Chapter 3
Species Richness and Size Distribution of Large Herbivores in the Himalaya

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Abstract Species diversity across several taxa ranging from plants to vertebrates is reported to decrease with altitude, or to show a mid-elevation peak in mountain systems. Plant biomass availability for herbivores is similarly expected to decline with altitude as temperature becomes limiting. However, the relationship between herbivore species richness and altitude has not been examined in detail. We show that while the overall regional pattern (gamma-richness) for 25 large-herbivore species (56 % grazers, 44 % browsers/mixed feeders) in the Western Himalayas shows a mid-elevation peak, the species richness of grazers increases nearly monotonically with altitude peaking at 4000–5000 m. Median body mass of herbivores decreased with altitude, suggesting greater suitability of higher elevations for smaller bodied herbivores. We propose that seasonal altitudinal migration patterns, biogeographic influences, increases in the abundance of graminoids, and an increase in plant nutrients with altitude might explain the unusual high grazer species richness at higher altitudes in the Himalayan Mountains.

Keywords Gamma-richness · Ungulate diversity patterns · Mid-domain effect · Herbivore species richness · Grazer diversity

Large-mammalian herbivores occupy half of the Earth's total land surface area and play significant ecological roles as modifiers of their landscapes, as dominant drivers of ecosystem function and as prey for large carnivores (Olff et al. 2002; Prins and Gordon 2008). Their economic importance is reflected in the fact that over

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one-fourth of the Earth's total land surface area is currently under managed grazing (Asner et al. 2004). Yet, the diversity of large wild herbivores across the world is threatened by human activities including anthropogenic habitat modification, hunting, and the competitive and other negative impacts of domestic herbivores (Prins and Gordon 2008, Kinnaird and O'brien 2012; Berger et al. 2013, also see Chaps. 1 and 11). Understanding the patterns and mechanisms underlying the diversity of large wild herbivores, therefore, has been a preoccupation of ecologists for almost 50 years now.

Analyses of large-herbivore species richness patterns traditionally focused on resource partitioning mechanisms that allow species of different body masses and adaptive syndromes (ruminants and hindgut fermenters, grazers and browsers; Clauss et al. 2008) to exploit different plant species or plant parts, thereby enabling niche differentiation and higher species packing (Jarman 1974; Jarman and Sinclair 1979; Vesey-Fitzgerald 1960). Based on patterns of body-mass structuring of large-herbivore assemblages, species interactions (competition and facilitation) were proposed to be the important underlying mechanisms for such niche differentiation and species richness (Prins and Olff 1998; Du Toit and Olff 2014). Gradients in moisture and nutrients in the soil available to plants were proposed as being the fundamental determinants of large-herbivore richness, with areas of intermediate moisture and high soil nutrients predicted to hold the highest potential herbivore richness globally (Olff et al. 2002).

In mountain systems, across a variety of taxa from plants to vertebrates, species diversity is generally a linearly decreasing function of altitude, or approximates a quadratic function with a mid-elevation peak (MacArthur 1972; Rahbek 2005, 1995; Stevens 1992; Namgail et al. 2012; Kraft et al. 2011; Tang et al. 2012; Presley et al. 2012). Temperature acts as an important limiting factor for plant growth at high elevations by reducing growing season length (Körner 2000; Mishra 2001; Hoch and Körner 2012). Consequently, for herbivores, plant biomass availability is expected to decline with altitude, and indeed, some of the lowest reported estimates of peak-season plant biomass come from ecosystems at high elevations (Mishra 2001). This pattern of reduced plant availability due to low temperature is further intensified in tropical mountains, where aridity additionally increases with altitude, particularly at higher elevations, despite reduced temperatures (Leuschner 2000). A hump shaped relationship between plant biomass and altitude has also been reported recently in the Western Trans-Himalayas (Namgail et al. 2012). However, the relationship between large-herbivore richness and altitude has remained unexplored.

We explored patterns of gamma-diversity of large herbivores in the highest mountain chain on earth, the Himalaya. Within vertical elevation bands of 1000 m in a 2.5 million km^2 region of the Western Himalaya-Tibetan Plateau complex (Fig. 3.1), we specifically examined patterns in richness and body mass distribution of all terrestrial large-mammalian herbivores (>2 kg). We also explored the relationships between observed richness patterns and potential correlates including climatic (temperature, precipitation, potential evapotranspiration) and biotic (plant species richness) variables, area within each band, and the geometrical constraints

