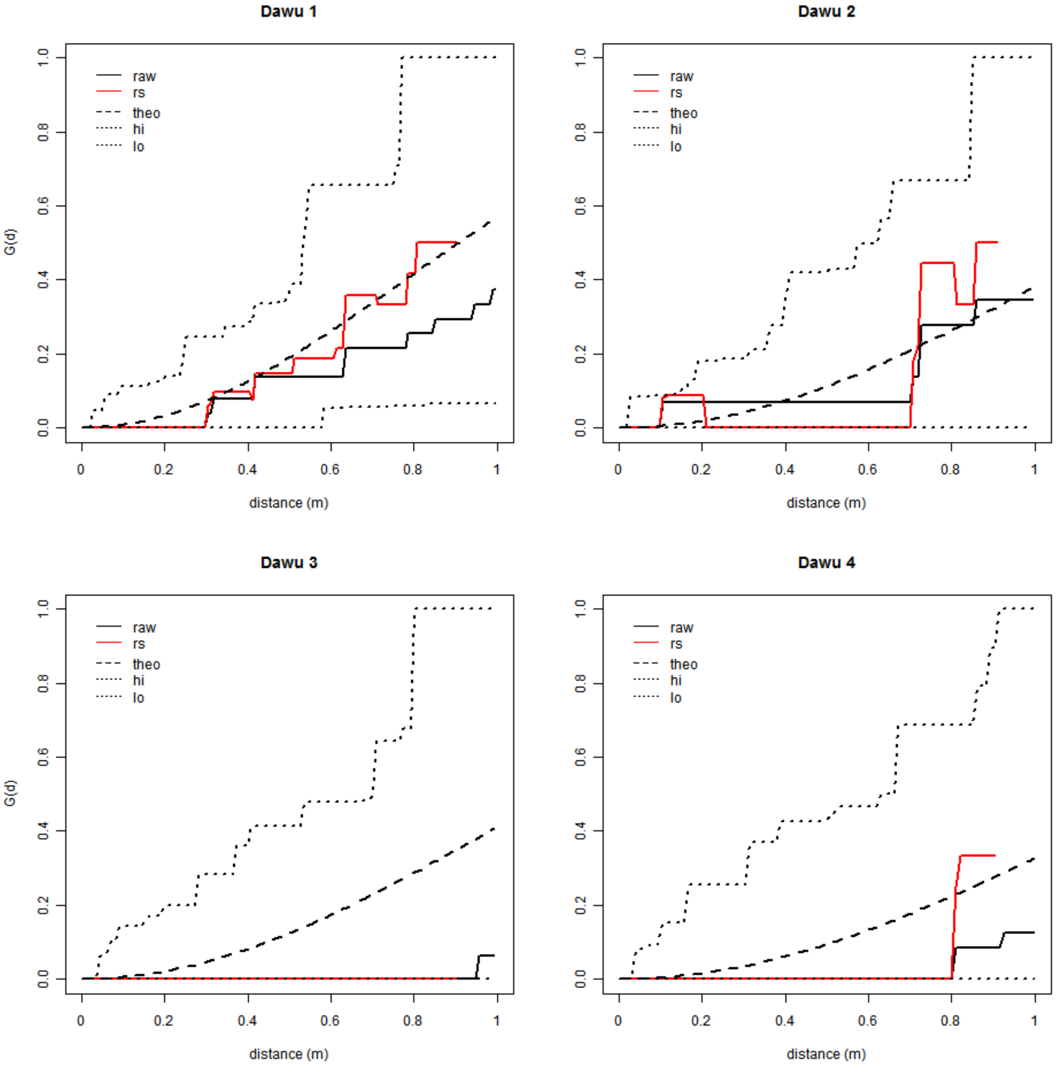


Figure 3.6. The cumulative distribution of nearest-neighbor distances. The G function by distance (in meters) is given for the theoretical CSR curve (theo), upper randomization envelope (hi), lower randomization envelope (lo), uncorrected estimate (raw) and border-correction (rs). For Dawu 3 and Dawu 4, the edge-correction falls on the lower randomization envelope.



Dawu 1

Dawu 2

Dawu 3

Dawu 4

Figure 3.7. The empty space function at four colonies. The F function by distance (in meters) is shown for the theoretical CSR curve (theo), upper randomization envelope (hi), lower randomization envelope (lo), uncorrected estimate (raw) and border-corrected estimate (rs).

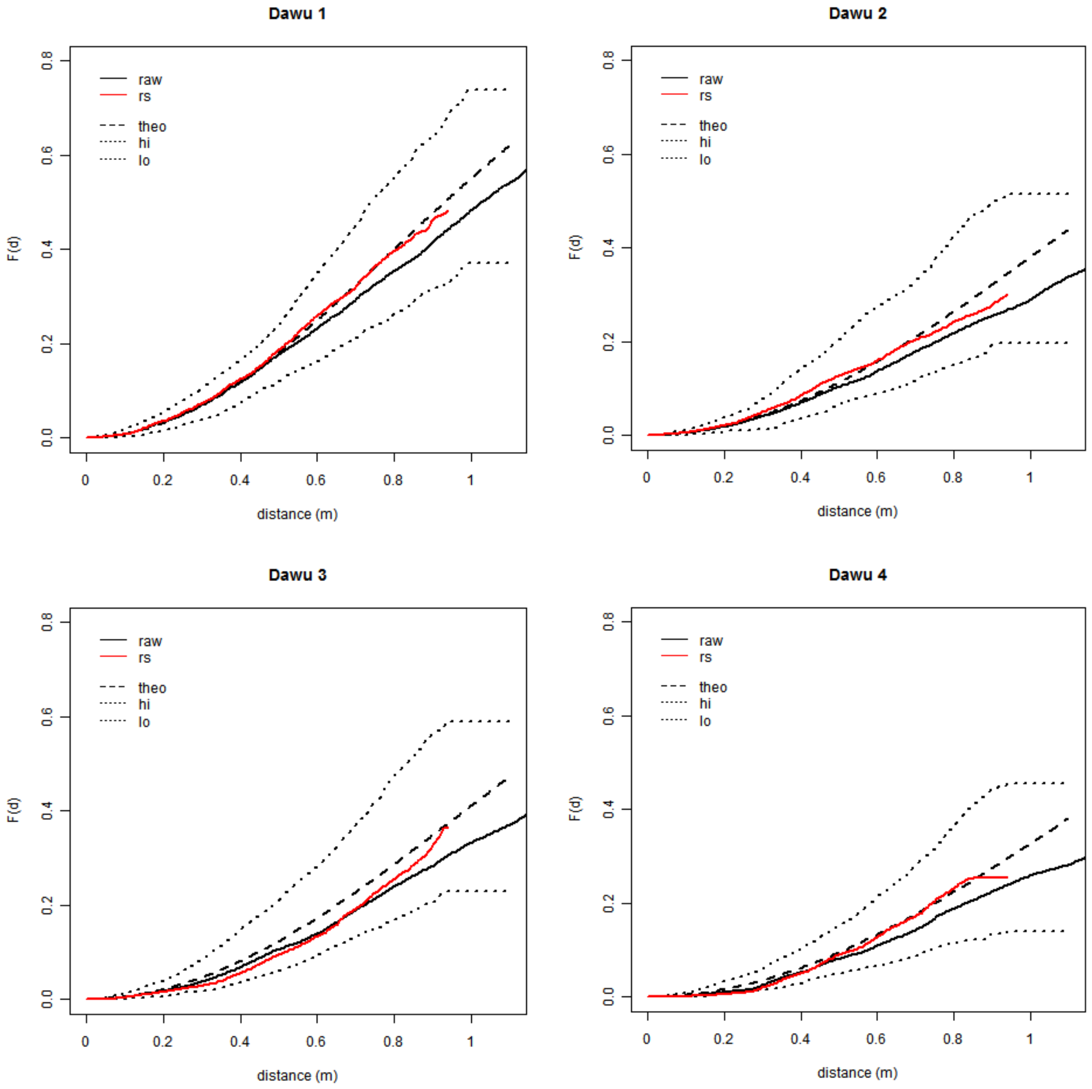


Figure 3.8. The J function (combined G and F function). The function by distance (in meters) is shown for the theoretical CSR curve (theo), upper randomization envelope (hi), lower randomization envelope (lo), uncorrected estimate (raw) and border-corrected estimate (rs).

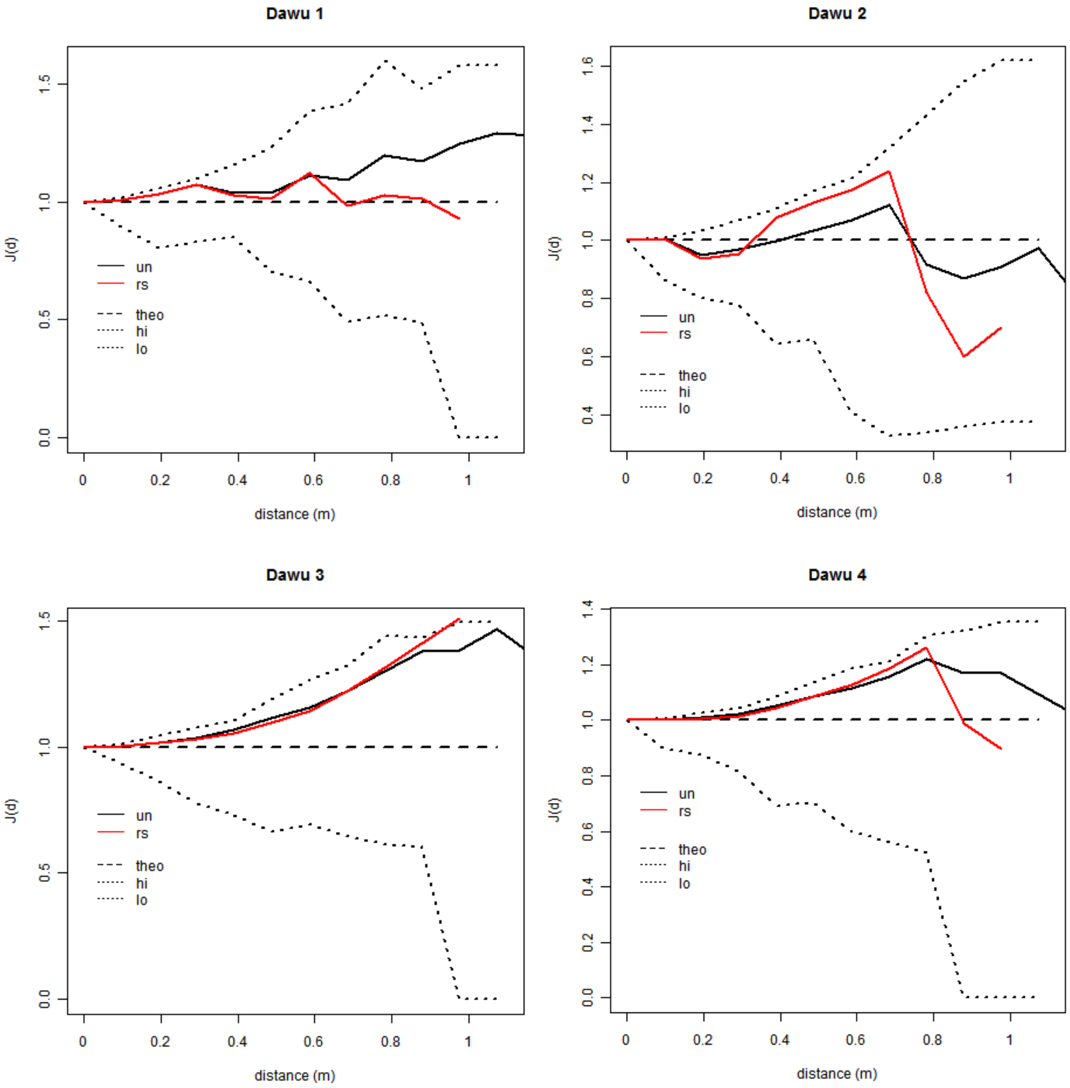


Figure 3.9. Reduced second moment function. Ripley's K by distance (in meters) is shown for the theoretical CSR curve (theo), upper randomization envelope (hi), lower randomization envelope (lo), uncorrected estimate (obs) and border-corrected estimate (border).

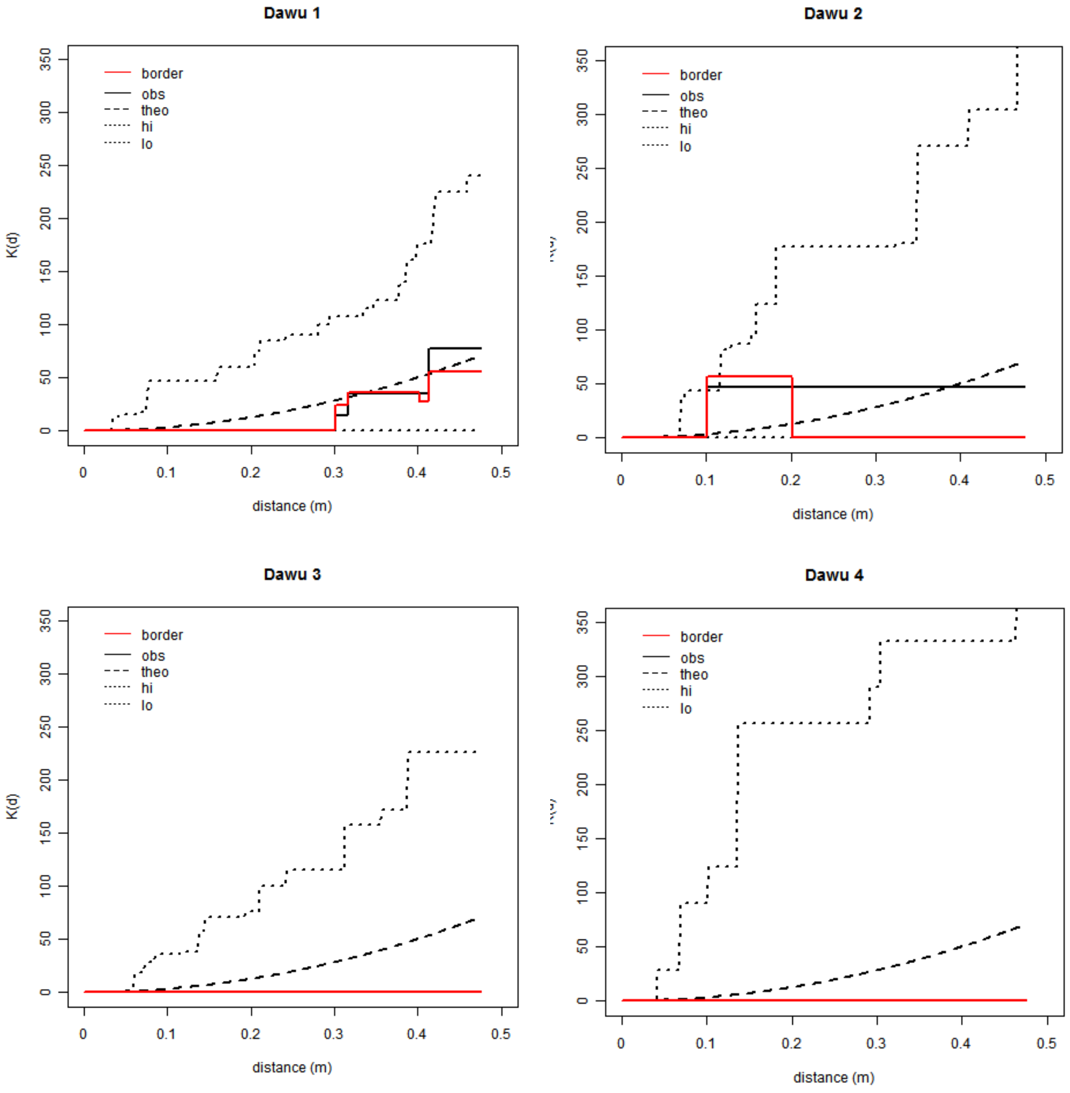
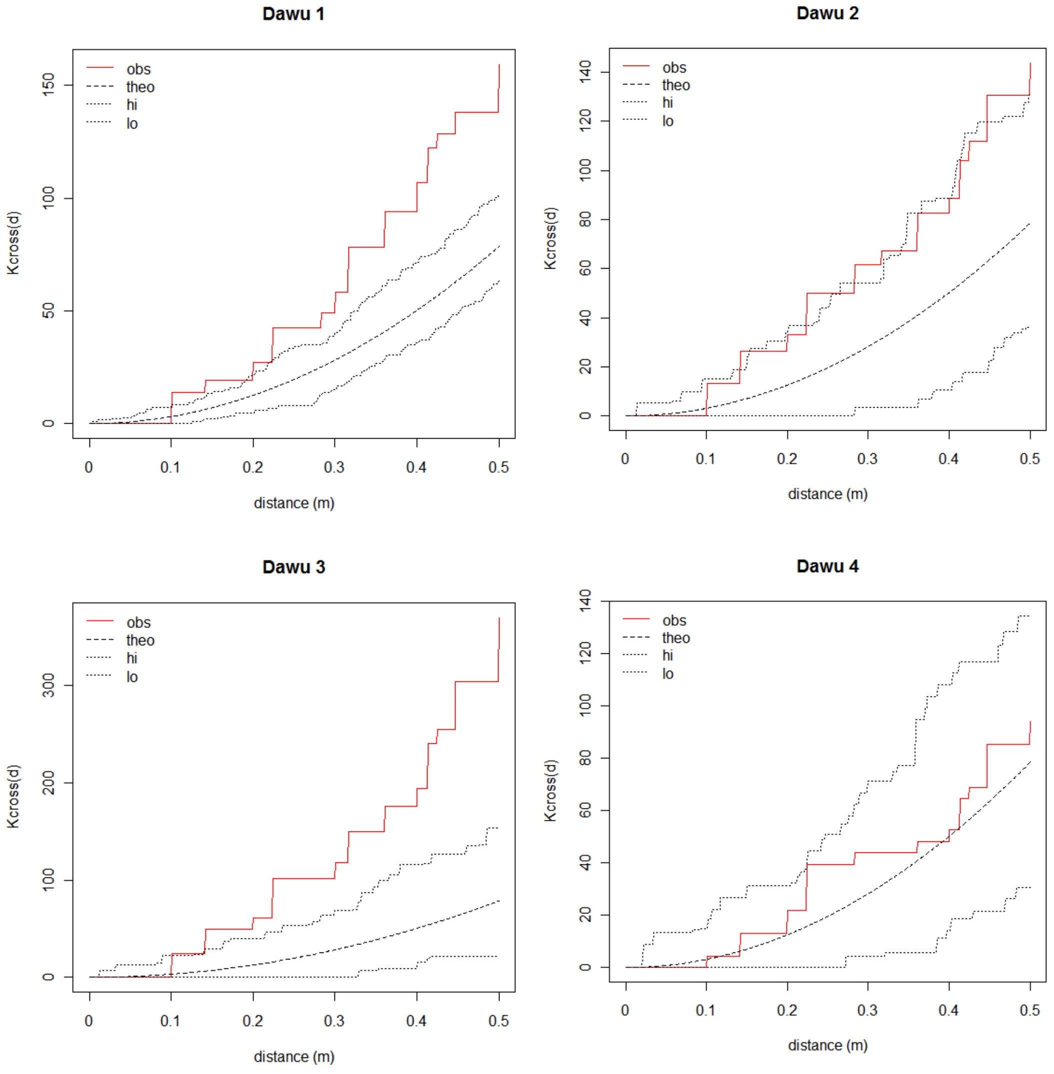


Figure 3.10. Kcross by distance (in meters) at four colonies. The function is shown for the theoretical CSR curve (theo), upper randomization envelope (hi), lower randomization envelope (lo), and uncorrected estimate (obs).


Dawu 1

Dawu 2

Dawu 3

Dawu 4

CHAPTER 4

Modeling effects of pika and livestock herbivory on pastureland of the Tibetan Plateau

INTRODUCTION

The Tibetan plateau stretches across 2.5 million km^2, dominating nearly a quarter of China's landscape; 70% of this area is characterized by high alpine grasslands (Miller 1995, Miller and Craig 1997). A primary resource user of this alpine habitat is the endemic plateau pika (Lagomorpha: *Ochotona curzoniae*), a small member of the order including rabbits that builds extensive underground burrow systems. Dense populations of these animals, which often exceed 300 per hectare, have long been considered a nuisance by local communities and governments (Formosov 1928, Ekvall 1968, Fan et al. 1999, Smith and Foggin 1999). Pikas are thought to compete with the local livestock for food and to overgraze the natural grasslands. Additionally, their burrows are said to cause soil erosion and rangeland degradation (Zhang et al. 1998, Fan et al. 1999). Potent chemicals, such as zinc phosphate, fluoroacetate, and botulin C toxin have been used in attempts to eradicate the pika locally, while simultaneously causing widespread environmental pollution (Fan et al. 1999) and reduction of the regional biodiversity and ecological functioning (Smith and Foggin 1999).

On the other hand, more and more evidence points to the keystone status of the plateau pika. Pikas are known as ecosystem engineers because of the importance of their burrows in providing nesting habitat for small birds in a treeless landscape (Lai and Smith 2003). The pika itself is the most abundant small mammal in the region. As such, it is an important food source for most regional carnivores and raptors (Schaller 1998, Smith and Foggin 1999, Lai and Smith 2003, Badingqiuying 2008). Without pikas, burrows may soon collapse and predators disappear. Pikas also contribute to ecosystem function in a number of other ways. For instance, species with similar ecological roles to the Tibetan pika, such as the American prairie dog, have been shown to influence plant species richness in inhabited areas (Whicker and Detling 1988, Fahnestock and Detling 2002). Pikas may play a similar role in their alpine meadow habitat.

Due to the high elevation (3500-5400m) and harsh conditions found on the plateau, most of this pastureland is not suitable for farming, but only for livestock production. In fact, Tibetan nomads have been grazing yak and sheep in coexistence with pikas for upwards of 8000 years (Miehe et al. 2009), and Tibetan pastoralism remains the primary human activity on the plateau (Ekvall 1968, Miller and Craig 1997). These nomads practice a transhumant system where livestock are shifted from summer to winter pastures with the changing of the seasons. Unlike transhumant systems in Africa and many arid regions of the world, forage availability is not limited by water availability, but by altitude (Meiners 1991). Livestock actually graze on senescent forage for most of the year (Goldstein et al. 1990).

One final important issue regarding pikas is the extent to which their dietary needs compete with those of Tibetan yak and sheep. Research suggests that only when livestock reach high densities are they likely to compete with pikas for food (Jiang and Xia 1987). This is because pikas graze selectively, and many of their food sources are passed over by yak and Tibetan sheep (Jiang and Xia 1987). Additionally, the competition for food between yak and Tibetan sheep is thought to be more intense than the competition between these domesticated animals and pikas (Jiang and Xia 1987). Recent government policy has been to settle Tibetan nomads and to fence rangelands

(Yeh 2003, 2005, Foggin 2008). However, it is likely that the fencing of rangelands, and corresponding increase in livestock density, is a source of overgrazing. Confounding matters, pikas tend to favor heavily grazed areas with low cover because there is a wider field of view for spotting predators (Bian et al. 1999). In this sense, large pika populations may be a result of overgrazing, rather than a cause (Smith and Foggin 1999).

CONCEPTUAL MODEL

The main resource in this system is the alpine grassland habitat. Plant availability is controlled by environmental conditions (primarily altitude and rainfall) and is strongly influenced by herbivore stocking rates. Livestock (controlled by pastoralists) and pikas are both resource users. Pika numbers are controlled by environmental conditions (e.g. snowstorms, rainfall), plant availability, natural predation, and poisoning policies. Other small mammalian herbivores are low in number compared to pikas, and can therefore be ignored. Livestock numbers are also controlled by environmental conditions and plant availability, as well as by their pastoralist managers. While wild ungulates are also common on the Tibetan plateau, they have restricted ranges and can therefore be left out of this simplified model. The pastoralists are in turn influenced by policies and livestock markets. Public infrastructure, in the form of markets and boundary enforcement, is provided by both pastoralists and local and regional governments. Figure 1 presents a conceptual model of this system.

