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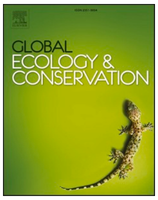

Original research article

Unveiling the mysteries of Asian herbivores resource partitioning in tropical wet-grassland ecosystem

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ABSTRACT

Ecological niche partitioning is fundamental for the coexistence of sympatric species. However, the relationship between herbivore body size and forage availability on resource segregation and selection remains debatable. This study quantifies the niche differentiation and selectivity of forage species consumed by six Asian large herbivores (SLH), including mega-herbivores like Greater one-horned rhino (*Rhinoceros unicornis*), Asian elephant (*Elephas maximus*) and Asiatic wild buffalo (*Bubalus arnee*), and meso-herbivores like swamp deer (*Rucervus duvaucelii*), hog deer (*Axis porcinus*) and sambar (*Rusa unicolor*) in tropical wet-grasslands of the Brahmaputra floodplains. We hypothesized that body size influences dietary niche breadth and interspecific dietary similarities or dissimilarities, while forage availability influences forage selectivity among Asian herbivores. We used micro-histological technique, harvest method and Jacobs Index to quantify SLH foraging patterns, forage availability and preference, respectively. Results of the study revealed high niche breadth for elephant ($0.56 > B_s \leq 0.74$) among mega-herbivores and for sambar ($0.49 > B_s \leq 0.64$) among meso-herbivores. SLH showed a significant positive correlation between body size and niche breadth in wet season. High dietary overlap was recorded between buffalo and hog deer (0.79–0.86) and swamp deer and hog deer (0.75–0.86) among SLH, rhino and buffalo (0.80–0.83) among mega-herbivores, and swamp deer and hog deer (0.75–0.86) among meso-herbivores. High dietary dissimilarity was recorded between elephant and swamp deer (36–37 %), elephant and buffalo (27–33 %), and swamp deer and sambar (27–29 %). Compared to dry season ($1354.54 \pm 641.30\ \mathrm{g\,m^{-2}}$), significantly higher biomass was recorded in wet season ($3026.93 \pm 1632.65\ \mathrm{g\,m^{-2}}$; $p < 0.05$). From dry to wet season, rhino, buffalo and hog deer shift their preferred forage from dicot to monocot. Dicot was the most preferred forage of elephant among mega-herbivores, and monocot of swamp deer and sambar among meso-herbivores. Mega- and meso-herbivores avoid invasives *Merremia umbellata* and *Mimosa* spp., while meso-herbivores avoid *Mikania micrantha*. Body size explains niche partitioning only for rhino, elephant and swamp deer. Forage availability contributed to niche breadth and forage preference. In conclusion, forage segregation, despite being challenging to interpret at taxonomic level, influences niche partitioning among mega- and meso-herbivores.

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1. Introduction

Resource selection and partitioning are integral to understanding plant-animal interactions (Marquis, 2010). Over time, various theories and explanations such as allometric theory (Kleiber, 1932), ecological succession (Vesey-FitzGerald, 1960), competitive exclusion principle (Hardin, 1960), and ecological separation (Lamprey, 1963) aided understanding of how mega- and meso-herbivores coexist with or without conflict; whereas, digestive physiology (Hofmann and Stewart, 1972), and Jarman–Bell principle (Bell, 1971; Jarman, 1974) explained how mega- and meso-herbivores segregate their resources. Resource-utilization concept suggests that two species cannot occupy a similar niche in a similar environment over long time scales without showing competition, which may result in the local extinction of other species (Hardin, 1960; MacArthur and Levins, 1967). Contrastingly, ecological niche partitioning predicts that sympatrically occurring species partition their resources spatially or temporally to coexist without competition (Pianka, 1969; Schoener, 1974). In limited resource conditions, coexisting species are expected to show natural selection by evolving themselves for niche partition (MacArthur and Levins, 1967).

Jarman–Bell principle (1974) proposed that compared to meso-herbivores (<500 kg), mega-herbivores (>1000 kg) are better equipped to satisfy their high metabolic requirement by feeding on low-quality forage (Bell, 1971; Jarman, 1974; Ahrestani and Sankaran, 2016), and ranging over larger areas (McNab, 1963; Ahrestani and Sankaran, 2016). To fulfil the metabolic requirements, mammals adjust their home ranges, resulting in a positive relationship between body size and home range (McNab, 1963; Odden and Wegge, 2007). Therefore, herbivores' body size helps to predict difficult aspects of community ecology (Odden and Wegge, 2007; Ahrestani and Sankaran, 2016).

Globally, Africa, and South and South East Asia represent a wide diversity of ungulates. Of 19 Asian terrestrial herbivores (body size>100 kg) representing South East Asia, 14 occur in India (Devi et al., 2022). Studies that suggest herbivores' body size plays significant role in segregation of resources, competition, and utilization of habitats have surfaced from Africa, Europe and North America (Ahrestani and Sankaran, 2016; Devi et al., 2022). In Asia, few studies illustrate dietary comparison of coexisting wild Asian large herbivores irrespective of body size (Dinerstein, 1980; Johnsingh and Sankar, 1991; Sankar, 1994; Steinheim et al., 2005; Pradhan et al., 2008), and fewer with respect to body size (Wegge et al., 2006; Ahrestani, 2009; Devi et al., 2022).

In areas where resource availability varies seasonally, foraging choice of herbivores varies spatio-temporally (Kleynhans et al., 2011). In temperate regions, forage availability is high during summer, while in tropical areas, forage availability is high during wet season due to seasonal rainfall (Ahrestani and Sankaran, 2016). Season governs the change in forage availability and quality (Owen-Smith, 1988; Ahrestani and Sankaran, 2016) and herbivores' body size influences forage selection process, which plays a crucial role in shaping plant communities (Marquis, 2010). Mega-herbivores with large body sizes (>1000 kg) and coarse feeding, utilize large quantities of dominant forage, which increases the plant diversity (Milchunas and Lauenroth, 1993). Contrastingly, meso-herbivores with intermediate body size (5–500 kg) and selective feeding, required qualitative forage, which decreases the plant diversity (Edwards and Crawley, 1999; Devi et al., 2022).

In India, terrestrial ecosystems are shared by multispecies assemblages of Asian mammalian herbivores of diverse body sizes, from mouse deer (2–4 kg) to Asian elephant (3000–5400 kg) (Devi et al., 2022). Tropical wet riverine grasslands of the Brahmaputra floodplains, are home to the world's largest population of Greater one-horned rhino, Asiatic wild buffalo and swamp deer, and is the only remaining habitat harbouring an assemblage of eight sympatrically occurring large herbivores (Devi, 2023; Sharma et al., 2023). Persistence of these multispecies systems in riverine grasslands without conflict and mechanisms facilitating stable coexistence of similar species are understudied (Ahrestani and Sankaran, 2016; Devi et al., 2022). Understanding of community ecology of mega- and meso-herbivores is fundamental for effectively managing herbivores and their associated habitat. Kaziranga National Park (KNP) in the Brahmaputra floodplains, with the world's largest population of Greater one-horned rhino and Asiatic wild buffalo, and significant population of elephant, swamp deer and hog deer (Devi et al., 2022) provides an opportunity to examine the community ecology of these mega- and meso-herbivores in a grassland ecosystem exposed to human pressure and susceptible to climate change.

