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Integrative modelling reveals mechanisms linking productivity and plant species richness

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How ecosystem productivity and species richness are interrelated is one of the most debated subjects in the history of ecology[1]. Decades of intensive study have yet to discern the actual mechanisms behind observed global patterns[2,3]. Here, by integrating the predictions from multiple theories into a single model and using data from 1,126 grassland plots spanning five continents, we detect the clear signals of numerous underlying mechanisms linking productivity and richness. We find that an integrative model has substantially higher explanatory power than traditional bivariate analyses. In addition, the specific results unveil several surprising findings that conflict with classical models[4–7]. These include the isolation of a strong and consistent enhancement of productivity by richness, an effect in striking contrast with superficial data patterns. Also revealed is a consistent importance of competition across the full range of productivity values, in direct conflict with some (but not all) proposed models. The promotion of local richness by macroecological gradients in climatic favourability, generally seen as a competing hypothesis[8], is also found to be important in our analysis. The results demonstrate that an integrative modelling approach leads to a major advance in our ability to discern the underlying processes operating in ecological systems.

Ecosystem productivity and species diversity are essential to the ability of natural systems to provide goods and services. Yet, for decades there has been debate over their interrelationship. In the 1970s and 1980s, conflicting models predicted that elevated productivity would lead to reductions in species richness[4–7]. Beginning in the mid-1990s, scientists started to seriously debate another possibility: that richness could promote productivity[9–12]. While experimental studies generally support a biodiversity enhancement of productivity[13,14], the precise strength of the effect in natural systems and the relationship of this process to other factors that can influence productivity remain major questions. Adding to the debate, macroecological theories propose that regional diversity is controlled by gradients in climatic favourability and evolutionary history[15] and that these larger-scale effects are important determinants of smaller-scale diversity patterns[8].

The search for a canonical bivariate productivity–richness relationship lies at the heart of the debate among ecologists. This pursuit is fuelled, in part, by the history of the discussion, which has focused on bivariate predictions[16]. At the same time, it is also seen by some as a means of assessing the overall importance of various mechanisms operating in natural systems. While many different mechanisms have been discussed, the primary competing theories make four main conflicting predictions: (1) richness and productivity should increase together with increasing resources and environmental favourability until limits to coexistence are reached at high productivity and richness declines, producing a humped-shape relationship[4–7,17]; (2) richness promotes productivity, leading to a positive relationship[6,9]; (3) richness and productivity increase together because climatic gradients in productivity lead to increased regional species pools, creating a positive relationship but from a separate mechanism[8]; and (4) the richness–productivity relationship will be of inconsistent form because the mechanisms controlling them vary in their scale-dependence and relative importance[18,19].

Empirical tests of the generality of hypothesized bivariate productivity–richness patterns have reported a wide variety of results and have produced substantial discussion[20–23]. Recent global studies[2,3] have disagreed with regard to whether a coherent pattern exists for natural grasslands. What has been agreed upon, however, is that the low explanatory power coming from conventional analyses suggests the need to pursue an integrative understanding of the causal mechanisms controlling productivity–richness relationships.

One potential explanation for why debate over mechanisms is proving difficult to resolve is because productivity and richness are jointly controlled by a complex network of processes[1,21,24–28]. Overcoming the challenge of evaluating more complex hypotheses requires both advanced statistical modelling approaches and large-scale systematic data collection efforts. Here, we used structural equation modeling[29] to integrate key predictions from competing theories into a multi-process hypothesis for evaluation. We then evaluated the hypothesis using data collected for that purpose by a global consortium, the Nutrient Network (http://nutnet.org). The data collected comprise samples

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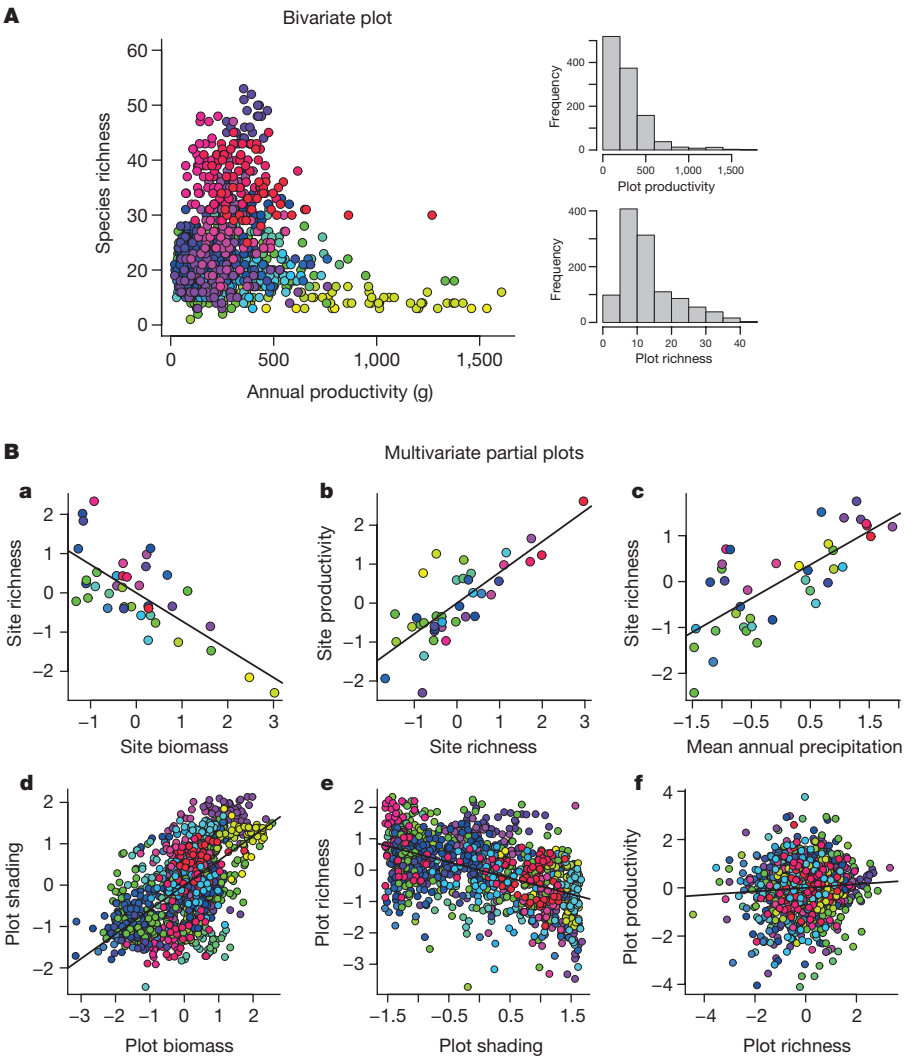

Figure 1 | Comparison between low-dimension (top panel) and high-dimension (bottom panel) examinations of data. A, Raw bivariate plot of above-ground productivity and species richness in 1-m^2 plots ($n = 1{,}126$). Different sites are represented in the graphs by different colours, assigned by mean site richness from low (yellow) to high (red). **B**, Plots **a**–**c** visualize site level partial relationships indicated by corresponding letters in Fig. 2 ($n = 39$ sites). Plots **d**–**f** visualize plot level partial relationships indicated by corresponding letters in Fig. 2 ($n = 1{,}126$ 1-m2 plots). Units are standardized residual deviations from predicted partial scores.

from 1,126 plots collected at 39 grass-dominated sites around the world. Variables measured include plant species richness, productivity (measured as the annual biomass increment), total biomass (the accumulated non-woody biomass, live and dead, including litter), along with many of the drivers hypothesized to be important for regulating their variations. Additional information is provided in the Methods.

To integrate theoretical expectations from competing theories, we mined the productivity–diversity literature to determine the main theoretical constructs discussed and the hypothesized interconnections between constructs (see Methods). We used this information to develop a structural equation meta-model that assimilates the essential theoretical constructs and hypothesized connections into a network of multivariate expectations (Extended Data Fig. 1, Extended Data Table 1 and Supplementary Information). This meta-model, along with the available data, guided our development of a structural equation model for empirical evaluation. We evaluated model-data consistency to determine whether there were missing linkages in the initial model as well as to determine the support for proposed links. We further addressed the question, 'what dimension of model (that is, number of parameters and linkages) is required to detect the signals in the underlying data?'. For this, we evaluated lower-dimensional versions of the model by removing linkages and re-evaluating against the data. More methodological detail is provided in the Methods and Supplementary Information.

A simple bivariate plot of richness against productivity (Fig. 1A) reveals little about the underlying mechanisms. Previous analyses of such bivariate relations have found it difficult to even detect significant associations[2,30]. However, our analysis based on an integrative model reveals strong, clear signals consistent with numerous proposed mechanisms, including several that are not at all suggested from the bivariate data.

First, we found clear evidence that the accumulation of total biomass (hereafter simply 'biomass') leads to a negative effect on species richness. At the site level, the partial effect (r_∂) of biomass on richness in the model was strong (Figs 1B, a and 2; $r_\partial = -0.77$). The reduction of richness was not found to be mediated by our one-time measurement of average shading at the ground surface, which was subsequently dropped from the model. At the plot level, however, we found evidence that biomass increases shading ($r_\partial = 0.56$), which in turn, decreases richness (Figs 1B, d, e and 2; $r_\partial = -0.34$). The negative effects of biomass on richness appear consistent with long-standing hypotheses that predict a hump-shaped productivity–richness relationship due to competitive dominance at high productivity[5,17]. However, while those hypotheses assume increasing competitive intensity with increasing productivity, our results reveal a linear effect across the full range of biomass observed in this study (Fig. 1B, a).

Second, we found a positive, linear enhancement of productivity by richness in the model. This effect was among the strongest found at the site-scale (Figs 1B, b and 2; $r_\partial = 0.67$), and was detectable, although weak, at the plot-scale (Figs 1B, f and 2; $r_\partial = 0.02$). A surprising feature of the site-level result is the apparent absence of a levelling off of the biodiversity enhancement of productivity at higher levels of richness. Such a continuous effect has been theorized for larger-scale studies and contrasts with the asymptotic levelling off usually

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Table 1 | Select standardized partial effect sizes (and standard errors) ranked by magnitude and proposed interpretations

Effect	Magnitude	Proposed interpretation
Site-scale		
Soil fertility → productivity	1.104 (0.220)	Productivity variations are most strongly related to spatial variations in site fertility.
Site biomass → richness	−0.771 (0.143)	High biomass sites have depressed species richness, presumably via some form of competitive dominance.
Site richness → productivity	0.671 (0.214)	Increasing richness contributes to higher productivity.
Climate → richness	0.669 (0.113)	Richness increases with increasing mean annual precipitation during warmest quarter.
Heterogeneity → richness	0.627 (0.119)	Species coexistence strongly regulated by within-site spatial heterogeneity in vegetation cover.
Climate → productivity	0.589 (0.195)	Combined effects of macrogradients in temperature and precipitation are moderately important in controlling site-to-site variations in productivity.
Soil suitability → richness	0.439 (0.107)	Richness increases with decreasing sand and silt content of soils.
Disturbance → richness	−0.251 (0.116)	Sites subject to strong anthropogenic alteration (for example, pasturing) notably lower in richness.
Disturbance → biomass	−0.185 (0.084)	Local grazing contributed to some biomass variation.
Correlation between soil fertility and soil suitability	−0.56 (0.109)	Influences of resources and filters on richness are distinct from those that regulate productivity.
Plot-scale		
Biomass → shading	0.559 (0.089)	Shading fairly strongly tied to biomass, although morphology and other features probably also important.
Soil suitability → richness	0.404 (0.074)	Plot-to-plot variations in richness tied to local variations in environmental edaphic filters.
Shading → richness	−0.342 (0.064)	Richness variations within site partially controlled by variations in competition via shading.
Soil suitability → shading	0.249 (0.098)	Variations in community traits driven by soil resources result in differences in amount of shading per gram.
Richness → productivity	0.017 (0.006)	Effects of natural plot-to-plot variations in richness can be discerned as an independent process in this sample.
Soil fertility → productivity	0.0 (NS)	Plot productivity largely determined by site-level productivity, with no significant local control.

Site-scale and plot-scale effects are presented separately.

found in experimental (smaller-scale) studies[13]. Previous attempts to isolate an effect of richness on productivity with observational data using simpler models have failed to do so (see Supplementary Information).

Third, we found strong and independent influences of macroclimate and soils on richness and productivity. The standardized effect sizes provide insights into the relative importance of these processes (Table 1). At the site level, productivity was most strongly related to soil fertility, while richness was most strongly related to climate and soil suitability, with heterogeneity and disturbance also important (Fig. 2). Rather than being made up of similar environmental factors, the soil environmental drivers of richness and productivity were negatively correlated at the site level (Table 1, $r_{\partial} = -0.56$), supporting previous claims of their semi-independence[21]. Thus, theories that presume a simultaneous increase in productivity and richness with increasing environmental favourability (see Supplementary Information) fail to correspond with the independent responses to environmental drivers observed in natural systems.