A simplified conceptual model of these alpine rangelands can be restricted to the primary resource (grassland plants) and resource users (livestock, pikas) (Figure 1, bold text). The alpine meadow resource can divided into two major types of forage:

graminoids, consisting grass-like herbaceous plants such as grasses and sedges, and forbs, consisting of mainly dicotyledonous herbaceous plants. Graminoids are the preferred forage for both pikas and livestock. Because forbs often contain toxic secondary compounds, these plants are frequently avoided by both pika and livestock. However, because pikas have the ability to gather plants and dry them in haypiles, thereby reducing the concentration of toxic chemicals (Dearing 1997), pika avoidance of forbs should be considered less extreme than that of ruminants. Other plant functional groups such as trees and shrubs can be ignored because trees are entirely lacking, while shrubs are usually restricted to north-facing slopes. Graminoids and forbs, then, are the primary resource constituents which compete for space, nutrients, water, etc. within the alpine habitat. Key questions that this mathematical model will address include conditions under which a more diverse, two competitor resource base would be stable; and the influences of herbivory by livestock and pikas on this system.

MATHEMATICAL MODEL

This model represents a highly simplified version of this ecosystem. Because the primary resource of interest is the condition of the alpine meadow habitat, rather than the abundances of livestock and pikas themselves, the state variables of the model were restricted to the two main forage components: namely, graminoids and forbs. These forage components compete for light, space and nutrients in the alpine meadow. Therefore, this system can be based on a standard Lotka-Volterra competition equation with graminoids (P_1) and forbs (P_2) as the primary competitors:

$$\dot{P}_1 = r_1 P_1 (1 - \alpha_{11} P_1 - \alpha_{12} P_2) \tag{1}$$

$$\dot{P}_2 = r_2 P_2 (1 - \alpha_{21} P_1 - \alpha_{22} P_2) \tag{2}$$

where r is the growth rate, and α is the competitive interaction (intraspecific for identical subscripts and interspecific for dissimilar subscripts). Consequently, this model will primarily quantify grassland productivity in terms of graminoid and forb aboveground biomass. Growth rate and competitive interactions will be treated as parameters. However, (P_1) and (P_2) are also acted upon by the resource users. Herbivory by pikas (H_1) and livestock (H_2), in addition to a metric of their preference for forage type, can be added in as a consumptive component:

$$\dot{P_1} = r_1 P_1(1 - \alpha_{11} P_1 - \alpha_{12} P_2) - \rho_{P1} H_1 P_1 - \gamma_{P1} H_2 P_1 \tag{3}$$

$$\dot{P_2} = r_2 P_2(1 - \alpha_{21} P_1 - \alpha_{22} P_2) - \rho_{P2} H_1 P_2 - \gamma_{P2} H_2 P_2 \tag{4}$$

where ρ is the preference of pikas for a forage type and γ reflects the preference of livestock. Although several other factors likely influence model relationships as well (for instance, forage competitive abilities may be influenced by the presence of pika burrows as new habitat or by livestock trampling and soil compaction) these processes will be ignored for the present so that a thorough anaylsis of a simplified model can be first constructed. After establishing these two basic equations, the model can be refined by eliminating nonessential parameters. The number of parameters can be reduced by three (number of equations + time) through a nondimensionalization process (see Appendix A).

$$\dot{P_1} = P_1(1 - P_1 - \alpha_{12} P_2) - \rho_{P1} H_1 P_1 - \gamma_{P1} H_2 P_1 \tag{5}$$

$$\dot{P_2} = r P_2(1 - \alpha_{21} P_1 - P_2) - \rho_{P2} H_1 P_2 - \gamma_{P2} H_2 P_2 \tag{6}$$

Equations 5 and 6 are the final system of equations to represent the rangeland conceptual model (Figure 1, bold text). Parameters can be interpreted as follows:

Table 4.1 List of parameter values and definitions.

Parameter	Definition
r	relative growth rate of forbs to graminoids
α_{12}	competitive effect of forbs on graminoids relative to intraspecific graminoid competition
α_{21}	competitive effect of graminoids on forbs relative to intraspecific forb competition
H_1	pika herbivory rate
H_2	livestock herbivory rate
ρ_{P1}	pika preference for graminoids relative to the growth rate of graminoids
ρ_{P2}	pika preference for forbs relative to the growth rate of forbs
γ_{P1}	livestock preference for graminoids relative to the growth rate of graminoids
γ_{P2}	livestock preference for forbs relative to the growth rate of forbs

MODEL ANALYSIS

For nonlinear systems, stability can only be evaluated where the system is unchanging; that is, at equilibrium points. Four fixed points of nondimensionalized equation 5 and 6 were found (Appendix B):

$$(0, 0) \tag{7}$$

$$(0, 1 - \rho_{P2}H_1 - \gamma_{P2}H_2) \tag{8}$$

$$(1 - \rho_{P1}H_1 - \gamma_{P1}H_2, 0) \tag{9}$$

$$\begin{gathered}\left(\frac{1 - \alpha_{12} + H_1(\alpha_{12}\rho_{P2} - \rho_{P1}) + H_2(\alpha_{12}\gamma_{P2} - \gamma_{P1})}{1 - \alpha_{12}\alpha_{21}},\right.\\ \left.\frac{1 - \alpha_{12} + H_1(\alpha_{21}\rho_{P1} - \rho_{P2}) + H_2(\alpha_{21}\gamma_{P1} - \gamma_{P2})}{1 - \alpha_{12}\alpha_{21}}\right)\end{gathered} \tag{10}$$

The stability at each fixed point can be assessed by taking the derivative of equation 5 and 6 in a Jacobean matrix (Appendix C). Equation (7) corresponds to a system without graminoids or forbs. This system has been overgrazed to the extent that no vegetation remains. Equation (8) corresponds to a system with only forbs. All graminoids have been consumed as a result of overgrazing. Equation (9) is the counterpoint of equation (8). In this case, forbs have been eliminated from the system and only graminoids remain. The most diverse resource base is represented by equation (10). Here both forbs and graminoids can coexist.

We can further assess the model by examining phase plane diagrams (Figure 2). Given two competitors (graminoids, P_1, and forbs, P_2), there are four possible outcomes (Figure 3). Either one or the other competitor always wins (cases 1 and 2), the competitors reach a stable equilibrium (case 3), or either competitor can win depending on the initial conditions (case 4). Each of these cases are examined with and without the effects of herbivory. For these cases, α_{12} and α_{21} were selected to create conditions under which one, both, or either competitor would "win" (reach stable equilibrium). Because both pikas and livestock prefer graminoids over forbs, ρ_{P1} and γ_{P1} were both set equal to 1. However, since pikas are able to tolerate increased amounts of toxins in forbs, pikas preference for forbs (ρ_{P2}) was set higher that that of livestock (γ_{P2}) (0.5 and 0.1, respectively). Changing values of the growth rate, r, does not change the stability of the system (compare Figure 3 with Figure 4). Increasing r merely increases the rate with which the system reaches stability. Therefore, r, was set at 1 for all analyses. H_1 and H_2 were set to zero unless effects of herbivory were included in the analysis.

In case 1, one competitor (graminoids) out competes the second competitor (forbs) (Figure 5; $\alpha_{12} = 0.5$, $\alpha_{21} = 2$). Therefore, there is only one stable point $(0, P_1)$, and the population of graminoids always exceeds that of forbs. The two species cannot coexist in the long term under these conditions. Graminoids dominate because their intraspecific competitive ability is lower than that of forbs. However, the addition of high levels of herbivory (Figure 5; $H_1 = H_2 = 0.4$) can cause a shift in stability from of the grassland from graminoid to forb dominance. This result makes intuitive biological sense because graminoids are the preferred forage for both herbivores. When herbivory levels are high enough, the natural competitive advantage of graminoids is not sufficient to overcome the impact of grazing herbivores, and the graminoid population declines.

Case 2 (Figure 6; $\alpha_{12} = 2, \alpha_{21} = 0.5$) represents the opposite situation: forbs are always dominant over graminoids. This system also only exhibits stability once one competitor is eliminated (in this case, $P_1 = 2$ and $P_2 = 0$). The parameter values indicate interspecific competition between both species is equal, but the intraspecific graminoid competition is larger than the intraspecific forb competition. Biologically, this means that graminoids are more self-limiting than forbs, hence the long-term persistence forbs alone. Unlike case 1, when herbivory is added here (Figure 6; $H_1 = H_2 = 0.4$), the nullclines shift to lower intercepts, but remained parallel to the original condition. Thus, the inclusion of herbivory does not influence the overall stability of the system; rather, in the case where the intraspecific competitive effects of one species is greater than the second, herbivory lowers the intercept (or abundance) of the winning competitor. In this scenario, the alpine habitat becomes a forb-dominated habitat regardless of herbivory levels.

The transition from graminoid to forb domination in this scenario can be more closely examined by plotting each of the variables over time (Figure 7). Although the population of graminoids always goes extinct, the rate at which the population goes extinct varies depending on the herbivore. Under livestock herbivory (Figure 7; $H_1 = 0$, $H_2 = 0 - 0.8$), the grassland population becomes dominated by forbs more quickly than under pika herbivory (Figure 7; $H_2 = 0$, $H_1 = 0 - 0.8$). Biologically, this result occurs because pikas remove more forbs from the system than do livestock, thereby lowering the rate at which conversion to forbs occurs. Consequently, the final biomass of forbs under pika herbivory alone is always lower than that of livestock herbivory alone.

Case 3 (Figure 8; $\alpha_{12} = \alpha_{21} = 0.5$) is the only circumstance under which two species can coexist in the long-term. Here the intraspecific competition of both species is greater than their interspecific competition. In other words, these two species regulate themselves better than they regulate each other. Therefore, the only stable point in this system is (P_1, P_2). As moderate levels of herbivory ($H_1 \prec 0.4$ and $H_2 \prec 0.4$) are added to this system, the nullclines for each competitor are pushed down, but the overall stability does not change (Figure 8). There is an overall tendency of the system to result in a forb dominated habitat as herbivory rates are varied. If high amounts of herbivory are added, the preferred competitor (in this case, graminoids) can be pushed to extinction. A stable habitat including both graminoids and forbs is only possible under moderate levels of grazing.

To further investigate the resistancy of coexistence to forb dominance, this case can also be plotted as variables over time (Figure 9). Under high levels of livestock grazing (Figure 9; $H_1 = 0$, $H_2 = 0 - 0.8$), graminoids quickly become extinct. However, under similar levels of pika grazing (Figure 9; $H_2 = 0$, $H_1 = 0 - 0.8$), not only does the system convert more slowly to forb dominace, but graminoids are not entirely eliminated from the grassland. Furthermore, the ratio of forbs to grasses is much lower in a system grazed by pikas than one grazed by livestock.

Lastly, for case 4 (Figure 10; $\alpha_{12} = \alpha_{21} = 2$), the intraspecific competition within each species is less than the interspecific competition between species. Under these parameters, only one species can survive. Thus, both $(0, 2)$ and $(2, 0)$ are stable points for (P_1, P_2). Which species will win out depends on the initial conditions of the system, or the direction of the initial perturbation. Similarly to case 3, stability is still possible under moderate levels of herbivory ($H_1 \prec 0.4$ and $H_2 \prec 0.4$), but the abundance of the winning competitor will be reduced. As in case 3, high levels of grazing by either herbivore will exclude graminoids.

CONCLUSION

Analysis of this model has shown that stability is primarily controlled by inter- and intraspecific competitive abilities of the forage components. The most diverse resource base, defined as a stable system of both graminoids and forbs, can occur only when the intraspecific competitive ability of each species is greater than their interspecific competitive effect. Under most cases, high levels of herbivory by either pika or livestock will drive the system to forb dominance. Heavy grazing pressure cannot result in a system dominated by graminoids, since these are the preferred forage type. However, low to moderate grazing levels do not necessarily lead to forb dominance. It is important to note that by observing the end result of long-term grazing to be a forb-dominated or “degraded” system, one cannot conclude whether this outcome was the result of pika or livestock overgrazing, or a combination of both. Rather, analysis of this model suggests that livestock grazing, rather than pika grazing, is more likely to convert a grassland to forb-dominance. Grazing by pikas may increase the resistance of this system to such dominance. In conclusion, this model does not implicate pikas per se as a cause of rangeland degradation from a two forage component stable system to one dominated by a single less desirable plant type. Rather, overgrazing by either pikas or livestock could remove graminoids as a forage source under these conditions.

Future avenues of exploration should include additional components of the conceptual model (Figure 1). In addition to the negative effects of pikas on alpine plants (represented by herbivory), pikas may also have positive influence upon their environment. By burrowing, they recycle deep alpine soil and may increase soil oxygenation and nutrient exchange. Plant productivity could be reflected by higher nutrient concentration of plants and soils near pika burrows. Furthermore, disturbance created by soil upheaval can create new habitat which may favor colonization by particular plant types. These impacts could be incorporated through additional variables linked to the current parameters in the system. Analysis of these components could lead to further insights on the relationship between forage competitors in this alpine system.

Figures

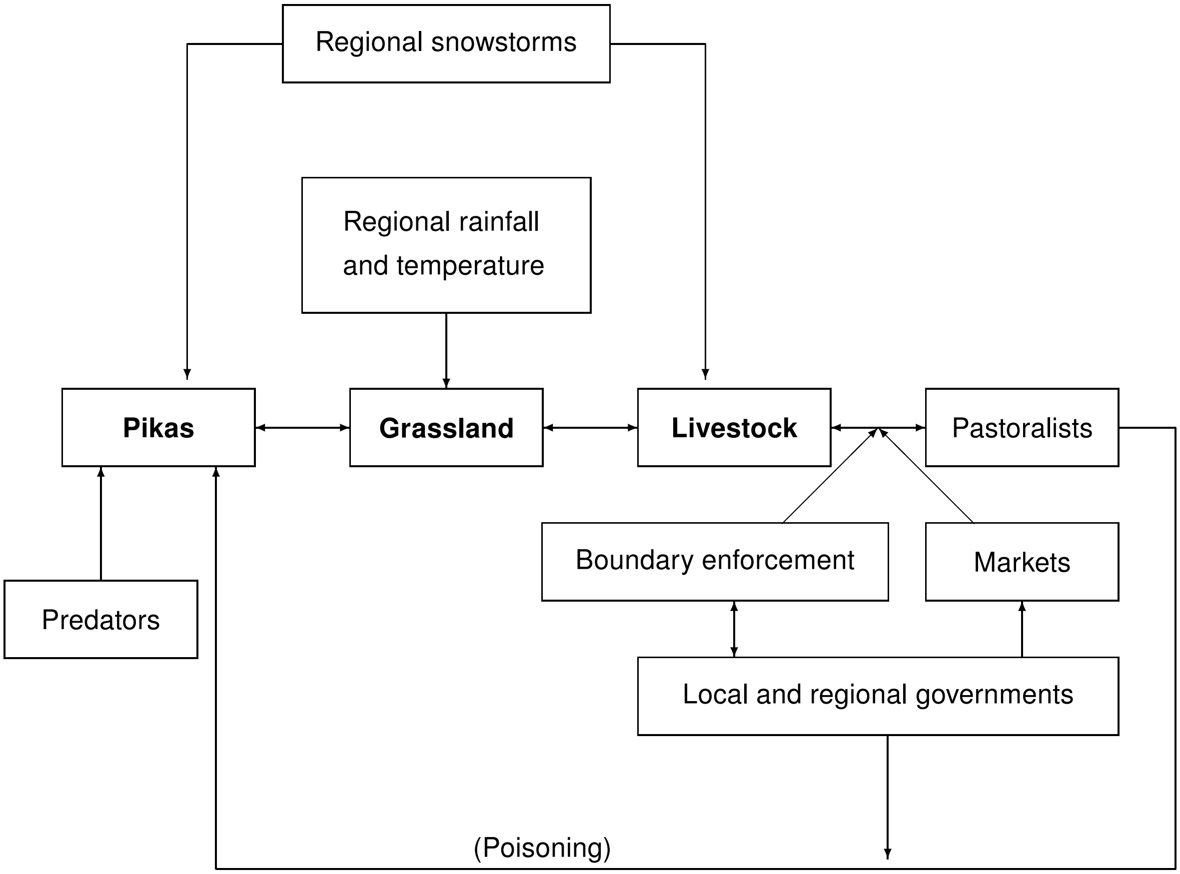


Fig. 1: A conceptual model of the pika-livestock-human social-ecological system on the Tibetan plateau. The resource base and resource users of a simplified conceptual model are shown in bold.

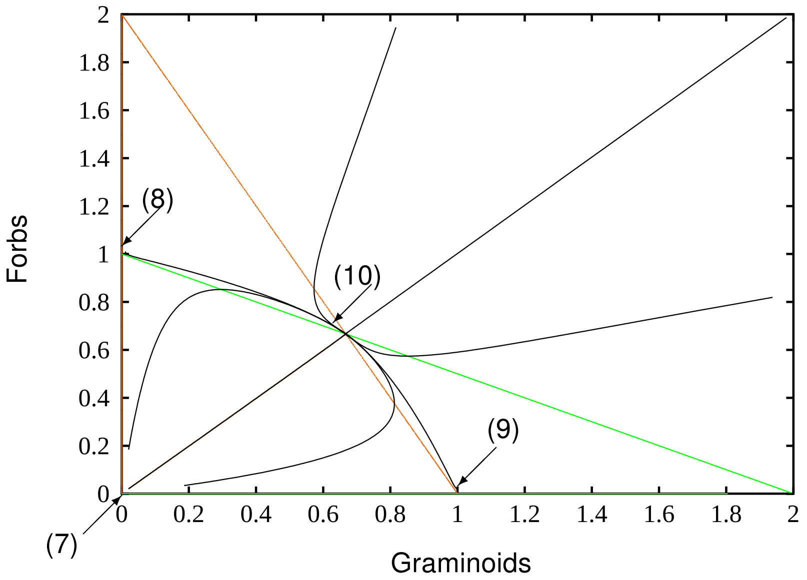
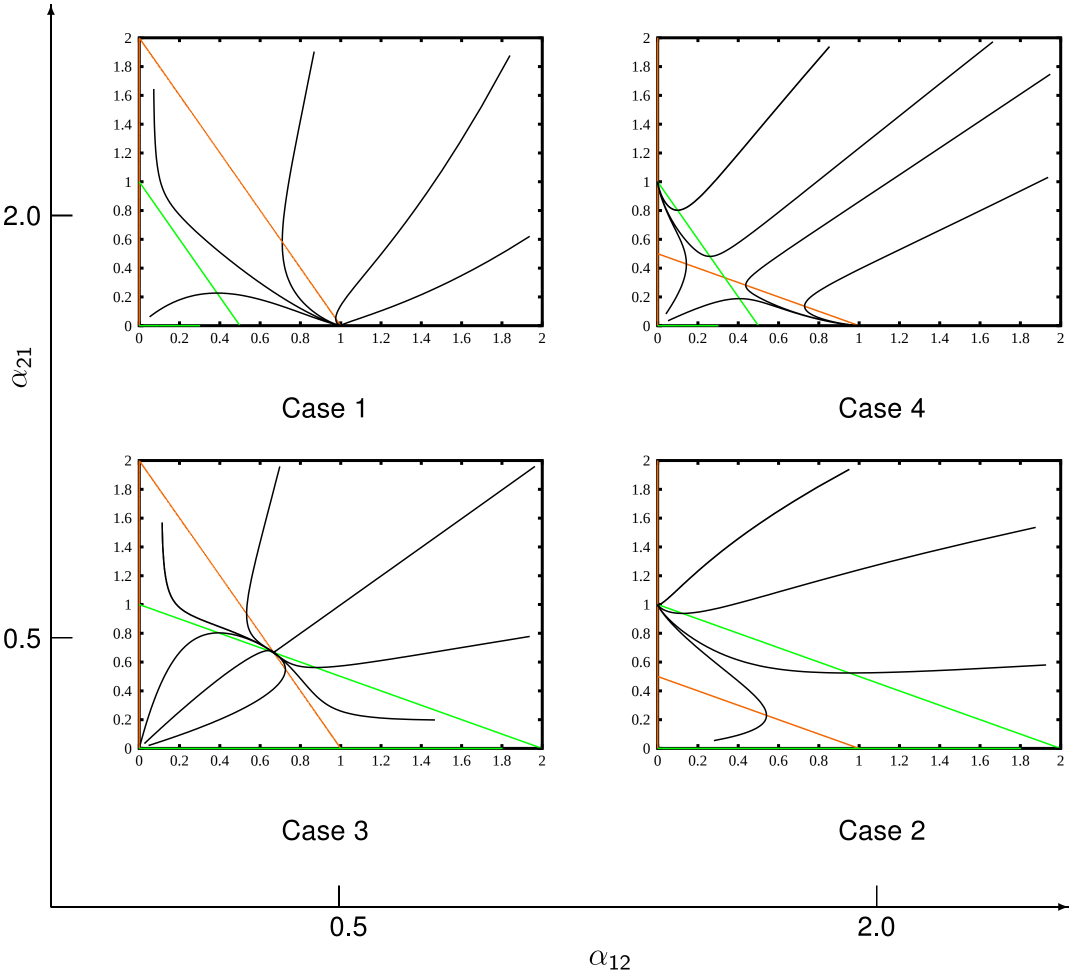


Fig. 2: Sample phase-plane diagram of graminoid and forb biomass. Potential stable points are labeled after equations (7), (8), (9), and (10). In this particular diagram, only points (7) and (10) are stable.



Case 1

Case 4

Case 3

Case 2

Fig. 3: Cases 1 - 4 of the standard Lotka-Volterra competition equations. In case 1 $\alpha_{12} = 0.5$ and $\alpha_{21} = 2$ and (9) is stable . In case 2 $\alpha_{12} = 2$ and $\alpha_{21} = 0.5$ and (8) is stable. In case 3 $\alpha_{12} = \alpha_{21} = 0.5$ and (10) is stable. In case 4 $\alpha_{12} = \alpha_{21} = 2$ and either (8) or (9) is stable, depending on initial conditions. Red and green lines represent forb and graminoid nullclines, respectively.

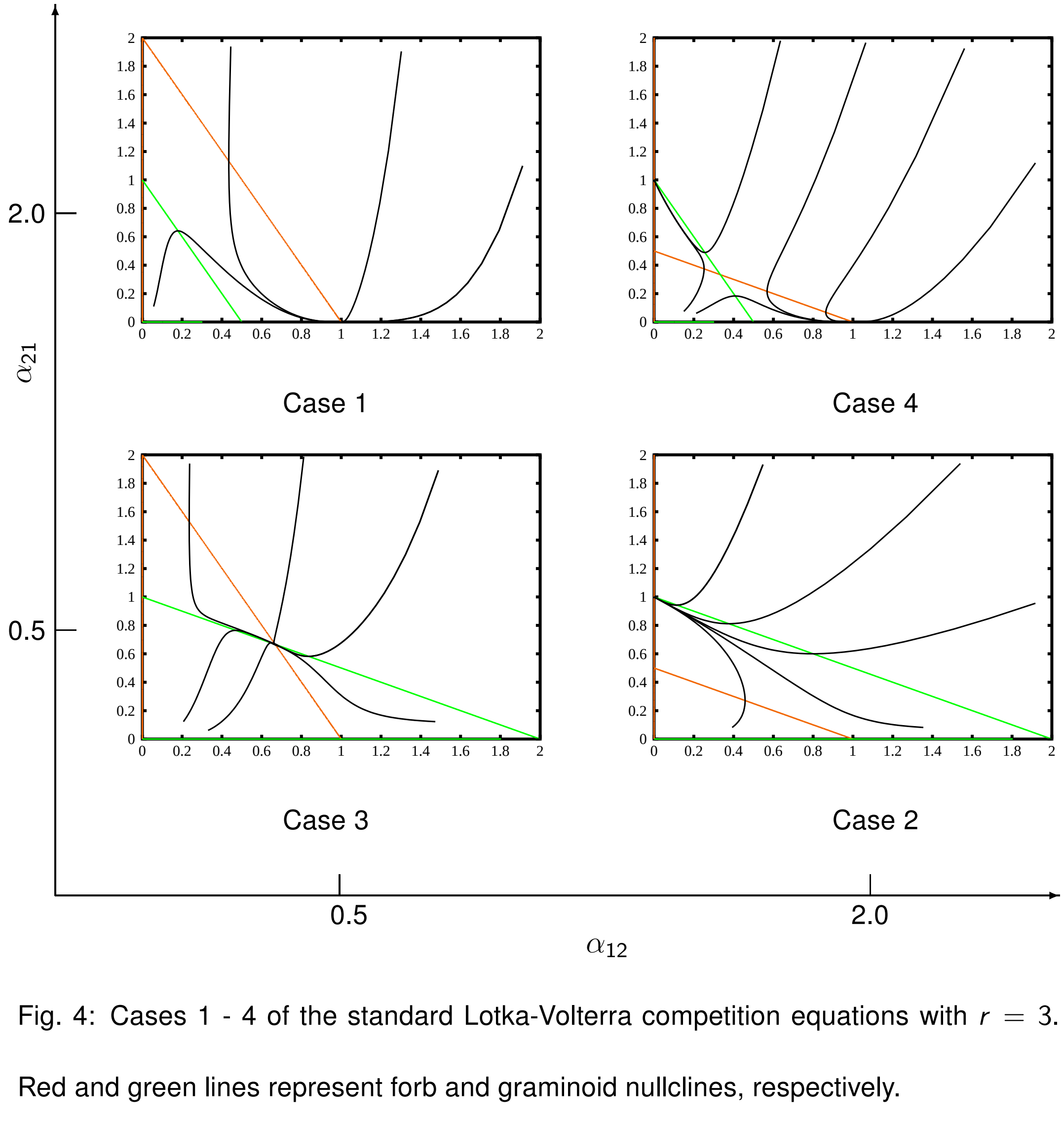


Fig. 4: Cases 1 - 4 of the standard Lotka-Volterra competition equations with $r = 3$. Red and green lines represent forb and graminoid nullclines, respectively.

