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Change in dominance determines herbivore effects on plant biodiversity

Sally E. Koerner^{1*Φ}, Melinda D. Smith^{2 Φ}, Deron E. Burkepile^{3 Φ}, Niall P. Hanan^{4 Φ}, Meghan L. Avolio^{5 Φ}, Scott L. Collins^{6 Φ}, Alan K. Knapp^{2 Φ}, Nathan P. Lemoine^{2 Φ}, Elisabeth J. Forrestel^{7 Φ}, Stephanie Eby^{8 Φ}, Dave I. Thompson^{9,10 Φ}, Gerardo Aguado-Santacruz¹¹, John P. Anderson¹², Michael Anderson¹³, Ayana Angassa¹⁴, Sumanta Bagchi¹⁵, Elisabeth S. Bakker¹⁶, Gary Bastin¹⁷, Lauren E. Baur⁶, Karen H. Beard¹⁸, Erik A. Beever¹⁹, Patrick J. Bohlen²⁰, Elizabeth H. Boughton²¹, Don Canestro²², Ariela Cesa²³, Enrique Chaneton²⁴, Jimin Cheng²⁵, Carla M. D'Antonio²⁶, Claire Deleglise²⁷, Fadiala Dembélé²⁸, Josh Dorrough²⁹, David Eldridge³⁰, Barbara Fernandez-Going³¹, Silvia Fernández-Lugo³², Lauchlan H. Fraser³³, Bill Freedman³⁴, Gonzalo Garcia-Salgado³⁵, Jacob R. Goheen³⁶, Liang Guo²⁵, Sean Husheer³⁷, Moussa Karembé³⁸, Johannes M. H. Knops³⁹, Tineke Kraaij⁴⁰, Andrew Kulmatiski¹⁸, Minna-Maarit Kytöviita⁴¹, Felipe Lezama⁴², Gregory Loucougaray²⁷, Alejandro Loydi⁴³, Dan G. Milchunas⁴⁴, Sue Milton⁴⁵, John W. Morgan⁴⁶, Claire Moxham⁴⁷, Kyle C. Nehring⁴⁸, Han Olf⁴⁹, Todd M. Palmer⁵⁰, Salvador Rebollo⁵¹, Corinna Riginos⁵², Anita C. Risch⁵³, Marta Rueda⁵⁴, Mahesh Sankaran^{55,56}, Takehiro Sasaki⁵⁷, Kathryn Schoenecker⁵⁸, Nick L. Schultz⁵⁹, Martin Schütz⁵³, Angelika Schwabe⁶⁰, Frances Siebert⁶¹, Christian Smit⁶², Karen A. Stahlheber⁶³, Christian Storm⁶⁰, Dustin J. Strong⁶⁴, Jishuai Su⁶⁵, Yadugiri V. Tiruvaimozhi⁵⁶, Claudia Tyler⁶⁶, James Val⁶⁷, Martijn L. Vandegehuchte^{53,68}, Kari E. Veblen¹⁸, Lance T. Vermeire⁶⁴, David Ward⁶⁹, Jianshuang Wu⁷⁰, Truman P. Young^{71,72}, Qiang Yu⁷³, Tamara Jane Zelikova⁷⁴

¹Department of Biology, University of North Carolina Greensboro, Greensboro, NC 27412,

USA

²Department of Biology and Graduate Degree Program in Ecology, Colorado State

University, Fort Collins, CO 80523, USA

³Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, Santa Barbara, CA 93016, USA

⁴Jornada LTER Program & Plant and Environmental Sciences Department, New Mexico State University, Las Cruces, NM 88003, USA

⁵Department of Earth and Planetary Sciences, John Hopkins University, Baltimore, MD 21218, USA

⁶Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA

⁷Department of Viticulture and Enology, University of California, Davis, Davis, CA 95616, USA

⁸Department of Marine and Environmental Sciences, Northeastern University, Boston MA 02115, USA

⁹South African Environmental Observation Network, Ndlovu Node, Scientific Services, Kruger National Park, Private Bag X1021, Phalaborwa 1390, South Africa

¹⁰School of Geography, Archaeology, and Environmental Studies, University of the Witwatersrand, Private Bag 3 WITS 2050, South Africa

¹¹Tecnológico Nacional de México/I.T. Roque, Carretera Celaya-Juventino Rosas Km. 8, Celaya, Gto. 38110, Mexico

¹²Jornada Basin LTER Program, New Mexico State University, Las Cruces, NM 88003, USA

¹³Wake Forest University, Department of Biology, 049 Winston Hall, Winston-Salem, NC 27109, USA

¹⁴Hawassa University, School of Animal and Range Sciences, Awassa, Ethiopia and Botswana University of Agriculture and Natural Resources, Gaborone, Botswana

- ¹⁵Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012, India
- ¹⁶Department of Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW),
Droevendaalsesteeg 10, 6708 PB Wageningen, The Netherlands
- ¹⁷Retired, PO Box 2886, Alice Springs NT 0871, Australia
- ¹⁸Department of Wildland Resources and Ecology Center, Utah State University, Logan, UT
84322, USA
- ¹⁹U.S. Geological Survey, Northern Rocky Mountain Science Center & Department of
Ecology, Montana State University, Bozeman, MT 59715, USA
- ²⁰Department of Biology, University of Central Florida, Orlando, FL 32816, USA
- ²¹Archbold Biological Station, MacArthur Agro-ecology Research Center, 123 Main Drive,
Venus, FL 33960, USA
- ²²UCSB Ken Norris Rancho Marino Reserve, 393 Ardath Dr., Cambria, CA 93428, USA
- ²³INTA Cuenca del Salado, Av. Belgrano 416, 7203 Rauch, Prov. de BsAs., Argentina,
grupo de Producción Vegetal.
- ²⁴IFEVA-CONICET, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín
4453, 1417 Buenos Aires, Argentina
- ²⁵State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau,
Northwest A&F University, Yangling 712100, China
- ²⁶Environmental Studies, University of CA, Santa Barbara 93106, USA
- ²⁷Université Grenoble Alpes, Irstea, UR LESSEM, 2 rue de la Papeterie-BP 76, F-38402 St-
Martin-d'Hères, France
- ²⁸Institut Polytechnique Rural / Institut de Formation et de Recherche Appliquée (IPR/IFRA),
Katibougou, Mali

- ²⁹Ecosystem Management Science, Science Division, NSW Office of Environment and Heritage, Merimbula , NSW, Australia
- ³⁰Centre for Ecosystem Studies, School of Biological, Earth and Environmental Sciences, University of NSW, Sydney, 2052, Australia
- ³¹Brackenridge Field Laboratory, University of Texas, Austin 78702, USA
- ^{32a} Island Ecology and Biogeography Group, Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias (IUETSPC), Universidad de La Laguna (ULL), Avda. Astofísico Francisco Sánchez s/n, La Laguna 38206, Canary Islands, Spain
- ³³Department of Natural Resource Sciences, Thompson Rivers University, Kamloops, BC, V2C0C8, Canada
- ³⁴Department of Biology, Dalhousie University, Halifax, Nova Scotia, B3H4R2, Canada
- ³⁵Department of Life Sciences, Alcalá University, Alcalá de Henares, 28805, Spain
- ³⁶Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA
- ³⁷New Zealand Forest Surveys, 15 McElwee Street, Napier, New Zealand
- ³⁸Université des Sciences, des Techniques et des Technologies (USTTB), Bamako, Mali
- ³⁹School of Biological Sciences, University of Nebraska, Lincoln, NE 68588, USA
- ⁴⁰School of Natural Resource Management, Nelson Mandela University, George, 6539, South Africa
- ⁴¹University of Jyväskylä, Department of Biological and Environmental Sciences, P.O. Box 35, FI-40014, University of Jyväskylä, Finland
- ⁴²Facultad de Agronomía, Universidad de la República. Av. Garzón 780, Montevideo, Uruguay

- ⁴³CERZOS-CONICET and DBByF, UNS. Camino La Carrindanga Km 7, Bahía Blanca,
Argentina
- ⁴⁴Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO, USA
(retired, current address PO Box 943, LaPorte CO 80535)
- ⁴⁵South African Environmental Observation Network (SAEON): Arid Lands Node, PO Box
47, Prince Albert 6930, South Africa
- ⁴⁶Department of Ecology, Environment and Evolution, La Trobe University, Bundoora 3086,
Victoria, Australia
- ⁴⁷Arthur Rylah Institute, Department of Environment, Land, Water and Planning, PO Box
137 Heidelberg 3084, Victoria, Australia
- ⁴⁸Dept. of Wildland Resources and Ecology Center, Utah State University, Logan, UT
84322, USA
- ⁴⁹Groningen Institute for Evolutionary Life Science, University of Groningen, PO Box
11103, 9700 CC Groningen, The Netherlands
- ⁵⁰Department of Biology, University of Florida, Gainesville, FL 32601, USA
- ⁵¹Department of Life Sciences, Alcala University, Alcalá de Henares, 28805, Spain
- ⁵²The Nature Conservancy, 258 Main Street, Lander, WY 82520, uSA
- ⁵³Research Unit Community Ecology, Swiss Federal Institute for Forest, Snow and
Landscape Research, Zürcherstrasse 111, CH-890 Birmensdorf, Switzerland
- ⁵⁴Department of Conservation Biology, Estación Biológica de Doñana CSIC, Calle Américo
Vespucio s/n, E-41092 Sevilla, Spain
- ⁵⁵School of Biology, University of Leeds, Leeds LS2 9JT, UK

- ⁵⁶National Centre for Biological Sciences, Tata Institute of Fundamental Research, GKVK Campus, Bellary Road, Bangalore 560065, India
- ⁵⁷Graduate School of Environment and Information Sciences, Yokohama National University, 79-7 Tokiwadai, Hodogaya, Yokohama 240-8501, Japan
- ⁵⁸U.S. Geological Survey, Fort Collins Science Center, and Colorado State University, Fort Collins, CO 80523, USA
- ⁵⁹School of Applied and Biomedical Science, Federation University, Ballarat 3353, Victoria, Australia
- ⁶⁰Department of Biology, Technische Universität Darmstadt, Schnittspahnstr. 10, 64287 Darmstadt, Germany
- ⁶¹Unit for Environmental Sciences and Management, North-West University, 11 Hoffman Street, Potchefstroom 2531, South Africa
- ⁶²Groningen Institute for Evolutionary Life Sciences, University of Groningen, PO Box 11103, Nijenborg 7, 9700 CC, Groningen, The Netherlands
- ⁶³University of Wisconsin Green Bay, Natural and Applied Sciences, 2420 Nicolet Dr. Green Bay WI 54311-7001, USA
- ⁶⁴USDA-ARS, Fort Keogh Livestock and Range Research Laboratory, Miles City, MT 59301, USA
- ⁶⁵College of Animal Science and Technology, Northwest A&F University, Yangling 712100, China
- ⁶⁶Earth Research Institute, University of California, Santa Barbara, CA 93106, USA
- ⁶⁷Office of Environment and Heritage, NSW, 32 Enterprise Way, Buronga, Australia

⁶⁸Terrestrial Ecology Unit, Department of Biology, Ghent University, K. L. Ledeganckstraat
35, 9000 Ghent, Belgium

⁶⁹Department of Biological Sciences, Kent State University, Kent OH 44242, USA

⁷⁰Lhasa National Ecological Research Station, Key Laboratory of Ecosystem Network
Observation and Modelling, Institute of Geographic Sciences and Natural Resources
Research, Chinese Academy of Sciences, Beijing 100101, China

⁷¹Department of Plant Sciences, University of California, Davis, CA 95616 USA,

⁷²Mpala Research Centre, P.O. Box 555, Nanyuki, Kenya

⁷³National Hulunber Grassland Ecosystem Observation and Research Station / Institute of
Agricultural Resources and Regional Planning, Chinese Academy of Agricultural
Sciences, Beijing 100081, China

⁷⁴Department of Botany, University of Wyoming, 1000 E. University Ave, Laramie WY
82071, USA

*Correspondence author. E-mail: Sally.Koerner@uncg.edu

^ΦGrazing Exclosure working group member

Herbivores alter plant biodiversity (species richness) in many of the world's ecosystems, but the magnitude and the direction of herbivore effects on biodiversity vary widely within and among ecosystems. One current theory predicts that herbivores enhance plant biodiversity at high productivity but have the opposite effect at low productivity. Yet, empirical support for the importance of site productivity as a mediator of these herbivore impacts is equivocal. Here, we synthesize data from 252 large-herbivore exclusion studies, spanning a 20-fold range in site productivity, to test an alternative hypothesis - that herbivore-induced changes in the competitive environment determine the response of plant biodiversity to herbivory irrespective of productivity. Under this hypothesis, when herbivores reduce the abundance (biomass, cover) of dominant species (e.g., because the dominant plant is palatable), additional resources become available to support new species, thereby increasing biodiversity. By contrast, if herbivores promote high dominance by increasing the abundance of herbivory-resistant, unpalatable species, then resource availability for other species decreases reducing biodiversity. We show that herbivore-induced change in dominance, independent of site productivity or precipitation (a proxy for productivity), is the best predictor of herbivore effects on biodiversity in grassland and savanna sites. Given that most herbaceous ecosystems are dominated by one or a few species, altering the competitive environment via herbivores or by other means may be an effective strategy for conserving biodiversity in grasslands and savannas globally.

Consumers play a critical role in determining the structure and functioning of most ecosystems¹. However, human activities have greatly altered top-down control by consumers with consequences for biodiversity and other ecosystem services not yet fully understood¹. In part,

this uncertainty arises because effects of consumers on biodiversity are highly variable in both aquatic and terrestrial ecosystems²⁻⁷. One theory predicts that the effects of herbivores on biodiversity (species richness, the number of species) vary with ecosystem productivity^{2,4,5,7-10}. In more productive systems, herbivory is expected to reduce the abundance of dominant species and increase biodiversity⁷. Dominant species often impact community structure¹¹, including species biodiversity, by monopolizing resources. Decreased dominance can be directly linked to increased availability of resources, including light, nutrients and water, leading to increased abundance of less common species, colonization by new species, and/or a decrease in local species extinctions⁷. In contrast, at low productivity, herbivores are predicted to decrease biodiversity by either 1) increasing dominance by grazing-tolerant species, which may reduce colonization rates or enhance extinctions of other species, or 2) not affecting dominance if species are unpalatable, but instead increasing extinctions of rare palatable species via consumption⁷. Collectively, these processes may result in a positive relationship between biodiversity and productivity with herbivory. However, deviations from this pattern are common, particularly in herbaceous plant communities (e.g.,^{7,12-14}). These discrepancies call into question the generality of productivity as a mediator of herbivore effects on biodiversity via the dominance mechanism. Indeed, high levels of plant community dominance are found in both high¹⁵ and low¹⁶ productivity systems, which suggests that changes in dominance may impact biodiversity directly and *irrespective* of productivity.

Here, we test for how changes in dominance determine biodiversity responses to herbivory, and whether this dominance mechanism is mediated by site productivity. We synthesized data from 252 grassland and savanna sites (Fig. 1; Supplementary Table 1-3) that includes 1,212 plots

sampled inside and outside of large-herbivore exclosures. These sites encompassed a broad range of environmental conditions across six biogeographic realms¹⁷. This dataset included measures of plant community composition from all sites and aboveground net primary productivity (ANPP) from half the sites, as well as a number of herbivore community and site characteristics (see Methods). To quantify herbivore-induced changes in biodiversity, we calculated the log response ratio ($\ln(G/UG)$) of plant species richness (average number of species per plot) outside (grazed, G) vs. inside (ungrazed, UG) exclosures. We used two common dominance metrics – Berger-Parker Dominance and Simpson’s Dominance¹⁸ – to evaluate changes in dominance with herbivory. Change of both metrics was calculated using log response ratios. We picked these two measures of dominance as both are robust to changes in richness at levels encompassed by our datasets (>5 ; ^{18,19}), and thus can vary independently of richness. Berger-Parker Dominance is a measure of the relative cover of the most abundant species agnostic of species identity, while Simpson’s Dominance is a measure of diversity that is highly sensitive to abundant species²⁰. We chose to focus on the Berger-Parker metric due to its simplicity and its mathematical independence from richness. However, Simpson’s Dominance, while more complicated, is a metric that can capture co-dominance by two or more species¹⁸. The inclusion of the Simpson’s Dominance metric in our analyses (see Supplementary Information) allowed us to examine the robustness of the patterns observed with the Berger-Parker dominance metric.

Results

Consistent with previous theory and several empirical studies^{2,8,9,13}, we found a positive relationship between changes in species richness in response to herbivores and ANPP, but the amount of variation explained was low (Fig. 2a). Contrary to theory, herbivory did not decrease

species richness at low productivity. Instead, herbivory had, on average, either neutral or positive effects on richness across the entire 20-fold range in ANPP. Because not all studies in our dataset measured ANPP, we used mean annual precipitation (MAP) as an ANPP proxy. This was possible due to the relationship between MAP and ANPP in our dataset (linear regression: $R^2=0.21$, $p < 0.001$, $F\text{-stat}_{106} = 27.63$) as well as in grasslands and savannas globally^{20,21}. Even with this expanded dataset, richness responses were poorly related to MAP (Fig. 2b), consistent with the weak relationship observed for ANPP.

