PLANT ECOLOGY

Worldwide evidence of a unimodal relationship between productivity and plant species richness

Lauchlan H. Fraser,[1*] Jason Pither,[2] Anke Jentsch,[3] Marcelo Sternberg,[4] Martin Zobel,[5] Diana Askarizadeh,[6] Sandor Bartha,[7] Carl Beierkuhnlein,[8] Jonathan A. Bennett,[9] Alex Bittel,[10] Bazartseren Boldgiv,[11] Ilsi I. Boldrini,[12] Edward Bork,[13] Leslie Brown,[14] Marcelo Cabido,[15] James Cahill,[9] Cameron N. Carlyle,[13] Giandiego Campetella,[16] Stefano Chelli,[16] Ofer Cohen,[4] Anna-Maria Csergo,[17] Sandra Díaz,[15] Lucas Enrico,[15] David Ensing,[2] Alessandra Fidelis,[18] Jason D. Fridley,[19] Bryan Foster,[10] Heath Garris,[20] Jacob R. Goheen,[21] Hugh A. L. Henry,[22] Maria Hohn,[23] Mohammad Hassan Jouri,[24] John Klironomos,[2] Kadri Koorem,[5] Rachael Lawrence-Lodge,[25] Ruijun Long,[26] Pete Manning,[27] Randall Mitchell,[20] Mari Moora,[5] Sandra C. Müller,[28] Carlos Nabinger,[29] Kamal Naseri,[30] Gerhard E. Overbeck,[12] Todd M. Palmer,[31] Sheena Parsons,[10] Mari Pesek,[10] Valério D. Pillar,[28] Robert M. Pringle,[32] Kathy Roccaforte,[10] Amanda Schmidt,[1] Zhanhuan Shang,[26] Reinhold Stahlmann,[8] Gisela C. Stotz,[9] Shu-ichi Sugiyama,[33] Szilárd Szentes,[34] Don Thompson,[35] Radnaakhand Tungalag,[11] Sainbileg Undrakhbold,[11] Margaretha van Rooyen,[36] Camilla Wellstein,[37] J. Bastow Wilson,[25,38] Talita Zupo[18]

The search for predictions of species diversity across environmental gradients has challenged ecologists for decades. The humped-back model (HBM) suggests that plant diversity peaks at intermediate productivity; at low productivity few species can tolerate the environmental stresses, and at high productivity a few highly competitive species dominate. Over time the HBM has become increasingly controversial, and recent studies claim to have refuted it. Here, by using data from coordinated surveys conducted throughout grasslands worldwide and comprising a wide range of site productivities, we provide evidence in support of the HBM pattern at both global and regional extents. The relationships described here provide a foundation for further research into the local, landscape, and historical factors that maintain biodiversity.

Despite a long history of research, the nature of basic patterns between environmental factors and biological diversity remain poorly defined. A notable example is the relationship between plant diversity and productivity, which has stimulated a long-running debate (*1*–*6*). A classic hypothesis, the humped-back model (HBM) (*7*), states that plant species richness peaks at intermediate productivity, taking above-ground biomass as a proxy for annual net primary productivity (*7*–*9*). This diversity peak is driven by two opposing processes. In unproductive ecosystems with low plant biomass, species richness is limited by abiotic stress, such as insufficient water and mineral nutrients, which few species are able to tolerate. In contrast, in the productive conditions that generate high plant biomass, competitive exclusion by a small number of highly competitive species is hypothesized to constrain species richness (*7*–*9*). Other mechanisms that may explain the unimodal relationship between species richness and biomass include disturbance (*7*, *10*), evolutionary history and dispersal limitation (*11*, *12*), and the reduction of total plant density in productive communities (*13*).

Since its initial proposal, a range of studies have both supported and rejected the HBM, and three separate meta-analyses reached different conclusions (*14*–*17*). Although this inconsistency may indicate a lack of generality of the HBM, it may instead reflect a sensitivity to study methodology, including the plant community types considered, the taxonomic scope, the range of site productivities sampled, the spatial grain and extent of analyses (*17*, *18*), and the particular measure of net primary productivity used (*19*). The questions therefore remain open as to what the form of the relationship between diversity and productivity is, and whether the HBM serves as a useful and general model for grassland ecosystem theory and management.

