Productivity Is a Poor Predictor of Plant Species Richness
Peter B. Adler, *et al.*
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Productivity Is a Poor Predictor of Plant Species Richness

Peter B. Adler,[1]* Eric W. Seabloom,[2] Elizabeth T. Borer,[2] Helmut Hillebrand,[3] Yann Hautier,[4] Andy Hector,[4] W. Stanley Harpole,[5] Lydia R. O'Halloran,[6] James B. Grace,[7] T. Michael Anderson,[8] Jonathan D. Bakker,[9] Lori A. Biederman,[5] Cynthia S. Brown,[10] Yvonne M. Buckley,[11] Laura B. Calabrese,[12] Cheng-Jin Chu,[13] Elsa E. Cleland,[14] Scott L. Collins,[11] Kathryn L. Cottingham,[15] Michael J. Crawley,[16] Ellen I. Damschen,[17] Kendi F. Davies,[18] Nicole M. DeCrappeo,[19] Philip A. Fay,[20] Jennifer Firn,[21] Paul Frater,[5] Eve I. Gasarch,[18] Daniel S. Gruner,[22] Nicole Hagenah,[23,24] Janneke Hille Ris Lambers,[25] Hope Humphries,[18] Virginia L. Jin,[26] Adam D. Kay,[27] Kevin P. Kirkman,[23] Julia A. Klein,[28] Johannes M. H. Knops,[29] Kimberly J. La Pierre,[23] John G. Lambrinos,[30] Wei Li,[5] Andrew S. MacDougall,[31] Rebecca L. McCulley,[32] Brett A. Melbourne,[18] Charles E. Mitchell,[33] Joslin L. Moore,[34] John W. Morgan,[35] Brent Mortensen,[5] John L. Orrock,[17] Suzanne M. Prober,[36] David A. Pyke,[19] Anita C. Risch,[37] Martin Schuetz,[37] Melinda D. Smith,[24] Carly J. Stevens,[38,39] Lauren L. Sullivan,[5] Gang Wang,[13] Peter D. Wragg,[2] Justin P. Wright,[40] Louie H. Yang[41]

For more than 30 years, the relationship between net primary productivity and species richness has generated intense debate in ecology about the processes regulating local diversity. The original view, which is still widely accepted, holds that the relationship is hump-shaped, with richness first rising and then declining with increasing productivity. Although recent meta-analyses questioned the generality of hump-shaped patterns, these syntheses have been criticized for failing to account for methodological differences among studies. We addressed such concerns by conducting standardized sampling in 48 herbaceous-dominated plant communities on five continents. We found no clear relationship between productivity and fine-scale (meters^{-2}) richness within sites, within regions, or across the globe. Ecologists should focus on fresh, mechanistic approaches to understanding the multivariate links between productivity and richness.

For more than three decades, ecologists have debated the role of primary productivity in regulating plant species richness at fine spatial scales (*1*, *2*). Although some studies have advocated multivariate approaches (*3*–*5*), much of the debate remains focused on evidence for a single, general relationship between productivity and richness. This classic productivity-richness relationship (PRR) is hump-shaped, with richness increasing at low to intermediate levels of productivity and decreasing at high productivity (*6*). The mechanisms invoked to explain the decreasing phase of the PRR in terrestrial plant communities have attracted the greatest controversy and include disturbance (*3*, *7*), competitive exclusion mediated by shifts in the identity or heterogeneity of limiting resources (*8*–*10*), and evolutionary history and dispersal limitation (*11*).

However, the theoretical justification for a hump-shaped PRR has been challenged (*12*), and the empirical evidence is mixed. For example, recent meta-analytical syntheses concluded that evidence for a single, canonical pattern was weak (*13*–*15*). A large percentage of studies exhibited negative, U-shaped, or nonsignificant PRRs in addition to unimodal and positive linear patterns, and the frequency of these various patterns depended on taxon and spatial scale. Subsequent critiques of the meta-analyses argued that the apparent lack of generality in PRRs might simply reflect methodological inconsistencies among the field studies (*16*, *17*). First, PRR studies vary widely in their choice of both the grain (the area of the sampling unit) and extent (the area over which sampling units are spread) (*15*, *18*). Because of the strong effects of area and heterogeneity on richness, such differences in scale confound cross-study comparisons (*19*). Second, many of the studies included in PRR meta-analyses did not measure primary production directly but used weakly related surrogates such as latitude, temperature, or altitude (*14*).

