

Received 9 October 2001; accepted 17 January 2002.

1. Sparks, R. S. J., Wilson, L. & Hulme, G. Theoretical modeling of the generation, movement, and emplacement of pyroclastic flows by column collapse. *J. Geophys. Res.* **83**, 1727–1739 (1978).
2. Valentine, G. A. & Wohletz, K. H. Numerical models of Plinian eruption columns and pyroclastic flows. *J. Geophys. Res.* **94**, 1867–1887 (1989).
3. Dobran, F., Neri, A. & Macedonio, G. Numerical simulation of collapsing volcanic columns. *J. Geophys. Res.* **98**, 4231–4259 (1993).
4. Neri, A. & Macedonio, G. Numerical simulation of collapsing volcanic columns with particles of two sizes. *J. Geophys. Res.* **101**, 8153–8174 (1996).
5. Oberhuber, J. M., Herzog, M., Graf, H. F. & Schwanke, K. Volcanic plume simulation on large scales. *J. Volcanol. Geotherm. Res.* **87**, 29–53 (1998).
6. Self, S., Wilson, L. & Nairn, I. A. Vulcanian eruption mechanisms. *Nature* **277**, 440–443 (1979).
7. Turcotte, D. L., Ockendon, H., Ockendon, J. R. & Cowley, S. J. A mathematical model of Vulcanian eruptions. *Geophys. J. Int.* **103**, 211–217 (1990).
8. Fagents, S. A. & Wilson, L. Explosive volcanic eruptions—VII. The ranges of pyroclastics ejected in transient volcanic explosions. *Geophys. J. Int.* **113**, 359–370 (1993).
9. Woods, A. W. A model of Vulcanian explosions. *Nucl. Eng. Des.* **155**, 345–357 (1995).
10. Kieffer, S. W. Fluid dynamics of the May 18 blast at Mount St. Helens. *US Geol. Surv. Prof. Pap.* **1250**, 379–400 (1981).
11. Wohletz, K. H., McGetchin, T. R., Sandford, M. T. & Jones, E. M. Hydrodynamic aspects of caldera-forming eruptions: numerical models. *J. Geophys. Res.* **89**, 8269–8285 (1984).
12. Neri, A., Di Muro, A. & Rosi, M. Mass partition during collapsing and transitional columns by using numerical simulations. *J. Volcanol. Geotherm. Res.* (in the press).
13. Neri, A. *Multiphase Flow Modelling and Simulation of Explosive Volcanic Eruptions*. Thesis, Illinois Inst. Technol. (1998).
14. Neri, A., Macedonio, G., Gidaspow, D. & Esposti Ongaro, T. *Multiparticle Simulation of Collapsing Volcanic Columns and Pyroclastic Flows* (Volcanic Simulation Group Report 2001–2, Istituto Nazionale di Geofisica e Vulcanologia, Pisa, 2001).
15. Amsden, A. A. & Harlow, F. H. *KACHINA: An Eulerian Computer Program for Multifield Fluid Flows* (Report LA-5680, Los Alamos National Laboratory, Los Alamos, 1974).
16. Rivard, W. C. & Torrey, M. D. *K-FIX: A Computer Program for Transient, Two-dimensional, Two-fluid Flow* (Report LA-NUREG-6623, Los Alamos National Laboratory, Los Alamos, 1977).
17. Gidaspow, D. *Multiphase Flow and Fluidization: Continuum and Kinetic Theory Descriptions* (Academic, New York, 1994).
18. Voight, B. *et al.* Magma flow instability and cyclic activity at Soufrière Hills Volcano, Montserrat. *Science* **283**, 1138–1142 (1999).
19. Wilson, L., Sparks, R. S. J. & Walker, G. P. L. Explosive volcanic eruptions IV. The control of magma properties and conduit geometry on eruption column behaviour. *Geophys. J. R. Astron. Soc.* **63**, 117–148 (1980).
20. Sparks, R. S. J. Causes and consequences of pressurisation in lava dome eruptions. *Earth Planet. Sci. Lett.* **150**, 177–189 (1997).
21. Devine, J. D., Rutherford, M. J. & Barclay, J. Changing magma conditions and ascent rates during the Soufrière Hills eruption on Montserrat. *GSA Today* **8**, 2–7 (1998).
22. Barclay, J. *et al.* Experimental phase equilibria constraints on pre-eruptive storage conditions of the Soufrière Hills magma. *Geophys. Res. Lett.* **25**, 3437–3440 (1998).
23. Murphy, M. D., Sparks, R. S. J., Barclay, J., Carroll, M. R. & Brewer, T. S. Remobilization of andesite magma by intrusion of mafic magma at the Soufrière Hills Volcano, Montserrat, West Indies. *J. Petrol.* **41**, 21–42 (2000).
24. Jaupart, C. & Allègre, C. J. Gas content, eruption rate and instabilities of eruption regime in silicic volcanoes. *Earth Planet. Sci. Lett.* **102**, 413–429 (1991).
25. Druitt, T. H. *et al.* *The Explosive Eruptions of August 1997* (Special Report 04, Montserrat Volcano Observatory, Salem, Montserrat, 1998).
26. Hoblitt, R. P. Observations of the eruptions of July 22 and August 7 1980 at Mount St Helens, Washington. *US Geol. Surv. Prof. Pap.* **1335**, (1986).
27. Wolf, T. Der Cotopaxi und seine letzte Eruption am 26 Juni 1877. *Neues Jb. Miner. Geol. Paläont.* **113**–167 (1878).
28. Taylor, G. A. The 1951 eruption of Mount Lamington, Papua. *Aust. Bur. Min. Resour. Geol. Geophys. Bull.* **38**, 1–117 (1958).
29. Formenti, Y. & Druitt, T. H. in *Abstracts and Addresses of the IAVCEI General Assembly 2000* 232 (Volcanological Survey of Indonesia, Bandung, Indonesia, 2000).
30. Melnik, O. & Sparks, R. S. J. Nonlinear dynamics of lava dome extrusion. *Nature* **402**, 37–41 (1999).

