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Forage quality in grazing lawns and tall grasslands in the subtropical region of Nepal and implications for wild herbivores

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ABSTRACT

Subtropical grasslands interspersed in forests often present mosaics of tall grasslands and grazing lawns with a high variation in structure, biomass and nutrient concentration. However, the impact of such variation on forage quality is still poorly known. We quantified physical and chemical properties of grasses of grazing lawns and tall grasslands, interspersed in the forested region of Bardia National Park, Nepal during the hot-dry season. This area falls within Cwa-climate (Köppen-Geigen climate classification). We found that grasses in grazing lawns had an average bulk density of ~5400 $g.m^{-3}$ whereas tall grasslands had an average bulk density of ~1000 $g.m^{-3}$ only. Forage in grazing lawns was comprised of a higher percentage of green leaf (up to 60%) compared to tall grassland (up to 40%). Phosphorus levels in green leaves were below maintenance requirements of wild herbivores (especially for grazers and mixed feeders) on both grazing lawns and tall grasslands. However, average crude protein levels in green leaves from both the grazing lawns and tall grasslands could meet the herbivores maintenance requirement (~7%). Only green leaves on grazing lawns had crude protein levels sufficient enough (9.7%) to meet the requirements of herbivores for maintenance and gestation, though not for lactation. We conclude that, during the hot-dry season, grazing lawns provide forage with a higher quantity and quality than tall grasslands. Consequently, grazing lawns can make a significant contribution to the maintenance or even growth of the grassland dependent wild ungulate population, such as chital (*Axis axis*), a primary prey species of the endangered tiger (*Panthera tigris*) in Bardia National Park. The insight of this study will provide a basis for restoring grazing lawns for quality forage, and aid in the conservation and management of wild grazers and mixed feeders.

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1. Introduction

Grasslands in the subtropical region of Nepal (and in India) can broadly be categorised into (i) floodplain grasslands dominating in riverbanks and floodplains and (ii) grasslands established in abandoned agricultural fields originated from human interventions such as land conversion (forest into agriculture), livestock grazing, thatch harvesting and burning (Peet et al., 1999). Grasslands established in abandoned agricultural fields frequently consist of mosaics of tall grasslands and grazing lawns (Ahrestani and Sankaran, 2016; Karki et al., 2000). This mosaic of tall grasslands and grazing lawns appears to be a key determinant for spatial and temporal heterogeneity of food resources that is necessary to meet the nutritional requirement of herbivore assemblages including grazers and mixed feeders (Ahrestani et al., 2012; Bonnet et al., 2010; Cromsigt et al., 2009; Hempson et al., 2015; Prins and Van Langevelde, 2008; Raynor et al., 2016; Verweij et al., 2006; Wilmshurst et al., 1999). Furthermore, a large number of empirical and experimental studies have pointed out that vegetation nutritive value is related to vegetation physical properties such as height, biomass, proportion of leaves over stem, and proportion of green parts over dry (Drescher et al., 2006a; Durant et al., 2004; Mårell et al., 2006) which in turn govern rates of daily energy intake (Laca et al., 2010; Mezzalira et al., 2017; Searle and Shipley, 2008; Spalinger and Hobbs, 1992). For instance, amount of green leaves and bulk density are critical parameters that largely influence bite rate and bite size and hence the intake in herbivores (Drescher et al., 2006a; Stobbs, 1973a, 1973b). Therefore, knowledge on the physical and chemical characteristics of grassland vegetation is essential to understand the nutritional value of the vegetation that is on offer as food to wild herbivores.

The ultimate aim of a foraging herbivore is to satisfy its energy requirements for maintenance and reproduction. The amount of energy obtained by an individual is determined by various factors, such as the animal's body size and digestive system (Gordon and Illius, 1996), parts of the plant consumed (Drescher et al., 2006b; Prins and Beekman, 1989), the nutritional value of the consumed forage in terms of nutrient and digestible energy content (Van Soest, 1982), and the quantity of the forage consumed (van Langevelde et al., 2008). Plant parts and growth stages of plants present great differences in its physical properties, chemical composition, and nutritional value. For instance, grasses in an early growth stage have a higher proportion of leaf over stem and have a higher digestibility than older grasses (Prins, 1996). Digestibility is inversely related to fibre content (Van Soest, 1982); which means digestible energy content in a forage decreases with age and biomass. Due to these variations in the quality and quantity of the forage, herbivores are predicted to select those grassland patches from which they can maximise their daily energy intake (Fryxell, 1991). McNaughton (1984), showed that herbivores on the African savanna can maximise their energy and nutrient intake from grazing lawns. However, grazing lawns demand a certain degree of frequent grazing pressure for their persistence and if grazing pressure is relaxed, fast growing tall grasses may replace grazing tolerant, high-quality grasses (Archibald, 2008; van Langevelde et al., 2008).

Grasslands in the subtropical region of Asia are dominated by an assemblage of herbivores belonging to grazers and mixed feeders (Ahrestani and Sankaran, 2016). This herbivore assemblage, however, has suffered dramatic population declines and range reductions due to changes in the extent of grasslands as a result of strong naturally (succession, and flood) and anthropogenically (cutting, fire, and conversion into agricultural land) induced dynamics (Ahrestani and Sankaran, 2016; Biswas et al., 2014; Ratnam et al., 2019). Local extinction of large grazers has happened too, leading to 'undergrazing' (Jhala et al., 2021; Subedi et al., 2013). Notably, tall grasslands have increased at the expense of grazing lawns (Peet et al., 1999), potentially, affecting forage quality and quantity for grazers and mixed feeders. Tall grasses with low nutrient and digestible energy content depress the intake rate of herbivores and thus hamper a positive energy balance for maintenance and production, especially in small and medium body-sized grazers and mixed feeders (Illius and Gordon, 1992; Wilmshurst et al., 2000). A handful of ecological investigations with chital (*Axis axis*) (Ahrestani et al., 2012; Moe and Wegge, 1994; Raman, 1997), gaur (*Bos gaurus*) (Ahrestani et al., 2012), and blackbuck (*Antilope cervicapra*) (Jhala, 1997) indicated that the amount of energy and nutrients consumed by these herbivores affects both their survival and reproduction. Hence, herbivores in the subtropical region are potentially limited in their numbers by the abundance of forage of high nutritional value.

Knowledge on the physical and chemical characteristics of grassland vegetation as food for herbivores is essential for understanding the nutritional value and availability of quality forage. However, studies on the nutritional quality of the different grassland states (grazing lawns and tall grasslands), are almost non-existent for the subtropical grasslands in Asia. Studies carried out in the subtropical Asian region have mostly focused either on vegetation classification (Dinerstein, 1979; Kumar et al., 2020; Lehmkuhl, 1994; Peet et al., 1999; Ratnam et al., 2016, 2011; Sankaran, 2009), or on herbivore foraging behaviour (Ahrestani et al., 2016, 2011; Moe, 1994; Moe and Wegge, 1997, 1994; Pokharel and Storch, 2016; Sankaran, 2009; Tuboi and Hussain, 2016; Wegge et al., 2006). Only a few studies have given strong attention to the chemical properties of grassland vegetation (Karki et al., 2000; Moe, 1994; Moe and Wegge, 2008). To our knowledge, the differences in chemical and physical properties between grazing lawns and tall grasslands in the sub-tropical region of South Asia have not yet been investigated.

Grasslands in the lowland Terai of Nepal are the last remaining examples of subtropical grasslands in the Indian subcontinent (Peet et al., 1997) and represent a globally important ecoregion, the 'Terai-Duar Savanna and Grasslands' (Olson and Dinerstein, 2002). In the past centuries, these grasslands extended across north-eastern India, lowland Terai of Nepal to northern Bangladesh. At present, these grasslands are entirely restricted to 10 protected areas in northern India and six protected areas within the Terai Arc Landscape in Nepal (Wikramanayake et al., 2010). A consequence of the loss of grasslands in the Terai Arc Landscape is a population decline and range reduction of a whole array of wild herbivores (Dinerstein, 1980; Karanth and Sunquist, 1992) and a near extinction of pigmy hog (*Porcula salvania*) (Jnawali et al., 2011). Therefore, a prerequisite for the conservation of these herbivores, and their predators such as the endangered tiger (*Panthera tigris*), is to understand the nutritional dynamics of the vegetation on the mosaic of tall and short grassland of the subtropical region.

We investigated the physical and chemical properties of two important grassland states, namely *grazing lawns* and *tall grasslands*, in

Bardia National Park (Bardia NP) lying within the Terai Arc Landscape in the subtropical region of Nepal. As mentioned before, grasslands established in the abandoned agricultural field within forests can occur in two different states, namely, the 'lawn state' and the 'tall grassland state'. We assessed which of these two grassland states offers food of sufficient quality and in such a quantity that they can meet the nutritional requirements for maintenance and reproduction of the herbivore assemblage that is (still) present. Given that deer are typically observed in grazing lawns, we expected grazing lawns, but not tall grasslands, to meet the nutritional requirements of herbivores for maintenance and reproduction. Our overarching goal was to understand the characteristics of subtropical grasslands to provide a basis for the restoration of grazing lawns as a management tool in the conservation of wild herbivores and their predators in this type of landscape.