We assessed the generality of the PRR and addressed previous methodological inconsistencies by conducting standardized, observational sampling in 48 herbaceous-dominated plant communities on five continents (Fig. 1 and table S1) (*20*). We sampled plant species richness in standard 1-m^2 quadrats located in blocks of 10 plots, holding grain constant and minimizing differences in extent across sites. In addition, we used the same protocol at all sites for estimating aboveground net primary production (ANPP) as peak–growing-season live biomass, an effective measure of ANPP in herbaceous vegetation (*21*), especially when consumption by herbivores is low (fig. S1).

Previous work indicated that the form of the PRR might vary with the spatial extent of sampling. Although significant PRRs have been observed at spatial extents ranging from individual

[1]Department of Wildland Resources and the Ecology Center, Utah State University, 5230 Old Main, Logan, UT 84322, USA. [2]Department of Ecology, Evolution, and Behavior, University of Minnesota, 1987 Upper Buford Circle, St. Paul, MN 55108, USA. [3]Institute for Chemistry and Biology of the Marine Environment, University of Oldenburg, Schleusenstrasse 1, Wilhelmshaven, D-26381, Germany. [4]Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, Zurich, 8057, Switzerland. [5]Department of Ecology, Evolution and Organismal Biology, Iowa State University, 133 Bessey Hall, Ames, IA 50011, USA. [6]Department of Zoology, Oregon State University, 3029 Cordley Hall, Corvallis, OR 97331, USA. [7]U.S. Geological Survey, National Wetlands Research Center, 700 Cajundome Boulevard, Lafayette, LA 70506, USA. [8]Department of Biology, 206 Winston Hall, Wake Forest University, Box 7325 Reynolda Station, Winston-Salem, NC 27109, USA. [9]School of Forest Resources, Box 354115, University of Washington, Seattle, WA 98195–4115, USA. [10]Department of Bioagricultural Sciences and Pest Management, Colorado State University, Campus Delivery 1177, Fort Collins, CO 80523–1177, USA. [11]School of Biological Sciences, The University of Queensland, St. Lucia, Queensland, 4072, Australia. [12]Department of Biology, MSC03-2020, University of New Mexico, Albuquerque, NM 87131, USA. [13]Ministry of Education Key Laboratory of Arid and Grassland Ecology, Lanzhou University, 222 Tianshui South Road, Lanzhou, Gansu, 730000, China. [14]Ecology, Behavior and Evolution Section, University of California, San Diego, 9500 Gilman Drive 0116, La Jolla, CA 92093, USA. [15]Department of Biological Sciences, 6044 Gilman Laboratory, Dartmouth College, Hanover, NH 03755, USA. [16]Department of Biological Sciences, Imperial College London, Silwood Park, Ascot, Berks, SL5 7PY, UK. [17]Department of Zoology, University of Wisconsin, 250 North Mills Street, Madison, WI 53704, USA. [18]Department of Ecology and Evolutionary Biology, RL-1 120, University of Colorado, 1560 30th Street, Boulder, CO, 80309, USA. [19]U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 3200 Southwest Jefferson Way, Corvallis, OR 97331, USA. [20]Grassland Soil and Water Research Lab, U.S. Department of Agriculture Agricultural Research Service (USDA ARS), 808 East Blackland Road, Temple, TX 76502, USA. [21]Queensland University of Technology, School of Biogeosciences, Brisbane QLD, 4001 Australia. [22]Department of Entomology, University of Maryland, 4112 Plant Sciences Building, College Park, MD 20742, USA. [23]School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg, KwaZulu-Natal, 3209, South Africa. [24]Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520, USA. [25]Department of Biology, University of Washington, Seattle, 24 Kincaid Hall, Seattle, WA 98195, USA. [26]Agroecosystem Management Research Unit, 137 Keim Hall, USDA ARS, Lincoln, NE 68583–0937, USA. [27]Department of Biology, University of St. Thomas, 2115 Summit Avenue, St. Paul, MN 55105, USA. [28]Natural Resource Ecology Laboratory, Colorado State University, Campus Delivery 1472, Fort Collins, CO 80523, USA. [29]School of Biological Sciences, 348 Manter Hall, University of Nebraska, Lincoln, NE 68588, USA. [30]Department of Horticulture, Oregon State University, 4017 Agricultural and Life Sciences Building, Corvallis, OR 97331, USA. [31]Department of Integrative Biology, University of Guelph, Guelph, Ontario, N1G 2W1, Canada. [32]Department of Plant and Soil Sciences, N-222D Agricultural Science Center North, University of Kentucky, Lexington, KY 40546–0091, USA. [33]Department of Biology, 411 Coker Hall, University of North Carolina at Chapel Hill, Chapel Hill, NC 27599–3280, USA. [34]School of Botany, University of Melbourne, Parkville, Victoria, 3010, Australia. [35]Department of Botany, La Trobe University, Bundoora, Victoria, 3086, Australia. [36]Commonwealth Scientific and Industrial Research Organisation Ecosystem Sciences, Private Bag 5, Wembley, Western Australia, 6913, Australia. [37]Community Ecology, Swiss Federal Institute for Forest, Snow and Landscape Research, Zuercherstrasse 111, Birmensdorf, ZH, 8903, Switzerland. [38]Department of Life Sciences, The Open University, Walton Hall, Milton Keynes, Buckinghamshire, MK7 6AA, UK. [39]Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK. [40]Department of Biology, Duke University, Durham, NC 27708, USA. [41]Department of Entomology, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA.

