

LETTER

Introduced grazers can restrict potential soil carbon sequestration through impacts on plant community composition

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Abstract

Grazing occurs over a third of the earth's land surface and may potentially influence the storage of 10^9 Mg year⁻¹ of greenhouse gases as soil C. Displacement of native herbivores by high densities of livestock has often led to overgrazing and soil C loss. However, it remains unknown whether matching livestock densities to those of native herbivores can yield equivalent soil C sequestration. In the Trans-Himalayas we found that, despite comparable grazing intensities, watersheds converted to pastoralism had 49% lower soil C than watersheds which retain native herbivores. Experimental grazer-exclusion within each watershed type, show that this difference appears to be driven by indirect effects of livestock diet selection, leading to vegetation shifts that lower plant production and reduce likely soil C inputs from vegetation by *c.* 25 gC m⁻² year⁻¹. Our results suggest that while accounting for direct impacts (stocking density) is a major step, managing indirect impacts on vegetation composition are equally important in influencing soil C sequestration in grazing ecosystems.

Keywords

Biodiversity, carbon dioxide, climate change, ecosystem function, ecosystem services, human natural ecosystems, land use change, livestock production, rangelands, wildlife conservation.

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INTRODUCTION

Carbon (C) sequestration has emerged as an important service provided by natural and managed ecosystems to mitigate current and projected climate change scenarios. Soils hold a vast potential for storing C (in excess of 10^{11} metric tons globally), and studies have estimated that adopting improved land management practices alone might offset about a third of the global annual greenhouse-gas emissions (e.g., Lal 2004). Over a quarter of the global potential for soil C storage may be influenced by grazing (Scurlock & Hall 1998), as it is the most geographically expansive land use today (Olf *et al.* 2002). Although mammalian herbivores convert consumed plants into CO₂ and other greenhouse gases such as methane (CH₄), studies have shown that grazing can often lower net ecosystem C emissions and promote soil C storage (e.g., Wilsey *et al.* 2002), especially in dry environments (Scurlock & Hall 1998; Allard *et al.* 2007; Derner & Schuman 2007). Thus, facilitating soil C storage through improved grazing

management (Pellant *et al.* 2005) is a very important component for offsetting greenhouse-gas emissions to mitigate climate change (Lal 2004).

Historically, grazing ecosystems in all continents have been severely impacted by human land use through conversion for livestock production. The replacement of native herbivores by excessive stocking densities of livestock (Prins 1992) has often resulted in overgrazing, consequent vegetation degradation, and ultimately in soil C loss (Conant *et al.* 2002; Pellant *et al.* 2005; FAO 2007; Reynolds *et al.* 2007). Reduction of livestock stocking densities to more sustainable levels is widely recommended as a policy to arrest, and possibly recover soil C losses (Conant *et al.* 2002; Pellant *et al.* 2005; FAO 2007). Yet, in the absence of direct comparisons of ecosystem function and services between managed ecosystems under livestock and natural ecosystems under native grazers, it remains uncertain whether managing stocking densities of livestock alone is sufficient to realize the full potential of soil C storage in grazing ecosystems (Milchunas *et al.* 1998).

Direct grazer impact on plant production, and thereby on potential soil C inputs, is likely mediated by grazing intensity, and has been extensively studied with theoretical models (e.g., de Mazancourt & Loreau 2000) and through experimentation (Milchunas & Lauenroth 1993). Grazers can also indirectly alter plant community composition through their diet selectivity (Augustine & McNaughton 1998; Ritchie & Olff 1999), and consequently influence soil C inputs (De Deyn *et al.* 2008). To date, although qualitative predictions do exist (Ritchie & Olff 1999), theoretical models are yet to explicitly incorporate the influence of diet selectivity on plant production as mediated by plant community composition. Although differences in such indirect effects between livestock and native herbivores have long been recognized (McNaughton 1986), current policy, worldwide, remains uninformed of their ecosystem consequences for plant production and soil C storage (Conant *et al.* 2002).

Based on first principles of consumer–resource interactions (Ritchie & Olff 1999; Casula *et al.* 2006), we evaluate a simple mathematical model to link herbivore diet selectivity and plant species composition (see model, Data S1). The model's predictions align with the hypothesis that diet differentiation among herbivores can have *compensatory* effects on plant communities and prevent directional shifts in composition, as opposed to *additive* effects in the absence of diet differentiation resulting in directional changes (Ritchie & Olff 1999). Using a herbivore-exclusion experiment nested within a natural experiment in the Trans-Himalayan grazing ecosystem in northern India, we investigated whether livestock and native grazers differ in their: (1) direct effects on potential soil C inputs (mediated by grazing intensity), and (2) indirect effects on potential soil C inputs (mediated by their effects on plant community composition).