2. Materials and methods

2.1. Study area

The study was carried out in Bardia NP which lies within the subtropical region in the western part of the Terai Arc Landscape of Nepal (centre of the park at 28^{0}23' N, 81^{0}30' E, elevation 100–200 m a.s.l., Fig. 1). The park supports the second-largest tiger population of Nepal with about 90 adult tigers (DNPWC and DFRS, 2018). The dominant habitat types are Sal (*Shorea robusta*) forest and mixed riverine forests along with floodplain grasslands and grasslands interspersed within forests especially in the abandoned agricultural fields (Dinerstein, 1979; Peet et al., 1999; Wegge et al., 2009). Grasslands established in abandoned agricultural field vary in size from 1 to 110 ha within the forest area and are dominated by an assemblage of *Imperata cylindrica* (L.), *Vetiveria zizanioides* (L.), *Saccharum spontaneum* (L.), *Saccharum bengalense* (Retz.), and *Narenga porphyrocoma* (Hance ex Trin.) Bor. (Peet et al., 1999).

Most of the grasslands within forest are believed to originate from shifting cultivation and were subsequently maintained either by grazing, harvesting, or by fire (Bell and Oliver, 1992; Peet, 1997). Following the establishment of the park and relocation of people and livestock out of the area, the park has carried out grassland management, following recommendations from research carried out in the early 1990s. A grassland management involved annual cutting (including thatch harvesting) and burning both by local people and by park staff which might have retarded the successional change towards forest (Lehmkuhl, 1994) and have also facilitated in a development of small patches of grazing lawns in the tall bunch-grass matrix (Fig. 2). These grazing lawns could have originated from

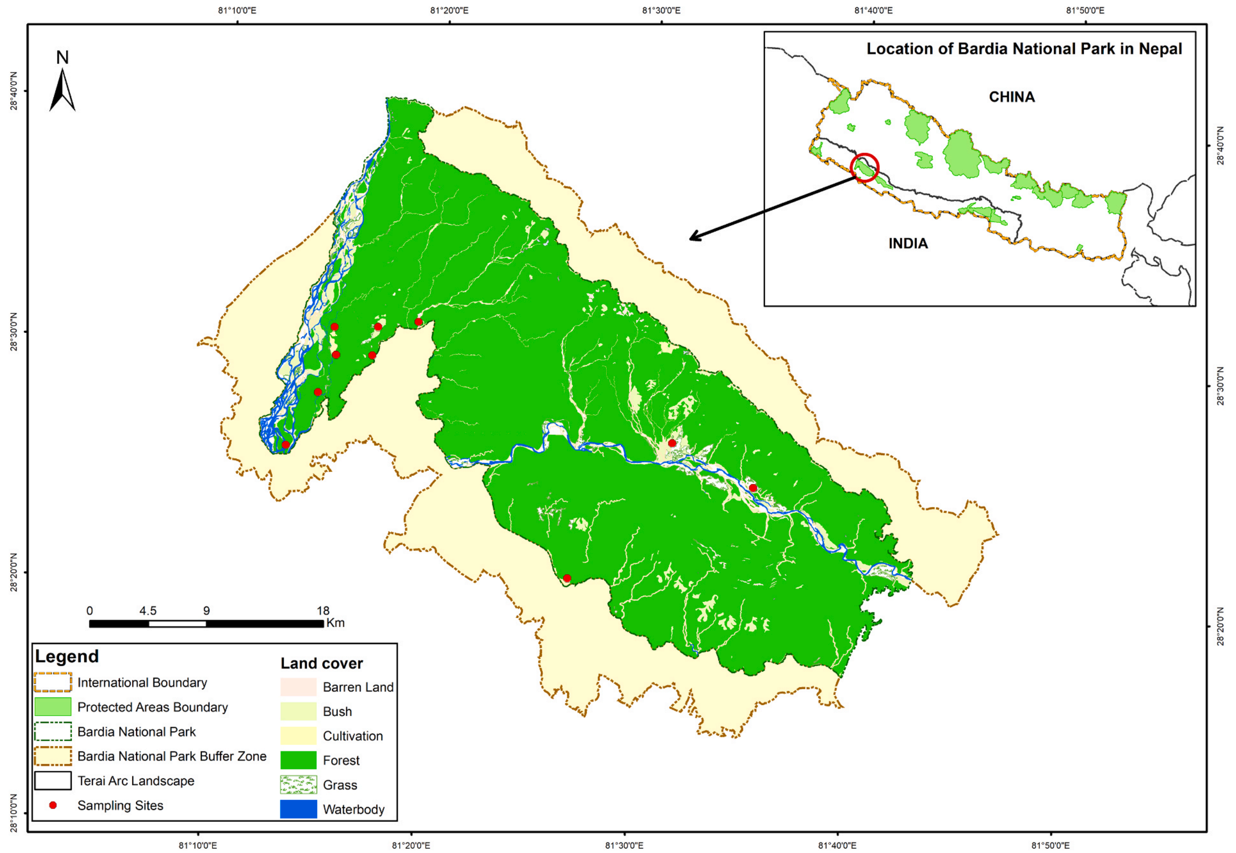

Fig. 1. Location of Bardia National Park within Nepal. Bardia National Park lies within Terai Arc Landscape in a Köppen classification Cwa-Climate. The figure shows the locations of grazing lawns and tall grassland surveyed.

grazing by deer immediately after patchy burning or cutting (Karki et al., 2000; Moe and Wegge, 1997). However, it is important to note here that during the 1990s, more than 30,000 people entered the park to harvest thatch grasses for 14 days but at present, people are allowed for three days only and the number of people entering the park for thatch collection has decreased drastically, possibly due to adoption of concrete houses with corrugated galvanised sheet roofs. A reduction of human activities (cutting and thatch harvesting) on the grasslands have facilitated the expansion and establishment of tall grasses and woody shrubs at the expense of grazing lawns.

The grasslands of Bardia NP are important foraging areas for deer of different body-sizes, viz., from smaller to larger – hog deer (*Axis porcinus*), chital, swamp deer (*Rucervus duvaucelii*), and sambar (*Rusa unicolor*) (Pokharel and Storch, 2016; Wegge et al., 2006, 2009). Chital is the most abundant and at the moment the primary prey species of the tiger in Bardia NP (Upadhyaya et al., 2018) with a reported density of 56 km^{-2} (DNPWC and DFRS, 2018). The area has three distinct seasons: the monsoon (June to September), dry winter (October to February) and the hot dry summer (March to May). The monthly mean temperature of the area ranges between 10 ^{0}C in January and 45 ^{0}C in June and the park receives a mean annual rainfall of ~1800 mm. According to the Köppen-Geigen climate classification, the area falls within a Cwa-climate: monsoon-influenced humid subtropical climate (Chen and Chen, 2013). Our investigations may thus be of relevance for a much wider area, as far as southern China and North-east India, which have similar conservation issues (e.g., management of the endangered Eld's deer (*Rucervus eldii*) (Tuboi and Hussain, 2016; Zhang et al., 2019). The forage qualities may vary markedly between seasons, but the hot dry season represents a nutrient bottleneck during which ungulates are most likely to be nutritionally stressed. Therefore, we conducted this study during the hot dry season (April – May) of 2019.

2.2. *Vegetation and soil sampling*

2.2.1. *Sampling protocol*

We carried out our study in those grasslands of Bardia NP that are established in abandoned agricultural field within the forested landscape which are believed to originate and maintained either by grazing, harvesting, or by fire (Bell and Oliver, 1992; Peet, 1997), hence, do not necessarily represent riverine floodplain grasslands developed in the riverbanks following river dynamics. Within the studied grasslands, we selected sampling sites in two conspicuous grassland states based on grassland characteristics, i.e., *grazing lawns* and *tall grasslands*; the latter were selected at minimally 50 m from the grazing lawns to allow for paired statistical analyses. We categorised *grazing lawns* as small (<1 hectare) areas containing short grasses with low stature growth form, growing closer to the ground with prostate leaves and tillers established and maintained through intensive grazing by wild herbivores. Grazing lawns currently occur as small areas in the tall bunch-grass matrix (Karki et al., 2000). We categorised *tall grasslands* as the grasslands in their tall state with tall bunch grasses (Fig. 2). The two grassland states have similar grass species composition (Table S2), but grazing lawns represent a short grassland state that have distinct growth forms due to frequent grazing (Hempson et al., 2015; Karki et al., 2000). The sampling locations for grazing lawns (n = 10) and tall grasslands (n = 10) were at the same topographic position in the landscape to minimise the confounding effect of topography and, for instance, depth of groundwater.

2.2.2. *Sward sampling*

We randomly laid down 1 m × 1 m quadrats with equally spaced grids of 10 cm × 10 cm (Goodall, 1952; Zwerts et al., 2015) in different direction in both the grazing lawns and tall grasslands. While laying down quadrats in the tall grasslands, we avoided areas that were either cut or burnt in the previous days to have a good representative samples of tall grasses. We laid down a total of 160 quadrats (eight in each sampling site) based on species effort curve (Krebs, 1999) and recorded bare ground, litter, animal droppings and vegetation. Within each quadrat, we used the point intercept method at 100 sampling points to assess the percentage cover of the different plant species. We only used vegetation hits for calculating the Shannon-Wiener diversity index (Peet, 1974) and species

Fig. 2. A typical grazing lawn interspersed within a tall grassland in Bardia National Park, Nepal.

richness (Chao index; Sarmah, 2017). We used grid corners as the point to record the hits.