We quantified the form and the strength of the richness-productivity relationship by using globally coordinated surveys (*20*), which yielded scale-standardized data and were distributed across 30 sites in 19 countries and six continents (Fig. 1). Collectively, our samples spanned a broad range of biomass production (from 2 to 5711 g m^{-2}) and grassland community types, including natural and managed (pastures and meadows) grasslands over a wide range of climatic zones (temperate, Mediterranean, and tropical), and altitudes (lowland to alpine) (table S1). Our protocol involved sampling 64 1-m^2 quadrats within 8-m-by-8-m grids (*18*, *21*). At each site, between 2 and 14 grids were sampled, thus resulting in 128 to 896 quadrats per site. In each 1-m^2 quadrat, we identified and counted all plant species and harvested above-ground biomass and plant litter. Litter production is a function of annual net primary productivity in grasslands and can have profound effects on the structure and functioning of communities, from altering nutrient cycling to impeding vegetative growth and seedling recruitment (*22*, *23*), thereby also playing a major role in driving community structure. Indeed, the HBM was originally defined in terms of live biomass plus litter material (*7*, *8*). Most of the sites in our survey were subject to some form of management, usually livestock grazing or mowing. In this respect, our sites are representative of most of the world's grasslands. Our sampling was conducted at

[1]Department of Natural Resource Sciences, Thompson Rivers University, Kamloops, BC, Canada. [2]Department of Biology, University of British Columbia, Okanagan campus, Kelowna, BC, Canada. [3]Department of Disturbance Ecology, BayCEER, University of Bayreuth, Bayreuth, Germany. [4]Department of Molecular Biology and Ecology of Plants, Tel Aviv University, Tel-Aviv, Israel. [5]Department of Botany, Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia. [6]Faculty of Natural Resources College of Agriculture and Natural Resources, University of Tehran, Iran. [7]MTA Centre for Ecological Research, Institute of Ecology and Botany, Vácrátót, Hungary, and School of Plant Biology, University of Western Australia, Crawley, Australia. [8]Department of Biogeography, BayCEER, University of Bayreuth, Bayreuth, Germany. [9]Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada. [10]Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66047, USA. [11]Department of Biology, National University of Mongolia, Ulaanbaatar, Mongolia. [12]Department of Botany, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil. [13]Department of Agricultural, Food and Nutritional Sciences, University of Alberta, Edmonton, AB, Canada. [14]Applied Behavioural Ecology and Ecosystem Research Unit, University of South Africa, Johannesberg, South Africa. [15]Instituto Multidisciplinario de Biología Vegetal (IMBIV-CONICET) and Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, Argentina. [16]School of Biosciences and Veterinary Medicine, University of Camerino, Camerino, Italy. [17]School of Natural Sciences, Trinity College Dublin, Dublin, Ireland. [18]Departamento de Botânica, UNESP - Univ. Estadual Paulista, Rio Claro, Brazil. [19]Department of Biology, Syracuse University, Syracuse, NY 13210, USA. [20]Department of Biology, University of Akron, Akron, OH 44325, USA. [21]Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA. [22]Department of Biology, University of Western Ontario, London, ON, Canada. [23]Department of Botany, Corvinus University of Budapest, Budapest, Hungary. [24]Department of Natural Resources, Islamic Azad University, Nour Branch, Iran. [25]Department of Botany, University of Otago, Dunedin, New Zealand. [26]International Centre for Tibetan Plateau Ecosystem Management, Lanzhou University, Lanzhou, China. [27]Institute of Plant Sciences, University of Bern, Altenbergrain 21, CH-3013, Bern, Switzerland. [28]Department of Ecology, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil. [29]Faculty of Agronomy, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil. [30]Department of Range and Watershed Management, Ferdowsi University of Mashhad, Iran. [31]Department of Biology, University of Florida, Gainesville, FL 32611, USA. [32]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA. [33]Laboratory of Plant Ecology, Hirosaki University, Hirosaki, Japan. [34]Institute of Plant Production, Szent István University, Gödöllő, Hungary. [35]Agriculture and Agri-Food Canada, Lethbridge Research Centre, Lethbridge, AB, Canada. [36]Department of Plant Science, University of Pretoria, Pretoria, South Africa. [37]Faculty of Science and Technology, Free University of Bozen-Bolzano, Bolzano, Italy. [38]Landcare Research, Dunedin, New Zealand.
***Corresponding author. E-mail: lfraser@tru.ca**

least 3 months after the last grazing, mowing, or burning event and at the annual peak of live biomass, which, when coupled with litter, constitutes a reliable measure of annual net aboveground production in herbaceous plant communities (*24*).

Our results strongly support the HBM of the plant richness-productivity relationship. By using a global-extent regression model (N = 9631 1-m^2 quadrats) (*21*), we found that plant richness formed a unimodal relationship with productivity (Fig. 2A) that is characterized by a highly significant concave-down quadratic regression [negative binomial generalized linear model (GLM); Table 1]. This relationship was not sensitive to the statistical model used; the hump-backed relationship was also evident when we used a negative binomial generalized linear mixed model (GLMM) that accommodated the hierarchical structure of our sampling design (grids nested within sites; Table 1 and fig. S1).

