Running Head: Can livestock be functional substitutes of native herbivores?

Functional substitutability of native herbivores by livestock for long-term soil carbon sequestration depends on microbial decomposers.

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Author contributions

S.R. and S.B. designed research; S.R. performed research; S.R. and S.B. analysed data; and S.R. and S.B. wrote the paper.

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ABSTRACT

The functional influence of native mammalian herbivores on ecosystem functions is declining as they get gradually replaced by domestic livestock who have become the predominant herbivores across the world. Alongside rewilding, restoration, and conservation, it is now important to address whether livestock can maintain erstwhile functions of the native herbivores they have displaced across the world's grasslands, savannas, and steppes. If yes, this has implications for the future of biodiversity, ecosystem functions and services, food-security, and other social and environmental dimensions. We test competing alternative hypotheses with a replicated, long-term, landscape-level experiment to ask whether livestock in the Trans-Himalayan ecosystem can match decadal-scale soil-C sequestration in soils under native herbivores. Over decadal time-scale (2006-16) livestock were imperfect substitutes since they could only attain three-fourths of the total soil-C stocks under native herbivores. Structural equation models supported the hypotheses that livestock alter soil microbial communities towards lower fungal abundance, which is detrimental for microbial carbon use efficiency (CUE) and for soil-C storage. This lag between livestock and native herbivores can be addressed through microbial restoration and rewilding of soil. Therefore, the idea of functional substitutability must be leveraged alongside microbial rewilding to restore and conserve ecosystem functions. Together they can reconcile conflicting demands from food-security and ecosystem services, and should become an integral part of nature-based climate solutions.

Keywords: Soil-respiration, Carbon use efficiency, Land-use, Grassland, Carbon-sequestration, 4-per-mille, Structural equation modelling (SEM).

INTRODUCTION

Large mammalian herbivores have undergone widespread declines in their abundance and distribution across the world's grasslands, steppes, and savannas. Pre-historic humans hunted many megafauna to extinction. More recently, humans have progressively replaced them with livestock across the world. Relatively intact assemblages of native herbivores are now increasingly confined to parks and reserves, where they continue to face many threats (Veldhuis et al. 2019). Elsewhere, livestock have not only become the most abundant herbivores, but they also represent the most geographically expansive land-use today (Asner et al. 2004; Bar-On, Phillips, and Milo 2018). Further displacement of native herbivores seems inevitable due to steadily rising demands for livestock-products to accommodate evolving human-diets (Thornton 2010; Leclère et al. 2020). This severely restricts and alters the erstwhile functional influence of native herbivores on ecosystem structure and functions, their broad influence on global biogeochemical cycles, and their influence on soil-C in particular (Brodie, Williams, and Garner 2021; Roy and Bagchi 2021).

Increasingly, it is important to ask whether livestock can maintain the functional roles of the displaced native herbivores (Lundgren et al. 2020; Malhi et al. 2016). If livestock can maintain ecological functions and services of their native counterparts, then such functional substitutability can have implications for the future of biodiversity, ecosystem functions and services, food-security, and other social and environmental dimensions (Willemen et al. 2020; Delabre et al. 2021; Western et al. 2020; Sayer et al. 2013; Veblen et al. 2016). The extent to which livestock can maintain ecosystem functions and services, particularly soil-C sequestration, becomes important to inform policies over sustainable use of grazing ecosystems and leverage their potential as natural climate solutions.

Opportunities to restore and maintain ecosystem processes using livestock as surrogates of displaced native herbivores arise from the mutual similarity in their functional

traits (Lundgren et al. 2020; Malhi et al. 2016; Schowanek et al. 2021). Indeed, traits are better predictors of ecosystem functions than taxonomic identity of species (Malaterre et al. 2019; Flynn et al. 2009; Hooper et al. 2005). Analyses of key traits, such as body size, diet-choice, and fermentation type, hypothesize that livestock can be approximate surrogates for native herbivores, i.e., nearest neighbors in trait-space (Malhi et al. 2016; Lundgren et al. 2020; Schowanek et al. 2021). However, empirical evidence on ecosystem functions and services is needed before these ideas can be implemented toward ecosystem management, and such evidence is lacking (Reinhart, Sanni Worogo, and Rinella 2021).

From this functional-substitutability hypothesis one can ask (Betts et al. 2021) – if there is sufficient overlap in trait-space between livestock and native herbivores, then to what extent can they act as surrogates? It is challenging to address this question because many modern livestock-production systems no longer have native counterparts within comparable ecological settings that can allow a fair comparison. Unlike intensive livestock production systems that are often associated with various forms of environmental degradation, traditional pastoral production systems where both livestock and native herbivores occur in multiple-use landscapes use (Sayer et al. 2013; Western et al. 2020; Asner et al. 2004; Veblen et al. 2016; du Toit, Kock, and Deutsch 2009) can be testbeds to assess whether livestock are good substitutes, or not. While this functional premise does not expect livestock to be perfect replacements for the displaced native herbivores (Sitters et al. 2020; Bagchi and Ritchie 2010b), it is important to estimate the degree to which their ecological roles are matched to identify gaps and shortfalls as well as the scope for improved livestock production systems (Sayer et al. 2013; Delabre et al. 2021; Western et al. 2020; Reinhart, Sanni Worogo, and Rinella 2021).