Our results show that failure to account for the variation in richness and productivity explained by the environmental drivers would make it difficult to detect the reciprocal influences of productivity and richness on each other. In fact, our capacity to isolate underlying processes was highly sensitive to model dimensionality, where dimensionality refers to the number of measured determinants of productivity and

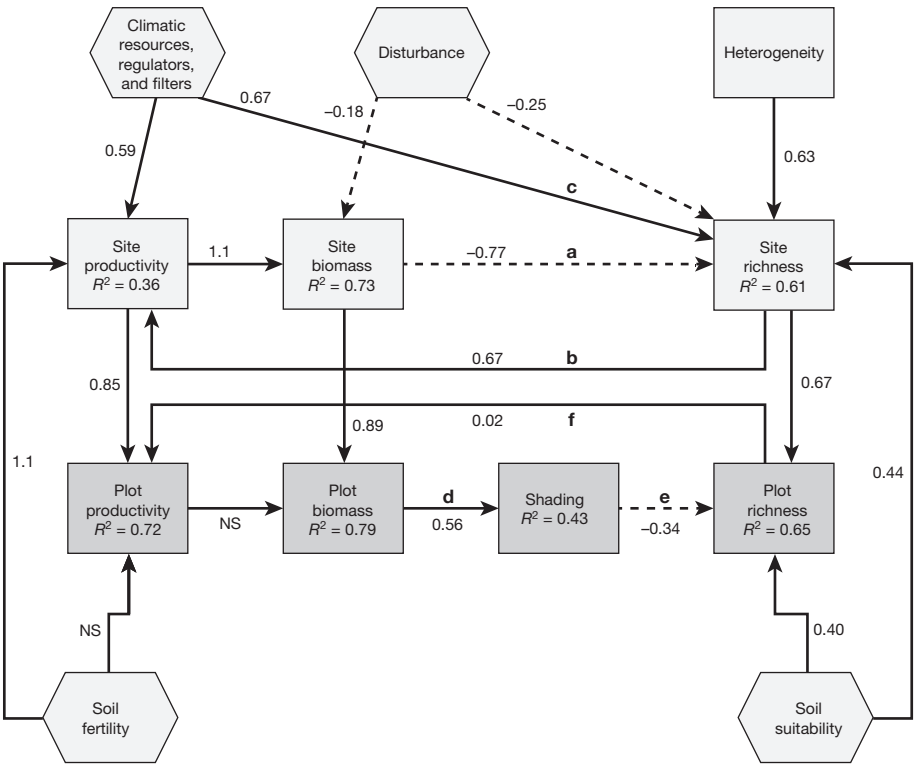

Figure 2 | Structural equation model representing connections between productivity and richness supported by the data. 'Biomass' refers to total above-ground accumulated biomass. Letters correspond to partial plots shown in Fig. 1B. Solid arrows represent positive effects, dashed arrows represent negative effects. For the site-level submodel, test statistic = 13.518, with 13 model degrees of freedom and $P = 0.409$ (indicating close model-data fit). For the plot-level submodel, robust test statistic = 21.907, with 16 model degrees of freedom and $P = 0.146$ (again indicating close model-data fit). Relative effect sizes presented in Table 1.

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richness included in the model (Extended Data Table 2). At both site and plot levels, models omitting either productivity or biomass (but not both) still permitted us to detect the feedback from richness to biomass production. Any other simplifications at the site-level, however, resulted in a failure to detect previously detected pathways and resulted in a dramatic loss of signal (as indicated by reduced values of R^2 in the model).

Regarding scale dependence, plot-level values of productivity, biomass, and richness were strongly related to site-level estimates (Fig. 2), as is common with hierarchical data. This should be interpreted as meaning much of the overall plot-to-plot variation in productivity, biomass, and richness can be ascribed to site-to-site variations in those properties. In this case, within-site variations in productivity were explained solely by site-level productivity, as there were no predictors for remaining among-plot variations. Within-site variations in richness, however, were additionally explained by within-site variations in soil suitability and shading. Also sensitive to scale was the strength of the feedback from richness to productivity, which was much stronger at the site scale. While multiple factors probably play a role in this scale-dependence, the simplest explanation here may be the smaller span of conditions sampled within sites compared with across sites.

Finally, in contrast to a bivariate model, which our analyses suggest can explain no more than 10% of the observed variation in richness, our structural equation model explains 61% of the variation in richness among sites, and 65% of the variation in richness among plots. An ability to explain a substantial portion of the variation in richness is tremendously important for potential conservation applications. Model complexity is also important because of its more detailed mapping onto nature, as our model can make statements about how both specific management actions (such as reduction of biomass through mowing or increase in soil fertility through fertilization), as well as shifts in climate conditions, may alter both productivity and species richness.

Our findings give reason for optimism about the future of ecology as a more precise and less ambiguous science. We show that many of the proposed processes connecting productivity and richness offered during previous decades operate simultaneously as parts of a whole system of effects. Details of the findings, however, refine many of our assumptions about how those processes operate. Our field's previous failure to resolve debate about productivity–richness relationships stems from a lack of integration of ideas and absence of simultaneous tests of their combined implications. By integrating and testing those ideas, our approach provides a systems-level understanding and improves our chances to foresee the possible consequences of human alteration of environmental factors, productivity, and richness now occurring worldwide.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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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 J.B.G. (gracej@usgs.gov).

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METHODS

Development of meta-model hypothesis. A review and accounting of the history of claims and disputed points in the published literature was developed before construction of the meta-model that guided this analysis (Extended Data Fig. 1 and Supplementary Information). During this review, attention was paid to the theoretical constructs invoked by various authors, since our goal was to provide a framework that had the potential to clarify and resolve disputed points. Attention was also paid to types of variable measured by different authors, as the relationship between constructs and measurements constitutes one of the several sources of ambiguity and confusion[31,32]. An in-depth description of the literature synthesized to generate the meta-model is presented in the Supplementary Information.

Data. Data collected by the Nutrient Network Cooperative[33] was used to design and evaluate a structural equation model based on the meta-model presented. The Nutrient Network is a distributed, coordinated research cooperative. Sites in the Network are dominated primarily by herbaceous vegetation and intended to represent natural/semi-natural grasslands and related ecosystems worldwide. Individual sites were selected to accommodate at least a 1,000 m^2 study design footprint. Most sites sampled vegetation in 2007, although 12 sites sampled in 2008 or 2009. No statistical methods were used to predetermine sample size. Samples were collected using a completely randomized block design. The standard design has three blocks and ten plots per block at each site, although some sites deviate slightly from this design. A few sites are grazed or burned before sampling, consistent with their traditional management. Further details on site selection and design can be found at http://www.nutnet.org/exp_protocol.

In this study, we analysed data from 39 of the 45 sites considered in ref. 2 possessing a complete set of covariates (Extended Data Table 3). While ref. 2 only examined bivariate relations between productivity and richness, our analyses brought in many additional variables (Extended Data Table 1) so that we could address the many hypotheses embodied in the meta-model. Individual plots with greater than 10% woody plant cover were omitted from consideration to maintain comparability in total biomass across plots. This step resulted in the removal of 73 plots, leaving 1,126 plots in the data set analysed. Four plots were omitted owing to incomplete plant data and one for incomplete light data. For two of the sites, live mass was estimated from total mass using available information on the proportion of live to total. One apparent measurement error was detected for light data and the associated plot removed from the analysed sample. Random imputation methods[34] were used for cases where there were missing soil measurements at a site. The decision to use this approach was based on weighing the demerits of deleting nearly complete multivariate data records versus introducing a modest amount of random error through the imputation process.

Study plots in this investigation had a perimeter of 5 m × 5 m and were separated by 1 m walkways. A single 1 m × 1 m subplot within each plot was permanently marked and sampled for species richness during the season of peak biomass. Sites with strong seasonal variation in composition were sampled twice during the season to assemble a complete list of species. To obtain an estimate of site-level richness, we used a jack-knife procedure[35]. (Because there have been some recent advances in the reduction of certain sources of bias in richness estimation[36], we checked our original results by computing site-level richness using the new iNEXT R package. The correlation between the two estimates of richness was found to be 0.972.)

Productivity and total above-ground biomass were sampled immediately adjacent to the permanent vegetation subplot. Vegetation was sampled destructively by clipping at ground level all above-ground biomass of individual plants rooted within two 0.1-m^2 (10 cm × 100 cm) strips. Harvested plant material was sorted into the current year's live and recently senescent material, and into previous year's growth (including litter). For shrubs and sub-shrubs, the current year's leaves and stems were collected. Plant material was dried at 60 °C to a constant mass and weighed to the nearest 0.01 g. We used the current year's biomass increment as our estimate of annual above-ground productivity, which commonly serves as a measurable surrogate for total productivity[37,38]. All sites used this protocol to estimate productivity (except for the Sevilleta, New Mexico, site which relied on species-specific allometric relationships[39]). Total above-ground biomass was computed as the sum of the current year's biomass and that from previous years and included remaining dead material (litter). Photosynthetically active radiation was measured at the time of peak biomass, both above the vegetation and at the ground surface, the ratio representing the proportion of available light reaching the ground. Degree of shading was computed as 1.0 minus the proportion of light reaching the ground.

Within each plot, 250 g of soil were collected and air dried for processing and soil archiving. Total soil %C and %N were measured using dry combustion gas chromatography analysis (COSTECH ESC 4010 Element Analyzer) at the University of Nebraska. All other soil analyses were performed at A&L Analytical Laboratory, Memphis, Tennessee, USA; these included the following: extractable soil phosphorus and potassium were quantified using the Mehlich-3 extraction method, and parts per million concentration estimated using inductively coupled plasma-emission spectrometry. Soil pH was quantified with a pH probe (Fisher Scientific) in a slurry made from 10 g dry soil and 25 ml of deionized water. Soil texture, expressed as the percentage sand, percentage silt, and percentage clay, was measured on 100 g dry soil using the Buoycous method. Further details on sampling methodology are at http://www.nutnet.org/exp_protocol.

Climatic characteristics were obtained for each site from version 1.4 of BioClim, which is part of the WorldClim[40] set of global climate layers at 1 km^2 spatial resolution. To represent measures of temperature and precipitation with meaningful relationships to plant growth in global grasslands, we selected mean temperature of the wettest quarter of the year (BIO8) and total precipitation of the warmest quarter of the year (BIO18). Climate values were extracted using universal transverse Mercator (UTM) coordinates collected near the centre of each site.

Several derived variables were developed to include in the modelling effort. To represent within-site heterogeneity, coefficients of variation were computed for the site-level model based on plot-to-plot variation in plot-level measures. This allowed us to examine the explanatory value of heterogeneity in soil nitrogen, phosphorus, potassium, and pH, as well as heterogeneity in biomass and light interception. Indices of total resource supply and resource imbalance were also calculated using the method of ref. 27 and evaluated for inclusion in our models.

Disturbance history information for the sites was converted into four binary (0,1) variables for analyses; information available included pretreatment history of (1) substantial anthropogenic alteration (for example, conversion to pasture), (2) grazing history, by wild or domestic animals, (3) active management (typically haying or mowing), and (4) fire. Current levels of herbivory were estimated by comparing biomass inside and outside exclosure plots located at each site.

Certain variables were constructed within the structural equation modeling process using the composite index development methods of ref. 41. Consideration of the ideas conveyed by the meta-model (Extended Data Fig. 1) and the specific situation being modelled suggested the need to develop index variables for soil fertility and soil suitability. Soil fertility indices were developed using all measured soil properties and were operationally defined as the drivers of productivity, controlling for all other effects on productivity in the model. Two indices were developed, one for site-to-site variations and another for plot-to-plot variations. Similarly, soil suitability indices were developed for the site- and plot-level data using all measured soil properties as potential contributors and operationally defined as the drivers of richness, controlling for all other effects on richness in the model.

Modelling with composites in structural equation models involved a two-step process. First, we constructed a fully specified structural equation model (as represented in Fig. 2), but providing a specific set of soil properties to serve as formative indicators for soil fertility and soil suitability. Variables that did not contribute to the total model (on the basis of model fit indices) were eliminated individually for the two composites being formed. The resulting prediction equations were used to compute index scores. Then, the model was reconstructed, substituting the indices in place of the collection of individual soil properties. Documentation of this process is provided in the Supplementary Information computer code (R script).

Analyses. A structural equation model was developed based on the ideas embodied in the meta-model, available data, and the principles and procedures laid out in ref. 42. Indicators for constructs were chosen from the set of variables available and quantities that could be computed from them (Extended Data Table 1). The modelling approach used was semi-exploratory in that while we worked to address the general hypothesis embodied in the meta-model, the precise variables (for example, mean annual precipitation versus mean annual precipitation in the warmest quarter of the year) to use for certain constructs (specifically, resource supplies and regulators) were determined empirically. Compositing techniques were used to estimate construct-level effects[41]. For comparative purposes, we analysed the bivariate pattern in Fig. 1A using a variety of regression models, including Ricker-type nonlinear models as well as second- and third-order polynomials. A three-parameter Ricker-type model provided the best fit for the data.