*To whom correspondence should be addressed. E-mail: peter.adler@usu.edu

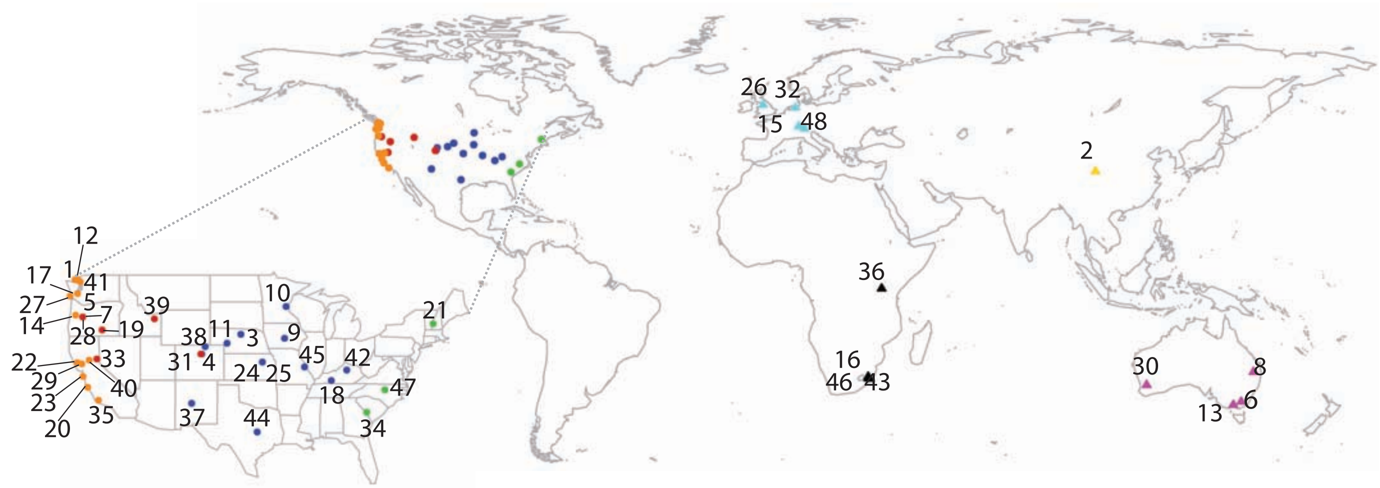

Fig. 1. Locations of the 48 Nutrient Network sites that provided data for this study. Numbers correspond to the "code" column in table S1. Colors and symbols represent the distinct biogeographic regions also shown in Fig. 3 (see Fig. 3 for key).