At a sampling grain of 1 m^2, 19 of 28 site level analyses (68%) yielded significant concave-down relationships (table S2 and Fig. 2A). This contrasts markedly with the results of Adler *et al.* (*1*), who found only 1 of their 48 within-site analyses to be significantly concave-down. We also found the form of the productivity-diversity relationship to be robust to sampling grain: by using grains of 1 m^2 up to 64 m^2, each time maintaining a global extent, we consistently found a significant concave-down relationship, although the proportion of variation explained tended to decrease with increasing grain (fig. S2).

The HBM predicts a boundary condition or upper limit to diversity that, in any given site, may not be realized for a variety of reasons (*18*). Consistent with this view, our global-extent association is characterized by a significant concave-down quantile regression (95th percentile) (Table 1), below which considerable scatter exists (Fig. 2A). This pattern was also insensitive to the statistical method used; a hierarchical Bayesian analysis that accommodated the nested sampling design and that enabled both the mean and the variance of species richness to be modeled more accurately against (log-transformed) biomass also revealed a significant 95th percentile quantile regression (fig. S3). Likewise, we found a significant, concave-down quantile regression (95th percentile) between the maximum (quadrat-scale) richness found within a grid and the total biomass of the same quadrat (Table 1 and fig. S4). Each of these approaches to characterizing boundary conditions suggests the existence of a "forbidden space," wherein high productivity precludes high local diversity. Furthermore, they suggest that extremely low-productivity sites rarely accommodate high diversity.

Why do our data show a hump-backed relationship, whereas those of Adler *et al.* (*1*) and related studies (*4*, *6*), do not? One possibility is that data limitations can thwart detection of the HBM (*18*). For example, the data used by Adler *et al.* differed from ours in the following potentially important ways: (i) They exhibited a maximum live biomass of only 1535 g^{-2} (ours was 3374 g^{-2}), (ii) litter was not included within the calculation of biomass, and (iii) sample size was limited to 30 quadrats per site (ours ranged from 128 to 894 quadrats per site; table S1). We conducted a form of sensitivity analysis in which we reran our statistical analyses using random subsets of our data that were constrained to exhibit similar properties to those of the Adler *et al.* data set. Specifically, after limiting the overall data set to less than 1535 g^{-2} and excluding litter, we randomly selected 30 quadrats per site 500 times, each time conducting the within-site regression analyses (N = 30 for each of the 28 site-level GLMs conducted per subsampling iteration). For each iteration, we also calculated the average range of biomass spanned by the 28 site-level relationships. Across the 500 iterations (one example set of outcomes is shown in Fig. 2B), the average proportion of significant concave-down, within-site regressions was 0.31 ± 0.003 (SEM), significantly less than our observed proportion of 0.68 (fig. S5). Moreover, when significant concave-down relationships were detected, they tended to span a broader range of biomass than the remaining forms (including nonsignificant relationships). Specifically, in 458 of the 500 iterations (92%), the mean biomass range of the concave-down regressions was larger than the mean of the remaining forms' biomass ranges (binomial test: $P < 2.2 \times 10^{-16}$). Last, the 48 within-site analyses of Adler *et al.* spanned, on average, a live biomass range of 428.7 g^{-2} ± 38.36 (range of 89 to 1217 g^{-2}). This is (i) less than half of the average range encompassed by our 28 site-level analyses shown in Fig. 2A (mean = 1067.5 g^{-2} ± 140.63; range of 286 to 3256 g^{-2}) and (ii) almost 50% narrower than the smallest average biomass range encompassed by our 500 random subset analyses (627.4 g^{-2}) (fig. S6). Taken together, these findings