Data were screened for distributional properties and nonlinear relations. Several variables were log-transformed as a result of evaluations (Extended Data Table 1). We used the R software platform[43] and the lavaan package[44] along with the lavaan.survey[45] package for our structural equation model analyses. For the plot-scale model, robust χ^2 tests, as implemented in the lavaan.survey package, were used to judge variable inclusion and model adequacy because of the nested nature of the plot-level data. Each link in the final model was evaluated for significant contribution to the model. Final model fit to data was very good for both submodels. Model fit indices were supplemented by using additional diagnostic evaluations that involve visualizing residual relationships

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to evaluate conditional independence[29]. These residual visualizations allowed, among other things, an ability to evaluate linearity assumptions and implement curve-fitting procedures if needed (which was only the case for the composite relationships in this case). Our structural equation model in this case is non-recursive and includes a causal loop. Models of this form are commonplace in structural equation model applications, although they come with some additional assumptions and requirements. Specifically, there is a requirement for unique predictors for the elements involved in loops, a requirement that was met in this case. Additional analysis details are documented in the R script used for the analysis (Supplementary Information).

Multi-level relations were incorporated into the architecture of our model. Several ways to incorporate both site- and plot-level variations in the model were considered and multiple approaches evaluated to ensure results are general. In the model form presented, we chose to follow modern hierarchical modelling principles and allow plot-level observations to depend on site-level parameters, since plots were nested within sites. The result of choosing this approach means site-level explanatory effects can filter down to the plot level while plot-level explanatory variables (for example, pathways from edaphic conditions to plot richness) explain additional plot-to-plot variations in responses that are not predicted from site-level (mean) conditions. Consistent with the capabilities of the structural equation model software used in our analyses (described below), we estimated site- and plot-level submodels using a two-stage approach, first estimating parameters for the site-level component and then using site productivity, biomass, and richness as exogenous predictors in the plot-level component. Comparisons with results from separate site- and plot-level models led to very similar conclusions, although the hierarchical approach used allowed a better integration of processes and greater variance explanation.

One of our objectives in this study was to assess the model dimensionality needed to detect the hypothesized signals in the data. To do this, we started with the most complete model (Fig. 2) and eliminated variables from the model (always retaining richness and some measure of biomass production, either productivity or total biomass). We then made any modifications needed to ensure adequate model-data fit for these reduced-form models. The consequences of model simplification was judged on the basis of signal retention, in particular a loss of capacity to detect signals associated with the remaining parts of the model.

Code availability. The computer script associated with the analyses in this paper is available as part of the Supplementary Information.

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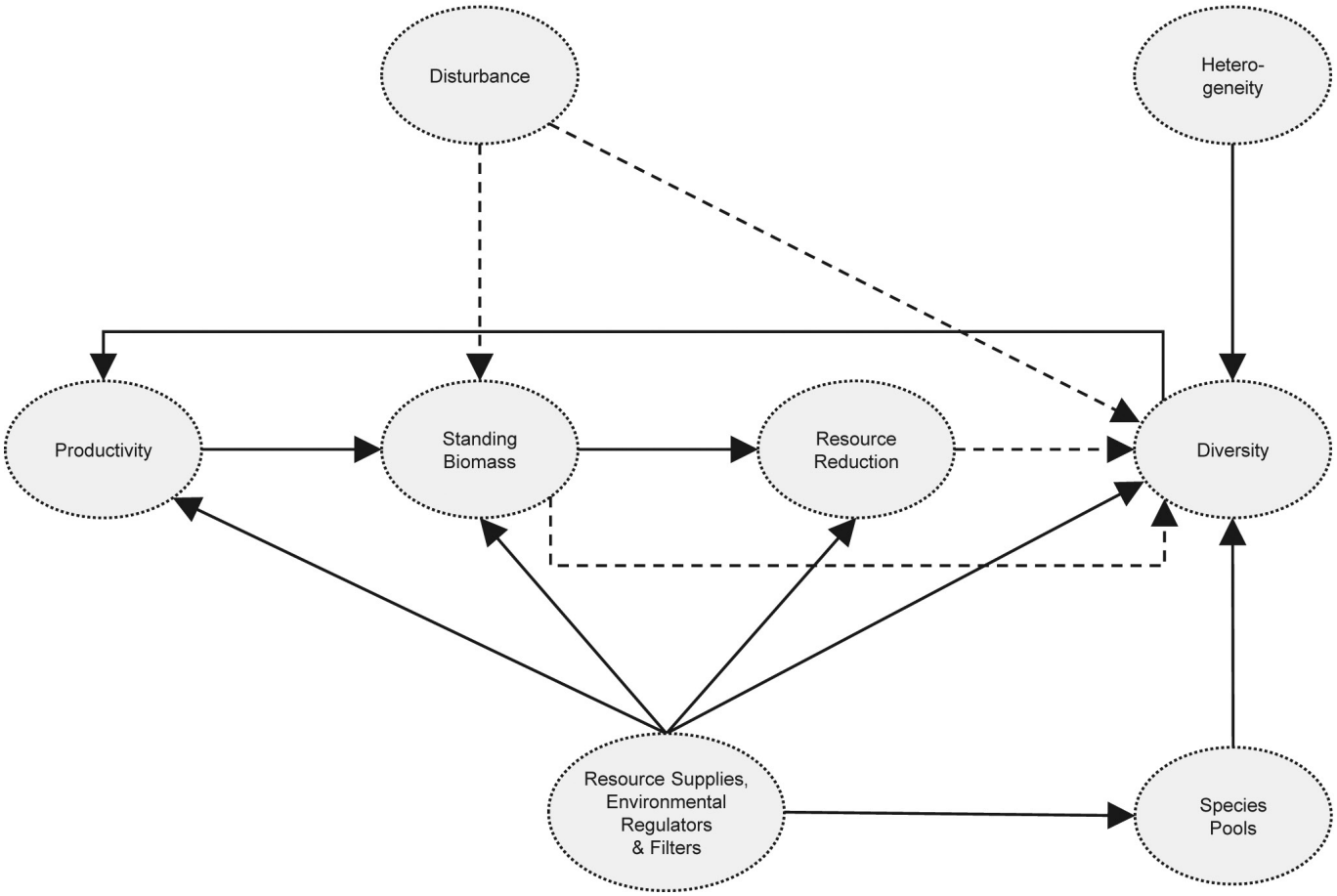

Extended Data Figure 1 | Structural equation meta-model showing hypothesized probabilistic expectations based on literature related to the productivity–diversity debate. Solid lines represent expected positive effects, dashed lines represent expected negative effects. Literature and meta-model development are discussed in the Supplementary Information. Specific implementations of this generalized model for particular cases will probably differ in detail as appropriate for the situation and available data.

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Extended Data Table 1 | Model variables and their indicators*

Model Variables	Indicator Variables	Units**
Site Richness (log)	estimated site richness	number/site
Site Biomass (log)	peak season total above-ground biomass, including litter	mean g/m^2
Site Productivity (log)	peak season live above-ground biomass increment	mean g/m^2
Plot Richness (log)	species in a plot	number/plot
Shading (log)	proportional reduction in light at ground surface	0.0 – 1.0
Plot Biomass (log)	peak season total above-ground biomass, including litter	g/m2 per plot
Plot Productivity (log)	peak season live above-ground biomass increment	g/m2 per plot
Climate Effect on Site Richness	mean precipitation in warmest quarter	mm
Climate Effect on Site Productivity	mean precipitation in warmest quarter temperature in wettest quarter	mm, ^{o}C
Disturbance Effect on Site Richness	history of major anthropogenic influences	0 or 1
Disturbance Effect on Site Biomass	herbivory (based on exclosure studies)	proportion
Heterogeneity	CV for variations in vegetation density among plots at a site (expressed in terms of canopy light interception variations)	unitless
Soil Suitability (site and plot-level)	*function of*(soil N, P, C, texture, pH) that maximizes richness, controlling for other conditions.	unitless
Soil Fertility (site and plot-level)	*function of*(soil N, P, C, texture, pH) that maximizes productivity, controlling for other conditions.	unitless

*The data are provided along with the Supplementary Information.
**Units given are for the raw (untransformed) variables.

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Extended Data Table 2 | Results of model dimensionality evaluations

Model Level	Model	Signals Lost	R^2 for Richness
Site-level	full model		0.62
	heterogeneity node eliminated	signal from disturbance to richness lost	0.33
	disturbance node eliminated	all paths retained	0.49
	climate node eliminated	signal from disturbance to richness lost; signal from richness to productivity lost	0.37
	soil fertility and suitability eliminated	signal from disturbance to richness lost; signal from richness to productivity lost; signal from climate to productivity lost	0.16
	biomass node eliminated	all signals were retained	0.50
	eliminate path from richness to productivity	significant misspecification, model fails to fit data unless path reinstated	
Plot-level	full model		0.67
	soil fertility and suitability eliminated	all signals were retained	0.51
	shading node eliminated	all signals were retained	0.56
	biomass node eliminated	no substantive signals lost	0.65
	productivity node eliminated	all signals were retained	0.67
	eliminate path from richness to productivity	significant misspecification, model fails to fit data unless path reinstated	

Models of different complexity were evaluated to determine the potential for model simplification. The bases for comparison were 'full models' for each site, as shown in Fig. 2. The consequences of removing various components of the models are summarized under the columns 'Signals lost' and 'R^2 for richness'.

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Extended Data Table 3 | Basic information on the study sites included in the final analyses

Site Code	Site Name	Continent	Region	Country	State	Site Lead PIs
amcamp.us	American Camp	North America	Pacific Coast (North America)	US	Washington	Jonathan D. Bakker; Janneke Hille Ris Lambers
azi.cn	Azi	Asia	Asia	CN	Gansu	Chengjin Chu; Qi Li; Wei Li; Gang Wen; Guozhen Du
barta.us	Barta Brothers	North America	Central plains (North America)	US	Nebraska	David Wedin
bldr.us	Boulder South Campus	North America	Central plains (North America)	US	Colorado	Kendi Davies; Brett Melbourne
bnch.us	Bunchgrass (Andrews LTER)	North America	Montane West (North America)	US	Oregon	Eric Seabloom; Elizabeth Borer
bogong.au	Bogong	Australia	Australia	AU	Victoria	John Morgan; Joslin L. Moore
bttr.us	Buttercup (Andrews LTER)	North America	Montane West (North America)	US	Oregon	Eric Seabloom; Elizabeth Borer
burrawan.au	Burrawan	Australia	Australia	AU	Queensland	Jennifer Firn; Yvonne Buckley
cbgb.us	Chichaqua Bottoms	North America	Central plains (North America)	US	Iowa	W. Stanley Harpole; Lori A. Biederman; Kirsten S. Hofmockel; Lauren Sullivan
cdpt.us	Cedar Point Biological Station	North America	Central plains (North America)	US	Nebraska	Johannes M. H. Knops
derr.au	Derrimut	Australia	Australia	AU	Victoria	John Morgan
elliot.us	Elliott Chaparral	North America	Pacific Coast (North America)	US	California	Elsa Cleland
fnly.us	Finley NWR	North America	Pacific Coast (North America)	US	Oregon	Eric Seabloom; Elizabeth Borer
gilb.za	Mt Gilboa	Africa	Sub-saharan Africa	ZA	KwaZulu-Natal	Peter D. Wragg
glac.us	Glacial Heritage	North America	Pacific Coast (North America)	US	Washington	Jonathan D. Bakker; Janneke Hille Ris Lambers
hall.us	Hall's Prairie	North America	Central plains (North America)	US	Kentucky	Rebecca L. McCulley; Jim Nelson
hart.us	Hart Mountain	North America	Montane West (North America)	US	Oregon	David Pyke; Nicole M. DeCrappeo
hnvr.us	Hanover	North America	Atlantic Coast (North America)	US	New Hampshire	Elizabeth M. Wolkovich; Kathryn L. Cottingham
kiny.au	Kinypanial	Australia	Australia	AU	Victoria	John Morgan
look.us	Lookout (Andrews LTER)	North America	Montane West (North America)	US	Oregon	Eric Seabloom; Elizabeth Borer
mtca.au	Mt. Caroline	Australia	Australia	AU	Western Australia	Suzanne M Prober
pape.de	Papenburg	Europe	Europe	DE	Lower Saxony	Helmut Hillebrand
sage.us	Sagehen Creek UCNRS	North America	Montane West (North America)	US	California	Daniel S. Gruner; Louie Yang
sava.us	Savannah River	North America	Atlantic Coast (North America)	US	South Carolina	John L. Orrock; Ellen I. Damschen; Lars Brudvig
sedg.us	Sedgwick Reserve UCNRS	North America	Pacific Coast (North America)	US	California	Carla M D'Antonio; W. Stanley Harpole; Elizabeth Borer; Eric Seabloom
sereng.tz	Serengeti	Africa	Sub-saharan Africa	TZ		T. Michael Anderson
sevi.us	Sevilleta LTER	North America	Central plains (North America)	US	New Mexico	Scott Collins; Laura Ladwig
sgs.us	Shortgrass Steppe LTER	North America	Central plains (North America)	US	Colorado	Cynthia S. Brown; Julia A. Klein; Dana M. Blumenthal; Alan Knapp
shps.us	Sheep Experimental Station	North America	Montane West (North America)	US	Idaho	Peter Adler
sier.us	Sierra Foothills REC	North America	Pacific Coast (North America)	US	California	Eric Seabloom; Elizabeth Borer; W. Stanley Harpole
smith.us	Smith Prairie	North America	Pacific Coast (North America)	US	Washington	Jonathan D. Bakker; Janneke Hille Ris Lambers
spin.us	Spindletop	North America	Central plains (North America)	US	Kentucky	Rebecca L. McCulley; Jim Nelson
summ.za	Summerveld	Africa	Sub-saharan Africa	ZA	KwaZulu-Natal	Peter D. Wragg
temple.us	Temple	North America	Central plains (North America)	US	Texas	Philip A Fay
trel.us	Trelease	North America	Central plains (North America)	US	Illinois	Andrew Leakey; Xiaohui Feng
tyso.us	Tyson	North America	Central plains (North America)	US	Missouri	John L. Orrock; Ellen I. Damschen; Tiffany Knight
ukul.za	Ukulinga	Africa	Sub-saharan Africa	ZA	KwaZulu-Natal	Nicole Hagenah; Kevin P Kirkman
unc.us	Duke Forest	North America	Atlantic Coast (North America)	US	North Carolina	Charles Mitchell; Justin Wright
valm.ch	Val Mustair	Europe	Europe	CH	Grisons	Anita C. Risch; Martin Schuetz