The present study was conducted in KNP, which focused on six Asian large herbivores (SLH) of different body sizes, specifically mega-herbivores — Greater one-horned rhino (*Rhinoceros unicornis*), Asian elephant (*Elephas maximus*) and Asiatic wild buffalo (*Bubalus arnee*), and meso-herbivores — swamp deer (*Rucervus duvaucelii*), hog deer (*Axis porcinus*) and sambar (*Rusa unicolor*) (Table S1). These SLH act as grazers and mixed feeders in KNP, which results in considerable seasonal variation in utilized forage species (Devi et al., 2022). Variations in foraging patterns can be influenced by body size, interactions like competition and predation, resource availability, plant height, nutrient content, gut physiology and herbivores' distribution (Pansu et al., 2019; Devi et al., 2022). The present study aims to provide information on community ecology of SLH in riverine grasslands of KNP with following research questions: (1) are there seasonal differences in niche breadth of mega- and meso-herbivores; (2) among mega and meso-herbivores (a) what is the degree of dietary overlap, (b) what is the degree of dietary dissimilarity, and (c) which forage species contribute most to diet dissimilarity; (3) are there differences in seasonal forage biomass in terms of (a) forage species consumed by mega- and meso-herbivores, and (b) growth forms *viz*., grasses, sedges, herbs, shrubs, climbers and trees; and (4) which forage species is most preferred and avoided by mega- and meso-herbivores, seasonally. We hypothesized (H_0) that with the increase in body size, there would be an increase in dietary niche breadth (H_1), species with similar body size would have the highest diet overlap, and vice-versa for dissimilar body size (H_2), and seasonal availability of forage would influence forage selectivity among SLH (H_3).

2. Material and methods

2.1. Study area

Study was conducted in KNP, Assam, northeastern India (26°34'–26°46'N; 93°08'–93°36'E). KNP, 429 km^2 in area, is dominated by wet grasslands interspersed with tropical moist deciduous to semi-evergreen forests and water bodies (Fig. 1). Conservation efforts in Kaziranga started with its declaration as a Reserve Forest (1908), subsequent redesignation as Wildlife Sanctuary (1950), then National Park (1974). After declaration as a UNESCO World Heritage Site (1985), it was declared a Tiger Reserve (2007). Climate in KNP is subtropical monsoon, divided into dry (October to March) and wet (April to September) seasons (Sharma et al., 2023). Annual rainfall ranges from 1592.8 to 2247.8 mm, with mean annual rainfall at 1802.7 ± 118.5 mm (Devi et al., 2022). Maximum temperature varies from 27°C to 39°C, and minimum temperature from 5°C to 23°C (Sharma et al., 2023).

KNP is a junction of the East Asia/Australia and Indo-Asian flyways. Annual floods aid grassland maintenance and replenish soil nutrients, however, high floods also lead to animal mortality (Devi, 2023). Controlled burning of tall grasslands, a well-established management practice, facilitates regeneration process and arresting succession (Sharma et al., 2023).

2.2. Faecal sample collection and micro-histology

Diet composition of mega- and meso-herbivores was examined using micro-histology technique (Tuboi and Hussain, 2016; Devi et al., 2022). The technique was based on two principles, which include preparation of plant reference slides (leaves, stems, flowers, and fruits) and its comparison to slides prepared from known faecal samples (Sparks and Malechek, 1968). Plant fragments in faeces were identified based on epidermal and cellular characteristics to estimate the frequency of occurrence of various forage fragments (Devi et al., 2022). Keys were referred to identify plant fragments at microscopic level (Satkopan, 1972; Johnson et al., 1983). Based on secondary literature and field observations, 75 reference plant samples were collected, identified taxonomically using Hajra and Jain (1994), oven-dried for ~48 hours at 60°C, kept in systematically-labelled paper bags, and transported to the base for micro-histological analysis (Devi et al., 2022).

For micro-histological examination, fresh faecal samples of SLH were collected for two-years, from November 2013 to May 2015 (except from June to October, high flooding time), which included sampling efforts of 307 days (rhino= 47 days, elephant= 56 days, buffalo=55 days, swamp deer=50 days, hog deer=51 days, and sambar=48 days). For each month, faecal samples were collected alternatively for fifteen days between 9:00 AM and 3:00 PM from the three forest ranges of KNP, namely Agoratoli (eastern range), Bagori (western range) and Kohora (central range) through vehicle and footpath surveys. Faecal samples of mega- and meso herbivores were collected opportunistically from random locations in tall and short grasslands and woodlands, except for the rhino, where latrine sites were used for the faecal samples collection (De Barba et al., 2010; Devi et al., 2022). During field survey, 1975 faecal samples of rhino (n=350), elephant (n=350), buffalo (n=325), swamp deer (n=325), hog deer (n=325) and sambar (n=300) were collected throughout study year (henceforth referred to as overall). In dry (November to March) and wet (April to May) seasons, 1500 and 475 faecal samples were collected, respectively (Table 1). Faecal samples were oven-dried at 60°C for 48 hours and grounded in a Micro-Willey mill (Devi et al., 2022). Five random faecal samples collected from similar locations and dates were mixed together to make one composite sample. We used 25 g of grounded faecal sample from each composite sample for micro-histological analysis (Devi et al., 2022). Five slides were produced from every composite sample and observed under microscope at 150X magnification. Observation fields with at least two identifiable fragments were considered for identification (Pradhan et al., 2008). Both identified and unidentified fragments were recorded to determine their frequency of occurrence in faecal sample (Sparks and Malechek, 1968).

2.3. Niche breadth

Niche breadth was calculated using Levins measure (Levins, 1968)

$$B = 1\Big/\sum P^2{}_j$$

where B is niche breadth, P_j the proportion of forage plants utilized by SLH with respect to growth forms such as grasses, sedges, climbers, herbs, shrubs, and trees. It was standardized following Hurlbert (1978)

$$B_s = \frac{(B-1)}{(n-1)}$$

where B_s represents standardized niche breadth, B niche breadth, and n number of forage plants utilized at least once by at least one large herbivore. Value of B_s ranges from zero (specialist feeder) to one (generalist feeder). Relationship between body size and standardized niche breadth was estimated using Pearson's correlation (r) analysis.

2.4. Dietary similarity and dissimilarity within and among guilds

Multivariate diet analysis was carried out using non-metric multidimensional scaling (NMDS) for the visualization of overlap, where samples were segregated based on their dissimilarity. In NMDS, Bray-Curtis similarity matrix was used to examine the overall