Acknowledgements

We thank our colleagues at Montserrat Volcano Observatory for their assistance, especially C. Bonadonna, T. Druitt, C. Harford, R. Herd, R. Luckett and R.E.A. Robertson, our colleagues during the August explosions. Support for monitoring was provided by the Department for International Development (UK), the British Geological Survey (BGS), the Seismic Research Unit of the University of the West Indies, and the US Geological Survey (USGS). A.C. and B.V. acknowledge support from the US NSF. A.N. and G.M. were assisted by the Istituto Nazionale di Geofisica e Vulcanologia, and Gruppo Nazionale per la Vulcanologia ING, Italy. B.V. was a Senior Scientist at Montserrat in 1997 with BGS, and was also affiliated with the USGS Volcano Hazards Program. We thank M. Rutherford for comments.

Competing interests statement

The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to A.B.C. (e-mail: aclarke@geosc.psu.edu).

.....
Global environmental controls of diversity in large herbivores

Han Offr*, Mark E. Ritchie† & Herbert H. T. Prins*

* Tropical Nature Conservation and Vertebrate Ecology Group, Wageningen University, Bornsesteeg 69, 6708 PD Wageningen, The Netherlands

† Department of Biology, Syracuse University, Syracuse, New York 13244, USA

Large mammalian herbivores occupy half of the earth's land surface and are important both ecologically and economically¹, but their diversity is threatened by human activities². 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 diversity¹³. 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 resources¹⁴. Previous results¹⁵ 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 moisture¹⁷ (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

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 sizes⁸.