A total of 39 sites from the Nutrient Network (http://nutnet.org) possessed sufficiently complete multivariate data to be incorporated into this analysis.

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MATERIALS AND METHODS

S1. History and Assessment of the Debate over the Connections between Productivity and Diversity

Initial Development of Theoretical Ideas

While many important, earlier precedents exist, we begin our chronology here with a paper published in 1973 by Grime[49]. In this paper, separate but "parallel" models were presented to explain the influences of environmental stress and disturbance on species richness. For both drivers, it was proposed that under the most favorable conditions (low stress or low disturbance), species richness will be low because of high rates of competitive exclusion. At high levels of stress (and thus low potential productivity) or high disturbance rates, diversity is predicted to be low because conditions are too severe for most species. Sites with intermediate levels of stress or disturbance, therefore, can be expected to have the highest species richness according to these models. While the influences of stress and disturbance were described separately, connections between the two were also proposed, in particular, that competitive exclusion at low disturbance rates depends on a site having a high potential productivity (low stress).

In response to Grime's paper, a rejoinder by Newman[50] brought into question a key mechanism proposed to cause the pattern – that competition intensity increases as stress declines and productivity goes up. Newman questioned the discounting of the importance of competition under less productive conditions where, for example, below-ground competition might be the predominant form. While Grime[51] offered counter arguments, it is instructive to note that this same issue was again raised a decade later and still remains an active topic today[52-55].

One of the next developments of the topic was a paper by Al-Mufti, Grime, and others[56]. Here it was proposed that the combined effects of stress and disturbance gradients on diversity could be summarized by a single community property, maximum total biomass, including both live and dead. This idea was developed further in Grime's 1979 book[57], leading to a formalization of the *humped-back model*. The pictorial representation of this model is an *x*-*y* (bivariate) plot, with variation in maximum potential species richness plotted along the *y*-axis and maximum total above-ground biomass plus litter (aka *total biomass*) on the *x*-axis. Overlays and accompanying descriptions suggest that stress and disturbance work together to control variation in total biomass and that with increasing biomass there is increasing dominance by the most productive species in the community. The model further hypothesizes that maximum potential richness peaks at low to intermediate levels of *x*, with the magnitude of potential richness depending on the degree of niche differentiation and rate of immigration for the sampled community. Importantly, discussions of underlying mechanisms were based on key propositions about life history tradeoffs, which themselves have been the source of substantial controversy.

At approximately the same time, other theoretical presentations of similar ideas were published. In 1978, Connell's exposition of what became known as the *intermediate disturbance hypothesis* [58]was published. While focusing on illustrations from tropical forests and coral reefs, similar arguments to those made by Grime in 1973[49] about

disturbance effects on richness were presented. Focus here was again placed on the need for some degree of disturbance to reduce the effects of competition in communities for the highest diversities to be observed.

In 1979, another model was offered by Huston[59], described as the *dynamic equilibrium model*. This paper built on the ideas of Grime and Connell to propose a formal relationship between the effects of disturbance and productivity (via influences on population growth rates). This paper focused on the role of the rate of competitive exclusion in non-equilibrium systems as a key determinant of diversity in natural communities. In this model, it was suggested that the effects of disturbance and productivity could potentially interact in complex ways, depending on the specifics of the disturbance regime.

Perhaps the next major event relative to the PRR discussion was the publication of an alternative theory for thinking about how competition relates to diversity by Tilman[60], the *resource ratio model*. Building on resource-based competition models, it was predicted that diversity would indeed peak at low to intermediate levels of resource supply rates. However, the controlling mechanism was suggested to not involve variations in competition intensity. Instead, variation in diversity was postulated to depend critically on spatial heterogeneity in the ratios of limiting resources. The mechanism proposed for this was derived from the presumption that there are greater opportunities for coexistence via exploitation of unique resource ratios, which decline with increasing resource supplies. A key element of the predictions that emanate from the resource ratio model depends on equilibrium assumptions, under which only unique resource ratio exploitation permits species persistence.

The 1980's was a decade in which debate over various aspects of these theories began to intensify. We interpret the various discussions that have taken place to be of two types. One type of argument has involved the empirical generality of predictions, which is seen by many as critical to the *importance* of proposed mechanisms (though a high degree of predictive/explanatory power is not required to suggest that a mechanism is simply *valid*). One exchange of this type can be seen reflected in a paper by Grime in1982[61] in which he attempted to clarify the meaning of his life-history mechanism in response to critiques by McNeilly[62] and van Andel and Jager[63] that question the conformity of individual species to predictions. Here, the tension between theory and empiricism that has continued to persist to the present day was clearly in evidence (see also Grime 1985[64], in which the author uses a golf analogy to compare concerns for discrepant examples rather than general patterns to "putting from the tee").

Another type of dispute about the relations between productivity and diversity involves a direct objection to elements of theory. For example, Thompson in 1987[65] presented a set of objections to Tilman's resource ratio model[60]. These included questioning both the reliance on equilibrium solutions and underlying assumptions about tradeoffs among traits and variations (or lack thereof) in competition intensity. Tilman[66] offered alternative perspectives on his model, as well as certain critiques of Grime's humped-back model assumptions[57]. A useful summary of the exchange is expressed in a quote

from Tilman, ". . . both Grime and I agree that soil nutrient levels, light, disturbance and competition are important factors influencing plant community structure. However, Grime and I disagree about the ways in which these factors interact to structure plant communities." In a joint response by Thompson and Grime in 1988[67], the authors felt that Grime's humped-back model was misrepresented by Tilman and no obvious resolutions were apparent. In that same year, Grime[68] reiterated a number of criticisms of Tilman's model approach and assumptions in a review of Tilman's second book on the subject[69]. Subsequent attempts to reconcile some parts of the dispute between Grime's and Tilman's models by Grace in 1990 and 1991[70,71] suggested that a portion of the apparent conflict is due to different perspectives and uses of terminology. In that effort, the difficulties posed by propositions that are only linguistically defined, as well as the role of defining examples, were brought to the forefront of the discussion.

In 1990, a new proposition about how species diversity relates to productivity was proposed by Taylor, Aarssen, and Loehle[72], who presented the *habitat templet model* as an alternative to Grime's and Tilman's models. In their new model, lower diversity at higher productivities is attributed not to higher competitive intensity, but to smaller pools of suitably evolved species. The basic argument made was that high-productivity conditions are naturally less common than less productive conditions, and as a result, there has been less evolutionary opportunity for a suitable pool of species to develop. This reference to the prospect that local richness patterns may be influenced by large-scale diversity patterns introduces some interesting alternative possibilities, which emerge as an additional theme in later studies (see below).

The mid-1990's ushered in a new, and at the time surprising, interest in the possibility that variations in diversity can drive productivity. While again, important precedents existed[73], it was experimental results from microcosms by Naeem et al. in 1994[74] and field experiments by Tilman et al. in 1996[75] that stimulated an explosion in interest in this possibility. Interest in this topic has stimulated a great deal of theoretical analysis and experimental study[76,77]. For a while, debate centered on the validity of experimental designs and interpretations (e.g., Huston 1997[78]), though subsequent disputes have been over the importance of this process relative to other controls on productivity[79]. There is now a very large body of literature on this subject recently reviewed in Cardinale et al. 2012[80].

The potential for components of diversity (including species richness, functional group richness, and genetic diversity) to influence productivity and many other aspects of ecosystem functioning has now been repeatedly demonstrated, though numerous exceptions, e.g., Wardle et al. (1997), Smith and Knapp (2003)[81,82], have also been reported. Not resolved, however, is either the quantitative importance in structuring natural ecosystems, or how to parse its effect from the presumed simultaneous influence of productivity on diversity. These are issues we address in this paper.

Also emerging in the 1990's (in this case with quite a long history of important precedents), was intensified interest in explicit linkages between large-scale and small-scale productivity-diversity relations[83]. A conspicuous empirical relationship that

contributed to this interest is the macro-pattern of increasing species richness with increasing energy[84] (Note that the word "energy" in this context is associated with gradients in evapotranspiration, which combine influences of precipitation and temperature.) Also supporting interest was the increasingly recognized need to consider the supply of species, or species pool, as a factor potentially limiting local richness[85-88].

While most of the prominent papers on the topic to this point advanced some model or point of view, a few took a neutral yet critical perspective. Abrams[89], for example, in 1995 reviewed competing ideas related to two major proposed relationships between productivity and the diversity of coexisting consumer species, monotonic and unimodal relationships. In his article, he argued that (a) there are many viable mechanisms that can produce monotonic curves in the presence of competition; (b) there is little empirical support for the hypothesis that productivity increases competitive exclusion by decreasing heterogeneity; and (c) there are numerous competing models that can predict unimodal curves. He argued that additional theoretical and empirical work is required to understand what relationships follow from different mechanisms of competition, and what relationships are most frequently observed under different observational protocols. In a review by Grace in 1999 that focused on herbaceous plant communities and small-scale patterns, it was also concluded that a multitude of competing models predict similar bivariate patterns for conflicting reasons[90]. In that paper it was argued that multivariate data would be required in order to make progress and methods such as structural equation modeling were needed to distinguish competing hypotheses. In perhaps the most explicit approach to this problem, Mouquet, Moore, and Loreau[91] performed modeling studies to examine the impacts of various mechanisms on predicted productivity-richness relationships. They concluded that there is no reason to expect a general pattern based on theory.

A More Serious Consideration of Evidence

The end of the century was marked by a spate of evaluations of the empirical support for a general relationship between productivity and diversity. As emphasis shifted from theoretical propositions to empirical evaluations, species richness became the most commonly used measure of diversity. One of the first major reviews of evidence was by Waide et al in 1999[92], who concluded "Reviews of the literature concerning deserts, boreal forests, tropical forests, lakes, and wetlands lead to the conclusion that extant data are insufficient to conclusively resolve the relationship between diversity and productivity, or that patterns are variable with mechanisms equally varied and complex." Following on the heels of that study was an investigation by Gross et al.[93] that concluded that attempts to discern a general relationship between productivity and richness would have to carefully consider scale and that certain scales may not show a consistent, coherent pattern. Mittelbach et al.[94] then used raw data to reexamine the relationship between species richness and productivity in 171 published studies, grouping results by a variety of scales. They concluded from this that the data themselves do not support a common general relationship and nearly all possible forms of curves (modal convex, positive, negative, modal concave, and none) were observed.

The claim that empirical data do not support the existence of a general relationship between productivity and richness by Waide et al.[92] and Mittelbach et al.[94] inspired a number of critical responses. In 2003, Whittaker and Heegaard[95], though in general agreement with Mittelbach et al.'s conclusions, were critical of the meta-analysis conducted and presented meta-analysis results of their own. Of special concern in their comments were (a) the treatment of scale, (b) surrogate measures of productivity, and (c) choices related to statistical analyses that might influence the complexity of pattern found. In a rejoinder to that article, Mittelbach[96] agreed with most points raised by Whittaker and Heegaard, but felt the latter authors had made recommendations that would generally favor the detection of monotonic relationships over other types.