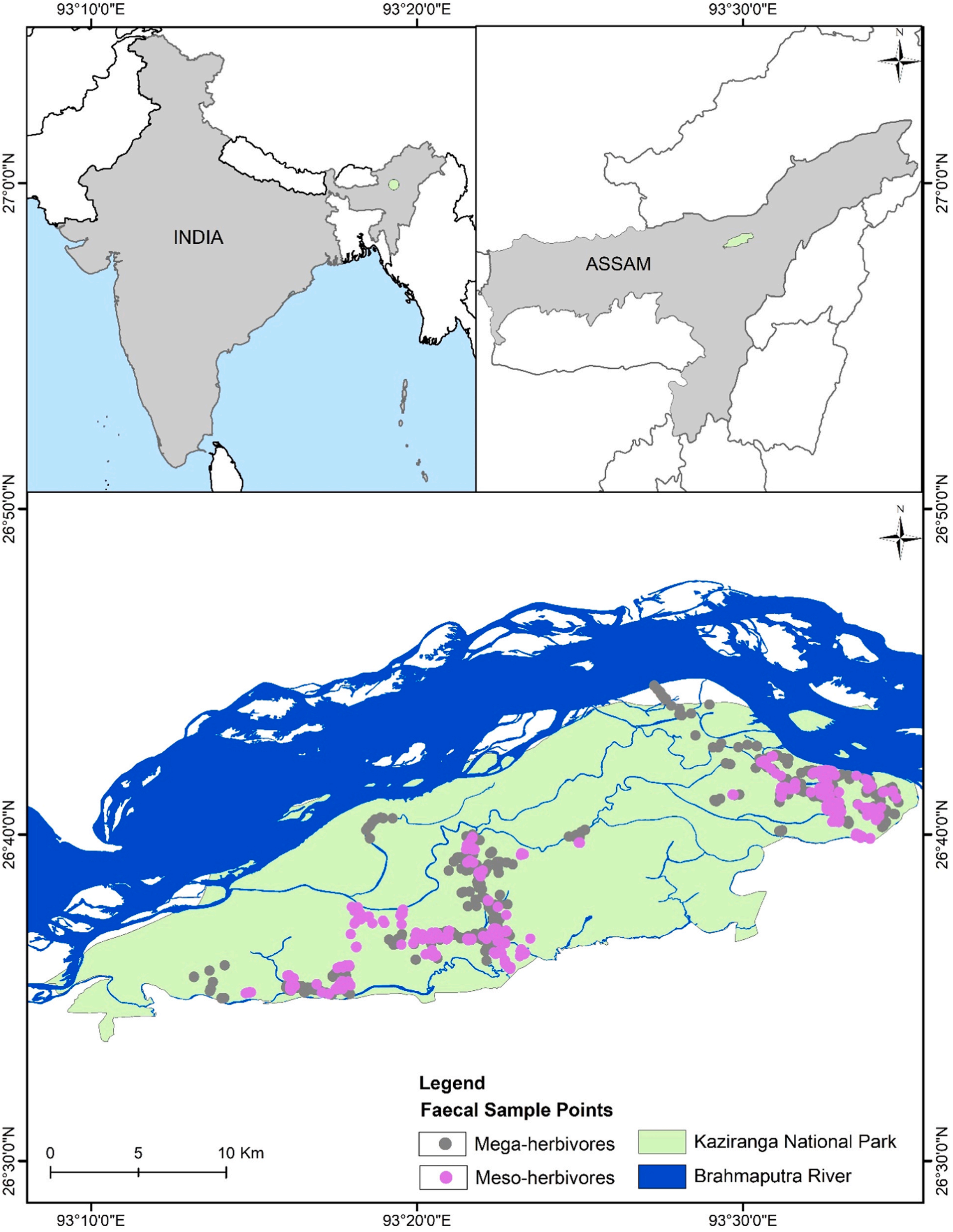

Fig. 1. Study area and GPS location of faecal sample collection in Kaziranga National Park, Assam, India.

Table 1
Faecal sample collection in Kaziranga National Park, Assam, India, from November 2013 to May 2015.

Species	Season	Sample collected	Composite samples	Slides Prepared	Slides Observation
Greater One-horned Rhino	Overall	350	70	350	3500
	Dry	250	50	250	2500
	Wet	100	20	100	1000
Asian Elephant	Overall	350	70	350	3500
	Dry	250	50	250	2500
	Wet	100	20	100	1000
Asiatic Wild Buffalo	Overall	325	65	325	3250
	Dry	250	50	250	2500
	Wet	75	15	75	750
Swamp Deer	Overall	325	65	325	3250
	Dry	250	50	250	2500
	Wet	75	15	75	750
Hog Deer	Overall	325	65	325	3250
	Dry	250	50	250	2500
	Wet	75	15	75	750
Sambar	Overall	300	60	300	3000
	Dry	250	50	250	2500
	Wet	50	10	50	500
Six Large Herbivores	Overall	1975	395	1975	19750
	Dry	1500	300	1500	15000
	Wet	475	95	475	4750

degree of similarity and dissimilarity in forage utilization of SLH, mega-herbivores and meso-herbivores (Kartzinel et al., 2015). In three-dimensional NMDS plots, herbivores were treated as samples and forage utilized as variables. Permutation-based non-parametric test, permutational multivariate analysis of variance (permANOVA) with 999 permutations was performed to test significance of differences within a group of SLH, mega-herbivores and meso-herbivores (Anderson and Walsh, 2013). The analysis was carried out in R (version 3.5.1) using package “vegan” (Oksanen et al., 2011).

We used Schoener index (SI) to examine diet overlap among SLH (Schoener, 1970; Mabragaña and Giberto, 2007). SI ranges from zero (no overlap) to one (complete overlap), while SI >0.6 indicates biologically significant diet overlap (Mabragaña and Giberto, 2007).

$$SI = 1 - 0.5\left(\sum_{i=1}^{n} |p_{iA} - p_{iB}|\right)$$

where SI represent Schoener Index, p_{iA} frequency of occurrence of i^{th} species utilized by species A and p_{iB} represents occurrence of i^{th} species utilized by species B (Schoener, 1970; Mabragaña and Giberto, 2007). SI was estimated using function R package “spaa” (version 0.2.2) (Zhang, 2013).

Rank-based permutation test, one-way analysis of similarities (ANOSIM), was used to test null hypothesis of no difference in forage utilized by SLH. Two-way ANOSIM was used to test null hypothesis of no difference in seasonal forage utilized by SLH. ANOSIM with 999 permutations ($p \leq 0.001$) and Bray Curtis distance was performed (Clarke, 1993). The global R statics in ANOSIM, ranging from 0 to 1, represent the degree of similarity to dissimilarity, respectively (Clarke, 1993; Mabragaña and Giberto, 2007; Anderson and Walsh, 2013). R statics <0.25, 0.26–0.5 and >0.5 were used to represent high, medium and low overlap, respectively (Gkenas et al., 2019). If results from ANOSIM were significant ($p \leq 0.001$), then similarity in percentages (SIMPER) was used to examine forage species contributing the most to dietary dissimilarity among SLH. Analysis of ANOSIM and SIMPER was carried out using Past3 (Hammer et al., 2001).

2.5. Forage availability

Aboveground biomass was estimated using harvest method from January 2014 to July 2015 (except from August to October, high flooding time) (Tuboi and Hussain, 2016). Ten exclosures of 10 m x 10 m were constructed in grasslands, and aboveground plants were harvested from 1 m x 1 m plots in three monthly replicates. Overall, 540 plots were harvested during the dry (n=300) and wet (n=240) seasons. The fresh-cut plants were sorted by species and weighed to record their wet weight, then oven-dried at 60°C to record their dry weight. Total biomass of plant species was calculated from differences recorded in wet and dry weight of individual plants. Based on forage plant consumption of SLH, only the biomass of 35 identified forage species consumed that also occurred in the plots, was calculated species-wise and in terms of six growth forms *viz.*, grasses, sedges, herbs, shrubs, climbers and trees. Mann-Whitney, a non-parametric test was performed to test significant differences between dry and wet season biomass. To calculate forage preference of SLH, only forage that contributed >1 % to biomass was used.

2.6. Forage preference

Jacobs Index (JI) was used to examine forage selection and strength of forage selection of SLH. Forage selectivity was examined in terms of forage species utilized more or less than its availability in environment. JI was estimated using the following formula (Jacobs, 1974)

$$D = \frac{(r_i - p_i)}{(r_i + p_i - 2r_ip_i)}$$

where D represents Jacobs forage selectivity index, r_i the proportion of i forage plant in diet of SLH, and p_i the proportional availability of i forage species in environment. D range from −1 to +1, where −1 (avoidance) indicates forage species utilized less than its availability, +1 (preference) indicates forage species utilized more than its availability, and 0 represents non-selective feeding, where forage species consumed in proportion to its availability (Jacobs, 1974). Bonferroni simultaneous confidence interval (CI) approach was used to test difference between availability of forage species in environment (proportion of available forage) and diet of study species (proportion of used forage) (Byers et al., 1984; Spencer et al., 2014). Forage species were considered to be avoided, when proportion of available forage species lies above CI estimated for its proportion of occurrence in diet, whereas forage species were considered to be preferred, when proportion of available forage species fell below CI estimated for its proportion of occurrence in diet (Neu et al., 1974; Byers et al., 1984; Spencer et al., 2014).