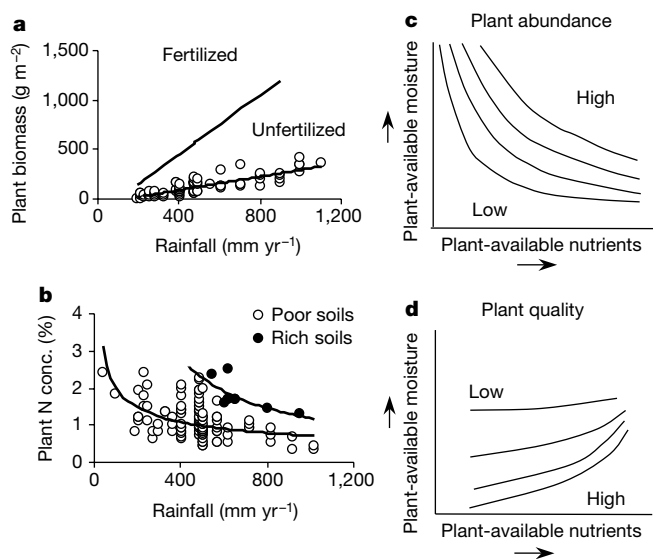


Figure 1 Plant biomass and tissue nitrogen content changes across rainfall gradients in Africa. **a**, Ungrazed plant biomass (V , open circles) increases with rainfall (M) on poor soils in West Africa ($V = -46.32 + 0.34M$; $n = 77$, $R^2 = 0.70$, $P < 0.001$) and fertilized patches at the same sites (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.

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

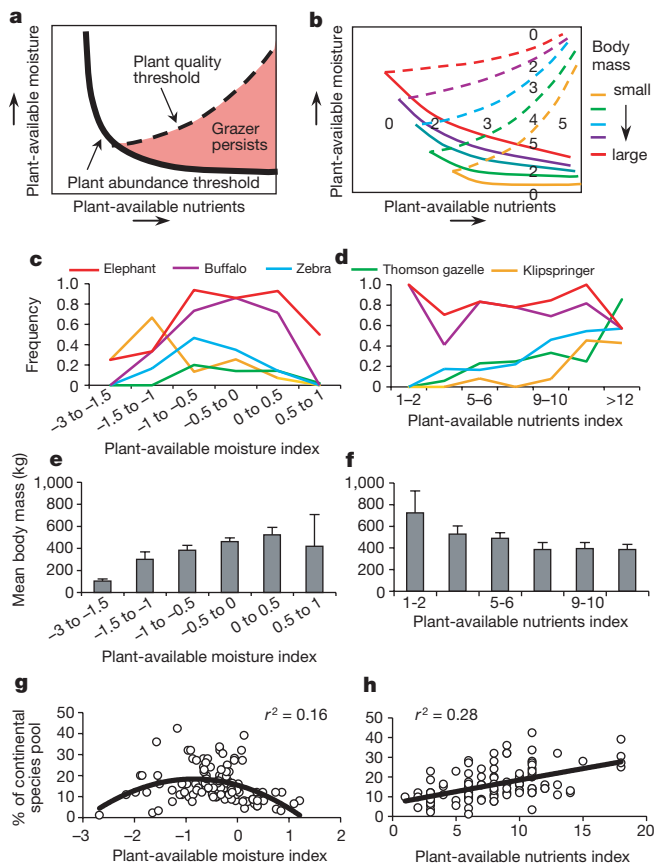


Figure 2 Predicted and observed patterns of herbivore diversity along gradients of plant-available moisture and nutrients. **a**, Threshold combinations of plant-available moisture and nutrients that allow a hypothetical herbivore to persist. Plant abundance and plant quality thresholds reflect shapes 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 \pm 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 ($\log_{10}[\text{precipitation}/\text{potential evapotranspiration}]$), $y = -3.81x^2 - 6.53x + 14.93$ (**g**), and plant-available nutrients (ref. 25, and Methods), $y = 1.10x + 6.79$ (**h**).

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 non-linearly (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 fertility²³. 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