Gillman and Wright in 2006[97] followed next with an examination of 159 productivity–plant species richness relationships from131 published studies. In their analyses they focused on the appropriateness of the surrogates used for productivity. They found only 60 of the reported relationships to be actual tests of productivity. The authors found that in studies that used data of continental to global extent, all productivity-richness relationships were positive, nearly all were positive in data sets of regional extent, and that unimodal relationships were not dominant even in studies of fine grain or small spatial extent. This study was among the first to suggest that the empirical form of fine-grain productivity-richness relationships may actually be monotonic positive instead of unimodal. The mechanistic basis for this claim was the contention that the importance of species pools typically predominates over local interactions in shaping observed patterns. Pärtel et al. in 2007[98] followed up on the idea in Gillman and Wright that species pools are predominantly important, but argued that historical effects on species pools create potentially complex productivity-richness relationships, not simply positive linear ones.

What came next was a collection of papers published in the form of a Forum in the journal *Ecology*[99]. The first paper in the selection by Whittaker[100] considered the value of meta-analysis and expressed concern that this means of drawing conclusions could overcome the many limitations of the individual studies treated in the meta-analysis. By-and-large, the other authors agree with the prescriptions given by Whittaker for better study designs and treatment of data, but disagreed with the notion that meta-analysis is not an appropriate means of reaching general results[101-105]. At the end of the set of papers, Whittaker[106] returned with a narrower focus on specific problems related to the meta-analyses involved in this debate. Again, the problem of drawing conclusions about "productivity" when the individual studies used different predictors was raised. Also reiterated was the great potential for two investigators to make many different decisions during meta-analysis and arrive at fundamentally different conclusions as a result. Central to these problems was the great variety of circumstances, sampling schemes, and measurements included in studies of productivity-richness relationships in the literature.

The very next year, Adler et al. (2011)[107] published results from a single, large study that involved a coordinated sampling of 1,600 plots from 48 herbaceous plant communities located on 5 continents across the world. In this study, considerable efforts were taken to address the many concerns raised in previous objections to attempts to make a general assessment. A standardized methodology was used for estimating annual plant production

and both plot-level and site-level species richness. A wide variety of analyses were conducted in an attempt to anticipate alternative perspectives that might be adopted by different investigators. For example, results were presented based on all sites, but also based on exclusion of highly anthropogenic sites or exclusion of the one salt marsh site that wound up being part of the study. Results showed modal, linear-positive, and null relationships depending on minor decisions about sample purity; however, in all cases variance explanation was very low. The paper's ultimate conclusion was that productivity is generally a weak predictor of richness and that instead of continuing to seek a general bivariate relationship between productivity and richness, ecologists should investigate the complex web of multivariate processes that regulate these system properties.

An interesting variety of reactions to the Adler et al. paper were published. Willig[108] concluded that because productivity and species richness are embedded in a multi-causal web of drivers and responses, "It should not be surprising that the relationship between biodiversity and productivity is complex, scale dependent, and context specific in nature." Others, however, took issue with the conclusions drawn by Adler et al., though for various and conflicting reasons. Pan et al.[109] performed an independent reanalysis of the data. They removed both the anthropogenic sites and the one salt marsh, classified the remaining 30 sites according to 12 vegetation types, and computed mean productivity and richness for each type. Based on these procedures, they claimed the data support a strong, positive linear relationship. Simultaneously, in a response by Fridley, Grime, Huston and others[110], an opposing interpretation was suggested. First, the authors argued that the range of values of productivity in the sample was inadequate for drawing general conclusions. An additional criticism was that Adler et al. used annual productivity instead of accumulated biomass (living plus dead) in the analyses. Further, they objected to the fact that some analyses omitted the anthropogenic sites and salt marsh. They then concluded that with these shortcomings removed, it was visually obvious that the data evidence a unimodal (humped-back) relationship.

In a rejoinder to the criticisms presented in 2012, Grace et al.[111] highlighted the fact that the two critiques argued on behalf of two contrasting interpretations of the same data. Pan et al.[109] argued that the data supported a positive linear relationship (and, it should be noted, ignored the fact that Adler et al.[107] presented this same curve as one of the possible outcomes from a selective analysis of the data). Fridley et al. [110], in contrast, argued that the data clearly showed a modal relationship (and also failed to comment on the fact that one of the analyses presented in Adler et al., which included all sites, did show a significant but weak modal relationship between productivity and richness). Grace et al. also offered an opinion for how contrasting opinions about the data could be drawn by different investigators. They framed the problem by distinguishing theory demonstrations from theory investigations as contrasting scientific motivations. They further argued that attachment to particular theoretical ideas can lead to a reliance on theory demonstrations, which selectively sift through data to find supporting evidence. Theory investigations, in contrast, have a different motivation - to evaluate the explanatory adequacy and limitations of theories so as to improve them; this was the motivation of Adler et al. Another distinction presented was that theory demonstrations generally seek qualitative

(yes/no) conclusions, whereas theory investigations seek to quantify the relative importance of different processes.

Following the above-described exchange, Pierce[112], in 2014, published a different reanalysis of the Adler et al. data, one that focused on analysis of the upper boundary of the relationship between productivity and richness. Also, Pierce emphasized one particular theory, Grime's humped-back model[57], which seeks only to explain maximum richness, thereby justifying the focus on boundary relations. Pierce used a method called "boundary regression" for his analysis. Using this technique and curve-fitting software, he claimed the Adler et al. plot-level and site-level data both show humped boundary relations with respective variance explanations of 88% and 97%. Pierce further argued that failure to support the humped-back model would do damage to conservation efforts. Grace et al.[113], in their response to Pierce, first focused on problems with the use of boundary regression, which depends strongly on an assumption of a uniformly-distributed *x*-variable. Using quantile regression, which is appropriate to the situation, Grace et al. were unable to detect significant boundary relations at either the plot-level or site-level. Grace et al. further argued that bivariate plots of data are fundamentally inadequate for the investigation of productivity-richness relations. Instead, they suggest that these two variables reside in a network of causal interrelations, requiring multivariate methods like structural equation modeling and the measurement of a full set of appropriate variables. Using this approach, Grace et al. translate Grime's humped-back model into a hypothesized causal network and test it using data from managed grasslands in Finland. They then used the ensuing structural equation model to illustrate the fallibility of bivariate patterns as indications of underlying processes. Once again, the theme presented is one that emphasizes the need for a different approach to evaluating theoretical ideas related to productivity and diversity.

Most recently, three additional papers have been published in response to Adler et al.[107]. First, Huston[114] has defended his dynamic equilibrium model as being conceptually valid and he reprinted the boundary regression results from Pierce as support (without reference to the problems with that analysis demonstrated by Grace et al.[113]). Fraser et al.[115], first called for a global sampling effort to provide a more extensive evaluation of the bivariate relationship between plant biomass and species richness. That sampling is now complete and the authors[116] present what they believe to be global support for a unimodal relationship between productivity and plant species richness in this larger sample. Further, they present this as strong support for Grime's humped-back model[57]. Interestingly, the patterns presented by Fraser et al. look very similar to the data patterns presented by Adler et al. superficially, though the emphasis in their conclusions is on the lower p-values in their study and the support for a global humped-back pattern.

As far as where we are at this point with the topic, Adler et al., the first paper in this most recent discussion, argued that "Rather than investing continued effort in attempting to identify a general [bivariate productivity-richness relationship], ecologists should focus on more sophisticated approaches already available for investigating the complex, multivariate processes that regulate both productivity and richness [i.e., structural equation modeling]." Several authors criticized this conclusion, while Grace et al.

followed this up with an illustration of how multivariate causal approach might clarify disputed issues and considerations of evidence. In the latest response to Adler et al., Fraser et al. continue to emphasize that there is a humped-shape relationship between productivity and diversity. However, at the end of their paper there is a call to move beyond the study of bivariate relations and they state, ". . . we recognize that . . . productivity accounts for a fairly low proportion of the overall variation in richness. . ." and ". . . we echo the call of Adler et al. for additional efforts to understand the multivariate drivers of species richness." Here we follow through on those suggestions. First, we develop a meta-model (a generalized model that describes a family of specific models with common general characteristics) based on our evaluation of the logical connections among theoretical constructs. We then develop a specific instantiation of that meta-model for the data from the Nutrient Network. After that, a specific structural equation model is evaluated and results obtained. We end by considering the consequences of using lower dimensional models to evaluate the data.

S2. A Meta-Model of Productivity-Diversity Interrelations

Overview

This paper addresses a several-decades-long debate over the meaning and value of various ecological models. Thus, it seems like an obvious point that approaches to conveying elements of causal hypotheses that are implicit rather than explicit are insufficient. To address this problem, we present our ideas about the interconnections between productivity and diversity using different forms of abstraction. First we describe a generalized meta-model of hypothesized interconnections among the key theoretical constructs. Meta-model development is often seen as one of the first steps in the structural equation modeling process[117]. It is the most general level of abstracting a system in terms of probabilistic causal networks. Meta-models also serve the purpose of generalizing across individual systems, which can differ from one another in particular features while sharing general properties. Second, we use the meta-model to guide the development of a specific structural equation model for the Nutrient Network data.

Meta-model Development

For our purposes here, theoretical "constructs" represent generalized entities of interest whose behaviors are to be studied. Thus, constructs are a subset of the broader idea of "concepts" where a formal approach to quantification is adopted. For more on this topic refer to Raykov and Marcoulides (2011)[118].

In developing a meta-model for structural equation modeling, we began by identifying the key theoretical constructs related to the purpose of the meta-model and then integrating the constructs into a hypothesized network of linkages. The criteria for decisions within this assembly process are presented in detail in Grace et al. 2015[119]. The resulting representation (Extended Data Fig. 1) is thought of as a "meta-model" in the sense that it represents a family of possible models for specific situations[120]. What is addressed by this approach is the recognition that ideas of general interest in ecology, like "disturbance", actually represent a family of related (but often subtly distinct) phenomena with some common shared property. This illustrates the notion of explicitly separating constructs from observations.

This separation of construct from observation is meant to draw attention to the importance of the measurement process and to reduce linguistic uncertainty[121], which is typically ignored in both ecology and biostatistics. There are two key concepts that relate to the mapping of data to constructs. Considering these issues leads us to treat observed variables as "indicators" of the theoretical constructs of interest. The concept of an indicator not only recognizes the potential for imperfect measurement, but also the presumption that observed manifestations are the result of underlying (latent) causal processes. When considering measurement adequacy, there are two properties of indicators to consider. One is validity, or whether the indicator actually represents the construct with which it is associated. The second property is reliability, which has to do with the repeatability of measurement. Perfect reliability suggests that different attempts to measure a construct (either with the same variable measured repeatedly or with alternative indicators) yield perfectly correlated sets of values. An important portion of the debate over productivity-diversity relations can be seen to emanate from a failure to explicitly consider such measurement issues. Here we attempt to make it explicitly clear that there may be several different ways to quantify a construct so that it is clear how models involving observed variables relate back to theory.

Our meta-model for understanding productivity-diversity interrelations is presented in Extended Data Fig. 1. In this figure we show hypothesized interconnections among key theoretical constructs (in dotted-outline ovals). The meta-model presented contains a number of theoretical constructs and represents a multivariate approach to the problem of understanding productivity-richness relations. Our decisions about what constructs to include are based on two criteria. First, resolving the ongoing debate will by necessity require consideration of certain key distinctions. Distinguishing resource supply from resource reduction, for example, aims to avoid confusion over the role of "resources." A second criterion is the irreducible complexity of Nature's data generating process. There has been a long history of attempts to reduce the relationship between productivity and diversity to a few dimensions (e.g., bivariate and 3-D plots). We have argued for higher-dimensional models in numerous previous commentaries on this issue[90,107,113]. Our intent here is to obtain a model that strikes a balance between realism and generality and that still allows empirical evaluations to resolve and distinguish key processes. To accomplish this, we have tried to represent the main, recurring theoretical entities in the above-described literature that represents the productivity-diversity debate.

Linkages among constructs are shown as directed arrows. We recognize that in specific systems there can be many additional processes at work besides the ones explicitly shown in this meta-model. Thus, the figure presents an underspecified, and thus easily falsified, hypothesis, with alternative models encompassed by the nested set of possibilities. For example, disturbance might influence resource supply or even environmental regulators in a specific system. Structural equation modeling permits the detection of such additional complexities for specific situations.

In the meta-model presented, the three exogenous (purely predictive) constructs are not assumed to be independent (uncorrelated), despite the fact that connections among them

are not shown. Rather, background interrelations among exogenous constructs are permitted. Such interrelations, if they occur, represent additional complexities that are beyond the explicit coverage of our presentation here and are dealt with implicitly (by allowing for correlated predictors). Aside from this, the hypothesized interconnections shown are still only a subset of the possible ones and we of course anticipate future versions of the meta-model that are more complex than this initial version.