We measured grass height at three random points within each 1 m × 1 m quadrat with a ruler to 0.5 cm precision. We chose three different points in different direction within a quadrat to measure the grass height. We assessed grazing intensity by visually estimating the bite marks (e.g., Sankaran, 2009) within a quadrat at a scale from 0 to 3 [i.e., 0 – not grazed, 1 – lightly grazed, up to 25% of quadrat area grazed; 2 – moderately grazed, (up to 50% grazed), and 3 – heavily grazed (more than 50% grazed)].

We clipped the vegetation at ground level in a 20 × 20 cm frame in the centre of each quadrat and determined fresh weight using a digital weighing scale [with a capacity of 600 g and accuracy of 0.5 mg; Brand: Equal (class II)] immediately after clipping. We hand-sorted the samples into green leaf, green stem, dry leaf and dry stem which were subsequently dried in the shade at ambient temperature (~30 °C) for five days until air-dry before recording the air-dry weight. Air-dried samples of green leaf and green stem were stored in paper bags for separate chemical analyses.

We clipped samples of four graminoids (viz., *I. cylindrica, V. zizanioides, Desmostachya bipinnata,* and *S. spontaneum*) from each grazing lawn and tall grassland sites for separate chemical analysis. These four grass species were the most abundant grass species in both the grasslands and occurred in all 20 sites (Table S2).

2.2.3. Soil sampling

We collected soil subsamples from each quadrat. While collecting soil subsamples, surface litter was removed, and the top 15 cm of soil was sampled using a shovel. A subsample of 15 cm long and 5 cm thick was unloaded in a bucket. We repeated the procedure in each quadrat. We mixed the subsamples thoroughly for those of 'lawns' and of 'tall grass' yielding 20 composite soil samples. We sieved the subsamples to remove roots, stones, pebbles and other non-soil materials. Quartering was done by dividing the thoroughly mixed soils into four equal parts. Two opposite quarters were discarded, the remaining two quarters were remixed, and the process was repeated until the sample reached 500 g. The soil samples (n = 20) were placed in airtight zip-lock plastic bags for chemical analyses. While packing, precaution was taken not to lose the moisture.

2.3. Chemical analysis

Air-dried green leaf and green stem were oven-dried for 48 h at 60 °C, grinded and sieved over a 2 mm sieve for chemical analysis. Crude protein (CP; defined as 6.25 x percentage nitrogen), phosphorus, acid detergent fibre (ADF), neutral detergent fibre (NDF) and silica were determined for green leaf and green stem. Nitrogen was determined by semi-micro Kjeldahl method in Dry-Block digester and phosphorus by tissue digestion in block digester (AOAC, 1990). NDF and ADF were measured by the methods described by Van Soest (1982). Silica concentration was determined by the gravimetric method (AOAC, 1990). All the measured nutrient concentrations were expressed as percentage dry matter (% DM). Soil pH was measured by the distilled water method (at a soil: water ratio of 1: 2.5) and soil moisture content in weight (w/w %) was calculated by the gravimetric method (Wilke, 2005). Soil organic matter was determined by the Walkely-Black wet combustion method (De Vos et al., 2007). Available phosphorus was determined by the modified Olsen's method and soil nitrogen (N) by spectrophotometric method (Schoenau and O'Halloran, 2008). Samples of vegetation and soils were chemically analysed by the Local Initiatives for Biodiversity, Research and Development (Li-Bird) in Pokhara, Nepal.

2.4. Data analyses

To compare the forage qualities between grazing lawns and tall grasslands, we quantified structural [aboveground biomass ($g.m^{-2}$), height (cm), bulk density ($g.m^{-3}$), and proportion of green leaf and stem (dimensionless)] and chemical parameters (w/w %) of the vegetation. We transformed the response variables to meet the statistical assumptions of normality and homogeneity of variances using log-transformation in most of the cases and arcsine transformation for proportion and percentage data (Wilson et al., 2013). Aboveground biomass, bulk density, and proportion of green leaf were compared between grazing lawns and tall grasslands using paired *t*-tests. We compared height and proportion of green stem using a Wilcoxon signed-rank test.

We used beta regression (Ferrari and Cribari-Neto, 2004), which is more flexible than transformation-based analyses for percentage or proportion data (Douma and Weedon, 2019), to quantify the effect of grassland states (grazing lawn vs. tall grassland) and grass parts (leaf vs. stem) on nutrient concentration in the forage. The statistical significance of the observed deviation between the grazing lawns and tall grasslands and between grass parts was investigated by a posthoc Tukey-test. Nutrient concentration of four graminoids (viz., *I. cylindrica, V. zizanioides, D. bipinnata,* and *S. spontaneum*) that were most abundant on both the grazing lawns and tall grasslands (Table S2) were compared to determine the within-species variation that occurred due to grassland state (grazing lawn vs. tall grassland). We compared soil properties of both grasslands to investigate the characteristics of underlying soils. Soil moisture was compared using a Wilcoxon signed-rank test. Other soil parameters (soil pH, soil organic matter, soil nitrogen and available phosphorus) were compared using paired *t*-tests. Descriptive statistics of transformed data were back-transformed and presented for interpretation (for instance, for the 95% confidence intervals).

We used a multivariate technique PCA (principal component analysis) to determine the correlation between forage characteristics and grassland state. All statistical tests were performed using R software (R Core Team, 2019). R package *vegan* 2.5.6 (Oksanen et al., 2019) was used for species diversity analysis and multivariate analysis. All graphs were produced in R using *ggplot2* (Wickham, 2016).

3. Results

3.1. Characteristics that differentiate grazing lawn from tall grassland

The PCA separated tall grasslands from grazing lawns (Fig. 3). Principal component 1 (Dim1) explained 48% of the variation and grouped grass height, biomass, NDF, ADF and proportion of green stem (right pole) versus grazing pressure, grass crude protein and phosphorus concentrations, vegetation species richness, and soil organic matter (left pole). Principal component 2 (Dim2) explained 13% of the variation and was mainly associated with proportion of green stem, species diversity, species richness, bulk density, proportion of green leaf and phosphorus concentration. Tall grasslands (black triangles with a darker ellipse in Fig. 3) were positively associated with the first axis of the PCA showing positive correlation with biomass, grass height, NDF and ADF concentrations, and proportion of green stem. Likewise, grazing lawns (grey dots with a lighter ellipse in Fig. 3) were positively correlated with bulk density, species richness, grazing pressure, crude protein and phosphorus concentration, proportion of green leaf and soil organic matter (Fig. 3 and Table S1).

3.2. Forage quality in grazing lawns and tall grasslands

Vegetation physical properties on grazing lawns were significantly different than on tall grasslands (Table 1). There was a difference in aboveground biomass between grazing lawns and tall grasslands. The ratio of aboveground biomass from grazing lawns to that from tall grasslands was 0.2 (95% CI: 0.15 – 0.28). Likewise, bulk density was significantly higher in grazing lawns than in their corresponding tall grasslands with a lawn-to-tall grass ratio of 5.4 (95% CI: 3.2–9.2). Vegetation height differed between grazing lawns and tall grasslands with a median difference of − 95.82 cm (85% CI: −119.9 to −86.09). Grasses on the grazing lawns had a higher percentage of green leaf (up to 60%) compared to those on tall grasslands (up to 40%). There was no difference in the proportion of green stem between grazing lawns and tall grasslands (Table 1).

