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Global environmental controls of diversity in large herbivores

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Large mammalian herbivores occupy half of the earth's land surface and are important both ecologically and economically[1], but their diversity is threatened by human activities[2]. We investigated how the diversity of large herbivores changes across gradients of global precipitation and soil fertility. Here we show that more plant-available moisture reduces the nutrient content of plants but increases productivity, whereas more plant-available nutrients increase both of these factors. Because larger herbivore species tolerate lower plant nutrient content but require greater plant abundance, the highest potential herbivore diversity should occur in locations with intermediate moisture and high nutrients. These areas are dry enough to yield high quality plants and support smaller herbivores, but productive enough to support larger herbivores. These predictions fit with observed patterns of body size and diversity for large mammalian herbivores in North America, Africa and Australia, and yield a global map of regions with potentially high herbivore diversity. Thus, gradients of precipitation, temperature and soil fertility might explain the global distribution of large herbivore diversity and help to identify crucial areas for conservation and restoration.

Previous studies have linked rainfall, soil fertility and primary productivity to total herbivore community biomass[3–5], plant quality[6–8] and species richness of herbivores[9–12], but have not explained why and how these factors affect herbivore diversity[13]. The ability of large herbivores (mass > 2 kg) to persist probably changes across gradients of plant abundance and quality. Plant productivity and quality are influenced by the availability of two principal plant resources, water and nutrients, and thus change across environmental gradients of these resources[14]. Previous results[15] have shown that plant abundance, as measured by the equilibrium biomass of ungrazed plants, increases linearly with rainfall—a crude measure of plant-available moisture. This increase is stronger at higher nutrient availability (Fig. 1a). However, leaf tissue nitrogen content, an index of plant quality to herbivores, decreases with plant-available moisture even though it also increases with plant-available nutrients (Fig. 1b). Similar patterns occur with plant phosphorus content[15,16].

These combined effects imply that plant abundance and nutrient content show different response surfaces to moisture and nutrients (Fig. 1c, d). Plant abundance is lowest at either low moisture or low nutrient availability, and highest when both are high (Fig. 1c). By contrast, plant nutrient content is lowest at combinations of high plant-available moisture and low nutrients, and highest at combinations of low plant-available moisture and high nutrients. We expect the contours of the response surface for plant nutrient content to be concave at low moisture and relatively horizontal at high moisture (Fig. 1d), because an increase in nutrients will increase plant nutrient content more strongly at low than at high moisture[17] (Fig. 1b).

The two response surfaces for plant abundance and nutrient content can be combined to define potential conditions for the presence of large herbivores. A given herbivore species must encounter plants of both sufficient abundance and quality to persist, and therefore may be constrained to persist only under certain conditions of plant-available moisture and nutrients. These conditions can be defined in a graphical model by two proposed

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thresholds of combinations of moisture and nutrients that allow plants of sufficient quality and abundance for a herbivore's persistence (Fig. 2a). A specific contour of the plant abundance response surface (Fig. 1c) will correspond to the plant abundance requirements of a herbivore, and represents the 'plant abundance threshold' of the herbivore. Similarly, a specific contour of the plant nutrient content response surface (Fig. 1d) will correspond to the plant quality requirements of a herbivore, and represents the 'plant quality threshold' of the herbivore.

The plant abundance threshold of a herbivore species is the minimum plant-available moisture, for a given nutrient availability, above which plant productivity will be sufficiently high to support a population of that herbivore species. Likewise, the plant quality threshold of a herbivore species is the maximum plant-available moisture, for a given nutrient availability, below which plant tissue is sufficiently nutrient-rich for that herbivore species to persist. Together, the quality and abundance thresholds define a 'wedge' of combinations of moisture and nutrients at which a herbivore species can persist (Fig. 2a).

The predicted potential diversity of different-sized herbivores at a certain combination of moisture and nutrients should reflect how many species can persist at those conditions. Larger herbivores require more abundant plants but can tolerate lower plant quality than smaller herbivores, whereas smaller herbivores can persist on less-abundant plants but only if the plants are of higher quality[3,8,18-20]. Thus, the plant abundance and quality thresholds should differ across orders of magnitude in herbivore body sizes[8].

The plant abundance threshold of larger herbivores will be shifted farther from the origin, but their plant quality threshold will be more horizontal and shifted to wetter conditions (Fig. 2b). Smaller herbivores should have abundance thresholds closer to the origin, plus more sharply concave quality thresholds shifted towards drier, more fertile conditions.

