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Moisture and nutrients determine the distribution and richness of India's large herbivore species assemblage

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Abstract

The goal of this study was to test whether body-mass based foraging principles, guided by plant available moisture (PAM) and plant available nutrients (PAN), could explain large mammalian herbivore species distribution and richness in India. We tested (1) whether the occurrence of larger-bodied herbivore species increases with PAM, but is independent of PAN, (2) whether the occurrence of smaller-bodied herbivore species decreases with PAM, but increases with PAN, and (3) whether herbivore species richness is highest in areas with intermediate PAM and high PAN. We analyzed the distribution and richness of the 16 large (>10 kg) herbivore species found in sub-Himalayan mainland India. Since the distributions of large herbivores in India have been altered by historic human activity, we only used India's largest 76 protected areas as data points, with respect to PAM ($\log_{10}$(rainfall/potential evapotranspiration)), PAN (soil cation exchange capacity), elevation, tree cover, and fire frequency. Using regression and null models to analyze the data, we found positive relations between PAM and the occurrences of the larger-bodied species (elephant and gaur), and negative relations between PAM and the occurrences of smaller-bodied species (chinkara, four-horned antelope and blackbuck). We also found positive relations between the occurrence of the smaller-bodied species and PAN. Large herbivore species richness in India is highest in Kanha and Indravati, areas with high PAN and intermediate PAM. We found that elevation, tree cover and fire frequency were insignificant predictors of herbivore species richness, although elevation and tree cover explained the distribution of a few species. Based on our null model analyses results, we conclude that moisture and soil nutrients are important in determining large herbivore species distribution and richness in sub-Himalayan India.

Zusammenfassung

Das Ziel dieser Untersuchung war es zu prüfen, ob Körpergewicht-basierte Prinzipien der Futtersuche, gesteuert durch pflanzenverfügbare Feuchtigkeit (PAM) und Nährstoffverfügbarkeit (PAN), die Verbreitung und den Artenreichtum herbivorer Großsäuger in Indien erklären können. Wir testeten, (1) ob das Auftreten der großen Herbivoren mit der PAM zunahm, während es unabhängig von PAN sein sollte, (2) ob das Auftreten der kleineren Herbivorenarten mit der PAM abnahm, aber mit der PAN zunahm, und (3) ob der Artenreichtum der Herbivoren am höchsten in Gebieten mit mittlerer PAM und hoher PAN war.

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Wir analysierten die Verbreitung und den Artenreichtum der 16 großen (>10 kg) Herbivorenarten, die in der Sub-Himalaya-Region Indiens gefunden werden. Da die Verbreitung der großen Herbivoren in Indien anthropogen beeinflusst wurde, nutzten wir nur die 76 größten Schutzgebiete Indiens als Datenpunkte und berücksichtigten PAM (log (Niederschlag/potentielle Evapotranspiration)), PAN (Kationenaustauschkapazität des Bodens), Höhe, Kronenbedeckung, und die Häufigkeit von Feuern. Wir setzten Regression und Null-Modelle ein, um die Daten zu analysieren, und wir fanden positive Beziehungen zwischen PAM und dem Auftreten der größeren Herbivoren (Elefant, Gaur) und negative Beziehungen zwischen PAM und dem Auftreten der kleineren Arten (Indische Gazelle, Vierhornantilope, Hirschziegenantilope). Wir fanden außerdem positive Beziehungen zwischen dem Auftreten der kleineren Arten und PAN. Der Artenreichtum der großen Herbivorenarten ist am größten in Kanha und Indravati, Regionen mit hoher PAN und mittlerer PAM. Wir fanden, dass die Höhe, Kronenbedeckung und Feuerhäufigkeit unbedeutende Prädiktoren des Artenreichtums der Herbivoren waren, auch wenn Höhe und Kronenbedeckung die Verbreitung einiger Arten erklärten. Aus den Ergebnissen unserer Null-Modell-Analysen schlossen wir, dass Feuchtigkeit und Nährstoffe im Boden wichtig sind für die Bestimmung der Verbreitung und den Artenreichtum der großen Herbivoren in der Sub-Himalaya-Region Indiens.