MATERIALS AND METHODS

Experimental design

The Trans-Himalayas of northern India provide a unique replicated natural experiment to evaluate grazer effects on potential inputs to soil C in natural ecosystems featuring native grazers, in comparison with managed ecosystems featuring introduced livestock. Here, local extinctions over the past 4–5 decades (Mishra *et al.* 2002) have established replicate watersheds grazed primarily by native species that are juxtaposed with watersheds that are managed for mixed-species of livestock by an indigenous subsistence-based pastoralist society (see map in Data S1). Some watersheds represent primarily natural ecosystems dominated by free ranging native species – yaks *Bos grunniens* (body weight 350 kg), bharal *Pseudois nayaur* (55 kg) and ibex *Capra sibirica*

(76 kg). Other watersheds are managed ecosystems dominated by mixed herds of cattle (250 kg), yak–cattle hybrids (250 kg), horses (220 kg), donkeys (90 kg), goats (30 kg) and sheep (35 kg) (see map, Data S1). This interspersion of natural and managed watersheds is reinforced by topographical barriers such as deep canyons and high ridges that restrict animal and human movement across the landscape. Consequently, these watersheds remain semi-isolated and serve as replicates of two alternative land uses – grazing by free ranging native herbivores, and grazing by husbanded livestock. Between 2005 and 2008, we used a 4-year manipulative herbivore-exclusion experiment nested within this natural experiment to evaluate the effects of native grazers and introduced livestock on plant production and community composition, both of which can co-determine potential C inputs to soils.

Based on previous work on animal distribution and abundance (Bagchi *et al.* 2004; Mishra *et al.* 2004), we identified different watersheds, each 4–6 km², in the Spiti region of northern India to serve as replicates within which to compare the effects of native herbivores ($n = 4$ natural watersheds) and introduced livestock ($n = 3$ managed watersheds) on potential soil C inputs via effects on plant production (see map, Data S1). Second, we verified, using dung counts in 3–4 plots (100 m² each) in each watershed (24 total), that the two watershed types were indeed differentially used by native grazers and introduced livestock. Initially, existing dung in the plots was gently crushed so that subsequent depositions could be distinguished. To avoid loss of dung due to decomposition, newly deposited dung was counted frequently (3–4 week intervals) between May and September 2005 to obtain a cumulative estimate for the growth season. Herbivore species were identified by the shape and size of their pellets. Third, we verified whether these watersheds were suitable replicates to assess differences in the effects of native and introduced herbivores on plant production and composition, and C inputs to soil. We measured several key edaphic factors, such as soil pH, electrical conductivity, texture, bulk density, cation exchange capacity and availability of major cations in the same plots following standard procedures (Robertson *et al.* 1999).

To evaluate herbivore effects on plant production and composition, we established permanent grazing exclosures in the watershed sites in 2005. In each watershed, we set up 3–4 permanent herbivore exclosures (100 m²) for a total of 24 fenced plots, each paired with an adjacent grazed control plot ($n = 48$ total plots). In each plot, we measured aboveground net primary production (ANPP) and grazing intensity (i.e., fraction of ANPP removed by grazers) at monthly intervals for three growth seasons (May through August, 2005–2008), using 1 m² temporary cages following McNaughton *et al.* (1996). In 2007, we measured

belowground production using 20 cm deep and 5 cm radius root ingrowth cores that were inserted in May and extracted in August. A pilot survey to determine the required depth of sampling revealed that more than 95% of root biomass is located within the top 15 cm of soil, and bedrock-depth is often approached at 20–22 cm, corroborating the findings of previous studies in the Tibetan highlands (Xu *et al.* 2004). Biomass data are reported as dry weight (g m^{-2}) of oven-dried samples (40 °C, 48 h).

Percent C content in soil, estimated for each paired-plot using an autoanalyzer (Carlo-Erba 1500, Milan, Italy), was multiplied by soil bulk density to estimate soil C stock per unit area up to 20 cm depth. Potential soil C input from vegetation was estimated as the product of dry weights and C content of plant tissue, plus the amount returned as dung in the grazed plots. To evaluate the effect of herbivore diet selectivity on vegetation composition, we documented plant species composition (and bare ground) in the same plots at 50 points along a 10 m line-intercept at peak standing biomass (August) between 2005 and 2008. Difference in plant species composition between paired fenced-and-control plots was calculated as the Bray–Curtis dissimilarity index

$$B_{jk} = \sum_{i=1}^n \frac{|y_{ij} - y_{ik}|}{(y_{ij} + y_{ik})},$$

where y_{ij} is the cover of i^{th} species in the j^{th} sample, and y_{ik} is the cover of i^{th} species in the k^{th} sample, summed across all n species. We sorted peak-season clipped aboveground biomass (1 m^2 plots) into major plant functional groups – grasses, sedges and forbs – and determined relative biomass from dried weights.

