

ARTICLE

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Replacing native grazers with livestock influences arthropods to have implications for ecosystem functions and disease

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Abstract

Grazing by large mammalian herbivores influences ecosystem structure and functions through its impacts on vegetation and soil, as well as by the influence on other animals such as arthropods. As livestock progressively replace native grazers around the world, it is pertinent to ask whether they have comparable influence over arthropods, or not. We use a replicated landscape-level, long-term grazer-exclusion experiment (14 years) to address how ground-dwelling arthropods respond to such a change in grazing regime where livestock replace native grazers in the cold deserts of the Trans-Himalayan ecosystem of northern India. We analyze spatial and temporal variation in the abundance of 25,604 arthropods sampled using pitfall traps across 2765 trap-days through the duration of the growing season spanning spring, summer, and autumn. These were from 88 operational taxonomic units covering six orders from 33 families (ants, wasps, bees, ticks and mites, spiders, grasshoppers, and beetles). We find that grazer assemblage—whether livestock or native herbivores—had a strong influence on both vegetation and arthropods. Partial redundancy analysis (RDA) showed that 53.6% of the spatial and temporal variation in arthropod communities could be explained by grazing and by grazer assemblage identity, alongside covariation with vegetation composition and soil variables. Structural equation models revealed that grazing and grazer assemblage identity have direct effects on arthropods, as well as indirect effects that are mediated through vegetation. Importantly, spiders (predators) were less abundant under livestock, whereas grasshoppers (leaf eaters) and ticks and mites (parasitic disease vectors) were more abundant, compared with native grazers. Reduction in spiders can fundamentally alter material and energy flow through the cascading effects of losing predators, and an abundance of grasshoppers may even contribute to vegetation degradation that is often associated with livestock. Parallelly, increases in ticks and mites lead to concerns over vector-borne disease that require planned interventions to align animal husbandry with One Health. Thus, losing native

Pronoy Baidya and Shamik Roy contributed equally to the work reported here.

grazers to livestock expansion can have wide-ranging repercussions via arthropods. This may not only affect ecosystem structure and functions, but also offer challenges and opportunities to mitigate risks from vector-borne disease.

KEY WORDS

large mammalian herbivores, one health, rangelands, tick-borne disease, trophic cascade, zoonosis

INTRODUCTION

Large mammalian herbivores exert a strong influence on the structure and functioning of grazing ecosystems. Since grazing is the most expansive land use, covering nearly 40% of the world's ice-free terrestrial surface (c. 50 million km² across grasslands, savannas, and shrub-steppes), grazers are an integral part of global biogeochemical cycles and the earth's climate system (Naidu et al., 2022; Schmitz et al., 2018). Grazers exert wide-ranging influence on vegetation, nutrient cycles, hydrology, fire regimes, and other related aspects of ecosystem structure and functions (Frank et al., 1998; Hobbs, 1996; Koerner et al., 2018; Olff & Ritchie, 1998; Trepel et al., 2024). In addition, grazers also influence ecosystem structure and function through their effects on other animals such as arthropods (Borer et al., 2012; Foster et al., 2014; van Klink et al., 2015; Zhu et al., 2023). Arthropods are ubiquitous, species-rich, functionally diverse, and perform several ecological functions such as nutrient cycling, pollination, seed dispersal, predation, herbivory, material and energy flow, alongside other roles as symbionts, pests, and disease vectors (Folgarait, 1998; McCary et al., 2021; Wong et al., 2019). Thus, interactions between grazers and arthropods have implications for sustainable land use, pest-control, zoonosis, and several other dimensions. Grazers can affect arthropods directly by reducing available food resources, as well as indirectly by altering vegetation structure and composition (Foster et al., 2014; van Klink et al., 2015; Zhu et al., 2023). Consequently, grazer effects on arthropods appear quite variable across different ecosystems, depending on the direction and magnitude of direct and indirect pathways (Borer et al., 2012; van Klink et al., 2015). In addition to grazing per se, another major source of variability is grazer identity, and this is linked to how different herbivores differ in their traits (Augustine & McNaughton, 1998; Bakker et al., 2006; Roy, Naidu, et al., 2023). For instance, small-bodied grazers tend to feed selectively on high-quality forage, whereas larger grazers can consume low-quality forage, and body size can lead to differences in their

impacts on vegetation composition (Bagchi & Ritchie, 2012; Lundgren et al., 2024; Olff & Ritchie, 1998). While trait-mediated effects of grazer identity on vegetation are becoming clear (Bakker et al., 2006; Price et al., 2022; Roy, Naidu, et al., 2023), we know comparatively less about how it can also influence arthropods (Pryke et al., 2016).

Across a wide range of environmental conditions, grazing alters plant communities (Bagchi & Ritchie, 2010; Koerner et al., 2018; Olofsson & Post, 2018), and this effect varies with grazer identity depending on their traits such as body size and diet selectivity (Augustine & McNaughton, 1998; Bagchi et al., 2012; Bakker et al., 2006; Lundgren et al., 2024; van der Plas et al., 2016; Young et al., 2010). A key consequence of grazing is a change in plant dominance, which alters the abundances of grazing-resistant and grazing-tolerant plants, which can in turn alter forage quality and quantity (Archibald et al., 2019; Atkinson et al., 2024; Koerner et al., 2018; Olff & Ritchie, 1998). Since arthropods also respond to plant communities, one can expect both grazing and grazer identity to have direct and indirect effects on arthropods (Borer et al., 2012; Pryke et al., 2016). For instance, grazing can have unequal effects on the abundance of different types of arthropods (leaf eaters, pollinators, detritivores, parasites, predators, etc.), which leads to restructuring of trophic-interactions in arthropod food webs (Zhu et al., 2023). Here, the underlying role of grazer identity is important because humans have progressively modified grazer assemblages across the world (Asner et al., 2004; Lundgren et al., 2020; Schowanek et al., 2021). Prehistoric humans may have altered Pleistocene grazer assemblages by hunting; modern humans have replaced wild grazers with domestic livestock around the world (Asner et al., 2004; Bar-On et al., 2018; Ripple et al., 2015; Schowanek et al., 2021). Further spread of livestock is anticipated, fueled by rising demands, socioeconomic growth, and evolving human diets (Godfray et al., 2010; Poore & Nemecek, 2018; Popkin, 1998; Svenning, Lemoine, et al., 2024; Thornton, 2010). Amidst the continuing decline in wild grazers and their replacement by livestock, it is important to ask how this change in grazer assemblage and identity affects ecological processes

associated with the interactions between large mammalian grazers and arthropods.