Regarding the nature of the hypothesized connections among constructs in the meta-model, relationships are probabilistic and directed arrows represent implied cause-effect influences as described by Pearl's structural-causal model[122]. In a sense, these relationships can be considered to be quasi-mechanistic in that we assume the real-world processes are some more-complex collection of mechanisms. We also assume that all direct links in the model are stand-ins for unobserved chains of cause-effect connections in the real world. Stated in another way, we assume actual causation occurs ultimately at some physical (e.g., quantum) level. At the level of the meta-model, we make no assumptions about the precise equational forms that will be used to represent mathematical relations, though specific models do of course.

Diversity

One of the focal components of the meta-model in Extended Data Figure 1 is the diversity construct. Diversity is a high-level construct made up of several component concepts, which include contributions from species richness and evenness, and also encompass functional, taxonomic, and genetic forms of diversity[123]. With regard to the productivity-diversity debate, species richness (or number of species in some unit area) is the most common variable measured and discussed. Species richness is also a fundamental causal driver of other diversity indices (e.g., Shannon diversity), which further justifies the attention this particular measure of diversity receives. For now, we will remain general in our discussion, assuming that dependencies that are specified will potentially apply to the whole suite of diversity measures. Issues of spatial scale relevant to this property, and others, are considered later.

The variety of species observed in a sample plot represent only a moment in time. Nonetheless, we must consider that differences among samples, at least over a substantial sample space, are conceptually connected to the issue of species coexistence. Theoretical considerations of diversity maintenance have led to the consensus conclusion that the maintenance of species diversity requires unique opportunities for each species (niche differences). The great variety of species that exist in real ecological communities has led many scientists to question how so many niches or opportunities for advantage could exist. Intuitive and informal explanations have been offered, with many suggesting that it involves the relaxation of competitive exclusion under disturbed or changing conditions. Decades of rigorous theoretical work has suggested, however, that simple ideas about non-equilibrium diversity maintenance are insufficient to explain coexistence. Levins (1979)[124] addressed the question of coexistence in variable environments and reached a fundamentally important conclusion: a level of diversity that would not persist at equilibrium may, nevertheless, persist if there is temporal variation *and nonlinear dynamics*. Chesson[125,126] has explored the requirements for coexistence and proposed that

there are three sets of sufficient conditions, (a) unique niche differences, which are sufficient in non-varying environments, (b) environmental fluctuations combined with nonlinear responses that differ among species, and (c) a combination of those conditions, which produces the "storage effect" (and which is also associated with fluctuating environments). More recently, proposals for diversity maintenance through neutral processes (Hubbell 2001[127]) have led to discussion of the relative roles of stabilizing versus equalizing effects (Adler et al. 2007[128]) and the challenges of empirically distinguishing among the numerous mechanisms.

It is not our purpose in this paper to model the full suite of coexistence mechanisms; rather, our purpose is to clarify issues related to the ongoing debate over observed productivity – richness relationships. In our meta-model, local diversity is controlled by inputs from a species pool and losses due to mortality of various sorts. While the exact mechanisms of coexistence are not addressed, we are interested in the dependency of diversity on various influences. A key contention of ours in all this is that we must consider and control for the multivariate effects of major influences if we are to isolate the empirical signals connecting productivity and diversity (Grace et al. 2014[113]). With regard to other major influences that we expect to help determine patterns of diversity, we begin with a consideration of the role of species pools.

Species Pools and Environmental Filters

It is convenient for our discussion to refer to the recent summary by Cornell and Harrison[129] (especially see their Fig. 1). A key assumption related to local diversity patterns is that the diversity in a community sample is derived from some larger pool of species that are both within dispersal distance and capable of living in the local environment ([72,85,87]). The separation of "unfiltered" and "filtered" species pools provides an important distinction. The critical point is the idea that the species found in a community sample are not just some subset of the species capable of having dispersed to that space, but that also are capable of establishing and surviving in the conditions that exist within the sample space. Here we imagine that any given subsample of space will likely include a smaller range of environmental conditions (and therefore niche space) than the larger area in which it is found. Here we extend the concept of dispersal to include both transport through space and transport in time via storage in propagule banks (e.g., the soil seed bank, which is a key regulator of richness for herbaceous plant communities). It has been suggested previously by Gough et al.[87] that the filtered species pool defines the maximum or "potential richness" for community samples. Recent discussions of "dark diversity" speak to the gap that exists between potential and realized diversity[130].

The filtered species pool is, by definition, some subset of the unfiltered pool. The unfiltered pool is the variety of species found in some larger area around the community sample space, but without regard for whether those species could actually establish successfully in a sample space in the absence of competition. Because unfiltered pools are more readily estimable (they are simply the list of species in some larger space), they are often the focus in empirical studies. We can, within the context of understanding community diversity, consider unfiltered pools at any scale to be a continuum of subsets

of the unfiltered pools at some larger scale. Generally, the assumption here is that as the scale (grain size) of a sample area increases, the span of variation in conditions increases, thereby permitting a larger number of species to be potentially included in the sample. Of course, we can expect there to be some larger number of species simply due to sample effects as well (e.g., Hubble 2001[127]).

At large scales, unfiltered pools are influenced by long-term processes such as speciation, migration, and extinction. Macroecological studies have revealed a number of large-scale relationships, such as increasing species richness along gradients in temperature and precipitation (Currie 1991[84]). These observed relationships suggest a number of possible causal mechanisms and much current work seeks to gain some greater insight into the roles of various alternatives (Hawkins et al. 2003, Currie et al. 2004, Qian and Kissling 2010)[131-133]. What is especially important to the focus of this paper is that there is an increasing recognition of the relevance of large-scale gradients in diversity for understanding community-level relationships when community samples span some substantial range of climate conditions[98,134,135].

Environmental filters on richness are well documented, even if comparatively little theoretical work has been conducted on this important topic. A recent, conspicuous example is from the work by Laliberte et al. [136] where it was shown through a rigorous consideration of alternative hypotheses that plant diversity along resource gradients associated with a >2-million-year dune chronosequence in an Australian biodiversity hotspot, was explained by environmental filtering from the regional flora, driven by soil acidification during long-term pedogenesis.

While it is reasonable to assume that the species in a community sample are drawn from some larger pool, accurately delimiting the filtered pool is a major challenge in the majority of situations. A number of studies have considered this problem and several have examined the empirical relationships between partially-filtered pools and local samples (reviewed in Cornell and Harrison 2014[129]). By “partially-filtered pools” we refer to cases where *a priori* criteria, such as soil pH (Partel et al. 2002[137]), soil salinity (Gough et al. 1994[87]), evolutionary histories (Harrison and Grace 2007[135]), or general community affinities, such as Ellenburg scores (Pärtel et al. 1999, Lewis et al. 2015)[138,139] are used. We feel that it is probably not reasonable to assume that these approaches are completely adequate, however. Multivariate studies of apparent environmental filtering for plant communities (e.g., Grace 1999, Grace et al. 2011)[90,140], as well as theoretical consideration of the filtering process[141,142], suggest that the actual environmental filtering influences are often complex and will be difficult to identify *a priori*. As a result, we assume that to an important degree the filtered pool will be unknowable in many cases and will therefore have to be treated as a latent entity.

In our meta-model, we deal with the latency of the filtered species pools by consolidating the various distinctions into two constructs, (1) environmental gradients and filters and (2) species pools. In this representation, we imagine that environmental gradients may, over the longer-term, influence the total unfiltered pool of species. Environmental conditions at the local conditions then act to filter the larger pool and determine the

fraction that may be in a local community. There may be cases where detailed measurements at different scales allow a full parsing of gradients and pools; however, here we provide a simpler conceptualization that does not fully specify or require such detailed information. For example, our meta-model is designed so as to allow us to not know the sizes of filtered pools for each community sample (which will often not be known), but to instead capture their effects through the signals from environmental variables (which are more commonly measurable). While the architecture of the meta-model consolidates the effects operating at different scales, it can be expanded for situations where multi-scale data on both species pools and environmental conditions are known (e.g., Harrison et al. 2006[143]).

The diversity observed in a community sample is generally presumed to be regulated by factors other than just the species pools of course. Cornell and Harrison (2014)[129] highlight the importance of competitive exclusion and disturbance. To this we add within-sample heterogeneity. We discuss the last of these first.

Spatial Heterogeneity

We expect, all other things equal, greater within-plot environmental heterogeneity should contribute to the support of a greater diversity of species (see review in Wilson 2000[144]). As a simple notion, we can anticipate that community samples that contain a wider range of abiotic conditions can be expected to include a greater range of niche space, and as a result, a greater opportunity for coexistence. As with all things, there are more complex nuances to the subject. One obvious nuance is that our measures of heterogeneity may not be the ones that are important to the community. Indeed, some have questioned whether we should necessarily expect heterogeneity to have a monotonically positive effect on diversity (Tamme et al. 2010, Seiferling et al. 2014)[145,146]. In a recent consideration of this question, Stein et al. (2014)[147] found, based on a meta-analysis of 192 published studies, strong empirical support for the general expectation of increasing species richness with increasing spatial heterogeneity. It should be clear that such an expectation depends upon isolating the effect of heterogeneity from correlated differences among samples and the absolute magnitude of effect can depend on spatial scale as well. While clearly this important topic deserves further consideration, in the context of our current discussion (Extended Data Fig. 1), we have the general expectation of a positive effect of spatial heterogeneity on diversity. Any given study, however, may produce data that reflects a more complex reality.

Disturbance

Disturbance constitutes an important theoretical construct commonly invoked in discussions of diversity (Pickett and White 1987[148]). Early ideas about the role of disturbance in communities (e.g., Connell 1978[58]; Huston 1979[59]) often emphasized the expectation of a unimodal response in diversity associated with intermediate frequencies and/or intensities of disturbance. The empirical literature, however, suggests the observed relationship between disturbance regimes and diversity is various (e.g., Mackey and Currie 2001[149]). There are multiple reasons why we might not see a common pattern of response in plots of disturbance versus diversity. Beyond obvious issues related to the comparability and appropriateness of individual studies, Miller et al. (2011)[150] point out

that "disturbance regime" is a heterogeneous collection of phenomena. Intensity, timing, duration, extent, and disturbance intervals represent importantly different aspects of the overall concept. Of course, we expect different types of disturbance (e.g., wildfire, agricultural practices, grazing, pollution events) to have qualitatively different influences on various systems properties (e.g., soil, seed banks, microclimates, architectures).

Empirical studies of diversity-disturbance relationships have tended to focus on net (bivariate) or three-dimensional (Huston 1994[151]) relationships. Within our basic meta-model, we represent the effects of disturbance on diversity as potentially involving multiple pathways of influence. Since disturbance is commonly defined in terms of direct loss of or damage to community biomass, we expect impacts on total biomass from recent disturbance events. These (and other) indirect influences on diversity should be distinguished from influences that operate on species diversity independent of any effects on community biomass. Since "disturbance" is only a general theoretical construct in our meta-model, it is permitted that different types of disturbances can have different effects on the system. Beyond that, it is possible for disturbance to have a more complex set of influences than shown explicitly in our meta-model. For example, fire as a disturbance can potentially influence nutrient supplies and growth conditions, which are not explicitly shown in our model. For the purposes of the basic meta-model presented, such influences are controlled for by permitting exogenous correlations. If our focus in this exercise was to more fully represent the potential effects of disturbance on diversity, we would provide a more explicit treatment of such possibilities.

Resources and Environmental Regulators

We have, thus far, focused on diversity and some exogenous factors that might help to regulate local levels and dynamics. We must first be clear that we expect responses to resources at the community level to be complex. While this is to be expected given the physiological diversity found at the community level, our own work (Harpole et al. 2011)[152], including our work with the Nutrient Network (Fay et al. 2015)[153] has shown this to be the case. We must also consider, of course, the regulation of productivity. While theoretical studies often emphasize resources, many non-resource conditions play a role. Obvious examples include ambient temperature, which regulates metabolism, but also influences chemical reactions as well. Soil systems are famously complex as collections of resources and non-resource regulators. Abiotic factors such as pH, Eh, cation exchange capacity, binding capacity, and many others can influence field productivity levels. Microbial and other biotic system regulators are, of course also ubiquitously important and can have a wide variety of possible effects. For this reason, in the general case, we use the umbrella concept of "resources and environmental regulators" to cover the wide variety of specific circumstances and can explain variations in community productivity.

Connections between Productivity and Richness: Competitive Exclusion and Interference

A key element of the debate over productivity – richness relations has to do with the question of how elevated biomass could be associated with lower species richness. In fact, a certain level of answer to that question is a primary focus of our meta-model and analysis. We considered many possible model conformations in constructing the meta-

model in Extended Data Figure 1. Decisions were influenced by the constraints imposed by our overall purpose and by the types of observations that are broadly collected for plant communities.