To evaluate differences in feeding complementarity between native grazers and livestock, we calculated diet selectivity over the three plant functional groups using Ivlev's index following Jacobs (1974), i.e., consumption relative to availability based on data on their foraging habits (Bagchi *et al.* 2004; Mishra *et al.* 2004). This index was calculated as

$$\frac{r - p}{r + p - 2rp},$$

where r is the proportion of an item in diet, and p is the proportional availability of the item in the environment (Jacobs 1974). These diet selectivity indices represent the relative consumption of plants, accounting for differences in their relative abundance, and hence their availability to grazers. In this way, diet selectivity, rather than herbivores' diet profile *per se*, indicates the grazers' impact on plant community structure and composition (McNaughton 1986; Augustine & McNaughton 1998; Olf & Ritchie 1998; Ritchie & Olf 1999). Ivlev's index scores are normalized between -1 and $+1$. Positive values for a plant type indicate

that herbivores consume it preferentially, i.e., in excess of their relative abundance. Similarly, a negative score indicates the tendency to avoid a plant type, leading to consumption that is lower than its relative abundance (Jacobs 1974). In this manner, herbivores may render competitive advantages to plants that are consumed less than their relative availability, thus exercising strong control over vegetation composition (Augustine & McNaughton 1998; Olf & Ritchie 1998; Ritchie & Olf 1999).

Data analysis

Effects of herbivore type (native vs. livestock) and grazing (grazed vs. ungrazed) on plant production, soil C and community composition were evaluated with repeated measures Analysis of variance on data collected over multiple growth seasons (2005–2008) using general linear models in SAS v. 9.1 (SAS Institute, Cary, NC, USA). To avoid pseudoreplication, each watershed was considered as a sampling unit ($n = 7$ total) and different exclosures within a watershed were considered sub-samples. Multiple comparisons of means were done using a Tukey–Kramer adjustment of error ($\alpha = 0.05$). Only main effects and interactions between the treatments are reported unless there were significant three-way interactions involving time. Data are reported as mean \pm SE.

RESULTS

Dung counts verified that three of our identified watersheds were primarily used by livestock, and the other four were primarily used by native grazers (Fig. 1a). The analysis of abiotic soil properties indicated that there were no systematic differences between the two types of watersheds in elevation and edaphic conditions such as soil pH, electrical conductivity, texture, bulk density, cation exchange capacity and availability of major cations (Table 1). The watersheds were, thus, comparable and suitable replicates to assess differences between direct and indirect impacts of native and introduced herbivores on soil C inputs from vegetation.

Comparison of the amount of plant production consumed in these two watershed types revealed they experienced similar grazing intensities during our study (herbivore type $F_{1,5} = 0.49$, $P = 0.51$, time $F_{2,3} = 0.62$, $P = 0.59$, interaction $F_{2,3} = 0.37$, $P = 0.72$, Fig. 1b). Despite similar grazing intensities (Fig. 1b) and comparable edaphic conditions (Table 1), soil C was 49% lower in the managed watersheds with livestock than in natural watersheds with native grazers ($F_{1,13} = 17.55$, $P = 0.001$, Fig. 2a). Under grazing, the average estimated soil C stock in natural watersheds was 1169 gC m^{-2} higher than in managed watersheds ($F_{1,13} = 12.54$, $P = 0.005$, Fig. 2b). In the

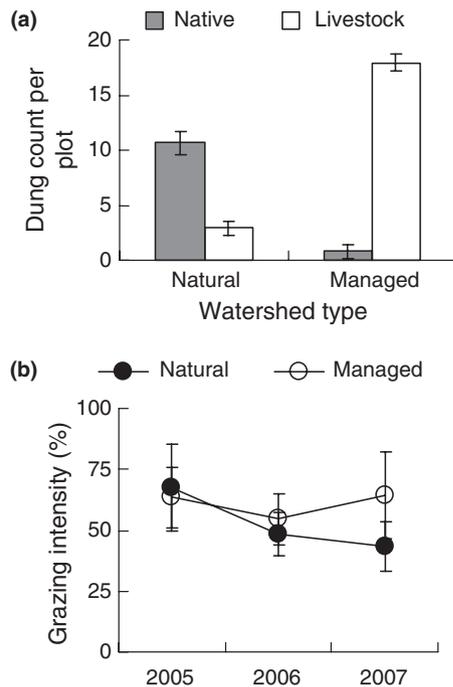


Figure 1 Dung counts of native herbivores and livestock (mean \pm SE in 100 m² plots) in natural and managed watersheds in the Spiti region of northern India (a). Based on percentage of plant production consumed, the natural and managed watersheds show comparable grazing intensities during 2005–2007 (b). The slight but non-significant decline in grazing intensity in natural watersheds in 2007 could be because of frequent visits to our plots (see text for details).

context of local extinctions of wildlife 4–5 decades ago, this difference can be seen as a relative loss ranging between 23.4 gC m⁻² year⁻¹ (over 50 years) and 29.2 gC m⁻² year⁻¹ (over 40 years).