Here, we ask whether livestock and native grazers differ in how they influence ground-dwelling arthropods. We assess this in a coupled human-and-natural ecosystem in the Trans-Himalaya of northern India. Here, the natural reference land-use features native grazers that are juxtaposed alongside human-altered ecosystems with livestock (Bagchi & Ritchie, 2010; Roy, Naidu, et al., 2023). Natural topography (rivers, ridges, canyons, etc.) present barriers that restrict frequent human and animal movement across the mountainous terrain and provide replicate watersheds of the two land uses: wildlife- and pastoral-use (Appendix S1: Figure S1). We use a long-term grazer-exclusion experiment (2005 onward, Bagchi & Ritchie, 2010, Roy, Karapurkar, et al., 2023) as it affords an opportunity to quantify the effect of grazing by livestock and by native herbivores on arthropod communities. Specifically, we ask (1) whether grazers have direct effects on ground-dwelling arthropod communities, as well as indirect effects mediated through vegetation and (2) whether these direct/indirect effects differ between the native and livestock grazer assemblages.

MATERIALS AND METHODS

Study area

We evaluate the effects of large mammalian herbivore identity on ground-dwelling arthropods in a coupled human-natural system around Kibber village (32° N, 78° E) in northern India. This site is at an elevation of 4200–4500 m above sea level in Spiti region of Trans-Himalaya (Appendix S1: Figure S1) and experiences semiarid climate that is characteristic of high-altitude cold deserts (Köppen class BWk). Vegetation is sparse shrub-steppes and consists of perennial grasses, sedges, forbs and shrubs; trees are very rare or absent. Watersheds at our study site are used by free-ranging native grazers, and these are juxtaposed with watersheds used by a multispecies livestock assemblage (Figure 1). The native herbivores are yak *Bos grunniens grunniens* that are related to wild yak *Bos grunniens mutus* (also named *B. grunniens* and *B. mutus*; Leslie et al., 2009), bharal *Pseudois nayaur*, and ibex *Capra sibirica*. Two other large herbivores (argali *Ovis ammon* and kiang *Equus kiang*) are found in adjacent areas, but Tibetan gazelle *Procapra picticaudata* and Tibetan antelope *Pantholops hodgsonii* have become locally extinct in recent decades (Roy, Naidu, et al., 2023). The livestock include mixed herds of cattle, yak-cattle hybrids, horses, donkeys, goats, and sheep. The multispecies livestock assemblage shows considerable trait overlap with native

herbivores in their body size, dietary guild, fermentation type, sexual dimorphism, graminoid consumption, and limb morphology (Lundgren et al., 2024; Roy, Naidu, et al., 2023). Over the past few decades, cumulative biomass of the livestock ($\sim 1.2 \times 10^5$ kg) has been similar to that of the native grazers ($\sim 1.1 \times 10^5$ kg) such that grazing intensity on vegetation is comparable where c. 60% of annual aboveground plant production is consumed in these watersheds (Bagchi & Ritchie, 2010; Roy, Naidu, et al., 2023; Singh et al., 2015). This ecosystem is highly seasonal, with temperatures ranging from -30°C in winters to 25°C in summers when winds can reach 12 km h^{-1} (Appendix S1: Figure S2). A short vegetation growth season extends from May till August, peaking by late July. By September, most plants begin to senescence, and the remaining litter biomass gets buried under snow during winter (November–March; Appendix S1: Figure S2).

Sampling of ground-dwelling arthropods

We used a replicated grazer-exclusion experiment with fenced and paired-adjacent control plots in the two types of watersheds—with either native or livestock herbivores—to estimate the interactions between grazers and ground-dwelling arthropods. A comparison of arthropod communities across these two herbivore assemblages may indicate differences brought upon by replacing wild herbivores with livestock and may also contain the legacy of any preexisting differences from when humans first colonized the region few thousand years ago (i.e., T_0). Since we do not have a reference-point for T_0 , we overlaid an herbivore-exclusion experiment in the alternative herbivore assemblage types to measure the impact that the two types of herbivores may have on arthropods (Bagchi & Ritchie, 2010; Roy, Naidu, et al., 2023). Fenced and control plots, each $10 \times 10 \text{ m}^2$, were set up starting in 2005, and after 14 years of the herbivore exclusion, we sampled $n = 20$ paired fenced-and-control plots for ground-dwelling arthropods using pitfall traps in 2018. This is a preferred method for sampling many types of arthropods in windblown areas, especially exposed mountain tops and in habitats with sparse vegetation (Santos & Fernandes, 2021). We sampled arthropods four times between June and September as different species complete their life cycle at different points in the growing season. At each site, based on a pilot study in 2017, we deployed four pitfall traps in the control plots and three traps in the paired-adjacent fenced plots (75-mL plastic cups, 10 m apart) for five days, each filled with 50 mL water and a few drops of liquid detergent to reduce surface tension (Appendix S1: Figures S3 and S4). Total sampling effort was 2800 trap-days ([4 control