Introduction

Understanding the distribution of species and species richness has been central to ecology and remains an active and dynamic research area given the changing patterns in local and global biodiversity (Rahbek 2005; Field et al. 2009). Studies from Africa, where large mammalian herbivore species richness is the highest in the world, have shown that the variation in the distribution of large herbivore species correlates significantly with the variation in the quality and quantity of forage (Coe, Cumming, & Phillipson 1976; East 1984; Fritz & Duncun 1994). An herbivore must encounter forage of sufficient quality (nutrient concentrations) and quantity (biomass density) to persist in an area. Since plant available moisture (PAM) and plant available nutrients (PAN) are the two principal determinants of plant quantity and quality (Milchunus, Forwood, & Lauenroth 1994; Milchunus, Varnamkhasti, Lauenroth, & Goetz 1995), PAM and PAN are therefore considered key determinants of the distribution of large herbivore species and richness.

Two foraging principles that relate species body mass to plant quality and quantity are integral to models that explain large herbivore species distribution, composition and richness (McNaughton, Ruess, & Seagle 1988; Prins & Olff 1998; Olff, Ritchie, & Prins 2002): larger-bodied species are capable of surviving on resources of lower quality better than smaller-bodied species; and, smaller-bodied species are capable of surviving in areas where plant quantity is insufficient to support larger-bodied species (Bell 1971; Jarman 1974; Demment & Van Soest 1985). The most recent model—Olff, Ritchie, & Prins 2002—argues that large herbivore species composition and richness on a continental scale can be explained on principles that relate species body mass, plant quantity and quality, and PAM and PAN. For example, the requirement for forage quantity increases with increasing species body mass, and given that plant quantity is positively related to PAM, it follows that the occurrence of larger-bodied herbivore species is positively related to PAM.

Also, despite the positive relation of forage quality and PAN, the occurrence of larger-bodied herbivore species should be independent of PAN because larger-bodied herbivore species are tolerant of lower forage quality. Therefore, the diversity of different-sized herbivores capable of surviving at the combination of PAM and PAN levels in an area reflects how many herbivore species (richness) can persist in that area.

Other environmental variables—like elevation (McCain 2007), tree cover (Riginos & Grace 2008), and fire frequency (Klop & Prins 2008)—are also known to explain the variation in large herbivore species richness. For example, Klop and Prins (2008) found that evapotranspiration and soil nutrients alone failed to predict the diversity patterns of grazing herbivores in West Africa; rather it was anthropogenic fires that modify the quality and structure of the herbaceous sward. The goal of this study is to test whether large mammalian herbivore species distribution and richness in the Indian sub-continent can be explained either by the body-mass based foraging principles, guided by PAM and PAN, or by other environmental variables (elevation, tree cover, and fire frequency). The Indian sub-continent with its rich large herbivore species assemblage—that is distributed over wide moisture and soil nutrient gradients and has a body mass range comparable to what is found in Africa—provides an ideal case for testing the following predictions with respect to the distribution of large mammalian species and their richness: (1) the occurrence of larger-bodied herbivore species (a) increases with PAM, but (b) is generally independent of PAN. Since smaller-bodied herbivores require high quality forage, and plant quality is negatively correlated to PAM, but is positively correlated to PAN (Walker & Langridge 1997), (2) the occurrence of a smaller-bodied herbivore species should (a) decrease with PAM, but (b) increase with PAN. Based on predictions 1 and 2, we also tested whether (3) the mean body mass of all species (not individuals) in an area would increase with PAM and then level off, but would decrease continuously with PAN. Finally we tested (4) whether large

mammalian herbivore species richness should be highest in areas with high PAN and intermediate PAM.

Methods

Data collection

We omitted India's Trans-Himalaya, Himalaya, and Coastal biogeographic zones from the analysis because of their inherent confounding abiotic factors of snow and flooded terrain. The study area, therefore, included the combined extent ($2,500,000 \, \text{km}^2$ land cover) of India's other 6 mainland biogeographic zones (Rogers & Panwar 1988): the Western Ghats and Northeast zones that are characterized by high rainfall and high biodiversity; the Deccan Peninsula, the largest zone, is characterized by volcanic soils and distinct wet and dry seasons; the Gangetic Plain encompasses the flood plain of the Ganges river; and the Indian Desert and Semi-arid zones are characterized by reduced rainfall.

We restricted our analyses to large mammalian herbivore species with mass >10 kg as the distribution data on the mouse deer (*Tragulus meminna*), which is <10 kg, is not well documented and had to be excluded. Therefore, the dataset included occurrence data of 16 large herbivores species from all ($n = 76$) protected areas >200 km^2 within the study area (see Appendix A: Tables 1 and 2; Fig. 1). The reason for choosing protected areas of a relatively large size was to reduce the probability of selecting areas that might have experienced recent extirpations, particularly of the largest species (Karanth, Nichols, Karanth, Hines, & Christensen 2010). The presence/absence of the species in the protected areas was determined by thoroughly referring to individual protected area reports and were verified by leading Indian wildlife experts (A. J. T. Johnsingh, J. C. Daniel, and T. R. Shankar Raman).