Herbivore-exclusion experiments revealed that this substantial difference in soil C can be attributed to differences in potential C inputs from plant production which was much higher in the natural watersheds with native herbivores. Total net primary production (TNPP), calculated as the sum of net belowground primary production (BNPP, Fig. 2c) and aboveground primary production (ANPP, Fig. 2d) was 40% higher in natural watersheds ($F_{1,10} = 5.86$, $P = 0.02$, Fig. 2c). TNPP was negatively impacted by grazing ($F_{1,10} = 4.55$, $P = 0.04$). Grazing had negative impacts on BNPP ($F_{1,10} = 5.36$, $P = 0.02$), and it was 40% higher in the natural watersheds than in managed watersheds ($F_{1,10} = 6.15$, $P = 0.01$, Fig. 2c). ANPP was small compared to BNPP but unlike BNPP, it was higher in the grazed plots ($F_{1,13} = 14.70$, $P = 0.002$, Fig. 2d). Also unlike BNPP, ANPP was higher in the managed watersheds with livestock ($F_{1,13} = 4.17$, $P = 0.06$). Importantly, following only 3 years of herbivore exclusion, BNPP and TNPP in the managed watersheds recovered to levels that are comparable to natural watersheds (Fig. 2c,e). C content of aboveground tissue ($43.2 \pm 0.4\%$), belowground tissue ($28.8 \pm 0.5\%$) and dung ($39.4 \pm 0.7\%$) was multiplied by respective dry weights to obtain potential C inputs from these sources (Table 2). There were no systematic differences in per cent C content of tissue and dung among the treatment categories ($P > 0.47$ in all comparisons). Under grazing, average potential C input to soil in natural watersheds was 103 gC m⁻² year⁻¹ higher than in the managed watersheds ($F_{1,10} = 5.77$, $P = 0.02$, Table 2).

Similar grazing intensities under comparable edaphic conditions would indicate that native herbivores and livestock may not differ substantially in their direct impacts on plant production and potential soil C inputs. Nevertheless, they may still differ in their indirect effects mediated by how they influence plant community composition. The two

Table 1 Comparison of managed watersheds (dominated by livestock) and natural watersheds (dominated by native herbivores) in the Spiti region of northern India. Mean and ± 1 SE of different parameters are reported along with P -values of one-way ANOVA

Parameter	Watershed type		P -value
	Managed	Natural	
Elevation (m above sea level)	4325 \pm 31	4358 \pm 40	0.44
pH	7.72 \pm 0.10	7.92 \pm 0.09	0.18
Electrical conductivity (m moh cm ⁻²)	0.14 \pm 0.01	0.15 \pm 0.01	0.30
Sand (%)	47.81 \pm 3.29	44.38 \pm 2.89	0.42
Silt (%)	34.20 \pm 1.48	33.23 \pm 1.30	0.61
Clay (%)	17.94 \pm 1.09	18.86 \pm 0.96	0.52
Texture (USDA category)	Sandy-loam	Sandy-loam	–
Bulk density (g cm ⁻³)	1.01 \pm 0.04	1.06 \pm 0.03	0.39
Cation exchange capacity (meq g ⁻¹)	13.02 \pm 0.72	12.36 \pm 0.63	0.51
Calcium (meq g ⁻¹)	8.21 \pm 0.36	8.47 \pm 0.32	0.58
Magnesium (meq g ⁻¹)	1.62 \pm 0.20	1.65 \pm 0.17	0.90
Bare ground (%)	19.8 \pm 3.2	27.6 \pm 2.6	0.006