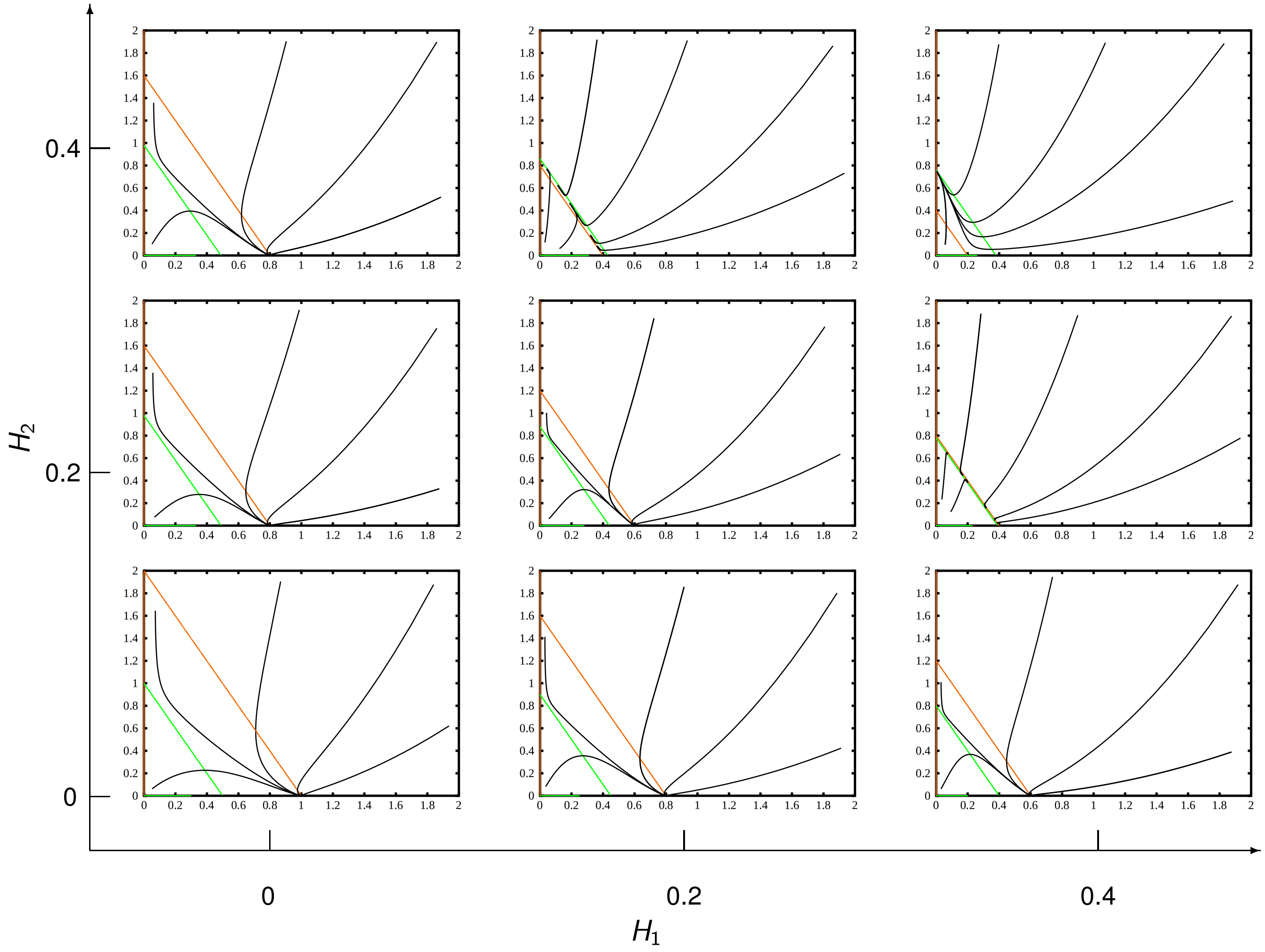


Fig. 5: Case 1 of the competition equations where $\alpha_{12} = 0.5$ and $\alpha_{21} = 2$. Red and green lines represent forb and graminoid nullclines, respectively. At low levels of herbivory (9) is stable, but at high levels of herbivory, (8) becomes stable.

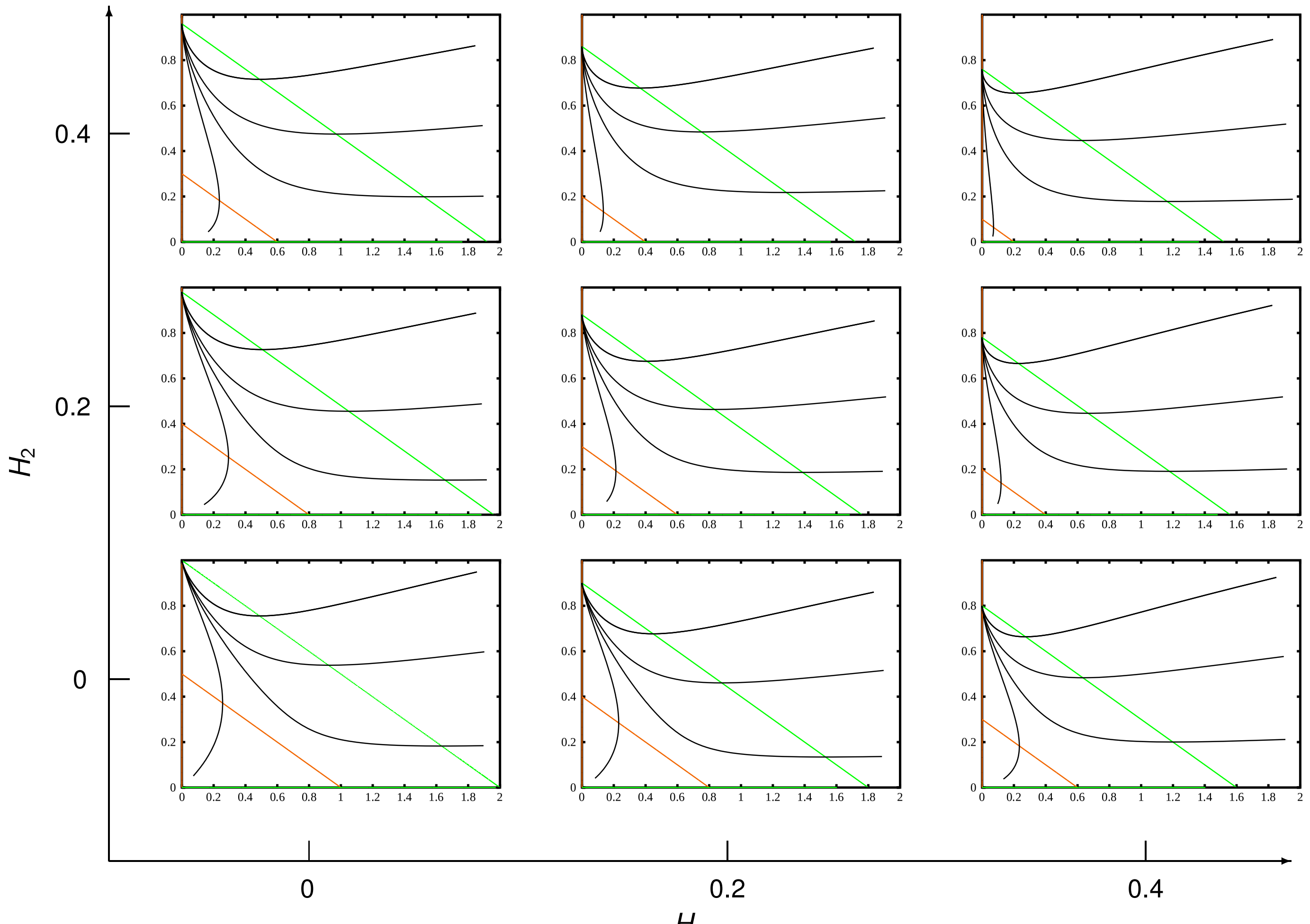


Fig. 6: Case 2 of the competition equations where $\alpha_{12} = 2$ and $\alpha_{21} = 0.5$. Red and green lines represent forb and graminoid nullclines, respectively. In this diagram only (8) is stable.

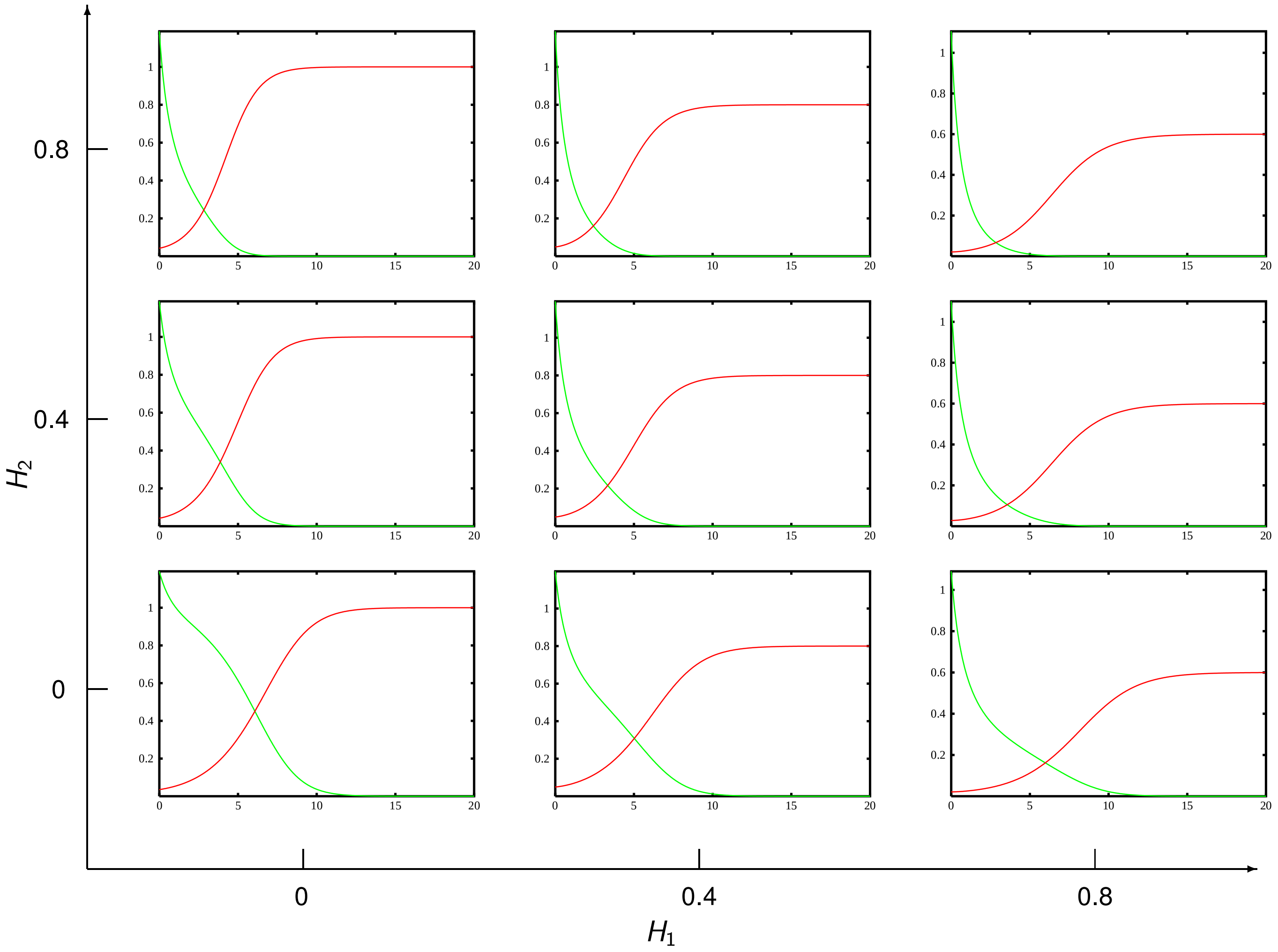


Fig. 7: Plot of P_1 (green) and P_2 (red) versus time for case 2 of the competition equations where $\alpha_{12} = 2$ and $\alpha_{21} = 0.5$.

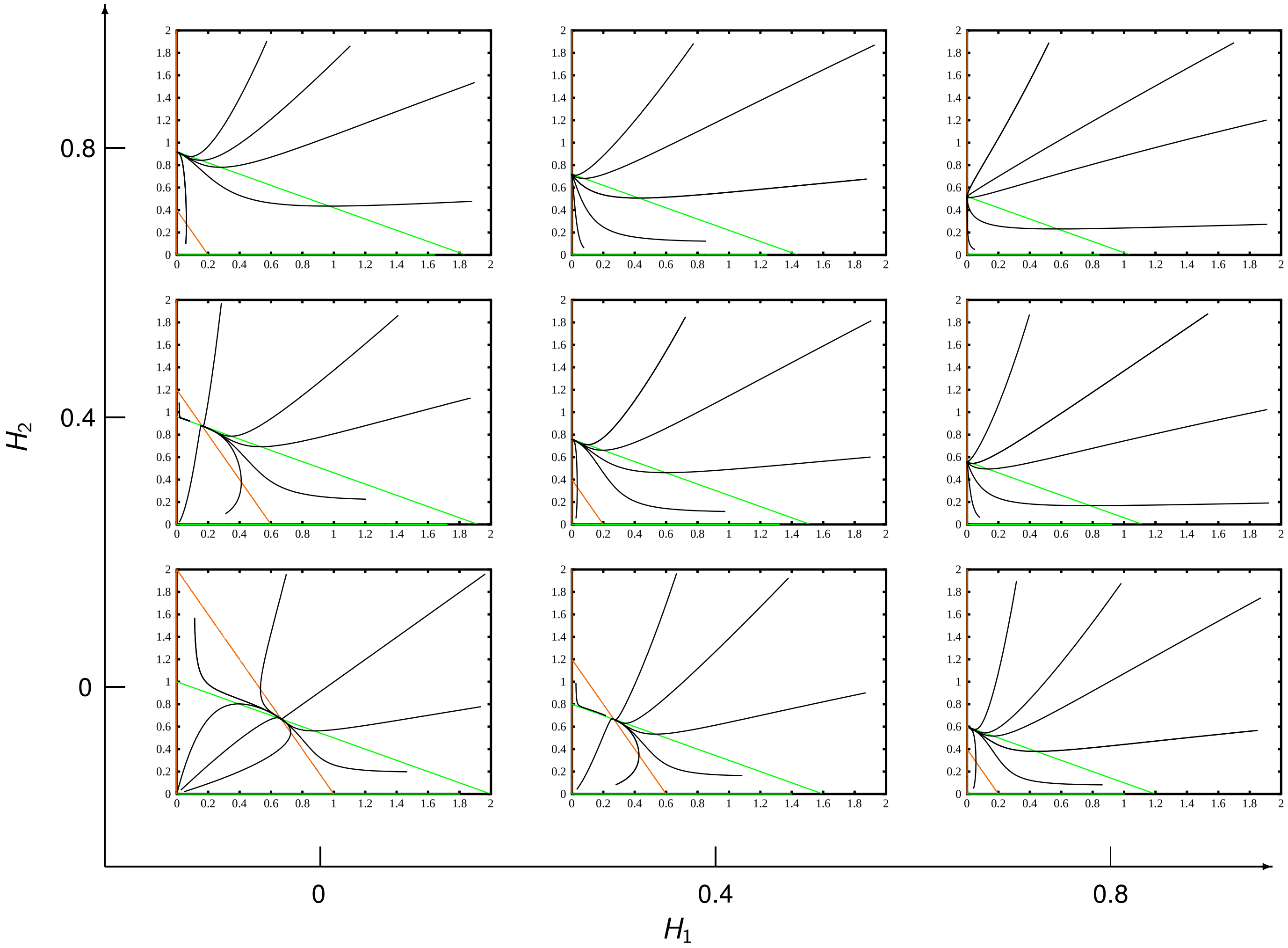


Fig. 8: Case 3 of the competition equations where $\alpha_{12} = \alpha_{21} = 0.5$. Red and green lines represent forb and graminoid nullclines, respectively. In this diagram (10) is stable at low levels of herbivory, and (9) is stable as herbivory increases.

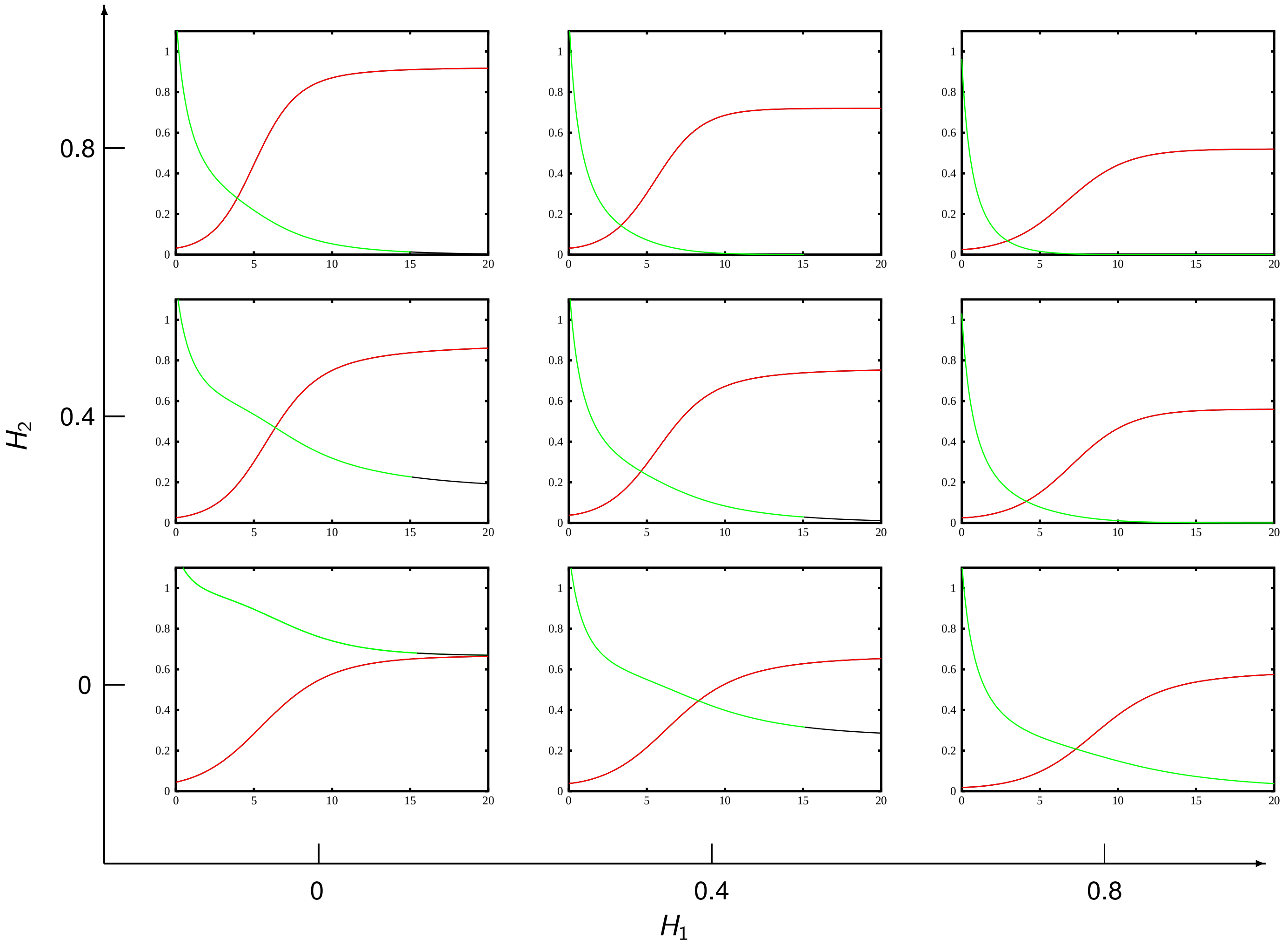


Fig. 9: Plot of P_1 (green) and P_2 (red) versus time for case 3 of the competition equations where $\alpha_{12} = 0.5$ and $\alpha_{21} = 0.5$.

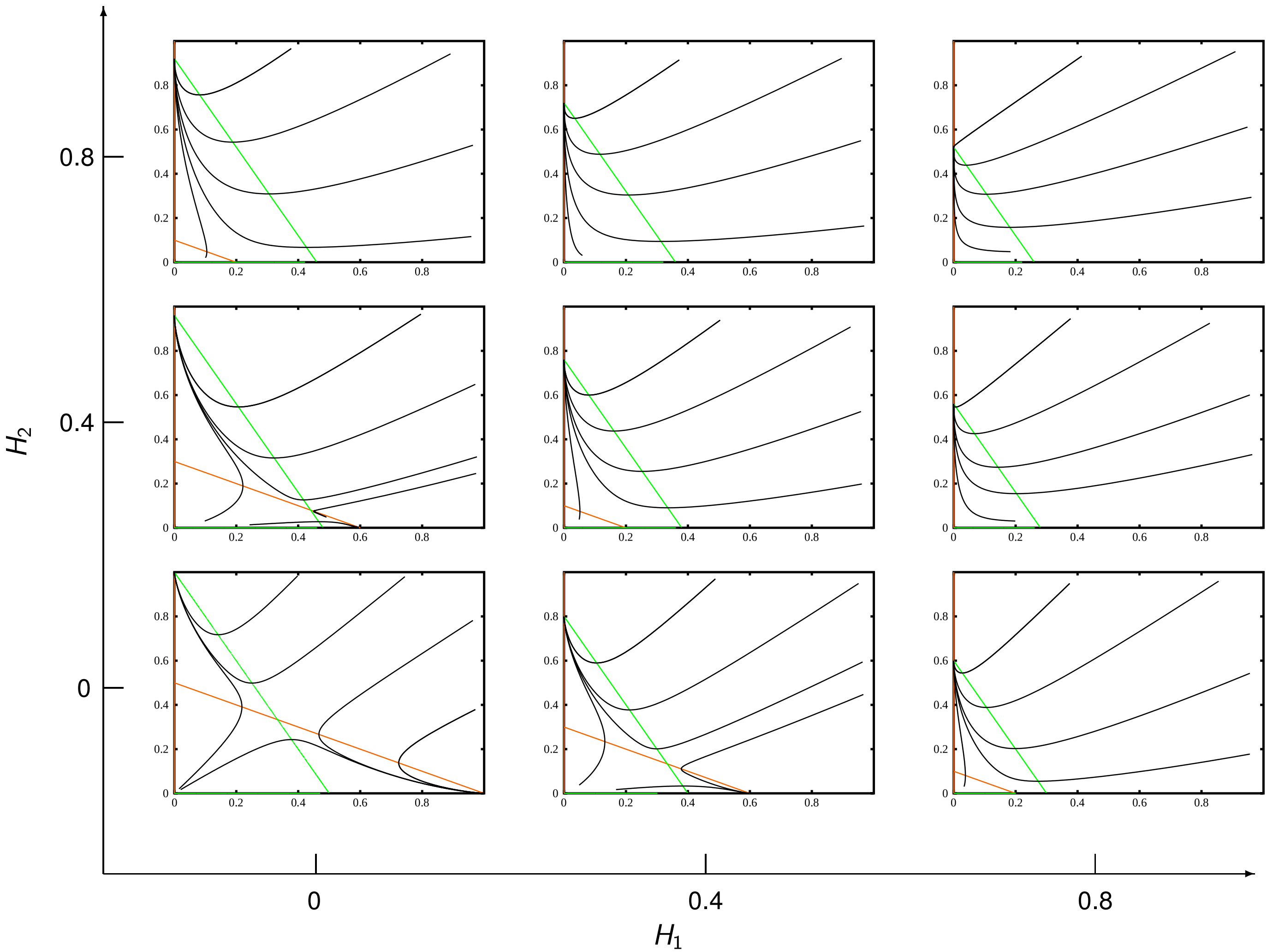


Fig. 10: Case 4 of the competition equations where $\alpha_{12} = \alpha_{21} = 2$. Red and green lines represent forb and graminoid nullclines, respectively. In this diagram both (8) and (9) are stable.