In contrast to the equivocal support for productivity influencing richness responses, we found a strong negative relationship between herbivore-induced changes in Berger-Parker dominance and the effect of herbivores on species richness (Fig. 2c). As predicted, when herbivores decreased dominance thereby reducing competition, species richness increased, but when herbivores increased dominance, thereby increasing the strength of competition, richness declined. Negative relationships between species richness and dominance are common (e.g.,^{11,12,22}), and this relationship was evident in both grazed and ungrazed plots in our data set as well (Fig. 2d). These patterns were even stronger when using Simpson's Dominance (Supplementary Figure 2; $r^2=0.192$ for BP Dominance and $r^2=0.299$ for S Dominance) suggesting that changes in co-dominance may be important in many of these grazing systems. Given this relationship and because we used measures of dominance that are mathematically independent of richness¹⁸, this suggests that changes in dominance can be causally linked to biodiversity responses to herbivory. Changes in Berger-Parker Dominance in response to grazing were not significantly related to either ANPP (Supplementary Figure 1a) or precipitation (Supplementary Figure 1b), suggesting

this pattern is independent of site productivity. Similarly, changes in Simpson's Dominance due to grazing were also not significantly related to ANPP or precipitation (Supplementary Figure 3).

Although univariate approaches can be informative, both productivity and change in dominance could jointly influence the biodiversity response to herbivory. Therefore, we utilized path analysis²³ to assess whether productivity mediates the effect of change in dominance on the richness responses to herbivory. Our *a priori* model included additional non-mutually exclusive factors that could influence the relationship between herbivory and species richness⁷, such as characteristics of the herbivore community (estimates of herbivore pressure, herbivore species richness, if herbivores were domesticated or not, and if browsers/mixed feeders were present in addition to grazers), the plant community (size of the species pool), and the duration of herbivore exclusion. See Methods for further detail. These metrics allowed us to explicitly contrast the effects of site-level productivity vs. change in dominance on the richness response to herbivory and include other factors that may affect both dominance and richness responses. We examined six alternative models (Fig. 3 & Supplementary Figure 4) to explicitly contrast the effects of changes in ANPP vs. dominance on the biodiversity response to grazing.

Our first model examined the widely-hypothesized relationship between precipitation, site productivity, and change in species richness (Fig. 3 – Model 1). This model also included characteristics of the herbivore community and the plant community (site-level richness) as well as accounted for correlations between input variables (Supplementary Table 4). Because productivity was not available from all sites, this initial model was limited to data from the 122 sites where ANPP was measured directly (see Methods; Data Subset 1 in Supplementary Table

3). As expected, precipitation was strongly related to productivity in this data set (Fig. 3 – Model 1), and consistent with our univariate analysis, we found a significant positive effect of site productivity on change in species richness. Grazing had neutral to mildly positive effects on richness at low productivity and a stronger positive effect at higher productivity. In addition, we found that grazing pressure negatively influenced the richness response, but to a lesser extent than productivity. Thus, at high grazing pressure, herbivores decreased richness irrespective of site productivity. Site-level species richness also affected how richness responded to herbivory. As site richness increased, herbivores had less of an effect on changes in species richness regardless of site productivity. Overall, this model explained 13% of variation in the richness response to herbivory.

In a second model (Fig. 3 – Model 2a) we added an estimate of site-level Berger-Parker dominance in the absence of grazing (averaged across all ungrazed plots at a site [U_{dom}]), as well as the change in dominance in response to grazing ($\ln(G_{dom}/U_{dom})$) to assess the relative effects of productivity vs. dominance on the richness response to herbivory (correlations between all input variables can be found in Supplementary Table 5). While site productivity was weakly correlated with changes in richness (Fig. 3 –Model 2a), both site-level dominance and the change in dominance were significantly and more strongly correlated with the richness response to grazing. That is, as site dominance increased, grazing had a stronger positive effect on species richness. Consistent with this relationship, the change in dominance due to herbivores was strongly related to changes in species richness. Thus, when grazing reduced dominance there was a strong increase in species richness. Similar to the previous model, grazing pressure remained significantly correlated with the change in species richness. In this model, other factors related to

the herbivore community were also significant (i.e., domestication and feeding guild), but their effects on change in richness were indirect via change in dominance. Also, site-level total species richness no longer directly or indirectly influenced change in species richness. Overall, inclusion of Berger-Parker dominance doubled the explanatory power of the change in species richness when compared to the model that only included productivity ($R^2=0.31$ vs. 0.13). When this second model included Simpson's Dominance instead of Berger Parker Dominance (Supplementary Figure 4a – Model 2b; Supplementary Table 6) explanatory power of the change in species richness increased ($R^2=0.39$), providing robust support for change in dominance as key to explaining changes in richness with herbivory. Additionally, ANPP no longer has any effect on change in richness from herbivory when Simpson's Dominance was included in the model.

Models 1, 2a, and 2b (Supplementary Information) were limited to the 122 sites that had productivity measurements. Because productivity is strongly correlated with MAP both in our data set (Fig. 3, Model 1 & 2) as well as more broadly²⁰, we used precipitation as a proxy for productivity in Model 3 & 4a and 4b (Supplementary Information). This allowed us to include 244 sites in the analysis (Data Subset 3 in Supplementary Table 3). In Model 3, we examined the relationship between precipitation and change in species richness without dominance (similar to Model 1 but utilizing a larger dataset) as well as accounted for correlations between input variables (Supplementary Table 7). Like with the ANPP dataset, Model 3 was only able to explain 11% of the variation in change in richness and there was no effect of precipitation in this model. When Berger-Parker dominance was included in the model (Model 4a; Supplementary Table 8), our explanatory power of change in richness more than doubled ($R^2=0.11$ vs. 0.26), and

when Simpson's Dominance was included (Supplementary Figure 4b: Model 4b; Supplementary Table 9) our explanatory power of change in richness more than tripled ($R^2=0.11$ vs. 0.36). Similar to Model 2, we again found that site-level Berger-Parker dominance and change in Berger-Parker dominance with herbivores were the main drivers of herbivory-induced changes in species richness ($R^2=0.26$). Precipitation, however, as a surrogate for productivity, had no significant effect in the model. Importantly, incorporating the larger dataset in Model 4a and Model 4b demonstrated that herbivore-driven changes in dominance exert stronger effects on richness change than site level dominance *per se* (standardized partial effect sizes of -0.35 vs. not significant, respectively). These models also identified a strong, negative relationship between site-level dominance and change in dominance (standardized partial effect size of -0.54 and -0.58). This occurred because change in dominance is expressed as a ratio of grazed to ungrazed dominance and indicates that grazers reduce dominance more in sites with higher dominance. With this more comprehensive data set, we identified additional factors with direct and indirect effects on richness response to herbivory. For example, grazers alone had a stronger impact on changes in species richness than when grazers and browsers were both present (standardized partial effect size for Herbivore Guild of -0.26 and $-.023$). This pattern suggests that grazers target dominant grasses that then outcompete subordinate species when released from herbivory. But, grazers and browsers may have less of a net effect on species richness due to compensatory feeding, supporting theory⁷ and patterns from previous experiments^{12,24,25}. Overall, the more data-rich models confirm the role of dominance in controlling the richness response to herbivory rather than productivity.

To further explore the relationship between community dominance and herbivory, we focused on palatability of the dominant species. Palatability strongly influences how a plant species responds to herbivory. Previous research has shown that herbivores reduce the dominance of palatable tall grasses in productive mesic grasslands of North America, resulting in increased biodiversity^{12,26}. Alternatively, large herbivores in a mesic South African savanna dominated by an unpalatable grass had only minor impacts on dominance and diversity¹². Dominant species can also be palatable but grazing-tolerant so that dominance increases with herbivory. Such is the case in East African mesic grasslands where large herbivores generate extensive grazing lawns in which a few grazing-tolerant grasses withstand high densities of large herbivores and high rates of consumption^{27,28}. Such grazing lawns exhibit both high dominance and low biodiversity²⁷. Finally, high dominance and low biodiversity also could occur if there is another species in the community capable of compensating for reduced abundance of the dominant species. Thus, including traits that confer palatability of dominant species into analyses may be key to a more detailed mechanistic understanding of herbivore effects on biodiversity.

Assessing the role of palatability in determining dominance responses to herbivory was not possible with our empirical analysis due to a lack of trait data for the whole suite of plant species. However, we incorporated palatability into a stochastic community assembly model to simulate the effect of herbivory on Berger-Parker dominance and richness independent of productivity. This model considered community assembly, as well as dominance and richness responses following grazing, as random processes (see Methods for details). Change in dominance was calculated using relative cover of the dominant species. In the model, changes in dominance and species richness can occur via competitor release, local extinction and new

species arrivals. We assessed three scenarios with the model: 1) all dominant species are palatable, *i.e.*, grazed (Fig. 4a), 2) all dominant species are unpalatable (Fig. 4b), and 3) communities have a random chance of being dominated by either a palatable or unpalatable species (Fig. 4c). We found that when all simulated communities were dominated by palatable species (Fig. 4a) or when communities were dominated by either a palatable or unpalatable species (Fig. 4c), the resulting ensembles of 1000 simulations generated richness and dominance responses to herbivory that were remarkably similar to empirical observations (Fig. 2c). In contrast, if the dominant species was unpalatable (leaving only less common species to be grazed), there were few instances where richness increased while dominance decreased (*i.e.*, few points in the upper left-hand quadrant of Fig 4b). These simulations are consistent with the biodiversity response to herbivory depending primarily on palatability of and subsequent response of the dominant species, irrespective of productivity.

Discussion

Our findings extend theory^{2,5,7,22,29} by identifying *change in community dominance*, and thus the competitive landscape, as the primary and generalizable mechanism underlying biodiversity response to herbivory. Change in dominance explains herbivore impacts on biodiversity – both positive and negative – globally across grasslands and savannas with 20-fold differences in productivity and vastly different biogeographic and evolutionary histories. This dominance mechanism is consistent with the light availability mechanism identified by Borer *et al.*⁵, because increases in dominance can increase light limitation³⁰. But dominance also changes with herbivory in sites where light is not limiting²⁷. Thus, the dominance mechanism applies to a wider range of ecosystems, reflecting competitive interactions for the availability of either

above- or below-ground resources⁷. This dominance mechanism is also consistent with the evolutionary history mechanism identified by Milchunas and colleagues^{13,31} as dominance and the traits of the dominant species, particularly those related to palatability, are determined by a site's evolutionary history. Strong community dominance by just a few species is a nearly universal feature of ecosystems^{15,22,29}, and dominant species are known to control most ecosystem processes^{22,32}. As a consequence, our results point to “dominance management” as an effective strategy for conserving species biodiversity and ecosystem functioning in grasslands and savannas globally.

References

- 1 Estes, J. A. *et al.* Trophic downgrading of planet Earth. *Science* **333**, 301-306, (2011).
- 2 Bakker, E. S., Ritchie, M. E., Olff, H., Milchunas, D. G. & Knops, J. M. H. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecol. Lett.* **9**, 780-788, (2006).
- 3 Proulx, M. & Mazumder, A. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* **79**, 2581-2592, (1998).
- 4 Worm, B., Lotze, H. K., Hillebrand, H. & Sommer, U. Consumer versus resource control of species diversity and ecosystem functioning. *Nature* **417**, 848-851, (2002).
- 5 Borer, E. T. *et al.* Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* **508**, 517-520, (2014).
- 6 Hillebrand, H. *et al.* Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences* **104**, 10904-10909, (2007).
- 7 Olff, H. & Ritchie, M. E. Effects of herbivores on grassland plant diversity. *Trends Ecol. Evol.* **13**, 261-265, (1998).
- 8 Osem, Y., Perevolotsky, A. & Kigel, J. Grazing effect on diversity of annual plant communities in a semi-arid rangeland: interactions with small-scale spatial and temporal variation in primary productivity. *J. Ecol.* **90**, 936-946, (2002).
- 9 Lezama, F. *et al.* Variation of grazing-induced vegetation changes across a large-scale productivity gradient. *Journal of Vegetation Science* **25**, 8-21, (2014).
- 10 Frank, D. A., McNaughton, S. J. & Tracy, B. F. The ecology of the Earth's grazing ecosystems. *Bioscience* **48**, 513-521, (1998).
- 11 McNaughton, S. J. & Wolf, L. L. Dominance and the niche in ecological systems. *Science* **167**, 131-139, (1970).
- 12 Koerner, S. E. *et al.* Plant community response to loss of large herbivores differs between North American and South African savanna grasslands. *Ecology* **95**, 808-816, (2014).
- 13 Milchunas, D. G. & Lauenroth, W. K. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecol. Monogr.* **63**, 327-366, (1993).
- 14 Eldridge, D. J., Poore, A. G. B., Ruiz-Colmenero, M., Letnic, M. & Soliveres, S. Ecosystem structure, function, and composition in rangelands are negatively affected by livestock grazing. *Ecol. Appl.* **26**, 1273-1283, (2016).
- 15 Smith, M. D. & Knapp, A. K. Dominant species maintain ecosystem function with non-random species loss. *Ecol. Lett.* **6**, 509-517, (2003).
- 16 Collins, S. L. & Xia, Y. Long-term dynamics and hotspots of change in a desert grassland plant community. *Am. Nat.* **185**, E30-E43, (2015).
- 17 Olson, D. M. *et al.* Terrestrial ecoregions of the world: A new map of life on earth. *Bioscience* **51**, 933-938, (2001).
- 18 Magguran, A. E. *Measuring Biological Diversity*. 264 (Wiley-Blackwell, 2003).
- 19 Smith, B. & Wilson, J. B. A consumer's guide to evenness indices. *Oikos*, 70-82, (1996).
- 20 Sala, O. E., Gherardi, L. A., Reichmann, L., Jobbágy, E. & Peters, D. Legacies of precipitation fluctuations on primary production: theory and data synthesis. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **367**, 3135-3144, (2012).

- 21 Forrestel, E. J. *et al.* Different clades and traits yield similar grassland functional responses. *P Natl Acad Sci USA* **114**, 705-710, (2017).
- 22 Grime, J. P. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* **86**, 902-910, (1998).
- 23 Grace, J. B. *et al.* Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature* **529**, 390-393, (2016).
- 24 Eby, S. *et al.* Grazing by a single herbivore species and fire frequency have differing impacts on plant community responses in North American and South African savanna grasslands. *Oecologia* **175**, 293-303, (2014).
- 25 Burkepile, D. E. *et al.* Fire frequency drives habitat selection by a diverse herbivore guild impacting top-down control of plant communities in an African savanna. *Oikos* **125**, 1636-1646, (2016).
- 26 Collins, S. L., Knapp, A. K., Briggs, J. M., Blair, J. M. & Steinauer, E. M. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* **280**, 745-747, (1998).
- 27 McNaughton, S. J. Serengeti grassland ecology - The role of composite environmental-factors and contingency in community organization. *Ecol. Monogr.* **53**, 291-320, (1983).
- 28 Plas, F., Howison, R. A., Mpanza, N., Cromsigt, J. P. & Olf, H. Different-sized grazers have distinctive effects on plant functional composition of an African savannah. *J. Ecol.* **104**, 864-875, (2016).
- 29 Whittaker, R. H. Dominance and diversity in land plant communities. *Science* **147**, 250-260, (1965).
- 30 Smith, M. D., Wilcox, J. C., Kelly, T. & Knapp, A. K. Dominance not richness determines invasibility of tallgrass prairie. *Oikos* **106**, 253-262, (2004).
- 31 Milchunas, D. G., Sala, O. E. & Lauenroth, W. K. A generalized model of the effects of grazing by large herbivores on grassland community structure. *Am. Nat.* **132**, 87-106, (1988).
- 32 Yang, Z. *et al.* Daytime warming lowers community temporal stability by reducing the abundance of dominant, stable species. *Global Change Biol.*, (2016).
- 33 Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**, 1965-1978, (2005).

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Author Contributions SEK managed the project including conceptualizing the questions, collecting and analyzing the data, developing the figures, and writing the manuscript. MDS conceptualized the questions and wrote the manuscript. DEB conceptualized the questions, collected the data, and wrote the manuscript. NPH performed simulations and wrote the manuscript. MLA & NPL executed the path analyses and developed figures. SLC & AKK wrote the manuscript. SE, EJF, DIT contributed to data collection and management. All authors who were not members from the Grazing Exlosure Working Group contributed data to the synthesis, and all authors (both members of the working group and not) edited the manuscript. See author contribution table (Supplementary Table 11) for complete list of contributions.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to SEK.

Competing Interests The authors declare no competing financial interests.

Data Availability While raw species abundances are not publicly available due to lack of permission from data owners (contact individual dataset owners listed in Supplementary Table 1), all data generated and analyzed during the current study (site level richness response to herbivory, site level Berger-Parker and Simpson's dominance response to herbivory, site ANPP, and site MAP) are provided in Supplementary Table 2.