3. Results

3.1. Niche breadth

Among SLH and mega-herbivores, elephant, with its largest body size, occupied widest niche overall (B_s=0.71), and in dry (B_s=0.74) and wet (B_s=0.56) seasons, while among meso-herbivores, sambar occupied widest niche overall (B_s=0.63), and in dry (B_s=0.64) and wet (B_s=0.49) seasons (Fig. 2). Among SLH and meso-herbivores, swamp deer occupied narrowest niche overall (B_s=0.43) and in dry season (B_s=0.42); while, hog deer, smallest among all study species, occupied narrowest niche in wet season (B_s=0.43). Among mega-herbivores, buffalo occupied narrowest niche overall (B_s=0.50), and in dry (B_s=0.50) and wet (B_s=0.49) seasons. Irrespective of season, niche breadth of rhino and buffalo among mega-herbivores, and hog deer and swamp deer among meso-herbivores indicate mixed feeding behaviour. Whereas, niche breadth of elephant and sambar indicates generalist feeding behaviour overall and in dry season, and mixed feeding in wet season. With respect to body size, niche breadth of SLH and mega-herbivores shows a significant strong positive correlation in wet season (SLH:- r=0.95, p=0.003; mega-herbivores:- r=1, p=0.04) and an insignificant positive correlation overall (SLH:- r=0.57, p=0.24; mega-herbivores:- r=0.90, p=0.28) and in dry season (SLH:- r=0.54, p=0.26; mega-herbivores:- r=0.89, p=0.30). Niche breadth of meso-herbivores shows an insignificant positive correlation overall (r=0.29, p=0.81), and in dry (r=0.20, p=0.87) and wet seasons (r=0.79, p=0.42).

3.2. Dietary similarity and dissimilarity within and among guilds

Overall, among SLH, NMDS plots illustrated high dietary similarities among buffalo, swamp deer and hog deer, and high dissimilarities among elephant and swamp deer (Fig. 3a). Similarly, NMDS plots illustrated high dietary similarities between mega- and meso-herbivores (Fig. 3b). Among mega-herbivores, NMDS plots illustrated high dietary similarities between rhino and buffalo, and high dissimilarities between elephant and buffalo (Fig. 3c). Among meso-herbivores, NMDS plots illustrated high dietary similarities between swamp deer and hog deer, and high dissimilarities between swamp deer and sambar (Fig. 3d). PermANOVA test indicated that diet differed significantly among SLH (adonis pseudo F_{1975}=39.53, df=5, R^2=0.091, $P \leq 0.001$), between guilds of mega- and meso-herbivores (adonis pseudo F_{1975}=54.79, df=1, R^2=0.027, $P \leq 0.001$) and within both guilds of mega-herbivores (adonis pseudo F_{1025}=39.51, df=2, R^2=0.071, $P \leq 0.001$) and meso-herbivores (adonis pseudo F_{950}=29.72, df=2, R^2=0.05, $P \leq 0.001$), with the overlap of forage species consumed by other study species with similar feeding strategies.

Overall, among SLH and meso-herbivores, pairwise maximum biologically significant diet overlap was recorded between swamp deer and hog deer (SI=0.86, ANOSIM R=0.08, p=0.001), and among mega-herbivores, between rhino and buffalo (SI=0.83, ANOSIM R=0.10, p=0.001). In dry season, buffalo and hog deer (SI=0.84, ANOSIM R=0.08, p=0.001) showed maximum pairwise diet overlap among SLH, rhino and buffalo (SI=0.80, ANOSIM R=0.14, p=0.001) among mega-herbivores, and swamp deer and hog deer (SI=0.84, ANOSIM R=0.08, p=0.001) among meso-herbivores. In wet season, rhino and buffalo (SI=0.80, ANOSIM R=0.08, p=0.001) showed maximum pairwise diet overlap among SLH and mega-herbivores, and hog deer and sambar among meso-herbivores (SI=0.76, ANOSIM R=0.15, p=0.001).

Among SLH, SIMPER revealed pairwise maximum average dietary dissimilarity between elephant and swamp deer overall (AD=36.18 %, SI=0.64, ANOSIM R=0.39, p=0.001), and in dry (AD=37.47 %, SI=0.63, ANOSIM R=0.47, p=0.001) and wet seasons (AD=36.46 %, SI=0.63, ANOSIM R=0.37, p=0.001). Overall, *Calamus tenuis*, *Hemarthria compressa* and *Saccharum* spp. significantly explained cumulative 28.26 % of differences in elephant and swamp deer diet; while in dry season, *H. compressa*, *C. tenuis* and *Dillenia indica* significantly explained cumulative 30.25 % of dietary differences, and in wet season, *Saccharum* spp., *Mallotus nudiflorus* and *C. tenuis* significantly explained cumulative 30.61 % of dietary differences (Tables 2, S2-S3).