PAM for each protected area was calculated as $\log_{10}$(annual rainfall/annual potential evapotranspiration). The values of PAM spanned many orders of magnitude and therefore we log transformed the PAM ratio (which increased its explanatory power in regressions). Rainfall data were derived from Hijmans, Cameron, Parra, Jones, and Jarvis (2005) WorldClim database at a spatial resolution 0.5×0.5 arc min ($1 \, \text{km} \sim 0.5$ arc min), and potential evapotranspiration (PET) from Ahn and Tateishi (1994) at a spatial grid cell resolution of 30×30 arc min. We chose Ahn and Teteishi's data despite its relatively coarse scale for two reasons: (1) because it has been used in other studies similar to ours (e.g., Klop & Prins 2008), and (2) because other well-known climatic and ecological datasets of finer scale, like WorldClim and MODIS NPP, do not have evapotranspiration data. Estimates of PAN were derived at a scale of 5×5 arc min from International Soil Reference and Information Centre's (ISRIC) global soil database (Batjes 2006). The ISRIC database provides data for total nitrogen ($\text{g} \, \text{kg}^{-1}$), organic carbon content ($\text{g} \, \text{C} \, \text{kg}^{-1}$), and cation

exchange capacity ($\text{cmol}_c \, \text{kg}^{-1}$), but not for phosphorous. To enable a comparison with predictions made by Olff et al. (2002) we used cation exchange capacity of the top 20 cm of soil as an index of PAN (Mengel & Krikby 2001). The PAM index for our sites ranged from −0.84 to 0.52 (see Appendix A: Fig. 2A) and the PAN index ranged from 3.2 to 42.5 (see Appendix A: Fig. 2B).

The coarse scale of the PET dataset allowed us to derive only one PET value for ∼70% of the protected areas. Also, all the three datasets (rainfall, evapotranspiration, and cation exchange capacity) were of different spatial resolutions. Therefore, given the constraining nature of the available data, we derived environmental data from a single centroid point (provided by UNEP's World Database on Protected Areas) in each protected area.

Data for elevation (m) were derived from the Global Land One-Kilometre Base Elevation (GLOBE) Digital Elevation Model (Hastings & Dunbar 1998); data for tree cover (%) from the Global Land Cover facility database (Hansen et al. 2003); and data for fire frequency (number of fires in seven years) from the Institute for Environment and Sustainability, Global Burnt Area database (Carmona-Moreno et al. 2005).

Statistical analysis

Since species occurrence data are binary in nature, predictions 1 and 2 were tested using multiple logistic regression models that analyzed the occurrence of individual species (see Appendix A: Table 1) as a function of PAM, PAN, tree cover, and elevation (We had to omit fire as a predictor variable in our logistic regression models as the range of the fire frequency data was small (0–3) and 67 sites had the value 0). Logistic regression models do not satisfactorily fit data of species that are either rare or widely distributed. Therefore, we present logistic regression results for those species that were found in 10–90% of the 76 areas analyzed, i.e., we do not report the inaccurate fits of logistic regression models for species found in less than 10% (rhino, wild buffalo, wild ass, barasingha, hog deer and Nilgiri Tahr) nor those found in over 90% (sambar, chital and wild pig).

To test prediction 3, we analyzed the mean body mass (mean BM) of all 16 large herbivore species (across species, not across individuals) present in each protected area as a function of PAM and PAN using ordinary least square (OLS) regression models. Elephants, because of their large body mass, have the capacity to significantly impact the mean BM of an area; to account for this effect, the presence of elephant was included as a binary factor in these models.

To test prediction 4, simple and multiple OLS regression models with stepwise variable selection were used to analyze species richness (of all 16 species) as a function of PAM, PAN, tree cover and elevation across sites. Since the data were spatial in nature, we repeated the multiple regression analysis with spatial simultaneous autoregressive (SAR) models that correct for potential spatial auto-correlation biases in datasets

Table 1. Results of fitting the absence/presence data of large (>10 kg) mammalian herbivore species found in the 76 largest (>200 km^2) protected areas in sub-Himalayan India to a multiple logistic regression model with predictor variables: plant available moisture (PAM) and nutrients (PAN), elevation (Elv) and tree cover (TCvr). Species are listed in the order of decreasing body mass.