Thus, the occurrence of larger herbivores is expected to increase with greater moisture, but to be relatively independent of plant-available nutrients. In contrast, smaller herbivores should decrease in occurrence with greater moisture and increase with greater nutrient availability. Therefore, the mean body size for all species
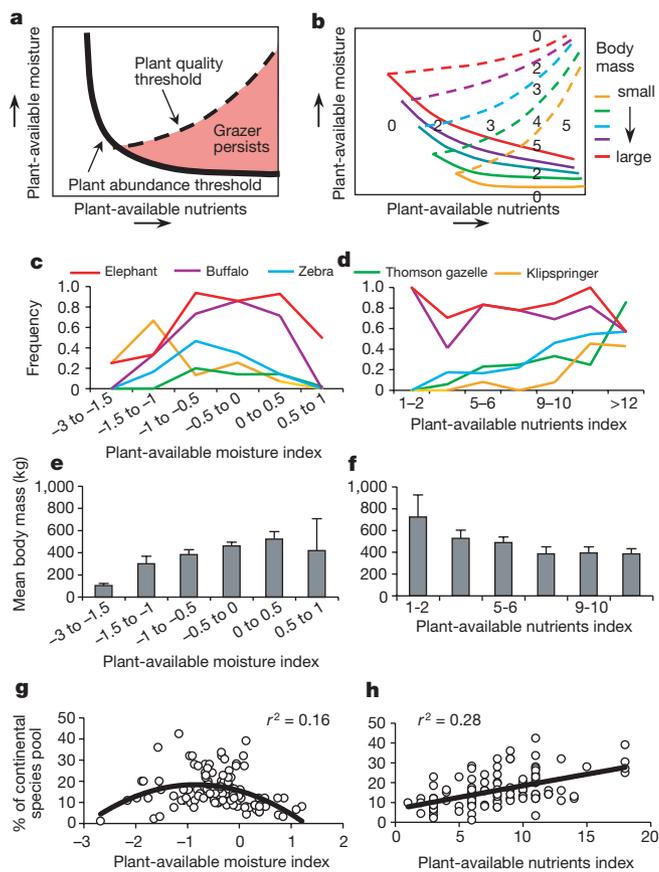
Figure 2 Predicted and observed patterns of herbivore diversity along gradients of plant-available moisture and nutrients. **a**, Threshold combinations of plant-available moisture and nutrients that allow a hypothetical herbivore to persist. Plant abundance and plant quality thresholds reflect shapes of the contours of the response surfaces for plant biomass and plant nutrient content, respectively. **b**, Hypothetical regions of persistence for six different species that differ in body mass, as defined by plant abundance thresholds (solid curves) and plant quality thresholds (dashed curves). Numbers indicate how many herbivore species can persist under different conditions of plant-available moisture and nutrients. Note the greater overlap in regions of persistence at intermediate plant-available moisture and high plant-available nutrients. **c**, **d**, Frequency of occurrence of five different-sized herbivore species (klipspringer, *Oreotragus oreotragus*; Thomson's gazelle, *Gazella thomsoni*; Burchell's zebra, *Hippotigris quagga*; Cape buffalo, *Syncerus caffer*; elephant, *Loxodonta africana*) among 85 African parks in different intervals of indices for plant-available moisture (**c**) and plant-available nutrients (**d**). **e**, **f**, Body mass (mean ± s.e.) of all species present in different intervals of indices for plant-available moisture (**e**) and plant-available nutrients (**f**). **g**, **h**, Observed large herbivore species richness, expressed as a percentage of the continental species pools from 118 sites in North America and Africa versus indices for plant-available moisture (log₁₀[precipitation/potential evapotranspiration]), $y = -3.81x^2 - 6.53x + 14.93$ (**g**), and plant-available nutrients (ref. 25, and Methods), $y = 1.10x + 6.79$ (**h**).
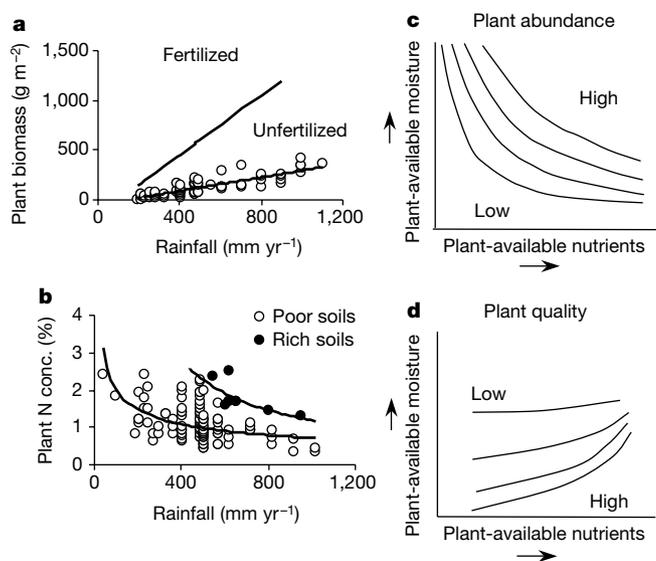