CHAPTER 5
Plateau pikas influence plant species diversity

INTRODUCTION

The concept of natural disturbance has been a topic of much discussion in community ecology. The exact nature of disturbance, along with description of its mechanisms and importance to diversity, has undergone radical change since disturbance was first defined by Cooper (Cooper 1926, Odum 1969) as “abrupt changes due to external causes.” These early treatments of disturbance as a large-scale disruption to community succession (White 1979) did not account for the wide variation in disturbance intensity and source (Connell 1978), nor did they acknowledge that ecological communities rarely exist in an equilibrium state (Sousa 1984). Current views recognize that ecological communities are both temporally dynamic and spatially heterogeneous (White 1979). Natural disturbance is an integral part of this system; and biotic disturbance, in particular, is seen as an endogenous ecological process (Huston 1979).

As perspectives on the nature of disturbance changed, so did descriptions of its mechanisms. Disturbance was promoted from a disruptive force to a mechanism of species maintenance (Grime 1973). The ideas of species maintenance and subsequent diversity rely strongly on coexistence mechanisms. In its simplest terms, species coexistence places two species of a similar trophic level within the same habitat (Gause 1934, Hardin 1960). If these species share similar resources, coexistence must overcome the diversity-depleting process of competition, in which a competitively superior species displaces the competitively inferior one (Shmida and Ellner 1984). One solution to this problem in nonequilibrium communities is niche differentiation, wherein each species specializes on a subset of the resources (Nicholson 1933, Odum

1969). Another solution concerns the dynamics of natural disturbance. Initially, these dynamics were described in terms of the trade-off between competitive ability and tolerance to disturbance (Grime 1973). Under the presence of moderate disturbance, the competitively inferior species may have an advantage. In this view, disturbance prevented the competitively superior species from dominating the community, and consequently encouraged species coexistence and diversity (Grime 1973, Horn 1975). Thus, a pattern of greater species diversity is expected under intermediate levels of disturbance (Roxburgh et al. 2004). This mechanism, and its corresponding prediction (Connell 1978), came to be known as the intermediate disturbance hypothesis (IDH) (1997). More recently, Chesson and Huntly (Pickett and White 1985) suggested revision of the IDH mechanism. They proposed IDH (their "successional mosaic hypothesis") maintains diversity not through suppression of a dominant species, but by generating environmental variation. Environmental variation is created through spatial patchiness (Roxburgh et al. 2004) and temporal variability, either working alone or together (Chesson and Huntly 1997). Thus, the major contribution of disturbance is the generation of novel microhabitats (White 1979). I use this framework to examine disturbance effects in alpine grasslands, specifically alpine meadows on the Tibetan plateau.

An important source of natural disturbance in grasslands is biotic disturbance by burrowing animals (Ahlbrandt et al. 1978). The topic of bioturbation as the "churning and stirring of sediment by organisms" (Ehrenberg 1954) has a long history. In marine biology and paleontology, bioturbation developed under the broad topic of *lebensspuren*, or traces of life (Frey 1973), which applied to both fossil and extant animals (Darwin 1881). In spite of initial attention (Meysman et al. 2006), the subject developed much more slowly in the terrestrial literature (Grinnell 1923, Jacot 1940, Thorp 1949, Hole 1981). Early works highlighted the role of burrowing animals in soil formation, and the equal consideration of their activities with those of plants (Naylor et al. 2002). The field is now well-developed (Kinlaw 1999, Whitford and Kay 1999) with numerous reviews on soil disturbance covering taxa from microbes to vertebrates in environments marine and terrestrial Table 5.1. Recent reviews focus on a subset of these organisms in particular habitats, such as arid (Zhang and Liu 2002, Hall and Lamont 2003) or alpine environments (Jones et al. 1994) (Table 5.2).

Bioturbation is often cited as a classic example of ecosystem engineering (Aho et al. 1998, Reichman and Seabloom 2002, Wright et al. 2002, Murdoch et al. 2009), especially in reference to mammals (Seabloom and Richards 2003). Extensive work has been done on North American pocket gophers (Miller et al. 2007) and prairie dogs (Abaturov 1972), as well as small mammals in Russia (1949). One animal which has not drawn equal attention as a biotic engineer is the plateau pika, *Ochotona curzoniae* (however, see an early reference in Thorp (Lai and Smith 2003, Smith and Lai 2005)). While the importance of plateau pika burrows to the animal community has lead to their label as an ecosystem engineer (Smith and Foggin 1999) and keystone species (Smith and Xie 2008), less work has focused on their importance in structuring the local plant community. As the most abundant small mammal on the Tibetan plateau (Schaller 1998), plateau pikas (hereafter, pikas) are transformative agents of the local community. Here, I examine the role that pika bioturbation plays in alpine meadow plant communities. Based on evidence from prairie dogs (Table 5.3), I hypothesized that pika burrowing generates novel microhabitat. Specifically, I predicted to find to increased plant species richness, diversity and composition in pika disturbed areas.

MATERIALS AND METHODS

Study Site

The Tibetan plateau is the world's largest low-latitude alpine region (Hu and Zhang 2004) and contains 40% of China's grasslands (Smith and Xie 2008). Plateau pikas are common in open grasslands (alpine meadow, meadow-steppe and desert-steppe) from 3000 to 5000 m (Smith et al. 1990). Where they are not poisoned, colonies have been reported to reach 380 individuals/ha (Kaiser et al. 2008). Alpine sedge meadows are dominated by low-growing *Kobresia* plants whose roots intertwine to form characteristic sod mats. Anthropogenic livestock grazing is closely associated with the development of these *Kobresia*-mats, some of which date back as far as 2000 years (Long et al. 1999). Thus, the breakup of these tightly-knit mats by burrowing animals may have important consequences on the plant community structure.

My research focused on the eastern Tibetan plateau, in Qinghai Province, People's Republic of China. I identified four distinct pika colonies (on-colony sites) approximately 3 km apart in unfenced *Kobresia*-sedge meadows between 3300 to 3800 m in elevation near Dawu Township (34º24'03" N, 100º21'38" E) in Golog County. These meadows also functioned as winter pasture for livestock (yak and sheep). Due to the high density of pikas in this area, I was only able to identify one nearby meadow without pikas to act as a control location (off-colony site). I chose the closest pika colony to function as a "treatment" (on-colony site). Vegetation was surveyed by placing small quadrats at 10 randomly-selected points along a 100 m transect (see below).

Data collection from June to early August in 2005 and 2006 was timed to coincide with the growing period (late May to mid-September). Biomass peaks in July for sedges and September for grasses (Liu et al. 2010b). Annual precipitation at this site is 420 – 560 mm (Dong et al. 2004b), most of which falls as rain from May to September (Dong et al. 2004b). Annual temperature ranges from -32 ºC to 25 ºC (Liu et al. 2010b), but there is no completely frost-free period (Chen et al. 2008).

Vegetation sampling

Due to the high abundance of species on these alpine meadows (Dohman 1968, van der Maarel and Titlyanova 1989, Kull and Zobel 1991), and overall low height of vegetation (< 5 cm), I used small nested quadrats (0.25 m^2) for plant surveys. This procedure is similar to that used in high small-scale diversity meadows in Europe (Stohlgren et al. 1999). Quadrats were surveyed for plant species identity, percent cover, percent bare ground, and average height of grasses and sedges. Photographs and vouchers of unknown plant specimens were taken to the Northwest Plateau Institute of Biology, Academia Sinica, for identification (Table D-1).

I used a nested quadrat design to collect data on incidence (presence-absence) as well as abundance (counts of individuals). Abundance data is notoriously difficult to collect in rhizomatous plant communities where individuals cannot be easily distinguished. To address this difficulty, each 0.25 m^2 quadrat was itself divided into 25 smaller 10-cm^2 sub-quadrats that were randomly sampled. I used frequency of occurrence of species in 11 evenly-spaced sub-quadrats as an approximate value for species abundance. While not a true abundance count, it does allow for equal comparison between communities.

Thus, each 0.25 m^2 quadrat contains the combined information from 11 10 cm x 10 cm sub-quadrats.

Placement of the quadrats at each site (on-colony and off-colony) followed a stratified random sampling design to account for any underlying environmental gradients. At each site, 10 randomly-selected points were identified along a 100 m transect for sampling within quadrats. However, the number of quadrats at each sampling point varied slightly with site type. Here, pika activity is considered as a treatment effect. At the on-colony site, I surveyed three quadrats at each of the 10 sampling points – one quadrat over disturbed ground adjacent to a pika burrow (treatment), a second quadrat at least 1 m from a pika burrow (control A), and a third quadrat also on undisturbed ground (control B). Every effort was made to center the “treatment” quadrat over soil excavated from a pika burrow, but this was not always possible to establish precisely, as older mounds tended to blend in to the surrounding meadow. The presence of a second control, or “third plot,” is necessary for clear evaluation of spatial heterogeneity (reviewed in Gotelli and Colwell 2001). I repeated the same procedure at the off-colony site, except that I surveyed only two quadrats at each sample point, neither of which fell over an area of pika disturbance. Thus, a total of 20 and 30 quadrats were sampled at each off-colony and on-colony site, respectively. Although the number of quadrats sampled varied with site type (on or off-colony), only areas of equal size were compared for data analysis (see below).

These quadrats can be considered as representing patch types in the local landscape – ground disturbed by pikas within the pika colony, undisturbed ground within the pika colony or undisturbed ground outside of the pika colony.

Comparisons were made between (1) a patch disturbed by pikas and a control patch within the pika colony, as an indicator of the within-colony treatment effect; (2) two control patches within the pika colony, as an indicator of within-colony background variation; (3) two patches at the control site, as an indicator of between-colony background variation; and (4) the combined patches from the on-colony site with those at the off-colony site, as an indicator of the between-colony treatment effect. As a result of this research design, I was able to draw conclusions on the impacts of pikas in two distinct spatial scales: first, the within-colony, or patch scale, where I intensively sampled quadrats both on and off an area of pika disturbance; and second, the between-colony scale, where effects of an entire pika colony site on the local landscape could be interpreted.

Data analysis

Multiple methods have been developed for describing species differences in various communities. These methods can be loosely grouped into descriptions of species richness (reviewed in Washington 1984), species diversity (reviewed in Koleff et al. 2003, Cardoso et al. 2009) and community similarity (Gotelli and Colwell 2001). At its most basic level, species richness can be defined as the total number of species in an area. In spite of this apparent simplicity, comparing richness between communities is fraught with difficulty (Gotelli and Colwell 2001). Some of these issues include differences in species density, unequal sampling effort, and insufficient sample size (Magurran 2004).

One method to measure richness in samples is to compare the shapes of species accumulation curves, which plot the cumulative number of species encountered during data collection (Gotelli and Colwell 2001). Because data were from non-contiguous quadrats, my results produced sample-based curves

(Gotelli and Colwell 2001). However, in their raw state, these curves actually represent sampling effort or density, rather than species richness (Magurran 2004). Rarefaction curves account for uneven sampling effort by plotting the expected number of species drawn from the total pool (Colwell 2006). I created smoothed accumulation and rarefaction curves using Monte Carlo sampling in the program EstimateS, version 8.0 (2001). I used sampling without replacement so that all samples would be included in each randomization and the final value would match the total number of observed species. To make suitable species richness comparisons, I rescaled the x-axis on these curves from samples to individuals using the average number of individuals per sample, as described in Gotelli and Colwell (Colwell 2006).

Total community richness can be calculated from observed species (S_{obs}) or by richness estimators. For generating richness estimators I sampled with replacement so that the variance could be meaningfully compared at the right side of the species accumulation curves between samples (Colwell 2006). As a result, these values may underestimate total species richness in the community (Walther and Moore 2005). Although S_{obs} has been shown to perform the worst of all estimators, there is no consensus on the “best” estimator for all situations or taxonomic groups (Magurran 2004). I used non-parametric estimators because they are potentially the most powerful (Walther and Moore 2005). Specifically, I chose Jack1, Jack2, and Chao2 based on their overall performance in plant taxa and randomized species accumulation curves (Magurran 2004). Variance could be compared with 95% confidence intervals only for Chao2. For comparison with other studies, I also report S_{obs} and its estimator, Mao Tau.

Although richness is informative, it does not account for all aspects of species heterogeneity. For example, two communities (e.g., community A and B) can have an equal number of individuals (e.g., 20) and species (e.g., two), yet differ in those species' relative abundances (e.g., community A has 10 individuals each species, while community B has 19 individuals of one and a single individual of the other species). Here, community A has an even distribution of species, while community B is dominated by a single species. Evenness measures the degree of similarity in species abundances between communities (Washington 1984, Mendes et al. 2008). Richness and evenness are often combined into a single measure, called a diversity index. Like richness estimators, there is no consensus on which diversity index functions best, although multiple reviews have assessed their relative merits (Washington 1984). I calculated two common indices that estimate the population diversity from multiple samples (Simpson 1949), Shannon's H diversity and Simpson's reciprocal D. Simpson's Index (Gini 1912), also called the Gini-Simpson Index (Washington 1984), is considered one of the best diversity indices (Washington 1984, Mendes et al. 2008) when used in it's reciprocal form (1/D). However, it is also criticized for its overemphasis of dominance over richness (Shannon 1949). The Shannon Index (Wiener 1948), or Shannon-Wiener Index (Mendes et al. 2008), on the other hand, considers richness and dominance equally (Washington 1984). Although not as biologically relevant (Magurran 2004), it is commonly used in the literature. I calculated diversity values for each quadrat and tested for effect of patch type using a one-way ANOVA for correlated samples, followed by Tukey's Honestly Significant Difference test (HSD) for differences between means. Aside from incorporating evenness into a diversity measure, I also directly evaluated trends in relative species abundance. Absolute abundances of identical plant species were compared graphically, while relative abundances over patch-types were used for statistical analyses with a Kolmogorov-Smirnov two sample test (Koleff et al. 2003, Cardoso et al. 2009).

The above measures all reflect alpha diversity, or diversity within a patch. The diversity between patches, or beta diversity, is a measure of the species turnover in the community. I took two approaches to measuring beta diversity. First, I determined classic similarity indices from pair-wise comparisons based on community similarity (1912). Specifically, I used classic Jaccard (1948) and Sørensen (Cardoso et al. 2009) similarity indices, both of which are commonly used, though Jaccard may be more robust to undersampling than Sørensen (Magurran 2004). The effect of pika disturbance by patch type was tested using a one-way ANOVA for correlated samples as described above. Secondly, I evaluated beta diversity by exploring changes to grain (patch) size. Initially, grain size was equal to the quadrat dimensions used for sampling. To increase grain size but keep spatial extent constant, I used combinations of two control patches or a control and burrow patch to recalculate species richness and diversity. I compared measures from these large-patches (colony scale) to the original patches (patch scale) to make inferences about species heterogeneity.

RESULTS

Species richness

On the pika colony, mean observed species richness differed significantly between patches at the colony scale (mean ± SE: control A=25.6±1.7, control B=25.7±1.8, burrow=18.4±2.5; one-way ANOVA for correlated samples: F=5.69, P<0.05). These differences can be attributed to the lower species richness on burrow patches (Tukey's HSD: H=6.35, $P<0.05$); the control patches were not significantly different from each other. Likewise, control patches from the off-colony site were not significantly different (mean ± SE: control A=8.9±1.0, control B=9.1±1.4; one-way-ANOVA for correlated samples: F=0.2, P=0.665). Variance on the burrow patches was approximately twice that of control patches on the pika colony (control A=28.3, control B=30.5, burrow=60.0). In sub-samples (10cm x 10cm) on the pika colony, species richness averaged 12.4±0.2 and 11.8±0.3 in controls patches and 5.8±0.4 in burrow patches (mean± standard error). These sub-samples ranged from completely bare soil (no species) to a maximum of 23 species. Control patches from the off-colony site had 10.9±0.2 and 10.8±0.2 species per $0.01m^2$ on average.

Species-area curves reflected trends similar to observed averages on the pika colony (Figure 5.1.). The accumulation of species over burrow patches was lower than over either control patch (Figure 5.1., patterned versus solid gray lines). When compared to off-colony control patches, species accumulation over on-colony patches was greater (Figure 5.1., gray versus black lines). On the other hand, rarefaction curves on the pika colony, which had been re-scaled to individuals, showed different trends (Figure 5.3). Rarefaction curves of burrow and control patches were not significantly different (Figure 5.3, patterned versus solid gray lines), and curves did not differ between the colony and off-colony site (Figure 5.3, gray versus black lines).

When considered at a larger grain size, different patterns emerged. The average species richness over combined controls on the pika colony was not significantly different from controls paired with burrow patches (one-way ANOVA for correlated samples: F=0.3, P=0.745). A species-area curve for combined burrow and control patches was distinctly higher than the combined controls at the off-colony site (Figure 5.2, gray versus black lines). Rarefaction curves re-scaled to individuals showed the same trend. Combined patches for the pika colony were significantly greater in richness than the off-colony site (95% confidence intervals on multiple runs, $P<0.05$; Figure 5.4, black versus gray lines).

Species Diversity

Mean species diversity in terms of Shannon's H and Simpson's D differed significantly between patch types within the pika colony (H: one-way ANOVA for correlated samples, $F=4.69$, $P<0.005$; D: one-way ANOVA for correlated samples, $F=7.35$, $P<0.005$). For both indices the diversity over burrow patches was significantly lower than control patches (Tukey's HSD; Figure 5.5, Figure 5.6). Diversity was not significantly different between control patches within the pika colony or at a nearby off-colony. Shannon diversity was significantly higher over the off-colony patches compared to the on-colony burrow patch.

When species diversity was considered at the next grain size, the trends reversed. Shannon diversity was significantly higher for combined patches on the pika colony compared to the off-colony site (one-way ANOVA for correlated samples, $F=4.81$, $P<0.01$). Differences between patch groupings within the pika colony were not significant (Tukey's HSD). Values for Simpson diversity were also lower over the off-colony site at this grain size, but not significantly so (Tukey's HSD).

Community Similarity

Similarity as measured by Jaccard's and Sørensen's index detected significant differences between patch types on the pika colony (one-way ANOVA for three correlated samples, Jaccard: $F = 26$, $P<0.0001$, Sørensen: $F= 13.7$, P=0.00024). For both measures, control patches were more similar to each other (mean ± SE: Jaccard= 61.8±1.9, Sørensen= 73.9±8.5) than either was to the burrow patch (mean ± SE: Jaccard= 40.1±4.8 and 43.8±4.8, Sørensen= 55.5±5.5 and 59.4±4.8). Post-hoc tests revealed that, for both measures, the control patches A and B were significantly more similar than controls compared to burrow patches (Tukey HSD, p<0.01). The same tests showed that similarity between control A patches and burrow patches was not significantly different from the similarity between control B patches and burrow patches (Figure 5.7).

A rank-abundance chart shows similar abundances for identical species in control patches within a pika community (Figure 5.8b). Burrow patches had lower species abundances, and these abundances had fewer similarities with control patches (Figure 5.8a). The largest differences in abundance were apparent for identical species over combined on-colony and off-colony patches (Figure 5.8c). Relative abundance was significantly different between control and burrow patches on the pika colony (Kolmogorov-Smirnov two sample test; Control A: K-S=245.2, P<0.05; Control B: K-S= 267.8, P<0.05). However, control patches A and B were not significantly different in terms of relative abundance (Kolmogorov-Smirnov two sample test, K-S=143.3, P>0.05). Likewise, control patches A and B at the off-colony site were not significantly different (Kolmogorov-Smirnov two sample test, K-S=36.8, P>0.05). A Whittaker, or rank/abundance plot (Chen et al. 2008), showed higher relative abundance of plant species over the pika colony (Figure 5.9).

DISCUSSION

Species richness was among the highest in the world for very small spatial scales (Table 5.4). I recorded a maximum of 23 different species in a

10cm x 10cm area. These richness values are in line with averages reported from alpine pasture in northeastern Qinghai (15.5–19.7 species per 0.01 m^2, Chen et al. (2008)). Other small-scale high-richness regions have been reported in European grasslands with calcareous soils (Myers and Harms 2009), longleaf pine savannas in Louisiana (Lamont et al. 1977) and Australian sand heaths (2001).

Although pika disturbance was predicted to increase plant species richness, my results did not match this expectation across all spatial scales. At the patch scale (0.25 m^2), I found significantly lower richness over disturbed patches compared to control patches within the pika colony. Yet, when richness at the same scale was plotted by individuals, rather than area, the differences in richness were no longer significant. These contradictory outcomes are most likely due to uneven species density between patch types. Density reflects the number of individuals in an area, rather than the number of species. As pointed out by Gotelli and Colwell (Mendes et al. 2008), variation in density can confound measurement of species richness. In areas of higher density more individuals are present, which increases the probability that more types of species will be found. Such a situation could easily arise under conditions of periodic natural disturbance, such as pika bioturbation. Near a pika burrow, excavated soil is constantly pushed to the surface where it smothers vegetation. Therefore, fewer individual plants will be present near pika burrows. Comparing total or average richness over different samples or areas reflects this density more than richness. A valid comparison of richness assumes equal densities and even distribution of species between patches. Because the rarefaction curves re-scale the x-axis from samples to individuals, these curves are often more informative than total richness or average richness measures. Therefore, differences in richness between patch types were probably a spurious consequence of uneven species abundances. On the other hand, more confidence can be placed in differences in richness at the combined patch or colony scale. Here, pika colony patches had significantly more species than off-colony sites. This outcome was the same even when the data were scaled to individuals using the rarefaction method.

Even if patches do not significantly differ in species richness, the question remains whether these communities are equally rich, yet different in composition. Species diversity incorporates information on richness as well as evenness in species distribution. Within the pika colony, I found significantly higher diversity over control patches than burrow patches. This result cannot be attributed to naturally high levels of patchiness, as diversity between control patches was not significantly different. This result adds further evidence that communities directly over burrow patches differ in composition from nearby patches.

If the control and burrow patches contained identical plant communities, then considering these two patches together (the colony scale) would yield identical results. That is, though the number of individuals has increased, their combined richness would be equal to their individual richness. However, this is not the case. At the colony scale, diversity over disturbed regions was higher than equally-sized control regions. Shannon diversity at this spatial extent was significantly greater over pika colony patches than off-colony patches.