Species	Intercept coeff.	Std. error	p	PAM coeff.	Std. error	p	PAN coeff.	Std. error	p	Elv. coeff.	Std. error	p	TCvr coeff.	Std. error	p
Asian elephant *Elephas maximus*	−0.13	1.03	0.90	6.06	2.29	0.008**	−0.12	0.06	0.03*	0.002	0.002	0.08*	0.007	0.02	0.71
Gaur *Bos gaurus*	−0.66	0.94	0.48	4.83	1.96	0.01**	−0.01	0.03	0.67	0.01	0.001	0.72	0.05	0.02	0.005**
Nilgai *Boselaphus tragocamelus*	0.13	0.89	0.88	−3.05	1.70	0.07*	0.11	0.05	0.02*	−0.002	0.001	0.09*	−0.01	0.02	0.33
Blackbuck *Antilope cervicapra*	−3.28	1.24	0.008**	−4.12	2.01	0.04*	0.03	0.03	0.23	0.0003	0.001	0.85	0.02	0.02	0.47
Muntjac *Muntiacus muntjac*	0.45	1.20	0.71	8.54	3.11	0.006**	0.02	0.03	0.50	0.002	0.002	0.23	0.02	0.02	0.44
Four-horned antelope *Tetracerus quadricornis*	−1.23	0.83	0.14	−0.28	1.33	0.83	0.08	0.03	0.02*	0.004	0.001	0.005**	−0.03	0.02	0.09*
Chinkara *Gazella bennetti*	−1.51	1.02	0.14	−5.93	2.38	0.01**	0.09	0.03	0.005**	0.0004	0.002	0.76	−0.03	0.02	0.05*

** ≤0.01.
* ≤0.1.

(Kissling & Carl 2008) using the software Spatial Analysis in Macroecology v4.0 (Rangel, Diniz-Filho, & Bini 2010).

Given our relatively small data set (16 species and a lack of data points for some combinations of PAM and PAN) we decided to check whether the environmental variables explain species richness better than could be observed by chance. We did this using a null model analysis based on randomly shuffling the species richness values with respect to the environmental variables. Doing this for 1000 different shufflings of the data yields a distribution of the R^2 values that would be expected by chance, to which we can compare the R^2 value obtained for the actual data. A similar analysis was carried out in which the presence/absence of each species was shuffled separately a 1000 times, species richness recalculated based on these shuffled data, and R^2 computed as before.

Besides the spatial autoregressive model analyses, all other statistical analyses were done in the R statistical programming environment (R Development Core Team, 2009).

Results

We found positive and mostly significant relations between the occurrence of the larger-bodied species (elephant and gaur) and PAM (Table 1; prediction 1a). However, the significant negative relation of the occurrence of elephants with PAN does not support prediction 1b, which is that the occurrence of larger-bodied species is independent of PAN. We also found mostly negative and significant relations between the occurrences of the smaller-bodied species (chinkara, four-horned antelope and blackbuck) and PAM, lending support to prediction 2a. The positive relation of the occurrence between the smaller-bodied species and PAN—significant for the two smallest species—lend support to prediction 2b. With respect to the other variables, only the following relations were significant: the positive relations of elevation to the occurrence of elephant, chital and four-horned antelope; the negative relation of elevation to nilgai; the positive relation of tree cover to the occurrence of gaur; and the negative relation of tree cover to that of the smaller four-horned antelope and chinkara (Table 1).