Figure Legends

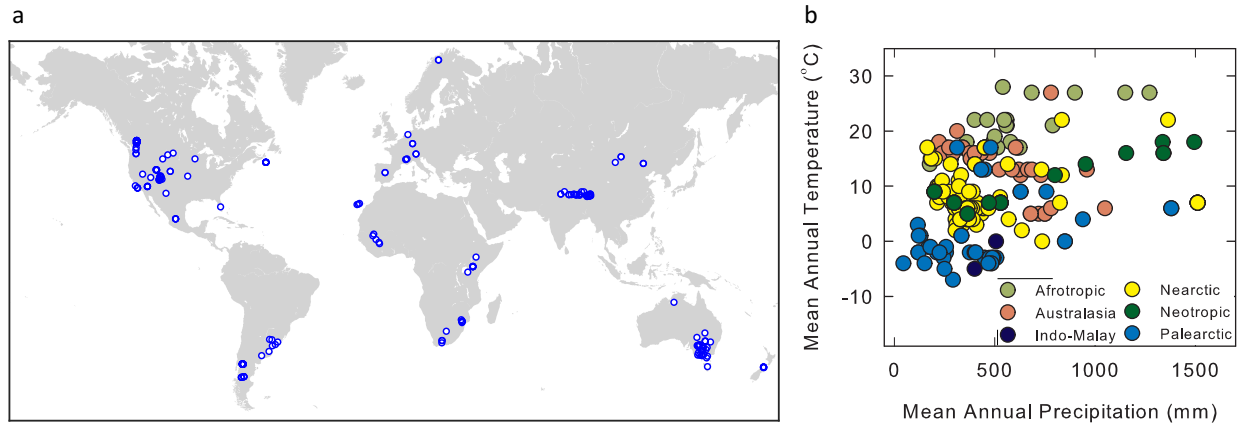


Figure 1. Location and climate of sites. **a**, Locations of the 252 grassland and savanna ecosystems where 1,212 grazed and ungrazed plots were located. All sites are represented by a single sized open blue circle. Areas where symbols overlap appear to be darker blue. **b**, These study sites represent six biogeographic realms and encompass broad gradients of mean annual temperature and precipitation. Additional site details are provided in Supplementary Tables 1 & 2.

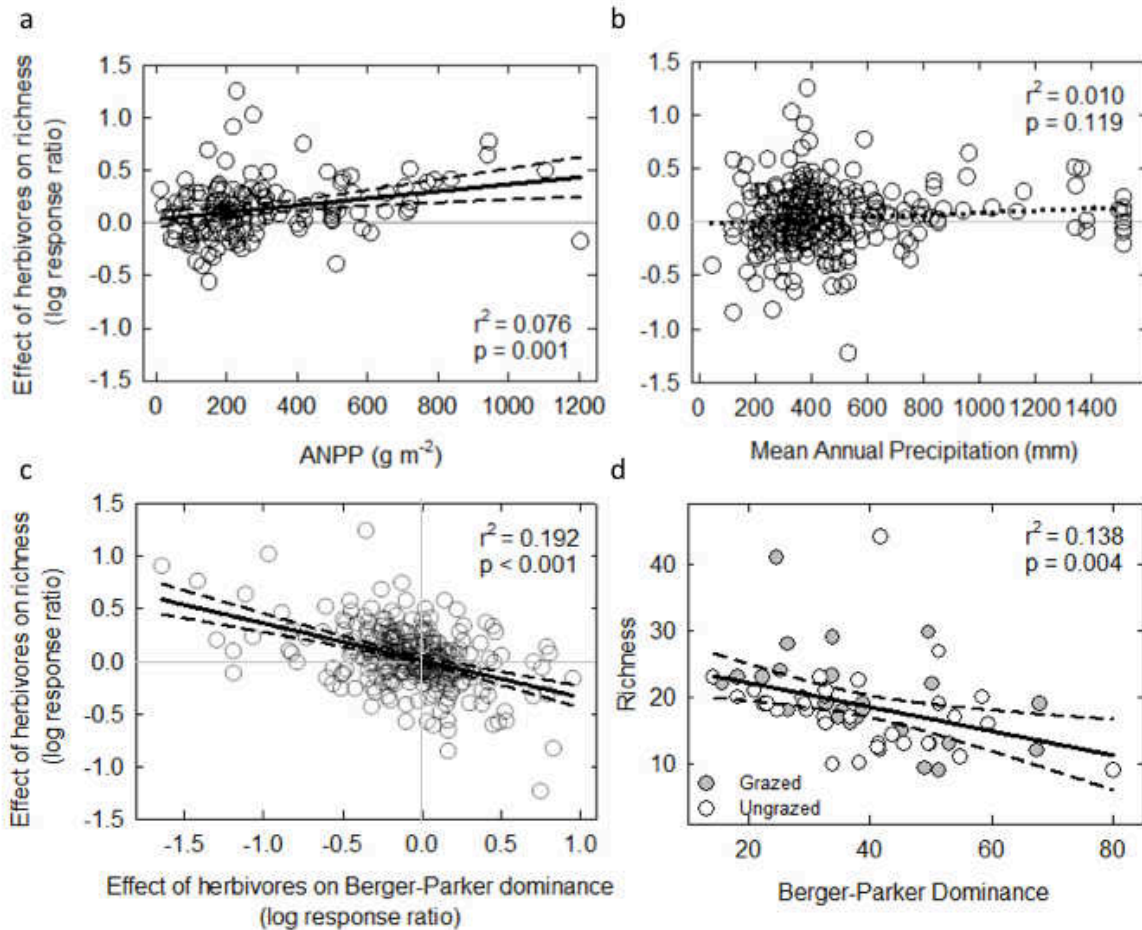


Figure 2. Herbivore effects on plant communities. **a**, Relationship between aboveground net primary production (ANPP) and the response of plant species richness to herbivory ($\ln(G/UG)$), where G is the average plant species richness in grazed plots and UG is the same measurement in ungrazed plots ($n=132$; Data Subset 1 in Supplementary Table 3). **b**, Relationship between mean annual precipitation and the response of plant species richness to herbivory ($n=244$; Data Subset 2 in Supplementary Table 3). **c**, Relationship between the change in dominance (Berger-Parker Dominance) and the change in species richness as a function of herbivory ($\ln(G/UG)$) ($n=252$; all data). **d**, Relationship between dominance (Berger-Parker Dominance) and species richness for grazed and ungrazed plots combined. This analysis is based only on studies with a common plot size of 25 m² ($n=58$). Dashed lines represent 95% confidence intervals.

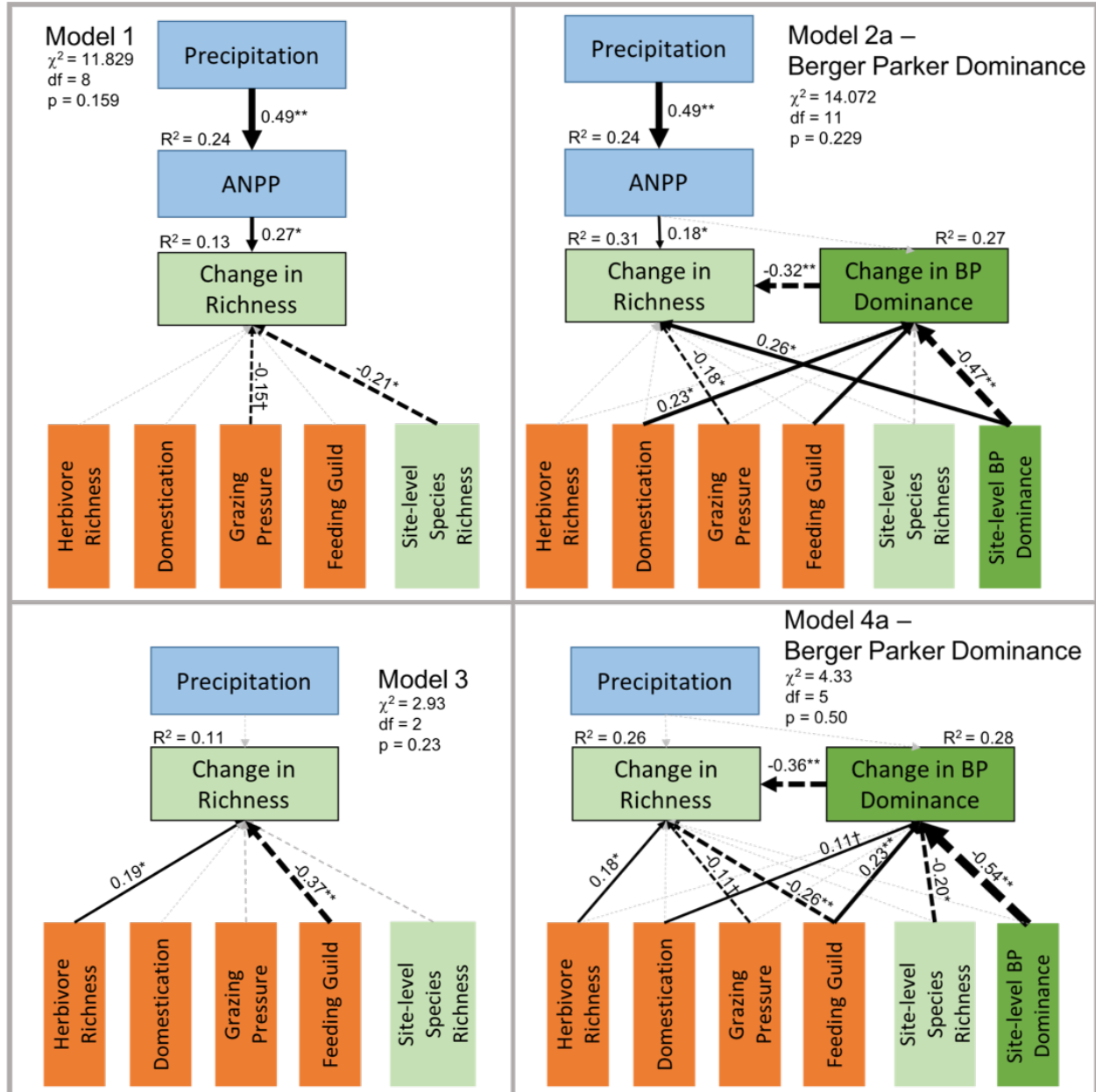


Figure 3. Drivers of plant richness response to herbivory. **a, b** Path analyses testing the importance of aboveground net primary productivity (ANPP, Model 1) and Berger-Parker dominance (Model 2a) on the change in species richness in response to herbivory. These models are restricted to sites where both ANPP and precipitation data were available (n=122; Data Subset 3 in Supplementary Table 3). See Supplementary Tables 4 & 5 for bivariate correlations

between input variables which were included in these models to improve model fit. **c,d** Path analyses testing the importance of productivity using precipitation as a proxy (Model 3) for productivity and Berger-Parker dominance (Model 4a) on the change in species richness in response to herbivory. These models use precipitation as a surrogate for ANPP allowing the use of more data (n=244; Data Subset 2 in Supplementary Table 3) . See Supplementary Table 7 & 8 for bivariate correlations between input variables which were included in these models to improve model fit. All models also test for the effects of site and herbivore characteristics (see Methods). **p<0.001, *p<0.05, †p<0.10. Non-significant relationships are shown in light gray dashed arrows, solid black arrows represent positive relationships and dashed black arrows represent negative relationships. Shown are standardized effect sizes, with arrow thickness proportional to the strength of the relationship. All models were a good fit to the data based on the χ^2 statistic (p>0.05 is good). See Supplementary Table 10 for additional model fit parameters for all four models.

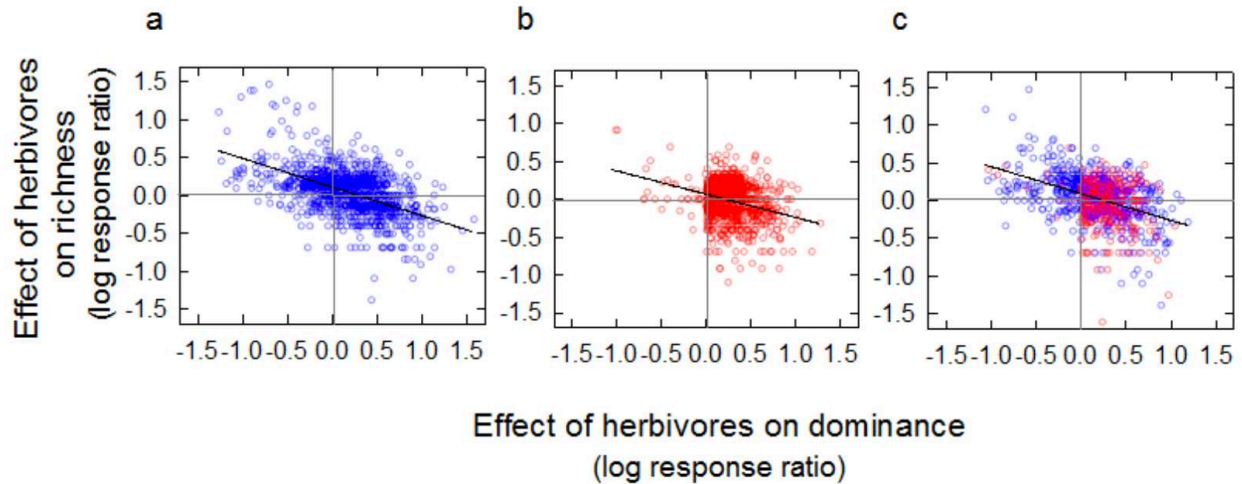


Figure 4. Simulation of plant community assembly in response to herbivory with three scenarios of palatability of the dominant species. a) In the first scenario, each assembled community has a dominant species that is grazed (blue), and all subordinate species have a 50% probability of being a grazed species. b) In the second scenario, each assembled community has a dominant species that is not grazed (red), and all subordinate species have a 50% probability of being a grazed species. c) In the third scenario, in each assembled community all plant species have 50% probability of being a grazed species including the dominant species. Blue dots represent communities that have a dominant species that is grazed. Red dots represent assembled communities in which the dominant species was ungrazed. All scenarios treat community assembly and dominance and richness responses following grazing as random processes (see details in methods).

METHODS

Data. We compiled a database (Grazing Exclosure Database = GEx) consisting of plant community composition data from 252 large vertebrate herbivore exclosure sites (Supplementary Tables 1 & 2). To be included in GEx, sites had to meet five criteria. (1) Exclosures had to be located in herbaceous-dominated communities - sites ranged from tallgrass prairie to alpine meadows to desert, but all are dominated or co-dominated by herbaceous species. (2) Large vertebrate herbivores (adult body mass >45 kg) had to be excluded from plots using fencing with adjacent plots exposed to herbivores. Herbivore type and number varies among the sites, including domesticated cattle, sheep, goats, burros, and horses, as well as native wildlife such as caribou, kangaroo, and the full complement of large African herbivores. The inside of the exclosure could not be manipulated or managed other than the removal of herbivore (*i.e.*, no mowing or burning that did not also occur outside the exclosure). (3) Data had to be collected after at least three years of exclusion of large herbivores. This was to ensure sufficient time for the plant community to respond to the absence of herbivores. (4) Paired plots inside and outside the exclosure had to be sampled at the same time and sampling intensity. (5) Community data had to be available at the species level. Data types include cover, line intercept, biomass, and pin hits (but not frequency or density), all of which were converted to relative abundance values.

Explanatory Variables. Several covariates were used in the analyses which described plant, experiment, and herbivore community characteristics. Site primary productivity was based on ungrazed vegetation, as reported by individual investigators for a subset of the sites ($n=132$). Individual investigators supplied precipitation data, while mean annual temperature (MAT) was based on WorldClim³³. Site-level richness and dominance were calculated using the species

composition data. Site richness was calculated as the total number of plant species found across all plots. Site dominance was calculated as the mean dominance across all ungrazed plots using Berger-Parker Dominance, which is the relative abundance of the most abundant species in the plot. Four variables were used to describe the herbivore community. Investigators provided an assessment of herbivory pressure (low, moderate, high) and species of large herbivores excluded. We converted herbivore species information into three variables: herbivore richness, feeding guild, and domestication. Herbivore richness is the number of large herbivore species excluded by the fences. Predominantly, these exclosures excluded grazers (feeding guild = 0), and when browsers or mixed feeders were present either in combination with grazers or alone (feeding guild = 1), we hypothesized this would have different effects on the herbaceous community. Domestication refers to human involvement with herbivore species presence and abundance. Native herbivores (wildlife) were coded as domestication = 0, while domesticated herbivores (e.g., cattle) or the combination of the two were coded as domestication = 1 as they were hypothesized to have different effects than native herbivores alone. Experiment length was the number of years post exclosure construction; this variable was included in many exploratory analyses but was never significant and often led to poor model fit to the data. Exclosure age was not significantly correlated with either change in richness or change in dominance. Therefore, exclosure age was dropped from all path analyses.