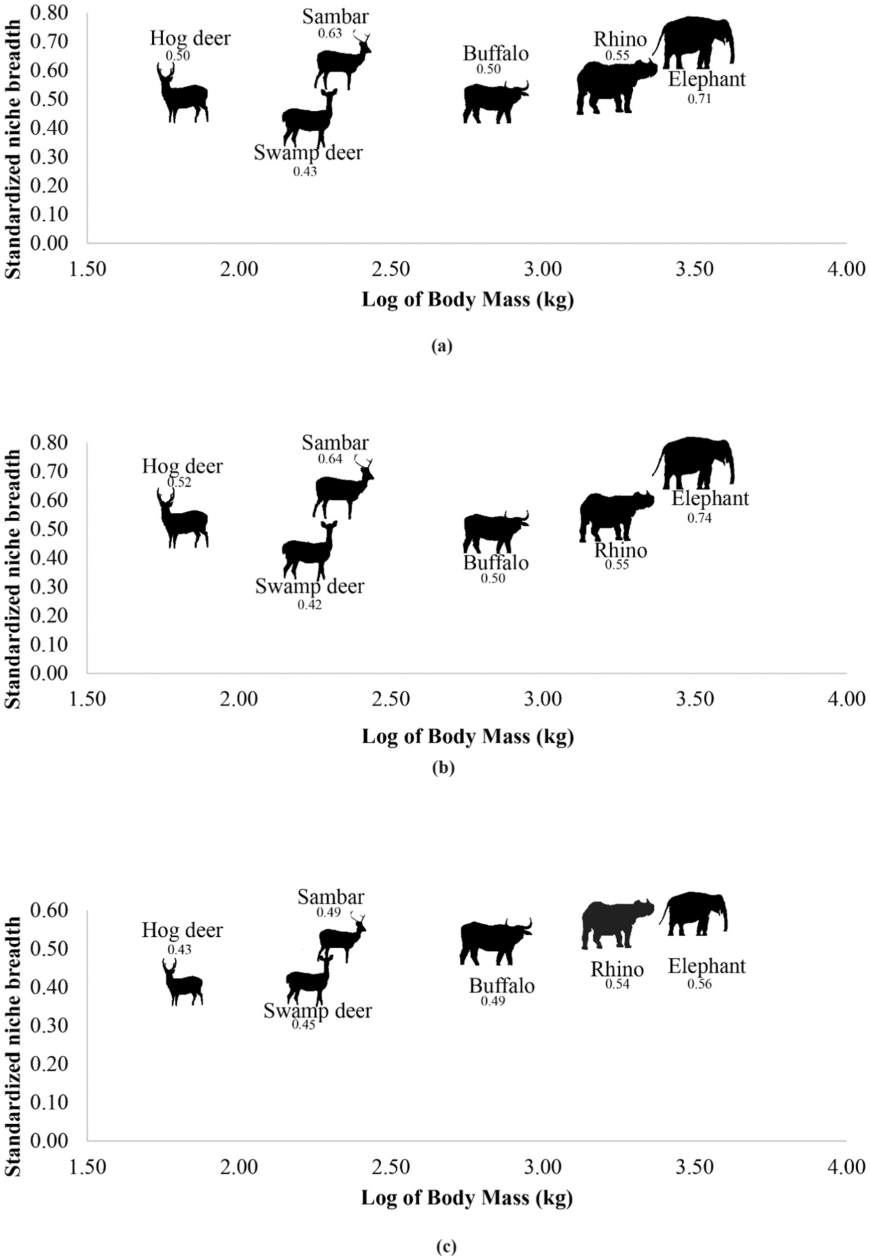

Fig. 2. Standardized niche breadth (B_s) of forage consumed in terms of growth forms by six large herbivores– **a)** overall, **b)** dry season and **c)** wet season in Kaziranga National Park, Assam, India.

Among mega-herbivores, elephant and buffalo showed pairwise maximum average dietary dissimilarity overall (AD=27.21 %, SI=0.73, ANOSIM R=0.27, p=0.001), and in dry (AD=28.92 %, SI=0.71, ANOSIM R=0.33, p=0.001) and wet seasons (AD=32.80 %, SI=0.67, ANOSIM R=0.28, p=0.001). *Calamus tenuis*, *H. compressa*, and *Echinochloa crus-galli* significantly explained cumulative 30.17 % and 32.66 % of differences in elephant and buffalo diet overall and in dry season, respectively, while *Saccharum* spp., *C. tenuis*, and *M. nudiflorus* significantly explained cumulative 28.70 % of dietary differences in wet season (Tables 2, S2-S3).

Among meso-herbivores, swamp deer and sambar showed pairwise maximum average dietary dissimilarity overall (AD=28.26 %, SI=0.72, ANOSIM R=0.23, p=0.001), and in dry (AD=28.99 %, SI=0.71, ANOSIM R=0.23, p=0.001) and wet seasons (AD=26.95 %, SI=0.73, ANOSIM R=0.26, p=0.001). Overall, *H. compressa*, *Saccharum* spp. and *Imperata cylindrica* significantly explained cumulative 23.52 % of differences in swamp deer and sambar diet, while in dry season, *H. compressa*, *Ziziphus jujuba* and *Cynodon dactylon* significantly explained cumulative 22.63 % of dietary differences, and in wet season, *Saccharum* spp., *I. cylindrica* and *H. compressa* significantly explained cumulative 32.42 % of dietary differences (Tables 2, S2-S3).

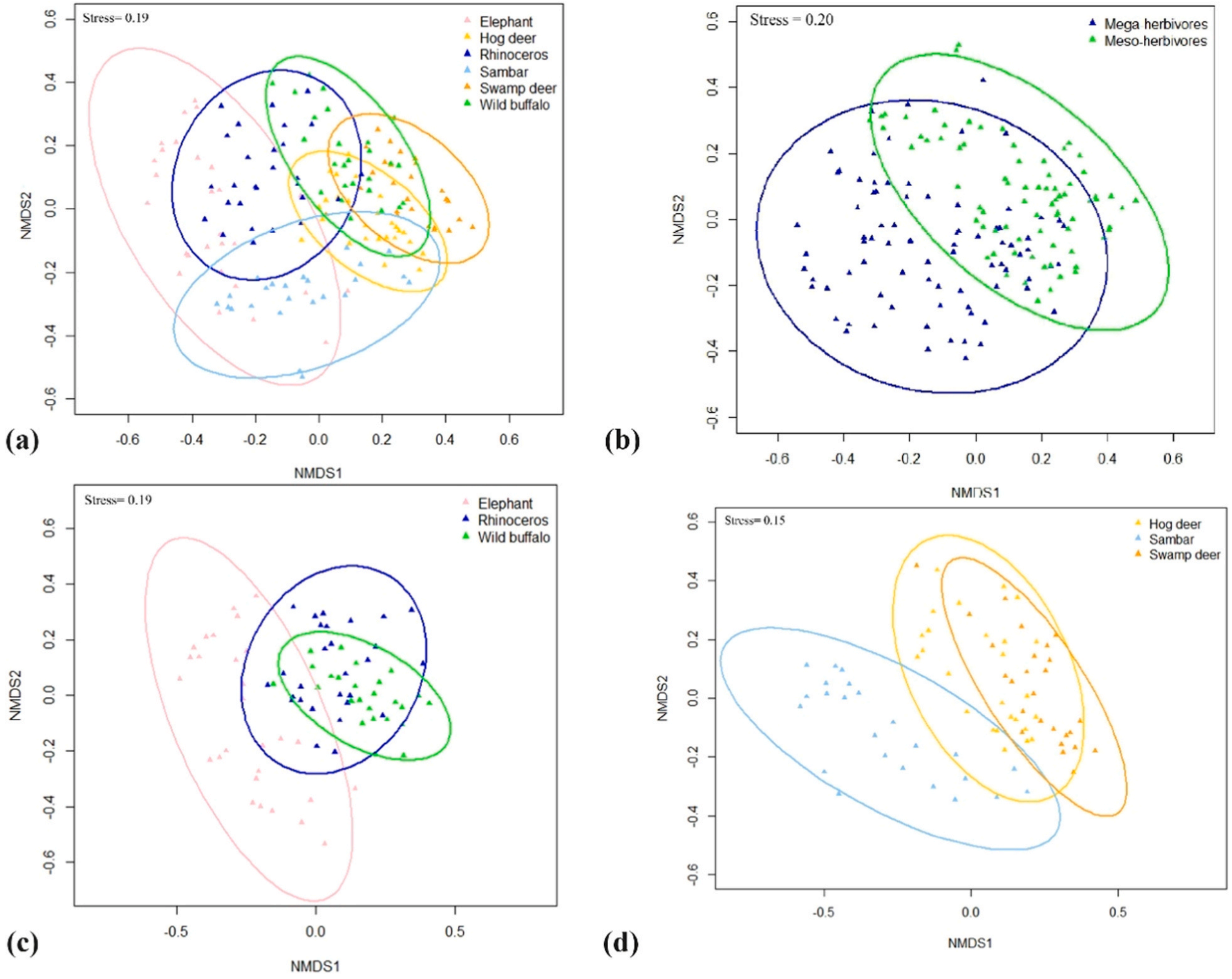

Fig. 3. NMDS ordination based on Bray–Curtis dissimilarity depicting overall diet partitioning among– **a)** six large herbivores (adonis pseudo $F_{1,\ 975}$=39.53, df=5, R^2=0.091, $P \leq 0.001$), **b)** mega-herbivores and meso-herbivores (adonis pseudo F_{1975}=54.79, df=1, R^2=0.027, $P \leq 0.001$), **c)** mega-herbivores (adonis pseudo $F_{1,\ 025}$=39.51, df=2, R^2=0.071, $P \leq 0.001$) and **d)** meso-herbivores (adonis pseudo F_{950}=29.72, df=2, R^2=0.05, $P \leq 0.001$).