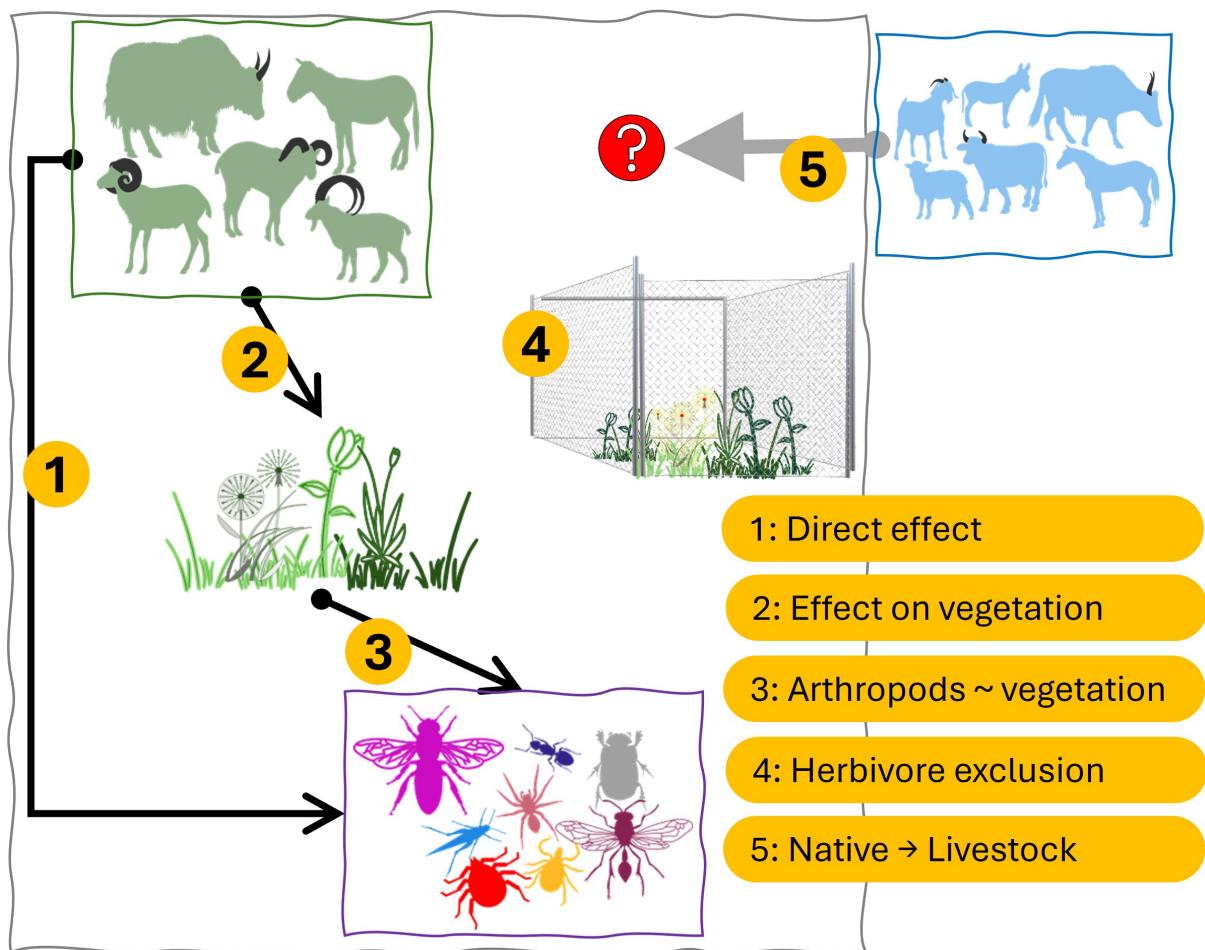


FIGURE 1 Different pathways through which large mammalian grazers can influence ground-dwelling arthropods. (1) Grazers can have direct impact on arthropods by altering available food resources. (2) Since grazers also alter vegetation structure and composition, (3) this can, in turn, influence arthropods. (4) These direct and indirect effects can be quantified through grazer-exclusion experiments. (5) Although these pathways can depend on grazer identity (livestock vs. wildlife), they remain less known. Here, we investigate whether livestock and native grazers have similar or different effects on arthropod communities. Illustrations were drawn by the authors (PB, SR, and SB).

traps \times 10 sites \times 2 land-use types \times 5 days \times 4 times] + [3 fenced traps \times 10 sites \times 2 land-use types \times 5 days \times 4 times]). We separated trapped specimens from soil debris, stored them in 70% ethanol, and subsequently identified them in the laboratory till family level based on regional databases (Chandra et al., 2018) and classified them into operational taxonomic units (OTUs). We pooled the specimens from the four control traps (quadruplets), and the corresponding three paired-adjacent fenced traps (triplets) at a site to target $n = 160$ samples to analyze the variation in arthropod abundance and community composition (2 paired-adjacent sets \times 10 sites \times 2 land-use types \times 4 times). One pair from this set was damaged and could not be retrieved after 5 days in one of the months, which yielded $n = 158$ samples and 2765 trap-days.

Plant and soil variables

We estimated vegetation composition using 50 points along a 10-m line intercept at each fenced and control plot in August, that is, during peak biomass (Bagchi & Ritchie, 2010). We also estimated plant biomass (peak season) by clipping green aboveground parts to ground level from $0.5 \times 0.5 \text{ m}^2$ quadrats and obtained their dry masses (in grams per square meter). We measured five edaphic variables that can influence ground-dwelling arthropods, namely, soil pH, moisture, texture, bulk density, and conductivity (van Klink et al., 2015). We measured soil moisture four times between June and September as volumetric water content with a 20-cm time domain reflectometry probe (Spectrum Technologies, USA). For the remaining variables, we collected soil

samples with a 5-cm diameter corer to 10 cm depth in August. We removed stones and rocks from the sample and air-dried them before transporting them for subsequent laboratory analysis following standard procedures (Robertson et al., 1999).