Here we address impacts of livestock and native herbivores on soil-C sequestration as grazing by large mammals is an important component of the global carbon cycle (Schmitz et

al. 2014; Roy and Bagchi 2021). We compare their ecological impacts in Spiti region of northern India, which is part of the greater Trans-Himalayan ecosystem spread across the Tibetan plateau and surrounding mountains. Soil-C sequestration in the Trans-Himalaya is particularly important under human land-use for livestock production and under ongoing climate change (Naidu and Bagchi 2021; Murthy and Bagchi 2018). We investigate long-term (decadal-scale) net soil-C sequestration under livestock and native herbivores, and their influence on key microbial decomposer functions related to the C-cycle (Falkowski, Fenchel, and Delong 2008; Roy and Bagchi 2021; Sinsabaugh et al. 2016). We take advantage of several key features in the Trans-Himalaya: (1) the livestock are a multi-species assemblage that show considerable trait-overlap with the native herbivores (Fig. 1), (2) livestock and native herbivores occupy distinct but juxtaposed watersheds with comparable environmental settings (Fig. S1-S4), (3) their abundances are comparable so that grazing pressure on vegetation is also similar (see Methods, Fig. S5). Absent major confounding influences, the livestock and native assemblages in Trans-Himalaya can help evaluate their functional substitutability (Lundgren et al. 2020; Malhi et al. 2016; Schowanek et al. 2021). Specifically, we investigate (1) whether, and by how much, does grazing by livestock and native herbivores differ in its influence on long-term (decadal-scale) soil-C sequestration, and (2) whether any differences can be attributed to how each assemblage influences microbial decomposer functions in soil.

MATERIALS AND METHODS

STUDY AREA

Traditional pastoral livestock production is the major land-use in Spiti region of the Trans-Himalayan grazing ecosystem. Watersheds near human settlements are used by a multi-species livestock assemblage, and these are juxtaposed with watersheds that retain native

herbivores (Fig. 1, Fig. S1). Natural terrain and barriers (canyons, rivers, high ridges) that restrict frequent animal movement, maintain replicate watersheds under two alternative types of herbivore assemblages (Fig. S1, S2). Historical local extinctions of native herbivores and their replacement by livestock over the past decades remains a major conservation challenge in this region (Namgail, Wieren, and Prins 2013; Mishra et al. 2002), and around the world (Western et al. 2020; Veblen et al. 2016). The extant native herbivores are ibex (*Capra sibirica*), bharal (*Pseudois nayaur*), and yak (*Bos grunniens grunniens*) that are related to wild yak (Bos grunniens mutus; also known as B. grunniens and B. mutus, respectively; Leslie and Schaller 2009). Currently, kiang (*Equus kiang*) are known from the fringes of study area, and there are sporadic reports of argali (*Ovis ammon*). But Tibetan antelope (*Pantholops hodgsonii*) and Tibetan gazelle (*Procapra picticaudata*) are no longer found in the region. The livestock consist of goat, sheep, donkey, horse, cattle and yak-cattle hybrids (Fig. 1). The livestock and native herbivores (after including kiang and argali) show sufficiently high overlap in key traits (Lundgren et al. 2020), such as body mass, dietary guild, fermentation type, sexual-dimorphism, graminoid, limb morphology (Fig. 1). In recent decades, total animal biomass has remained comparable (6.9×104 kg for native and 7.2×104 kg for livestock; Bagchi and Ritchie 2010b; 2010a; Singh, Sharma, and Babu 2015), such that grazing pressure on vegetation has also remained similar for sufficiently long periods (Fig. S5).

The two types of watersheds are comparable in their abiotic conditions (Fig. S3–S4). Climate in Spiti is cold and semi-arid with temperature ranging from 25 °C in summer to below -30 °C in winters (Fig. S6). Precipitation occurs as winter-snow (100-200 cm yr^{-1}) and summer-rain (150-300 mm yr^{-1}), and vegetation growth-season is short (May-August, Fig. S6). Vegetation of this treeless landscape consists of grasses (*Poa*, *Elymus*, *Festuca*), sedges (*Carex*, *Kobresia*), forbs and shrubs (*Artemisia*, *Lindelofia*, *Caragana*). Both types of

watersheds have an overlapping pool of plant species; livestock watersheds are dominated by sedges and grasses with higher ground cover as well as higher aboveground plant biomass than grass-and-forb vegetation in the native watersheds (Fig. S5, Bagchi and Ritchie 2010b).

SOIL CARBON

Between 2006 and 2016, we measured soil-C at regular intervals in four watersheds with native herbivores, and another four watersheds with livestock (Fig. S1, S2). In each watershed, we set up 3-4 replicated permanent plots (10×10 m^2), for a total of n=15 plots under native herbivores, and another n=15 plots under livestock. We collected soils with a 5 cm diameter and 20 cm deep cores, and measured carbon content (TruSpec, Leco, USA, and Elementar Analysensysteme, GmbH, Germany) to compare long-term soil-C stocks (mg C cm^{-3}) under livestock and native herbivores.