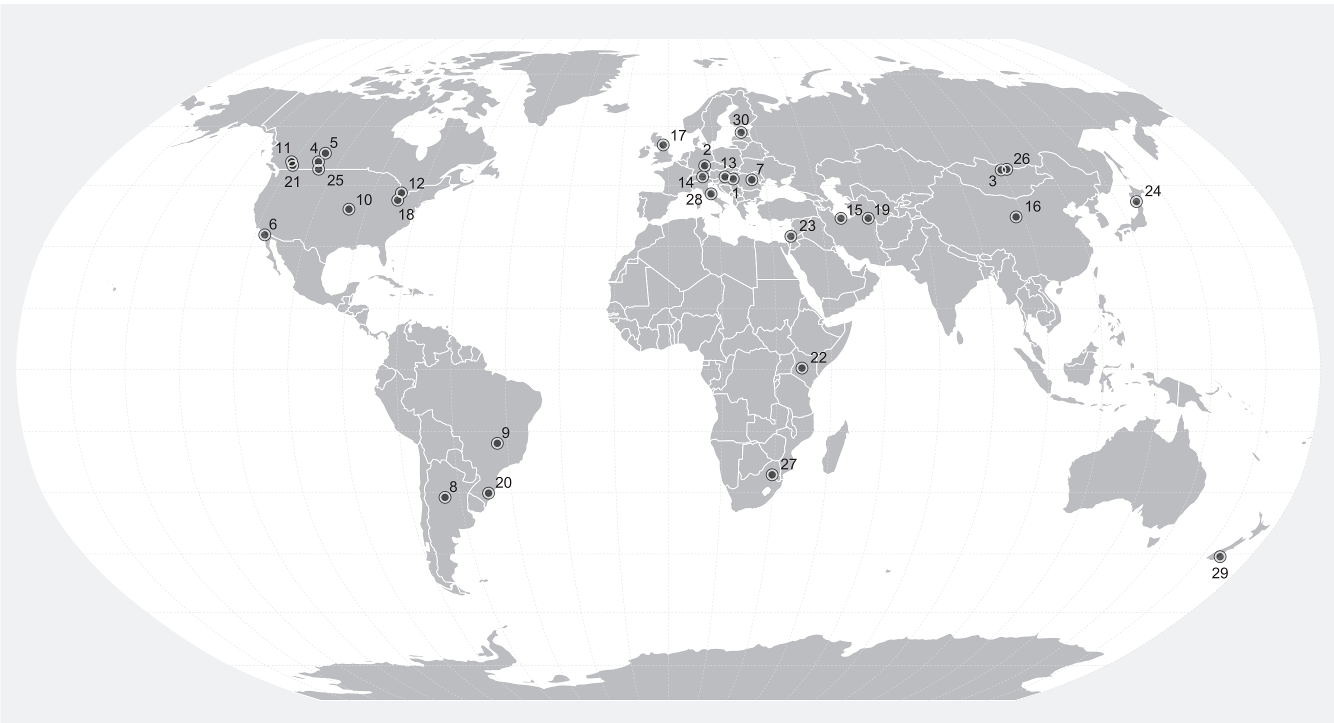

Fig. 1. Site locations. Locations of the geographic centroids of the 30 study sites, which include 151 sampling grids. Some points overlap and are therefore indistinguishable. Additional site details are provided in table S1. Map is displayed using the Robinson projection.

strongly suggest that we were able to detect more concave-down relationships because of the greater sample sizes and biomass ranges in our analysis.

It has been suggested (2) that some previous studies, including Adler *et al.* (1), failed to support the HBM because they excluded litter. Although we do find a significant concave-down relationship at the global extent using only live biomass (Table 1), a comparison of models using biomass versus biomass and litter (both N = 9,631) shows total biomass to provide a far better fit [residual deviance = 10,105 (live) versus 10,037 (total); Vuong z-statistic for comparing non-nested models: −13.4; P < 0.001]. It has also been suggested that previous surveys failed to adequately represent high-productivity communities. Indeed, our high-biomass quadrats (1011 samples were over 1000 g^{-2}, ~10% of the 9631 samples; maximum of 5711 g^{-2}) contributed considerably to the right-hand part of the fitted humped-back regression. This could be a reason why the data set of Adler *et al.* (1) (in which only 0.5% of samples were over 1000 g^{-2} with a maximum of 1534 g^{-2}) failed to support the HBM. Our results therefore show that a test of the HBM in herbaceous plant communities yields the expected pattern when it is robust and comprehensive, spans a wide range of biomass production (from 1 to at least 3000 dry g^{-2} year^{-1}), and provides sufficient replication of quadrats along the productivity gradient.