Data analysis

Our overall objective was to determine the relative importance of five variables in explaining the observed variability in arthropods communities, namely, grazing (fenced/control), grazer assemblage identity (native/livestock), season (growing season June–September), background edaphic variables (soil texture, pH, soil moisture, and bulk density), and vegetation. From this, we infer the direct and indirect influence of grazers on the arthropod community. We used General Linear Models (GLMs) to account for the paired structure of the data (with Gaussian errors for continuous variables and Poisson errors for count data) with season (June, July, August, September), grazing (fenced/control), and grazer assemblage identity (native/livestock) as fixed effects, alongside identity of the paired fenced/control plots as a random-effect to assess their role in explaining the observed variation in species richness of ground-dwelling arthropods. Similarly, we used a corresponding GLM with grazing (fenced/control), and grazer assemblage identity (native/livestock) as fixed effects, alongside plot-identity as the random-effect to assess herbivore effects on species richness and biomass of plant communities. We used “lme4” library, followed by post hoc comparisons of groups in “multcomp” with $\alpha = 0.05$. We verified whether the data met the assumptions of GLMs from the distribution of the model residuals, and the data did not require transformations.

We used ordination with principal coordinates analysis (PCoA) of pair-wise Bray–Curtis dissimilarity of samples to visualize arthropod species composition across seasons, grazing treatment, and grazer assemblage identity in a multivariate space summarized as two axes (Legendre & Legendre, 2012). We used PERMANOVA to assess the effects of grazer assemblage identity, grazing, and season on the beta-diversity of the arthropods with “adonis2” function. We used ordination and PERMANOVA for plant community composition as well. We used partial redundancy analysis (RDA) to estimate the relative importance of background spatial autocorrelation among samples across the landscape, background edaphic variables, growth season, grazer exclusion, grazer assemblage identity, and plant composition in explaining variation among the ground-dwelling arthropods (Borcard et al., 1992; Legendre & Legendre, 2012). A baseline RDA model contained the spatial and edaphic variables; we

included latitude/longitude of the sampling locations as Universal Transverse Mercator (UTM) coordinates. The edaphic variables were soil pH, electrical conductivity, bulk density, soil moisture, and soil texture (sand, silt, and clay) (Appendix S1: Figure S5). To this baseline model, we added seasons (four months during the growth season), grazing treatment (two categories), herbivore assemblages (two categories), and plant community composition to quantify the variation explained by them separately, as well as when they are included together.

We used permutation-based distance-based structural equation models (dbSEMs) to evaluate whether and how grazers and herbivore assemblage identity affects species richness and composition of arthropods directly, as well indirectly through effects on vegetation composition and edaphic factors (Fourtune et al., 2018; Jabot et al., 2020; Roy, Karapurkar, et al., 2023). We included sand content for soil texture in this analysis because of its autocorrelation with clay and silt content. The paths in the dbSEM were motivated by examples in the available literature on processes that can influence arthropod communities (Figure 1). An omnibus model with three sets of paths related to vegetation, that is, plant species richness, vegetation composition, and vegetation biomass, became overfitted (Fourtune et al., 2018; Jabot et al., 2020). So, we simplified the model to exclude unimportant paths (Borer et al., 2012; Roy & Bagchi, 2022). Specifically, we excluded paths involving plant biomass to avoid model overfitting since it did not vary with grazer assemblage (neither as main effect, nor an interaction, see *Results*). We assessed and interpreted the goodness of fit for each path using standardized root mean square residual (SRMR) with value below 0.08, average root mean square error of approximation (RMSEA) below 0.1, and the confirmatory fit index (CFI) above 0.9 (Pouget et al., 2021) using the “lavaan” package in R (Rosseel, 2012). Lastly, to assess differences in abundance across arthropod groups, we used GLM (Poisson distribution) to evaluate the influence of arthropod group identity, season, grazing and herbivore assemblage on the abundance of guilds; here alongside the main effects, we used plot-identity as the random-effect.

RESULTS

From the 158 samples across 2765 trap-days, we classified 25,604 individuals of ground-dwelling arthropods into 88 OTUs belonging to six orders covering 33 families (Appendix S1: Table S1). Hymenoptera (ants, bees, and wasps) had the highest number of OTUs followed by Coleoptera (beetles) and Araneae (spiders); the generalist ant *Formica candida* (Smith, 1878) was the most abundant species (Appendix S1: Figure S6).

Arthropod diversity

Species richness of the ground-dwelling arthropods varied between 3 and 24 per plot (14 ± 4 [mean \pm SD], Figure 2), and this variation was explained by a two-way season \times assemblage interaction ($\chi^2_1 = 11.72$, $p = 0.008$; Appendix S1: Table S3). Arthropod richness was higher in control plots under native grazers at the end of the growing season (Figure 2).

In multivariate space summarized with PCoA (Figure 2), variation in arthropod community composition was explained a two-way season \times assemblage interaction (PERMANOVA: $F_{3,142} = 3.36$, $p = 0.001$; Appendix S1: Table S3). Broadly, ants, beetles, ticks, and mites were more abundant in the middle of the growth season; bees and grasshoppers became abundant later in the season, and spiders were less abundant at the end of season (Appendix S1: Figure S6). The baseline RDA showed that variation in arthropod communities was neither explained by potential spatial autocorrelation in the samples ($F_{2,155} = 1.59$, $p = 0.173$; Appendix S1: Table S2), nor by background influence from the abiotic variables alone ($F_{7,150} = 1.11$, $p = 0.300$; Appendix S1: Table S2, Figure S5). Inclusion of growth season, grazing, vegetation composition, and herbivore assemblage identity to the baseline model explained 53.6% of the variation in arthropod communities ($F_{37,120} = 3.75$, $p = 0.001$; Appendix S1: Table S2).

Vegetation parameters

Plant species richness varied between 3 and 10 species/plot (6 ± 2 species/plot; Figure 3), and this was explained by a two-way grazing \times assemblage interaction ($\chi^2_1 = 5.98$, $p < 0.015$; Appendix S1: Table S3). In the control plots, plant species richness was higher under native grazers (Figure 3). Vegetation composition varied between sedge-dominated and grass-dominated ground cover (Appendix S1: Figure S7). This variation in vegetation composition was associated with grazer assemblage identity ($F_{1,18} = 24.47$, $p = 0.001$; Figure 3; Appendix S1: Table S3, Figure S7). Peak-season vegetation biomass varied between 12.8 and 61.6 g m⁻² (30.6 ± 11.1 g m⁻²; Figure 3), and this variation was explained by herbivore exclusion alone ($\chi^2_1 = 6.96$, $p = 0.008$; Appendix S1: Table S3) as there were no effects due to interactions.