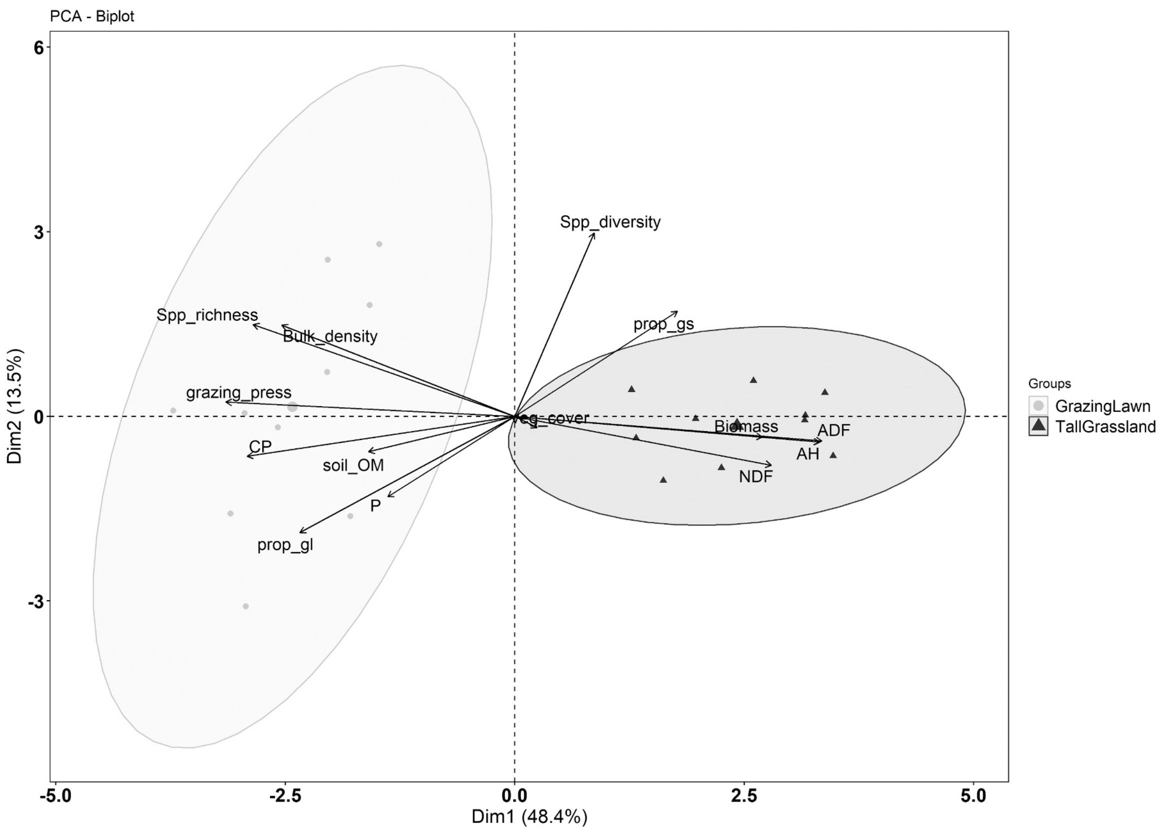

Fig. 3. Principal component analysis (PCA) for variables related to forage physical and chemical properties between grazing lawns and tall grasslands from Bardia National Park. Grazing lawns are indicated by grey dots and tall grasslands by black triangles. The ellipses indicate the 95% confidence intervals. The length of the solid arrows is proportional to its importance and the angle between two arrows reflects the magnitude of the correlation between variables. Response variables are coded as: AH = average height, Biomass = aboveground biomass, Bulk_Density = bulk density, prop_gl = proportion of green leaf, prop_gs = proportion of green stem, veg_cover = percentage vegetation cover, grazing_press = grazing pressure, soil_OM = soil organic matter, CP = crude protein in vegetation, P = Phosphorus concentration in vegetation, NDF = neutral detergent fibre, ADF = Acid detergent fibre, Spp_diversity = Shannon diversity index, and Spp_richness = Chao1 index of species richness.

Table 1
Comparison of physical parameters of forage in Bardia National Park (Nepal) of grass in grazing lawns and of tall grasslands. Note that confidence limits (CI) are asymmetrical because of back-transformation.

Physical parameters	Grazing lawns (GL)		Tall grasslands (TG)		Test statistics
	Mean	95% CI	Mean	95% CI	
Aboveground biomass ($g.m^{-2}$)	200	134–270	922	602–1480	Paired *t*-test (t = - 11.55, df = 9, *P* < *0.001*) ***
Bulk density ($g.m^{-3}$)	5432	4024–8103	992	735–1480	Paired *t*-test (t = 7.32, df = 9, *P* < *0.001*) ***
Average height (cm)	4.0	3.0–5.0	100	87–120	Wilcoxon signed-rank test (*Z = 0, N = 10, P = 0.002*) **
Proportion of green leaf	0.5	0.4–0.6	0.30	0.3–0.4	Paired *t*-test (t = 3.7, df = 9, *P* = *0.004*) **
Proportion of green stem	0.15	0.04–0.2	0.23	0.2–0.3	Wilcoxon signed-rank test (*Z = 9, N = 10, P = 0.10*) ***ns***

*, **, *** indicate significant difference at $P < 0.05$, < 0.01, and < 0.001, respectively. ***ns*** - indicates non-significant.

We found significant differences in vegetation nutrient concentration between grass parts (green leaf vs. green stem) and grassland states (grazing lawns vs. tall grasslands) (Table 2). Vegetation CP levels were higher in grazing lawns compared to tall grassland and in green leaves compared to green stem (Beta regression, $z = -5.7$, $P < 0.001$, and Beta regression, $z = -9.7$, $P < 0.001$, respectively; Table 2). The phosphorus level in lawn grass leaf and stem samples were significantly higher than in their corresponding tall grass samples (Beta regression, $z = -3.6$, $P < 0.001$), whereas, there was no difference in grass parts phosphorus levels within grasslands (Beta regression, $z = -0.73$, $P = 0.46$). Likewise, NDF, and ADF concentration of green leaf and green stem were significantly lower than in their corresponding tall grass samples (Beta regression, $z = 4.15$, and 6.7, and $P < 0.001$, respectively), however, the NDF and ADF concentration of grass parts were similar within grazing lawns and tall grasslands [Beta regression, $z = 1.7$ ($P = 0.08$) and 1.9 ($P = 0.058$), respectively]. Silica concentration in the vegetation was significantly higher in green leaf in both the grasslands (Beta regression, $z = -4.9$, $P < 0.001$), but remained proportionately the same between grassland states (Beta regression, $z = 0.05$, $P = 0.95$).

We found noticeable differences in chemical composition of the four graminoids that were most abundant in both grassland states viz., *I. cylindrica, V. zizanioides, D. bipinnata,* and *S. spontaneum* (Fig. 4). These species represented on average 73% and 78% of all grass species on grazing lawns and tall grasslands, respectively. *I. cylindrica* was the most abundant species in both grassland states which represented 62% and 30% of all grass species, respectively (Table S2). We found a higher concentration of CP in *I. cylindrica*, *S. spontaneum*, and *V. zizanioides* on grazing lawns than on tall grasslands (Fig. 4, a). *V. zizanioides* on grazing lawns had significantly higher phosphorus concentration than on tall grassland (Fig. 4, b). Likewise, *I. cylindrica*, and *S. spontaneum* on grazing lawns had lower NDF and ADF than on tall grasslands (Fig. 4, c and d). We further found that *S. spontaneum* had a significantly higher concentration of silica on grazing lawns than on tall grasslands (Fig. 4, e).

3.3. Underlying soil properties

Soils of grazing lawns and tall grasslands did not differ significantly (Table 3) in terms of soil moisture, pH, soil and available phosphorus. Soil organic matter differed significantly between grazing lawns and tall grasslands with lawns having higher loads than tall grasslands (Table 3).

4. Discussion

4.1. Forage quality in grasslands of Terai Arc Landscape

We analysed the physical and chemical composition of grassland vegetation from grazing lawns and tall grasslands in Bardia NP during the hot-dry season and found markedly different physical and chemical compositions. We found that grazing lawns were characterised by high bulk density, high proportion of green leaves, a high concentration of CP and phosphorus, and lower concentration of NDF and ADF. From the herbivore perspective, these are all desired characteristics. Hence, as expected, grazing pressure was higher in grazing lawns than in encroaching tall grasslands. The grazing lawns occurred in soils with a higher organic matter, and they had a higher species richness. Tall grasslands, on the other hand, had higher biomass, NDF and ADF. These findings corroborate the

Table 2
Chemical concentrations (dw/dw) (mean, 95% CI) of grass parts sampled from grazing lawns and tall grasslands. Note that confidence limits (CI) are asymmetrical because of back-transformation. Letters within the rows indicate significant differences at alpha = 0.05 (beta regression followed by Tukey-test).

Chemical parameters	Grazing lawns		Tall grasslands	
	Green leaf	Green stem	Green leaf	Green stem
Crude Protein (%)	9.7 (8.9–10)^{d}	6.5 (5.1–7.9)^{b}	7.7 (7.1–8.3)^{c}	4.2 (3.7–4.6)^{a}
Phosphorus (%)	0.2 (0.16–0.21)^{c}	0.2 (0.16–0.23)^{bc}	0.15 (0.12–0.18)^{ab}	0.13 (0.1–0.16)^{a}
NDF (%)	76 (74–77)^{a}	75 (71–79)^{ab}	78 (77–79)^{bc}	80 (79–81)^{c}
ADF (%)	36 (35–38)^{a}	36 (32–40)^{a}	41 (40–42)^{b}	44 (42–46)^{b}
Silica (%)	2.8 (2.4–3.1)^{b}	2.2 (1.7–2.7)^{a}	3 (2.6–3.4)^{b}	2 (1.6–2.2)^{a}