Competitive exclusion has been cited as the primary factor driving low species numbers at

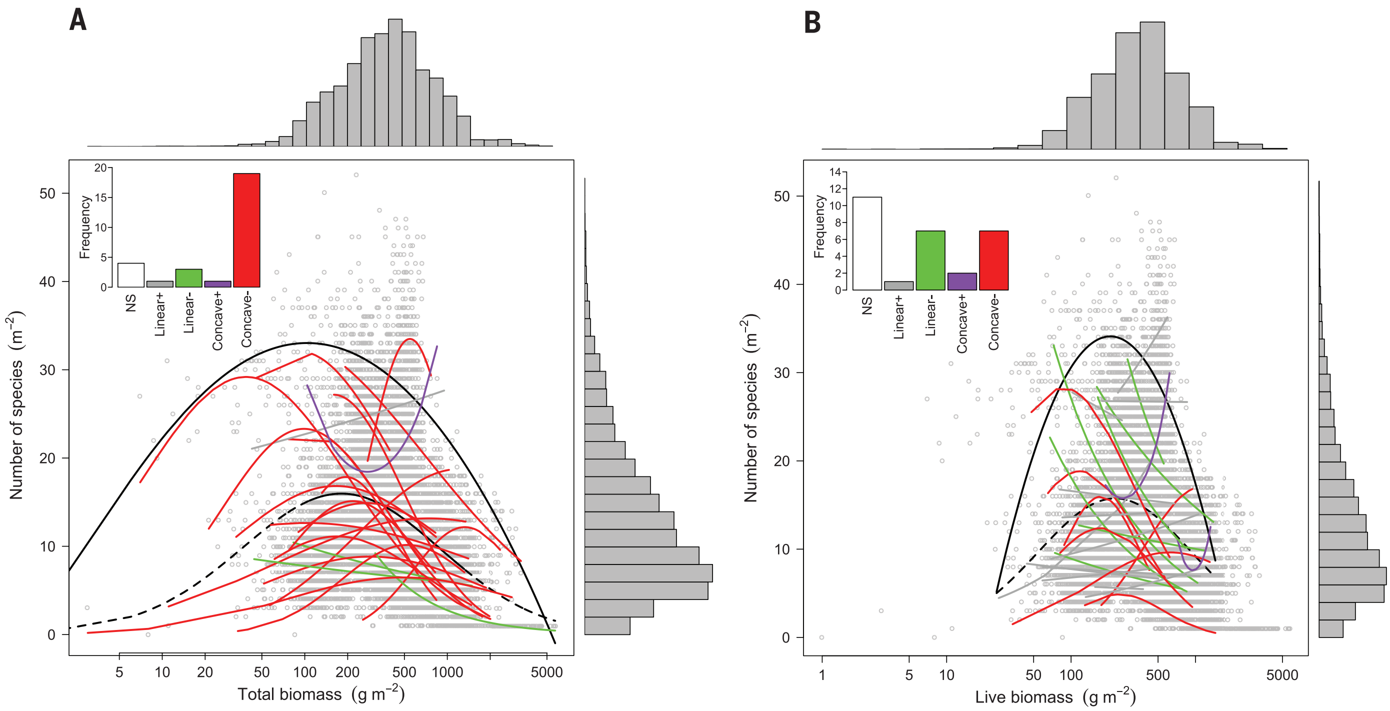

Fig. 2. Biomass production as a function of species richness. (**A**) Biomass production-species richness relationships for 28 study sites. Solid black line indicates significant quantile regression (95th percentile) of overall relationship (quadratic coefficient P < 0.001; N = 9631 quadrats). Dashed black line, significant negative binomial GLM (quadratic coefficient P < 0.001; N = 9631). Colored lines indicate significant GLM regressions (Poisson or quasi-Poisson), with N ranging from 128 to 894 quadrats. (Inset) The frequencies of each form of relationship observed across study regions. NS, not significant. (**B**) Same as (A) but the results are derived from the analysis of an example, random subsample of the complete data set that satisfies the following criteria: litter biomass excluded, quadrats with biomass >1534 g^{-2} excluded, and including 30 (randomly selected) quadrats per site (total N = 840). These criteria match the characteristics of the data set used by Adler *et al.* (1).

Table 1. Regression results. Results of regression analyses of the relationship between productivity and species richness, measured at a global extent and a sampling grain of 1-m^2 quadrat. Total biomass = live biomass + litter biomass. All linear and quadratic term coefficients were highly significant (P < 0.001).

Productivity measure	Type of regression	Sample size	Test of model fit	Intercept estimate ± SEM	Linear term coefficient ± SEM	Quadratic term coefficient ± SEM
Total biomass	negative binomial GLM (log-link function)	9631 quadrats	likelihood ratio stat. = 1602.2	−2.52 ± 0.235	4.69 ± 0.186	−1.04 ± 0.037
Total biomass	negative binomial GLMM (log-link function) random effects: grid nested in site	9631 quadrats 151 grids 28 sites	likelihood ratio stat. = 114.0	0.91 ± 0.191	1.33 ± 0.133	−0.29 ± 0.028
Total biomass	quantile (95th percentile)	9631 quadrats	pseudo-F statistic = 179.1	−12.9 ± 7.159	45.6 ± 5.833	−11.3 ± 1.173
Live biomass	negative binomial GLM (log-link function)	9644 quadrats	likelihood ratio stat. = 950.3	−2.03 ± 0.212	4.27 ± 0.178	−0.96 ± 0.037

high plant biomass (7, 8, 25). However, in the case of nitrogen addition the negative relationship between productivity and species richness has been shown to diminish over time [(26), but see (27, 28)]. It may be that low species richness in high-productivity conditions arises in part because most such habitats are anthropogenic, and there are few species in the local pool adapted to these conditions (11, 12). If so, it is possible that species will eventually immigrate from distant pools, so that the right-hand part of the hump will then flatten out.