Table 2
Overall, pairwise diet overlap among six large herbivores using Schoener's Index (0=no overlap, 0.60=biological significant overlap, 1=complete overlap), R-statistic values in ANOSIM test based on Bray-Curtis similarity matrix (permutation=999) and average dissimilarity and diet taxa contributions to dissimilarity in SIMPER.

Group	SI	R ANOSIM	SIMPER				
			Cum. AD	Forage Species	AD	Cont%	Cum%
Ele-HD	0.68	0.35	32.19	*Calamus tenuis*	4.00	12.42	12.42
				Hemarthria compressa	3.82	11.85	24.27
				Saccharum spp.	2.62	8.15	32.42
Ele-Rhi	0.76	0.21	23.95	*Calamus tenuis*	3.91	16.31	16.31
				Cynodon dactylon	1.46	6.09	22.40
				Amaranthus spinosus	1.09	4.56	26.95
Ele-Sam	0.75	0.20	24.70	*Calamus tenuis*	3.95	16.01	16.01
				Mallotus nudiflorus	1.13	4.59	20.60
				Solanum americanum	1.08	4.36	24.96
Ele-SD	0.64	0.39	36.18	*Calamus tenuis*	3.98	10.99	10.99
				Hemarthria compressa	3.79	10.48	21.46
				Saccharum spp.	2.46	6.79	28.26
Ele-WB	0.73	0.27	27.21	*Calamus tenuis*	3.99	14.65	14.65
				Hemarthria compressa	2.33	8.56	23.21
				Echinochloa crus-galli	1.89	6.96	30.17
HD-Rhi	0.74	0.21	25.94	*Hemarthria compressa*	3.17	12.23	12.23
				Saccharum spp.	1.84	7.10	19.33
				Carex vesicaria	1.45	5.60	24.93
HD-Sam	0.77	0.16	22.85	*Hemarthria compressa*	2.83	12.38	12.38
				Saccharum spp.	2.30	10.05	22.42
				Cynodon dactylon	1.70	7.44	29.87
HD-SD	0.86	0.08	14.03	*Imperata cylindrica*	1.92	13.69	13.69
				Tetrastigma dubium	0.81	5.81	19.49
				Kyllinga brevifolia	0.68	4.86	24.36
HD-WB	0.86	0.06	14.29	*Saccharum* spp.	1.54	10.80	10.80
				Hemarthria compressa	1.49	10.45	21.24
				Ziziphus jujuba	0.81	5.70	26.94
Rhi-Sam	0.78	0.14	22.45	*Ziziphus jujuba*	1.79	7.96	7.96
				Cynodon dactylon	1.68	7.47	15.44
				Amaranthus spinosus	1.12	5.01	20.44
Rhi-SD	0.71	0.24	29.12	*Hemarthria compressa*	3.15	10.82	10.82
				Imperata cylindrica	1.86	6.40	17.22
				Carex vesicaria	1.84	6.31	23.53
Rhi-WB	0.83	0.10	16.93	*Hemarthria compressa*	1.69	9.96	9.96
				Carex vesicaria	1.38	8.12	18.08
				Amaranthus spinosus	1.09	6.43	24.50
Sam-SD	0.72	0.23	28.26	*Hemarthria compressa*	2.81	9.94	9.94
				Saccharum spp.	2.13	7.54	17.48
				Imperata cylindrica	1.71	6.04	23.52
Sam-WB	0.78	0.15	22.50	*Cynodon dactylon*	1.80	7.99	7.99
				Ziziphus jujuba	1.58	7.01	15.00
				Hemarthria compressa	1.34	5.97	20.96
SD-WB	0.82	0.10	17.73	*Imperata cylindrica*	1.65	9.30	9.30
				Hemarthria compressa	1.48	8.35	17.64
				Saccharum spp.	1.38	7.79	25.43

Rhi- Greater one-horned rhino, Ele- Asian Elephant, WB- Asiatic Wild Buffalo, SD- Swamp Deer, HD- Hog Deer, Sam- Sambar, SI- Schoener Index, Cum. AD- Cumulative Average Dissimilarity, AD - Average Dissimilarity, Cont%- dissimilarity contribution percentage of a forage species, Cum%- dissimilarity cumulative percentage

3.3. Forage availability

Overall, mean biomass of 4381.47±2268.4 g m^{-2} was recorded. Between dry and wet seasons, there was a significant difference in mean biomass (Mann–Whitney, $p<0.05$), as compared to dry season (1354.54±641.30 g m^{-2}), higher biomass was recorded in wet season (3026.93±1632.65 g m^{-2}) (Tables S4 & S5). Compared to other growth forms, highest mean biomass was recorded for grasses overall (6607.17±931.74 g m^{-2}), and in dry (3595.24±508.63 g m^{-2}) and wet (10372.09±826.5 g m^{-2}) seasons. Between dry and wet seasons, there was a significant difference in mean biomass of the six growth forms (Kruskal-Wallis, $H=194.38$, $df=5$, $p<0.05$). There were significant seasonal differences only in mean biomass of grasses & grasses and herbs & herbs (Mann–Whitney, $p<0.05$), and no significant seasonal difference in biomass of sedges & sedges, climbers & climbers, shrubs & shrubs and trees & trees (Mann–Whitney, $p>0.05$). Irrespective of season, tall grass *Saccharum* spp. and short grass *Hemarthria compressa* contributed the most to available forage biomass (Table S4). Of 35 forage species, only 11 species *viz.*, *Alpinia nigra*, *Carex vesicaria*, *C. dactylon*, *Flemingia lineata*, *H. compressa*, *Litsea salicifolia*, *Merremia umbellata*, *Mikania micrantha*, *Mimosa* spp., *Paspalum conjugatum*, and *Saccharum* spp., contributed >1 % to forage biomass.