Given that one of the frequently debated issues is the role of resources versus productivity versus accumulated biomass in regulating species richness, we felt it necessary to be sure all these were represented in the meta-model. Resources are defined as those material substances that contribute to growth (sometimes equated with "potential" productivity). The concept of total biomass encompasses the accumulation of material. There are several possibilities here, but we chose to follow some basic ideas that arise from competition theory. Fundamental ideas related to resource competition generally hypothesize a chain of causal connections in which (a) resource supply determines rates of production, (b) annual production increment contributes to the accumulation of total biomass, (c) accumulated biomass drives community-level resource uptake, (d) uptake leads to reduced resource concentrations, and (e) long-term resource concentrations determine species success, and thereby, diversity dynamics. To these, we add the potential for resource supplies and environmental regulators to influence all of the other nodes in that chain. We would like to emphasize that this representation is a huge over-simplification of the potential mechanisms. We briefly discuss each of the linkages here.

As stated above, we expect productivity to be related positively to resource supply, but also influenced strongly by non-resource regulators (e.g., soil salinity, pH, Eh as well as the activities of soil biota). We also expect the combination of factors comprising the relevant resources and regulators to be complex and difficult to predict based on simple notions of resource-regulation. For this reason, our application of this meta-model to the Nutrient Network data considered a number of variables presumed to be related to either resource supply or resource use regulation, as well as various ways of combining them. We generally expect it will be the scientist's task in any particular application to discover the specific factors contributing to the regulation of productivity, treating the collection as a composite latent factor (Grace and Bollen 2008)[154].

The interrelation between production and biomass is potentially more complex than the above-described causal chain. It is certainly the case that total community biomass is the accumulation of production, but while biomass accumulates asymptotically in the absence of mortality and disturbance, productivity, which is a rate function, can vary in more complex ways. For example, it is well documented that the harvest of plant communities can temporarily increase production (McNaughton 1979)[155]. This means that short-term production can be influenced by biomass levels. What one will observe in data relationships will be a function, therefore, of both the time span over which production is accumulated and the particular time at which the relationship is examined (e.g., shortly after a disturbance versus at quasi-equilibrium). Our meta-model is meant to represent a broad range of possibilities and does not impose a strong assumption on the form of empirical relationship that will be observed. Note, however, in the development of our specific structural equation model (discussed below), we assume a simple unidirectional relationship between productivity (which was measured in our case as the

annual production increment) and total biomass accumulation (which is the sum of annual production and any biomass, living or dead, carried over from previous years.

The capacity for biomass to lead to reductions in species richness is a key point of departure for some investigators. There are many known mechanisms whereby biomass can impact the processes that regulate recruitment, mortality, and coexistence in plant communities (see for one of many examples the 2013 *Functional Ecology* special issue on Mechanisms of Plant Competition Volume 27 issue 4. http://onlinelibrary.wiley.com/doi/10.1111/fec.2013.27.issue-4/issuetoc). Despite this, some theoretical analyses have suggested that variations in biomass cannot lead to impacts on species richness (Gross and Cardinale 2007)[156]. We feel it is necessary to confront this issue directly, lest that suggestion lead to doubts about the suitability of our meta-model.

Gross and Cardinale (2007)[156] claim, ". . . these results call into question any mechanistic interpretations of empirical relationships that present species richness as a function of community biomass." We think this suggestion is indefensible for several reasons. On first principles, we object to the idea that equilibrium results from a very simplistic model can be used to establish what *can't* happen in nature. We think this is a misuse of theoretical analysis. Second, there is no inherent difference in the interpretation of a path from richness to productivity than there is from biomass to richness. Both are mediated by some additional latent chain of events that must take place before an effect can be propagated. Most importantly, however, their contention is refuted by a very large body of factual, experimental evidence. Causal analysis of their model (Grace unpublished) leads to the prediction that direct manipulations of biomass in natural plant communities cannot produce changes in species richness. If we are able to decrease or increase biomass in controlled experiments and observe an unambiguous response in species richness, such evidence demonstrates a causal connection from biomass to richness and refutes their contention.

The most common forms of biomass manipulation in experimental studies involve clipping/mowing and litter removal or addition. There have been some experiments that have moved plants to change light profiles and have observed richness responses (e.g., Hautier et al. 2009)[157], but we consider this to be a related yet slightly different change to the system. We discount the results of studies involving fertilization, burning, or grazing as providing direct evidence as to whether biomass manipulations lead to richness responses. Rather, we take the strict view that direct manipulations of biomass provide an unambiguous test.

Examining the literature provides abundant evidence of richness responses to biomass manipulations. To quote from one review of the role of dead plant biomass in herbaceous communities, Facelli and Pickett (1991)[158] state, "Litter accumulation may reduce species richness in grasslands (Facelli et al., 1988; Penfound, 1964; Watt, 1974)[159-161], oldfields (Facelli et al., 1987; Carson & Peterson, 1990)[162,163], lacustrine wetlands (van der Valk, 1986)[164], salt marshes (Haslam, 1971)[165], and in pit-and-mound complexes in temperate forest (Beatty & Sholes, 1988)[166]. Litter removal usually increases species diversity and

the number of flowering species in grasslands (Penfound, 1964[160]; Weaver & Rowland, 1952)[167]." To provide a more detailed evaluation of such general contentions, we conducted a cursory review of the literature that has experimentally examined the consequences of biomass manipulations for species richness in plant communities (Table S1). The great majority of results have shown increases in species richness as a result of biomass reductions, both for removal of dead and living above-ground material. Further, those studies that have added dead plant material have observed reductions in species richness in response. Based on these results, we think it would be inappropriate to postulate no potential effect of biomass variations on species richness in our meta-model, at least for higher plant communities.

Table S1. Illustrative examples of biomass manipulation experiments.

Study*	System	Manipulation	Findings
Antonsen and Olsson 2005[168]	subalpine grassland in Norway	mowing	After 2 years, richness was higher in mowed plots than in controls.
Beltmann et al., 2003[169]	limestone meadow in Ireland	mowing, either in spring and/or fall	Mowing in spring and fall consistently promoted richness.
Bobbink et al. 1987[170]	chalk grasslands in The Netherlands	clipping and mowing	Biomass removal caused richness increase.
Burton et al. 2014[171]	forest ground-layer communities in Wisconsin, USA	forest gap creation	Subsequent increases in understory productivity were associated with declines in species richness and increased rates of local extinction.
Carson and Peterson 1990[163]	former agricultural field in New Jersey, USA	litter addition and removal	Spring and fall litter removal increased richness initially, but not permanently. Overall, results were complex.
Clark and Tilman 2010[172]	former agricultural field in Minnesota, USA	litter removal	Litter removal caused small increase in richness.
Collins et al., 1998[173]	tallgrass prairie in Kansas, USA	mowing with cut biomass removed	Mowing increased richness compared to controls.
Dewey et al. 2006[174]	experimental herb communities in Utah, USA	mowing	Mowing along with irrigation reduced richness.
Dzwonko and Gawronski 2002[175]	woodland understory in Poland	litter removal for 15 years	Litter removal led to richness increase.
Eek and Zobel 2001[176]	wooded meadow in western Estonia	cessation of annual mowing	Richness did not respond to any of the treatments.
Fang et al. 2013[177]	semiarid temperate	N addition	Attributed 52.3% of the variation in

	steppe in China		species richness to litter accumulation.
Fenner and Palmer 1998[178]	conservation meadow, England	mowing	Mowing led to increased richness.
Foster and Gross 1998[179]	former agricultural field, Michigan, USA	litter removal	Litter removal increased richness.
Fynn et al. 2004[180]	tropical grassland in South Africa	long-term (>50 mowing)	Grass species richness declined in the absence of disturbance, whereas forb species richness was unaffected.
Gardiner and Vaughan 2009[181]	former pasture in England	mowing and shrub removal	Mowing and shrub removal doubled richness.
Gerard et al., 2008[182]	floodplain meadow in Belgium	mowing and flooding	Combination of mowing with periodic flooding (which supplied propagules) increased species richness.
Goldberg and Barton 1992[183]	review of field competition experiments in plant communities	various manipulations of biomass	In all relevant studies, richness was significantly higher in plant removal treatments than in controls.
Gough and Grace 1997[184]	coastal marsh in Louisiana, USA	vine removal	Vine removal caused an initial increase in species richness until dominant grasses took over and richness declined.
Jensen and Meyer 2001[185]	fen in northwestern Germany	mowing, thinning, litter removal	Litter removal and mowing increased richness.
Jutila and Grace 2002[186]	tallgrass prairie in Texas, USA	biomass manipulations by various means	The more complete biomass removal was, the more seeding emergence was observed and the higher the species richness. Results could be explained quantitatively by the cummulative light penetration to the soil surface during the experiment.
Kolos and Banaszuk 2013[187]	wet meadows in Poland	mowing	Mowing enhanced richness, though results complicated by hydrologic regime.
Maron and Jefferies 2001[188]	coastal prairie grasslands in California, USA	mowing with clippings removed	Species richness increased by treatment relative to control plots.
Melman et al. 1988[189]	roadside vegetation in The Neterlands	mowing with clippings removed	Richness increased.
Sandel and Corbin 2014[190]	coastal grasslands in California, USA	mowing	Richness responses were scale-dependent and complex. Disturbance either increased

			or had no effect on richness,
Socher et al., 2012[191]	grasslands in three regions of Germany	mowing	Mowing generally reduced richness.
Socher et al., 2013[192]	150 grasslands in Germany	mowing	Reactions to mowing were mixed and varied among regions.
Valko et al., 2012[193]	meadows in NE Hungary	mowing	Mowing increased richness.
Wang et al., 2010[194]	alpine meadow in China	litter removal	Richness increased in response to litter removal.
Xiong et al., 2003[195]	wet grassland in England	biomass removal and litter removal	Litter removal led to increased total richness.
Yang et al., 2012[196]	semi-arid steppe in China	mowing one of the treatments	Mowing increased stability, and in turn, richness.

* A literature search was conducted to located experimental field studies in which grassland plant biomass was directly manipulated. Only studies that involved biomass removal, clipping, mowing, or haying were considered (e.g., studies involving herbivore exclusion or fire were not considered). A Google Scholar search for "allintitle: (mowing OR haying OR litter) AND (diversity OR richness)" was conducted. Resulting papers that met the criteria for inclusion were examined in order to find additional relevant studies.

Now, to be clear, for those not familiar with structural equation models, please be aware that inclusion of an arrow in our meta-model from biomass through resource reduction to richness only means that such an effect is *permitted*, not that it is assumed. Empirical evaluation will determine whether responses to other drivers in the model (e.g., resources and regulators) provide a complete explanation for their observed association. Thus, inclusion of a pathway from biomass to richness *allows* us to test the hypothesis. Omitting that pathway would attempt to *prevent* us from such a test (though model-data discrepancies could still be evidenced if the data support an effect).

Returning to further discuss the mechanisms whereby biomass might impact richness, one category of mechanisms deals with resources. Generally, we expect total resource uptake to depend on community biomass. For resources that depend on metabolically-active tissues (e.g., water or nutrient uptake in plants), both community biomass and per-unit resource demand could contribute to uptake. Other resources, such as light, are reduced by a more simple physical process such as direct interception, which can be accomplished by both dead and living materials. Generally, we expect resource reduction to be somewhat proportional to accumulated biomass, but it also could be influenced by productivity-driven resource uptake. Again, numerous complexities are to be expected, but it is typically assumed that as community biomass increases, limitation will shift from soil conditions to shading. This can have major implications for both the potential for coexistence (through loss of niche dimensionality[197]) and for recruitment opportunities.

Other mechanisms are known whereby variations in biomass influence species richness. In plant communities, the recruitment process is a large regulator of species richness at local scales[186]. Germination inhibition is known to be enforced by various canopy-influenced physical cues such as damped temperature fluctuations and shifts in the red to far-red ratios of light spectra. Such cues enable seeds in the seed bank to time their germination to periods when there is a sufficient gap for successful establishment. These mechanisms are not regulated by resource levels per se but represent more of an avoidance of competition. Physical effects of litter may also play a role, especially for species that have difficulty penetrating litter layers. Allelochemical effects, including those that involve microbial components, represent yet another category of well-studied mechanisms whereby community biomass might affect species richness (e.g., Wardle et al. 2011)[198]. Thus, it is quite possible that there may be effects of biomass on diversity that are not mediated through resource reductions (represented by the direct arrow from biomass to diversity in Extended Data Fig. 1).

Connections between Productivity and Richness: Biodiversity Enhancement of Productivity

Of great interest during the past two decades have been mechanisms whereby community diversity might promote productivity. We feel sufficient experimentation has been done to demonstrate the potential for diversity to promote productivity in plant communities. We refer the interested reader to reviews of the potential mechanisms behind such effects[76,77,80] and include an arrow from diversity to productivity in the meta-model. Some interesting studies have been conducted to evaluate the potential for various mediators to explain experimental diversity effects on community stability (Mazencourt et al. 2013[199]).

Other Complexities

It is important to recognize that our meta-model, while designed to accommodate a large number of effects, does not attempt to explicitly address all possibilities so as to retain focus on key issues that have been debated. Some that come to mind include: (a) dependency of productivity on the species pool, (b) effects of disturbance on resource supply, environmental drivers, heterogeneity, and species pools, (c) effects of species pools on plant traits and subsequently on resource reduction, and (d) effects of diversity explicitly on community composition.