The Shannon-Weiner (H) diversity index considers richness and dominance equally (Jost 2006). It is technically a measure of uncertainty in the identity of a sample; higher values indicate less certainty due to increased possibilities (Mendes et al. 2008). Unlike Shannon-Weiner, Simpson's index (1/D) places more weight on species dominance than richness (Koleff et al. 2003). Differences in diversity as measured by Simpson's reciprocal index were not as consistent as Shannon's. This result suggests that differences in diversity may be due more to variation in species identity than species evenness. Alternatively, large differences in evenness between colony and off-colony may mask differences in species identity.

Both Jaccard and Sørensen are classic measures of continuity that reflect species turnover, or beta diversity, within a community (Shi 1983, Bian et al. 1994). Significantly higher values indicate a more similar community between control patches than between control and burrow patches. The relative abundance of plant species differed significantly between control and burrow patches. The high beta diversity cannot be attributed to background turnover in the landscape, as the turnover of control patches was not significantly different. Although pika bioturbation increased bare patches on the colony, the overall abundance of plants at this site was higher than the off-colony site. While having lower diversity than adjacent control patches, burrow patches were still significantly richer than off-colony control patches.

Another possible explanation for increased overall richness is that pikas preferentially inhabit regions of higher plant diversity. Under this scenario, the plant community (in terms of its richness, diversity or composition) is not a result of pika bioturbation action, but a consequence of habitat choice. I will refer to these two alternatives as the "habitat choice" and "bioturbation action" models. In support of the first model, plateau pikas are known to exhibit habitat selection preferences. For example, pikas are known to inhabit areas of lower plant height, which are typically regions of higher livestock grazing (2001). This effect possibility cannot be conclusively ruled-out without experimental tests. Ideally, this would involve replicates of grazing exclosures, controlling for pika and livestock abundance.

Without these results, we can only speculate whether pikas are causal factors of species differences. However, I have several reasons to believe these results may reflect a causal, rather than correlative, relationship. First, under the habitat choice scenario, dispersing individuals would preferentially establish burrows in species-rich regions. However, the addition of disturbance alone necessarily decreases species abundance. Therefore, if pika bioturbation does not contribute to diversity (as it would not in a purely a habitat-choice model), over time these regions should have *lower* diversity than nearby uninhabited areas Gotelli and Colwell (2008). This finding was not the case for my results. Although it is possible that species loss under the habitat-choice model would result in regions of equal diversity, the landscape would either have to exist in an unusual high state of patchiness or pika disturbance would have had very little impact for the community to remain more diverse after the addition of disturbance. Second, pikas were found to not only increase diversity, but also increase variability within these patches. This outcome is expected under the bioturbation-action model because disturbance generates novel microhabitats which increase variability. Unless the habitat-choice model includes selection for both diverse as well as spatially variable patches, it will not fulfill this expectation. Finally, only the bioturbation-action model explains differences in species composition. Novel microhabitats could act as refugia for rare species. Under the habitat-choice model, the species-rich region selected by pikas would simply contain more species than a nearby species-poor area. However, these species need not be compositionally different; the species-poor community could merely be a subset of the richer community. Some other explanatory factor would be required to explain compositional differences. It is more likely the off-colony site is the result of poisoning than habitat avoidance by pikas.

Chen et al. (Chen et al. 2008) attribute high plant species richness on Tibetan alpine meadows to two factors: seasonal grazing and plant community structure. Livestock grazing on standing dead biomass during the winter creates gaps and removes plant litter, which facilitates light penetration at the start of the next growing season. These spaces are equally likely to be filled by grazing tolerant or intolerant plants because grazing pressure is absent during the summer. A second process is the overall low height of the plant community (5-20cm, 3.0-3.3g biomass per 0.01 m^2), which reduces competition for light that would result from shading (1940). To these factors, I would like to include natural disturbance as a generator of novel microhabitat. In combination with the above factors, pika bioturbation makes a rich community even richer.

CONCLUSION

When considered together, these results suggest that pika disturbance increases plant species diversity at the local landscape level, but not at the patch scale. However, this does not establish a direct causal relationship between pika activity and species richness. My results clearly support that community differences are correlated with pika bioturbation. The activity of pikas appears to generate novel microhabitats which lead to increased richness in the plant community. These results should be substantiated through experimental tests of the potential causal mechanisms.

Table 5.1. Broad-scale reviews with a focus on terrestrial bioturbation. These articles cover a wide range of taxa, from plant and microbes to invertebrates and vertebrates. Specialized vocabulary used by the authors to refer to soil disturbance is given under "neologisms."

Source	Scope	Examples discussed	Neologisms
Jacot (1949)	Terrestrial invertebrates and vertebrates	mammal (cow, rodent), bird, reptiles, toad, insect, mollusk, nematode, earthworm	geenton
Thorp (1978)	Mainly terrestrial invertebrates and vertebrates	earthworm, ant, termite, crustacean, rodent	
Ahlbrandt et al. (1981)	Terrestrial Invertebrates burrowing on inland sand dunes	sand wasp, camel cricket, crane fly larvae, tiger beetle larvae, ants, termite, wolf spider	bioturbation[1]
Hole (1987)	Mainly terrestrial vertebrates and invertebrates that affect soil	earthworm, insect, spider, bird, mammals (rodent, elephant, bison)	amphihabitant, exopedonic, endopedonic
Andersen (1988)	Terrestrial fossorial herbivores	rodent, nematode, insect (beetle, fly, cicada, moth and butterfly)	fossorial herbivore, excavator, tunneler
Viles (1991)	Terrestrial micro-organisms, plants, vertebrates and invertebrates		biogeomorphology
Meadows and Meadows (1993)	Terrestrial and aquatic burrowing invertebrates and vertebrates	meiofaua, nematode, insect (beetle, wood-borer, ant), fish, mammal (rabbit, badger, rodent)	bioturbation, fossorial
Hansell (1995)	Nests and burrows of terrestrial arthropods, birds and mammals	spider, wasp, ambrosia beetle, termites, ants, honeybee, bird, mammals (rodent, badger)	
Butler (2002)	Terrestrial vertebrates and invertebrates	mammal, bird, reptile, amphibian	zoogeomorphology
Naylor (2002)	Marine and terrestrial micro-organisms, plants, vertebrates and invertebrates	microfilm, coral reef, lichen, beaver, goose	bioerosion, bioconstruction, bioprotection

Table 5.1 Continued.

Johnson (2003)	Conceptual models of bioturbation	earthworm	biomantle, bioturbation, dynamic denudation, floralturbation, faunalturbation, pedoturbation, pedogeomorphic agent
Gabet et al. (2006)	Terrestrial plants, invertebrates and vertebrates	earthworm, ant, termite, rodent	bioturbation
Meysman et al. (1923)	Marine and terrestrial invertebrates and vertebrates	mammal (rodents, dugong) earthworm, crustacean, stingray	biogenic disturbance, bioturbation, bio-irrigation

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[1] The term "bioturbation" was probably in use before this time

Table 5.2. Reviews focused on terrestrial bioturbation by mammals.

Source	Scope	Examples discussed	Notes
Grinnell (1972)	Burrowing rodents in California	ground squirrel, kangaroo mouse, pocket mouse, kangaroo rat, pocket gopher (*Thomomys* spp.)	animal "workings," such as mounds and burrows
Abaturov (1990)	Small mammals in Russian forest and semi-desert	mole (*Talpia europea*), ground squirrel (*Spermophilus pygmaeus*)	
Reichman and Smith (1999)	Burrowing mammals	rodent (Bathyergidae, Ctenomyidae, Geomyidae, Muridae, Octodontidae), aardvark, pangolin, armadillo, some foxes	fossorial, subterranean
Whitford and Kay (1999)	Mammals in deserts	echidna, rodent (Bathyergidae, Geomyidae, Heteromyidae, Hystricidae, Sciuridae) jackrabbit, fox, badger, aardvark	biopedturbation
Dickman (1999)	Rodents	rodent (Castoridae, Geomyidae, Heteromyidae, Hystricidae, Sciuridae)	allogenic engineering, biotic engineering
Kinlaw (2002)	Vertebrates in arid environments	reptile, gopher tortoise, gecko, wombat, rodent (prairie dog, gerbil, kangaroo-rat)	primary modifier, secondary modifier
Zhang and Liu (2003)	Small mammals in North America and China	rodent (pocket gopher, vole), plateau pika, vole	
Hall and Lamont (2008)	Mammals in alpine areas	*Spermophilus* spp., *Marmota* spp., *Ursus arctos horribilus*, *Bos grunniens*	

Table 5.3. Ecological impacts of bioturbation by prairie dogs.

Impact	Source
Soil mixing, oxygenation and water infiltration	Grinnell 1923, Whicker and Detling 1988, Huntly and Reichman 1994, Kotliar et al. 1999
Plant diversity, turnover	Archer et al. 1987, Coppock et al. 1983a, Whicker and Detling 1988, Stapp 1988, Ceballos et al. 1999, Kotliar et al. 1999, Fahnestock and Detling 2002
Plant growth, forage quality	Aho et al. 1998, Coppock et al. 1983a, Ingham and Detling 1984, Uresk 1985

Table 5.4. Locations of high species diversity reported in the literature. Table is based on Chen et al. (2008) and shows study site (altitude), dominant vegetation type and diversity measures. The altitude of coastal sites was assumed to be at sea level. Abbreviations for countries are CZE, Czech Republic; EST, Estonia; NLD, Netherlands; PRC, China; and SWE, Sweden. S is the size of quadrat in m^2, N is the number of quadrats, and R is mean species richness. Richness is given as an average, a range, and/ or a maximum value (in parenthesis).

Study area	Vegetation type	S	N	R	Source
Dawu, PRC (3300-3800 m)	Winter grazed *Kobresia* meadow inhabited by plateau pikas	0.01	110	5.8-12.3 (23)	this research
Haibei, PRC (4000 m)	Winter grazed alpine meadow dominated by *Festuca ovina* and *Stipa aliena*	0.01	80	19.1-19.7 (30)	Chen et al. (1991)
Laelatu, EST (0 m)	Wooded meadow of *Sesleria coerulea–Filipendula hexapetala*	0.01	30	4.0–17.7 (25)	Kull and Zobel (1993)
Limburg, NLD (130-170 m)	Chalk grassland of *Mesobrometum erecti*	0.01	50	5.85–12.87	Willems et al. (1993)
Öland, SWE (0 m)	Alvar habitat of *Veronica spicata–Avenula pratensis*	0.01	40	12.1–16.3 (29)	van der Maarel & Sykes (1995)
"	"	0.01	10-35	9.5–13.1	van der Maarel et al. (1995)
"	"	0.01	10	11.2, 12.5, 13.3*	Wilson et al. (1999)
Saaremaa & Muhu, EST (0 m)	Alvar type grassland of *Filipendula hexapetala–Trifolium montanum*	0.04	10	10–25	Pärtel and Zobel (2000)
Hanila, EST (0 m)	Alvar grassland of *Filipendula-Trifolium montani*	0.01	60	13.2–17.1	Zobel et al. (2001)
CZE (400 m)	*Bromus erectus* and *Carex montana* dominated grassland	0.015…§	1	29	Klimeš et al. (1966, 1969)

*Data from three different sites

§ 0.015625

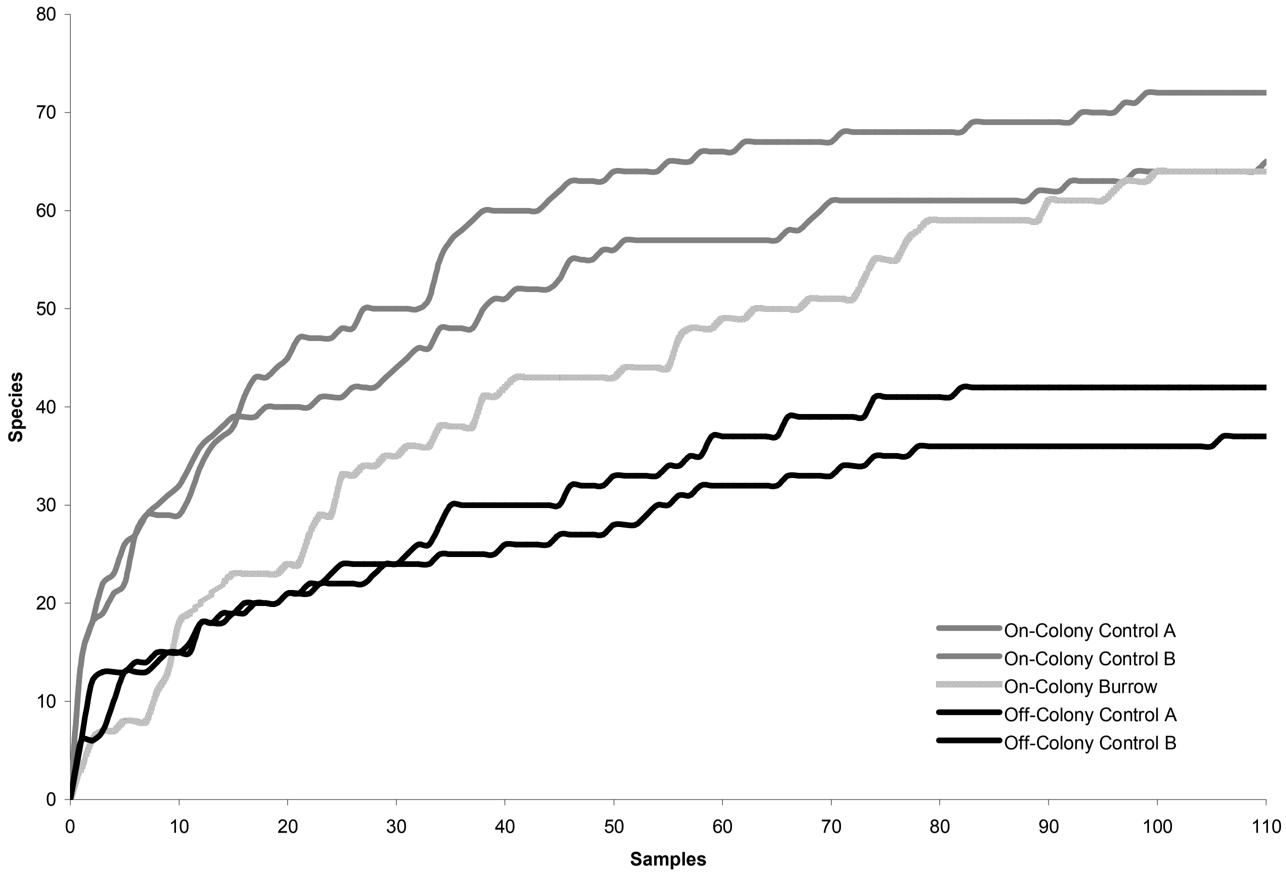


Figure 5.1. Species-area curve (or collector's curve) for patches on a pika colony (gray lines) and at a nearby off-colony site (black lines). Burrow patches (patterned line) contained disturbance from pika burrowing, but control patches (solid lines) did not. Species are shown as a running total.

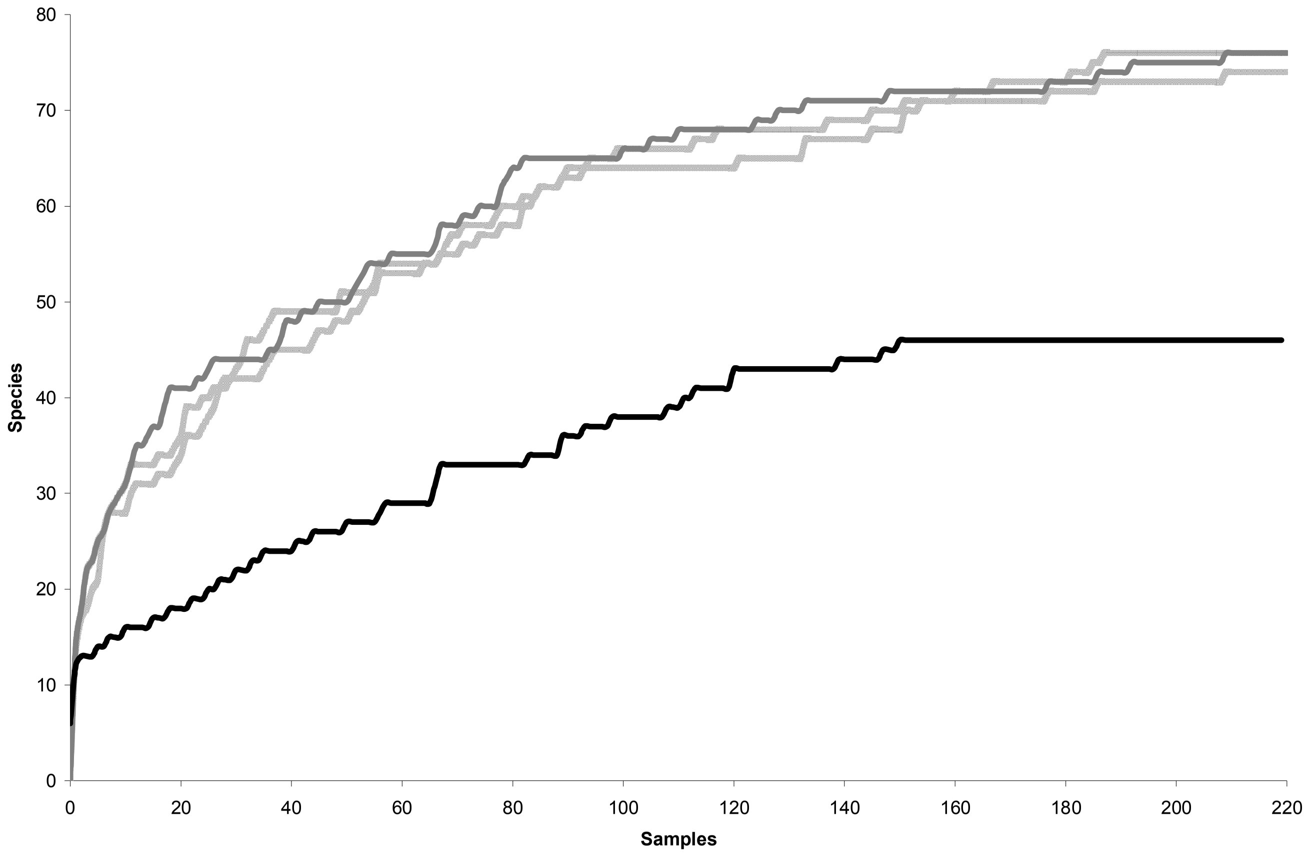


Figure 5.2. Species-area curve (or collector’s curve) for a pika colony (gray lines) and nearby off-colony site (black line). The pika colony is shown as multiple separate lines (control + burrow = patterned gray line, control + control = solid gray line) so that sampling area remains equal. Species are shown as a running total.

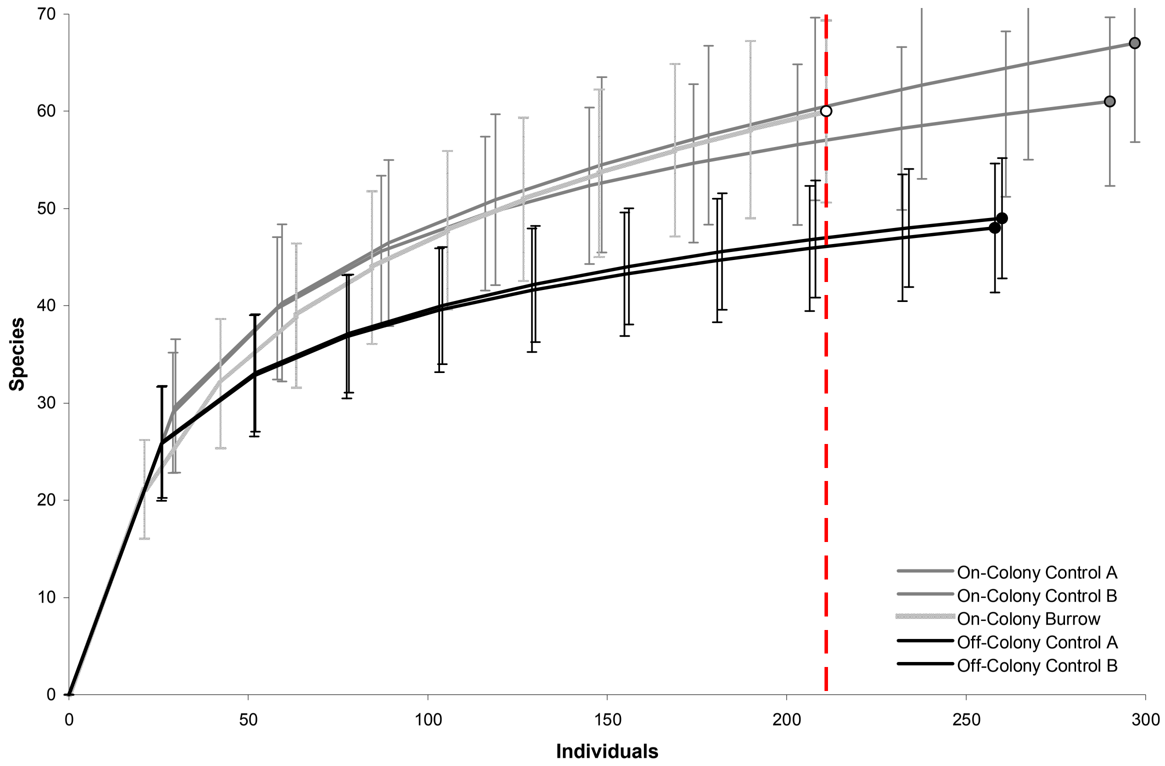


Figure 5.3. Species-accumulation (rarefaction) curve for observed plant species in different patches on a pika colony (gray lines) and at a nearby off-colony site (black lines). Burrow patches (patterned line) contain disturbance from pika burrowing, but control patches (solid lines) do not. Samples were pooled and analyzed in random order without replacement over 1000 runs. The x-axis was re-scaled from samples to individuals using the average number of individuals per sample. The vertical line indicates the rarified value at which patches should be compared. Overlapping error bars (95% confidence intervals) indicate there is no significant difference in richness between patch types.

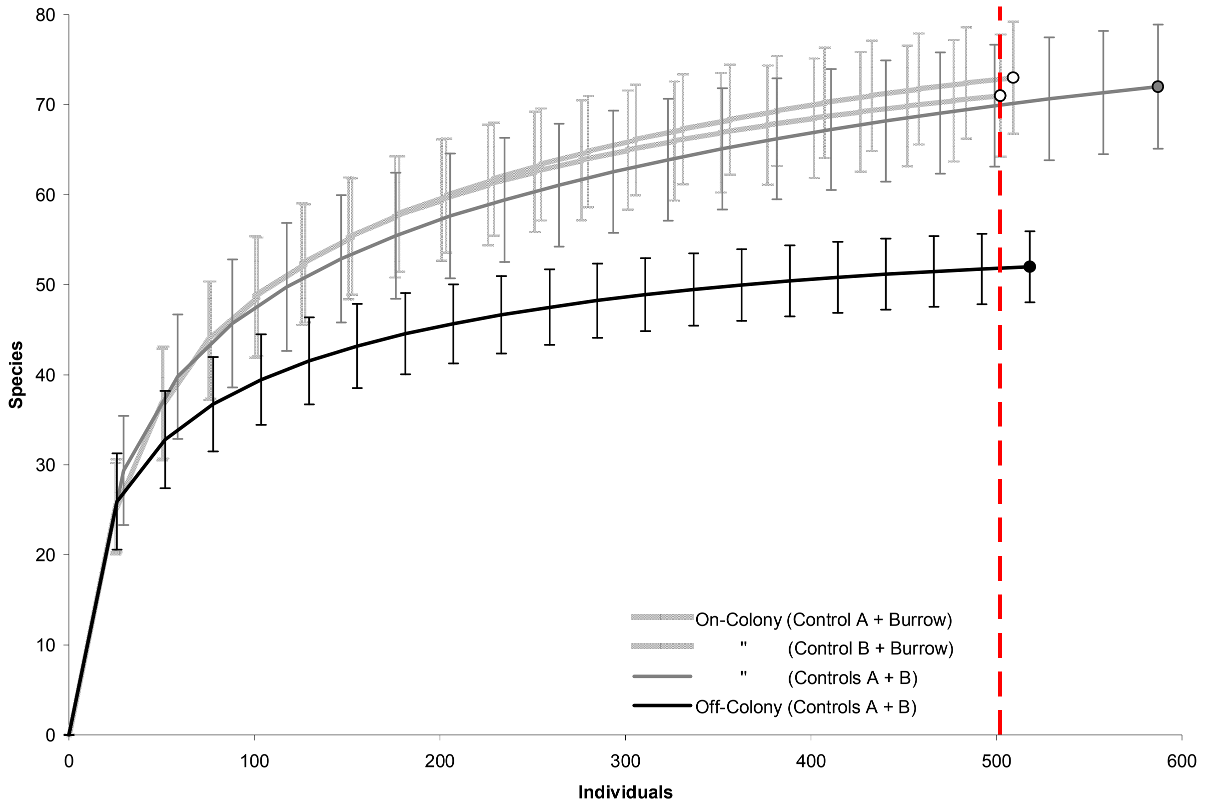


Figure 5.4. Species-accumulation (rarefaction) curve for observed plant species on a pika colony (gray lines) and a nearby off-colony site (black line). The pika colony is shown as multiple lines (control and burrow = patterned gray lines, two controls = solid gray line) to keep sampling areas equal. Samples were pooled and analyzed in random order without replacement over 1000 runs. The x-axis was re-scaled from samples to individuals using the average number of individuals per sample. The vertical line shows the rarified value at which patches should be compared. Non-overlapping error bars (95% confidence intervals) indicates the pika colony contains significantly more species (p<0.05) than the off-colony site.