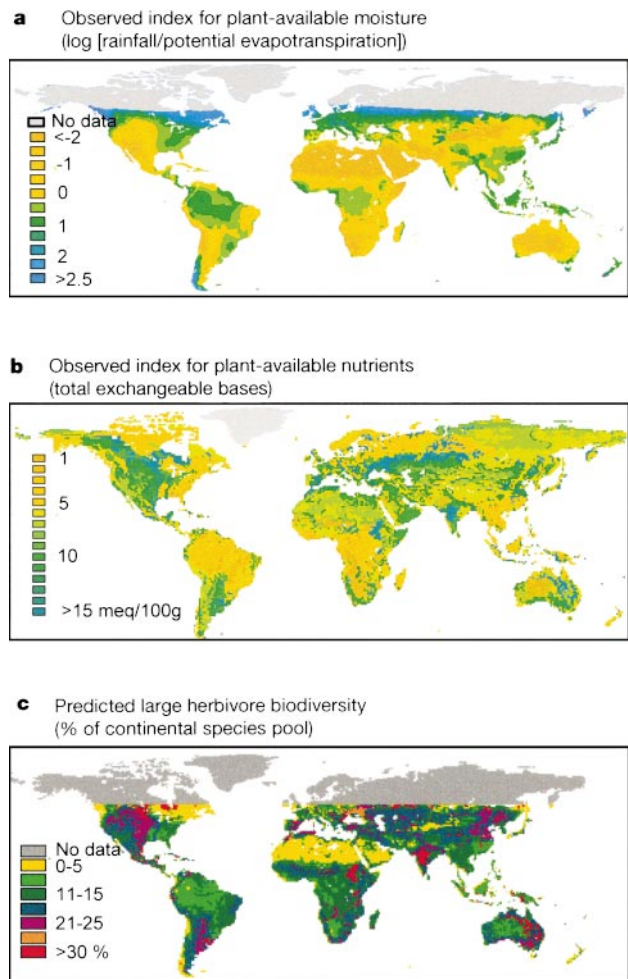


Figure 3 Global distribution of large herbivore diversity, as predicted by indices for plant-available moisture and nutrients using a regression model obtained from data for African and North American parks. **a, b**, Maps of observed water supply and soil fertility indices, respectively. **c**, Map 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	<i>t</i>	<i>P</i>
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 hotspots²⁴. Current land-use practices²⁵ 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 log₁₀ of the ratio of actual rainfall over potential evapotranspiration using published maps²⁶. 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, assigned²⁵ to 1° by 1° cells. Plant-available nutrients were assumed to be proportional to the sum of soil cations Ca²⁺, Mg²⁺, 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% × 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.

Received 28 September; accepted 6 December 2001.