Grazer effects on arthropods

The dbSEM indicated a nonrandom match between the data and the hypothesized paths (SRMR = 0.004, RMSEA = 0.005, p [RMSEA] > 0.999, CFI > 0.999,

$\chi^2_6 = 7.88$, $p = 0.247$). Path coefficients suggested that herbivore assemblage identity has both direct and indirect effects on ground-dwelling arthropod communities (Figure 4). Grazer assemblage directly influenced arthropod species richness (Native vs. Livestock \rightarrow Arthropod species richness; Figure 4) as well as arthropod community composition (Native vs. Livestock \rightarrow Arthropod species composition; Figure 4). The indirect effects of grazer assemblage identity on arthropods were primarily mediated through their influence on vegetation composition (Native vs. Livestock \rightarrow Plant species composition \rightarrow Arthropod species richness) and on plant species richness (Native vs. Livestock \rightarrow Plant species richness \rightarrow Arthropod species composition). Grazer exclusion influenced vegetation composition (Fenced vs. Control \rightarrow Plant species composition; Figure 4) but did not show any other effects on arthropods via plant communities and edaphic factors. In addition, there were influences from prevailing environmental conditions such as seasonality, soil moisture content, and texture (Figure 4).

The sampled arthropods belonged to seven broad taxonomic groups (Figure 5; Appendix S1: Figure S6, Table S1). Variation in abundance of these groups was explained by group identity, season, grazing, and grazer assemblage identity due to a complex four-way interaction ($\chi^2_{18} = 81.90$, $p < 0.001$; Appendix S1: Table S3) such that many variables appear influential. Importantly, ticks (Ixodidae), and mites (Dermanyssidae) were more abundant under livestock compared with native grazers; grasshoppers were more abundant, and spiders were less abundant (Figure 5).

DISCUSSION

The data broadly support the expectation that spatial and temporal variability of arthropod communities (Figure 1) would be explained by grazing and grazer assemblage identity (Figure 2). When analyzed individually, arthropod species richness varied more strongly with grazer assemblage identity than with grazing, per se. Additionally, there were marked seasonal differences in arthropod community composition across months (Figure 2), which relate to the life cycles of different taxa and the timing of their metamorphic stages through the growth season. Once again, arthropod community composition appeared more strongly influenced by grazer assemblage identity than by grazing, per se (Figure 2). These results are consistent with studies in other regions where grazers not only influenced their ecosystem directly, but also by their simultaneous influence on other animals such as