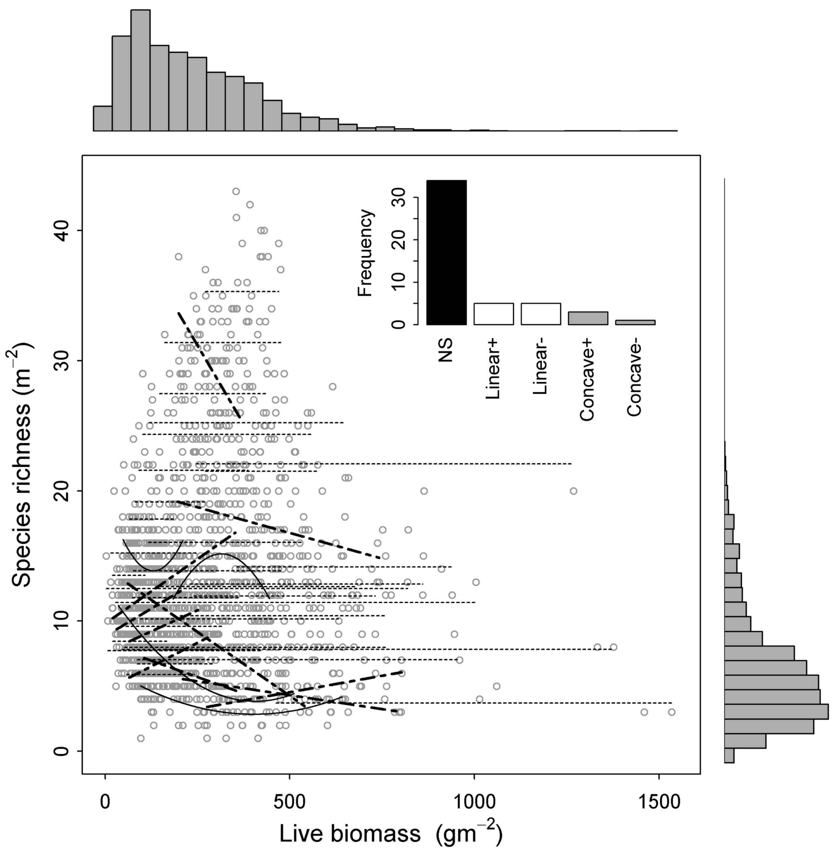

Fig. 2. Within-site relationships between productivity, measured as peak live biomass (dry weight) and species richness. The inset shows the frequencies of relationships that were nonsignificant (NS, thin dashed lines), positive or negative linear (thick dashed lines), and concave-up (+) or -down (–) (solid curves). Statistical results and separate figures for each of the 48 sites are available in table S2 and fig. S1, respectively. The marginal histograms show the frequency of species richness and peak live biomass across all sites.

plots located within one community to means of sites spread across continents, the hump-shaped pattern has emerged most frequently in studies that cross community boundaries (*14*, *22*). PRRs described within communities may be weaker because of the potential for limited variation in productivity among sampling plots as well as measurement error on individual samples (*22*) and because mechanisms involving variation in species pools and dispersal are excluded. We tested for scale-dependence by characterizing the shape of the PRR at three spatial extents: (i) The within-site extent compares richness and productivity sampled in individual plots; (ii) the regional extent compares site-level averages for 1-m^2 richness and productivity among sites occurring within a biogeographic province; and (iii) the global extent compares site-level averages for richness and productivity among all sites.

The 48 within-site PRRs took all possible shapes in parametric regressions of species richness on productivity (Fig. 2, fig. S2, and tables S2 and S3). The most common relationship was nonsignificant (34 sites), 5 sites had a positive linear pattern, 5 sites had a negative linear pattern, 3 sites were concave-up (U-shape), and 1 site was concave-down (the classical hump shape). Repeating this analysis with quasipoisson regression (*20*) gave similar results (34 nonsignificant, 5 positive linear, 6 negative linear, 2 concave-up, and 1 concave-down). We did not find factors that explained the variation in the shape of the within-site PRRs. For example, if unproductive sites had positive linear PRRs and highly productive sites had negative PRRs, then there should be a correlation between site-level productivity and the slope of the within-site linear relationship (*18*). We found no such pattern (correlation coefficient $r = 0.07$, $df = 46$, $P = 0.62$), nor were sites that spanned larger ranges in productivity more likely to show significant PRRs. Specifically, the probability of finding a non-null PRR was unrelated to the range of ANPP within a site (logistic regression $P = 0.20$).