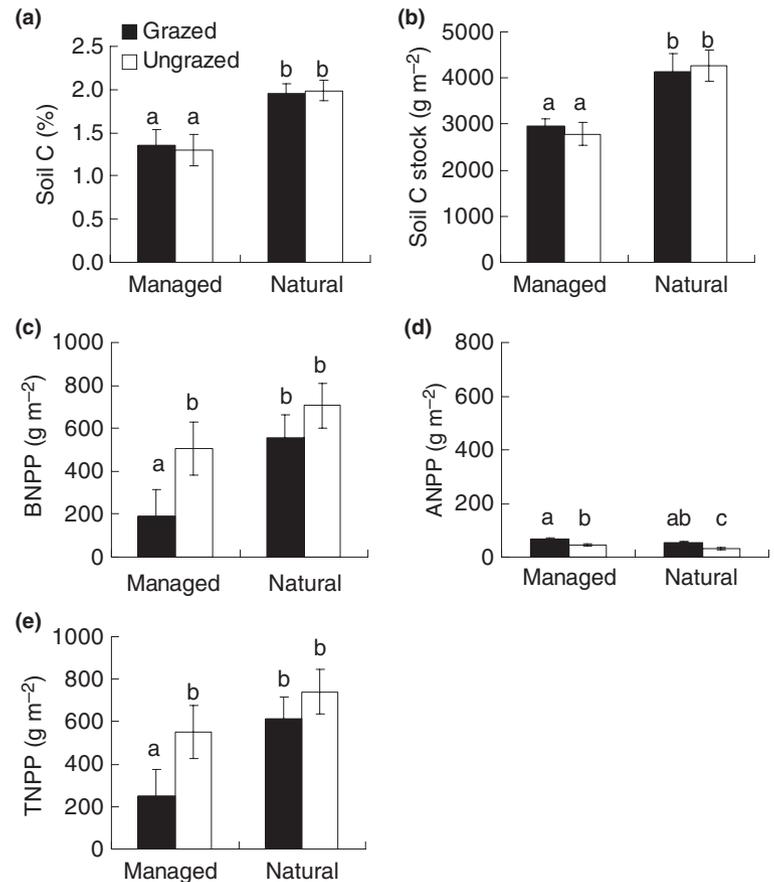


Figure 2 Differences in soil C content by weight (a) and total soil C stock up to 20 cm depth (b) in Spiti region of northern India between managed watersheds with livestock and natural watersheds with native herbivores. Differences in belowground net primary production (BNPP, c), aboveground net primary production (ANPP, d), and total net primary production (TNPP = ANPP + BNPP, e) in grazed and ungrazed plots from two types of watersheds. Different letters represent differences in multiple comparisons of means.

Table 2 Estimated annual C inputs (gC m⁻²) from aboveground and belowground production and through return of dung in Spiti region of northern India (mean ± 1 SE) for four treatment categories. Under grazing, average C input in natural watersheds with native grazers was 103 gC m⁻² higher than in managed watersheds with livestock

Grazing	Watershed type	Source of C input			Total (sum)
		Aboveground	Belowground	Dung	
Grazed	Managed	13 ± 1	55 ± 10	5 ± 1	73 ± 10 ^a
Grazed	Natural	10 ± 1	160 ± 29	6 ± 1	176 ± 21 ^b
Ungrazed	Managed	19 ± 2	147 ± 32	0 (NA)	166 ± 33 ^b
Ungrazed	Natural	15 ± 1	202 ± 36	0 (NA)	217 ± 37 ^b

Letters in superscript indicate differences in means from multiple-comparison tests.

types of watersheds had remarkable differences in their vegetation composition despite sharing an overlapping and relatively small pool of 39 plant species, of which only 8 contributed to > 10% of community biomass as the others were rare (see species list in Data S1). Summarized into functional types, while the natural watersheds with native grazers were co-dominated by grasses and forbs in 2005 (Fig. 3a), the managed watersheds with livestock were dominated by sedges (Fig. 3a). Between 2005 and 2008, exclusion of livestock in managed watersheds led to much

stronger shifts in vegetation composition than the exclusion of native grazers in natural watersheds. Bray–Curtis dissimilarity in plant species composition in paired grazed-and-ungrazed plots was higher in managed watersheds ($44.1 \pm 5.1\%$) compared to natural watersheds ($27.3 \pm 4.5\%$, repeated measures ANOVA over 4 years $F_{1,5} = 8.68$, $P = 0.03$). This difference in compositional change is summarized as relative biomass of plant functional types (Fig. 3b). Large compositional changes were driven by substantial increases in forbs at the expense of sedges in the

managed watersheds (Fig. 3b). In comparison, compositional changes in the natural watersheds were much smaller (Fig. 3b). Thus, community composition in managed watersheds approached that in the natural watersheds after only 4 years of herbivore exclusion (Fig. 3b). This differential response from forbs was particularly important because soil C was positively correlated with BNPP ($r = 0.61$, $P = 0.002$), and with relative abundance of forbs ($r = 0.45$, $P = 0.03$) as BNPP, in turn, was correlated with relative abundance of forbs ($r = 0.57$, $P = 0.004$). Thus, the strong recovery in forbs allowed the ungrazed vegetation communities in the managed watersheds to not only resemble the natural watersheds in composition (Fig. 3b), but also emulate them in total plant production (Fig. 2c–e).