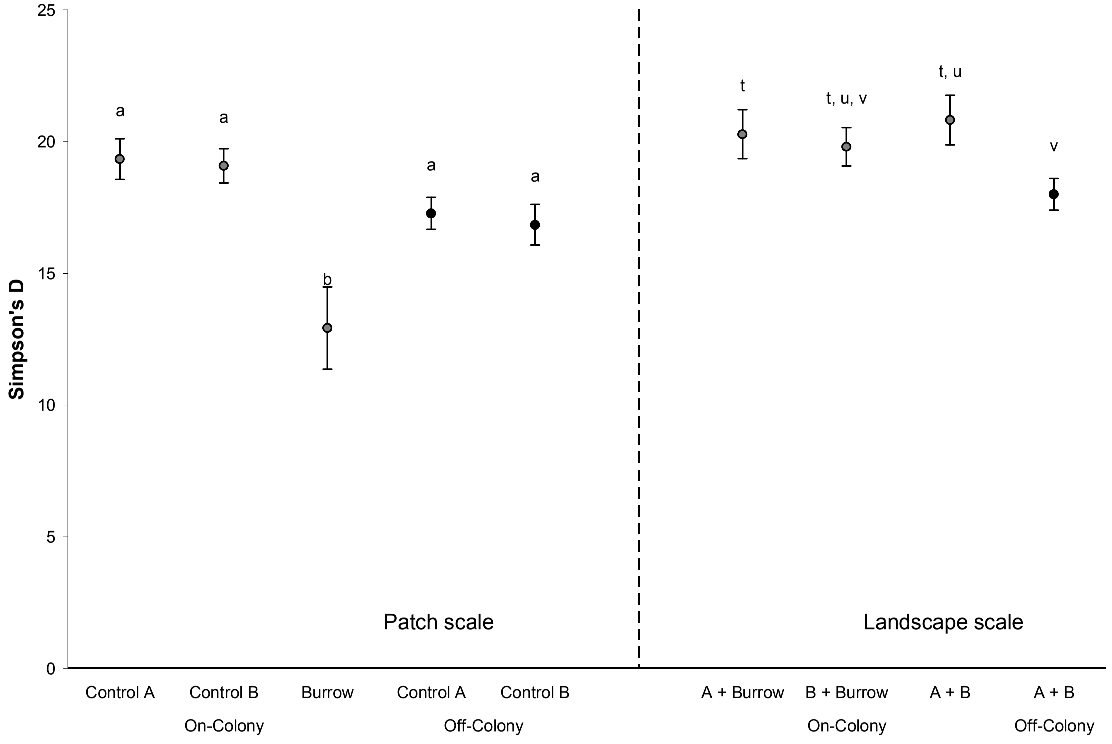


Figure 5.5. Simpson's reciprocal diversity for average species diversity on patches at two spatial scales. Error bars show standard error. Patch types with different letters are significantly different at $p<0.01$ for a – b and $p<0.05$ for t – v (Tukey's HSD).

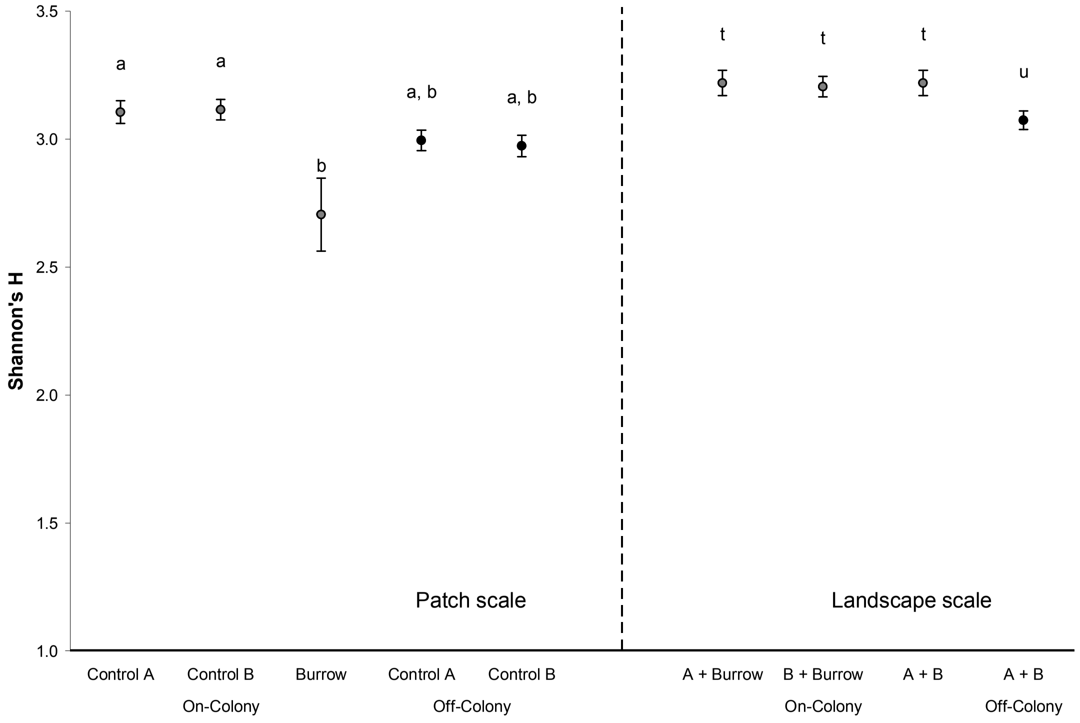


Figure 5.6. Shannon diversity for average species diversity on patches at two spatial scales. Error bars show standard error. Patch types with different letters are significantly different at $p<0.05$ (Tukey's HSD).

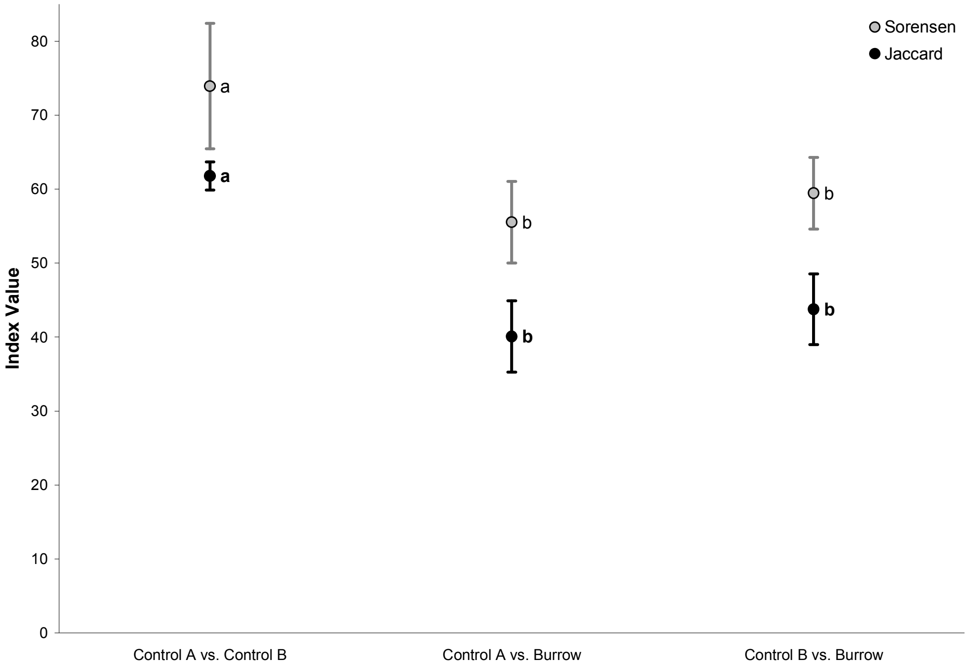
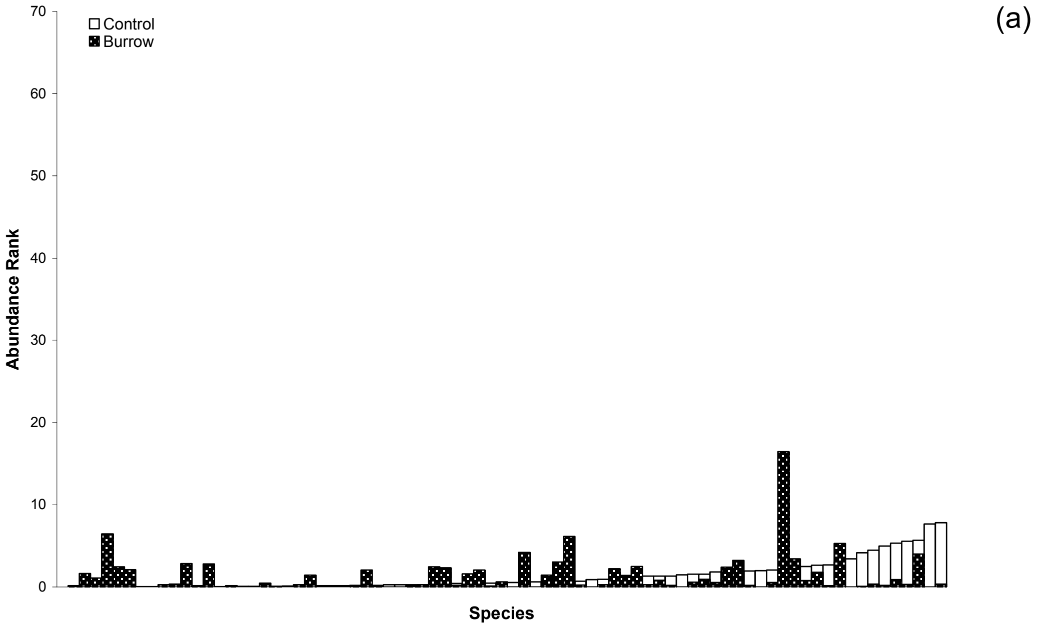
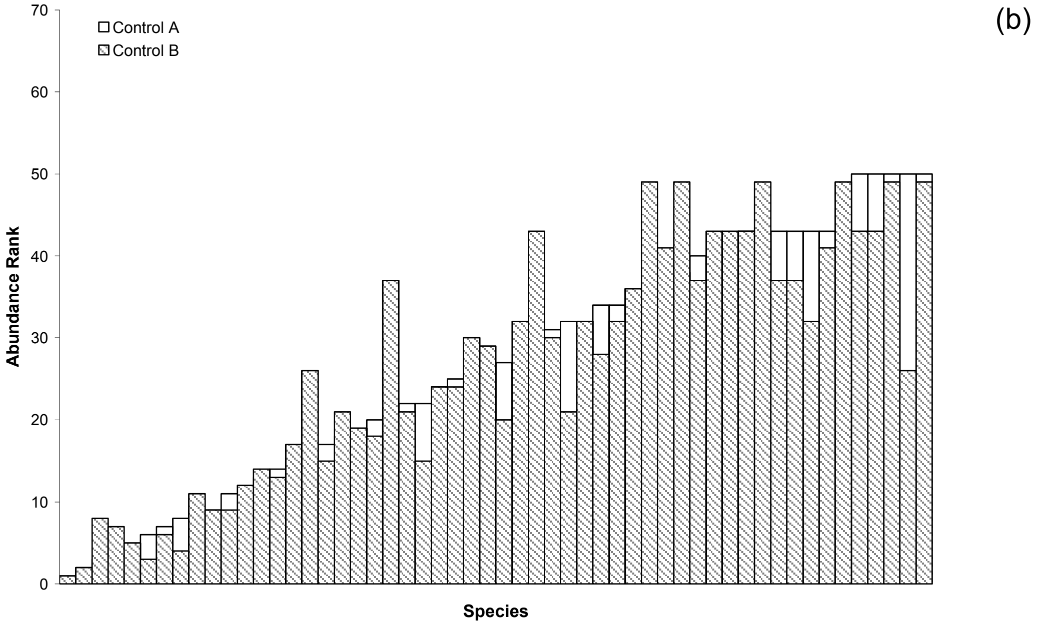


Figure 5.7. Measures of community similarity for Jaccard (bold) and Sorensen (grey) indices on a pika colony. Comparisons were made between control patches (Control A vs. Control B) and between control and burrow patches (Control A vs. Burrow, Control B vs. Burrow). The control patches were more similar to each other than either was to the burrow patch. Identical letters within a similarity measure are not significantly different at $p < 0.01$ (Tukey's HSD).


(a)
Control
Burrow
Abundance Rank
Species
0
10
20
30
40
50
60
70


(b)
Control A
Control B
Abundance Rank
Species
0
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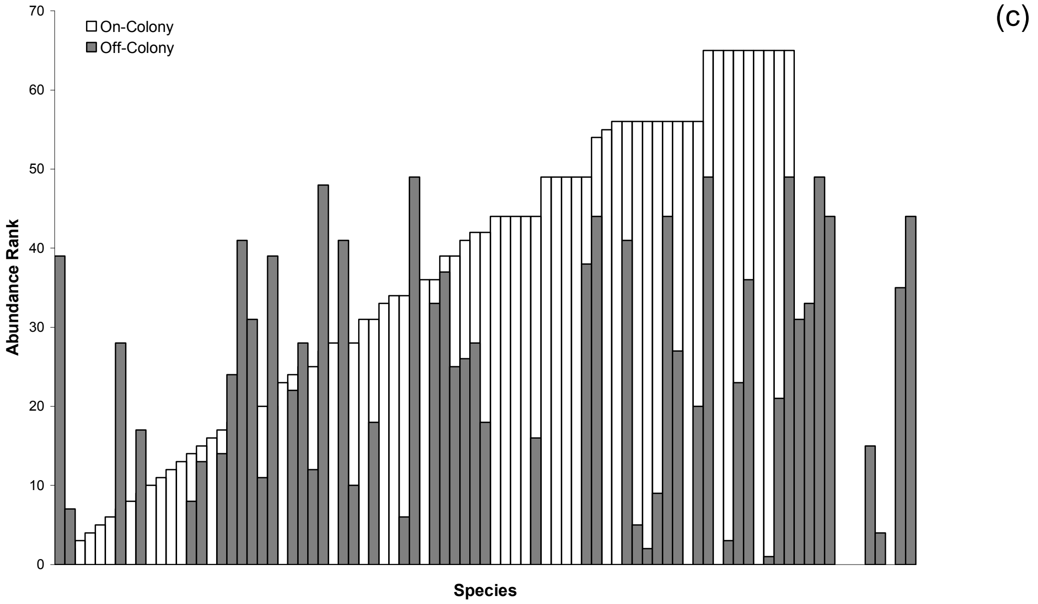

Figure 5.8. Abundance rank of identical species over different patch types. Comparisons are shown between control and burrow patches on a pika colony (a), two control patches on a pika colony (b), and the pika colony and a nearby off-colony site (c).

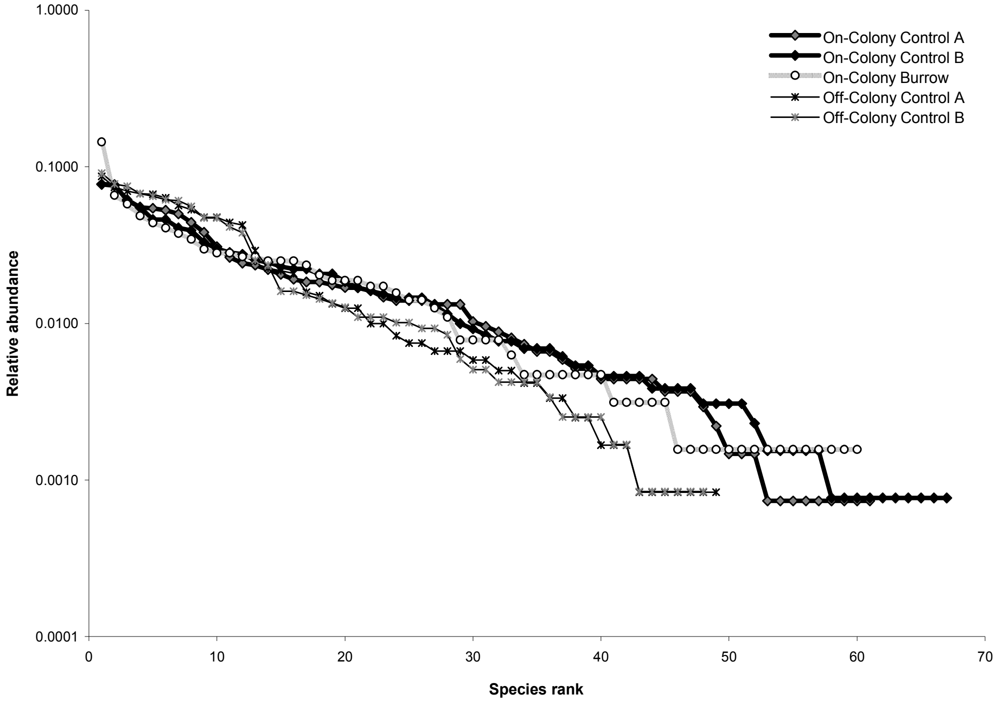

Figure 5.9. Whittaker plot (rank/abundance plot) of patches on a pika colony (thick lines) and a nearby off-colony site (thin lines). The y-axis shows relative abundance of species on a logarithmic scale and the x-axis shows species ranked from most to least abundant. The relative abundance of plants on burrow patches was significantly different from control patches (Kolmogorov-Smirnov, $P<0.05$). Control patches were not significantly different within the on-colony or off-colony site (Kolmogorov-Smirnov, $P>0.05$).

CHAPTER 6
Conclusions

Plateau pikas excavate vast burrow complexes in alpine meadows on the Tibetan Plateau. They are the most abundant small animal in this environment, and their colonies can reach over 300 individuals/ha. Previous research has labeled these animals as both a keystone species and allogenic engineer. I find that plateau pikas function as keystone engineers by increasing plant species diversity, enhancing soil mixing, and boosting water infiltration, and contributing novel microhabitats.

Results of this research indicate that pika colonies have both patch-level and local landscape-level effects. At the small patch scale, their burrowing does generate bare patches in soil and areas of reduced species richness. However, these outcomes are reversed at higher spatial scales. Nonlinearity is a common attribute of ecological communities. In landscape ecology, this phenomenon is termed the Modifiable Areal Unit Problem. Because pikas limit plant growth only in areas of very small spatial extent, the impact of a pika colony is not equal to that of a disturbed patch.

A major contribution of pika disturbance is increased spatial heterogeneity, which likely underlies differences in the plant community. These findings suggest that the positive impact of plateau pikas on rangeland resources has been undervalued. In concurrence with other studies, this work concludes that plateau pikas provide valuable ecosystem services on the Tibetan plateau.

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APPENDIX A

Table A-1. The evolution of the keystone species concept through its major interpretations. Representative species are listed, along with relevant quotes and neologisms introduced by the author(s).

Author, **neologism(s)**	Quote	Example
Paine (1972) **keystone species, keystone predator**	*Within both these fairly or very complex systems the species composition and physical appearance were greatly modified by the activities of a single native species high in the food web. These individual populations are the **keystone** of the community's structure, and the integrity of the community and its unaltered persistence through time, that is, stability, are determined by their activities and abundances* (1969)	seastar, *Piaster*
Dayton (1974) **foundation species**	*…most of the communities so studied have **key or foundation species** which have roles in the maintenance of the community disproportionate to the abundance or biomass of the species. ...I will refer to the group of critical species which define much of the structure of a community as "**foundation**" species*	urchin, *Strongylocentrotus*
Estes and Palmisano (1977)	*The sea otter is an important species in determining structures and dynamic relations within nearshore communities, and so fits Paine's … concept of a **keystone species**.*	sea otter, *Enhydra lutris*
Holt (1980) **keystone prey**	*A prey species with a high relative value for* r/a *is a "**keystone**" species in the community (sensu Paine, 1969), inasmuch as its properties both control the density of the predator and restrict the range of parameters open to other prey.*	snowshoe hare, *Lepus americanus*
Gilbert (1981) **mobile link, keystone mutualist**	*…I call such organisms "**mobile links**" because through their foraging movements, they are of mutual concern to the reproduction of many different unrelated plants which, in turn, support otherwise independent food webs. ….**Keystone mutualists** are those organisms, typically plants, which provide critical support to large complexes of mobile links.*	canopy tree *Casearia corymbosa*
Noy-Meir (Naiman et al. 1986)	*… the more predator-tolerant prey B can be called a "**keystone species**," since its introduction allows stable coexistence of A with the predator, which is impossible in the absence of B.*	

Table A-1. Continued

(1990) **keystone modifier**	*Overall, our field observations and data show that beaver, through their feeding and dam-building activities, act as a **keystone species** (sensu Paine 1966, 1969, 1974) to affect ecosystem structure and dynamics far beyond their immediate requirements for food and space.*	beaver, *Castor canadensis*
Brown and Heske (1986) **keystone guild**	*In the present case, the "keystone" organism whose removal caused large changes in ecosystem structure and dynamics was not a single species, but a guild of three taxonomically related and ecologically similar kangaroo rat species. …. In this ecosystem kangaroo rats are a **keystone guild**: through seed predation and soil disturbance they have major effects on biological diversity and biogeochemical processes.*	kangaroo rats, *Dipodomys* spp.
Terborgh (1986) **keystone plant resources**	***Keystone plant resources** are thus characterized as playing prominent roles in sustaining frugivores through periods of general food scarcity. An additional key feature of these resources is reliability.*	palm nuts, figs, nectar
Wells et al. (1992) **transformer species**	*However, 47 of the species were identified as weeds of concern to conservationists, that **transform** habitats or landscapes… i.e. change the character, condition, form or nature of a natural ecosystem over a substantial area. … neither the alien nor the **transformer species** dealt with here should be regarded as the only ones in southern Africa.*	invasive plant *Acacia baileyana*
Lamont (1992) **first-, second-, and third-order keystones species; third-order keystone guild**	*I therefore define a **first-order (arch) keystone species** as essential as essential for the continued presence of one other species within an ecosystem. A **first-order keystone guild** becomes a group of functionally related species, individually or collectively responsible for the continued presence of another species. A **second-order (vault) keystone** has an essential (usually the same) function for a few species….A **third-order (cathedral) keystone species** has a prime role in functioning of the ecosystem, consistent with the original concept of keystone species (Paine 1969). …A **third-order keystone guild** is a group of functionally-related species that has a prime role in functioning of the ecosystem.*	wasps that pollinate *Drakea*; *Verticordia nitens*; *Banksia speciose*

Table A-1. Continued

Holling (1993) **extended keystone hypothesis**	*The **Extended Keystone Hypothesis**: All terrestrial ecosystems are controlled and organized by a small set of key plant, animal, and abiotic processes. They form interacting clusters of relationships, each of which determines the temporal and spatial structure over a constrained range of scales. The overall extent of these influences covers at least centimetres to hundreds of kilometres in space and months to centuries in time.*	disturbance mechanisms of macroscopic plants
Bond (1994)	*…such an agent is a keystone since its elimination or addition will change the abundance of competitive dominants and thus result in successional change with local loss of species*	
Jones et al. (1994) **keystone engineer**	*Our views are very close to Holling's (1992) Extended Keystone Hypothesis…. We would add two points. First a critical, but not exclusive controlling mechanism is some form of engineering; and second, we believe that **keystone engineers** occur in virtually all habitats on earth, not just terrestrial ones*	
Menge et al. (1992, 1995)	*…communities may be affected by strong or weak predation, and those with strong predation may be under the influence of either **keystone** or diffuse **predation**.*	seastar, *Piaster*
Walker (1996)	*… the best return for conservation effort will come from concentrating on ensuring the welfare of those species that are sole representatives of functional groups—by definition, **keystone species**. These groups are those in which there is no redundancy.*	
Power et al. (1996)	*…we define a **keystone species** as one whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance.*	
Folke et al. (1997) **keystone process species**	*A limited number of organisms and groups of organisms seem to drive or control the critical processes necessary for ecosystem functioning, while the remaining organisms exist in the niches formed by these **keystone process species**. Such organisms modify, maintain, and create habitats.*	migratory insectivorous birds

Table A-1. Continued

De Leo and Levin (1999) **keystone group**	*In most cases, it is indeed groups of species, rather than individual species, that assume importance, forming "**keystone groups**" or "functional groups," a generalization of the notion of keystone species.*	
Piraino and Fanelli (1999) **'key' species**	*…Those species driving ecosystem processes or energy flows are generally referred as "**key" species**, but only a few of them are keystones*	seastar, *Piaster*
Jordán et al. (2000)	*A species can be considered as **keystone** for it is in a key position in the food flow network and/or for it is responsible for large fluxes of matter and energy.*	
Kotliar (2005)	*…I propose that a third criterion be incorporated into the definition: **keystone species** perform roles not performed by other species or processes.*	prairie dogs, *Cynomys* spp.
Ebenman and Jonsson (2003)	*We chose here to define **keystone species** as a species whose loss is likely to trigger a significant number of secondary extinctions.*	
Davic (1994)	*…a **keystone species** is a strongly interacting species whose top-down effect on species diversity and competition is large relative to its biomass dominance within a functional group.*	

Table A-2. Methods of *a priori* keystone species identification.