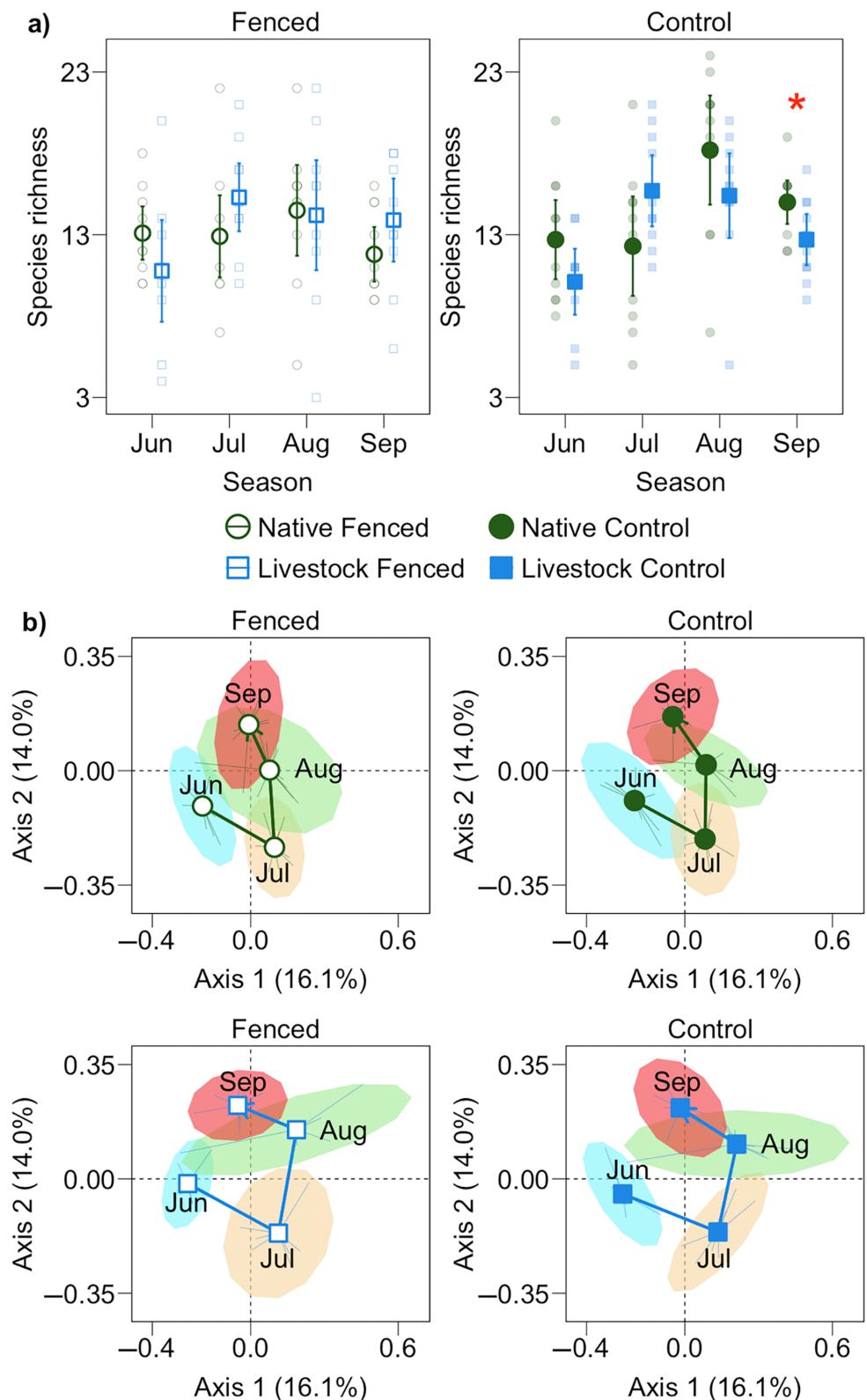


FIGURE 2 Ground-dwelling arthropod (a) species richness and (b) species composition summarized as ordination by principal coordinates analysis (PCoA) across the growth season under fenced and control plots in watersheds with native herbivores and livestock in Spiti region of northern India. Species richness and composition varied between native and livestock watersheds and with growth season. These did not vary between fenced and control plots. Data (mean \pm 95% CI) are from $n = 20$ paired fenced-and-control plots. The asterisk denotes a significant difference between groups in post hoc comparisons ($\alpha = 0.05$).

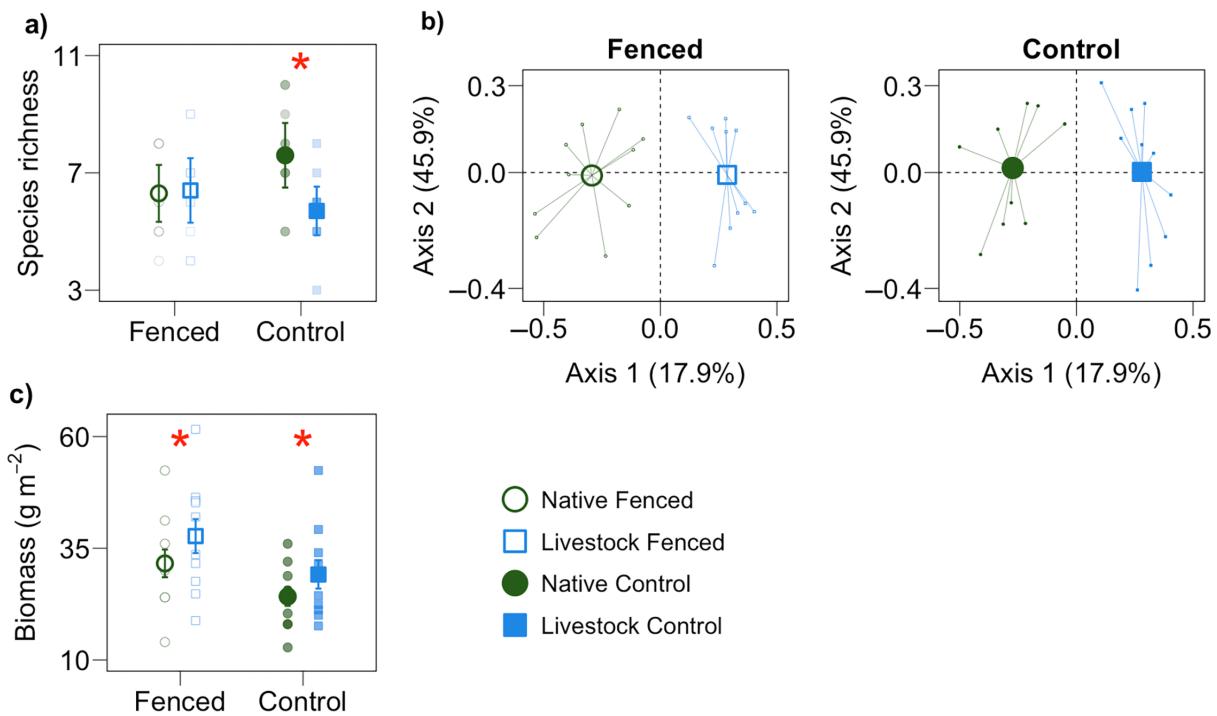


FIGURE 3 (a) Plant species richness, (b) vegetation composition summarized as ordination by principal coordinates analysis (PCoA), and (c) peak-season plant biomass under fenced and control plots in watersheds with native herbivores and livestock in Spiti region of India. Plant species richness and vegetation composition varied between native and livestock plots, but not with grazer exclusion. Plant biomass varied with grazer exclusion. Data (mean \pm 95% CI) are from $n = 20$ paired fenced-and-control plots. An asterisk denotes a significant difference between groups in post hoc comparisons ($\alpha = 0.05$).

arthropods (Foster et al., 2014; van Klink et al., 2015; Zhu et al., 2023). Patterns in the different aspects of vegetation were similar to that seen among arthropods, where grazer assemblage had a stronger influence on plant species richness, and vegetation composition than grazing (Figure 3). This supports the idea that grazer effects on vegetation depends on their identity (and traits) such that different assemblages can differ in their ecological impacts (Bagchi et al., 2012; Bakker et al., 2006; Price et al., 2022; Roy, Naidu, et al., 2023). Specifically, such dependency on grazer assemblages posits that livestock may not be perfect ecological substitutes for native wildlife, particularly for arthropods (Lundgren et al., 2024; Trepel et al., 2024). The ecological differences between domestic and native grazers have implications for several ongoing discussions, such as wildlife extinctions due to livestock expansion (Asner et al., 2004; Bar-On et al., 2018; Ripple et al., 2015; Schowanek et al., 2021), and rewilding efforts to restore ecological functions and services (Cromsigt et al., 2018; Kristensen et al., 2022; Pryke et al., 2016; Svenning, Lemoine, et al., 2024). These differences also have relevance for the rising importance of livestock in food security (Godfray et al., 2010; Poore & Nemecek, 2018; Popkin, 1998; Thornton, 2010), which often comes at the cost of ecological degradation around the world (Asner et al., 2004,

Bar-On et al., 2018; Ripple et al., 2015; Schowanek et al., 2021). Therefore, continued investment in the rewilding of megafauna, as well as seeking improvements in how livestock are managed, could have positive effects on the arthropod communities (Svenning, Buitenhof, et al., 2024; Svenning, Lemoine, et al., 2024).