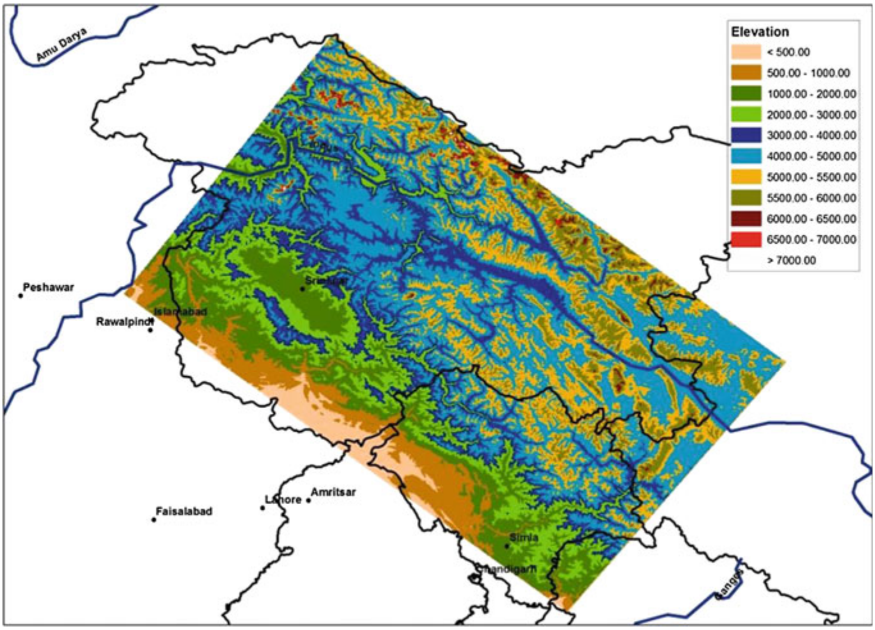

Fig. 3.1 Map of the Western Himalayan region showing the area under different elevation bands

of range-size distribution, commonly called the mid-domain effect (Colwell et al. 2004; Currie and Kerr 2008; Letten et al. 2013). We then separately examined the altitudinal richness patterns of grazers and browsers (including mixed feeders), since species belonging to these morpho-physiological types have different nutritional strategies (Clauss et al. 2008; Duncan and Poppi 2008), and can be expected to respond differently to elevation gradients. For instance, a greater occurrence of shrubs at relatively lower or mid-elevations could be expected to lead to greater browser richness compared to grazers.

We focused on the Western Trans-Himalayan region of India as the large-herbivore assemblage of this region is relatively well documented. From published records as well as our own observations and knowledge of the altitudinal range of the Western Himalayan large herbivores, we assigned presence/absence for each species within each of the 1000 m elevation bands. Information from only the Western Himalaya was used since the lower latitudes and higher precipitation of the Eastern Himalaya make the elevation bands incomparable. Further, the entire large-mammalian assemblage of the Eastern Himalayan region still remains poorly documented, and even within the last 10 years, several new ungulate records have been reported from the region (Datta et al. 2003; Mishra et al. 2006), and even a large primate species new to science has been described (Sinha et al. 2005).

The bands were deliberately chosen at a coarse resolution to minimize errors in this preliminary analysis. Each species was categorized as a grazer or a browser/mixed feeder based on information on species diets in the literature. Species such as the bharal *Pseudois nayaur*, which are grazers but include some browse in the diet when grass availability is low, were classified as grazers rather than mixed feeders/browsers (Mishra et al. 2004; Suryawanshi et al. 2010). Information on species adult body mass was also obtained from the literature, and where ranges were reported, these were first averaged within each sex, and then across sexes. Information on climatic variables was obtained from the FAO climate database, and extracted for each altitudinal zone of the study area using the new New_LocClim software for local climate estimation (http://www.fao.org/sd/). The data for each altitudinal zone came from 5 points (each point representing averaged data from 1 to 7 weather stations located within the study site or nearby) distributed across the gradient of altitude, latitude, and longitude within each elevation band. These data from 5 locations were averaged for each band. Climate data were not available for the highest elevation band (5000–6000 m). Plant species richness within each elevation band was estimated from Grytnes and Vetaas (2002). Although their data came from further east in the Himalayas, we expect the altitudinal pattern in plant species richness within our study area to be similar. This assumption is supported by data on woody plant species richness estimated from Oommen and Shanker (2005)—which came partly from our focal area (though not extending to the highest elevation band)—that were well correlated (Pearson's R = 0.74, P = 0.07) with those of Grytnes and Vetas (2002). The area within each altitudinal band was calculated based on a digital map of the region (Fig. 3.1). Predicted large-herbivore species richness along the elevation gradient due to geometrical constraints of range size was estimated through Monte Carlo simulations using the RangeModel software, with altitudinal ranges and mid-points for each species forming the input data (Colwell 2008; Colwell et al. 2004).