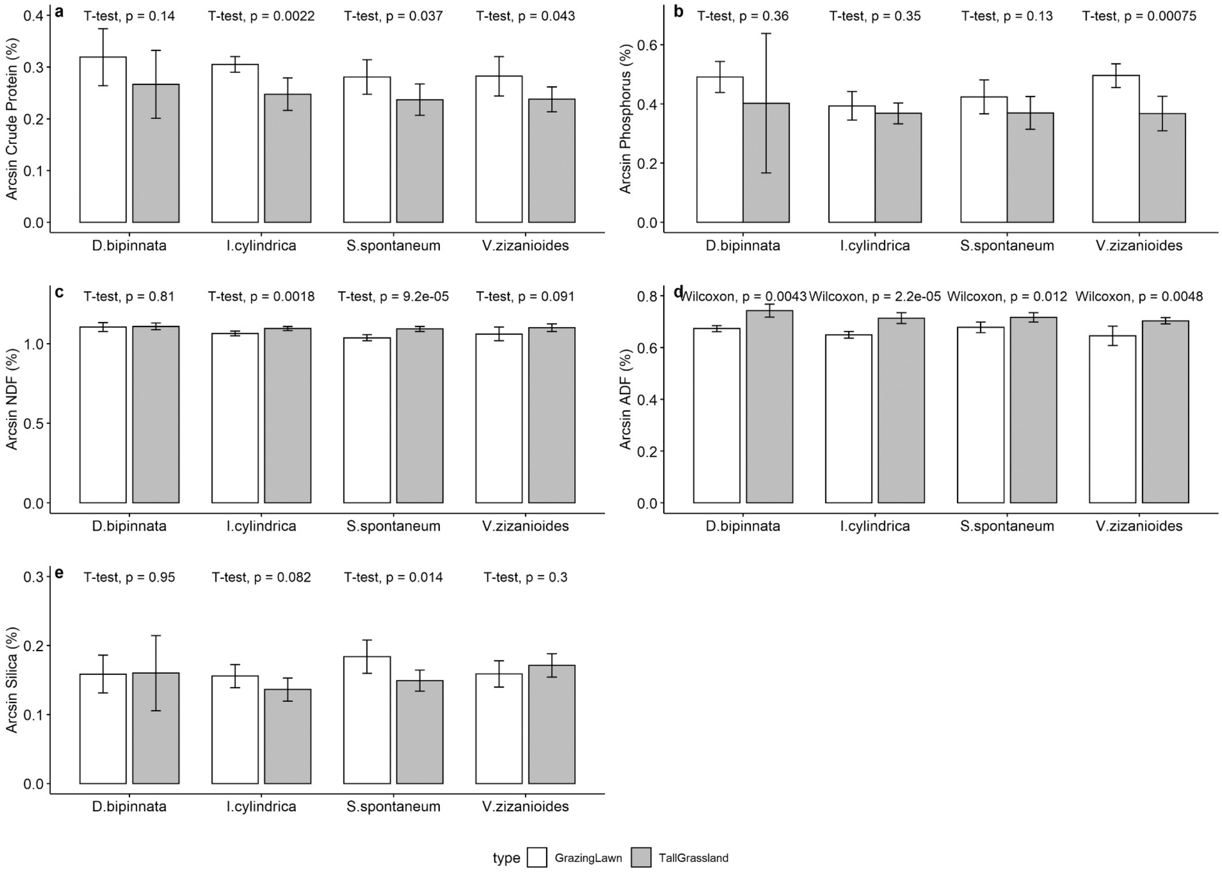

Fig. 4. : Comparison of nutrient concentration (a) Crude protein (b) phosphorus (c) NDF (d) ADF and (e) silica of grass species that are most abundant in grazing lawns and tall grasslands. Error bars indicate 95% confidence limits.

Table 3
Underlying soil properties (mean, 95% CI) of grazing lawn and tall grassland. Note that confidence limits (CI) are asymmetrical because of back-transformation.

Soil properties	Grazing lawns	Tall grasslands	Test statistics
Soil Moisture (%)	8 (4.8–12)	6 (3.0–10)	Wilcoxon signed-rank test (*Z = 46, N = 10, P = 0.05*) **ns**
Soil pH	7.4 (7.2–7.6)	7.5 (7.3–7.6)	Paired *t*-test (t = - 0.91, df=9, *P = 0.38*) **ns**
Soil Organic Matter (%)	1.4 (1.2–2.0)	1.0 (0.7–1.4)	Paired *t*-test (t = 3.73, df = 9, *P = 0.004*) **
Soil Nitrogen (%)	0.15 (0.15–0.23)	0.15 (0.09–0.23)	Paired *t*-test (t = 1.01, df = 9, *P = 0.33*) **ns**
Available phosphorus (ppm)	15 (9.2–20)	17 (9.8–24)	Paired *t*-test (t = - 1.3, df = 9, *P = 0.22*) **ns**

** indicates significant difference at $P < 0.01$. ***ns*** indicates non-significant.

previous studies in grazing lawns from other parts of the world, viz., African savannas (Archibald, 2008; Arnold et al., 2014; Cromsigt et al., 2017; Cromsigt and Olff, 2008; Grant and Scholes, 2006; Hempson et al., 2015; McNaughton, 1984; Veldhuis et al., 2016, 2014; Verweij et al., 2006), and Asia (Ahrestani et al., 2011; Karki et al., 2000; Moe and Wegge, 2008) where grazing lawns are characterised by short, grazing-tolerant grasses with higher nutrient concentrations and digestible energy content, higher biomass per volume and higher proportions of leaves to stems. Our study expands the findings from much drier savannas into dry monsoon grasslands that reflect past human interventions (Kumar et al., 2020; Ratnam et al., 2019, 2016). Indeed, our study area with Cwa-climate (monsoon-influenced humid subtropical climate) has an average of 1800 mm annual precipitation. Very few studies (Karki et al., 2000; Moe and Wegge, 2008, 1997; Wegge et al., 2006) have been executed in the Terai-Duar Savanna and Grasslands with such a Cwa-climate, and thus, our study adds to insights gained in other areas far outside the climate envelope of savannas (cf. Sankaran et al., 2005). Moreover, we draw attention to the fact that floristically the grassland states within forested landscape in the Terai-Duar Savanna and Grasslands are not different, but that lawns and tall grasslands represent two alternative states of a similar plant community. This is a marked difference from the iconic Serengeti ecosystem where the grazing lawns are floristically different from the tall grasslands (Cromsigt et al., 2017). And yet, despite the floristic similarity, we show a similar nutritional elevation in these man-made grazing lawns as found in African savanna grazing lawns.

4.2. The implications of improved forage quality

Depending on herbivore mouth dimensions, the higher bulk density on grazing lawns will enable higher intake rates per bite compared to tall grass swards (Drescher et al., 2006a; Laca et al., 1992; Stobbs, 1973a, 1973b). Moreover, the higher proportion of green leaf in grazing lawns will ensure that each bite will contain more green leaf, and hence will lead to higher rates of energy gain. Likewise, the improved leaf quality metrics (higher CP and phosphorus and lower percentage of NDF and ADF) of grazing lawns should ensure higher digestibility and nutrient intake compared to that from tall grasslands. Hence, grazing lawns are likely important nutrient sources from where herbivores can maximise the concentration of protein and phosphorus in their diet.

Chital, the most abundant primary prey of the tiger in the Bardia NP, utilises open grassland heavily for grazing (Moe and Wegge, 1997, 1994; Pokharel and Storch, 2016). If we estimate the daily requirement of nitrogen for an adult female chital with an average body mass of 50 kg from the known allometric relationship (Ahrestani et al., 2012; Prins, 1996; Prins and Van Langevelde, 2008), then she requires 7.6% CP for maintenance, 9.2% CP for reproduction and 11.8% CP for lactation, respectively. Chital can meet their nitrogen requirement from the grazing lawns for maintenance and reproduction, however, grass nitrogen is still below requirement for lactating females even from grazing lawns (Table 2). Likewise, phosphorus is a limiting factor for herbivores in the grasslands of the Bardia NP as the forage generally does not meet the minimum requirement reported for ruminants (0.2 – 0.4%; Moe, 1994). These requirements of nutrients are derived from livestock industry norms and may be too high for wild ruminants (e.g., Wallis De Vries et al., 1999). Notwithstanding these limitations, chital and other deer can obtain higher levels of nitrogen and phosphorus in the forage from the grazing lawns compared to the tall grasslands during the nutrient-bottleneck period i.e., during the hot-dry season. The hot-dry season is the peak lactating period of the deer when females require high nutrients compared to other seasons. Ahrestani et al. (2012) reported that chital in South Indian tiger reserves have parturition peak timing between February–April, the season when available plant quality was above the minimum required by lactating females. Likewise, Mishra (1982a,1982b) documented a distinct seasonal pattern of breeding cycle in chital with December – March in Chitwan. The chital in Bardia NP also exhibited a peak parturition period between January – March (80% in the second week of February) where majority of Does were observed with fawns (pers. obs.), the season when grassland were preferentially used by chital in Bardia NP (Moe and Wegge, 1994). Hence, the availability of required nutrients during the nutrient-bottleneck season will influence both the survival and fitness of lactating females and fawns which have an implication on the species population dynamics. If nutrition falls below the minimum requirements, physiological functions like maintenance, growth, reproduction, and lactation are compromised (Kiffner and Lee, 2019; Van Soest, 1982) which may lead to poor health and reproduction of herbivores and might have a cascading negative effect on the tiger population due to food availability.