Figure 1 Plant biomass and tissue nitrogen content changes across rainfall gradients in Africa. **a**, Ungrazed plant biomass (V, open circles) increases with rainfall (M) on poor soils in West Africa ($V = -46.32 + 0.34M$; $n = 77$, $R^2 = 0.70$, $P < 0.001$) and fertilized patches at the same sites (only the regression line is available)[15,16]. **b**, Whole-plant tissue nitrogen content (N) at the same sites (open circles) decreases across the same rainfall gradient on poor soils ($N = 15.99M^{-0.45}$; $n = 117$, $R^2 = 0.22$, $P < 0.001$), as it does on rich soils from East Africa ($N = 822.14M^{-0.95}$; $M^2 = 0.57$, $P = 0.02$)[26-30]. Plant tissue phosphorus content on poor West African soils responded similarly to rainfall as tissue nitrogen content[15,16]. **c**, **d**, Hypothetical response surfaces for plant biomass (**c**; abundance) and plant nutrient content (**d**) to plant-available moisture (balance of rainfall and potential evapotranspiration) and plant-available nutrients, inferred from observed data in **a** and **b**. Contour shapes in **c** reflect the joint limitation of plant biomass by water and soil nutrients. Contour shapes in **d** reflect the observed data in **b**, which show that plant nutrient content increases with plant-available nutrients more rapidly at low than at high plant-available moisture.

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is expected first to increase rapidly with plant-available moisture and then to level off, but to decrease continuously with plant-available nutrients (Fig. 2b).

The trade-off in requirements for plant quantity and quality for different-sized herbivores ultimately predicts general patterns of herbivore diversity across gradients of water availability and soil nutrients. At a given nutrient concentration, herbivore species richness is predicted to peak at intermediate moisture because both small and large species occur together (Fig. 2b). For a given moisture, however, herbivore species richness should increase continuously with greater nutrients because more smaller species are added (Fig. 2b). The highest herbivore diversity is thus expected in locations that are not so wet and/or infertile that average plant quality would be too low to sustain smaller herbivores, and also not so dry and/or infertile that plant productivity would be insufficient to sustain larger herbivores (Fig. 2b). This prediction is insensitive to the shapes of the contours of plant abundance and nutrient content (Fig. 1a–d).

We tested our predictions by compiling a data set of the observed occurrence and species richness of all terrestrial mammalian herbivores with a mass greater than 2 kg (grazers, mixed feeders and browsers) in 33 different protected natural areas in North America and 85 such areas in sub-Saharan Africa (Methods). For every site, we calculated indices for plant-available moisture and nutrients (Methods), and graphed changes in individual species, mean body mass and species richness along these gradients. We expressed species richness as a proportion of the total species richness per continent to standardize for differences between the two continents in size and biogeographical history[21,22].

Observed frequencies of occurrence of five different-sized grazing mammals, chosen as representative examples, in 85 parks in Africa support our predictions for individual species (Fig. 2c, d). Large species (Cape buffalo and elephant) peaked in occurrence at higher plant-available moisture than did intermediate-sized herbivores (zebra, Thomson's gazelle), which in turn peaked in occurrence at higher water availability than did a small species (klipspringer). In addition, logistic regression showed that occurrence of the two largest species was independent of plant-available nutrients ($P > 0.05$), but that occurrence of the smaller three species increased with increasing plant-available nutrients ($P < 0.05$). As we predicted, the mean body mass of all species present at a site increased with increasing plant-available moisture, and decreased with increasing plant-available nutrients (Fig. 2e, f).