We found that grazers influence both plants and arthropods, and these align with the expected direct and indirect effects. In the RDA, more than half the variation in arthropod abundance and composition was explained by covariation with the other variables, chiefly—grazing and grazer assemblage identity. This points toward potential causal linkages between them, which were targets of the various paths tested through dbSEM. Indeed, the data supported various paths to suggest that these interactions may not appear in the data due to random chance alone (Figure 4). Most importantly, the paths help in visualizing the different anticipated and observed impacts of grazers (Figures 1 and 4), which point at the direct influence of grazers on arthropods alongside their influences mediated through vegetation, as well as the background role of seasonality and soil properties (Foster et al., 2014; van Klink et al., 2015; Zhu et al., 2023). Influences mediated through vegetation could be due to the differences in diet selectivity in

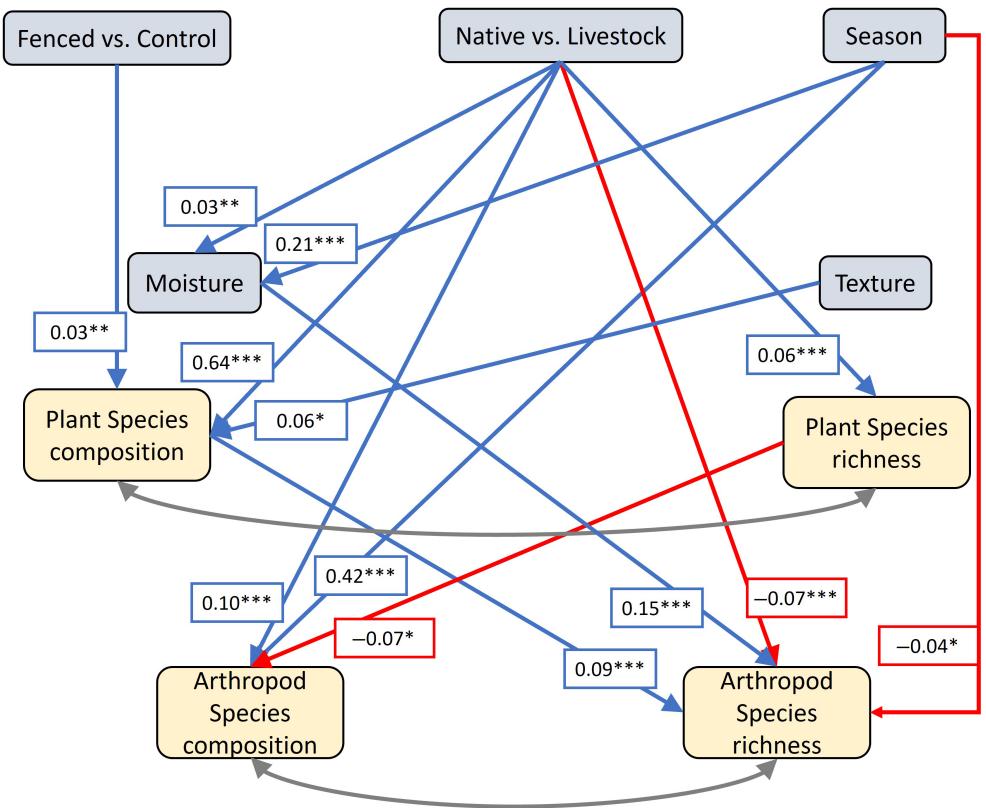


FIGURE 4 Summary of distance-based structural equation model (dbSEM) to evaluate the influence of grazer assemblage identity when native herbivores are replaced by livestock on the ground-dwelling arthropods communities. Unidirectional arrows represent hypothesized causal paths, and bidirectional arrows represent correlated paths where two variables can influence one another. Values represent standardized path coefficients and asterisks represent statistical significance (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$). Modeled paths from grazing (fenced/control) to arthropods were nonsignificant and are not shown. Diagnostics for the model were standardized root mean square residual (SRMR) = 0.004, root mean square error of approximation (RMSEA) = 0.005, p (RMSEA) > 0.999, confirmatory fit index (CFI) > 0.999, $\chi^2 = 7.877$, df = 6, p (χ^2) = 0.247. Overall, grazer assemblage identity had direct as well as indirect effects mediated through plant community and edaphic factor on the arthropod communities.

herbivores that alters the relative abundance of sedges, grasses, and forbs in the two types of watersheds (Figure 3; Appendix S1: Figure S7) (Bagchi & Ritchie, 2010; Roy, Naidu, et al., 2023). These differences in vegetation persisted even after 14 years of herbivore exclusion and can also explain the similarity in arthropod community between grazed and ungrazed plots (Figure 2).

All arthropod groups did not respond in the same way to the two types of land use (Figure 5). The arachnids—spiders, ticks, and mites—showed a strong and systematic variation which was attributable to human alteration of ecosystems where native grazers are replaced by livestock. Lower abundance of spiders under livestock, compared with native grazers, indicates a loss of the ecological function of predation. As predators, spiders influence material and energy flow in the same way as the wolves in a forest and sharks in the ocean (Hawlena et al., 2012; Ripple et al., 2014; Schmitz et al., 1997). Thus, human land use can not only have

well-known cascading effects via large-bodied predators, but also through smaller predators such as spiders. The loss of spiders points toward direct alterations in material and energy flow in landscapes dominated by livestock, compared with native herbivores (Figure 5), alongside indirect effects mediated through the landscape of fear with consequences for ecosystem processes (Gaynor et al., 2019; Hawlena et al., 2012). Further, as this may also favor spiders' leaf-eating prey, such as grasshoppers and several beetles (Figure 5). This may also be linked to vegetation degradation that is frequently associated with livestock but cannot be readily attributed to poor management alone (Maestre et al., 2022; Naidu et al., 2022). Across the Central Asian highlands, vegetation degradation over the past decades is often decoupled with the density and distribution of livestock (Murthy & Bagchi, 2018; Zheng et al., 2006), and identifying whether the underlying mechanisms involve interactions between grazers and grasshoppers may become targets for future research.