Although many sites provided multiple years of data, here we present only the most recent year of data collected from each site. For analyses involving ANPP, a subset of sites was used ($n=132$; Data Subset 1 in Supplementary Table 3), while nearly all sites were included in analyses using only precipitation ($n=244$; 8 sites were strategically placed in topographic locations that were either wetter or drier than expected based on precipitation and were therefore

only used in the ANPP analysis but not the precipitation analyses; Data Subset 2 in Supplementary Table 3). Likewise, when models included both ANPP and precipitation a subset was used ($n=122$; Data Subset 3 in Supplementary Table 3). When models did not include either ANPP or precipitation as predictors, we used all sites in the database ($n=252$).

Response Variables. The majority of sites had a single exclosure ($n=132$). When more than one exclosure was built in the same year, each exclosure and corresponding paired plot was considered a block. When multiple subplots were sampled within each exclosure or paired plot, species abundance was summed for each species across the subplots, to obtain species data at the plot level (i.e., 1 plot per block). Plant community richness and dominance were calculated at the plot level for inside and outside the exclosure. Plant community richness was calculated as the number of species in the plot in that year. Dominance was quantified in two ways. Berger-Parker Dominance (BP Dominance) was calculated as the maximum relative abundance of the most abundant species in each plot. Simpson's Dominance was calculated as

$$D_{simp} = \sum_{s=1}^S p_s^2$$

where S is the number of species in the sample and p_s is the proportional abundance of the s^{th} species. To quantify herbivore-induced changes in biodiversity, we calculated the log response ratio ($\ln(G/UG)$) of plant species richness outside (grazed, G) vs. inside (ungrazed, UG) each exclosure. Change in community dominance with herbivory (both Berger Parker and Simpson's) was also estimated by using this log response ratio. The log response ratios were then averaged across blocks to obtain a single value for each site.

Analyses. We developed linear models using R (version 3.1; R Foundation for Statistical Computing). We used the `lm` R function to analyze the relationships between the effect of herbivores on richness (log response ratio) and ANPP (Fig. 2a), MAP (Fig. 2b), and effect of herbivores on dominance (log response ratio; Fig. 2c), as well as for the relationship between dominance and richness (Fig. 2d).

To determine the relative importance of various proposed explanatory variables on the richness response to herbivory (log response ratio), we used path analysis conducted in AMOS v7 (SPSS, Chicago, IL, USA). We contrasted the effects of site-level productivity vs. dominance on species-richness response to herbivory utilizing two alternative models. All models also included hypothesized influential covariates such as characteristics of the herbivore community, the plant community, and experimental duration. Data were screened for distributional properties and nonlinear relations. Site-level plant richness and herbivore richness were log-transformed as a result of these evaluations. While site level dominance and richness theoretically could be driven by precipitation, the correlations between site-level richness and precipitation (Pearson correlation coefficient = 0.357; linear regression $R^2 = .126$) and between site-level Berger-Parker dominance and precipitation (Pearson Correlation Coefficient = -0.246; linear regression $R^2 = .06$) within our dataset were low. Therefore, these relationships were dropped from the path analysis due to replication constraints. Model 1 examined the widely hypothesized relationship between precipitation, ANPP, and change in species richness (Fig. 3a). Because ANPP was not available from all sites, this model used data from 122 of the 252 sites where ANPP was measured and precipitation was a good proxy for ANPP. Model 2a (Fig. 3b) used the same data as Model 1 but included an estimate of site level Berger-Parker dominance in the absence of grazing (U_{dom}), as well as the change in Berger-Parker dominance in response to grazing

($\ln(G_{\text{dom}}/U_{\text{dom}})$) to assess the relative effects of ANPP vs. Berger-Parker dominance on richness response to herbivory. Model 2b - Simpson's (Supplementary Figure 4a) was the same as Model 2a but included an estimate of site level Simpson's dominance in the absence of grazing (U_{SimpDom}), as well as the change in Simpson's dominance in response to grazing ($\ln(G_{\text{SimpDom}}/U_{\text{SimpDom}})$) to assess the relative effects of ANPP vs. Simpson's dominance on richness response to herbivory. Because ANPP is strongly correlated with MAP both in our data set (Fig. 3A & B) as well as more broadly²⁰, we used precipitation as a proxy for ANPP, allowing us to run similar models again but including 244 sites in the analysis (Model 3 & 4a and 4b). Several input variables were correlated (based on AMOS recommendations for correlated variables that improve model fit), therefore, included as such in the models (Supplementary Table 4-9). All models were a good fit to the data, according the X^2 statistic with $P > 0.05$ as well as other measures of goodness of fit (see Supplementary Table 10).

Null Model Simulation. To explore possible mechanisms for observed herbaceous community responses to herbivory, we created a simple community assembly and grazing response model in which idealized plant communities first assemble stochastically, with each new species assigned a canopy cover drawn from a negative binomial distribution (mean cover, $\mu = 15\%$; dispersion = 1.0) until the collective canopy cover = 100% of available space, after which time no further species can be added. The grazing process is then simulated with (i) species in the community assigned as “palatable” or “unpalatable” using a random binomial process ($P=0.5$), and (ii) reduction in cover of palatable species simulated as a random-uniform process where ~50% of palatable species are excluded by grazing (i.e. cover reduced to 0%), and the cover of the remaining palatable species is reduced by 50-99% of their original extent. The community

response to the resources made available through grazing-induced loss in plant cover is then simulated via the effect of two mechanisms: (i) competitive release of ungrazed species (“growth response”) and (ii) establishment of novel species (i.e. species assumed to have been absent in the ungrazed community, but available in the regional species pool; “immigration response”). The growth and immigration responses are simulated alternately until the resulting community again occupies all available space, with each ungrazed species increasing its cover in proportion to the grazing-induced loss in total cover in the plot, and new immigrants arriving via the negative binomial stochastic process used in the original community assembly.

Supplementary Table 1. Site locations and contact researcher. Sites are organized first by Biogeographic Realm and then by site mean annual precipitation (MAP; low to high); additionally, Site # and organization are consistent between Supplementary Tables 1-3.

Site #	Site Name	Country	Lat	Long	Contact
Afrotropics					
1	Tierberg_Karoo_Research_Centre	South Africa	-33.2	22.4	Sue Milton
2	KarooNP_Sandrivier	South Africa	-32.3	22.3	Tineke Kraaij
3	KarooNP_Lammertjiesleegte	South Africa	-32.3	22.6	Tineke Kraaij
4	Pniel	South Africa	-28.6	24.4	David Ward
5	Kruger_Letaba	South Africa	-23.8	31.4	Frances Siebert
6	Mali_Korokodjo	Mali	15.3	-9.5	Niall Hanan, Moussa Kareembe, Fadia Dembele
7	Kruger_Nwan	South Africa	-24.5	31.9	Sally Koerner, Melinda Smith
8	Kenya_North	Kenya	0.5	36.9	Jacob R. Goheen, Todd M. Palmer, Robert M. Pringle
9	Ethiopia	Ethiopia	4.8	38.4	Ayana Angassa
10	Mpala	Kenya	0.3	36.9	David Augustine
11	Kruger_Buff	South Africa	-24.4	31.8	Stephanie Eby, Melinda Smith
12	Kruger_Marheya	South Africa	-24.5	31.8	Sally Koerner, Melinda Smith
13	Kruger_Satara	South Africa	-24.4	31.7	Sally Koerner, Melinda Smith
14	Kruger_Nkuhlu	South Africa	-25	31.8	Frances Siebert
15	Mali_Lakamane	Mali	14.6	-9.9	Niall Hanan, Moussa Kareembe, Fadia Dembele
16	Kenya_Central	Kenya	0.4	36.9	Jacob R. Goheen, Todd M. Palmer, Robert M. Pringle
17	KLEE_cattle (O vs. C)	Kenya	0.3	36.8	Corinna Riginos, Kari E. Veblen, Truman Young
18	KLEE_wildlife (O vs. MW)	Kenya	0.3	36.8	Corinna Riginos, Kari E. Veblen, Truman Young
19	Kenya_South	Kenya	0.3	36.9	Jacob R. Goheen, Todd M. Palmer, Robert M. Pringle
20	Serengeti_Nutnet	Tanzania	-2.3	34.5	Mike Anderson
21	Mali_Neguela	Mali	12.9	-8.5	Niall Hanan, Moussa Kareembe, Fadia Dembele
22	Mali_Tiorola	Mali	11.6	-7.1	Niall Hanan, Moussa Kareembe, Fadia Dembele
23	Mali_Tiendaga	Mali	11	-6.8	Niall Hanan, Moussa Kareembe, Fadia Dembele
24	Mananga_High	South Africa	-24.4	31.7	Deron Burkepile
25	Mananga_Low	South Africa	-24.4	31.9	Deron Burkepile
26	Satara_North_High	South Africa	-24.4	31.9	Deron Burkepile
27	Satara_North_Low	South Africa	-24.4	31.7	Deron Burkepile
28	Satara_South_High	South Africa	-24.5	31.9	Deron Burkepile
29	Satara_South_Low	South Africa	-24.4	31.7	Deron Burkepile
30	Shibotawna_High	South Africa	-24.4	31.7	Deron Burkepile
31	Shibotawna_Low	South Africa	-24.4	31.9	Deron Burkepile
Australasia					
32	AUS_FowlersGap	Australia	-31.1	141.7	David Eldridge
33	AUS_Mallee	Australia	-34.2	142.5	David Eldridge
34	AUS_Arumpo	Australia	-33.9	143	David Eldridge
35	AUS_Kimberley	Australia	-32.5	145.6	David Eldridge
36	AUS_Ag_Biod	Australia	-34.1	142.5	David Eldridge
37	AUS_Buronga	Australia	-34.2	142.2	James Val
38	AUS_Murray	Australia	-34.3	141.8	John Morgan, Nick Schultz
39	AUS_Hattah	Australia	-34.7	142.3	John Morgan, Nick Schultz
40	AUS_Wapweelah	Australia	-29.3	145.5	David Eldridge
41	AUS_Yathong_large	Australia	-32.6	145.6	David Eldridge
42	AUS_Yathong_small	Australia	-32.5	145.6	David Eldridge
43	AUS_Werrai	Australia	-35.4	144.6	David Eldridge
44	AUS_OBriens	Australia	-36.2	144.4	John Morgan, Nick Schultz
45	AUS_Pinegrove	Australia	-36.2	144.4	John Morgan, Nick Schultz
46	AUS_Paradise	Australia	-34.8	144.8	David Eldridge
47	AUS_Kinypanial	Australia	-36.3	143.8	John Morgan, Nick Schultz
48	AUS_CYP	Australia	-35	146.5	David Eldridge
49	AUS_Savernake	Australia	-35.8	146	David Eldridge
50	AUS_Inverleigh	Australia	-38.1	144.1	John Morgan, Nick Schultz

51	AUS_Warrambeen	Australia	-37.9	143.9	John Morgan, Nick Schultz
52	AUS_Berry	Australia	-32.9	148.1	David Eldridge
53	AUS_Darlington	Australia	-37.9	143	Claire Moxham, Josh Dorrrough
54	AUS_Grampians	Australia	-37.1	142.4	John Morgan, Nick Schultz
55	AUS_Craigieburn	Australia	-37.6	144.9	John Morgan, Nick Schultz
56	Molesworth_ST	New Zealand	-42.2	172.8	Sean Husheer
57	Molesworth_SW	New Zealand	-42.1	172.9	Sean Husheer
58	AUS_Hamilton	Australia	-37.8	142.1	Claire Moxham, Josh Dorrrough
59	Molesworth_CC	New Zealand	-42.2	172.9	Sean Husheer
60	AUS_Birregurra	Australia	-38.3	146.7	Claire Moxham, Josh Dorrrough
61	Molesworth_HG	New Zealand	-42.1	172.9	Sean Husheer
62	Molesworth_SD	New Zealand	-42.2	172.9	Sean Husheer
63	VictoriaRiverResearchStation	Australia	-16.1	131	Gary Bastin
64	Molesworth_PT	New Zealand	-42.3	173	Sean Husheer
65	AUS_WilsonsPromontory	Australia	-38.9	146.2	John Morgan, Nick Schultz
<hr/>					
Indo-malay					
66	India_Kibber	India	32.3	78	Sumanta Bagchi
67	India_Nutnet	India	32.3	78	Mahesh Sankaran, V. T. Yadugiri
<hr/>					
Nearctic					
68	MNP_14mileTank	USA	35.4	-115.4	Erik Beever
69	MNP_TenmileTank	USA	35.3	-115.4	Erik Beever
70	MNK_16mileTank	USA	35.3	-115.5	Erik Beever
71	MNP_30	USA	35.2	-115.5	Erik Beever
72	Park Pasture	USA	38	-109.7	Kyle Nehring, Kari E. Veblen, Jane Zelikova
73	Cisco Wash 1	USA	39	-109.4	Kyle Nehring, Kari E. Veblen, Jane Zelikova
74	Cisco Wash 2	USA	39	-109.4	Kyle Nehring, Kari E. Veblen, Jane Zelikova
75	Cisco Mesa	USA	39.1	-109.4	Kyle Nehring, Kari E. Veblen, Jane Zelikova
76	Sand Flat	USA	38	-109.9	Kyle Nehring, Kari E. Veblen, Jane Zelikova
77	N_Clan	USA	39.8	-117.7	Lauren Baur, Kate Schoenecker
78	Hotel Mesa	USA	38.8	-109.2	Kyle Nehring, Kari E. Veblen, Jane Zelikova
79	Westwater	USA	39.2	-109.2	Kyle Nehring, Kari E. Veblen, Jane Zelikova
80	Horse Pasture	USA	39.1	-109.6	Kyle Nehring, Kari E. Veblen, Jane Zelikova
81	Buckhorn	USA	38.9	-109.2	Kyle Nehring, Kari E. Veblen, Jane Zelikova
82	Jornada	USA	32.6	-106.7	John Anderson
83	Neponset	USA	38	-109.6	Kyle Nehring, Kari E. Veblen
84	Dry Valley	USA	38.2	-109.4	Kyle Nehring, Kari E. Veblen, Jane Zelikova
85	Canada_Currie	Canada	50.7	-120.5	Lauchlan Fraser
86	Canada_LGS.6	Canada	50.7	-120.4	Lauchlan Fraser
87	DeseretLow	USA	41.4	-111.4	Elisabeth Bakker, Mark Ritchie
88	DeseretSage	USA	41.2	-111.1	Elisabeth Bakker, Mark Ritchie
89	Kate Hollow	USA	41.3	-111.2	Kyle Nehring, Kari E. Veblen
90	Canada_Dewdrop.2	Canada	50.8	-120.6	Lauchlan Fraser
91	Canada_Ils1	Canada	50.8	-120.4	Lauchlan Fraser
92	Salt Creek Mesa	USA	38.9	-109.2	Kyle Nehring, Kari E. Veblen, Jane Zelikova
93	Short Grass Steppe	USA	40.8	-104.8	Elisabeth Bakker, Daniel Milchunas
94	Stanley Park	USA	38.8	-109.1	Kyle Nehring, Kari E. Veblen, Jane Zelikova
95	Canada_hav	Canada	50.1	-120.5	Lauchlan Fraser
96	Canada_hbb	Canada	50.1	-120.5	Lauchlan Fraser
97	Canada_MG1.LDB	Canada	50.8	-120.4	Lauchlan Fraser
98	Canada_MG2.LDB	Canada	50.8	-120.4	Lauchlan Fraser
99	House Park	USA	38	-109.9	Kyle Nehring, Kari E. Veblen, Jane Zelikova
100	Canada_hkb	Canada	50.1	-120.5	Lauchlan Fraser
101	Canada_MG3.LDB	Canada	50.7	-120.4	Lauchlan Fraser
102	Canada_Goose.Lake	Canada	50.1	-120.4	Lauchlan Fraser
103	Canada_Lundbom.Lake	Canada	50.1	-120.6	Lauchlan Fraser
104	N_Sulphur	USA	38.6	-113.9	Lauren Baur, Kate Schoenecker
105	North Cottonwood	USA	38.2	-109.7	Kyle Nehring, Kari E. Veblen, Jane Zelikova
106	Canada_gooselake2	Canada	50.1	-120.4	Lauchlan Fraser