GRAZING-EXCLUSION EXPERIMENT

We distinguish whether any observed difference in soil-C between the watersheds is merely an artefact of pre-existing site-specific conditions, or it can be attributed to grazing by the alternative herbivore assemblages. For this, starting in 2005, we set up experimental grazer-exclusion with a paired-adjacent fence at each location (also 10×10 m^2, each). In 2017, after up to 12 years of herbivore-exclusion, we estimated grazer-effects on key soil microbial functions in the paired-adjacent fenced and control plots.

SOIL MICROBIAL FUNCTIONS

We estimated the response of key soil microbial functions to grazing, that are related to the carbon cycle and net soil-C sequestration: (1) Basal respiration (BR), (2) Potential, or substrate-induced respiration (SIR), (3) Soil microbial community composition, broadly as

fungal and bacterial fractions, (4) Microbial biomass-C and N (MBC and MBN), (5) labile Carbon (LC) and labile Nitrogen (LN) pools of soil organic matter, (6) Metabolic quotient (qCO_2), and (7) Microbial carbon use efficiency (CUE). Since these microbial processes have seasonal dynamics (Bagchi et al. 2017), we measured them at five time points during the growing season, between May and September. We followed standard laboratory protocols to measure these microbial variables (Robertson et al. 1999; Bagchi et al. 2017; Roy and Bagchi 2021). Briefly, for BR we used alkali-trap method where we incubated 4 g soil at 60% water holding capacity and measured respired CO_2 (mg C g^{-1} soil day^{-1}). Similarly, we measured potential microbial respiration (mg C g^{-1} soil day^{-1}) using substrate-induced respiration (SIR) after adding 0.5% (w/v) of glucose to soil.

We estimated broad microbial community composition as fungal and bacterial contributions to potential respiration under selective inhibition using Streptomycin (anti-bacterial) and Cycloheximide (anti-fungal). We used chloroform fumigation-extraction to estimate MBC (mg C g^{-1} soil), and MBN (mg N g^{-1} soil). We measured SOM from weight loss on ignition at 450 °C after 4 h. We measured labile and recalcitrant fractions (mg g^{-1} soil) of SOM using two-step hydrolysis with H_2SO_4. We estimated metabolic quotient as the ratio of BR and MBC (qCO_2, respiration per unit biomass, hr^{-1}). We estimated CUE from established relationships between key microbial extracellular enzymes (carbon-acquiring Beta-glucosidase, alongside nitrogen-acquiring Leucine aminopeptidase and *N*-acetyl glucosaminidase), MBC and MBN, and labile fractions of C and N in SOM (Sinsabaugh et al. 2013; 2016). We measured activity of the three enzymes using their specific fluorogenic substrates (4-MUB beta-D-glucopyranoside for Beta-glucosidase, L-Leucine-7-amido-4-methylcoumarin hydrochloride for Leucine aminopeptidase, and 4-MUB N-acetyl-beta-D-glucosaminide for N-acetylglucosamindase) (German et al. 2011; Stone et al. 2012) in soils from growth season of 2017. These parameters influence microbial metabolism to determine

their investment in growth (G) and respiration (R), so that $\mathrm{CUE} = \frac{\mathrm{G}}{\mathrm{G+R}}$ (Sinsabaugh et al. 2013; 2016). Theoretically CUE can range between 0 and 1, i.e., nil to perfect efficiency, with higher values indicating greater potential for C-sequestration. But, CUE in nature generally does not exceed 0.6, and the global average is estimated at 0.5±0.25 SD (Manzoni et al. 2012; Sinsabaugh et al. 2013; 2016).

SOIL MICROBIAL DNA

Based on patterns seen in fungal and bacterial contribution to soil respiration, we evaluated community composition in more detail using their DNA markers in 2019 (Bru, Martin-Laurent, and Philippot 2008; Maestre et al. 2015; Fierer et al. 2005). We collected soils from ten paired-plots at four time points during the growing season and extracted microbial DNA using MOBIO Power Soil DNA Extraction Kit following manufacturer's protocols. Next, we quantified the Internal Transcribed Spacer (ITS-1 and ITS-2) regions of rRNA for fungal abundance, and region of 16s rRNA for bacterial abundance with qPCR (Bru, Martin-Laurent, and Philippot 2008; Maestre et al. 2015; Fierer et al. 2005). We used these genetic data to confirm whether DNA-based estimates align with respiration-based estimates of fungal and bacterial abundance. Additional details of laboratory analyses are in Appendix.

DATA ANALYSIS

We evaluated competing hypotheses (Tredennick et al. 2021) to determine whether the observed variation in the data merely represent site-specific and time-specific heterogeneity between replicates, or it is necessary to invoke herbivore assemblage-type (livestock or native) as an explanatory variable. We used a linear mixed-effects model to evaluate long term trends in soil-C and grazer-exclusion effects on each microbial variable. For soil-C, we used a null-model $\left(M_0^{soilC}\right)$ with time (years, 2006-16) and plot identity as random-effects to

account for background variation due to sampling locations and times. This model was evaluated against the alternative competing model $\left(M_A^{soilC}\right)$ which included assemblage-type as a fixed-effect, alongside both random-effects. We compared both models using parsimony, goodness-of-fit, and likelihood-ratio test (i.e., AIC, RMSE, and LR). Next, we determined whether there was gain or loss of soil-C with a separate model where time (years) was a fixed-effect and plot identity as random effect.