Mean body mass (BM) of species increased with PAM in areas both with and without elephants (Fig. 1A), supporting prediction 3. However, once the presence of elephants was accounted for, PAN did not appear to affect mean BM (Fig. 1B). The models of individual predictor variables that best fit the species richness distribution were: a parabolic function of PAM (Fig. 2A), a linear function of PAN (Fig. 2B), a linear function of elevation ($0.002\,\text{Elv} + 5.96$, $r^2 = 0.09$, $p = 0.01$), and a linear function of tree cover ($0.03\,\text{Tcvr} + 5.90$, $r^2 = 0.16$, $p < 0.001$). The contribution of PAM^2 and PAN were more significant than that of PAM in the multiple regression model that best fit the richness data (Table 2); Fig. 2D illustrates the extent to which this model predicted species richness. We also found: adding PAN^2 did not improve
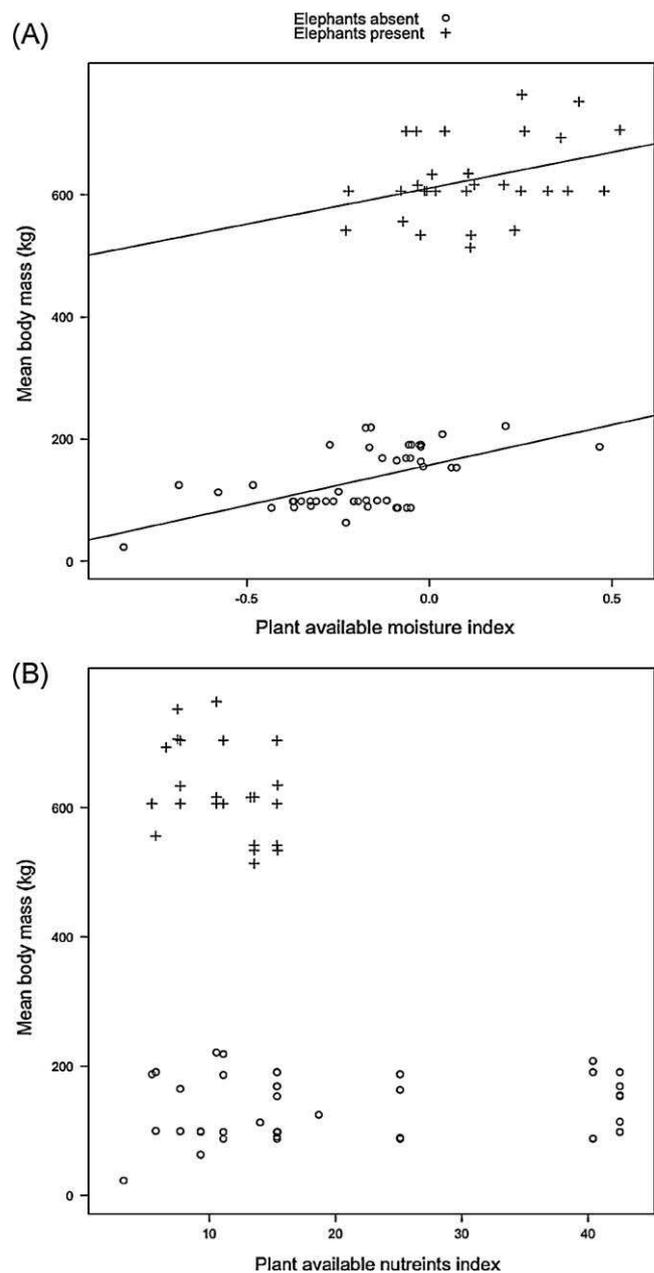

Fig. 1. Mean body mass (across species, not individuals) of large (>10 kg) mammalian herbivore species found in each of 76 Indian protected areas (>200 km^2) in sub-Himalayan India plotted against (A) plant available moisture (PAM) index $= \log_{10}$(rainfall/potential evapotranspiration), and (B) plant available nutrients (PAN) index $=$ cation exchange capacity, $\text{cmol}_c\,\text{kg}^{-1}$. In (A) linear functions positively relate mean body mass to PAM in areas both with elephants ($r^2 = 0.09$, $p = 0.06$) and without elephants ($r^2 = 0.33$, $p < 0.001$). In (B), after accounting for the presence of elephants, mean body mass is not related to PAN.