The regional species pool for the entire 2.5 million km^2 study area comprised 25 large-herbivore species (Table 3.1), with each elevation band holding a subset ranging from 28 to 56 % of the total pool. Fifty six percent of the species were grazers, the remaining 44 % being browsers/mixed feeders. Across this stretch of the Western Himalaya-Tibetan plateau complex (Fig. 3.1), the species richness of large herbivores was highest within the 3000–4000 m band (Fig. 3.2)—which also harbors the tree line—consistent with the commonly observed diversity pattern in mountains with a peak at mid-elevations (Rahbek 1995, 2005). Surprisingly, even within the 5000–6000 m band (5500 m being the limit to plant growth), where the growing season length is one–fifth of that at lower altitudes, species richness of large herbivores was still quite high (Fig. 3.2). In contrast, species richness was considerably lower at low elevations, i.e., 1000–2000 m band, where a significant number of species were lost when compared to the mid-elevation band of 3000–4000 m (Fig. 3.2). The observed altitudinal species richness pattern appeared to be correlated with climatic variables, particularly potential evapotranspiration and annual temperature, although the relationships were not statistically significant (Table 3.2). No relationship could be detected between overall herbivore species richness and plant species richness, the area within each elevation band, or the geometrical constraints imposed by range-size distribution (Table 3.2, Fig. 3.2).

Table 3.1 Large-herbivore species occurring in the 2.5 million km^2 Western Himalayan study site, their diet (G: grazer, B: browser or mixed feeder), and their occurrence (+ present, . absent) in 1000 m elevation bands across the altitudinal gradient (*A* <1000 m, *B* 1001–2000 m, *C* 2001–3000 m, *D* 3001–4000 m, *E* 4001–5000 m, and *F* 5001–6000 m)

Species	Mean body mass (kg)	Diet	Altitudinal zone in m above mean sea level					
			A	B	C	D	E	F
Elephas maximus	3000	B	+	.	.	.	.	.
Bos grunniens	413	G	.	.	.	+	+	+
Equus kiang	275	G	.	.	.	+	+	+
Cervus unicolor	250	B	+	+	+	+	.	.
Boselaphus tragocamelus	180	B	+	.	.	.	.	.
Cervus elaphus	154	B	.	+	+	+	.	.
Sus scrofa	125	B	+	+	+	.	.	.
Nemorhaedus sumatraensis	95	B	.	.	+	+	.	.
Ovis ammon	87	G	.	.	.	.	+	+
Capra sibirica	76	G	.	.	+	+	+	+
Hemitragus jemlahicus	75	G	.	.	+	+	.	.
Capra falconeri	71	B	.	.	+	+	.	.
Axis axis	70	G	+	+	.	.	.	.
Ovis vignei	60	G	.	.	+	+	+	.
Pseudois nayaur	55	G	.	.	+	+	+	+
Pantholops hodgsoni	32	G	.	.	.	.	+	+
Muntiacus muntjak	25	B	+	+	+	.	.	.
Nemorhaedus goral	25	G	+	+	+	.	.	.
Procapra picticaudata	14	B	.	.	.	.	+	+
Moschus chrysogaster	10	B	.	.	+	+	+	.
Marmota caudata	8.5	G	.	.	.	+	+	+
Marmota himalayana	6	G	.	.	.	.	+	+
Lepus capensis	4.5	G	.	.	.	+	+	+
Lepus oiostolus	3	B	.	.	.	+	+	+
Lepus nigricollis	2.1	G	+	+	+	.	.	.

The median body mass of the species assemblage decreased with altitude, the decline being particularly sharp between the 3000–4000 and 4000–5000 m band, suggesting greater suitability of higher elevations for smaller bodied herbivores (Fig. 3.3).

Further analyses revealed that the combined diversity of browsers and mixed feeders showed a mid-elevation peak in the 2000–3000 m band, with a steeper loss of species at higher altitudes when compared to grazers (Fig. 3.4). This pattern in browser diversity was positively correlated with plant species richness, but was also consistent with the predictions of the mid-domain effect (Table 3.2). Browser

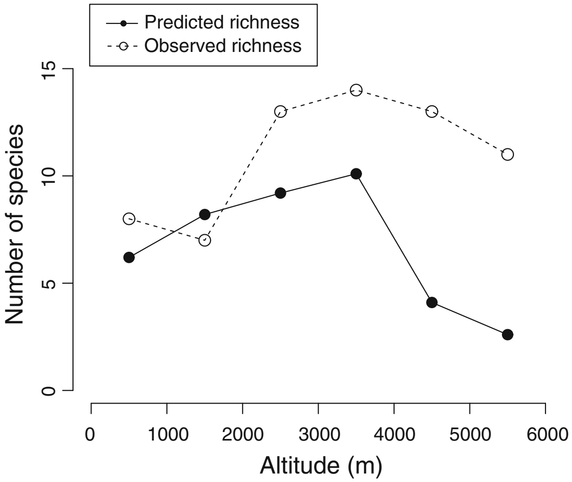

Fig. 3.2 Large-herbivore species richness within each altitudinal zone in the Western Himalaya (*open circles*). *Closed circles* depict the expected null distribution generated by mid-domain effects or geometrical constraints of range size