We estimated grazer-effect on each microbial variable as the log-ratio of values in the fenced and paired-adjacent control plots i.e., $\Delta = \ln\left(\frac{\mathrm{Grazing_i}}{\mathrm{Fenced_i}}\right)$ for the ith pair, and calculated the mean and 95% CI of the log-ratio (Roy and Bagchi 2021). As earlier, we first evaluated a null-model to assess whether the observed variation in grazer-effects can simply be attributed to heterogeneity across sampling locations and times (months, May-September). As the null-model for the jth microbial variable $\left(M_0^j\right)$, we used plot identity and month as random-effects. In the competing alternative model for each variable $\left(M_A^j\right)$, we included herbivore assemblage-type as a fixed-effect alongside the random-effects. As before, we used AIC, RMSE and LR for model comparison to judge whether herbivore assemblage-type is a necessary explanatory variable for the data (Tredennick et al. 2021). We assessed whether data met statistical assumptions from the observed and theoretical quantiles of residuals (Schielzeth et al. 2020); the variables required no further transformation (Δ is already in ln-scale). We used 'nlme' library in R (Pinheiro et al. 2020) to perform these analyses.

We assessed the inter-relationships between grazer-effects (Δ) on different microbial variables with structural equations models (SEM). SEM help evaluate hypothesized pathways over how change in one variable can influence another (Grace 2006). We identified SEM paths from *a-priori* examples in the literature (Fig. S8). To avoid multicollinearity in SEM arising from redundancy among variables, we removed those variables which were either

highly correlated with each other (|r| > 0.49), or were derived from each other (Fig. S9). So, ΔSIR, ΔB, ΔMBN, and ΔqCO_2 were not included in this step, and we built SEM using ΔMBC, ΔLN, ΔLC and ΔF. We did not use genetic data from ITS and 16s rRNA in the SEM because these were collected from a subset of plots (10 fenced and control pairs in each watershed) and were also not from the same year as the other microbial variables. As earlier, we evaluated two competing SEMs – with and without herbivore assemblage-type as an explanatory variable, i.e., SEM_0 and SEM_A. We incorporated SEM paths as mixed-effects models for each variable as piece-wise structural equations (Lefcheck 2016). We assessed goodness of fit with Fisher's C statistic (Roy and Bagchi 2021; Shipley 2009) and report standardised path coefficients alongside their statistical significance (α=0.05). When SEM paths are supported by data, then they offer a plausible explanation for the underlying process. When SEM paths are not supported, it suggests that the hypothesized process may not give rise to the observed data.

RESULTS

LONG-TERM TREND IN SOIL-CARBON

Model comparison showed that spatio-temporal heterogeneity was not sufficient to explain long-term variation in soil-C, and it could instead be attributed to herbivore assemblage-type. There was stronger support for M_A^{soilC} than for M_0^{soilC} (difference in AIC=-25.3, and diffrence in RMSE=-0.61, and LR=27.3, P<0.001). Soils under native herbivores stored 7.7±1.5 SE more carbon (mg C cm^{-3}) than under livestock ($F_{1,176}$=26.6, P<0.001). Effectively, areas under livestock could realize up to 71% of the soil-C found under native herbivores (Fig. 2).

SOIL MICROBIAL RESPONSES TO GRAZING

Analysis of grazer-effects revealed that the observed difference in soil-C (Fig. 2) was related to how soil microbes respond to grazing by livestock or native herbivores (Fig. 3). Livestock and native herbivores had comparable effects on B, 16s rRNA abundance, MBC, MBN, LC, LN, and qCO_2 (Fig. 3, Table S1). For these seven variables, the competing alternative models were not supported, and their variability could be attributed to spatio-temporal heterogeneity rather than to assemblage-type (Fig. 3, Table S1). But livestock and native herbivores differed in their influence on BR, SIR, F, ITS abundance, and CUE. For these five variables, there was stronger support for the competing models than the null models (Table S1), as assemblage-type was an important explanatory variable over and above background spatio-temporal heterogeneity (Fig. 3). Grazing by livestock increased both basal and potential microbial respiration (BR and SIR), compared to grazing by native herbivores (Fig. 3). But grazing by livestock reduced both the fungal fraction of microbial respiration and abundance of fungal genetic markers (F and ITS). Respiration-based estimates of fungal and bacterial fractions were consistent with DNA-based estimates (Fig. 3). Grazing by livestock reduced CUE compared to native herbivores (Fig. 3).

INTER-RELATIONSHIPS BETWEEN SOIL MICROBIAL RESPONSES

To assess how differences in grazer-effects on one microbial variable may influence other variables, we evaluated two competing SEM models. The null model was supported by the data (SEM_0: Fisher's C = 3.34, P=0.503, df = 4, AIC = 69.34). This showed, regardless of herbivore assemblage-type, grazer-effects on microbial community composition (fungal fraction) affects CUE, and grazers also influence the labile-C pool via their effects on microbial biomass and labile-N (Fig. 4). The alternative competing model was also supported by the data (SEM_A: Fisher's C = 2.108, P=0.716, df = 4, AIC = 88.11). It showed that change in assemblage-type can influence CUE via its effect on microbial community composition

(Fig. 4). Specifically, change in herbivore-assemblage from native to livestock has negative influence on fungal abundance, which in turn is detrimental for CUE (Fig. 4). Both SEM models indicate that direction and magnitude of grazer-effects are consistent with the premise that higher CUE under native herbivores improves net soil-C storage, compared to livestock (Fig. 2, Fig. 4).