We tested the regional relationship between site-level–average species richness (meters^{-2}) and average biomass production in the three biogeographic provinces of North America in which we had more than four sites (Fig. 3). For the 11 Pacific coast sites, located west of the Cascade/Sierra Mountain ranges and dominated by non-native species (along with one salt

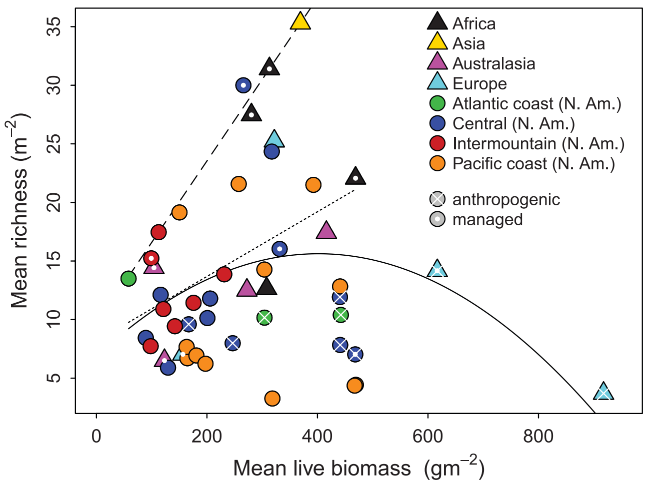

Fig. 3. Global relationship between mean productivity, measured as peak live biomass (dry weight), and mean species richness (meters^{-2}) at each site. White dots indicate managed sites (burned regularly or grazed by domestic livestock) and crosses indicate sites of anthropogenic origin (pastures, old fields, and restored prairies). The solid curve shows the quadratic relationship between productivity and richness with all sites included; the dotted line shows the linear relationship that remains when the anthropogenic sites are removed; and the dashed line shows the 0.95 quantile regression with all sites included. N. Am., North America.

marsh), there was no significant quadratic (t = –1.0, P = 0.33) or linear (t = –0.27, P = 0.79) effect of productivity on richness. Removing the highly productive salt marsh site did not change this result. Results for the seven Intermountain West sites located between the Cascade/Sierra and Rocky Mountains were similar: Neither the quadratic (t = 0.52, P = 0.63) nor linear (t = 0.14, P = 0.89) effects of productivity were significant, and removing the one site grazed by domestic livestock did not change this result. For the 13 Central Region grassland sites east of the Rockies and west of the Appalachian Mountains, we did find evidence of a hump shape, with a significant quadratic effect of productivity on richness (t = –2.35, P = 0.041). However, when we removed five sites of anthropogenic origin (restored prairies, pastures, or old fields), the quadratic term was no longer significant (t = –0.177, P = 0.87), whereas the linear term was significant (t = 2.5, P = 0.046).

At the global extent (Fig. 3), the quadratic effect of productivity on richness was significant (t = –2.39, P = 0.021). However, this hump-shaped model, which ignored uncertainty in estimates of site means, explained little variation in average species richness (coefficient of determination R^2 = 0.11). Furthermore, the pattern was sensitive to land-use history. When we removed nine sites of anthropogenic origin and the one salt marsh, the quadratic effect was no longer significant (t = –1.36, P = 0.18), but a positive linear effect was significant (t = 2.61, P = 0.013).

An alternative hypothesis states that productivity sets the upper limit on richness, with stochastic forces such as disturbance causing deviations below this limit (*3*, *23*). We tested for a hump-shaped constraint on maximum richness by conducting quantile regressions on our data at within-site and global extents (we did not have sufficient data to address the regional extent). At the within-site extent, results for the 0.95 quantile regressions were similar to our standard regression analysis, with 39 nonsignificant tests, 2 positive linear, 5 negative linear, 1 concave-up, and 1 concave-down pattern (fig. S2). The use of lower quantiles (0.7, 0.8, 0.9) generated fewer significant PRRs. At the global extent (Fig. 3), the quadratic effect was not significant (t = –1.63, P = 0.11); instead, a positive linear trend emerged (t = 2.19, P = 0.034). Testing the relationship between mean productivity at a site and maximum richness observed at that site (fig. S3) produced a similar nonsignificant quadratic effect (t = –1.50, P = 0.14) and marginally significant linear effect (t = 2.01, P = 0.051).