107	Canada_Mara.1	Canada	50.7	-120.5	Lauchlan Fraser
108	Harts Point	USA	38	-109.5	Kyle Nehring, Kari E. Veblen, Jane Zelikova
109	Texas Flat	USA	41.3	-111.2	Kyle Nehring, Kari E. Veblen, Jane Zelikova
110	FortKeogh	USA	46.4	-105.9	Lance Vermeire, Dustin Strong
111	CPER	USA	40.8	-104.7	David Augustine, Dan Milchunas
112	Steamboat Mesa	USA	37.6	-109.8	Kyle Nehring, Kari E. Veblen, Jane Zelikova
113	Wild Cow Point	USA	37.9	-110	Kyle Nehring, Kari E. Veblen, Jane Zelikova
114	N_Pryor	USA	45.1	-108.3	Lauren Baur, Kate Schoenecker
115	Canada_Dewdrop.1	Canada	50.8	-120.7	Lauchlan Fraser
116	Canada_Illrs	Canada	50.8	-120.4	Lauchlan Fraser
117	Canada_LG5.LDB	Canada	50.7	-120.4	Lauchlan Fraser
118	Canada_Summit.North	Canada	50.1	-120.4	Lauchlan Fraser
119	Canada_LG4.LDB	Canada	50.7	-120.4	Lauchlan Fraser
120	Canada_Repeter	Canada	50.1	-120.4	Lauchlan Fraser
121	Canada_LGS.4	Canada	50.7	-120.4	Lauchlan Fraser
122	Canada_UG2.LDB	Canada			Lauchlan Fraser
123	Harts Draw	USA	38	-109.5	Kyle Nehring, Kari E. Veblen, Jane Zelikova
124	Canada_LG2.LDB	Canada	50.7	-120.4	Lauchlan Fraser
125	Canada_Powerline	Canada	50.1	-120.4	Lauchlan Fraser
126	Canada_hsr	Canada	50.1	-120.5	Lauchlan Fraser
127	Canada_MGBR.1	Canada	50.8	-120.4	Lauchlan Fraser
128	Canada_LG1.LDB	Canada	50.7	-120.4	Lauchlan Fraser
129	Canada_MGBR.2	Canada	50.8	-120.4	Lauchlan Fraser
130	Canada_LGS.5	Canada	50.7	-120.4	Lauchlan Fraser
131	Canada_UG3.LDB	Canada			Lauchlan Fraser
132	Canada_LG3.LDB	Canada	50.7	-120.4	Lauchlan Fraser
133	Canada_Redhil	Canada	50.8	-120.4	Lauchlan Fraser
134	Canada_Frolek	Canada	50.8	-120.4	Lauchlan Fraser
135	Canada_Long.lake.6	Canada	50.8	-120.4	Lauchlan Fraser
136	N_Theodore	USA	47	-103.4	Lauren Baur, Kate Schoenecker
137	The Dip	USA	37.7	-110	Kyle Nehring, Kari E. Veblen
138	Canada_LGS.1	Canada	50.7	-120.4	Lauchlan Fraser
139	Canada_Summit.South	Canada	50.1	-120.4	Lauchlan Fraser
140	California_Sedgwick_Airstrip	USA	34.7	-120	Carla Dantonio, Claudia Tyler, Barbara Fernandex-Going
141	California_Sedgwick_Lisque	USA	34.7	-120	Carla Dantonio, Claudia Tyler, Barbara Fernandex-Going
142	California_Sedgwick_Mesa	USA	34.7	-120	Carla Dantonio, Claudia Tyler, Barbara Fernandex-Going
143	Lost Park	USA	41.4	-111.1	Kyle Nehring, Kari E. Veblen, Jane Zelikova
144	Canada_LGS.2	Canada	50.7	-120.4	Lauchlan Fraser
145	Canada_TMV	Canada	50.8	-120.4	Lauchlan Fraser
146	N_Spring	USA	38	-108.6	Lauren Baur, Kate Schoenecker
147	Canada_Drum	Canada	50.1	-120.7	Lauchlan Fraser
148	Canada_Illw	Canada	50.8	-120.4	Lauchlan Fraser
149	Canada_FLHT.2	Canada	50.7	-120.4	Lauchlan Fraser
150	Canada_Long.lake.5	Canada	50.8	-120.4	Lauchlan Fraser
151	Canada_fht1	Canada	50.7	-120.4	Lauchlan Fraser
152	Canada_Long.lake.4	Canada	50.8	-120.4	Lauchlan Fraser
153	Mexico_LaColorada	Mexico	22	-102.3	Gerardo Armando Aguado Santacruz
154	Mexico_LaMesa	Mexico	22	-102.3	Gerardo Armando Aguado Santacruz
155	Mexico_LaPresa	Mexico	22	-102.3	Gerardo Armando Aguado Santacruz
156	Mexico_Vaquerias	Mexico	22	-102.3	Gerardo Armando Aguado Santacruz
157	Canada_LGS.3	Canada	50.7	-120.4	Lauchlan Fraser
158	Canada_UG1.LDB	Canada			Lauchlan Fraser
159	Washington_OakCreek	USA	46.7	-120.8	Andrew Kulmatiski
160	Washington_Wenas	USA	46.8	-120.7	Andrew Kulmatiski
161	California_Sedgwick	USA	34.7	-120	Carla Dantonio, Karen Stahlheber
162	Washington_LTMurray	USA	48	-120.8	Andrew Kulmatiski
163	DeseretHigh	USA	41.4	-111.4	Elisabeth Bakker, Mark Ritchie
164	California_RanchoMarino	USA	35.5	-121.1	Carla Dantonio, Barbara Fernandex-Going, Don Canestro

165	Washington_Sinlahekin	USA	48.7	-120.7	Andrew Kulmatiski
166	CedarCreek	USA	45.1	-93.2	Elisabeth Bakker, Jean Knops
167	Konza	USA	39.1	-96.6	Sally Koerner, Melinda Smith
168	KonzaPrairie	USA	39.1	-96.6	Elisabeth Bakker, Jean Knops
169	MAERC	USA	27.1	-81.2	Elizabeth Boughton, Patrick Bohlen
170	NS_East Light BIO	Canada	44	-59.8	Bill Freedman
171	NS_Main Station Dry Heath	Canada	43.9	-60	Bill Freedman
172	NS_Main Station Grassland	Canada	43.9	-60	Bill Freedman
173	NS_Main Station Mesic Heath	Canada	43.9	-60	Bill Freedman
174	NS_West Light	Canada	43.9	-60	Bill Freedman
175	NS_Wind Turbine (a)	Canada	43.9	-60	Bill Freedman
176	NS_Wind Turbine (b)	Canada	43.9	-60	Bill Freedman
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Neotropic					
177	Argentina_RMcl84	Argentina	-45.4	-70.3	Cesa Ariela
178	Argentina_S18	Argentina	-45.4	-70.3	Cesa Ariela
179	Argentina_S19	Argentina	-45.4	-70.3	Cesa Ariela
180	Argentina_S20	Argentina	-45.4	-70.3	Cesa Ariela
181	Argentina_S12	Argentina	-41.1	-70.6	Cesa Ariela
182	Argentina_S13	Argentina	-41.1	-70.6	Cesa Ariela
183	Argentina_S14	Argentina	-41.1	-70.6	Cesa Ariela
184	Argentina_S15	Argentina	-41.1	-70.6	Cesa Ariela
185	Argentina_S16	Argentina	-41.1	-70.6	Cesa Ariela
186	Argentina_S17	Argentina	-41.1	-70.6	Cesa Ariela
187	Argentina_ML	Argentina	-45.6	-71.4	Cesa Ariela
188	Argentina_S21	Argentina	-45.6	-71.4	Cesa Ariela
189	Argentina_S22	Argentina	-45.6	-71.4	Cesa Ariela
190	Argentina_S1	Argentina	-41.1	-70.9	Cesa Ariela
191	Argentina_S2	Argentina	-41.1	-70.9	Cesa Ariela
192	Argentina_S3	Argentina	-41.1	-70.9	Cesa Ariela
193	Argentina_S10	Argentina	-41.1	-71	Cesa Ariela
194	Argentina_S11	Argentina	-41.1	-71	Cesa Ariela
195	Argentina_S4	Argentina	-41.1	-71.1	Cesa Ariela
196	Argentina_S5	Argentina	-41.1	-71.1	Cesa Ariela
197	Argentina_S6	Argentina	-41.1	-71.1	Cesa Ariela
198	Argentina_S7	Argentina	-41.1	-71.1	Cesa Ariela
199	Argentina_S8	Argentina	-41.1	-71	Cesa Ariela
200	Argentina_S9	Argentina	-41.1	-71.1	Cesa Ariela
201	Argentina_Sierra	Argentina	-38.1	-62	Alejandro Loydi
202	LasChilcas	Argentina	-36.5	-58.5	Enrique Chaneton
203	Uruguay_Relincho	Uruguay	-34.3	-57	Felipe Lezama
204	Argentina_ElPalmar	Argentina	-31.9	-58.3	Felipe Lezama
205	Uruguay_Quebrada	Uruguay	-32.9	-54.5	Felipe Lezama
206	Uruguay_SUL	Uruguay	-33.9	-55.6	Felipe Lezama
207	Uruguay_Glencoe	Uruguay	-32	-57.2	Felipe Lezama
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Palarctic					
208	Tibet_Site25_Rutog_Rusong	China	33.3	79.7	Jianshuang Wu
209	Mongolia_BGgrassland	Mongolia	43.9	103.5	Takehiro Sasaki
210	Tibet_Site10_Gegyai_Xiongbar	China	32.1	81.8	Jianshuang Wu
211	Tibet_Site24_Gegyai_Xiongbar2	China	32.1	81.8	Jianshuang Wu
212	Mongolia_Mgshrubland	Mongolia	45.8	106.2	Takehiro Sasaki
213	Mongolia_Mgairport	Mongolia	45.8	106.3	Takehiro Sasaki
214	Tibet_Site23_Gegyai_Wenbudangsang	China	32.1	82.9	Jianshuang Wu
215	Tibet_Site22_Gerze_Gerze	China	32.3	84.1	Jianshuang Wu
216	Tibet_Site21_Gerze_Dongcuo	China	32.3	84.4	Jianshuang Wu
217	Tibet_Site20_Gerze_DongcuoTemple	China	32	85.1	Jianshuang Wu
218	Tibet_Site19_Nyima_Zhongcang2	China	32	85.4	Jianshuang Wu
219	Tibet_Site9_Nyima_Zhongcang	China	32	85.1	Jianshuang Wu
220	Tibet_Site18_Nyima_Erjiu2	China	32.3	86.7	Jianshuang Wu

221	Tibet_Site6_Shuanghu_Beicuo	China	33.2	87.7	Jianshuang Wu
222	Tibet_Site7_Nyima_Erjiu	China	31.9	86.9	Jianshuang Wu
223	Tibet_Site8_Nyima_Arsuo	China	31.9	86.6	Jianshuang Wu
224	Tibet_Site17_Shuanghu_Shuanghu	China	33.2	88.8	Jianshuang Wu
		Canary			
225	CanaryIsland_Valle	Islands	28.1	-17.3	Silvia Fernandez-Lugo
226	China_LC	China	43.6	116.7	Qiang Yu
227	China_SG	China	43.5	116.6	Qiang Yu
228	Tibet_Site5_Bangoin_Marqian	China	31.8	89.9	Jianshuang Wu
229	Tibet_Site16_Bangoin_Pubao2	China	31.4	90.3	Jianshuang Wu
230	Tibet_Site4_Bangoin_Pubao	China	31.4	90.3	Jianshuang Wu
231	Spain_ChapineriaHP	Spain	40.4	-4.2	Marta Rueda
232	Spain_ChapineriaLP	Spain	40.4	-4.2	Marta Rueda
233	Tibet_Site3_Bangoin_Pengcuo_South	China	31.4	91	Jianshuang Wu
		Canary			
234	CanaryIsland_Teno	Islands	28.3	-16.8	Silvia Fernandez-Lugo
235	Tibet_Site15_Bangoin_Beilar	China	31.4	91	Jianshuang Wu
236	Tibet_Site2_Amdo_Cuomar	China	32.3	91.5	Jianshuang Wu
237	Tibet_Site14_Nagqu_Namarqie	China	31.6	91.5	Jianshuang Wu
		Canary			
238	CanaryIsland_Anaga	Islands	28.5	-16.2	Silvia Fernandez-Lugo
239	Tibet_Site1_Amdo_Bangai	China	32.3	91.9	Jianshuang Wu
240	Tibet_Site12_Amdo_Marluo	China	32.3	91.9	Jianshuang Wu
241	Lapland_Jehkas	Finland	69.1	20.8	Minna-Maarit Kytöviita
242	Lapland_Saana	Finland	69.1	20.8	Minna-Maarit Kytöviita
243	Tibet_Site11_Amdo_Guozur	China	31.7	91.8	Jianshuang Wu
244	Tibet_Site13_Nagqu_Nagqu	China	31.7	92	Jianshuang Wu
245	Germany1	Germany	49.9	8.7	Angelika Schwabe, Christian Storm
246	Germany2	Germany	49.9	8.7	Angelika Schwabe, Christian Storm
247	Junner Koeland	Netherlands	52.5	6.5	Elisabeth Bakker, Han Oloff
248	SwissNP_Short	Switzerland	46.7	10.3	Anita Risch, Martin Schuetz, Martijn Vandegehuchte
249	SwissNP_Tall	Switzerland	46.7	10.3	Anita Risch, Martin Schuetz, Martijn Vandegehuchte
250	France_Heath	France	45.1	6.1	Claire Deleglise, Gregory Loucougaray
251	France_Mesic	France	44.9	5.5	Claire Deleglise, Gregory Loucougaray
252	France_Xeric	France	44.9	5.5	Claire Deleglise, Gregory Loucougaray

Supplementary Table 2. Site characteristics. Sites are organized first by Biogeographic Realm and then by site mean annual precipitation (MAP; low to high); additionally, Site # and organization are consistent between Supplementary Tables 1-3.

Site #	Site Name	MAP (mm)	MAT (°C)	ANPP (g/m ²)	Excl. Age	Site Richness	Site BP Dom	Site Simp Dom	Richness Response	BP-Dom Response	Simp Dom Response
Afrotropics											
1	Tierberg_Karoo_Research_Centre	176	14		28	16	36.9	0.25	-0.15	0.12	0.16
2	KarooNP_Sandrivier	196	17		11	54	26.5	0.16	0.02	0.11	0.01
3	KarooNP_Lammertjiesleegte	282	15		11	64	35.7	0.21	-0.17	0.17	0.22
4	Pniel	360	18		5	8	68.2	0.52	-0.14	-0.05	-0.03
5	Kruger_Letaba	400	22	118	12	75	53.0	0.30	0.00	-0.11	-0.21
6	Mali_Korokodjo	427	28	243	4	48	15.8	0.08	-0.25	-0.31	0.00
7	Kruger_Nwan	463	22	500	9	36	42.1	0.28	0.11	0.13	0.14
8	Kenya_North	493	18	512	6	33	31.5	0.17	-0.39	0.30	0.48
9	Ethiopia	500	19		30	31	30.4	0.16	-0.07	0.08	0.30
10	Mpala	514	17		4	45	35.2	0.19	-0.11	-0.14	-0.09
11	Kruger_Buff	547	22	487	7	46	64.6	0.53	0.49	-0.19	-0.29
12	Kruger_Marheya	557	21	560	7	32	76.8	0.64	0.28	-0.27	-0.35
13	Kruger_Satara	559	22	609	9	24	78.3	0.68	-0.10	0.01	0.01
14	Kruger_Nkuhlu	560	21	372	10	179	13.2	0.04	0.23	-0.73	-0.38
15	Mali_Lakamane	577	27	228	4	54	12.6	0.07	0.11	0.19	0.01
16	Kenya_Central	578	18	1204	6	32	40.3	0.23	-0.17	-0.21	-0.16
17	KLEE_cattle (O vs. C)	613	17		18	29	37.6	0.22	-0.03	-0.12	-0.08
18	KLEE_wildlife (O vs. MW)	613	17		18	36	37.6	0.22	0.06	-0.08	-0.11
19	Kenya_South	625	17	722	6	35	59.6	0.43	0.20	-0.48	-0.58
20	Serengeti_Nutnet	789	21	166	5	23	34.9	0.20	0.14	-0.12	-0.05
21	Mali_Neguella	868	27	421	2	56	18.5	0.08	0.12	-0.34	-0.15
22	Mali_Tiorola	1043	27	718	4	61	15.9	0.07	0.13	-0.24	-0.09
23	Mali_Tiendaga	1132	27	573	4	72	14.1	0.07	0.10	-0.20	-0.21
24	Mananga_High		22	311	7	44	41.5	0.26	0.16	-0.03	0.07
25	Mananga_Low		22	93	7	31	45.6	0.29	-0.13	-0.02	0.01
26	Satara North_High		22	769	7	21	73.3	0.60	0.39	-0.34	-0.40
27	Satara North_Low		22	504	5	26	60.6	0.43	0.14	-0.44	-0.42
28	Satara South_High		22	790	7	21	71.2	0.55	0.41	-0.23	-0.42
29	Satara South_Low		22	553	7	26	49.8	0.32	0.45	-0.17	-0.24
30	Shibotawna_High		22	517	7	31	35.3	0.24	0.12	0.23	0.22
31	Shibotawna_Low		22	135	7	16	52.6	0.42	-0.09	-0.22	-0.32
Australasia											
32	AUS_FowlersGap	223	18		12	53	34.7	0.20	0.10	-0.33	-0.33
33	AUS_Mallee	240	16	73	17	15	71.3	0.52	0.18	0.06	0.13
34	AUS_Arumpo	245	17		28	30	36.7	0.22	-0.24	0.14	0.09
35	AUS_Kimberley	245	17		12	78	16.1	0.06	-0.06	-0.34	-0.19
36	AUS_Ag_Biod	246	17		5	58	29.6	0.15	-0.17	0.05	0.10
37	AUS_Buronga	260	17		13	35	25.1	0.13	-0.82	0.82	1.00
38	AUS_Murray	272	17	172	15	12	87.8	0.78	0.32	0.01	0.01
39	AUS_Hattah	293	16	171	9	26	39.2	0.25	0.21	-1.30	-1.33
40	AUS_Wapweelah	312	20		19	31	28.0	0.19	0.00	0.70	0.66
41	AUS_Yathong_large	340	17		10	34	52.0	0.35	-0.61	0.15	0.52
42	AUS_Yathong_small	340	17		31	77	37.2	0.22	-0.27	0.36	0.53
43	AUS_Werrai	375	16	54	5	21	37.3	0.20	-0.16	-0.35	-0.23
44	AUS_OBriens	381	15	407	4	26	26.4	0.14	-0.05	-0.04	-0.13
45	AUS_Pinegrove	381	15	162	10	22	19.5	0.10	-0.33	0.70	0.70
46	AUS_Paradise	400	16		65	24	37.7	0.19	0.41	-0.07	-0.06
47	AUS_Kinypanial	409	15	208	12	34	18.6	0.08	0.00	0.15	0.01
48	AUS_CYP	432	16	73	10	54	33.6	0.19	0.06	-0.40	-0.56
49	AUS_Savernake	475	16		7	67	37.3	0.23	0.00	0.00	0.01