We have shown a global-scale concave-down unimodal relationship between biomass production and richness in herbaceous grassland communities. However, the original HBM (7) is vaguely articulated by the standards of modern ecological theory, and it is clear that more work is needed to determine the underlying causal mechanisms that drive the unimodal pattern (1, 6, 17, 18). We recognize that, in our study and many others, productivity accounts for a fairly low proportion of the overall variation in richness and that many other drivers of species richness exist (28–30). Accordingly, we echo the call of Adler *et al.* (1) for additional efforts to understand the multivariate drivers of species richness.

REFERENCES AND NOTES

1. P. B. Adler *et al.*, *Science* **333**, 1750–1753 (2011).
2. J. D. Fridley *et al.*, *Science* **335**, 1441 (2012).
3. X. Pan, F. Liu, M. Zhang, *Science* **335**, 1441 (2012).
4. J. B. Grace *et al.*, *Science* **335**, 1441 (2012).
5. S. Pierce, *Funct. Ecol.* **28**, 253–257 (2014).
6. J. B. Grace, P. B. Adler, W. S. Harpole, E. T. Borer, E. W. Seabloom, *Funct. Ecol.* **28**, 787–798 (2014).
7. J. P. Grime, *J. Environ. Manage.* **1**, 151–167 (1973).
8. M. M. Al-Mufti, C. L. Sydes, S. B. Furness, J. P. Grime, S. R. Band, *J. Ecol.* **65**, 759–791 (1977).
9. Q. Guo, W. L. Berry, *Ecology* **79**, 2555–2559 (1998).
10. J. H. Connell, *Science* **199**, 1302–1310 (1978).
11. M. Zobel, M. Pärtel, *Glob. Ecol. Biogeogr.* **17**, 679–684 (2008).
12. D. R. Taylor, L. W. Aarssen, C. Loehle, *Oikos* **58**, 239–250 (1990).
13. J. Oksanen, *J. Ecol.* **84**, 293–295 (1996).
14. G. G. Mittelbach *et al.*, *Ecology* **82**, 2381–2396 (2001).
15. L. N. Gillman, S. D. Wright, *Ecology* **87**, 1234–1243 (2006).
16. M. Pärtel, L. Laanisto, M. Zobel, *Ecology* **88**, 1091–1097 (2007).
17. R. J. Whittaker, *Ecology* **91**, 2522–2533 (2010).
18. L. H. Fraser, A. Jentsch, M. Sternberg, *J. Veg. Sci.* **25**, 1160–1166 (2014).
19. B. J. Cardinale, H. Hillebrand, W. S. Harpole, K. Gross, R. Ptacnik, *Ecol. Lett.* **12**, 475–487 (2009).
20. L. H. Fraser *et al.*, *Front. Ecol. Environ* **11**, 147–155 (2013).
21. Materials and methods are available as supplementary materials on *Science* Online.
22. A. K. Knapp, T. R. Seastedt, *Bioscience* **36**, 662–668 (1986).
23. B. L. Foster, K. L. Gross, *Ecology* **79**, 2593–2602 (1998).
24. M. Oesterheld, S. J. McNaughton, in *Methods in Ecosystem Science*, O. E. Sala, R. B. Jackson, H. A. Mooney, R. Howarth, Eds. (Springer-Verlag, New York, 2000), chap. 2, pp. 151–157.
25. T. K. Rajaniemi, *J. Ecol.* **90**, 316–324 (2002).
26. F. Isbell *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **110**, 11911–11916 (2013).
27. K. N. Suding *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **102**, 4387–4392 (2005).
28. T. L. Dickson, K. L. Gross, *Oecologia* **173**, 1513–1520 (2013).
29. P. Chesson, *Annu. Rev. Ecol. Syst.* **31**, 343–366 (2000).
30. K. J. Gaston, *Nature* **405**, 220–227 (2000).