Overall, we found no consistent, general relationship between productivity and richness of herbaceous-dominated plant communities at the local, regional, or global extent. When we used both standard and quantile regressions, nonsignificant relationships were most common. Although linear or hump-shaped patterns occurred in particular cases, no strong correlates explained these idiosyncrasies. Furthermore, consideration of land-use history and management changed the form of the regional and global scale relationships. Despite using consistent and appropriate data-collection methods, our results show even less support for a general PRR than did previous synthesis efforts based on meta-analysis (*13*–*15*), indicating that inadequate or noncomparable data are not the explanation for the lack of a general PRR.

If theory provided a strong prediction for the form of the PRR, then deviations from the expected pattern would be informative. However, ecologists have proposed many competing models that predict every form of the PRR (*12*). Furthermore, recent work has emphasized that productivity does not have a direct, mechanistic effect on fine-scale species richness, but rather a complex set of interactions links the two variables (*5*, *24*). For example, productivity and richness each respond to the supply rate as well as the stoichiometry of resources (*25*–*27*), with variation in these factors leading to different forms of the PRR. In addition, richness may respond more strongly to disturbance, habitat heterogeneity, and biogeographic and assembly history (*3*, *11*, *28*–*30*) than to productivity. Finally, richness is not simply a function of productivity but it may feed back to influence productivity (*31*). The weak and variable PRRs we found are consistent with these hypotheses.

Rather than investing continued effort in attempting to identify a general PRR, ecologists should focus on more sophisticated approaches already available for investigating the complex, multivariate processes that regulate both productivity and richness (*5*, *25*, *26*). Coordinated, global networks represent a research approach that will be invaluable not only for addressing longstanding debates about the generality of empirical patterns but also for testing the underlying mechanisms.

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Supporting Online Material
www.sciencemag.org/cgi/content/full/333/6050/1750/DC1
Materials and Methods
Figs. S1 to S3
Tables S1 to S3
References (*32*–*34*)

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African Wild Ungulates Compete with or Facilitate Cattle Depending on Season

Wilfred O. Odadi,[1]* Moses K. Karachi,[2] Shaukat A. Abdulrazak,[3] Truman P. Young[1,4]*

Savannas worldwide are vital for both socioeconomic and biodiversity values. In these ecosystems, management decisions are based on the perception that wildlife and livestock compete for food, yet there are virtually no experimental data to support this assumption. We examined the effects of wild African ungulates on cattle performance, food intake, and diet quality. Wild ungulates depressed cattle food intake and performance during the dry season (competition) but enhanced cattle diet quality and performance during the wet season (facilitation). These results extend our understanding of the context-dependent–competition-facilitation balance, in general, and are critical for better understanding and managing wildlife-livestock coexistence in human-occupied savanna landscapes.

Savannas cover ~20% of the global land surface and occur more extensively in Africa than in any other continent (*1*). These ecosystems vitally support large proportions of the world's human, livestock, and wildlife populations (*1*). In savannas worldwide—and especially in the ungulate-rich African savannas (*2*)—domestic and wild herbivores commonly share food and other resources. Such sharing of habitat by guilds of herbivores can result in varied interactions ranging from negative (competition) to positive (facilitation) (*3*).

In savanna rangelands worldwide, management decisions are based on the supposition that wild fauna and domestic stock compete for forage resources, but there are little experimental data to support this assumption. For competition to occur, a shared resource must be in short supply, and its joint exploitation by two or more herbivore species must lead to reduced performance (such as survivorship, fecundity, or weight gain) of at least one species (*3*). Although changes in several factors—including food availability, quality, and intake—can alter herbivore performance, a change in one or more of these factors without an effect on performance of the species involved is not in itself evidence of competition (*3*).

The food habits of domestic and wild ungulates—and dietary overlap between these herbivore guilds—have been studied widely (*4*–*7*). In addition, the effects of wildlife on livestock food habits and foraging patterns have been documented (*8*, *9*). However, the critical assessment of whether or not wild ungulates alter livestock performance has rarely been carried out, and never in a tropical savanna biome. Yet, such an appraisal is urgently needed to guide management efforts toward enhancing wildlife-livestock coexistence in human-occupied landscapes, especially in the African savanna biome, which hosts the last remnants of an intact large herbivore fauna.