50	AUS_Inverleigh	523	13	306	11	18	93.8	0.88	0.24	-1.07	-1.69
51	AUS_Warrambeen	587	13	944	12	30	91.2	0.83	0.77	-1.42	-2.27
52	AUS_Berry	605	17		7	79	16.7	0.08	0.30	-0.50	-0.36
53	AUS_Darlington	620	13	500	3	29	40.5	0.28	0.05	-0.43	-0.73
54	AUS_Grampians	629	12	44	6	35	20.8	0.09	-0.15	-0.61	-0.40
55	AUS_Craigieburn	665	13	350	8	29	18.5	0.11	0.08	0.80	0.69
56	Molesworth_ST	680	5		19	66	19.8	0.10	0.06	0.19	0.14
57	Molesworth_SW	680	5		13	17	24.5	0.18	-0.09	0.19	0.16
58	AUS_Hamilton	686	13	242	3	22	39.8	0.27	0.33	-0.58	-0.73
59	Molesworth_CC	720	5		19	28	26.3	0.12	-0.27	0.08	0.24
60	AUS_Birregurra	730	12	712	3	23	33.4	0.26	0.10	0.23	-0.07
61	Molesworth_HG	750	5		19	48	16.2	0.08	-0.35	0.16	0.26
62	Molesworth_SD	750	5		19	25	24.5	0.16	-0.20	0.14	0.14
63	VictoriaRiverResearchStation	780	27	108	29	20	62.4	0.44	-0.11	0.20	0.30
64	Molesworth_PT	780	6		14	21	46.2	0.25	0.06	-0.46	-0.31
65	AUS_WilsonsPromontory	960	13	941	16	23	75.9	0.60	0.65	-1.12	-1.73
Indo-malay											
66	India_Kibber	400	-5	55	5	34	39.4	0.27	0.19	-0.07	-0.13
67	India_Nutnet	507	0	55	4	15	46.9	0.32	-0.08	0.07	0.17
Nearctic											
68	MNP_14mileTank	164	17		22	13	45.3	0.32	0.53	-0.61	-0.62
69	MNP_TenmileTank	181	15		22	14	35.4	0.24	-0.08	0.14	0.02
70	MNK_16mileTank	184	15		22	7	52.4	0.37	0.22	-0.20	-0.33
71	MNP_30	203	15		22	21	42.0	0.31	-0.32	0.41	0.42
72	Park Pasture	213	7		56	27	28.9	0.18	-0.05	-0.25	-0.19
73	Cisco Wash 1	215	10		51	16	41.4	0.27	-0.08	0.01	0.15
74	Cisco Wash 2	215	10		51	24	58.5	0.37	-0.11	-0.50	-0.46
75	Cisco Mesa	223	10		53	21	32.8	0.23	-0.06	0.32	0.22
76	Sand Flat	225	8		51	28	51.4	0.30	0.10	-0.45	-0.46
77	N_Clan	229	8		23	22	41.3	0.26	-0.29	0.18	0.29
78	Hotel Mesa	237	11		51	32	21.0	0.12	0.29	0.23	0.19
79	Westwater	242	9		51	20	33.8	0.25	0.59	0.14	-0.18
80	Horse Pature	270	8		48	23	54.0	0.35	0.11	-0.33	-0.25
81	Buckhorn	272	9		51	29	32.5	0.20	0.34	-0.25	-0.29
82	Jornada	280	14		23	43	63.3	0.51	-0.09	0.05	0.11
83	Neponset	286	7		20	26	14.2	0.07	0.00	0.45	0.30
84	Dry Valley	293	9		35	18	59.5	0.39	-0.21	-0.18	-0.14
85	Canada_Currie	304	6	155	73	12	76.1	0.59	0.11	-1.19	-1.27
86	Canada_LGS.6	304	6	187	10	16	73.4	0.56	0.07	-0.18	-0.32
87	DeseretLow	305	2	125	7	18	52.5	0.36	0.24	-0.20	-0.15
88	DeseretSage	305	4	47	7	27	32.8	0.19	0.09	-0.15	-0.08
89	Kate Hollow	310	3		20	23	24.7	0.10	0.20	-0.45	-0.34
90	Canada_Dewdrop.2	320	6	164	37	13	70.0	0.51	0.09	-0.83	-0.84
91	Canada_Ils1	320	6	198	13	16	47.3	0.40	0.59	-0.11	-0.42
92	Salt Creek Mesa	320	11		43	23	32.8	0.16	-0.10	0.00	0.25
93	Short Grass Steppe	322	8	91	7	48	56.3	0.39	-0.21	0.09	0.07
94	Stanley Park	322	10		54	24	45.6	0.34	0.38	0.40	0.34
95	Canada_hav	327	4	202	13	20	32.9	0.18	0.11	-0.10	-0.21
96	Canada_hbb	327	4	248	13	14	54.8	0.37	0.18	-0.24	-0.25
97	Canada_MG1.LDB	327	6	231	30	16	55.0	0.36	-0.21	0.00	0.02
98	Canada_MG2.LDB	327	6	215	30	20	45.6	0.26	0.18	0.11	0.12
99	House Park	327	8		55	35	31.8	0.16	0.23	0.06	-0.02
100	Canada_hkb	328	4	276	13	11	88.9	0.80	1.03	-0.97	-1.29
101	Canada_MG3.LDB	328	6	250	30	21	73.4	0.55	-0.06	-0.57	-0.87
102	Canada_Goose.Lake	329	4	284	78	24	71.3	0.52	-0.11	-1.19	-1.29
103	Canada_Lundbom.Lake	329	4	191	26	9	58.5	0.38	0.32	0.04	0.07
104	N_Sulphur	332	7		82	20	38.2	0.26	-0.07	0.27	0.31
105	North Cottonwood	332	12		55	25	36.7	0.23	0.06	-0.32	-0.24

106	Canada_gooselake2	334	4	252	5	18	22.3	0.16	0.06	0.50	0.27
107	Canada_Mara.1	334	6	158	73	16	57.2	0.37	-0.15	0.30	0.49
108	Harts Point	338	7		53	15	49.6	0.34	0.00	0.07	0.20
109	Texas Flat	338	3		55	25	23.0	0.14	0.15	0.78	0.71
110	FortKeogh	339	7	124	20	48	49.0	0.35	0.00	0.05	0.08
111	CPER	340	8	70	72	78	46.3	0.31	0.08	0.23	0.25
112	Steamboat Mesa	345	9		45	20	29.6	0.21	-0.06	0.16	0.01
113	Wild Cow Point	349	8		55	25	29.2	0.21	0.05	0.11	-0.15
114	N_Pryor	352	6		22	66	38.1	0.24	0.07	-0.10	-0.17
115	Canada_Dewdrop.1	353	6	84	37	9	51.7	0.38	0.41	0.00	-0.05
116	Canada_IIrs	353	6	312	30	16	51.9	0.33	0.24	-0.34	-0.60
117	Canada_LG5.LDB	362	6	219	30	12	88.8	0.79	0.32	-0.14	-0.26
118	Canada_Summit.North	362	4	340	41	17	44.0	0.26	0.29	-0.84	-0.81
119	Canada_LG4.LDB	364	6	147	30	17	58.5	0.40	0.69	-0.26	-0.44
120	Canada_Repeter	364	4	319	39	12	39.1	0.31	0.49	-0.45	-0.71
121	Canada_LGS.4	365	6	127	10	12	72.2	0.55	0.29	-0.19	-0.28
122	Canada_UG2.LDB	365		179	30	13	43.1	0.32	0.37	-0.42	-0.72
123	Harts Draw	372	9		56	18	54.8	0.37	0.44	-0.37	-0.24
124	Canada_LG2.LDB	373		189	30	12	72.2	0.56	0.11	0.07	0.10
125	Canada_Powerline	373	4	219	13	15	79.6	0.65	0.92	-1.65	-1.70
126	Canada_hsr	375	4	211	13	20	52.1	0.30	-0.18	-0.19	-0.11
127	Canada_MGBR.1	375	6	288	30	20	57.8	0.38	0.00	-0.18	-0.33
128	Canada_LG1.LDB	376	6	115	30	9	78.6	0.63	0.29	-0.63	-0.80
129	Canada_MGBR.2	376	6	271	30	21	30.3	0.20	-0.19	-0.08	-0.07
130	Canada_LGS.5	383	6	173	10	12	71.6	0.56	-0.25	-0.52	-0.60
131	Canada_UG3.LDB	383		229	26	15	98.2	0.97	1.25	-0.36	-0.67
132	Canada_LG3.LDB	384	6	153	30	13	57.6	0.38	-0.10	-0.11	-0.15
133	Canada_Redhil	384	6	314	50	16	45.8	0.27	0.06	0.08	0.09
134	Canada_Frolek	388	6	294	51	18	56.0	0.35	0.31	-0.82	-0.89
135	Canada_Long.lake.6	388	6	230	30	22	47.9	0.27	-0.10	-0.06	-0.12
136	N_Theodore	389	6		68	111	41.7	0.24	-0.07	-0.48	-0.47
137	The Dip	390	9		20	25	18.2	0.08	0.14	0.00	0.03
138	Canada_LGS.1	391	6	88	10	16	68.2	0.49	0.24	-0.16	-0.24
139	Canada_Summit.South	391	4	418	41	14	60.5	0.40	0.75	-0.13	-0.23
140	California_Sedgwick_Airstrip	401	14	271	13	30	65.4	0.55	0.34	-0.22	-0.33
141	California_Sedgwick_Lisque	401	14	271	16	56	43.3	0.26	0.19	-0.08	-0.14
142	California_Sedgwick_Mesa	401	14	271	16	54	61.5	0.42	0.47	-0.89	-1.00
143	Lost Park	409	3		55	15	80.0	0.65	0.29	-0.17	-0.27
144	Canada_LGS.2	412	6	163	10	10	43.7	0.27	0.18	0.07	0.22
145	Canada_TMV	412	6	221	19	17	30.7	0.16	-0.13	0.03	0.03
146	N_Spring	413	7		12	46	43.7	0.27	0.10	-0.17	-0.14
147	Canada_Drum	434	5	99	15	13	46.7	0.34	-0.10	0.31	0.24
148	Canada_IIw	434	6	206	30	13	25.4	0.17	-0.09	0.17	0.08
149	Canada_FLHT.2	441	6	188	10	14	57.8	0.42	0.20	0.25	0.30
150	Canada_Long.lake.5	441	6	208	30	17	49.1	0.29	0.12	-0.22	-0.27
151	Canada_fht1	448	6	247	10	18	67.1	0.48	0.27	-0.21	-0.35
152	Canada_Long.lake.4	448	6	198	30	15	32.5	0.18	0.07	0.30	0.38
153	Mexico_LaColorada	450	17	114	6	34	37.9	0.19	-0.37	-0.20	-0.23
154	Mexico_LaMesa	450	17	100	5	13	53.9	0.33	-0.20	-0.20	-0.07
155	Mexico_LaPresa	450	17	132	7	37	41.6	0.24	-0.41	-0.10	-0.16
156	Mexico_Vaquerias	450	17	88	6	31	27.2	0.19	0.29	0.00	-0.22
157	Canada_LGS.3	469	6	176	10	20	43.9	0.31	0.35	0.26	0.17
158	Canada_UG1.LDB	469		255	30	12	85.0	0.73	0.26	-0.23	-0.45
159	Washington_OakCreek	526	7	200	51	45	10.0	0.06	0.14	-0.07	-0.04
160	Washington_Wenas	526	8	13	31	27	25.3	0.16	0.32	-0.35	-0.41
161	California_Sedgwick	565	14	287	16	37	44.6	0.30	0.04	-0.13	-0.25
162	Washington_LTMurray	569	4	22	31	29	23.0	0.15	0.16	-0.03	-0.19
163	DeseretHigh	635	2	203	7	33	30.8	0.19	0.10	-0.26	-0.30

164	California_RanchoMarino	733	13	422	7	42	50.1	0.33	0.03	-0.18	-0.24
165	Washington_Sinlahekin	737	0	97	51	64	22.1	0.14	-0.16	0.06	0.02
166	CedarCreek	825	7	222	7	84	22.9	0.13	0.03	0.42	0.39
167	Konza	835	12	525	8	95	53.7	0.36	0.39	-0.48	-0.61
168	KonzaPrairie	835	22	302	7	56	28.0	0.17	0.33	-0.02	-0.24
169	MAERC	1364	22	1105	13	25	63.6	0.51	0.50	0.22	0.23
170	NS_East Light BIO	1511	7		20	19	48.8	0.30	0.00	-0.79	-0.70
171	NS_Main Station Dry Heath	1511	7		20	26	27.4	0.17	-0.10	0.04	0.08
172	NS_Main Station Grassland	1511	7		20	19	36.6	0.21	0.13	0.06	0.10
173	NS_Main Station Mesic Heath	1511	7		20	26	25.6	0.11	0.09	-0.18	0.11
174	NS_West Light	1511	7		10	19	58.6	0.37	-0.21	-0.57	-0.67
175	NS_Wind Turbine (a)	1511	7		4	21	32.1	0.18	-0.06	0.03	0.26
176	NS_Wind Turbine (b)	1511	7		4	25	35.7	0.19	0.23	-0.18	-0.13
Neotropic											
177	Argentina_RMcl84	199	9		15	31	28.0	0.16	-0.11	0.17	0.23
178	Argentina_S18	199	9		47	18	35.2	0.23	-0.22	0.24	0.20
179	Argentina_S19	199	9		27	19	25.4	0.17	-0.57	0.48	0.62
180	Argentina_S20	199	9		15	15	32.2	0.22	-0.34	0.04	0.10
181	Argentina_S12	297	7		59	9	62.7	0.48	-0.56	0.16	0.28
182	Argentina_S13	297	7		59	11	53.1	0.39	-0.16	0.15	0.08
183	Argentina_S14	297	7		59	11	64.5	0.46	-0.42	-0.32	-0.26
184	Argentina_S15	297	7		59	17	36.1	0.20	-0.31	0.07	0.26
185	Argentina_S16	297	7		59	14	61.3	0.44	-0.01	-0.33	-0.31
186	Argentina_S17	297	7		59	16	61.6	0.44	-0.13	-0.29	-0.35
187	Argentina_ML	365	5		14	35	54.3	0.33	-0.10	-0.24	-0.35
188	Argentina_S21	365	5		14	25	61.4	0.40	-0.02	-0.30	-0.46
189	Argentina_S22	365	5		14	21	39.6	0.25	-0.19	0.42	0.44
190	Argentina_S1	472	7		59	25	27.5	0.16	-0.40	0.37	0.55
191	Argentina_S2	472	7		59	20	48.5	0.35	0.08	0.16	0.07
192	Argentina_S3	472	7		59	18	73.2	0.56	-0.60	0.07	0.14
193	Argentina_S10	530	7		59	15	44.0	0.27	-1.23	0.74	1.16
194	Argentina_S11	530	7		59	18	45.9	0.34	-0.20	-0.25	-0.26
195	Argentina_S4	530	7		59	18	69.0	0.53	-0.11	0.06	0.07
196	Argentina_S5	530	7		59	22	62.5	0.44	-0.57	0.03	0.10
197	Argentina_S6	530	7		59	17	77.1	0.60	-0.57	-0.11	-0.14
198	Argentina_S7	530	7		59	20	42.5	0.26	-0.37	-0.03	0.07
199	Argentina_S8	530	7		59	13	48.1	0.32	-0.33	-0.22	-0.06
200	Argentina_S9	530	7		59	17	40.0	0.27	-0.20	0.25	0.19
201	Argentina_Sierra	800	12	500	16	61	26.6	0.13	0.07	0.10	0.21
202	LasChilcas	953	14	530	21	54	21.5	0.13	0.42	0.05	-0.10
203	Uruguay_Relincho	1155	16	655	11	91	24.7	0.12	0.29	-0.09	-0.24
204	Argentina_ElPalmar	1338	18	720	30	90	36.7	0.22	0.51	-0.32	-0.36
205	Uruguay_Quebrada	1341	16	585	6	92	24.2	0.10	-0.05	-0.10	-0.07
206	Uruguay_SUL	1341	16	707	13	59	25.6	0.12	0.34	0.44	0.45
207	Uruguay_Glencoe	1495	18	650	18	94	33.3	0.14	0.11	-0.84	-0.78
Palerarctic											
208	Tibet_Site25_Rutog_Rusong	45	-4		4	3	60.9	0.45	-0.41	0.15	0.27
209	Mongolia_BGgrassland	116	3		9	23	61.9	0.46	-0.07	-0.05	-0.03
210	Tibet_Site10_Gegyai_Xiongbar	120	-2		3	8	68.4	0.52	-0.85	0.16	0.25
211	Tibet_Site24_Gegyai_Xiongbar2	120	-2		4	8	67.6	0.48	-0.13	0.06	0.11
212	Mongolia_Mgshrubland	121	1		9	28	62.1	0.45	0.58	-0.46	-0.62
213	Mongolia_Mgairport	130	1		35	18	44.9	0.29	0.10	0.16	0.31
214	Tibet_Site23_Gegyai_Wenbudangsang	150	-4		4	7	81.3	0.69	0.41	-0.50	-0.57
215	Tibet_Site22_Gerze_Gerze	170	-1		4	9	37.3	0.23	-0.47	0.52	0.70
216	Tibet_Site21_Gerze_Dongcuo	180	-1		4	8	34.5	0.28	0.29	0.46	0.16
217	Tibet_Site20_Gerze_DongcuoTemple	212	-2		4	14	56.6	0.36	0.29	-0.12	-0.20
218	Tibet_Site19_Nyima_Zhongcang2	220	-2		4	11	66.8	0.48	-0.25	-0.43	-0.42
219	Tibet_Site9_Nyima_Zhongcang	225	-2		3	9	76.6	0.61	0.29	0.02	0.02