DISCUSSION

Previous studies from around the world have emphasized that grazing by large mammalian herbivores leads to net soil-C storage (Sitters et al. 2020; Derner, Augustine, and Frank 2019; Liu et al. 2020; Witt et al. 2011), and grazing ecosystems should be integral to nature-based climate solutions (Willemen et al. 2020; Roy and Bagchi 2021; Reinhart, Sanni Worogo, and Rinella 2021). But it has remained unclear whether this service can be maintained when natural ecosystems are repurposed for livestock production. And if so, then to what extent?

Our results address several aspects of functional substitutability of native herbivores by livestock. We find that a multi-species assemblage of livestock can have remarkable functional similarities with the native assemblages they displace (Fig. 1). And, at comparable abundances, both assemblages gain soil-C (Fig. 2) at approximately 1‰ to reiterate the role for grazing ecosystems in nature-based climate solutions (Naidu and Bagchi 2021; Willemen et al. 2020; Reinhart, Sanni Worogo, and Rinella 2021). But livestock do not emerge as perfect substitutes since they achieve only about three-fourths of the soil-C stock, compared to the native herbivores (Fig. 2). Nevertheless, consistent with the functional substitutability hypothesis, a key ecosystem service provided by native herbivores, soil-C sequestration, can also be partly realized in livestock-production systems. This can have implications for how we manage environmental impacts of food (Willemen et al. 2020; Delabre et al. 2021; Sayer

et al. 2013; Western et al. 2020; Veblen et al. 2016), and meet the rising demand for livestock-products in the coming decades (Thornton 2010; Leclère et al. 2020).

To determine the scope of improved management, it is important to identify the potential drivers and mechanisms that explain why livestock lag native herbivores in soil-C sequestration. Prevailing management practices have largely focused on two such aspects: overgrazing and plant community change which result in altered C-input to soil from plants (Bagchi and Ritchie 2010b; Reinhart, Sanni Worogo, and Rinella 2021). However, this prevailing focus on C-input alone can be simplistic and inadequate since it does not account for subsequent catabolism of carbon by microbes in soil (Roy and Bagchi 2021). Our results from the grazer-exclusion experiment (Fig. 3) identify soil microbial responses as the proximate explanation for why livestock are not perfect substitutes for native herbivores (Fig. 3). Tests of the competing hypotheses addresses whether the observed patterns in soil-C reflects idiosyncratic and/or pre-existing differences between watersheds, or they are linked to identity of the grazing herbivores. We attribute this missing soil-C to how microbial soil processes respond to grazing when native herbivores are replaced by livestock (Fig. 3-4). However, this still leaves the possibility that livestock watersheds may have been historically overgrazed, and their soils have not yet recovered. Even though vegetation may recover from historical overgrazing, it may take much longer for soil microbial functions to recover (López Zieher, Vivanco, and Yahdjian 2020). Seen together, these highlight the importance of soil microbial restoration in tandem with management of grazing intensity and stocking rates.

CUE is a fundamental microbial trait that controls residence time of carbon in the soil, and determines the flow of carbon through ecosystems (Six et al. 2006; Sinsabaugh et al. 2013; Falkowski, Fenchel, and Delong 2008). The direction and magnitude of difference in microbial community change under livestock reduces CUE (Fig 3-4), and this is consistent

with lower soil-C stocks (Fig. 2) because fungi are known to have higher CUE than bacteria (Six et al. 2006; Fontaine et al. 2004).

Several overlapping mechanisms can alter microbial communities towards lower fungi, and their individual roles may not be easily disentangled from each other. First, plant community differences – higher abundance of sedges under livestock (Bagchi and Ritchie 2010b) – can affect microbes because sedges have lower lignin and higher soluble carbohydrate content than forbs or grasses (Wardle, Bonner, and Barker 2002; Hobbie 1996). Relatively high-quality litter-inputs from them can result in 'priming' effects (Fontaine et al. 2004) which favor bacteria over fungi. Indeed, we found higher microbial-respiration rates under livestock despite no difference in the labile-C pool (Fig. 3). Second, as discussed above, microbial communities may have not yet recovered from any historical overgrazing in the past (López Zieher, Vivanco, and Yahdjian 2020), even though vegetation biomass does not indicate overgrazing is currently a concern (Fig. S5). Third, veterinary care offered to the livestock leads to inadvertent release of antibiotics and other drugs to the soil from their dung, and this can alter microbial communities towards lower CUE (Wepking et al. 2019). Such overlapping factors need to be addressed together to improve soil-C sequestration, rather than in isolation.