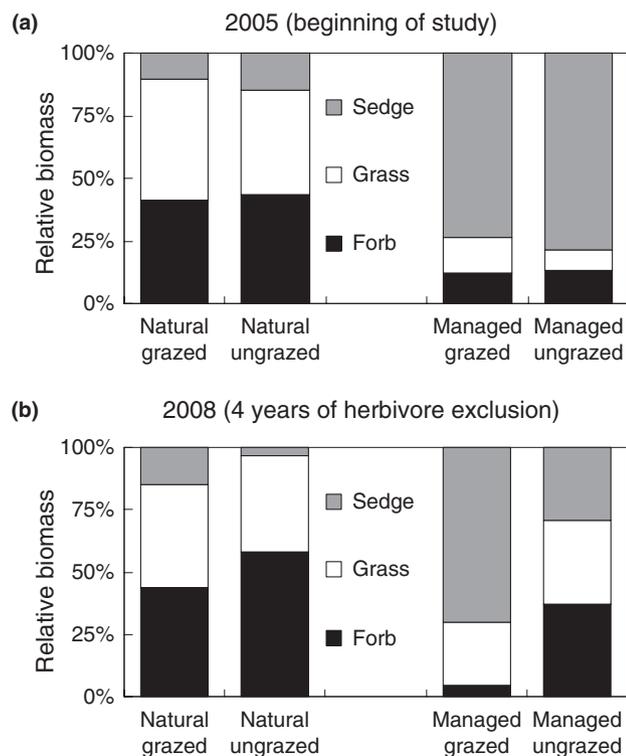


Figure 3 Differences in response of grazed and ungrazed vegetation community following in two types of watersheds, summarized into average relative biomass of three functional groups. Initially in 2005, plots in managed watersheds were dominated by sedges, while plots in natural watersheds were co-dominated by grasses and forbs (a). After 4 years of herbivore exclusion, ungrazed plots in natural watersheds showed minor changes in relative abundance; whereas, those in managed watersheds showed a strong recovery by forbs (b). This recovery by forbs allowed the ungrazed plots in managed watersheds to emulate vegetation composition in the natural watersheds, and even approximate them in plant production (Fig. 2). Variation around mean was analysed using repeated measures ANOVA on Bray–Curtis similarity index (see text for statistical tests).

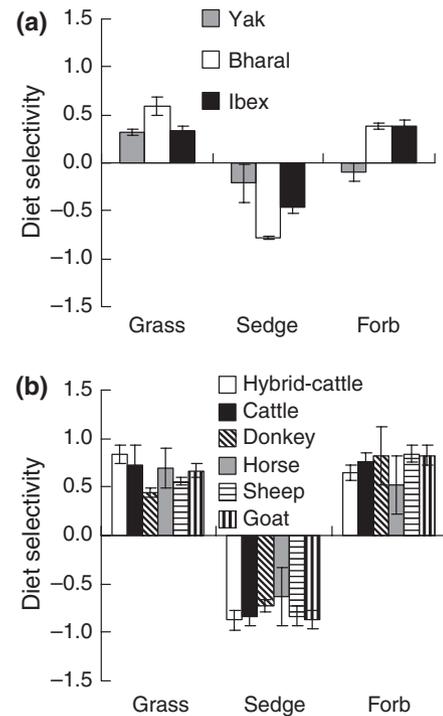


Figure 4 Differences in diet selectivity (Ivlev's index) among native herbivores (a) and introduced livestock (b) in Spiti region in northern India. Native herbivores differ in their selectivity towards grasses, sedges and forbs (a), while the livestock do not (b). The net effect of livestock over grasses and forbs is greater than native herbivores, and may allow sedges to dominate. These patterns in diet selection are consistent with vegetation composition and recovery seen in Fig. 3.

Finally, evaluation of diet selectivity revealed that these differences in vegetation composition between natural and managed watersheds are likely due to levels of feeding complementarity, i.e., consumption relative to availability (Fig. 4a,b). Native herbivores displayed greater feeding complementarity and differed from one another in their diet selectivity (Fig. 4a). On the other hand, livestock showed mutually similar diets and a high level of redundancy among themselves (Fig. 4b).

DISCUSSION

The distribution of animals across a mountainous landscape in the Spiti region of northern India provides an opportunity to investigate whether native grazers and introduced livestock have different direct and/or indirect effects on soil C in their respective watersheds. These watersheds do not differ systematically in terms of geologically determined edaphic conditions (Table 1) and have comparable grazing intensities (Fig. 1b). Yet, the natural watersheds hold 49% higher soil C than managed watersheds (Fig. 2a,b). This

difference may arise from reduced C inputs due to lowered production (Fig. 2c–e, Table 2) stemming from strong compositional shifts caused by livestock compared to native grazers (Fig. 3a,b). High preference for forbs, together with the collective avoidance of sedges by all livestock is consistent with the trend seen in vegetation composition shifts (Fig. 3a,b). These compositional changes also dovetail with the recovery in plant production (Fig. 2c–e).

As the livestock-induced vegetation shift towards dominance by sedges can account for the difference in production, the central issue in this study is whether the consequent reduction in C inputs (Table 2) can explain the actual difference in soil C stocks (Fig. 2b). Studies have indicated that approximately a quarter of the C input from plant production gets incorporated as soil C (e.g., Ganjgunte *et al.* 2005). So, on average (Table 2), soils in natural watersheds may incorporate more than twice as much of net production as soil C (average $44 \text{ gC m}^{-2} \text{ year}^{-1}$) compared to the managed watersheds (average $19 \text{ gC m}^{-2} \text{ year}^{-1}$). Some of this soil C may be sequestered for prolonged periods, while the rest may be respired through microbial metabolism to determine whether or not there is net C storage or loss. Possibly, either type of watershed may be storing and/or losing soil C. However, these results indicate that the natural watersheds are, at least, losing less soil C than the managed watersheds and the difference in potential soil C inputs from vegetation between the watersheds is $25 \text{ gC m}^{-2} \text{ year}^{-1}$. So, the difference of 1169 gC m^{-2} in soil C stock between the watershed types (Fig. 2b) could have resulted because the natural watersheds have avoided a relative loss of 23.4 and $29.2 \text{ gC m}^{-2} \text{ year}^{-1}$ compared to the managed watersheds over the past 40–50 years. This calculated range is consistent with the estimated $25 \text{ gC m}^{-2} \text{ year}^{-1}$ difference in soil C inputs from production ($19 \text{ gC m}^{-2} \text{ year}^{-1}$ in managed watersheds as opposed to $44 \text{ gC m}^{-2} \text{ year}^{-1}$ in natural watersheds). So, the changes in production (Fig. 2c–e, Table 2) and composition (Fig. 3) might account for the difference in soil C stocks between the watersheds (Fig. 2). Therefore, the observed difference in soil C stocks (Fig. 2a,b) appears to be primarily driven by differences in the indirect effects of native and livestock grazers (Fig. 4a,b), mediated by their influence over vegetation composition (Fig. 3a,b); and not their direct impacts alone (Fig. 1b).