Consistent with these results for individual species and mean body mass, and with our predictions of diversity patterns (Fig. 2b), we found that total herbivore species richness (as a percentage of the continental species pool) for Africa and North America together peaked at intermediate plant-available moisture (Fig. 2g) and increased continuously with plant-available nutrients (Fig. 2h). Multiple regression analysis (Table 1) showed that herbivore species richness increased linearly with plant-available nutrients and nonlinearly (as a quadratic function) with plant-available moisture, and that each had a significant effect. Separate herbivore diversity

patterns for Africa and North America were similar. This pattern is unlikely to be caused by plant diversity (leading to more resource types), because plant diversity is typically highest at low soil fertility[23]. It is also unlikely to be caused by non-food differences between habitats (for example, shelter to predation) as the patterns shown in Fig. 2g and h did not change substantially when the analysis was restricted to include only sites that were primarily grassland.

On a global scale, this empirical regression model (Table 1) predicts that there are regions that can support high herbivore diversity when applied to maps of our indices for plant-available moisture and nutrients (Methods and Fig. 3). To validate our regression model with independent data, we predicted large herbivore species richness (as a percentage of continental pool) for ten preserves and natural areas in Australia on the basis of our global
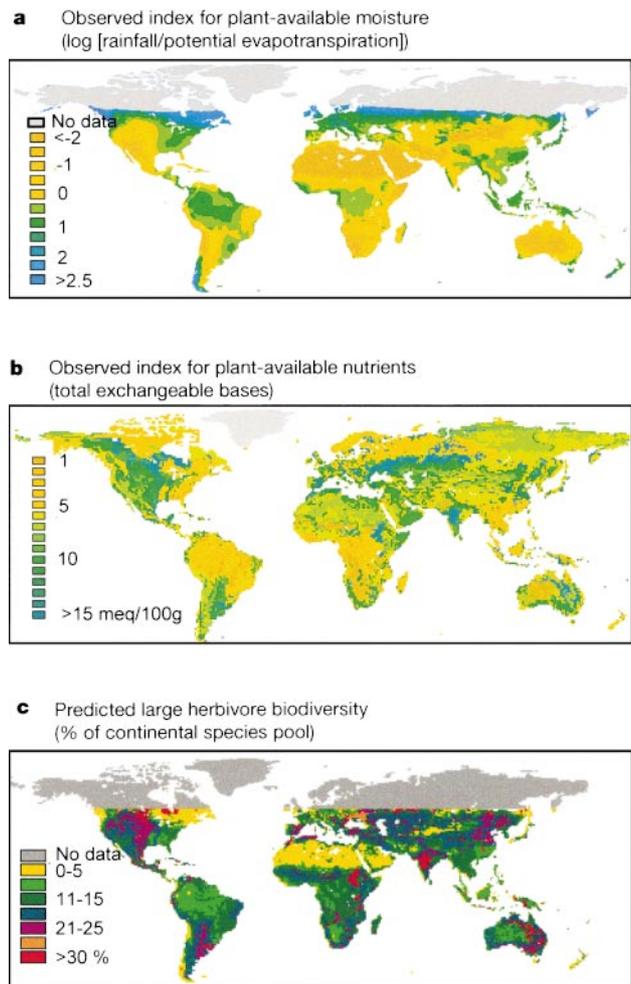

a Observed index for plant-available moisture (log [rainfall/potential evapotranspiration])

No data
<-2
-1
0
1
2
>2.5

b Observed index for plant-available nutrients (total exchangeable bases)

1
5
10
>15 meq/100g

c Predicted large herbivore biodiversity (% of continental species pool)

No data
0-5
11-15
21-25
>30 %

Figure 3 Global distribution of large herbivore diversity, as predicted by indices for plant-available moisture and nutrients using a regression model obtained from data for African and North American parks. **a**, **b**, Maps of observed water supply and soil fertility indices, respectively. **c**, Map of species richness of large herbivores, as a percentage of continental species pool (Methods), predicted from indices for plant-available moisture and nutrients using the multiple regression model (Table 1, Fig. 2d). Continental species pools are North America, 25; Africa, 99; Central and South America, 18; Europe, 5; Middle East, 11; North Africa, 8; India, 10; Northern Asia and Far East, 31; southeast Asia and Indonesian archipelago, 10; Australia, 59. All maps represent a planar projection, at a resolution of 0.5° longitude/latitude (**a**) or 1° longitude/latitude (**b**, **c**). No data for potential evapotranspiration are available for the boreal zones in **a**, hence no diversity predictions could be made for this region (**c**).