the multiple regression model (F-test, $p = 0.86$); the interaction PAM $\times$ PAN term was insignificant and was therefore dropped from the model; and that adding elevation (F-test, $p = 0.62$), tree cover (F-test, $p = 0.97$), and fire frequency (F-test, $p = 0.60$) individually, nor collectively (F-test, $p = 0.91$),
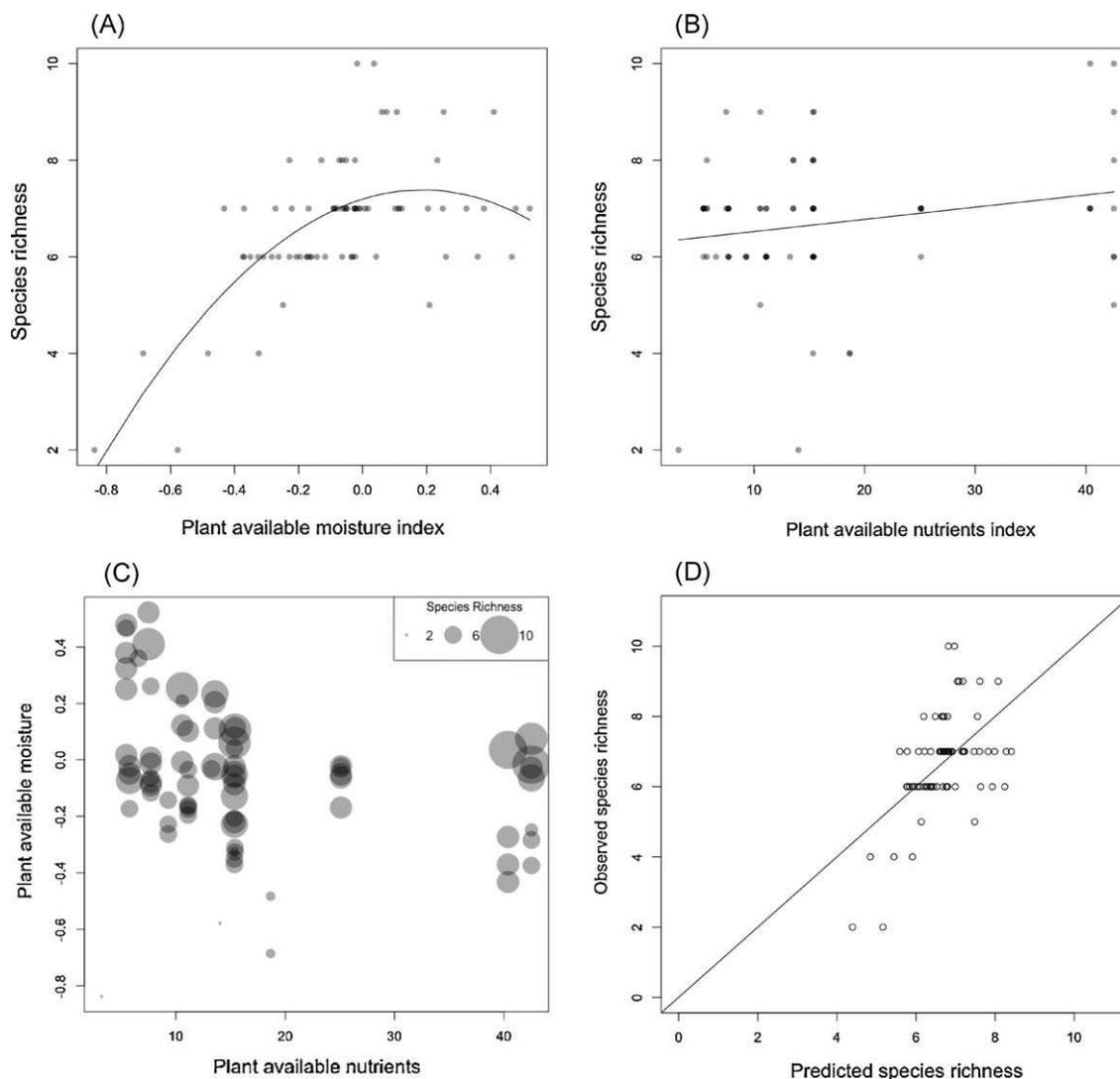
Fig. 2. Large (>10 kg) mammalian herbivore species richness found in 76 protected areas (>200 km^2) in sub-Himalayan India as a function of (A) plant available moisture (PAM) index = $\log_{10}$(rainfall/potential evapotranspiration), $-5.92\,\text{PAM}^2 + 2.15\,\text{PAM} + 7.21$, $r^2 = 0.53$, $p < 0.001$; (B) plant available nutrients (PAN) index = cation exchange capacity (cmol$_c$ kg^{-1}), $0.02\,\text{PAN} + 6.21$, $r^2 = 0.05$, $p < 0.05$; (C) PAM and PAN; bubble size is proportionate to species richness, which is highest (10) in areas with high PAN and intermediate PAM; (D) the correlation (Pearson's $r = 0.77$, $p < 0.001$) between predicted and observed species richness; diagonal line in graph depicts equality, predicted species richness = $6.54 + 2.72\,\text{PAM} + 0.04\,\text{PAN} - 4.62\,\text{PAM}^2$, $R^2 = 0.54$, $p < 0.001$.

improved the model. Although adding protected area size improved the model according to the F-test ($p = 0.04$), it improved the adjusted R^2 from 0.598 to only 0.602. We also found evidence for prediction 4, which was that large herbivore species richness is highest in areas with intermediate levels of PAM and high levels of PAN (Fig. 2C).