Another major question is why do livestock have such different effects on vegetation than native herbivores? When herbivore species differ in diet selection, they may exert *compensatory* effects on plant species composition which do not drive directional vegetation shifts (Ritchie & Olff 1999). On the contrary, herbivore species lacking feeding complementarity may propagate *additive* effects resulting in directional vegetation shifts (Ritchie & Olff 1999). These expectations are consistent with consumer–resource theory (see mathematical model, Data S1), and receive support

from our data (Fig. 4a,b). Therefore, unlike the *compensatory* effects of native herbivores on plant communities, *additive* effects from livestock induce a shift towards increased abundance of sedges (Fig. 3a,b) at the expense of forbs, which reduces plant production, particularly belowground, and potentially accounts for the C inputs to soil (Fig. 2, Table 2). These data, thus, demonstrate how indirect effects mediated by diet selectivity may drive vegetation composition change (Augustine & McNaughton 1998; Ritchie & Olff 1999) with potential consequences for soil C storage (De Deyn *et al.* 2008). They also explain the particularly strong recovery seen in forbs (Fig. 3a,b), allowing BNPP and TNPP in the managed watersheds to resemble that in the natural watersheds (Fig. 2c–e). Together, these results show how trophic interactions have ecosystem consequences (Duffy *et al.* 2007).

The replacement of native herbivores by livestock diminishes the potential of plant communities to facilitate soil C storage. There may be several potential mechanisms contributing to this phenomenon such as (1) inherent differences in edaphic conditions between the watersheds; (2) differences in soil erosion; (3) differences in grazing intensity; and (4) differences in production that eventually influence soil C inputs. First, we found that edaphic conditions are an unlikely explanation as these conditions were similar between watershed types (Table 1). Secondly, if soil erosion was an important factor in this system, the watersheds with higher bare ground should have had lower soil C. But, as natural watersheds had higher bare ground than managed watersheds (Table 1), the data are inconsistent with the possibility that soil erosion plays an important role. On the other hand, the difference in potential C storage (Fig. 2a) does appear to be related to differences in potential C input from plant production (Table 2). Therefore, the role of grazing intensity needs to be further evaluated. Grazing intensities were comparable between the different watersheds, at least during the study period (Fig. 1b). A slight, but non-significant difference in grazing intensity in the natural watersheds during 2007 (Fig. 1b) is perhaps due to an extraneous event. During 2005 and 2006, we observed the native herbivores grazing adjacent to the exclosures. However, between May and June 2007, a separate experiment required making frequent visits to the plots (every 2–3 days), and we noticed that the native grazers, especially bharal, were grazing 60–100 m away from the exclosures, rather than in closer proximity. The livestock were relatively unaffected by our presence.

Historical grazing intensity

Although we do not have direct estimates of historical grazing intensities as our data are limited to the study period (Fig. 1b), we can draw secondary inferences from livestock

census data. Annual livestock census (1996 onwards) in the villages in our study area (map, Data S1) indicate that total biomass of livestock animals, distributed among the different livestock types, has remained steady at $66\,800 \pm 3320$ kg for over a decade now (for census data at different times since 1996, see Mishra 2001; Bagchi & Mishra 2006). This low variation for over a decade is likely because pastoralists are limited by agricultural hay as feed for their herds during the winter. As agricultural production across the Trans-Himalayan region is primarily subsistence-based, it probably imposes a limit on per-capita livestock holdings (see Mishra 2001; Mishra *et al.* 2003; and Namgail *et al.* 2007 for various socio-economic data on agro-pastoral subsistence economies) and these watersheds may have experienced similar grazing over a considerable period of time. In this context, reviews have shown that grazing has the highest positive effect on soil C in dry environments such as the Trans-Himalayas (< 400 mm annual precipitation, Derner & Schuman 2007), where the average turnover time of soil C is 10–30 years (Raich & Schlesinger 1992). So, current levels of soil C (Fig. 2a,b) may potentially reflect the cumulative effects of grazing over relatively short periods of time and the influence of far-history may not be critically important. Far-history would be more important in swamps and wetlands, where residence time of soil C can be > 500 years (Raich & Schlesinger 1992). More importantly, studies in other parts of the Tibetan plateau have found that soil C recovery is accomplished within *c.* 15 years since plants communities can recover from past disturbances in that time (Li *et al.* 2009); and we found significant community change within only 4 years (Fig. 3a,b). If the role of far-history were crucial, then its influence would have been reflected as a large discrepancy between our estimates of soil C inputs from vegetation, and actual differences in soil C stocks.