4.3. Management implications

Tall grasslands in the study region with higher quantity but of lower quality vegetation are less beneficial for the small and medium body-sized herbivores. The forage requirement of these wild herbivores is different from large roughage feeders such as gaur, arna (*Bubalus arnee*), greater one-horned rhinoceros (*Rhinoceros unicornis*), and Asian elephant (*Elaphas maximus*) (Ahrestani et al., 2016, 2012; Pradhan et al., 2008; Wegge et al., 2006) because of body mass and digestive physiology (Illius and Gordon, 1992; Prins and Olff, 1998). The former require higher quality forage for their maintenance and production. At present, there is a relatively low density of large roughage grazers in this subtropical region that at high density can possibly create, and certainly maintain grazing lawns (Ahrestani et al., 2016) but currently are unable to do so (often because they occur in such a low density that they are functionally extinct). In contrast to African white rhinoceroses (*Ceratotherium simum*), greater one-horned rhinoceroses do not closely crop the sward. Furthermore, greater one-horned rhinoceros graze pre-dominantly on the riverine tall grassland dominated by *S. spontaneum* (Pradhan and Wegge, 2007). Indeed, they appear to chomp off grasses to reach the sweet base of stems and are thus very atypical "grazers" (pers. obs.). With the existing rhinoceros density of 0.3 km^{-2} in Bardia NP (Subedi et al., 2013) and with their grazing modus, it is therefore unlikely that they could create and maintain grazing lawns. Also, Asian elephants have never been reported to convert forests into grasslands (Pradhan et al., 2008). Medium body-sized herbivores do not seem to be able to create or maintain grazing lawns in the Terai grasslands. Thus, the Department of National Parks and Wildlife Conservation and National Trust for Nature Conservation of Nepal, may benefit from translocating large mammals like greater one-horned rhinoceros, arna and gaur in order to maintain and expand the necessary lawns.

Our study suggests that the mosaic of tall grassland and grazing lawns found in the study region is not caused by edaphic factors, such as soil nutrients, soil pH, or soil moisture (Table 3). This is in contrast to the conclusion by others that grazing lawns are often formed in areas where soil mineral concentrations are higher e.g., volcanic soils, sodic sites, near termite moulds, near elephant or rhinoceros dung piles, and abandoned kraals (Cromsigt et al., 2017; Fox et al., 2015; Grant and Scholes, 2006). We did find higher loads of soil organic matter in the soil under grazing lawns as compared to that of tall grasslands. This could however be due to the supplementation of dung and urine from herbivores to the lawns while grazing (Moe and Wegge, 2008). Moreover, high nutrient maintenance costs of continuously growing grasses in grazing lawns can only be achieved if there is sufficient nutrients to sustain it which could only be achieved with continual nutrient replenishment through dung and urine inputs. The improved nutritional properties of individual grass species when growing in grazing lawns, may be a result of plant phenology brought about by frequent grazing.

We, thus, posit that the grazing lawns in the Cwa-climate grasslands result from patch-selective grazing immediately after patchy burning or cutting and not by differences in underlying soil properties, but that some soil differentiation occurs after these lawns have formed and a positive feedback loop through a dung feedback cycle (or mineralization cycle) starts. We do not yet know how persistent these mosaics are, but from experience we know that the landscape patterns can be reset every year by a fire. Like African savannas, fire is an integral component of the subtropical grasslands (Ratnam et al., 2019; Sankaran, 2005). After burns, the entire burnt area consists of nutritious new re-sprout (Donaldson et al., 2018; Moe and Wegge, 1997) which interrupt the positive interaction between grazing and grazing lawns by diffusing the grazing pressure away from the lawns (Archibald et al., 2005; Van Langevelde et al., 2003).

The very high growth rate and fast production of combustible materials due to hot and humid growing season of this location as characterised by the Cwa-climate make these grasslands fundamentally different from savanna grasslands in arid and semi-arid ecosystems. This implies that African savanna studies on lawns cannot yield sufficient insight into how grazing lawns come into existence in the highly productive subtropical grasslands. Apart from major fires, we suspect that past agricultural practices in what are now the grasslands in the park and the ongoing grassland management by the park (cutting and burning) and thatch harvesting by local people are likely to be of utmost importance to understand the present-day functioning of grazing lawns for the prey-base of tigers in areas where the large roughage feeders are now absent or in low density.

5. Conclusion

Grazing lawns constitute an important nutritional supplement to burning and grass cutting for maintaining abundant population of small to medium sized ungulates. Management actions such as large-scale burning may diffuse grazing pressure and lead to the disappearance of these lawns. Efforts to maintain these grazing lawns could prevent herbivores from needing to supplement their diet elsewhere in the park either with browse, forest grasses or agricultural crops. Hence, as long as the roughage grazers are absent, regular management of these highly productive subtropical grasslands is essential to maintain grazing lawns in the national parks of the Terai Arc Landscape.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01747.

References

Ahrestani, F.S., Sankaran, M., 2016. The Ecology of Large Herbivores in South and Southeast Asia. Springer.

Ahrestani, F.S., Heitkönig, I.M.A., Prins, H.H.T., 2011. Herbaceous production in South India-limiting factors and implications for large herbivores. Plant Soil 349, 319–330. https://doi.org/10.1007/s11104-011-0876-x.

Ahrestani, F.S., Van Langevelde, F., Heitkönig, I.M.A., Prins, H.H.T., 2012. Contrasting timing of parturition of chital Axis axis and gaur Bos gaurus in tropical South India - the role of body mass and seasonal forage quality. Oikos 121, 1300–1310. https://doi.org/10.1111/j.1600-0706.2011.20244.x.

Ahrestani, F.S., Heitkönig, I.M.A., Matsubayashi, H., Prins, H.H.T., 2016. Grazing and browsing by large herbivores in South and Southeast Asia. In: The Ecology of Large Herbivores in South and Southeast Asia. Springer, pp. 99–120.

AOAC, 1990. Official methods of analysis. Assoc. Anal. Chem.

Archibald, S., 2008. African grazing lawns—how fire, rainfall, and grazer numbers interact to affect grass community states. J. Wildl. Manag. 72, 492–501. https://doi.org/10.2193/2007-045.

Archibald, S., Bond, W.J., Stock, W.D., Fairbanks, D.H.K., 2005. Shaping the landscape: fire – grazer interactions in an African Savanna. Ecol. Appl. 15, 96–109. https://doi.org/10.1890/03-5210.

Arnold, S.G., Anderson, T.M., Holdo, R.M., 2014. Edaphic, nutritive, and species assemblage differences between hotspots and matrix vegetation: two African case studies. Biotropica 46, 387–394. https://doi.org/10.1111/btp.12116.

Bell, D., Oliver, W.L.R., 1992. Northern Indian tall grasslands: management and species conservation with special reference to fire.

Biswas, T., Ramsey, R.D., Bissonette, J.A., Symanzik, J., 2014. Integration of two spectral indices to monitor loss of moist grasslands within the Jaldapara Wildlife Sanctuary, India. Int. J. Remote Sens. 35, 1038–1063.

Bonnet, O., Fritz, H., Gignoux, J., Meuret, M., 2010. Challenges of foraging on a high-quality but unpredictable food source: the dynamics of grass production and consumption in savanna grazing lawns. J. Ecol. 98, 908–916. https://doi.org/10.1111/j.1365-2745.2010.01663.x.

Chen, D., Chen, H.W., 2013. Using the Köppen classification to quantify climate variation and change: an example for 1901–2010. Environ. Dev. 6, 69–79.

Cromsigt, J.P.G.M., Olff, H., 2008. Dynamics of grazing lawn formation: an experimental test of the role of scale-dependent processes. Oikos 117, 1444–1452. https://doi.org/10.1111/j.0030-1299.2008.16651.x.

Cromsigt, J.P.G.M., Prins, H.H.T., Olff, H., 2009. Habitat heterogeneity as a driver of ungulate diversity and distribution patterns: Interaction of body mass and digestive strategy. Divers. Distrib. 15, 513–522. https://doi.org/10.1111/j.1472-4642.2008.00554.x.

Cromsigt, J.P.G.M., Veldhuis, M., Stock, W., Roux, E., le, Gosling, C., Archibald, S.A.L.L.Y., Cromsigt, J., Archibald, S., Owen-Smith, N., 2017. The functional ecology of grazing lawns—how grazers, termites, people, and fire shape HiP's savanna grassland mosaic. Conserv. Africa's mega-diversity Anthr. Hluhluwe-iMfolozi Park story. Cambridge Univ. Press, Cambridge, UK, pp. 135–160.

De Vos, B., Lettens, S., Muys, B., Deckers, J.A., 2007. Walkley–Black analysis of forest soil organic carbon: recovery, limitations and uncertainty. Soil Use Manag. 23, 221–229.

Dinerstein, E., 1979. An ecological survey of the Royal Karnali-Bardia Wildlife Reserve, Nepal. Part I: vegetation, modifying factors, and successional relationships. Biol. Conserv. 15, 127–150.

Dinerstein, E., 1980. An ecological survey of the Royal Karnali-Bardia Wildlife Reserve, Nepal. Biol. Conserv. 18, 5–37. https://doi.org/10.1016/0006-3207(80)90063-4.