The $R^2 = 0.57$ derived from fitting a multiple regression model to the actual species richness data (Table 1), was nearly twice that of the highest recorded $R^2 = 0.3$ from the null model analyses of 1000 direct simulations of species richness; <0.1% of 1000 the R^2 were >0.2. The results of the 1000 indirect simulations of species richness (derived from shuffling the presence/absence data of the individual species) were similar; highest $R^2 = 0.25$ and <0.05% of the 1000 R^2

values were >0.2. These results demonstrate that there is a low probability that the distribution of large herbivore species richness in India as a function of PAM and PAN is due to chance.

Protected area size was included in the multiple logistic regression models used to fit individual species occurrence, but was found to be an insignificant explanatory variable for all species. Also, no significant correlation between species richness and protected area size was found (Kendall's tau = 0.05, $p = 0.55$). These results suggest that reserve size did not play a role in either species distribution or richness despite the wide protected area size range (259–7506 km^2). Results from trying to fit a spatial simultaneous autoregressive (SAR) model were near identical to results from fitting

Table 2. Results of fitting an ordinary least square (OLS) multiple regression model (top) and a spatial simultaneous autoregressive (SAR) model (bottom) to large herbivore species richness found in 76 Indian protected areas in Sub-Himalayan India as a function of plant available moisture (PAM: linear and quadratic) and plant available nutrients (PAN: linear) and the interaction of PAM and PAN.

Factor	Regression coefficient	Standard error	t	p
Ordinary least squares multiple regression model				
Intercept	6.42	0.23	28.32	<0.001
PAM (linear)	1.97	0.69	2.85	0.006
PAM (quadratic)	−4.21	1.08	−3.88	<0.001
PAN (linear)	0.05	0.01	4.02	<0.001
PAM × PAN	0.07	0.05	1.53	0.13
$R^2 = 0.57$				
Spatial multiple autoregressive model				
Intercept	6.53	0.56	11.60	<0.001
PAM (linear)	1.92	0.76	2.52	0.014
PAM (quadratic)	−4.22	1.21	−3.50	<0.001
PAN (linear)	0.04	0.01	3.36	0.001
PAM × PAN	0.06	0.05	1.15	0.26
$R^2 = 0.57$ (predictor variables)				
$R^2 = 0.53$ (predictor variables + space)				

an ordinary least square multiple regression model (Table 2) to species richness data and no strong autocorrelation was found in the residuals, suggesting that spatial autocorrelation was not a confounding issue with the data.

Discussion

The results lend support to the overarching proposition that body-mass based foraging principles in relation to PAM and PAN are capable of explaining the occurrence of differently sized mammalian herbivore species in India. The positive relation between the occurrence of larger-bodied species and PAM (prediction 1a) could be explained by the positive effect that PAM has on plant quantity; only higher plant biomass levels can support the energy requirements of larger-bodied species (Demment & Van Soest 1985). Both the absence of smaller-bodied species (chinkara, blackbuck and four-horned antelope) in areas of high PAM and the negative relation between their occurrence and PAM (prediction 2a) could be explained by the negative effect that PAM has on plant quality, i.e., increasing PAM results in increasing plant biomass, which dilutes plant nutrient concentrations to levels that are sub-optimal for smaller-bodied species. Finding elephants in areas of low PAN, and PAN having no effect on explaining gaur occurrence (Table 1), both lend support to the principle that larger-bodied herbivores can tolerate low plant quality because of their lower metabolic requirements per unit body mass. The positive effect that PAN has on plant quality can explain the positive relation of the occurrence of the smallest species (chinkara and four horned antelope) with that of PAN (prediction 2b). These findings are consistent with the understanding that smaller-bodied species, because of their higher metabolic requirements per unit body mass, favour areas with high plant quality (Jarman 1974).

Not all the relations between species occurrence and PAM and PAN, however, conform to our predictions. The negative relation between the occurrence of elephant and PAN does not conform to prediction 1b, which is that the occurrence of larger-bodied species should be independent of PAN levels. Also, the significant positive relation between the occurrence of muntjac and PAM is different from the negative relations between PAM and the occurrence of the other small-bodied species. These contradictions suggest that despite the general patterns of the influence of environmental controls on species richness being true, ecological processes at aggregation levels below that of the subcontinent also influence species distribution.

Protected areas with intermediate PAM and high PAN (the protected areas of Kanha and Indravati; Fig. 2C) support the richest (10 species) large herbivore assemblages in India (prediction 4). Intermediate PAM levels ensure sufficient plant quantity levels to support the energy requirements of both small as well as large-bodied species like the gaur, while the high PAN levels help support multiple species over a wide body mass range. It is important to note, however, that the data analyzed included neither areas that have both low PAM and high PAN nor areas that have both high PAM and high PAN. Also, PAM = −0.4 (Fig. 2A) appears to be a threshold above which the relation between PAM and species richness becomes less prominent.