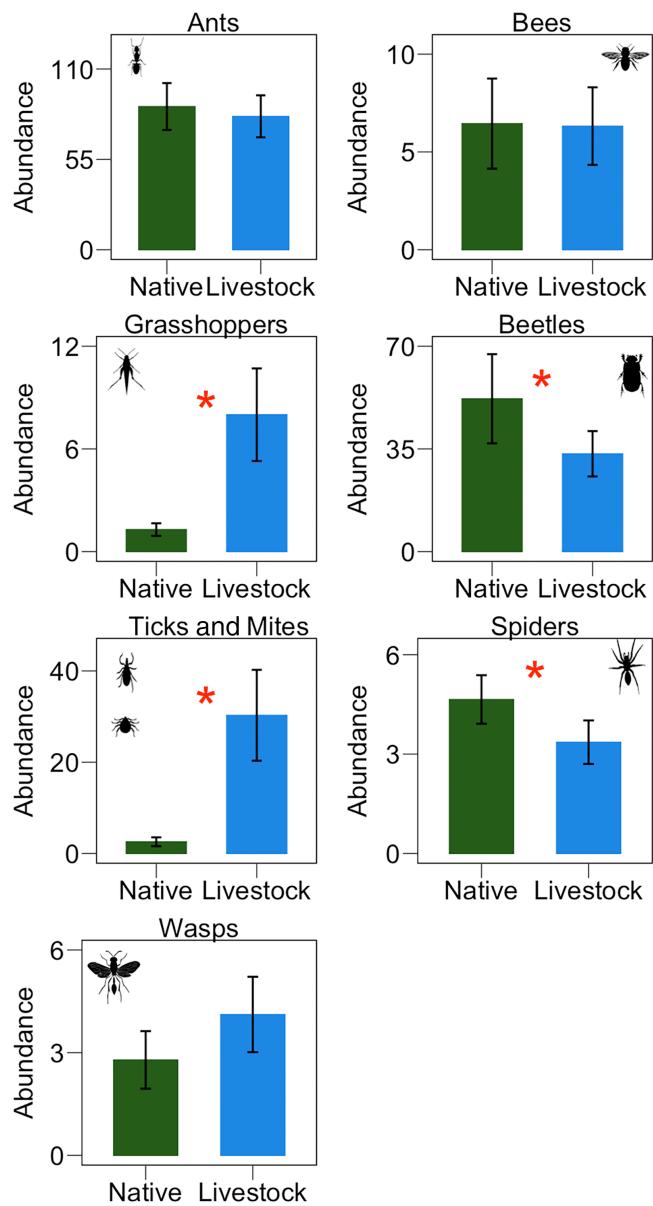


FIGURE 5 Abundance of ground-dwelling arthropods classified into different taxonomic groups in watersheds with native herbivores and livestock in Spiti region of northern India. Data (mean \pm 95% CI) are averaged across seasons for $n = 20$ paired fenced-and-control plots. Beetles and spiders were more abundant under native than livestock, whereas grasshoppers, ticks, and mites were more abundant under livestock than native grazers. An asterisk denotes a significant difference between groups in post hoc comparisons ($\alpha = 0.05$). Illustrations were drawn by the authors (PB, SR, and SB).

While one can envision the mechanisms where a decline in spiders would result in cascading effects such as an increase in grasshoppers (Hawlena et al., 2012), our data do not directly offer a clear explanation about why spiders are lower under livestock. Plausibly, spiders might prefer grass-dominated patches that are structurally heterogeneous with

irregularly spaced tussocks, rather than fairly homogeneous sedge meadows, as differences in vegetation structure can affect prey capture. These likely explanations need further investigations to identify how the underlying mechanisms involve grazers, vegetation, and spiders.

Second, higher abundance of ticks and mites under livestock, compared with native grazers, indicates increase in parasitism. Pertinently, as blood-feeders, ticks and mites are vectors for a wide range of diseases (Estrada-Peña & De La Fuente, 2014). Disease transmission between wildlife and livestock can not only have long-lasting repercussions on ecosystems (Holdo et al., 2009; Monk et al., 2022), but also be consequential for One Health (Cunningham et al., 2017; Titcomb et al., 2017). Ticks are the most important disease vectors for wild and domestic animals, in fact over 80% of the cattle in the world are likely affected by ticks; they are also a threat for humans similar to mosquitoes (Rochlin & Toledo, 2020; Titcomb et al., 2017), particularly in regions that are high-risk but lack resources and infrastructure to mitigate zoonotic threats (Purseid et al., 2020). Encouragingly, recent efforts in the Trans-Himalaya point toward a growing recognition of the ecological dimensions of disease (Khanyari et al., 2024), and this affords a scope to address the implications of ticks and mites to strengthen One Health frameworks. For instance, improvements in animal husbandry that reduce ectoparasite loads to mitigate vector-borne risks can become targets for planned interventions. This also calls for monitoring and surveillance of vector-borne disease risks in coupled human-and-natural ecosystems that have a prominent interface between wild animals, domestic livestock, and humans (Purseid et al., 2020; Titcomb et al., 2017).

In conclusion, we find that livestock expansion at the cost of native wildlife has implications for ecosystem structure and functions due to their differential influence on arthropods. These differences offer challenges and opportunities for improved land management and animal husbandry within the One Health framework.

AUTHOR CONTRIBUTIONS

Pronoy Baidya, Jalmesh Karapurkar, Shamik Roy, and Sumanta Bagchi conducted fieldwork and labwork. Shamik Roy, Sumanta Bagchi, and Pronoy Baidya analyzed the data. Shamik Roy and Sumanta Bagchi wrote the first draft. All authors contributed to revisions.

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CONFLICT OF INTEREST STATEMENT

As the handling editor for the special issue (Applied Ecology in India), Sumanta Bagchi did not oversee the peer review of the manuscript. The authors declare no other conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from Zenodo: <https://doi.org/10.5281/zenodo.14192912>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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