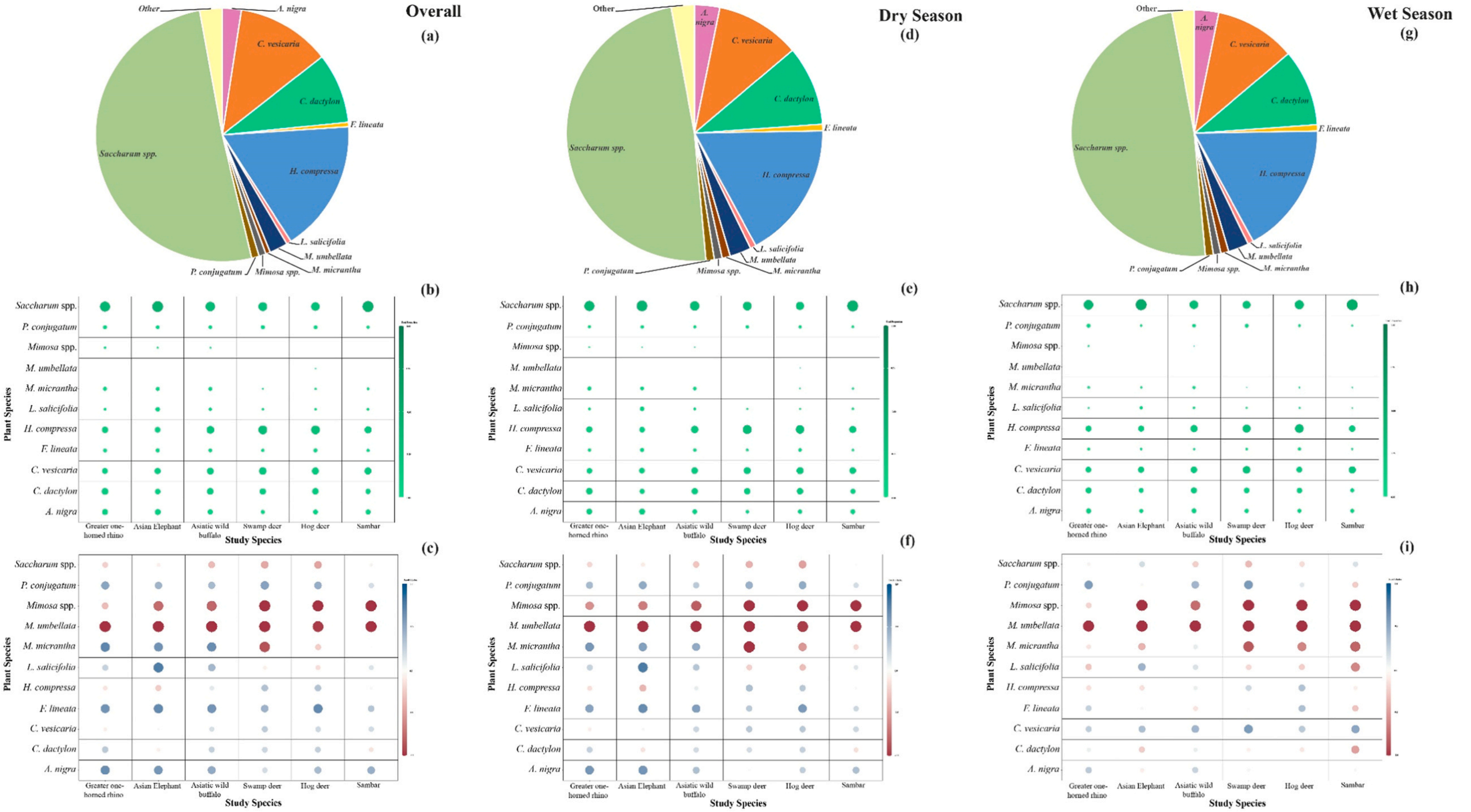

Fig. 4. Availability, utilization and selectivity of forage plants contributing >1 % to six large herbivore diet 1) overall– **a)** proportion of available forage biomass, **b)** proportion of forage utilized by six large herbivores, **c)** forage preference index of six large herbivores; 2) dry season– **d)** proportion of available forage biomass, **e)** proportion of forage utilized by six large herbivores, **f)** forage preference index of six large herbivores; 3) wet season– **g)** proportion of available forage biomass, **h)** proportion of forage utilized by six large herbivores and **i)** forage preference index of six large herbivores in Kaziranga National Park, Assam, India.

3.4. Forage preference

Overall, *L. salicifolia* was most preferred by elephant (D=0.76), *M. micrantha* by rhino (D=0.70) and buffalo (D=0.66), *F. lineata* by hog deer (D=0.69), *P. conjugatum* by swamp deer (D=0.53), and *A. nigra* by sambar (D=0.46) (Fig. 4, Tables S6-S11). *Merremia umbellata* was completely avoided (D=-1) by rhino, elephant, buffalo, swamp deer and sambar, and avoided by hog deer (D=-0.97). *Mimosa* spp. was completely avoided by meso-herbivores, and avoided by buffalo (D=-0.77), elephant (D=-0.75) and rhino (D=-0.33). In dry season, *L. salicifolia* was most preferred by elephant (D=0.76), *A. nigra* by rhino (D=0.61) and sambar (D=0.36), *F. lineata* by hog deer (D=0.59) and buffalo (D=0.56), and *P. conjugatum* (D=0.44) by swamp deer. *Merremia umbellata* was completely avoided by rhino, elephant, buffalo, swamp deer and sambar, and avoided by hog deer (D=-0.96). Similarly, *Mimosa* spp. was completely avoided by meso-herbivores, and avoided by buffalo (D=-0.82), elephant (D=-0.67) and rhino (D=-0.56). Although preferred by rhino (D=0.61), elephant (D=0.55) and buffalo (D=0.49), *M. micrantha* was completely avoided by swamp deer, and avoided by hog deer (D=-0.53) and sambar (D=-0.19). In wet season, *P. conjugatum* was most preferred by rhino (D=0.57), buffalo (D=0.42) and swamp deer (D=0.59), *C. vesicaria* by sambar (D=0.51), *L. salicifolia* by elephant (D=0.43), and *F. lineata* by hog deer (D=0.36). *Merremia umbellata* was completely avoided by both mega- and meso-herbivores. *Mimosa* spp. was completely avoided by meso-herbivores and elephant, and avoided by buffalo (D=-0.75) and rhino (D=-0.21). Overall and in dry season, the most consumed and available tall grass, *Saccharum* spp. was utilized less than its availability by both mega and meso-herbivores, whereas in wet season, it was utilized more than its availability only by elephant (D=0.19) and sambar (D=0.16).

4. Discussion

Niche is an integral element in ecology that helps in understanding community dynamics. Spatio-temporal resource utilization plays an important role in gaining insight into a species niche. Our study partially supports the hypothesis that body size influences niche breadth (H_1) due to a significant positive correlation between body size of SLH and niche breadth during the wet season. We recorded that elephant among SLH and mega-herbivores, and sambar among meso-herbivores have the highest niche breadth. Ahrestani et al. (2012) conducted a study in South India and also reported the highest habitat niche breadth for elephants and sambar. Our study reported that in dry season, niche breadth of sambar was almost as high as that of elephant, which may be attributed to limited resources, larger home ranges compared to other herbivores and flexibility in forage utilization (Sukumar, 1990; Banerjee, 2001; Ahrestani, 2009; Devi et al., 2022). In wet season, rhino, buffalo and sambar have niche breadth as high as that of elephant possibly due to high resource availability, and easy accessibility of diverse nutritive green forage, primarily due to high moisture content and controlled burning of wet grasslands (Pathak et al., 2018; Devi et al., 2022; Sharma et al., 2023). Besides forage availability, the seasonal changes in the niche breadth of mega- and meso-herbivores might be attributed to mouth size, gut physiology, and predation risk (Devi et al., 2022).

Our study revealed significant dietary overlap among SLH irrespective of seasons and mixed results for hypothesis that species with similar body sizes have highest diet overlap, and vice-versa for dissimilar body sizes (H_2). Such diverse foraging patterns might be due to resource availability, diverse body size, interactions like competition and predation, feeding style, plant height, nutrient content, gut physiology and herbivores' distribution (Pansu et al., 2019; Devi et al., 2022; Fynn and Provenza, 2023). Generally, a high dietary overlap can be interpreted as competition and segregation when resources are limited and abundant, respectively (Gotelli and Graves, 1996; Mysterud, 2000). Thus, availability of forage, particularly monocots and grasses, may be the primary reason for high dietary overlap, as it forms a major portion of diet of SLH (Devi et al., 2022). High dietary overlap may also occur because large herbivores can reduce competition and facilitate other herbivores by utilizing different parts of same forage species or segregate resources at spatio-temporal gradients (Bell, 1971; Pansu et al., 2019). Also compared to mega-herbivores, the meso-herbivores are most vulnerable to predation, and to avoid predation, meso-herbivores utilize similar habitats and resources as that of mega-herbivores, which might result in high dietary overlap (Sinclair et al., 2003). Besides this, grazing and mixed feeding styles might be responsible for the high dietary overlap among mega- and meso-herbivores (Devi et al., 2022). Biologically significant dietary overlap in the present study cannot be interpreted as competition due to abundant forage, even at the end of the dry season, and good physical condition of herbivores (field observation), which was also supported by Banerjee (2001) that despite utilizing similar habitats, rhino, buffalo, swamp deer and hog deer in KNP, showed no competition.