- Owen-Smith, N. *Megaherbivores. The Influence of Very Large Body Size on Ecology* (Cambridge Univ. Press, Cambridge, 1988).
- Prins, H. H. T. The pastoral road to extinction: Competition between wildlife and traditional pastoralism in East Africa. *Environ. Conserv.* **19**, 117–123 (1992).
- Bell, R. H. V. in *Ecology of Tropical Savannas* (eds Huntly, B. J. & Walker, B. H.) 193–216 (Springer, Berlin, 1982).
- East, R. Rainfall, nutrient status and biomass of large African savannah mammals. *Afr. J. Ecol.* **22**, 245–270 (1984).
- McNaughton, S. J., Oesterheld, M., Frank, D. A. & Williams, K. J. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* **341**, 142–144 (1989).
- Coe, M. in *Nitrogen as an Ecological Factor* (eds Lee, J. A., McNeill, J. & Rorison, I. H.) 345–368 (Oxford, Blackwell, 1983).
- Du Toit, J. T. & Owen-Smith, N. Body size, population metabolism and habitat specialization among large African herbivores. *Am. Nat.* **133**, 736–740 (1989).
- Belovsky, G. E. Optimal foraging and community structure: The allometry of herbivore food selection and competition. *Evol. Ecol.* **11**, 641–672 (1997).
- Western, D. & Ssemakula, J. The future of savanna ecosystems: ecological islands or faunal enclaves? *Afr. J. Ecol.* **19**, 7–19 (1981).
- Huston, M. A. *Biological Diversity. The Coexistence of Species on Changing Landscapes* (Cambridge Univ. Press, Cambridge, 1994).
- Danell, K. L. P. & Niemela, P. Species richness in mammalian herbivores: patterns in the boreal zone. *Ecography* **19**, 404–409 (1996).
- Rosenzweig, M. L. *Species Diversity in Space and Time* (Cambridge Univ. Press, Cambridge, 1995).
- Prins, H. H. T. & Olfh, H. in *Dynamics of Tropical Communities* (eds Newbery, D., Prins, H. H. T. & Brown, G.) 449–489 (Blackwell Science, Oxford, 1998).
- Walker, B. H. & Langridge, J. L. Predicting savanna vegetation structure on the basis of plant available moisture (PAM) and plant available nutrients (PAN): A case study from Australia. *J. Biogeogr.* **24**, 813–825 (1997).
- Breman, H. & De Wit, C. T. Rangeland productivity and exploitation in the Sahel. *Science* **221**, 1341–1347 (1983).
- Breman, H. & Krul, J. M. in *La Productivité de Pâturages Sahéliens. Une Etude des Sols, des Végétations et de l'Exploitation de cette Ressource Naturelle* (eds Penning de Vries, F. W. T. & Djiteye, M. A.) 322–345 (Pudoc, Wageningen, 1991).
- Milchunas, D. G., Varnamkhandi, A. S., Lauenroth, W. K. & Goetz, H. Forage quality in relation to long-term grazing history, current-year defoliation, and water resource. *Oecologia* **101**, 366–374 (1995).
- Jarman, P. J. The social organization of antelope in relation to their ecology. *Behaviour* **48**, 215–267 (1974).
- Van Soest, P. J. *Nutritional Ecology of the Ruminant: Ruminant Metabolism, Nutritional Strategies, the Cellulolytic Fermentation and the Chemistry of Forages and Plant Fibres* (O & B Books, Corvallis, 1982).
- Belovsky, G. E. Generalist herbivore foraging and its role in competitive interactions. *Am. Zool.* **26**, 51–69 (1986).
- Owen-Smith, N. Pleistocene extinctions: The pivotal role of megaherbivores. *Paleobiology* **13**, 351–362 (1987).
- Eisenberg, J. F. *The Mammalian Radiations. An Analysis of Trends in Evolution, Adaptation, and Behaviour* (Athlone, London, 1981).
- Huston, M. A. Biological diversity, soils and economics. *Science* **262**, 1676–1680 (1993).
- Myers, N., Mittelmeier, R. A., Mittelmeier, C. G., da Fonseca, G. A. B. & Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000).
- Alcamo, J. *et al.* Modeling the global society-biosphere-climate system: Part 2. Computed scenarios. *Water Air Soil Poll.* **76**, 37–78 (1994).
- Murray, M. G. in *Serengeti II. Dynamics, Management and Conservation of an Ecosystem* (eds Sinclair, A. R. E. & Arcese, P.) 231–256 (Univ. Chicago Press, Chicago, 1995).
- Kinyamario, J. I. & Macharia, J.-N. M. Aboveground standing crop, protein content and dry matter digestibility of a tropical grassland range in the Nairobi National Park, Kenya. *Afr. J. Ecol.* **30**, 33–41 (1992).
- Prins, H. H. T. *Ecology and Behaviour of the African Buffalo. Social Inequality and Decision Making* (Chapman & Hall, London, 1996).
- van Wijngaarden, W. Elephants–Trees–Grass–Grazers, relationships between climate, soils, vegetation and large herbivores in a semi-arid savanna ecosystem (Tsavo, Kenya). (ITC Publication no. 4, Enschede, 1985).
- Voeten, M. M. Living with wildlife. Coexistence of wildlife and livestock in an East African savanna ecosystem. *Tropical Resource Management Papers* no. 29 (Wageningen Univ., Wageningen, 1999).

Acknowledgements

We thank E. S. Bakker, J. P. Bakker, W. J. Bond, F. S. Chapin III, G. E. Belovsky, S. J. McNaughton, D. Milchunas, N. Owen-Smith, F. J. Weissing and D. Tilman for comments; M. A. Huston for soil fertility data; and R. Leemans for temperature and rainfall data. Financial support was provided by the Dutch NWO (WOTRO and ALW), Wageningen University, the NSF, the Utah Agricultural Experiment Station, and the Utah State University Ecology Center.

Competing interests statement

The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to H.O. (e-mail: han.olff@staf.ton.wau.nl).