Our results from alternative competing SEMs offer insights into how net soil-C sequestration can be improved (Fig. 4). Since replacing native herbivores with livestock is detrimental for CUE, promoting wildlife conservation over livestock-production would favor soil-C (SEM_A, Fig. 4). This would compromise livelihoods and food-security, and it circles back to the inconsistencies and conflicts between the goals of conservation and human land-use. The null model (SEM_0, Fig. 4) can offer insights into ways to resolve these conflicting demands on land-use. It suggests altered microbial communities compromise CUE regardless of whether the community shift is a fallout of land-use, or not. This opens opportunities for

restoration of microbial communities to sustain ecosystem services under human land-use (Wubs et al. 2016; Paluch, Thomsen, and Volk 2013; Mills et al. 2017). Admittedly, there are many gaps in our current understanding of structure-function relationships for hyper-diverse microbial communities (Bier et al. 2015). Yet, there are encouraging signs that effective restoration can be achieved even with incomplete taxonomic knowledge (Wubs et al. 2016; Paluch, Thomsen, and Volk 2013). Since livestock already deliver 71% of the ecosystem service provided by native herbivores, further incorporating microbial restoration of soils into livestock-production may offset the 29% lag against native herbivores.

In conclusion, our results highlight: (1) multi-species and functionally diverse assemblages of livestock can partly approximate the ecological roles of native herbivores, and (2) restoration and rewilding of soil microbial communities may enable livestock to emulate the services provided by native herbivores. Alongside continued management of stocking rates, functional substitutability and microbial restoration in-tandem may help reconcile rising demands for livestock-products with conservation of ecosystem functions and services.

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Figures

Fig. 1

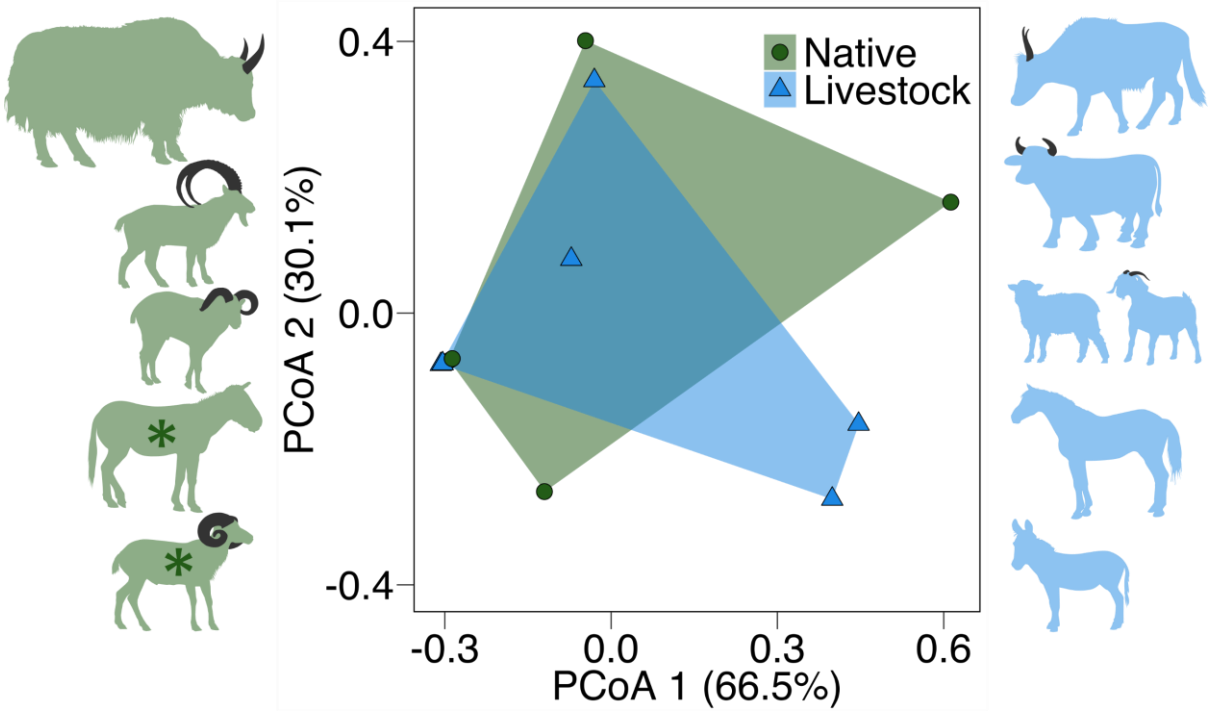

Figure 1. Trait space of livestock and native herbivores in Spiti, India. We find there is considerable overlap in multidimensional trait space between native herbivores (green) and livestock (blue). Native herbivores in the study area are ibex, bharal, yak; asterix (kiang, argali) indicates that these animals are found in nearby regions. The livestock consist of goat, sheep, donkey, horse, cattle and yak-cattle hybrids. Six traits were used to construct the trait-space: body mass, dietary guild, fermentation type, sexual-dimorphism, graminoid, and limb morphology following (Lundgren et al. 2020) with Principal Coordinates Analysis on the Gower's distance matrix.