DNPWC, DFRS, 2018. Status of Tigers and Prey in Nepal 2018. Dep. Natl. Park. Wildl. Conserv. Dep. For. Soil Conserv. Minist. For. Environ. Kathmandu, Nepal.

Donaldson, J.E., Archibald, S., Govender, N., Pollard, D., Luhdo, Z., Parr, C.L., 2018. Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns. J. Appl. Ecol. 55, 225–235.

Douma, J.C., Weedon, J.T., 2019. Analysing continuous proportions in ecology and evolution: a practical introduction to beta and Dirichlet regression. Methods. Ecol. Evol. 10, 1412–1430.

Drescher, M., Heitkönig, I.M.A., Raats, J.G., Prins, H.H.T., 2006a. The role of grass stems as structural foraging deterrents and their effects on the foraging behaviour of cattle. Appl. Anim. Behav. Sci. 101, 10–26. https://doi.org/10.1016/j.applanim.2006.01.011.

Drescher, M., Heitkönig, I.M.A., Van Den Brink, P.J., Prins, H.H.T., 2006b. Effects of sward structure on herbivore foraging behaviour in a South African savanna: an investigation of the forage maturation hypothesis. Austral Ecol. 31, 76–87. https://doi.org/10.1111/j.1442-9993.2006.01552.x.

Durant, D., Fritz, H., Duncan, P., 2004. Feeding patch selection by herbivorous Anatidae: the influence of body size, and of plant quantity and quality. J. Avian Biol. 35, 144–152.

Ferrari, S., Cribari-Neto, F., 2004. Beta regression for modelling rates and proportions. J. Appl. Stat. 31, 799–815.

Fox, H.V., Bonnet, O., Cromsigt, J.P.G.M., Fritz, H., Shrader, A.M., 2015. Legacy effects of different land-use histories interact with current grazing patterns to determine grazing lawn soil properties. Ecosystems 18, 720–733.

Fryxell, J.M., 1991. Forage quality and aggregation by large herbivores. Am. Nat. 138, 478–498. https://doi.org/10.1086/285227.

Goodall, D., 1952. Some considerations in the use of point quadrats for the analysis of vegetation. Aust. J. Biol. Sci. 5, 1–41. https://doi.org/10.1071/BI9520001.

Gordon, I.J., Illius, A.W., 1996. The nutritional ecology of African ruminants: a reinterpretation. J. Anim. Ecol. 18–28.

Grant, C.C., Scholes, M.C., 2006. The importance of nutrient hot-spots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. Biol. Conserv. 130, 426–437.

Hempson, G.P., Archibald, S., Bond, W.J., Ellis, R.P., Grant, C.C., Kruger, F.J., Kruger, L.M., Moxley, C., Owen-Smith, N., Peel, M.J.S., Smit, I.P.J., Vickers, K.J., 2015. Ecology of grazing lawns in Africa. Biol. Rev. 90, 979–994. https://doi.org/10.1111/brv.12145.

Illius, A.W., Gordon, I.J., 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. Oecologia 89, 428–434.

Jhala, H.Y., Qureshi, Q., Jhala, Y.V., Black, S.A., 2021. Feasibility of reintroducing grassland megaherbivores, the greater one-horned rhinoceros, and swamp buffalo within their historic global range. Sci. Rep. 11, 1–15.

Jhala, Y.V., 1997. Seasonal effects on the nutritional ecology of blackbuck Antelope cervicapra. J. Appl. Ecol. 34, 1348–1358. https://doi.org/10.2307/2405252.

Jnawali, S.R., Baral, H.S., Lee, S., Acharya, K.P., Upadhyay, G.P., Pandey, M., Shrestha, R., Joshi, D., Lamichhane, B.R., Griffiths, J., Khatiwada, A.P., Amin, R. (Compilers), 2011. The Status of Nepal ' s Mammals: The National Red List Series. Pref. by Simon M. Stuart Chair IUCN Species Surviv. Comm. Status Nepal's Mamm. Natl. Red List Ser. 276. https://doi.org/10.13140/2.1.4619.0881.

Karanth, K.U., Sunquist, M.E., 1992. Population structure, density and biomass of large herbivores in the tropical forests of Nagarahole, India. J. Trop. Ecol. 8, 21–35.

Karki, J.B., Jhala, Y.V., Khanna, P.P., 2000. Grazing Lawns in Terai Grasslands, Royal Bardia National Park, Nepal1. Biotropica 32, 423–429. https://doi.org/10.1111/j.1744-7429.2000.tb00489.x.

Kiffner, C., Lee, D.E., 2019. Population dynamics of browsing and grazing ungulates in the anthropocene. In: The Ecology of Browsing and Grazing II. Springer, pp. 155–179.

Krebs, J.C., 1999. Ecological Methodology, xii. Addison Wesley, Menlo Park, California, p. 620.

Kumar, D., Pfeiffer, M., Gaillard, C., Langan, L., Martens, C., Scheiter, S., 2020. Misinterpretation of Asian savannas as degraded forest can mislead management and conservation policy under climate change. Biol. Conserv. 241, 108293.

Laca, E.A., Ungar, E.D., Seligman, N., Demment, M.W., 1992. Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. Grass Forage Sci. 47, 91–102. https://doi.org/10.1111/j.1365-2494.1992.tb02251.x.

Laca, E.A., Sokolow, S., Galli, J.R., Cangiano, C.A., 2010. Allometry and spatial scales of foraging in mammalian herbivores. Ecol. Lett. 13, 311–320. https://doi.org/10.1111/j.1461-0248.2009.01423.x.

Lehmkuhl, J.F., 1994. A classification of subtropical riverine grassland and forest in Chitwan National Park, Nepal. Vegetatio 111, 29–43. https://doi.org/10.1007/BF00045575.

Mårell, A., Hofgaard, A., Danell, K., 2006. Nutrient dynamics of reindeer forage species along snowmelt gradients at different ecological scales. Basic Appl. Ecol. 7, 13–30. https://doi.org/10.1016/j.baae.2005.04.005.

McNaughton, S.J., 1984. Grazing lawns: animals in herds, plant form, and coevolution. Am. Nat. 124, 863–886.

Mezzalira, J.C., Bonnet, O.J.F., Carvalho, P.C. d F., Fonseca, L., Bremm, C., Mezzalira, C.C., Laca, E.A., 2017. Mechanisms and implications of a type IV functional response for short-term intake rate of dry matter in large mammalian herbivores. J. Anim. Ecol. 86. https://doi.org/10.1111/1365-2656.12698.

Mishra, H.R., 1982a. Balancing human needs and conservation in Nepal's Royal Chitwan Park (rhinoceros, tiger). Ambio 11, 246–251.

Mishra, H. R., 1982b. The ecology and behaviour of chital (Axis axis) in the Royal Chitwan National Park, Nepal: with comparative studies of hog deer (Axis porcinus), sambar (Cervus unicolor) and barking deer (Muntiacus muntjak).

Moe, S.R., 1994. The importance of aquatic vegetation for the management of the Barasingha Cervus-Duvauceli in Nepal. Biol. Conserv. 70, 33–37.

Moe, S.R., Wegge, P., 1994. Spacing behaviour and habitat use of axis deer (Axis axis) in lowland Nepal. Can. J. Zool. 72, 1735–1744.

Moe, S.R., Wegge, P., 1997. The effects of cutting and burning on grass quality and axis deer (Axis axis) use of grassland in lowland Nepal. J. Trop. Ecol. 13, 279–292. https://doi.org/10.1017/S0266467400010452.

Moe, S.R., Wegge, P., 2008. Effects of deposition of deer dung on nutrient redistribution and on soil and plant nutrients on intensively grazed grasslands in lowland Nepal. Ecol. Res. 23, 227–234. https://doi.org/10.1007/s11284-007-0367-y.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., 2019. vegan: Community Ecology Package. R package version 2.5–6. 2019.