Author	Index/ Method	Quote
Tanner et al. (1996)	Sensitivity analysis	*We suggest that, for certain assemblages, this* [identification of keystones] *can also be done by means of a sensitivity analysis of a matrix of transition probabilities.*
Power et al. (1999)	Community importance	*In mathematical terms,* $CI = [d(trait)/dp]\ [1/(trait)]$ *where p is the proportional abundance (in most cases, proportional biomass relative to the total biomass of all other species in the community) of the species whose abundance is modified. Trait refers to a quantitative trait of a community or ecosystem.*
Jordán et al. (2001)	Keystone indices in food web networks	*We characterize species by three keystone indices:* K_b *for bottom-up,* K_t *for top-down and K for bidirectional processes (where* $K = K_b + K_t$*).*
Solé and Montoya (2002)	topological analysis of ecological networks	*In this respect, our approximation to the fragility of species-rich food webs through topological changes may help to design new methods for* a priori *identification of keystone species. We can identify such species as highly connected because of the effects of their removal in terms of secondary extinctions and food-web fragmentation.*
Jordán and Scheuring (2004)	topological analysis of ecological networks	*Although the study of large and complex networks may help ecologists in answering certain questions, we suggest that for evaluating the role of a species in a community (i.e. identifying keystones), ecology needs a more local view on the network of interspecific interactions ….We argue that considering either only direct partners or the whole community is not the key to assessing the importance of a species. Rather, a "meso-scale" view is proposed: it should be taken into account that the strength of indirect effects is generally thought to be decreasing with the length of the pathway.*
Okey et al. (2005)	Removal simulations using Ecopath and Ecosim	*We used the interaction strength index (ISI), the sum of all resulting relative changes in the system (the total absolute relative changes in all but the removed group). The 'keystone' index is the ISI expressed in terms of the relative biomass of the respective groups ….*

Table A-2. Continued

Christianou and Ebenman (2006)	topological analysis of ecological networks, including interaction strength	*In this study we investigate the role of interaction strength between species (measured as the per capita effects of one species on another). In particular, we explore how the number and position of strong and weak links affect the response of model communities to species loss.*
Jordán et al. (2006)	topological analysis of ecological networks	*We present a detailed network analysis based on pure topology (partly extended also to a weighted network)…. We use a variety of network indices from local to global ones, including node degree, keystone indices, centrality indices and the most general topological importance indices derived from matrix algebra.*
Libralato et al. (2007)	Network mixed trophic impact analysis with Ecosim	*The high general agreement between the mixed trophic impacts estimated by the mass-balance routine, Ecopath, and the observed relative changes in the biomasses obtained with long-term Ecosim simulations, allowed use of the mixed trophic impact matrix* ***M*** *as a straightforward basis to quantify the effect one functional group has on all the other groups in the ecosystem. Thus, the method proposed allows estimating the keystoneness of the species or group of species in a model without having to perform the time-dynamic simulations, as performed, e.g. by Okey et al. (2004a), thus avoiding differences induced by different simulation protocols.*
Estrada (2008)	Generalized keystone index from combination of other centrality measures	*Here we study several centrality measures which can be grouped as local or global as well as our "meso-scale" centrality index…. A generalized centrality index is derived by means of factor analysis which resumes the information contained in the six-centrality measures analyzed here.*
Jordán et al. (2003)	Comparison of structural and functional indices	*In this paper we calculate 13 structural and 5 functional importance indices for the trophic components of an ecosystem model and examine their relationships…. Our primary finding is that unweighted indices of the interaction web structure of a community show no correlation with any of the functional indices.*

APPENDIX B

Table B-1. Percentage of organic matter in alpine meadow soils in Qinghai province. Organic matter (SOM) is shown as percent of soil content. The range of soil depth (Depth) sampled is reported in cm. Locality is reported to the administrative level reported by the authors. Sampling in Haibei Alpine Research Station was located in Menyuan County. NR indicates information not reported by the author.

SOM	Depth	Habitat	Site	Source
2.49	0–30	Alpine meadow, <15% plant cover	Darlag County	Wang et al. (2003)
3.80	0–30	Alpine meadow, 15–30% plant cover	Darlag County	Wang et al. (2003)
4.33	0–30	Alpine meadow, 30–50% plant cover	Darlag County	Wang et al. (2003)
4.41	0–30	Alpine meadow, 50–70% plant cover	Darlag County	Wang et al. (2003)
7.19	0–30	Alpine meadow, 70–90% plant cover	Darlag County	Wang et al. (2003)
10.03	0–30	Alpine meadow, >90% plant cover	Darlag County	Wang et al. (2002)
12.12	—	Alpine meadow	Qinghai	Wang et al. (2002)
10.18	—	Sub-alpine meadow	Qinghai	Wang et al. (2002)
3.12	—	Alpine steppe	Qinghai	Wang et al. (2002)
6.74	—	Mountain meadow	Qinghai	Wang et al. (2002)
6.53	—	Meadow	Qinghai	Wang et al. (2004a)
15.68	0–5	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
13.07	0–5	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
11.89	0–5	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
10.34	0–5	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
9.77	5–10	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
9.09	5–10	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
8.53	5–10	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
7.81	5–10	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
7.29	10–20	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
5.98	10–20	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)

5.51	10–20	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
4.58	10–20	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2003)
17.9	0–5	Alpine meadow, no zokor colonies	Haibei Research Station	Zhang and Liu (2003)
15.6	6–10	Alpine meadow, no zokor colonies	Haibei Research Station	Zhang and Liu (2003)
14.5	11–15	Alpine meadow, no zokor colonies	Haibei Research Station	Zhang and Liu (2003)
13.5	16–20	Alpine meadow, no zokor colonies	Haibei Research Station	Zhang and Liu (2003)
11.5	> 20	Alpine meadow, no zokor colonies	Haibei Research Station	Zhang and Liu (2003)
13.5	0–5	Alpine meadow, active zokor colony	Haibei Research Station	Zhang and Liu (2003)
13.5	6–10	Alpine meadow, active zokor colony	Haibei Research Station	Zhang and Liu (2003)
12.9	11–15	Alpine meadow, active zokor colony	Haibei Research Station	Zhang and Liu (2003)
12.9	16–20	Alpine meadow, active zokor colony	Haibei Research Station	Zhang and Liu (2003)
12.3	> 20	Alpine meadow, active zokor colony	Haibei Research Station	Zhang and Liu (2003)
13.2	0–5	Alpine meadow, abandoned zokor colony	Haibei Research Station	Zhang and Liu (2003)
15.1	6–10	Alpine meadow, abandoned zokor colony	Haibei Research Station	Zhang and Liu (2003)
14.6	11–15	Alpine meadow, abandoned zokor colony	Haibei Research Station	Zhang and Liu (2003)
14.5	16–20	Alpine meadow, abandoned zokor colony	Haibei Research Station	Zhang and Liu (2003)
13.2	> 20	Alpine meadow, abandoned zokor colony	Haibei Research Station	Zhang and Liu (1993)
17.92	0–20	Alpine meadow, no zokor colonies	Haibei Research Station	Wang et al. (1993)
14.83 - 15.67	0–20	Alpine meadow, zokor mounds	Haibei Research Station	Wang et al. (2008b)
10.27	0–40	*Kobresia humilis* meadow	Haibei Research Station	Wang (2008b)
11.99	0–40	*Kobresia pygmaea* meadow	Haibei Research Station	Wang (2008b)
24.91	0–40	*Kobresia tibetica* swamp meadow	Haibei Research Station	Wang (2008b)
10.23	0–40	*Potentilla fruticosa* shrub	Haibei Research Station	Wang (2008)
8.86	—	*Kobresia* alpine meadow	Dawu	Xu et al. (2008)
7.22	—	*Kobresia* alpine meadow	Dawu	Xu et al. (2008)
5.36	—	*Kobresia* alpine meadow	Dawu	Xu et al. (2004a)

Table B-2. Total nitrogen (%) in alpine meadows of the Tibetan plateau. The range of soil depth (Depth) sampled is reported in cm. Locality is reported to the administrative level reported by the authors. Haibei Research Station is located in Menyuan County. Darlag County, Dawu Township, and Menyuan County are located in Qinghai Province and Nagqu County is in the Tibetan Autonomous Region.

Total N	Depth	Habitat	Site	Source
0.62	0–5	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
0.59	0–5	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
0.54	0–5	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
0.51	5–10	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
0.44	5–10	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
0.39	5–10	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
0.42	5–10	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
0.36	10–20	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
0.32	10–20	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
0.30	10–20	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
0.26	10–20	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2003)
0.13	0–30	Alpine meadow, <15% plant cover	Darlag County	Wang et al. (2003)
0.23	0–30	Alpine meadow, 15–30% plant cover	Darlag County	Wang et al. (2003)
0.27	0–30	Alpine meadow, 30–50% plant cover	Darlag County	Wang et al. (2003)
0.20	0–30	Alpine meadow, 50–70% plant cover	Darlag County	Wang et al. (2003)
0.38	0–30	Alpine meadow, 70–90% plant cover	Darlag County	Wang et al. (2003)
0.48	0–30	Alpine meadow, >90% plant cover	Darlag County	Wang et al. (2008b)
0.55	0–40	*Kobresia humilis* meadow	Haibei Research Station	Wang (2008b)
0.58	0–40	*Kobresia pygmaea* meadow	Haibei Research Station	Wang (2008b)
1.21	0–40	*Kobresia tibetica* swamp meadow	Haibei Research Station	Wang (2008b)
0.48	0–40	*Potentilla fruticosa* shrub	Haibei Research Station	Wang (2008)
0.53	—	*Kobresia* alpine meadow	Dawu	Xu et al. (2008)
0.40	—	*Kobresia* alpine meadow	Dawu	Xu et al. (2008)
0.36	—	*Kobresia* alpine meadow	Dawu	Xu et al. (2005)
0.54	0–10	Alpine Kobresia meadow	Darlag County	Wang et al. (2005)

0.39	0–10	Alpine Kobresia meadow	Darlag County	Wang et al. (2005)
0.50	10–20	Alpine Kobresia meadow	Darlag County	Wang et al. (2005)
0.36	10–20	Alpine Kobresia meadow	Darlag County	Wang et al. (2008)
0.62	0–18	*Kobresia pygmaea* mat, footslope 10°S	Nagqu County	Kaiser et al. (2008)
0.19	18–31	*Kobresia pygmaea* mat, footslope 10°S	Nagqu County	Kaiser et al. (2008)
0.05	31–45	*Kobresia pygmaea* mat, footslope 10°S	Nagqu County	Kaiser et al. (2008)
0.01	45–70+	*Kobresia pygmaea* mat, footslope 10°S	Nagqu County	Kaiser et al. (2008)
0.55	0–15	*Kobresia pygmaea* mat, valley bottom	Nagqu County	Kaiser et al. (2008)
0.26	15–25	*Kobresia pygmaea* mat, valley bottom	Nagqu County	Kaiser et al. (2008)
0.17	25–40	*Kobresia pygmaea* mat, valley bottom	Nagqu County	Kaiser et al. (2008)
—	40–70+	*Kobresia pygmaea* mat, valley bottom	Nagqu County	Kaiser et al. (2008)
0.19	0–15	*Kobresia pygmaea* mat, river floodplain	Nagqu County	Kaiser et al. (2008)
0.18	15–60	*Kobresia pygmaea* mat, river floodplain	Nagqu County	Kaiser et al. (2008)
0.02	60–72	*Kobresia pygmaea* mat, river floodplain	Nagqu County	Kaiser et al. (2008)
—	72–76	*Kobresia pygmaea* mat, river floodplain	Nagqu County	Kaiser et al. (2008)
—	76–90+	*Kobresia pygmaea* mat, river floodplain	Nagqu County	Kaiser et al. (2008)
1.14	0–30	*Kobresia schoenoides* swamp, basin	Nagqu County	Kaiser et al. (2008)
0.07	30–70+	*Kobresia schoenoides* swamp, basin	Nagqu County	Kaiser et al. (1993)

Table B-3. Amount of plant-available nitrogen (N) in alpine meadows of the Tibetan plateau in Qinghai Province. Available N is reported in mg/kg. The range of soil depth (Depth) sampled is reported in cm. Locality is reported to the administrative level reported by the authors. Haibei Research Station is located in Menyuan County. Darlag County, Dawu Township, and Menyuan County are located in Qinghai Province and Nagqu County is in the Tibetan Autonomous Region.

N	Depth	Habitat	Site	Source
50.9	0–20	Alpine meadow, no zokor colonies	Haibei Research Station	Wang et al. (1993)
69.3 - 78.8	0–20	Alpine meadow, zokor mounds	Haibei Research Station	Wang et al. (2004a)
546.3	0–5	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
392.2	0–5	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
469.2	0–5	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
518.2	0–5	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
392.2	5–10	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
322.2	5–10	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
350.2	5–10	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
364.2	5–10	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
238.1	10–20	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
252.1	10–20	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
224.1	10–20	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2004a)
294.1	10–20	*Kobresia parva* alpine meadow	Darlag County	Dong et al. (2008b)
30.6	0–40	*Kobresia humilis* meadow	Haibei Research Station	Wang (2008b)
36.5	0–40	*Kobresia pygmaea* meadow	Haibei Research Station	Wang (2008b)
80.9	0–40	*Kobresia tibetica* swamp meadow	Haibei Research Station	Wang (2008b)
31.6	0–40	*Potentilla fruticosa* shrub	Haibei Research Station	Wang (2008)
398.1	—	*Kobresia* alpine meadow	Dawu	Xu et al. (2008)
304.0	—	*Kobresia* alpine meadow	Dawu	Xu et al. (2008)
212.8	—	*Kobresia* alpine meadow	Dawu	Xu et al. (2005)

Table B-4. Reported values of above-ground percent carbon, nitrogen, and C:N ratios in alpine meadows on the Tibetan plateau. Darlag County is located in Qinghai Province and Tianzhu County in Gansu.

Overall	Grass	Sedge	Forbs	Habitat	Site (Sampling Date)	Source
Carbon						
—	40.48	41.47	43.93	*Kobresia* alpine meadow	Darlag County (August)	Wang et al. (2005)
—	38.69	—	40.79	*Kobresia* alpine meadow	Darlag County (August)	Wang et al. (2007)
25.27	—	—	—	Alpine Meadow	Multiple	Zhang et al. (2006)
43.5	43.6	—	43.5	Steppe, meadow, desert grassland	Multiple (July/ August)	He et al. (2005)
Nitrogen						
—	1.27	1.22	1.53	*Kobresia* alpine meadow	Darlag County (August)	Wang et al. (2005)
—	1.49	—	1.60	*Kobresia* alpine meadow	Darlag County (August)	Wang et al. (1999)
—	1.64	1.93	2.39	Alpine Meadow	Tianzhu County (August)	Long et al. (1999)
—	1.06	1.41	1.76	Alpine Meadow	Tianzhu County (September)	Long et al. (1999)
—	0.65	0.80	1.17	Alpine Meadow	Tianzhu County (October)	Long et al. (2006)
2.86	2.40	—	3.06	Steppe, meadow, desert grassland	Multiple (July/ August)	He et al. (2005)
C:N						
—	31.92	34	28.75	*Kobresia* alpine meadow	Darlag County (August)	Wang et al. (2005)
—	25.93	—	25.53	*Kobresia* alpine meadow	Darlag County (August)	Wang et al. (2006)
17.0						He et al. (e. g.
	19.6	—	16.0	Steppe, meadow, desert grassland	Multiple (July/ August)	Wang and Fu 2004)

APPENDIX C

Nondimensionalization

To nondimensionalize equation 5 and 6, we first replace each variable by the nonparameterized version, represented by "*":

$$\begin{aligned}
\dot{P}_1^* U_{P1} &= r_1 U_{P1} P_1^* (1 - \alpha_{11} U_{P1} P_1^* - \alpha_{12} U_{P1} P_2^*) - \rho_{P1} H_1 U_{P1} P_1^* - \gamma_{P1} H_2 U_{P1} P_1^* \\
\dot{P}_1^* &= r_1 P_1^* (1 - \alpha_{11} U_{P1} P_1^* - \alpha_{12} U_{P1} P_2^*) - \rho_{P1} H_1 P_1^* - \gamma_{P1} H_2 P_1^* \\
\dot{P}_2^* U_{P2} &= r_2 U_{P2} P_2^* (1 - \alpha_{21} U_{P2} P_1^* - \alpha_{22} U_{P2} P_2^*) - \rho_{P2} H_1 U_{P2} P_2^* - \gamma_{P2} H_2 U_{P2} P_2^* \\
\dot{P}_2^* &= r_2 P_2^* (1 - \alpha_{21} U_{P2} P_1^* - \alpha_{22} U_{P2} P_2^*) - \rho_{P2} H_1 P_2^* - \gamma_{P2} H_2 P_2^*
\end{aligned}$$

Now we can choose values of U to eliminate two of the parameters in the set α_{11}, α_{12}, α_{21}, α_{22}.

$$\begin{aligned}
U_{P1} = &\quad \tfrac{1}{\alpha_{11}} \\
U_{P2} = &\quad \tfrac{1}{\alpha_{22}} \\
\dot{P}_1^* = &\quad r_1 P_1^* (1 - P_1^* - \tfrac{\alpha_{12}}{\alpha_{11}} P_2^*) - \rho_{P1} H_1 P_1^* - \gamma_{P1} H_2 P_1^* \\
\dot{P}_2^* = &\quad r_2 P_2^* (1 - \tfrac{\alpha_{21}}{\alpha_{22}} P_1^* - P_2^*) - \rho_{P2} H_1 P_2^* - \gamma_{P2} H_2 P_2^*
\end{aligned}$$

To eliminate the final parameter, we can rescale time $\dfrac{dP^*}{dt}$ in terms of $\dfrac{dP^*}{d\tau}$:

$$\begin{aligned}
\frac{dP^*}{d\tau} = &\quad \frac{dP^*}{dt} * \frac{dt}{d\tau} \\
\frac{dP^*}{dt} = &\quad \frac{dP^*}{d\tau} * \frac{d\tau}{dt} \\
\frac{dP^*}{dt} = &\quad \frac{dP^*}{d\tau} * U_t
\end{aligned}$$

$$\begin{aligned}
\frac{dP_1^*}{d\tau} = &\quad \tfrac{r_1 P_1^*}{U_t} (1 - P_1^* - \tfrac{\alpha_{12}}{\alpha_{11}} P_2^*) - \tfrac{\rho_{P1}}{U_t} H_1 P_1^* - \tfrac{\gamma_{P1}}{U_t} H_2 P_1^* \\
\frac{dP_2^*}{d\tau} = &\quad \tfrac{r_2 P_2^*}{U_t} (1 - \tfrac{\alpha_{21}}{\alpha_{22}} P_1^* - P_2^*) \tfrac{\rho_{P2}}{U_t} H_1 P_2^* - \tfrac{\gamma_{P2}}{U_t} H_2 P_2^*
\end{aligned}$$

We can choose U_t so that $U_t = r_1$:

$$\frac{dP_1^*}{d\tau} = P_1^*(1 - P_1^* - \frac{\alpha_{12}}{\alpha_{11}}P_2^*) - \frac{\rho_{P1}}{r_1}H_1P_1^* - \frac{\gamma_{P1}}{r_1}H_2P_1^*$$
$$\frac{dP_2^*}{d\tau} = \frac{r_2}{r_1}(1 - \frac{\alpha_{21}}{\alpha_{22}}P_1^* - P_2^*) - \frac{\rho_{P2}}{r_1}H_1P_2^* - \frac{\gamma_{P2}}{r_1}H_2P_2^*$$

As a final step, we can remove "*" and rename the nondimensionalized parameters:

$$\dot{P_1} = \quad P_1(1 - P_1 - \alpha_{12}P_2) - \rho_{P1}H_1P_1 - \gamma_{P1}H_2P_1$$

$$\dot{P_2} = \quad rP_2(1 - \alpha_{21}P_1 - P_2) - \rho_{P2}H_1P_2 - \gamma_{P2}H_2P_2$$

where $r = \frac{r_2}{r_1}$, $\alpha 12 = \frac{\alpha 12}{\alpha 11}$, $\alpha 21 = \frac{\alpha 21}{\alpha 22}$, $\rho_{P1} = \frac{\rho_{P1}}{r_1}$, $\rho_{P2} = \frac{\rho_{P2}}{r_1}$, $\gamma_{P1} = \frac{\gamma_{P1}}{r_1}$ and $\gamma_{P2} = \frac{\gamma_{P2}}{r_1}$

.