Fig. 2

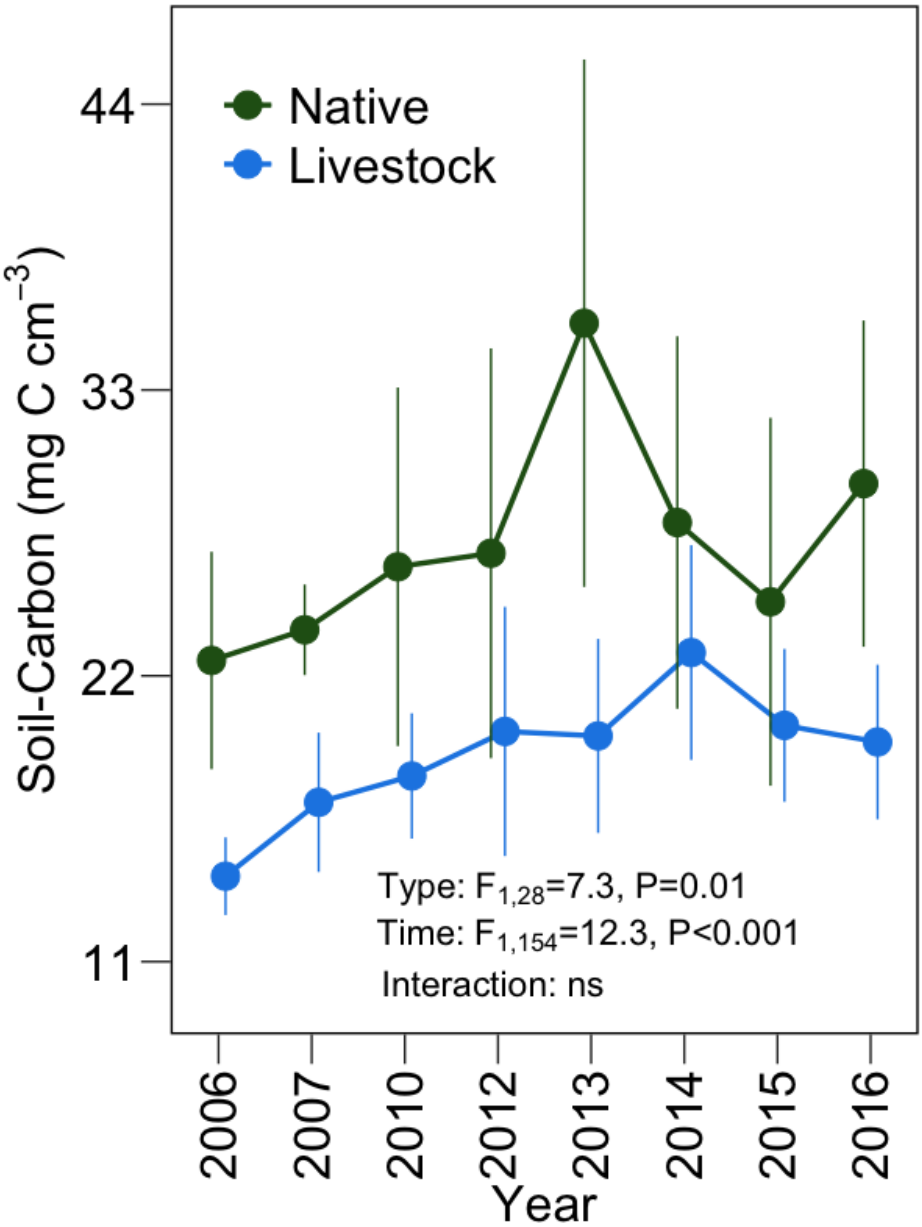

Figure 2. Long-term change in soil-C (mean ± 95CI) under grazing by native herbivores and livestock in Spiti, India. Watersheds with livestock had overall lower soil-C than those with native herbivores, but both gained soil-C during the decade at approximately 1‰.