We used a controlled replicated experiment to assess whether or not medium-sized wild ungulates (>20 kg; plains zebra *Equus burchelli*, Grevy's zebra *E. grevyi*, African buffalo *Syncerus caffer*, eland *Tragelaphus oryx*, hartebeest *Acelaphus buselaphus*, oryx *Oryx gazella*, and Grant's gazelle *Gazella granti*) and megaherbivores (African elephant *Loxodonta africana* and giraffe *Giraffa camelopardalis*) compete with cattle in a savanna ecosystem in Kenya. Specifically, we hypothesized that if these ungulates compete with cattle, food availability and quality should decrease in the shared foraging areas, resulting in reductions in food intake, diet quality, and most importantly, weight gain of cattle. Additionally, we hypothesized that these effects would reduce after experimental exclusion of megaherbivores, especially elephants, because of their documented seasonal resource overlap with cattle (*10*). Last, we expected greater competitive effects during the dry season, when food is less abundant.

We compared cattle weight gain, organic matter food intake (OMI), diet selection, dietary digestible organic matter (DOM), crude protein (CP), DOM/CP ratio, and herbage cover in treatment plots that cattle accessed exclusively and those they shared with wild ungulates, excluding or including megaherbivores, during wet and dry seasons (*11*). Consistent with our hypothesis, cattle experienced depressed weight gain when they shared foraging areas with wild herbivores during the dry season (Fig. 1A), providing evidence of competition. In contrast, this pattern was reversed in the wet season, with increased cattle performance in the shared treatments (Fig. 1B), demonstrating a surprising facilitative interaction that was nearly great enough to overcome the preceding season's competition.

Competition was associated with depressed food intake in the shared treatments (Table 1), which corresponded with reductions in cover and selection by cattle of *Pennisetum stramineum* (Fig. 2, A to C), suggesting that wildlife and cattle competed for this grass. For all other major herbaceous species, cover was not significantly different among herbivore treatments (table S1). Relative bites on *Themeda triandra* increased in the treatment accessible to all three guilds of herbivores during wet season, but no other major plant species showed treatment effects on either relative bites or selection by cattle (tables S2 and

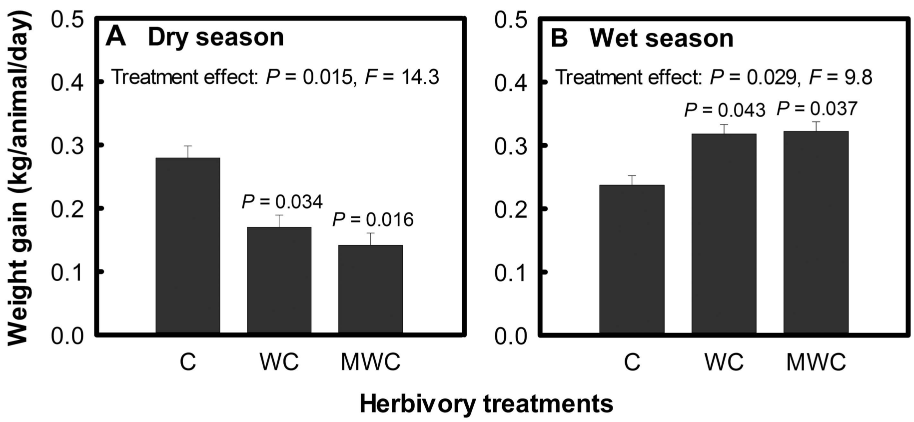

Fig. 1. Weight gain of cattle within treatment plots they accessed exclusively (C) and those they shared with wild herbivores, with megaherbivores absent (WC) or present (MWC). (**A**) During dry season. (**B**) During wet season. Error bars are SEM (n = 3 experimental blocks). The P values over the WC and MWC treatments are for comparisons with treatment C (Tukey's post hoc test).

[1]Mpala Research Centre, Post Office Box 555, Nanyuki 10400, Kenya. [2]Natural Resources Department, Egerton University, Post Office Box 536, Egerton 20115, Kenya. [3]National Council for Science and Technology, Post Office Box 30623, Nairobi 00100, Kenya. [4]Department of Plant Sciences, University of California, Davis, CA 95616, USA.

*To whom correspondence should be addressed. E-mail: woodadie@yahoo.com (W.O.O.); tpyoung@ucdavis.edu (T.P.Y.)