220	Tibet_Site18_Nyima_Erjiu2	245	-3	4	5	86.5	0.76	0.00	-0.12	-0.19
221	Tibet_Site6_Shuanghu_Beicuo	250	-5	3	9	65.8	0.46	0.00	-0.07	-0.07
222	Tibet_Site7_Nyima_Erjiu	258	-1	3	6	64.3	0.47	0.18	0.09	0.10
223	Tibet_Site8_Nyima_Arsuo	258	-2	3	8	48.1	0.30	-0.47	0.11	0.23
224	Tibet_Site17_Shuanghu_Shuanghu	292	-7	4	9	76.1	0.59	-0.12	-0.51	-0.78
225	CanaryIsland_Valle	313	17	174	4	92	40.7	0.23	0.00	0.07
226	China_LC	334	1	150	29	30	27.6	0.16	-0.56	0.53
227	China_SG	334	1	150	28	28	34.3	0.20	-0.30	0.79
228	Tibet_Site5_Bangoin_Marqian	376	-2	3	16	50.5	0.34	0.08	-0.34	-0.22
229	Tibet_Site16_Bangoin_Pubao2	400	-2	4	16	39.7	0.29	0.15	-0.07	-0.18
230	Tibet_Site4_Bangoin_Pubao	405	-2	3	22	37.1	0.21	0.22	-0.31	-0.43
231	Spain_ChapineriaHP	433	13	837	6	56	28.2	0.17	0.42	-0.25
232	Spain_ChapineriaLP	433	13	230	6	42	22.2	0.12	-0.16	0.95
233	Tibet_Site3_Bangoin_Pengcuo_South	448	-3	3	19	34.0	0.18	-0.27	0.18	0.28
234	CanaryIsland_Teno	450	13	6	136	24.8	0.11	-0.03	-0.05	0.07
235	Tibet_Site15_Bangoin_Beilar	450	-3	4	27	21.4	0.11	-0.05	0.75	0.83
236	Tibet_Site2_Amdo_Cuomar	468	-4	3	29	32.2	0.18	0.51	0.02	-0.23
237	Tibet_Site14_Nagqu_Namarqie	475	-3	4	11	57.8	0.38	0.00	-0.24	-0.30
238	CanaryIsland_Anaga	480	17	256	4	114	25.7	0.10	-0.09	0.31
239	Tibet_Site1_Amdo_Bangai	484	-4	3	29	61.2	0.39	-0.29	-0.30	-0.50
240	Tibet_Site12_Amdo_Marluo	484	-4	4	33	38.5	0.18	0.24	-0.19	-0.24
241	Lapland_Jehkas	489	-3	185	11	32	76.1	0.59	0.11	-0.11
242	Lapland_Saana	489	-3	185	11	33	76.2	0.59	-0.10	-0.01
243	Tibet_Site11_Amdo_Guozur	494	-3	4	23	37.6	0.21	-0.10	-0.12	-0.19
244	Tibet_Site13_Nagqu_Nagqu	508	-3	4	21	40.2	0.24	-0.60	0.44	0.58
245	Germany1	629	9	11	105	19.6	0.09	0.18	0.36	0.26
246	Germany2	629	9	14	55	51.3	0.35	0.13	-0.08	-0.14
247	Junner Koeland	758	9	463	7	42	52.0	0.38	0.21	0.01
248	SwissNP_Short	850	0	401	5	113	21.8	0.11	0.00	0.01
249	SwissNP_Tall	850	0	500	5	117	25.5	0.12	0.02	0.06
250	France_Heath	940	4	320	30	80	30.6	0.15	0.11	-0.23
251	France_Mesic	1380	6	220	30	75	25.7	0.11	0.01	0.08
252	France_Xeric	1380	6	130	30	64	16.1	0.08	-0.09	0.25

Supplementary Table 3. Data Subsets. In this manuscript, different subsets of data were used depending on if the analysis required a site level estimate of ANPP (Subset 1), a site level estimate of MAP (used as a proxy for ANPP; Subset 2), or both ANPP and MAP estimates (Subset 3). Sites are organized first by Biogeographic Realm and then by site mean annual precipitation (MAP; low to high); additionally, Site # and organization are consistent between Supplementary Tables 1-3.

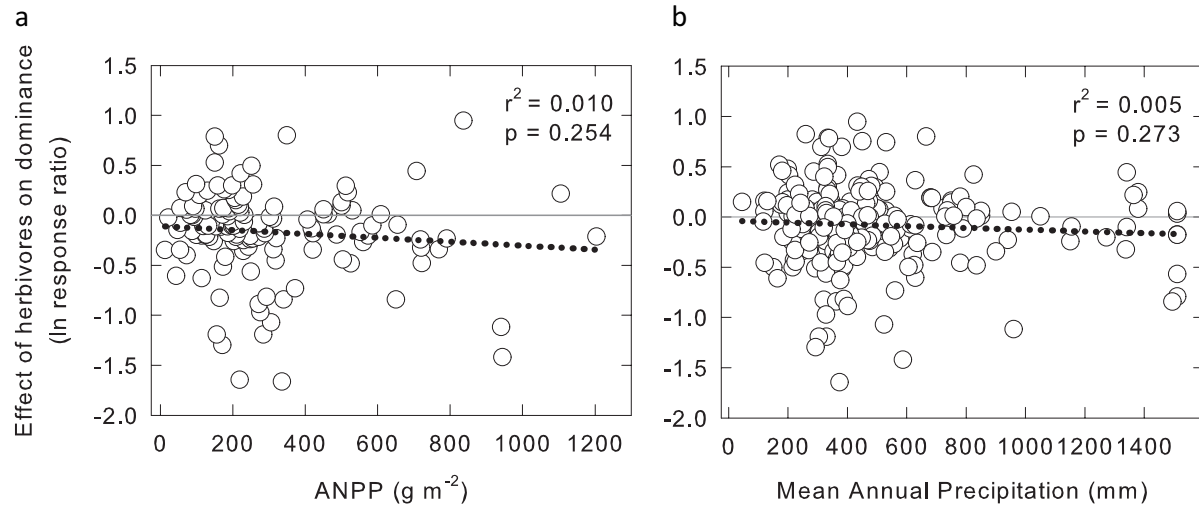
Site #	Site Name	Data Subset 1 [Used in analyses which required site level ANPP estimate]	Data Subset 2 [Used in analyses which required site level MAP]	Data Subset 3 [Used in analyses which required both site level ANPP & MAP]
Afrotropics				
1	Tierberg_Karoo_Research_Centre	No	Yes	No
2	KarooNP_Sandrivier	No	Yes	No
3	KarooNP_Lammertjiesleegte	No	Yes	No
4	Pniel	No	Yes	No
5	Kruger_Letaba	Yes	Yes	Yes
6	Mali_Korokodjo	Yes	Yes	Yes
7	Kruger_Nwan	Yes	Yes	Yes
8	Kenya_North	Yes	Yes	Yes
9	Ethiopia	No	Yes	No
10	Mpala	No	Yes	No
11	Kruger_Buff	Yes	Yes	Yes
12	Kruger_Marheya	Yes	Yes	Yes
13	Kruger_Satara	Yes	Yes	Yes
14	Kruger_Nkuhlu	Yes	Yes	Yes
15	Mali_Lakamane	Yes	Yes	Yes
16	Kenya_Central	Yes	Yes	Yes
17	KLEE_cattle (O vs. C)	No	Yes	No
18	KLEE_wildlife (O vs. MW)	No	Yes	No
19	Kenya_South	Yes	Yes	Yes
20	Serengeti_Nutnet	Yes	Yes	Yes
21	Mali_Neguela	Yes	Yes	Yes
22	Mali_Tiorola	Yes	Yes	Yes
23	Mali_Tiendaga	Yes	Yes	Yes
24	Mananga_High	Yes	No	No
25	Mananga_Low	Yes	No	No
26	Satara_North_High	Yes	No	No
27	Satara_North_Low	Yes	No	No
28	Satara_South_High	Yes	No	No
29	Satara_South_Low	Yes	No	No
30	Shibotawna_High	Yes	No	No
31	Shibotawna_Low	Yes	No	No
Australasia				
32	AUS_FowlersGap	No	Yes	No
33	AUS_Mallee	Yes	Yes	Yes
34	AUS_Arumpo	No	Yes	No
35	AUS_Kimberley	No	Yes	No
36	AUS_Ag_Biod	No	Yes	No
37	AUS_Buronga	No	Yes	No
38	AUS_Murray	Yes	Yes	Yes
39	AUS_Hattah	Yes	Yes	Yes
40	AUS_Wapweelah	No	Yes	No
41	AUS_Yathong_large	No	Yes	No
42	AUS_Yathong_small	No	Yes	No
43	AUS_Werrai	Yes	Yes	Yes
44	AUS_OBriens	Yes	Yes	Yes

45	AUS_Pinegrove	Yes	Yes	Yes
46	AUS_Paradise	No	Yes	No
47	AUS_Kinypanial	Yes	Yes	Yes
48	AUS_CYP	Yes	Yes	Yes
49	AUS_Savernake	No	Yes	No
50	AUS_Inverleigh	Yes	Yes	Yes
51	AUS_Warrambeen	Yes	Yes	Yes
52	AUS_Berry	No	Yes	No
53	AUS_Darlington	Yes	Yes	Yes
54	AUS_Grampians	Yes	Yes	Yes
55	AUS_Craigieburn	Yes	Yes	Yes
56	Molesworth_ST	No	Yes	No
57	Molesworth_SW	No	Yes	No
58	AUS_Hamilton	Yes	Yes	Yes
59	Molesworth_CC	No	Yes	No
60	AUS_Birregurra	Yes	Yes	Yes
61	Molesworth_HG	No	Yes	No
62	Molesworth_SD	No	Yes	No
63	VictoriaRiverResearchStation	Yes	Yes	Yes
64	Molesworth_PT	No	Yes	No
65	AUS_WilsonsPromontory	Yes	Yes	Yes
<hr/>				
Indo-malay				
<hr/>				
66	India_Kibber	Yes	Yes	Yes
67	India_Nutnet	Yes	Yes	Yes
<hr/>				
Nearctic				
<hr/>				
68	MNP_14mileTank	No	Yes	No
69	MNP_TenmileTank	No	Yes	No
70	MNK_16mileTank	No	Yes	No
71	MNP_30	No	Yes	No
72	Park Pasture	No	Yes	No
73	Cisco Wash 1	No	Yes	No
74	Cisco Wash 2	No	Yes	No
75	Cisco Mesa	No	Yes	No
76	Sand Flat	No	Yes	No
77	N_Clan	No	Yes	No
78	Hotel Mesa	No	Yes	No
79	Westwater	No	Yes	No
80	Horse Pature	No	Yes	No
81	Buckhorn	No	Yes	No
82	Jornada	No	Yes	No
83	Neponset	No	Yes	No
84	Dry Valley	No	Yes	No
85	Canada_Currie	Yes	Yes	Yes
86	Canada_LGS.6	Yes	Yes	Yes
87	DeseretLow	Yes	Yes	Yes
88	DeseretSage	Yes	Yes	Yes
89	Kate Hollow	No	Yes	No
90	Canada_Dewdrop.2	Yes	Yes	Yes
91	Canada_Ils1	Yes	Yes	Yes
92	Salt Creek Mesa	No	Yes	No
93	Short Grass Steppe	Yes	Yes	Yes
94	Stanley Park	No	Yes	No
95	Canada_hav	Yes	Yes	Yes
96	Canada_hbb	Yes	Yes	Yes
97	Canada_MG1.LDB	Yes	Yes	Yes
98	Canada_MG2.LDB	Yes	Yes	Yes
99	House Park	No	Yes	No
100	Canada_hkb	Yes	Yes	Yes

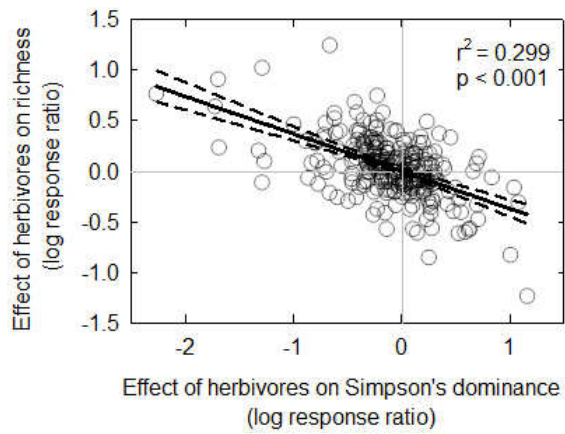
101	Canada_MG3.LDB	Yes	Yes	Yes
102	Canada_Goose.Lake	Yes	Yes	Yes
103	Canada_Lundbom.Lake	Yes	Yes	Yes
104	N_Sulphur	No	Yes	No
105	North Cottonwood	No	Yes	No
106	Canada_gooselake2	Yes	Yes	Yes
107	Canada_Mara.1	Yes	Yes	Yes
108	Harts Point	No	Yes	No
109	Texas Flat	No	Yes	No
110	FortKeogh	Yes	Yes	Yes
111	CPER	Yes	Yes	Yes
112	Steamboat Mesa	No	Yes	No
113	Wild Cow Point	No	Yes	No
114	N_Pryor	No	Yes	No
115	Canada_Dewdrop.1	Yes	Yes	Yes
116	Canada_Illrs	Yes	Yes	Yes
117	Canada_LG5.LDB	Yes	Yes	Yes
118	Canada_Summit.North	Yes	Yes	Yes
119	Canada_LG4.LDB	Yes	Yes	Yes
120	Canada_Repeter	Yes	Yes	Yes
121	Canada_LGS.4	Yes	Yes	Yes
122	Canada_UG2.LDB	Yes	Yes	Yes
123	Harts Draw	No	Yes	No
124	Canada_LG2.LDB	Yes	Yes	Yes
125	Canada_Powerline	Yes	Yes	Yes
126	Canada_hsr	Yes	Yes	Yes
127	Canada_MGBR.1	Yes	Yes	Yes
128	Canada_LG1.LDB	Yes	Yes	Yes
129	Canada_MGBR.2	Yes	Yes	Yes
130	Canada_LGS.5	Yes	Yes	Yes
131	Canada_UG3.LDB	Yes	Yes	Yes
132	Canada_LG3.LDB	Yes	Yes	Yes
133	Canada_Redhil	Yes	Yes	Yes
134	Canada_Frolek	Yes	Yes	Yes
135	Canada_Long.lake.6	Yes	Yes	Yes
136	N_Theodore	No	Yes	No
137	The Dip	No	Yes	No
138	Canada_LGS.1	Yes	Yes	Yes
139	Canada_Summit.South	Yes	Yes	Yes
140	California_Sedgwick_Airstrip	Yes	Yes	Yes
141	California_Sedgwick_Lisque	Yes	Yes	Yes
142	California_Sedgwick_Mesa	Yes	Yes	Yes
143	Lost Park	No	Yes	No
144	Canada_LGS.2	Yes	Yes	Yes
145	Canada_TMV	Yes	Yes	Yes
146	N_Spring	No	Yes	No
147	Canada_Drum	Yes	Yes	Yes
148	Canada_Illw	Yes	Yes	Yes
149	Canada_FLHT.2	Yes	Yes	Yes
150	Canada_Long.lake.5	Yes	Yes	Yes
151	Canada_fht1	Yes	Yes	Yes
152	Canada_Long.lake.4	Yes	Yes	Yes
153	Mexico_LaColorada	Yes	Yes	Yes
154	Mexico_LaMesa	Yes	Yes	Yes
155	Mexico_LaPresa	Yes	Yes	Yes
156	Mexico_Vaquerias	Yes	Yes	Yes
157	Canada_LGS.3	Yes	Yes	Yes
158	Canada_UG1.LDB	Yes	Yes	Yes