In addition to the indirect impacts on soil C sequestration, livestock husbandry may also have other incidental effects, such as nutrient redistribution. Overnight dung deposition by livestock in village corrals can result in a net C loss from rangelands (Augustine *et al.* 2003). While this does contribute towards the difference in soil C between the two watershed types, it is a much smaller contribution compared to the reduction in plant production. The average difference in plant production between the livestock-watersheds and the native-watersheds is 360 g m^{-2} (Fig. 2e). Even if all livestock dung was deposited in village corrals, the plant biomass equivalent would be $10\text{--}20\text{ g m}^{-2}$ (Fig. 1b), which is < 2% of the difference in production (Fig. 2e). Clearly, difference in total production, which is an order of magnitude greater, is likely to be a larger determinant of the difference in soil C among the watersheds (Fig. 2a,b), compared to nutrient redistribution via dung deposition in corrals. The suppression of forbs by livestock is consistent

with reports, where belowground biomass allocation by forbs appears as an important determinant of soil C inputs (De Deyn *et al.* 2008). Our results are also consistent with studies from other regions of the greater Trans-Himalayan ecosystem on grazer impacts on above- (Klein *et al.* 2007) and belowground production (Gao *et al.* 2008) and vegetation composition (Bai *et al.* 2004).

The apparent lack of feeding complementarity among livestock compared to native grazers (Fig. 4a,b) cannot be attributed to lower functional diversity in morphological traits as the livestock demonstrate a greater range of body size, cranio-dental anatomy, and digestive physiology, than the native species assemblage. A more likely explanation for this lack of complementarity is changes in foraging behaviour through temporary inflation of densities due to husbandry (Du Toit & Cumming 1999; Coppolillo 2000; Rook *et al.* 2004). Individuals in tightly packed mixed-species herds of livestock tend to become less selective when foraging. This behaviour is often the basis for pastoral land management (McNaughton 1986), as it may promote aboveground production, but the belowground consequences can go unnoticed (Fig. 2c,d). Other benefits of such herding include better control over animal movement over difficult mountainous terrain, and protection from predators (Bagchi & Mishra 2006). To verify whether husbandry can indeed alter foraging behaviour, we inspected data from a neighbouring area in Spiti region where villagers allow some horses to range freely, while intensively herding the rest with other animals. Consistent with the expected trend (Du Toit & Cumming 1999; Coppolillo 2000; Rook *et al.* 2004), diet selection by the herded horses was noticeably different from their free ranging counterparts (see Data S1).

Replacing native herbivores by livestock may severely restrict the ability of grazing ecosystems to sequester soil C, and thereby their potential to offset greenhouse-gas emissions. Worldwide, there are several well-documented instances of directional vegetation change following the introduction of non-native grazers at high stocking density (e.g., in Australia, Andrew & Lange 1986; North America, Grover & Musick 1990; Africa, Jeltsch *et al.* 1997; South America, Cabral *et al.* 2003). As the possibility for securing new areas inviolate of human impacts is rapidly diminishing, there is an urgent need to realize the full potential of coupled human natural ecosystems to provision ecosystem services (e.g., preventing cascading effects of disease transmission from livestock to wildlife to promote soil C storage in the Serengeti ecosystem, Holdo *et al.* 2009). As managing grazing intensity alone (Fig. 1b) may not be enough to realize the full potential of soil for C sequestration (Scurlock & Hall 1998; Lal 2004), wildlife conservation appears to be the preferred land use. But, removing livestock altogether would be detrimental to pastoral livelihoods. This implicit

trade-off and the ensuing dilemma may be resolved by generating new incentives for community-based wildlife conservation that attempt to secure a network of small but strategically chosen areas to be maintained free of livestock use (Mishra *et al.* 2010). As conserving native herbivores translates into a relative average gain of at least 25 g m⁻² year⁻¹ of soil C, as in the Serengeti (Holdo *et al.* 2009), emerging C credit markets could help alleviate the economics costs of choosing between alternative land-use practices (Nelson *et al.* 2009) – viz., wildlife conservation and livestock production. If anticipated policy changes over market-trade in soil C (e.g., Nelson *et al.* 2009) recognize C offsets arising from land use that prevents loss of soil C (Fig. 2a), then the revenue generated from trading C credits might provide strong incentives for conserving native wildlife as well as for improving livestock husbandry practices in a manner that facilitates soil C storage in different grazing ecosystems around the world.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Data S1 Map of study area in Spiti region, northern India (32° N, 78° E), mathematical model for *additive* vs. *compensatory* effects of herbivores, comparison of diet selection among free ranging and herded livestock, list of plant species recorded during vegetation sampling, and Supporting References.

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