Swamp deer are obligatory grassland species that mostly use short grassland as a foraging ground; similarly, rhino, elephant and sambar utilize mixed habitats as forage ground, including tall grassland, short grassland and woodland (Banerjee, 2001; Ahrestani and Sankaran, 2016); in present study, this might be contributing to highest pairwise dissimilarities of rhino, elephant and sambar with swamp deer. Besides major consumption of shrub *C. tenuis* by elephant, the highest pairwise dissimilarities of buffalo, swamp deer and hog deer with elephant may also be attributed to the use of short grassland as a foraging ground by swamp deer, both tall and short grassland by buffalo, and mixed habitat by hog deer (Banerjee, 2001). With their larger body size and home range, elephants have more opportunities to explore mixed habitats, including woodland, tall and short grasslands for forage (Sukumar, 1990; Banerjee, 2001; Ahrestani and Sankaran, 2016). Our results suggest that body size, resource availability, and, possibly, habitat utilization and home range are responsible for dietary similarities and dissimilarities among SLH. In most parts of the world, rhinos and buffalo no longer coexist with elephants, swamp deer, hog deer and sambar (Pradhan et al., 2008); therefore, little is known about the degree of determinants of inter- and intra-specific diet variation among these herbivores. Many studies have quantified dietary overlap in terms of growth forms, monocots (graze) and dicots (browse), and stable carbon isotopes, which makes it challenging to provide comparative quantification of diet from different studies as they are unlikely to be informative (Sankar, 1994; Pradhan et al., 2008; Ahrestani, 2009); hence, this study quantifies it at taxonomic level.

Our study recorded a significant increase in available forage biomass from dry to wet season, probably due to precipitation, fertile alluvial soil and controlled burning (Sharma et al., 2023). Grasses contributed the most to available forage biomass compared to other growth forms. This study supports the hypothesis that seasonal availability of forage influences forage selectivity of mega- and meso-herbivores (H_3), as based on forage availability, both mega- and meso-herbivores switched their most preferred forage from browse to graze, and vice-versa. Irrespective of season, dicot was the most preferred forage of elephant (*L. salicifolia*), whereas monocots were the most preferred forage of swamp deer (*P. conjugatum*) and sambar (*A. nigra* and *C. vesicaria*). From dry to wet season, rhino, buffalo and hog deer shift their most preferred forage from dicot to monocot, possibly due to a significant increase in availability and nutrient quality of grasses (Devi et al., 2022). As compared to monocots, dicots have high soluble cell concentration and nitrogen content, which might benefit large herbivores, however, they also have high lignin and secondary metabolites, which might be disadvantageous for large herbivores as it requires a lot of energy to detoxify (Devi et al., 2022). Despite contributing most to available and utilized forage biomass of SLH, *Saccharum* spp. was avoided by SLH, except elephant among mega-herbivores and sambar among meso-herbivores in wet season, possibly because both elephant and sambar switched their diet from browse to graze in wet season primarily due to high availability, palatability and nutritional quality of *Saccharum* spp. (Devi et al., 2022).

Irrespective of season, invasive *Mimosa* spp. was completely avoided by meso-herbivores, and avoided by mega-herbivores, possibly due to the high availability of *Mimosa* spp. throughout the year, or its nutrient quality (Guyton et al., 2020). *Mikania micrantha* was almost avoided by SLH overall, and in dry and wet seasons, who utilized it less than its availability, and completely avoided by swamp deer in dry season. A reason for its consumption may be its entanglement with principal forage *Saccharum* spp. and other forage species (Ram, 2008). Overall, and in both seasons, *M. umbellata* was completely avoided by mega- and meso-herbivores, except hog deer. Results from forage availability indicate that the high availability of aforementioned invasive species, irrespective of season, might be a reason for their consumption by SLH. Suggesting that biological invasion can possibly alter feeding ecology of mega- and meso-herbivores by limiting the available resources (Bhatt et al., 1994; Raghubanshi et al., 2005; Ahrestani, 2009).

5. Conclusion and conservation implications

In grassland ecosystem, the annual cycle of dry (drought period) and wet season (high precipitation resulting in floods) combined with management practices such as controlled burning and removal of invasive plants determines the quantity and quality of forage available for wild herbivores of varied body sizes (Devi et al., 2022, Sharma et al., 2023; Fynn and Provenza, 2023). Forage availability, quality, and body size have been the cornerstone of understanding the foraging ecology of large herbivores (Devi, 2023). Present study provides insights into how coexisting sympatric large herbivores change their seasonal dietary overlap and forage selection with respect to body size and forage availability. Dietary niche breadth significantly increased with body size, only in resource-rich wet season. However, niche breadth of elephant, hog deer and sambar decreased from dry to wet season. Only rhino, elephant and swamp deer showed high dietary overlap with herbivores of similar body sizes and lowest dietary overlap for dissimilar body sizes. From dry to wet season, mega-herbivores shift their most preferred forage from browse to graze, and meso-herbivores, especially swamp deer, showed more affinity toward grasses.

The study revealed that proliferation of invasives like *Mimosa* spp., *M. micrantha* and *M. umbellata*, may impact foraging ecology of herbivores. Limited studies have studied the physiological impacts on large herbivores from foraging on invasives, therefore, scientific studies on management of plant community dynamics in riverine grasslands are required for maintaining and enhancing grassland integrity and long-term management of herbivores. To ensure forage availability to mega- and meso-herbivores, recommendations provided by IPCC (2022), such as establishment of seed bank and reseeding combined with invasive uprooting, may be implemented. With the world's largest global population of rhino and buffalo, and a significant population of elephant, swamp deer, hog deer and sambar, the riverine grasslands of KNP is a key protected area in Asia. In the current era of polycrisis, including climate change and habitat degradation, the information gathered from this study is useful in providing key scientific and ecological insights on globally threatened Asia's large herbivores and formulating informed policy and management interventions that require baseline information on the species inhabiting the area. Based on the outcomes of the present study, Park managers can formulate effective herbivore species-specific conservation action plans, conservation strategies to address the feeding ecology of Asian large herbivores and to improve herbivore species-specific relocation programmes.

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CRediT authorship contribution statement

Anita Devi: Investigation, Methodology, Data curation, Formal analysis, Software, Visualization, Writing - Original Draft, **Monika Sharma**: Investigation, Methodology, Data Curation, Formal analysis, Writing - Original Draft, **Ruchi Badola**: Conceptualization, Funding acquisition, Supervision, Project administration, Writing - Review & Editing, **Syed Ainul Hussain**: Conceptualization, Validation, Resources, Supervision, Project administration, Funding acquisition, Writing - Review & Editing.

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.

Data availability

Data will be made available on request.

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Ethical approval

To conduct research, permission was obtained on 20th August 2013 in O.O No. 868 from the Principal Chief Conservator of Forest (Wildlife) & Chief Wildlife Warden, Assam, under section 12 of the Indian Wild Life (Protection) Act, 1972, to collect the biological samples and establish exclosures to estimate the biomass productivity. Similarly, a permission was acquired from Director, Kaziranga National Park, Assam in a permission letter no. KNP/FG.647/WII/Research dated 31st October 2013.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e03079.

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