Fig. 3

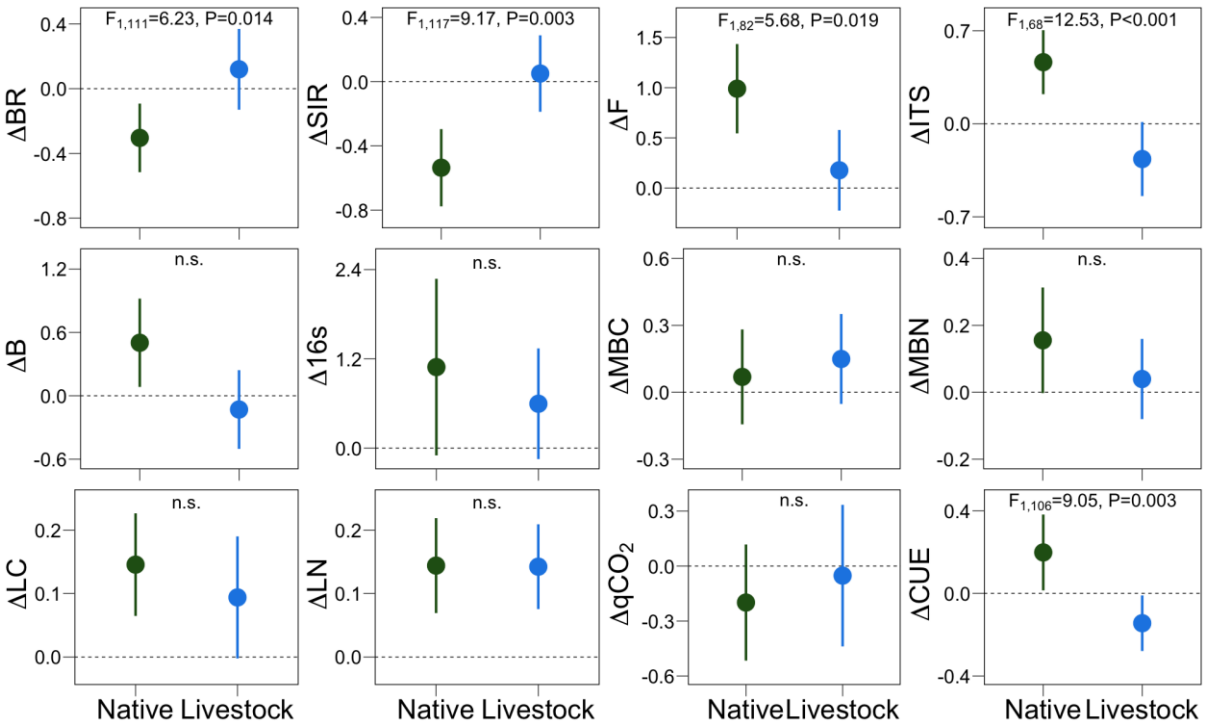

Figure 3. Grazer-effect ($\Delta = ln\left(\frac{grazed}{fenced}\right)$, as mean ± 95CI) of livestock and native herbivores on twelve soil microbial variables in Spiti, India. The parameters are basal microbial respiration (BR); potential microbial respiration (SIR); Fungal fraction (F); ITS gene abundance (ITS); Bacterial fraction (B); 16s gene abundance (16s); Microbial Biomass Carbon (MBC); Microbial Biomass Nitrogen (MBN), Labile-C (LC); Labile-N (LN); Metabolic quotient (qCO_2); microbial carbon use efficiency (CUE). Direction and magnitude of differences in BR, SIR, F, and ITS abundance varied with herbivore-assemblage type. But the remaining variables were not influenced by herbivore-assemblage type.

Fig. 4

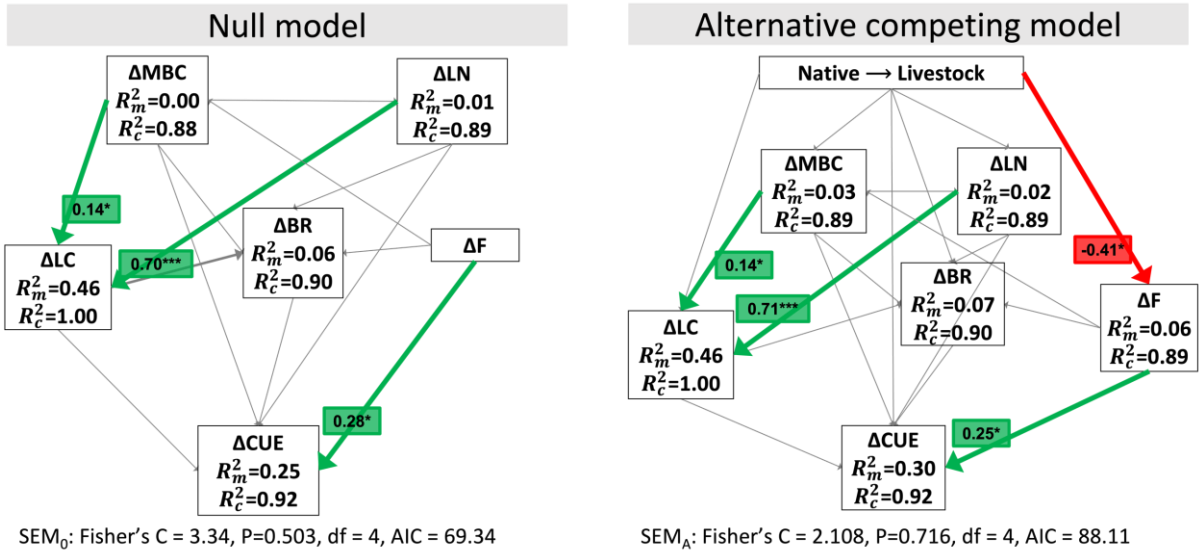

Figure 4. Mixed-effects structural equation models to evaluate two competing hypotheses – with and without herbivore assemblage-type as an explanatory variable, i.e., SEM_A and SEM_0. For each variable, grazer-effect (Δ, ln response-ratio) was calculated from grazed and ungrazed paired plots. ΔBR: basal respiration, ΔMBC: microbial biomass-C, ΔLC: labile-C, ΔLN: labile-N, ΔF: fungal biomass, ΔCUE: carbon use efficiency. In SEM_A, as herbivore-assemblage goes from native to livestock ΔF decreases that leads to a decrease in ΔCUE. Alternatively, in SEM_0, increase in ΔF increases ΔCUE independent of herbivore-assemblage type. Green and red arrows represent significant positive and negative standardized path coefficients respectively, while grey arrows represent non-significant paths ($\alpha = 0.05$). Marginal and conditional R^2 for microbial variables is reported in the corresponding box. Asterix represent statistical significance (*** $P \leq 0.001$, ** $P \leq 0.01$, and * $P \leq 0.05$).