Table 1 Dependence of species richness on water and soil

Coefficient	Regression coefficient	Standard error	t	P
Constant	8.091	1.483	5.46	< 0.001
Soil fertility index (linear)	1.031	0.181	5.70	< 0.001
Water availability index (linear)†	−3.639	1.489	−2.45	0.016
Water availability index (quadratic)	−2.897	0.877	−3.30	< 0.001

Results of the multiple regression analysis of the dependence of large herbivore species richness (given as a percentage of the continental species pool; see Methods) on indices of water availability and soil fertility are shown.
† This linear coefficient was negative, despite a unimodal relationship (Fig. 2e), because water availability indices were mainly negative (potential evapotranspiration > rainfall).

map of plant-available moisture and nutrient indices. We found a strong correspondence between predicted and observed diversity ($R^2 = 0.69$, $P = 0.003$, $n = 10$). Regions of known high herbivore diversity in other regions and continents[1,10,22] also seem to correspond to areas that are classified as having high potential diversity by our global map. These include the Argentinian pampa, Gir Forest of India, steppes of Khazakstan and Mongolia, Cordillera of Spain, and the coastal region of Morocco and Algeria (Fig. 3c).

Extrapolating the predictions of our model to the global map yields potentially important insights about the global status of large herbivore conservation. For example, the prime regions for large herbivore diversity can host potentially more than 25% of the species in a continental species pool, but comprise only about 5% of the investigated land of the world (see Fig. 3c). Fewer than 2% of the prime regions for large herbivore diversity overlap with regions designated as 'general purpose' biodiversity hotspots[24]. Current land-use practices[25] suggest that more than half of the area of these prime regions has been already converted to agriculture and lost its herbivore diversity. Another 25% of these prime regions may be converted to agriculture in the next 25 yr. Thus, less than 1.2% of the earth's surface might remain to support uniquely diverse, grazing ecosystems by 2025. Some regions, such as the northern Great Plains in North America, might be highly suitable for restoring large herbivore diversity if agriculture were to be abandoned.

Our approach is powerful because it identifies how plant resources constrain the distribution of herbivores of different sizes. We can use this functional relationship to predict patterns in large herbivore diversity on a global scale. Similar approaches might be applied to other groups of organisms to help to identify crucial areas for current conservation and future restoration of biodiversity. □

Methods

Data sources

Main data sources for species occurrences in protected areas in North America (34 sites) and Africa (85 sites) were the Man and Biosphere Species Database (http://ice.ucdavis.edu/mab) and the UNEP-WCMC Protected Areas Database (http://www.unep-wcmc.org). Only mammalian herbivores > 2 kg that eat graminoids, forbs and/or woody plants were recorded. We restricted the analysis to this size class because the records of smaller herbivores (small mammals, insects) in these areas are incomplete. Species that eat mostly seeds and fruits were not included as it is unclear whether the food abundance and quality patterns shown in Fig. 1a and b also hold for these food types. We included only wilderness areas, national parks and national monuments and wildlife management areas (International Union for the Conservation of Nature (IUCN)) categories I, II or III or IV).

Plant-available moisture index

The plant-available moisture index for each protected area was calculated as the monthly average of the $\log_{10}$ of the ratio of actual rainfall over potential evapotranspiration using published maps[26]. Data of potential evapotranspiration and therefore our moisture index and diversity prediction were not available for the polar region, as the calculation method is inappropriate for areas with long-term snow cover.

Plant-available nutrients index

Data on plant-available nutrients are based on the FAO-UNESCO Soil Map of the World, assigned[25] to 1° by 1° cells. Plant-available nutrients were assumed to be proportional to the sum of soil cations Ca^{2+}, Mg^{2+}, Na^+ and K^+ or total exchangeable bases (TEB), which is calculated from base saturation, BS% = [(TEB/CECsoil)×100], and soil exchange capacity (soil CEC) according to TEB = (BS%/100)×3.5OC% + [(Clay% x CECclay)/100)], where OC% is the percentage of organic carbon in the soil, Clay% is the percentage of clay content and CECclay is the approximate cation exchange capacity for the dominant clay mineral.

Species frequency of occurrence

The frequency of occurrence of individual herbivore species is the proportion of parks that contain a particular species in each of six intervals of plant-available moisture index, and seven intervals of plant-available nutrients index. Patterns were robust to our choice of interval sizes. For each interval, we also calculated the mean body mass of all species present. Because Africa (99 large herbivore species) and North America (25 large herbivore species) differ in their continental species pools and local species richness, owing in part to extinction of 50% of the species in North America since the last glaciation, the species richness at each park was expressed as a percentage of the continental species pool. This

crudely standardizes diversity relative to the potential number of species that could be present theoretically at a site.

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Competing interests statement

The authors declare that they have no competing financial interests.

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