Table 3.2 Correlation coefficients (Pearson's R) of the relationship between large-herbivore species richness and independent climatic, geometric, and biotic variables across an elevation gradient in the Western Himalaya (see Fig. 3.1)

	All species	Grazers	Browsers
Mean temperature	−0.850	−0.975*	0.158
Precipitation	−0.561	−0.826	0.461
Potential evapotranspiration (PET)	−0.849	−0.819	−0.145
Mid-domain effect (MDE)	0.128	−0.425	0.884*
Log area	0.498	0.808	−0.532
Plant species richness	0	−0.554	0.893**

*$P \leq 0.05$, **$P \leq 0.01$

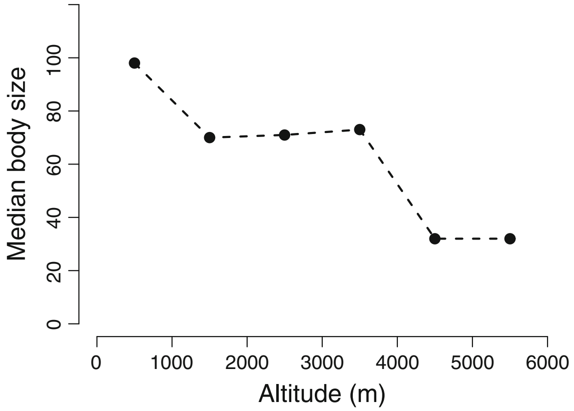

Fig. 3.3 Median body mass of the large-herbivore assemblage within 1000 m *vertical bands* across an elevation gradient in the Western Himalaya

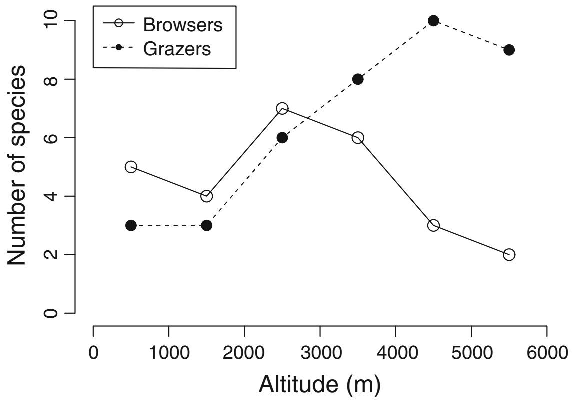

Fig. 3.4 Species richness of large-bodied grazers and browsers within 1000 m *vertical bands* across an elevation gradient in the Western Himalaya

species diversity was not correlated with climatic or biotic variables (Table 3.2). On the other hand, grazer species showed a sharp, near monotonic increase in diversity with elevation reaching their peak at 4000–5000 m (Fig. 3.4). The observed pattern in grazer diversity was negatively correlated with temperature (Table 3.2). Grazers did not show any relationship with plant species richness (Table 3.2). Even though we only compared grazer species diversity with overall plant species richness, we expect grass species richness to show a similar pattern with altitude as overall plant species richness (see Namgail et al. 2012).

The relatively high overall herbivore species richness at higher altitudes was surprising. Even more surprising and perhaps counterintuitive was the continuous increase in the grazer species richness with altitude. Temperature was the only significant correlate of grazer species richness. Seasonal altitudinal migration by herbivores of the high elevation bands could, presumably, be one mechanism allowing diversity at high altitudes. Variation in biogeographic histories, which we did not consider in our analysis, could be another explanation for the relatively high diversity at high altitudes.

We also propose that increase in plant nutrients with altitude may be an important mechanism of large-herbivore diversity in high mountain systems. It is empirically well established that the nutrient content of plants, especially the nitrogen content of leaves tends to increase with altitude independently of nutrient availability in the soil (Koerner 1989; Morecroft and Woodward 1996). This increase in nitrogen content has been linked to increased carboxylation efficiency at higher altitudes (Friend et al. 1989; Friend and Woodward 1990). This suggests that large-herbivore diversity in high mountains can be relatively greater at higher elevations than at mid-elevations, as long as there is sufficient plant biomass to support herbivore populations. Grazers and relatively smaller bodied herbivores are presumably better able to respond to increased plant nutrition at higher elevations as (i) climatic regimes may lead to a predominance of grassland systems at higher altitudes, especially above the tree line, and, (ii) the reduction in plant biomass with altitude limits species richness of larger bodied herbivores more than that of smaller bodied herbivores at higher elevations.

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