ACKNOWLEDGMENTS

We are grateful to all of the people who helped in the collection and processing of the samples, including L. Alabiso-Cahill, D. Ariunzaya, M. R. Ávila, J. C. R. Azambuja, L. Bachinger, I. Badamnyambuu, K. Baethke, J. Batbaatar, S. Ballelli, K. Bayarkhuu, G. Bertone, V. Besnyői, C. L. Bonilha, G. Boorman, R. A. X. Borges, T. Broadbent, R. Canullo, J. Carding, B. Casper, K. Castillioni, M. Cervellini, G. Charles, G. Chiara, E. Cleland, R. Cornfoot, G. Crowder, A. I. Csathó, L. Demeter, M. Demski, M. Deutschlander, S. Donnelly, A. L. P. Dresseno, S. Enkhjin, O. Enkhmandal, T. Erdenebold, L. Erdenechimeg, B. Erdenetsetseg, J. K. Fedrigo, A. C. Ferreira, Z. Foldvari, L. Fourie, B. Fraser, J. Galdi-Rosa, E. Gorgone-Barbosa, R. Greuel, A. Guido, É. György, D. Hall, A. Hassan, J. Házi, R. Henkin, S. Hoffmann, T. Jairus, M. Jankju, Ü. Jõgar, T. Jongbloets, M. Juhász, C. F. Jurinitz, V. R. Kakroudi, A. Kelemen, T. Khandarmaa, E. Khash-Erdene, C. Koch, C. Komoly, S. Kurukura, P. Liancourt, S. Lima, A. Lkhagva, M. Lucrecia Lipoma, D. Lkhagvasuren, J. Lombardi, M. Eugenia Marcotti, J. McPhee, B. McWhirter, L. Menezes, J. McCulloch, M. Mesdaghi, I. Máthé, M. Messini, M. Mistral, C. Moffat, M. Mohamed, L. Mugwedi, J. Padgham, P. Padilha, S. Paetz, S. Pagmadulam, G. Pec, C. Peconi, G. Péter, S. Piros, V. C. Pistóia, L. Pyle, M. Randall, M. Ninno Rissi, R. G. Rolim, M. Ross, T. Salarian, S. Sandagdorj, S. Sangasuren, C. Santinelli, C. Scherer, G. H. M. Silva, M. G. Silva, T. Smith, S. Solongo, F. Spada, R. Stahlmann, J. Steel, M. Sulyok, A. Sywenky, G. Szabó, L. Szabules, V. Tomlinson, J. Tremblay-Gravel, G. Ungvari, O. Urangoo, M. Uuganbayar, M. S. Viera, C. E. Vogel, D. Wallach, R. Wellstein, J. I. Withworth Hulse, and Z. Zimmermann. This work was supported in part by the Canada Research Chair Program, Canadian Foundation for Innovation (CFI), and a Natural Sciences and Engineering Research Council Discovery Grant (NSERC-DG) of Canada awarded to L.H.F., and Thompson Rivers University; a CFI and NSERC-DG awarded to J.P.; the University of Tartu, Estonia, and a European Regional Development Fund: Centre of Excellence FIBIR awarded to M.Z. and M.M.; a Hungarian National Science Foundation (OTKA K 105608) awarded to S.B.; Taylor Family-Asia Foundation Endowed Chair in Ecology and Conservation Biology and University of Mongolia's Support for High Impact Research program awarded to B.B.; the Rangeland Research Institute, University of Alberta, Canada; CONICET, Universidad Nacional de Córdoba, FONCyT, and the Inter-American Institute for Global Change Research (with support of NSF) awarded to S.D., L.E., and M.C.; a NSERC-DG awarded to J.C.; State Nature Reserve "Montagna di Torricchio" and University of Camerino, Italy; Hungarian University of Transylvania, Romania; a Fundação Grupo Boticário, Brazil (0153_2011_PR) awarded to A.F.; NSF DEB-1021158 and DEB-0950100 awarded to B.F.; UHURU: NSERC and CFI awarded to J.R.G. and the University of Wyoming; an NSERC-DG awarded to H.A.L.H.; an NSERC-DG awarded to J.K.; a National Natural Science Foundation of China grant (No. 41171417) awarded to R.L.; Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Brazil (n. 307719/2012-0) awarded to S.M.; CNPq, Brazil (grants 403750/2012-1 and 307689/2014-0) awarded to V.P.; University of Florida and a NSF DEB 1149980 awarded to T.P.; Princeton Environmental Institute and a NSF DEB 1355122 awarded to R.M.P.; a CONYCIT Becas-Chile Scholarship awarded to G.C.S. Data and R scripts associated with this paper are deposited in the Dryad repository (http://datadryad.org/).

SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/349/6245/302/suppl/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S6
Tables S1 and S2
References (31–36)

29 April 2015; accepted 15 June 2015
10.1126/science.aab3916

ICE SHEETS

Reverse glacier motion during iceberg calving and the cause of glacial earthquakes

T. Murray,[1]* M. Nettles,[2] N. Selmes,[1] L. M. Cathles,[3] J. C. Burton,[4] T. D. James,[1] S. Edwards,[5] I. Martin,[5] T. O'Farrell,[6] R. Aspey,[6] I. Rutt,[1] T. Baugé[7]

Nearly half of Greenland's mass loss occurs through iceberg calving, but the physical mechanisms operating during calving are poorly known and in situ observations are sparse. We show that calving at Greenland's Helheim Glacier causes a minutes-long reversal of the glacier's horizontal flow and a downward deflection of its terminus. The reverse motion results from the horizontal force caused by iceberg capsize and acceleration away from the glacier front. The downward motion results from a hydrodynamic pressure drop behind the capsizing berg, which also causes an upward force on the solid Earth. These forces are the source of glacial earthquakes, globally detectable seismic events whose proper interpretation will allow remote sensing of calving processes occurring at increasing numbers of outlet glaciers in Greenland and Antarctica.

One-third to one-half of Greenland's total mass loss occurs through iceberg calving at the margins of tidewater-terminating glaciers (1, 2). Recent rapid changes in glacier dynamics are associated with increased calving rates (3–5) and increased rates of glacial earthquakes (6). At large glaciers with near-grounded termini, calving typically occurs when buoyancy forces cause icebergs that are the full thickness of the glacier to capsize against the calving front (6–9). This type of calving is associated with glacial earthquakes (6, 7, 10), long-period seismic emissions of magnitude ~5 that are observed globally (11). These earthquakes have expanded northward and increased sevenfold in number during the past two decades (6, 12, 13), tracking changes in glacier dynamics, the retreat of glacier fronts, and increased mass loss (6, 14). Buoyancy-driven calving represents an increasingly important source of dynamic mass loss (6–8) as glacier fronts throughout Greenland have retreated to positions near their grounding lines (15). However, because of the difficulty of instrumenting the immediate near-terminus region of these highly active glaciers, few direct observations of the calving process are available, limiting development of the deterministic calving models required for improved understanding of controls on dynamic ice-mass loss. Detailed knowledge of the glacial earthquake source would allow quantification of calving processes for a large

Science

Worldwide evidence of a unimodal relationship between productivity and plant species richness

Lauchlan H. Fraser, Jason Pither, Anke Jentsch, Marcelo Sternberg, Martin Zobel, Diana Askarizadeh, Sandor Bartha, Carl Beierkuhnlein, Jonathan A. Bennett, Alex Bittel, Bazartseren Boldgiv, Ilsi I. Boldrini, Edward Bork, Leslie Brown, Marcelo Cabido, James Cahill, Cameron N. Carlyle, Giandiego Campetella, Stefano Chelli, Ofer Cohen, Anna-Maria Csergo, Sandra Díaz, Lucas Enrico, David Ensing, Alessandra Fidelis, Jason D. Fridley, Bryan Foster, Heath Garris, Jacob R. Goheen, Hugh A. L. Henry, Maria Hohn, Mohammad Hassan Jouri, John Klironomos, Kadri Koorem, Rachael Lawrence-Lodge, Ruijun Long, Pete Manning, Randall Mitchell, Mari Moora, Sandra C. Müller, Carlos Nabinger, Kamal Naseri, Gerhard E. Overbeck, Todd M. Palmer, Sheena Parsons, Mari Pesek, Valério D. Pillar, Robert M. Pringle, Kathy Roccaforte, Amanda Schmidt, Zhanhuan Shang, Reinhold Stahlmann, Gisela C. Stotz, Shu-ichi Sugiyama, Szilárd Szentes, Don Thompson, Radnaakhand Tungalag, Sainbileg Undrakhbold, Margaretha van Rooyen, Camilla Wellstein, J. Bastow Wilson and Talita Zupo

Science **349** (6245), 302-305.
DOI: 10.1126/science.aab3916

Grassland diversity and ecosystem productivity

The relationship between plant species diversity and ecosystem productivity is controversial. The debate concerns whether diversity peaks at intermediate levels of productivity —the so-called humped-back model—or whether there is no clear predictable relationship. Fraser *et al.* used a large, standardized, and geographically diverse sample of grasslands from six continents to confirm the validity and generality of the humped-back model. Their findings pave the way for a more mechanistic understanding of the factors controlling species diversity.

Science, this issue p. 302