Calculation of Fixed Points

The fixed points of nondimensionalized equation 5 and 6 are be determined as follows:

$$\dot{P_1} = P_1(1 - P_1 - \alpha_{12}P_2) - \rho_{P1}H_1P_1 - \gamma_{P1}H_2P_1$$

$$0 = P_1(1 - P_1 - \alpha_{12}P_2) - \rho_{P1}H_1P_1 - \gamma_{P1}H_2P_1$$

The solution to the above equation is either $0 = P_1$ or $0 = (1 - P_1 - \alpha_{12}P_2 - \rho_{P1}H_1 - \gamma_{P1}H_2)$. Solving for the nontrivial solution:

$$0 = 1 - P_1 - \alpha_{12}P2 - \rho_{P1}H_1 - \gamma_{P1}H_2 \tag{11}$$
$$P_1 = 1 - \alpha_{12}P2 - \rho_{P1}H_1 - \gamma_{P1}H_2$$

In the case where $P_2 = 0$ we are left with:

$$P_1 = 1 - \rho_{P1}H_1 - \gamma_{P1}H_2$$

Complementary equations can be found for P_2:

$$\begin{aligned}
\dot{P_2} &= P_2(1-\alpha_{21}P_1-P_2)-\rho_{P2}H_1P_2-\gamma_{P2}H_2P_2 \\
0 &= P_2(1-\alpha_{21}P_1-P_2-\rho_{P2}H_1-\gamma_{P2}H_2) \\
0 &= 1-\alpha_{21}P_1-P_2-\rho_{P2}H_1-\gamma_{P2}H_2 \qquad (12) \\
P_2 &= 1-\alpha_{21}P_1-\rho_{P2}H_1-\gamma_{P2}H_2 when P_1 \neq 0 \\
P_2 &= 1-\rho_{P2}H_1-\gamma_{P2}H_2 when P_1 = 0
\end{aligned}$$

We can also solve for the fixed points when both $P_1 \neq 0$ and $P_2 \neq 0$:

$$\begin{aligned}
P_1 &= 1-\alpha_{12}P_2-\rho_{P1}H_1-\gamma_{P1}H_2 \\
P_1 &= 1-\alpha_{12}(1-\alpha_{21}P_1-\rho_{P2}H_1-\gamma_{P2}H_2)-\rho_{P1}H_1-\gamma_{P1}H_2 \\
P_1 &= 1-\alpha_{12}+\alpha_{12}\alpha_{21}P_1+\alpha_{12}\rho_{P2}H_1+\alpha_{12}\gamma_{P2}H_2-\rho_{P1}H_1-\gamma_{P1}H_2 \\
P_1-\alpha_{12}\alpha_{21}P_1 &= 1-\alpha_{12}+\alpha_{12}\rho_{P2}H_1+\alpha_{12}\gamma_{P2}H_2-\rho_{P1}H_1-\gamma_{P1}H_2 \\
P_1(1-\alpha_{12}\alpha_{21}) &= 1-\alpha_{12}+\alpha_{12}\rho_{P2}H_1+\alpha_{12}\gamma_{P2}H_2-\rho_{P1}H_1-\gamma_{P1}H_2 \\
P_1 &= \frac{1-\alpha_{12}+H_1(\alpha_{12}\rho_{P2}-\rho_{P1})+H_2(\alpha_{12}\gamma_{P2}-\gamma_{P1})}{(1-\alpha_{12}\alpha_{21})}
\end{aligned}$$

The complementary equation for P_2 is:

$$P_2 = \frac{1-\alpha_{12}+H_1(\alpha_{21}\rho_{P1}-\rho_{P2})+H_2(\alpha_{21}\gamma_{P1}-\gamma_{P2})}{(1-\alpha_{12}\alpha_{21})}$$

Stability Evaluation of Fixed Points

The stability at each fixed point can be assessed by taking the derivative of equation 5 and 6 in a Jacobean matrix:

$$J = \begin{pmatrix} \frac{\delta P_1}{\delta P_1} & \frac{\delta P_1}{\delta P_2} \\ \frac{\delta P_2}{\delta P_1} & \frac{\delta P_2}{\delta P_2} \end{pmatrix} \qquad (13)$$

$$\begin{aligned}
\frac{\delta P_1}{\delta P_1} &= \frac{\delta}{\delta} P_1(P_1 - P_1^2 - \alpha_{12}P_1P_2 - \rho_{P1}H_1P_1 - \gamma_{P1}H_2P_1) = 1 - 2P_1 - \alpha_{12}P_2 - \rho_{P1}H_1 - \gamma_{P1}H_2 \\
\frac{\delta P_1}{\delta P_2} &= \frac{\delta}{\delta} P_2(P_1 - P_1^2 - \alpha_{12}P_1P_2 - \rho_{P1}H_1P_1 - \gamma_{P1}H_2P_1) = -\alpha_{12}P_1 \\
\frac{\delta P_2}{\delta P_1} &= \frac{\delta}{\delta} P_1(P_2 - \alpha_{21}P_1P_2 - P_2^2 - \rho_{P2}H_1P_2 - \gamma_{P2}H_2P_2) = -\alpha_{21}P_2 \\
\frac{\delta P_2}{\delta P_2} &= \frac{\delta}{\delta} P_2(P_2 - \alpha_{21}P_1P_2 - P_2^2 - \rho_{P2}H_1P_2 - \gamma_{P2}H_2P_2) = 1 - \alpha_{21}P_1 - 2P_2 - \rho_{P2}H_1 - \gamma_{P2}H_2 \\
J &= \begin{pmatrix} 1 - 2P_1 - \alpha_{12}P_2 - \rho_{P1}H_1 - \gamma_{P1}H_2 & -\alpha_{12}P_1 \\ -\alpha_{21}P_2 & 1 - \alpha_{21}P_1 - 2P_2 - \rho_{P2}H_1 - \gamma_{P2}H_2 \end{pmatrix}
\end{aligned} \tag{14}$$

Each of the four fixed points should then be evaluated using the Jacobean:

Point $(0, 0)$

$$J_{(0,0)} = \begin{pmatrix} 1 - 2P_1 - \alpha_{12}P_2 - \rho_{P1}H_1 - \gamma_{P1}H_2 & -\alpha_{12}P_1 \\ -\alpha_{21}P_2 & 1 - \alpha_{21}P_1 - 2P_2 - \rho_{P2}H_1 - \gamma_{P2}H_2 \end{pmatrix}$$

$$J_{(0,0)} = \begin{pmatrix} 1 - \rho_{P1}H_1 - \gamma_{P1}H_2 & 0 \\ 0 & 1 - \rho_{P2}H_1 - \gamma_{P2}H_2 \end{pmatrix}$$

where $\lambda_1 = 1 - \rho_{P1}H_1 - \gamma_{P1}H_2$ and $\lambda_2 = 1 - \rho_{P2}H_1 - \gamma_{P2}H_2$. This point will be stable when both λ_1 and $\lambda 2$ are less than zero:

$$\begin{aligned}
\lambda_1 &\prec 0 \\
1 - \rho_{P1}H_1 - \gamma_{P1}H_2 &\prec 0 \\
\rho_{P1}H_1 + \gamma_{P1}H_2 &\succ 1
\end{aligned}$$

$$\begin{aligned}
\lambda_2 &\prec 0 \\
1 - \rho_{P2}H_1 - \gamma_{P2}H_2 &\prec 0 \\
\rho_{P2}H_1 - \gamma_{P2}H_2 &\succ 1
\end{aligned}$$

The point $(0,0)$ is stable when the sum of herbivory on forage type multiplied by preference for that forage type is less than 1. This situation reflects circumstances when grazing pressure is so high that all forage is driven to zero biomass.

Point $(0, P_2)$

$$J_{(0,P_2)} = \begin{pmatrix} 1-\alpha_{12}(1-\rho_{P2}H_1-\gamma_{P2}H_2) & 0 \\ \text{-}\alpha_{21}(1-\rho_{P2}H_1-\gamma_{P1}H_2) & \begin{matrix} 1-2(1-\rho_{P2}H_1-\gamma_{P2}H_2) \\ -\rho_{P2}H_1-\gamma_{P2}H_2 \end{matrix} \end{pmatrix}$$

$$= \begin{pmatrix} \begin{matrix} 1-\alpha_{12}+\alpha_{12}\rho_{P2}H_1+\alpha_{12}\gamma_{P2}H_2 \\ -\rho_{P1}H_1-\gamma_{P1}H_2 \end{matrix} & 0 \\ \text{-}\alpha_{21}(1-\rho_{P2}H_1-\gamma_{P2}H_2) & \begin{matrix} \text{-}1+2\rho_{P2}H_1+2\gamma_{P2}H_2 \\ -\rho_{P2}H_1-\gamma_{P2}H_2 \end{matrix} \end{pmatrix}$$

$$= \begin{pmatrix} \begin{matrix} 1-\alpha_{12}+H_1(\alpha_{12}\rho_{P2}-\rho_{P1}) \\ +H_2(\alpha_{12}\gamma_{P2}-\gamma_{P1}) \end{matrix} & 0 \\ \text{-}\alpha_{21}(1-\rho_{P2}H_1-\gamma_{P2}H_2) & \text{-}1+\rho_{P2}H_1+\gamma_{P2}H_2 \end{pmatrix}$$

where $\lambda_1 = 1-\alpha_{12}+H_1(\alpha_{12}\rho_{P2}-\rho_{P1})+H_2(\alpha\gamma_{P2}-\gamma_{P1})$ and $\lambda_2 = -1+\rho_{P2}H_1+\gamma_{P2}H_2$

.

This point will be stable when both λ_1 and λ_2 are less than zero:

$$1-\alpha_{12}+H_1(\alpha_{12}\rho_{P2}-\rho_{P1})+H_2(\alpha_{12}\gamma_{P2}-\gamma_{P1}) \prec 0$$

$$\alpha_{12}-H_1(\alpha_{12}\rho_{P2}-\rho_{P1})-H_2(\alpha_{12}\gamma_{P2}-\gamma_{P1}) \succ 1 \tag{15}$$

$$\text{-}1+\rho_{P2}H_1+\gamma_{P2}H_2 \prec 0$$

$$\rho_{P2}H_1+\gamma_{P2}H_2 \prec 1 \tag{16}$$

Given these circumstances, point $(0,0)$ and $(0,P2)$ cannot both be stable because equations (15) and (16) are contradictory.

Point $(P_1, 0)$

$$\begin{aligned} J_{(P_1,0)} &= \begin{pmatrix} \begin{array}{c} 1-2(1-\rho_{P1}H_1-\gamma_{P1}H_2) \\ -\rho_{P1}H_1-\gamma_{P1}H_2 \end{array} & \text{-}\alpha_{12}(1-\rho_{P1}H_1-\gamma_{P1}H_2) \\ 0 & \begin{array}{c} 1-\alpha_{21}(1-\rho_{P1}H_1-\gamma_{P1}H_2) \\ -\rho_{P2}H_1-\gamma_{P2}H_2 \end{array} \end{pmatrix} \\ &= \begin{pmatrix} \begin{array}{c} 1-2+2\rho_{P1}H_1+2\gamma_{P1}H_2- \\ \rho_{P1}H_1-\gamma_{P1}H_2 \end{array} & \text{-}\alpha_{12}(1-\rho_{P1}H_1-\gamma_{P1}H_2) \\ 0 & \begin{array}{c} 1-\alpha_{21}+\alpha_{21}\rho_{P1}H_1-\alpha_{21}\gamma_{P1}H_2 \\ -\rho_{P2}H_1-\gamma_{P2}H_2 \end{array} \end{pmatrix} \\ &= \begin{pmatrix} \text{-}1+\rho_{P1}H_1+\gamma_{P1}H_2 & \text{-}\alpha_{12}(1-\rho_{P1}H_1-\gamma_{P1}H_2) \\ 0 & \begin{array}{c} 1-\alpha_{21}+H_1(\alpha_{21}\rho_{P1}-\rho_{P2}) \\ +H_2(\alpha_{21}\gamma_{P1}-\gamma_{P2}) \end{array} \end{pmatrix} \end{aligned}$$

where $\lambda_1 = -1+\rho_{P1}H_1+\gamma_{P1}H_2$ and $\lambda_2 = 1\alpha_{21}+H_1(\alpha_{21}\rho_{P1}-\rho_{P2})+H_2(\alpha_{21}\gamma_{P1}-\gamma_{P2})$

.

This point will be stable when both λ_1 and λ_2 are less than zero:

$$\begin{aligned} \text{-}1+\rho_{P1}H_1\gamma_{P1}H_2 &\prec 0 \\ \rho_{P1}H_1+\gamma_{P1}H_2 &\succ 1 \qquad (17) \end{aligned}$$

$$\begin{aligned} 1-\alpha_{21}+H_1(\alpha_{21}\rho_{P1}-\rho_{P2})+H_2(\alpha_{21}\gamma_{P1}-\gamma_{P2}) &\prec 0 \\ \alpha_{21}+H_1(\alpha_{21}\rho_{P1}-\rho_{P2})+H_2(\alpha_{21}\gamma_{P1}-\gamma_{P2}) &\prec 1 \qquad (18) \end{aligned}$$

Point $(P_1, 0)$ also cannot be stable while point $(0, 0)$ is stable because equations (17) and (15) are contradictory.

Point (P_1, P_2)

$$J_{(P_1,(P_2)} = \begin{pmatrix} \begin{array}{c} 1-2P_1\text{-}\alpha_{12}P_2-\rho_{P1}H_1 \\ -\gamma_{P1}H_2 \end{array} & \text{-}\alpha_{12}P_1 \\ \text{-}\alpha_{21}P_2 & \begin{array}{c} 1-\alpha_{21}P_1-2P_2-\rho_{P2}H_1 \\ -\gamma_{P2}H_2 \end{array} \end{pmatrix} \qquad (19)$$

From equations (11) and (12) we know that at equilibrium $1-P_1-\alpha_{12}P_2-\rho_{P1}H_1-\gamma P1H_2$ and $1-P_2-a_{21}P_1-\rho_{P2}H_1-\gamma_{P2}H_2$ equal zero. Therefore, equation (19) can be rewritten as follows:

$$\begin{aligned}
J_{(P_1,P_2)} &= \begin{pmatrix} \begin{array}{c}(1 - P_1 - \alpha_{12}P_2 - \rho_{P1}H_1 \\ - \gamma_{P1}H_2) - P_1\end{array} & \text{-}\alpha_{12}P_1 \\ \text{-}\alpha_{21}P_2 & \begin{array}{c}(1 - P_2 - \alpha_{21}P_1 - \rho_{P2}H_1 \\ - \gamma_{P2}H_2) - P_2\end{array} \end{pmatrix} \\
&= \begin{pmatrix} \text{-}P_1 & \text{-}\alpha_{12}P_1 \\ \text{-}\alpha_{21}P_2 & \text{-}P_2 \end{pmatrix} \qquad (20) \\
&= \begin{pmatrix} \text{-}(1 - \rho_{P1}H_1 - \gamma_{P1}H_2) & \text{-}\alpha_{12}(1 - \rho_{P1}H_1 - \gamma_{P1}H_2) \\ \text{-}\alpha_{21}(1 - \rho_{P2}H_1 - \gamma_{P2}H_2) & \text{-}(1 - \rho_{P2}H_1 - \gamma_{P2}H_2) \end{pmatrix} \\
&= \begin{pmatrix} \text{-}1 + \rho_{P1}H_1 + \gamma_{P1}H_2 & \text{-}\alpha_{12} + \alpha_{12}\rho_{P1}H_1 + \alpha_{12}\gamma_{P1}H_2 \\ \text{-}\alpha_{21} + \alpha_{21}\rho_{P2}H_1 + \alpha_{21}\gamma_{P2}H_2 & \text{-}1 + \rho_{P2}H_1 + \gamma_{P2}H_2 \end{pmatrix}
\end{aligned}$$

$$\begin{aligned}
T &= \text{-}1 + \rho_{P1}H_1 + \gamma_{P1}H_2 - 1 + \rho_{P2}H_1 + \gamma_{P2}H_2 \\
&= \text{-}2 + H_1(\rho_{P1} + \rho_{P2}) + H_2(\gamma_{P1} + \gamma_{P2}) \\
D &= (\text{-}1 + \rho_{P1}H_1 + \gamma_{P1}H_2)(\text{-}1 + \rho_{P2}H_1 + \gamma_{P2}H_2) - (\text{-}\alpha_{12} + \alpha_{12}\rho_{P1}H_1 + \alpha_{12}\gamma_{P1}H_2) \\
&\quad (\text{-}\alpha_{21} + \alpha_{21}\rho_{P2}H_1 + \alpha_{21}\gamma_{P2}H_2) \\
&= 1 - \rho_{P1}H_1 - \rho_{P2}H_2 + \rho_{P1}\rho_{P2}H_1^2 - \gamma_{P1}H_2 - \gamma_{P2}H_2 + \gamma_{P1}\gamma_{P2}H_2^2 + \gamma_{P1}\rho_{P2}H_1H_2 + \\
&\quad \gamma_{P2}\rho_{P1}H_1H_2 - \alpha_{12}\alpha_{21} + alpha_{12}\alpha_{21}\rho_{P1}H_1 + \alpha_{12}\alpha_{21}\rho_{P1}H_2 + \alpha_{12}\alpha_{21}\rho_{P2}H_1 - \\
&\quad \alpha_{12}\alpha_{21}\rho_{P1}\rho_{P2}H_1^2 - \alpha_{12}\alpha_{21}\gamma_{P1}\rho_{P2}H_1H_2 + \alpha_{12}\alpha_{21}\gamma_{P2}H_2 - \alpha_{12}\alpha_{21}\gamma_{P2}\rho_{P1}H_1H_2 - \\
&\quad \alpha_{12}\alpha_{21}\gamma_{P1}\gamma_{P2}H_2^2 \\
&= 1 - \rho_{P1}H_1 - \rho_{P2}H_2 + \rho_{P1}\rho_{P2}H_1^2 - \gamma_{P1}H_2 - \gamma_{P2}H_2 + \gamma_{P1}\gamma_{P2}H_2^2 + \gamma_{P1}\rho_{P2}H_1H_2 + \\
&\quad \gamma_{P2}\rho_{P1}H_1H_2 - \alpha_{12}\alpha_{21} + \alpha_{12}\alpha_{21}\rho_{P1}H_1 + \alpha_{12}\alpha_{21}(\rho_{P1}H_2 + \rho_{P2}H_1 - \rho_{P1}\rho_{P2}H_1^2 - \\
&\quad \gamma_{P1}\rho_{P2}H_1H_2 + \gamma_{P2}H_2 - \gamma_{P2}\rho_{P1}H_1H_2 - \gamma_{P1}\gamma_{P2}H_2^2) \\
&= (1 - \alpha_{12}\alpha_{21})(1 - \rho_{P1}H_1 - \rho_{P2}H_1 - \rho_{P1}\rho_{P2}H_1^2 - \gamma_{P1}H_2 - \gamma_{P2}H_2 + \gamma_{P1}\gamma_{P2}H_2^2 + \\
&\quad \gamma_{P1}\rho_{P2}H_1H_2 + \gamma_{P2}\rho_{P1}H_1H_2)
\end{aligned} \qquad (21)$$

$$\begin{aligned}
\lambda_{1,2} &= \frac{T \pm \sqrt{(T^2 - 4D)}}{2} \\
&= \tfrac{1}{2}(-2 + H_1\Phi + H_2\Theta) \ \pm \ \tfrac{1}{2}\Big[(-2 + H_1\Phi + H_2\Theta)^2 \ - 4\big((1 - \alpha_{12}\alpha_{21})(1 - \\
&\quad H_1\Phi - H_2\Theta + H_1H_2(\gamma_{P1}\rho_{P2} + \gamma_{P2}\rho_{P1}) - H_1^2\rho_{P1}\rho_{P2} + H_2^2\gamma_{P1}\gamma_{P2})\big)\Big]^{-\frac{1}{2}}
\end{aligned} \qquad (22)$$

where $(\rho_{P1} + \rho_{P2}) = \Phi$ and $(\gamma_{P1} + \gamma_{P2}) = \Theta$.

This last point is stable when equation (22) is less than zero. However, because is no straightforward interpretation of (22), it may be helpful to look at an earlier version, equation (20). By solving for the trace and determinant at this equation, we can evaluate the stability of the fixed point using a stability diagram for two dimensional continuous systems.

$$\begin{aligned} T &= \text{-}P_1 - P_2 \\ T &= \text{-}(P_1 + P_2) \qquad (23) \\ D &= (\text{-}P_1)(\text{-}P_2) - (\text{-}\alpha_{21}P_2)(\text{-}\alpha_{12}P_1) \\ D &= P_1P_2(1 - \alpha_{21}\alpha_{12}) \qquad (24) \end{aligned}$$

Equation (23) suggests the trace is positive as long as $(P1 + P2)$ is negative. However, because a negative biomass does not make biological sense, the trace will always be negative. Therefore, the trace determinant value will fall in regions **I** (stable spiral), **II** (stable node), or **III** (saddle point) of typical trace-determinant diagram. Given that P_1 and P_2 are positive numbers, the determinant (24) will be negative if $\alpha_{21}\alpha_{12}$ is greater than one, corresponding to region **III** (saddle point). α_{21} and α_{12} can be expressed as ratios of interspecific competition to intraspecific competition:

$$\begin{aligned} \alpha_{21}\alpha_{12} &\succ 1 \\ \left(\frac{\alpha_{21}}{\alpha_{11}}\right)\left(\frac{\alpha_{12}}{\alpha_{22}}\right) &\succ 1 \\ \left(\frac{\alpha_{21}}{\alpha_{11}}\right) &\succ \left(\frac{\alpha_{22}}{\alpha_{12}}\right) \\ \alpha_{12}\alpha_{21} &\succ \alpha_{22}\alpha_{12} \qquad (25) \end{aligned}$$

For $\alpha_{21}\alpha_{12}$ to be greater than one, the product of interspecific competition must be larger than the product of intraspecific competition. Therefore, the system will be unstable (a saddle point) if interspecific competition is larger than intraspecific competition. The trace determinant value will fall in regions I (stable spiral) or II (stable node) if $\alpha_{21}\alpha_{12}$ is less than one. In this case, the product of interspecific competition is less than the product of intraspecific competition. Therefore, the system will be a stable node (or spiral) if intraspecific competition is greater than interspecific competition.

APPENDIX D

Table D-1. List of plants collected in Dawu Township. Type A plants were found only at the on-colony site, type B only at the off-colony site and type C on both sites.

Family	Species	Type
Apiaceae	*Pleurospermum camtschaticum*	C
	Pleurospermum hedinii	A
Asteraceae	*Ajania khartensis*	C
	Anaphalis lactea	C
	Aster flaccidus	A
	Leontopodium pusillum	C
	Saussurea arenaria	C
	Saussurea leontodontoides	B
	Saussurea superba	C
	Taraxacum leucanthum	C
Boraginaceae	*Microula tibetica*	A
Brassicaceae	*Draba lanceolata*	A
	Hedinia tibetica	A
	Lepidium apetalum	A
Caprifoliaceae	*Lonicera rupicola*	C
Caryophyllaceae	*Melandrium apetalum*	A
	Silene conoidea	C
	Stellaria sagioroides	A
Chenopodiaceae	*Axyris amaranthoides*	A
	Chenopodium glaucum	A
Cyperaceae	*Carex moorcraftii*	C
	Kobresia humilis	C
	Kobresia macrantha	C
	Kobresia pygmaea	C
	Scirpus distigmaticus	C
Elaeagnaceae	*Hippophae rhamnoides*	A
Fabaceae	*Amblytropis diversifolia*	C
	Astragalus fenzeliarus	C
	Astragalus sp. 1	C
	Astragalus sp. 2	A
	Oxytropis glabra	C
Gentianaceae	*Comastoma pulmonarium*	C
	Gentiana leucomelaena	A
	Gentiana sp.	C
	Gentiana squarrosa	C
	Gentiana straminea	C
	Gentianopsis paludosa	B
Iridaceae	Iris sp.	A
Lamiaceae	*Ajuga lupulina*	A
	Elsholtzia densa	A
	Lamiophlomis rotata	C

Table D-1. Continued.

Liliaceae	*Allium sikkimense*	B
	Polygonatum sibiricum	C
Morinaceae	*Morina kokonorica*	A
Papaveracaae	*Hypecoum leptocarpum*	A
Poaceae	Compressed purple	C
	Elymus nutans	C
	Koenigia pilosa	A
	Poa bomiensis	B
	Ptilagrostis concinna	C
	Stipa sp.	A
Polygonaceae	*Polygonum sibiricum*	A
Primulaceae	*Androsace gmelinii var. geophila*	A
	Androsace marie	C
	Glaux maritima	C
	Pomatosace filicula	A
Ranunculaceae	*Aconitum pendulum*	A
	Aconitum sp.	C
	Delphinium caeruleum	A
	Delphinium densiflorum	A
	Ranunculus brotherusii	C
	Ranunculus membraneous	C
	Ranunculus nephelogenes	C
	Thalictrum rutifolium	C
	Callianthemum pimpinetloides	B
Rosaceae	*Potentilla anserina*	C
	Potentilla nivea	C
	Potentilla saundersiana	C
Rubiaceae	*Galium verum*	A
Saxifragaceae	*Parnassia trinervis*	C
	Saxifraga stolonifera	C
Scrophulariaceae	*Euphrasia pectinata subsp pectinata*	A
	Euphrasia pectinata	A
	Lancea tibetica	C
	Pedicularis kansuensis	B
	Pedicularis lyrata	C
	Pedicularis sp.	A
	Veronica ciliata	C