Olson, D.M., Dinerstein, E., 2002. The Global 200: priority ecoregions for global conservation. Ann. Missouri Bot. Gard. 199–224.
Peet, N., 1997. Biodiversity and management of tall grasslands in Nepal School of Biological Sciences. Biodivers. Manag. Tall Grassl. Nepal.
Peet, N.B., Watkinson, A.R., Bell, D.J., Sharma, U.R., 1997. The management of tall grasslands for the conservation of biodiversity and sustainable utilization. Sci. Manag. Rep. Prep. Dep. Natl. Park. Wildl. Conserv. HMG, Nepal.
Peet, N.B., Watkinson, A.R., Bell, D.J., Kattel, B.J., 1999. Plant diversity in the threatened sub-tropical grasslands of Nepal. Biol. Conserv. 88, 193–206. https://doi.org/10.1016/S0006-3207(98)00104-9.
Peet, R.K., 1974. The measurement of species diversity. Annu. Rev. Ecol. Syst. 285–307.
Pokharel, K.P., Storch, I., 2016. Habitat niche relationships within an assemblage of ungulates in Bardia National Park. Nepal. Acta Oecol. 70, 29–36.
Pradhan, N.M.B., Wegge, P., 2007. Dry season habitat selection by a recolonizing population of Asian elephants Elephas maximus in lowland Nepal. Acta Theriol. 52, 205–214.
Pradhan, N.M.B., Wegge, P., Moe, S.R., Shrestha, A.K., 2008. Feeding ecology of two endangered sympatric megaherbivores: Asian elephant Elephas maximus and greater one-horned rhinoceros Rhinoceros unicornis in lowland Nepal. Wildl. Biol. 14, 147–154.
Prins, H., 1996. Ecology and Behaviour of the African Buffalo: Social Inequality and Decision Making. Springer Science & Business Media.
Prins, H.H.T., Beekman, J.H., 1989. A balanced diet as goal of grazing: the food of the Manyara buffalo. J. Afr. Ecol. 129–147.
Prins, H.H.T., Olff, H., 1998. Species richness of African grazer assemblages: towards a functional explanation. In: Dynamics of Tropical Communities. Cambridge University Press, pp. 449–490. https://doi.org/10.1017/CBO9781107415324.004.
Prins, H.H.T., Van Langevelde, F., 2008. Assembling a diet from different places. In: Resource Ecology. Springer, pp. 129–155.
R. Core Team, 2019. R: A language and environment for statistical computing.
Raman, T.R.S., 1997. Factors influencing seasonal and monthly changes in the group size of chital or axis deer in southern India. J. Biosci. 22, 203–218.
Ratnam, J., Bond, W.J., Fensham, R.J., Hoffmann, W.A., Archibald, S., Lehmann, C.E.R., Anderson, M.T., Higgins, S.I., Sankaran, M., 2011. When is a 'forest'a savanna, and why does it matter? Glob. Ecol. Biogeogr. 20, 653–660.
Ratnam, J., Tomlinson, K.W., Rasquinha, D.N., Sankaran, M., 2016. Savannahs of Asia: antiquity, biogeography, and an uncertain future. Philos. Trans. R. Soc. B Biol. Sci. 371, 20150305.
Ratnam, J., Sheth, C., Sankaran, M., 2019. African and Asian Savannas: cmparisons of vegetation composition and drivers of vegetation structure and function. Savanna Woody Plants Large Herbiv. 25–49.
Raynor, E.J., Joern, A., Nippert, J.B., Briggs, J.M., 2016. Foraging decisions underlying restricted space use: effects of fire and forage maturation on large herbivore nutrient uptake. Ecol. Evol. 6, 5843–5853. https://doi.org/10.1002/ece3.2304.
Sankaran, M., 2005. Fire, grazing and the dynamics of tall-grass savannas in the Kalakad-Mundanthurai Tiger Reserve. South India Conserv. Soc. 4–25.
Sankaran, M., 2009. Diversity patterns in savanna grassland communities: implications for conservation strategies in a biodiversity hotspot. Biodivers. Conserv. 18, 1099–1115.
Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., 2005. Determinants of woody cover in African savannas. Nature 438, 846–849.
Sarmah, C.K., 2017. Chao, jackknife and bootstrap estimators of species richness. IJAMAA 12, 7–15.
Schoenau, J.J., O'Halloran, I.P., 2008. Sodium bicarbonate-extractable phosphorus. Soil Sampl. Methods Anal. 2.
Searle, K.R., Shipley, L.A., 2008. The comparative feeding bahaviour of large browsing and grazing herbivores. In: The Ecology of Browsing and Grazing. Springer, pp. 117–148.
Spalinger, D.E., Hobbs, N.T., 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. Am. Nat. 140, 325–348. https://doi.org/10.1086/285415.
Stobbs, T.H., 1973a. The effect of plant structure on the intake of tropical pastures. I. Variation in the bite size of grazing cattle. Aust. J. Agric. Res. 24, 809–819.
Stobbs, T.H., 1973b. The effect of plant structure on the intake of tropical pastures. II.* Differences in sward structure, nutritive value, and bite size of animals grazing Setaria anceps and Chloris gayana at various stages of growth. Aust. J. Agric. Res. 24, 821–829.
Subedi, N., Jnawali, S.R., Dhakal, M., Pradhan, N.M.B., Lamichhane, B.R., Malla, S., Amin, R., Jhala, Y.V., 2013. Population status, structure and distribution of the greater one-horned rhinoceros *Rhinoceros unicornis* in Nepal. Oryx 47, 352–360. https://doi.org/10.1017/S0030605313000562.
Tuboi, C., Hussain, S.A., 2016. Factors affecting forage selection by the endangered Eld's deer and hog deer in the floating meadows of Barak-Chindwin basin of North-east India. Mamm. Biol. 81, 53–60.
Upadhyaya, S.K., Musters, C.J.M., Lamichhane, B.R., de Snoo, G.R., Thapa, P., Dhakal, M., Karmacharya, D., Shrestha, P.M., de Iongh, H.H., 2018. An insight into the diet and prey preference of tigers in Bardia National Park, Nepal. Trop. Conserv. Sci. 11, 1940082918799476.
van Langevelde, F., Drescher, M., Heitkönig, I.M.A., Prins, H.H.T., 2008. Instantaneous intake rate of herbivores as function of forage quality and mass: effects on facilitative and competitive interactions. Ecol. Modell. https://doi.org/10.1016/j.ecolmodel.2007.12.009.
Van Langevelde, F., Van De Vijver, C.A.D.M., Kumar, L., Van De Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J., 2003. Effects of fire and herbivory on the stability of savanna ecosystems. Ecology 84, 337–350.
Van Soest, P.J., 1982. Nutritional Ecolo gy of the Ruminant, O & B Books, Inc., Corvallis, OR, 374.
Veldhuis, M.P., Howison, R.A., Fokkema, R.W., Tielens, E., Olff, H., 2014. A novel mechanism for grazing lawn formation: large herbivore-induced modification of the plant-soil water balance. J. Ecol. 102, 1506–1517. https://doi.org/10.1111/1365-2745.12322.
Veldhuis, M.P., Fakkert, H.F., Berg, M.P., Olff, H., 2016. Grassland structural heterogeneity in a savanna is driven more by productivity differences than by consumption differences between lawn and bunch grasses. Oecologia 182, 841–853. https://doi.org/10.1007/s00442-016-3698-y.
Verweij, R.J.T., Verrelst, J., Loth, P.E., Heitkönig, I.M.A., Brunsting, A.M.H., 2006. Grazing lawns contribute to the subsistence of mesoherbivores on dystrophic savannas. Oikos 114, 108–116. https://doi.org/10.1111/j.2006.0030-1299.14209.x.
Wallis De Vries, M.F., Laca, E.A., Demment, M.W., 1999. The importance of scale of patchiness for selectivity in grazing herbivores. Oecologia 121, 355–363. https://doi.org/10.1007/s004420050939.
Wegge, P., Shrestha, A.K., Moe, S.R., 2006. Dry season diets of sympatric ungulates in lowland Nepal: competition and facilitation in alluvial tall grasslands. Ecol. Res. 21, 698–706.
Wegge, P., Odden, M., Pokharel, C.P., Storaas, T., 2009. Predator-prey relationships and responses of ungulates and their predators to the establishment of protected areas: a case study of tigers, leopards and their prey in Bardia National Park, Nepal. Biol. Conserv. 142, 189–202. https://doi.org/10.1016/j.biocon.2008.10.020.
Wickham, H., 2016. ggplot2: Elegant Graphics fr Data Analysis. Springer.
Wikramanayake, E., Manandhar, A., Bajimaya, S., Nepal, S., Thapa, G., Thapa, K., 2010. The Terai Arc Landscape: a tiger conservation success story in a human-dominated landscape. In: Tigers of the World. Elsevier, pp. 163–173.
Wilke, B.-M., 2005. Determination of chemical and physical soil properties. In: Monitoring and Assessing Soil Bioremediation. Springer, pp. 47–95.
Wilmshurst, J.F., Fryxell, J.M., Farm, B.P., Sinclair, A.R.E., Henschel, C.P., 1999. Spatial distribution of Serengeti wildebeest in relation to resources. Can. J. Zool. 77, 1223–1232. https://doi.org/10.1139/cjz-77-8-1223.
Wilmshurst, J.F., Fryxell, J.M., Bergman, C.M., 2000. The allometry of patch selection in ruminants. Proc. R. Soc. London. Ser. B Biol. Sci. 267, 345–349.
Wilson, E., Underwood, M., Puckrin, O., Letto, K., Doyle, R., Caravan, H., Camus, S., Bassett, K., 2013. The arcsine transformation: has the time come for retirement. Unpubl. manuscript, Meml. Univ. Newfoundland, Newfoundl. Labrador, Canada.
Zhang, H., Zhang, S., Fu, M., Chang, H., He, G., Hou, R., Pan, R., Li, B., Guo, S., 2019. Habitat manipulation preferred by Eld's Deer in Hainan Island, China. J. Nat. Conserv. 48, 21–26. https://doi.org/10.1016/j.jnc.2019.01.004.
Zwerts, J.A., Prins, H.H.T., Bomhoff, D., Verhagen, I., Swart, J.M., De Boer, W.F., 2015. Competition between a lawn-forming Cynodon dactylon and a tufted grass species Hyparrhenia hirta on a south-African dystrophic savanna. PLoS One 10. https://doi.org/10.1371/journal.pone.0140789.