With respect to the environmental variables besides PAM and PAN, elephants are known to occur in higher altitude areas while nilgai are not (Prater 1997; Sukumar 2008), which explains their respective occurrence being positively and negatively related to elevation (Table 1). The positive relations between elevation and the occurrence of four-horned antelope and chital, however, are not consistent with the observed disassociation of these species with higher altitude areas (Prater 1997). The positive relation between the occurrence of gaur

and forest cover is consistent with their known association with forested areas (Prater 1997), but as Schaller (1967) has pointed out this could be because much of the gaur's former grasslands have been converted to agriculture. The negative relations between the occurrence of four-horned antelope and chinkara, though, validate their known associations with low-elevation areas (Prater 1997).

Although Klop and Prins (2008) found that fire played a prominent role in determining herbivore species richness in West Africa, the effect of fire frequency on species richness in India was insignificant (see Section 'Results'). Elevation too was a weak predictor, whereas tree cover, relative to PAN and elevation, was a much better predictor of species richness. This stronger relationship of tree cover to species richness could be interpreted as forested areas having a diversity of habitats providing a higher number of niches for large herbivore species. Although there exists little evidence demonstrating the impact of competition or facilitation within herbivore assemblages (Arsenault & Owen-Smith 2002), we acknowledge the potential these ecological forces might have had in shaping herbivore assemblages in India. For example, the analysis by Fritz, Duncun, Gordon, and Illius (2002) of herbivore assemblages in Africa provides evidence of competition between megaherbivores and smaller herbivore species.

While it is not possible to directly compare results of this study with the predictions made by Olff et al. (2002) for India—they used a pool of 10 species while we used 16—their predictions of the distribution of species richness differed from actual species richness. For example, they predicted low species richness for the Western Ghats, an area in which species richness is in fact relatively high. This is not entirely surprising, given that a recent study by Field et al. (2009) argues that care is needed when making global predictions based on local knowledge, and that a thorough analysis using different techniques while accounting for confounding and other potential correlates is required if we are to extrapolate predictions. We tried addressing Field et al.'s concerns by analyzing the distribution of species and richness with environmental variables other than PAN and PAM, and eliminating other variables like the size of protected areas and spatial auto-correlation, while the results of the null model analyses show that species richness is significantly more related to PAM and PAN than would be expected by chance.

It is possible that cation exchange capacity does not accurately reflect PAN in some areas. However, we found weak correlations of species richness with total soil nitrogen ($r = 0.28$, $p = 0.01$) and soil organic carbon content ($r = 0.29$, $p = 0.01$), and no correlation with soil C:N ($r = -0.09$, $p = 0.43$). Also, the species pool for this study might appear small in comparison to Africa, where the large herbivore species pool is ∼90 species. However, the large herbivore species assemblage in India has remained unchanged for at least the last 100 years, if not more (Prater 1997), and therefore was a valid test case for the theory which explains large herbivore species richness at a countrywide spatial scale. What would be worthwhile investigating in the future is whether the species richness in a large protected area with multiple habitat types can be explained as a function of the intra-site variability in environmental factors. While expanding the theory to account for intra-site environmental variability, we should also pay attention to addressing the aspect that sometime different sites with the same species assemblages have different species abundances. However, neither did the data that was available to us allow for such analyses, nor were we trying to answer questions pertaining to niche partitioning of species at a local scale.

Finally, this discussion would not be complete without acknowledging the potential that human activity might have had in shaping the current distribution of large herbivores in India. Studies have shown that human practices such as livestock grazing (Madhusudan 2004) and habitat fragmentation (Karanth, Nichols, Hines, Karanth, & Christensen 2009) correlate with the distribution of mammalian species in India. Furthermore, the reduction in the historical ranges of the different species (Karanth et al. 2010), especially the larger-bodied species like elephant (Sukumar 2008), probably contributed in restricting the range of PAM and PAN represented in the dataset. Testing this study's predictions with species' historical ranges, however, is impossible given the lack of standardized data of the historical distributions of the species and that of PAM and PAN from India. The lack of historical data on accurate distributions of the species does not allow for verifying past local extirpations of species either, which is why we chose protected reserves of relatively large size as this study's data points as they are the most likely to have their historical large herbivore species assemblage intact.

In conclusion, this study provides insight into how environmental variables, with a special focus on PAM and PAN, play a role in influencing the large herbivore species distribution and richness in India.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2011.08.008.

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