159	Washington_OakCreek	Yes	Yes	Yes
160	Washington_Wenas	Yes	Yes	Yes
161	California_Sedgwick	Yes	Yes	Yes
162	Washington_LTMurray	Yes	Yes	Yes
163	DeserethHigh	Yes	Yes	Yes
164	California_RanchoMarino	Yes	Yes	Yes
165	Washington_Sinlahekin	Yes	Yes	Yes
166	CedarCreek	Yes	Yes	Yes
167	Konza	Yes	Yes	Yes
168	KonzaPrairie	Yes	Yes	Yes
169	MAERC	Yes	Yes	Yes
170	NS_East Light BIO	No	Yes	No
171	NS_Main Station Dry Heath	No	Yes	No
172	NS_Main Station Grassland	No	Yes	No
173	NS_Main Station Mesic Heath	No	Yes	No
174	NS_West Light	No	Yes	No
175	NS_Wind Turbine (a)	No	Yes	No
176	NS_Wind Turbine (b)	No	Yes	No
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Neotropic				
177	Argentina_RMcl84	No	Yes	No
178	Argentina_S18	No	Yes	No
179	Argentina_S19	No	Yes	No
180	Argentina_S20	No	Yes	No
181	Argentina_S12	No	Yes	No
182	Argentina_S13	No	Yes	No
183	Argentina_S14	No	Yes	No
184	Argentina_S15	No	Yes	No
185	Argentina_S16	No	Yes	No
186	Argentina_S17	No	Yes	No
187	Argentina_ML	No	Yes	No
188	Argentina_S21	No	Yes	No
189	Argentina_S22	No	Yes	No
190	Argentina_S1	No	Yes	No
191	Argentina_S2	No	Yes	No
192	Argentina_S3	No	Yes	No
193	Argentina_S10	No	Yes	No
194	Argentina_S11	No	Yes	No
195	Argentina_S4	No	Yes	No
196	Argentina_S5	No	Yes	No
197	Argentina_S6	No	Yes	No
198	Argentina_S7	No	Yes	No
199	Argentina_S8	No	Yes	No
200	Argentina_S9	No	Yes	No
201	Argentina_Sierra	Yes	Yes	Yes
202	LasChilcas	Yes	Yes	Yes
203	Uruguay_Relincho	Yes	Yes	Yes
204	Argentina_ElPalmar	Yes	Yes	Yes
205	Uruguay_Quebrada	Yes	Yes	Yes
206	Uruguay_SUL	Yes	Yes	Yes
207	Uruguay_Glencoe	Yes	Yes	Yes
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Palarctic				
208	Tibet_Site25_Rutog_Rusong	No	Yes	No
209	Mongolia_BGgrassland	No	Yes	No
210	Tibet_Site10_Gegyai_Xiongbar	No	Yes	No
211	Tibet_Site24_Gegyai_Xiongbar2	No	Yes	No
212	Mongolia_Mgshrubland	No	Yes	No
213	Mongolia_Mgairport	No	Yes	No
214	Tibet_Site23_Gegyai_Wenbudangsang	No	Yes	No

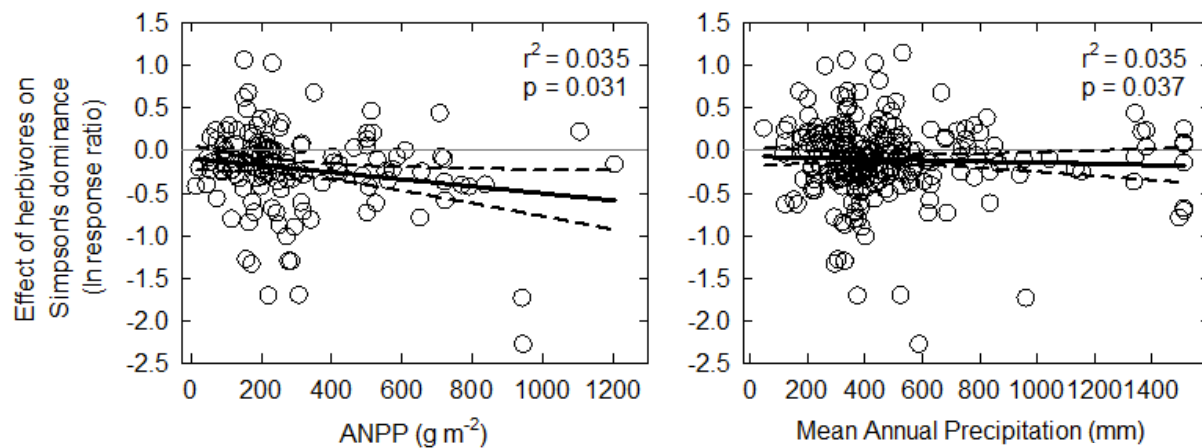
215	Tibet_Site22_Gerze_Gerze	No	Yes	No
216	Tibet_Site21_Gerze_Dongcuo	No	Yes	No
217	Tibet_Site20_Gerze_DongcuoTemple	No	Yes	No
218	Tibet_Site19_Nyima_Zhongcang2	No	Yes	No
219	Tibet_Site9_Nyima_Zhongcang	No	Yes	No
220	Tibet_Site18_Nyima_Erjiu2	No	Yes	No
221	Tibet_Site6_Shuanghu_Beicuo	No	Yes	No
222	Tibet_Site7_Nyima_Erjiu	No	Yes	No
223	Tibet_Site8_Nyima_Arsuo	No	Yes	No
224	Tibet_Site17_Shuanghu_Shuanghu	No	Yes	No
225	CanaryIsland_Valle	Yes	Yes	Yes
226	China_LC	Yes	Yes	Yes
227	China_SG	Yes	Yes	Yes
228	Tibet_Site5_Bangoin_Marqian	No	Yes	No
229	Tibet_Site16_Bangoin_Pubao2	No	Yes	No
230	Tibet_Site4_Bangoin_Pubao	No	Yes	No
231	Spain_ChapineriaHP	Yes	Yes	Yes
232	Spain_ChapineriaLP	Yes	Yes	Yes
233	Tibet_Site3_Bangoin_Pengcuo_South	No	Yes	No
234	CanaryIsland_Teno	No	Yes	No
235	Tibet_Site15_Bangoin_Beilar	No	Yes	No
236	Tibet_Site2_Amdo_Cuomar	No	Yes	No
237	Tibet_Site14_Nagqu_Namarqie	No	Yes	No
238	CanaryIsland_Anaga	Yes	Yes	Yes
239	Tibet_Site1_Amdo_Bangai	No	Yes	No
240	Tibet_Site12_Amdo_Marluo	No	Yes	No
241	Lapland_Jehkas	Yes	Yes	Yes
242	Lapland_Saana	Yes	Yes	Yes
243	Tibet_Site11_Amdo_Guozur	No	Yes	No
244	Tibet_Site13_Nagqu_Nagqu	No	Yes	No
245	Germany1	No	Yes	No
246	Germany2	No	Yes	No
247	Junner Koeland	Yes	Yes	Yes
248	SwissNP_Short	Yes	Yes	Yes
249	SwissNP_Tall	Yes	Yes	Yes
250	France_Heath	Yes	Yes	Yes
251	France_Mesic	Yes	Yes	Yes
252	France_Xeric	Yes	Yes	Yes



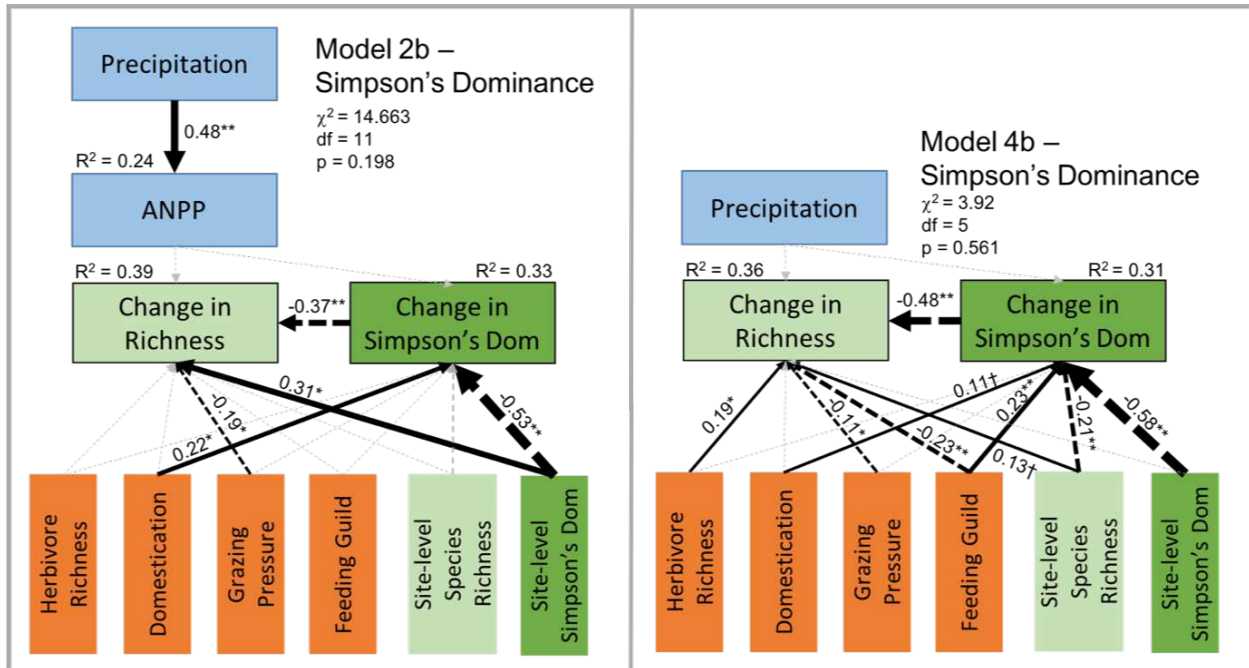
Supplementary Figure 1. Effects of ANPP and mean annual precipitation on Berger-Parker dominance response to herbivory. **a**, The relationship between aboveground net primary production (ANPP) and the response of plant-species dominance (Berger-Parker) to herbivory ($\ln(G/UG)$), where G is the average plant species dominance in grazed plots and UG is the same measurement in ungrazed plots ($n=132$; Data Subset 1 in Supplementary Table 3). **b**, The relationship between mean annual precipitation and the response of plant species dominance (Berger-Parker) to herbivory ($n=246$; Data Subset 2 in Supplementary Table 3).



Supplementary Figure 2. Relationship between the change in Simpson's dominance and the change in species richness as a function of herbivory ($\ln(G/UG)$) ($n=252$; all data).



Supplementary Figure 3. Effects of ANPP and mean annual precipitation on Simpson's dominance response to herbivory. **a**, The relationship between aboveground net primary production (ANPP) and the response of plant-species dominance (Simpson's) to herbivory ($\ln(G/UG)$), where G is the average plant species dominance in grazed plots and UG is the same measurement in ungrazed plots (n=132; Data Subset 1 in Supplementary Table 3). **b**, The relationship between mean annual precipitation and the response of plant species dominance (Simpson's) to herbivory (n=246; Data Subset 2 in Supplementary Table 3).



Supplementary Figure 4. Drivers of plant richness response to herbivores. **a** Path analyses testing the importance of aboveground net primary productivity (ANPP) and Simpson's dominance (Model 2b - Simpson's) on the change in species richness in response to herbivory. These models are restricted to sites where both ANPP and precipitation data were available ($n=122$; Data Subset 3 in Supplementary Table 3). **b** Path analyses testing the importance of productivity using precipitation as a proxy for productivity and dominance (Model 4b - Simpson's) on the change in species richness in response to herbivory ($n=244$; Data Subset 2 in Supplementary Table 3). See Supplementary Table 6 & 9 for bivariate correlations between input variables which were included in these models to improve model fit. All models also test for the effects of site and herbivore characteristics (see Methods). ** $p < 0.001$, * $p < 0.05$, † $p < 0.10$. Non-significant relationships are shown in light gray dashed arrows, solid black arrows represent positive relationships and dashed black arrows represent negative relationships. Shown are standardized effect sizes, with arrow thickness proportional to the strength of the relationship. All models were a good fit to the data based on the χ^2 statistic ($p > 0.05$ is good). See Supplementary Table 10 for additional model fit parameters for all four models.

Supplementary Table 4. Correlated variables included in Model 1 that improve model fit between exogenous and endogenous variables in the path analysis. Included correlations are denoted by estimates present.

	Precipitation	Herbivore richness	Domestication	Grazing pressure	Feeding guild	Species richness	Error of ANPP
Precipitation						0.549	
Herbivore richness			-0.519	-0.013	-0.519	0.175	0.135
Domestication				-0.113	-0.499	-0.236	
Grazing pressure					-0.036		
Feeding guild						0.245	-0.165
Species richness							0.025
Error of ANPP							

Supplementary Table 5. Correlated variables included in Model 2a that improve model fit between exogenous and endogenous variables in the path analysis. Included correlations are denoted by estimates present.

	Precipitation	Herbivore richness	Domestication	Grazing pressure	Feeding guild	Species richness	Plant BP dominance	Error of ANPP
Precipitation						0.550	-0.326	
Herbivore richness			-0.519	-0.021	0.590	0.174	0.031	0.135
Domestication				-0.103	-0.499	-0.234		
Grazing pressure					-0.036			
Feeding guild						0.243	-0.162	-0.165
Species richness							-0.536	0.025
Plant BP dominance								0.208
Error of ANPP								

Supplementary Table 6. Correlated variables included in Model 2b - Simpson's that improve model fit between exogenous and endogenous variables in the path analysis. Included correlations are denoted by estimates present.

	Precipitation	Herbivore richness	Domestication	Grazing pressure	Feeding guild	Species richness	Plant Simpson's dominance	Error of ANPP
Precipitation						0.548	-0.304	
Herbivore richness			-0.519	-0.021	0.590	0.179	0.015	0.135
Domestication				-0.100	-0.501	-0.244		
Grazing pressure					-0.038			
Feeding guild						0.249	-0.144	-0.165
Species richness							-0.530	0.025
Plant Simpson's dominance								0.231
Error of ANPP								

Supplementary Table 7. Correlated variables included in Model 3 that improve model fit between exogenous and endogenous variables in the path analysis. Included correlations are denoted by estimates present.

	Precipitation	Herbivore richness	Domestication	Grazing pressure	Feeding guild	Species richness
Precipitation		-0.185		-0.125	-0.207	0.388
Herbivore richness			-0.407	0.027	0.569	0.092
Domestication				-0.116	-0.274	-0.250
Grazing pressure					0.025	
Feeding guild						0.050
Species richness						

Supplementary Table 8. Correlated variables included in Model 4a that improve model fit between exogenous and endogenous variables in the path analysis. Included correlations are denoted by estimates present.

	Precipitation	Herbivore richness	Domestication	Grazing pressure	Feeding guild	Species richness	Plant BP dominance
Precipitation		-0.190		-0.127	-0.224	0.397	-0.275
Herbivore richness			-0.406	0.031	0.569	0.076	
Domestication				-0.121	-0.274	-0.235	
Grazing pressure					0.036		0.129
Feeding guild						0.011	
Species richness							-0.536
Plant BP dominance							

Supplementary Table 9. Correlated variables included in Model 4b -Simpson's that improve model fit between exogenous and endogenous variables in the path analysis. Included correlations are denoted by estimates present.

	Precipitation	Herbivore richness	Domestication	Grazing pressure	Feeding guild	Species richness	Plant Simpson's dominance
Precipitation		-0.191		-0.127	-0.223	0.395	-0.275
Herbivore richness			-0.407	0.030	0.569	0.079	
Domestication				-0.117	-0.275	-0.246	
Grazing pressure					0.034		0.121
Feeding guild						0.017	
Species richness							-0.538
Plant Simpson's dominance							

Supplementary Table 10. Goodness of fit metrics suggest all path analysis models are a good fit to the data – Normalized Fit Index = 0.971 (>0.95 is considered a good fit); Tucker Lewis Index = 0.991 (>0.95 is considered a good fit); Root-Mean Square Error of Approximation = 0.040 (<0.05 is considered a good fit) with a PCLOSE = 0.588 (PCLOSE is the probability that RMSEA = 0.05, if PCLOSE > 0.05, the model is considered a good fit).

	Model 1	Model 2a	Model 2b	Model 3	Model 4a	Model 4b
NFI	0.951	0.962	0.963	0.988	0.991	0.992
TLI	0.938	0.961	0.957	0.957	1.011	1.016
RMSEA	0.062	0.048	0.052	0.044	0.00	0.000
(PCLOSE)	(0.339)	(0.467)	(0.428)	(0.419)	(0.771)	(0.808)