Also of potential importance in the interpretation of richness variations is the role of sampling effects, in particular the dependence of number of species observed on the number of individuals sampled (Gotelli and Colwell 2001[200]). In animal and forest community assessments, for example, it is often possible to count the numbers of individuals sampled and then express the number of species on that basis (say, number of species per 1,000 individuals). One of the extensions of this idea is the “more individuals” hypothesis (e.g., Evans et al. 2005) which states that with increasing productivity there should be more individuals and automatically more species per area or volume sampled. However, the linkage of numbers of individuals to biomass/productivity in herbaceous plant communities is not at all straightforward. The most commonly invoked role for number of individuals in the productivity-richness debate is Oksanen’s

(1996)[201] expectation that high productivity leads to *fewer* individuals (rather than more individuals) because of dominance by a few large individuals. From this logic, the sampling-driven relationship of richness to productivity might be expected to be negative rather than positive because of biomass-driven thinning. For herbaceous grasslands dominated by perennials such as studied here, it is impractical to consistently measure the number of individuals for two reasons. First, many of the species are clonal, making it impossible (short of genetic sampling of the entire communities) to estimate the numbers of individuals. Second, it is almost universally ignored that seeds are live plants too and the suppression of germination by established vegetation is a form of cryptic competition that is disproportionately important in regulating richness. So, one would really need to know a number of hard-to-measure system properties to make interpretational use of the any estimates of numbers of individuals. This is a fertile area for further study, but not explicitly represented in the meta-model used in this study of grasslands dominated by perennial plants.

Spatial Scale

The wide variation in productivity-richness bivariate patterns observed has stimulated discussion about scale-dependence. Most conspicuously, macroecological studies with large spans and grain (plot) sizes have frequently shown clearly positive relationships (Currie et al. 2004[132]). Studies involving smaller grain sizes have, as discussed earlier, shown various patterns, with theoretical interest primarily focused on unimodal patterns. The span of the sample has also been part of the discussion, especially for local-scale, small plot studies. Most of the emphasis here has related to the signal-to-noise issue of containing enough range of conditions in productivity so as to find statistically significant correlations with richness.

In addition to the potential effects of sample characteristics on bivariate patterns, some interest has also developed as to processes that might have predictable influences at different scales. One facet of this issue relates to how species richness scales up nonlinearly (Loreau and Moquet 1999[202]). Regarding other mechanisms, Chase and Liebold (2002)[203] and Chalcraft et al. (2004)[204] have illustrated that a dependence on sample scale can be produced because of an increase in species turnover and the resulting dissimilarity in local species composition with increasing productivity. Chase and Ryberg (2004)[205] have further concluded that whether or not scale-dependence is observed in productivity–diversity relationships will depend, at least in part, on the degree of connectivity among localities within regions. McBride et al. (2014)[206] have shown that geographic features, such as the size of ecoregions, can drive variations in the patterns.

Scale-dependence in the magnitude of influence of diversity on productivity has also received attention. Bond and Chase (2002)[207] have proposed that we should expect a hump-shaped relationship between diversity and ecosystem functioning at local scales, but a linear increase of functioning with diversity at regional scales due to regional complementarity. The presumed mechanism behind this effect is that at low diversity, adding species increases complementarity while at high diversity, excess species can actually decrease productivity. Overall, Cardinale et al. (2012)[80] have suggested “At

larger spatial scales and with greater temporal fluctuations, more environmental heterogeneity may increase opportunities for species to exploit more niches. Consistent with this argument, a growing body of research now shows that the net effects of biodiversity on ecosystem functions grow stronger as experiments run longer. Limited data also support the notion that diversity effects grow stronger at larger spatial scales and with greater resource heterogeneity."

Recently, Chase and Knight (2013) [208]have proposed that to derive an unambiguous estimate of the effect sizes of environmental drivers on species diversity, comparisons need to be based on a scale-independent metric, such as Hurlbert's Probability of Interspecific Encounter[209]. This will require a change in the way data are collected and analyzed.

In developing our meta-model, we have strived to be general enough to accommodate specific models developed from data at multiple scales. A discussion of specific sampling scale recommendations is beyond the scope of our study. Rather, we expect that the ideas we present will have to be adapted to fit the particular features of any multi-scale sampling of data. It is not our intention to imply that quantitative relations will be scale-invariant, but expect that the principles proposed above will be reflected in multi-scale applications (though very dependent on the particulars of the study).

S3. Additional Background about Structural Equation Model Development and Evaluation

Development of a structural equation model based on a hypothesized meta-model or causal diagram invariably involves simplification. While the meta-model is meant to describe the data-generating process, there are always parts of that process that are hidden or omitted from the measurement process. In this case, the most conspicuous missing component from our structural equation model is a node for the species pools. The Nutrient Network data include richness estimates at both the plot and site level; thus, site richness can serve as the estimate of the species pool for plots. However, sites were not selected as representative of some larger type, nor are they nested within known larger natural units. Thus, coherent estimates of species pools for sites are lacking in this application.

To elaborate on that issue a little further, a number of studies have estimated the sizes of species pools and examined the relationships with higher-level conditions as well as local richness. However, the estimation of meaningful species pool sizes is challenging, perhaps even problematic (Grace 2001a)[141]. When a species is missing from a sample unit, but within some larger area, is it because of limits to dispersal, restrictive local conditions, by chance, or competitive exclusion within the unit? Rarely do we have the knowledge it takes to estimate filtered species pools in a way that cannot be criticized (Grace 2001a)[141]. It has been our considerable experience that the environmental "filters" that filter species richness for real communities are very complex and difficult to anticipate fully (Gough, Grace, and Taylor 1994, Grace and Pugesek 1997, Grace and Jutila 1999, Harrison et al. 2006, Grace et al. 2011)[87,140,143,210,211]. Fortunately, certain rules exist within SEM for model simplification via node absorption (Pearl 2009)[122]. First

of all, SEM is based on covariances/correlation relationships and the concept of "indicator" variables[212]; thus, while it may be an impediment to variance explanation, it is not a fatal flaw that we do not have estimates of species pools, but rely instead on estimates of factors that correlate with the species pools. In this case, we rely on environmental variables, particularly those related to major climate gradients in temperature and precipitation, to serve as indicators for the filtering process. The partial plot showing increasing richness with increasing precipitation (Fig. 1-Part II- Plot C) suggests a major gradient in species pool sizes may have been captured by the available indicators.

Another way in which our specific structural equation model (Fig. 2) is more simplified than we would like relates to measures of resource reduction. The only measure of resource reduction available was a single estimation of the percent of full sun reaching the soil surface, which we converted to a measure of shading. At the plot-level, our measure of shading was sufficient to serve as a complete mediator, explaining the decline in richness with increasing biomass. At the site level, shading was predicted by biomass and richness was predicted by shading, to a degree. However, shading was not sufficiently strongly associated with biomass or richness to serve as a complete mediator. To avoid making the model unnecessarily complicated, we chose to remove the shading node from the site-level portion of the model. We hypothesize that shading may well be among the key factors whereby productive sites end up with reduced richness (e.g., Jutila and Grace 2002, Hautier et al. 2009, Borer et al. 2014)[157,186,213], but results suggest at the very least that our single measure for one growing season does not provide a *sufficient* explanation.

Here we provide additional explanation for the methods we used to create indices for *Soil Fertility* and *Soil Suitability*. We started by defining a theoretical construct "*Soil Fertility*" that describes the edaphic conditions that explain variations in community productivity, controlling for effects on productivity due to variations in climate, disturbance, and richness. It was our assumption that this construct might be made up by a collection of factors (supplies of various resources, textural properties that influence water holding capacity, and other conditions influencing the soil ecosystem). The theoretical construct "*Soil Suitability*" was created to represent the oft-observed influence of soil conditions on potential species richness controlling for non-edaphic factors (Grace 1999, 2001).

In order to create indices to represent soil fertility and suitability, we used the method of "composite estimation" (Grace and Bollen 2008, Grace et al. 2010). Composites possess the properties of "directed components" in that they represent the combined information in a set of predictors that explains variation in some response or set of response variables. Thus, they are fundamentally different from either fixed-weight indices or principal components, the latter being an attempt to describe the information in a set of predictors ignoring any relation to response variables. However, like principal components, one gains insight into their interpretive meaning through examination of loadings (correlations with predictors) rather than weights (precisely how they are computed). Composites can be used to serve a number of purposes in structural equation models.

Generally, they permit us to estimate the influences of collections of variables. In this case, we used them to represent latent complex entities. They also can be used to allow for the interpretation of nonlinear effects. For more on modeling with composite variables, one can refer to our tutorials at www.nwrc.usgs.gov/SEM.

Regarding presentations, we chose to omit from Figure 2, which presents the main SEM results, three items included in the model results (Table S2). First we controlled for error correlates between productivity and biomass since these variables were computed from overlapping information. Second, we omitted from the diagram exogenous correlations, which are freely allowed in the lavaan software. Third, at the plot level we found that shading depended not only on biomass but on the soil conditions as well. We interpret this effect as a soil-associated influence on plant species that appears to influence the per-gram shading of the canopy. Attempts to determine some simple general explanation for this effect were not successful, so we treat this as a background control feature of the study.

Table S2. Results for site-scale and plot-level components of the structural equation model. Variable descriptions are given in Extended Data Table 1. Only the unstandardized parameter estimates are presented here, along with their standard errors, Z-values (equivalent to t-values), and associated probabilities. Standardized parameter estimates derived from the unstandardized ones are presented in Table 1 and Figure 2.

```
SITE-SCALE RESULTS (select)
lavaan (0.5-15) converged normally after 230 iterations

  Number of observations                            39
  Estimator                                         ML
  Minimum Function Test Statistic               13.518
  Degrees of freedom                                13
  P-value (Chi-square)                           0.409

Parameter estimates:
                   Estimate  Std.err  Z-value  P(>|z|)
Regressions:
  SiteRich ~
    SiteBiomass      -0.742    0.138   -5.380    0.000
    Heterogeneity     0.583    0.111    5.258    0.000
    Disturb.anthr    -0.127    0.059   -2.165    0.030
    SiteSoilSuit      0.999    0.244    4.102    0.000
    ClimateOnRich     0.099    0.017    5.909    0.000
  SiteBiomass ~
    SiteProd          1.422    0.166    8.561    0.000
    Disturb.herbv    -0.028    0.013   -2.210    0.027
  SiteProd ~
    SiteRich          0.530    0.169    3.131    0.002
    SiteSoilFert      1.006    0.200    5.022    0.000
    ClimateOnProd     0.986    0.327    3.015    0.003

Select Correlations of Interpretive Interest:
    SiteSoilSuit WITH SiteSoilFert   = -0.56
    SiteSoilSuit WITH ClimateOnProd  =  0.30ns
    SiteSoilFert  WITH ClimateOnProd = -0.52
    ClimateOnProd WITH ClimateOnRich = -0.43

Complete List of Correlations:
            lhs op            rhs est.std    se       z pvalue
    SiteBiomass ~~       SiteProd  -0.463 0.176  -2.632  0.008
  Heterogeneity ~~ Disturb.anthro   0.394 0.135   2.915  0.004
  Heterogeneity ~~   SiteSoilSuit  -0.356 0.140  -2.547  0.011
  Heterogeneity ~~  ClimateOnRich   0.242 0.151   1.605  0.108
  Heterogeneity ~~ Disturb.herbiv  -0.187 0.155  -1.209  0.226
  Heterogeneity ~~   SiteSoilFert   0.379 0.137   2.767  0.006
  Heterogeneity ~~  ClimateOnProd  -0.324 0.143  -2.261  0.024
 Disturb.anthro ~~   SiteSoilSuit  -0.171 0.155  -1.102  0.270
 Disturb.anthro ~~  ClimateOnRich   0.331 0.143   2.323  0.020
 Disturb.anthro ~~ Disturb.herbiv  -0.398 0.135  -2.949  0.003
 Disturb.anthro ~~   SiteSoilFert   0.389 0.136   2.862  0.004
 Disturb.anthro ~~  ClimateOnProd   0.023 0.160   0.145  0.885
   SiteSoilSuit ~~  ClimateOnRich  -0.168 0.156  -1.078  0.281
   SiteSoilSuit ~~ Disturb.herbiv   0.180 0.155   1.160  0.246
   SiteSoilSuit ~~   SiteSoilFert  -0.563 0.109  -5.146  0.000
```

SiteSoilSuit	~~	ClimateOnProd	0.296	0.146	2.023	0.043
ClimateOnRich	~~	Disturb.herbiv	0.003	0.160	0.019	0.985
ClimateOnRich	~~	SiteSoilFert	0.379	0.137	2.763	0.006
ClimateOnRich	~~	ClimateOnProd	-0.435	0.130	-3.355	0.001
Disturb.herbiv	~~	SiteSoilFert	-0.211	0.153	-1.379	0.168
Disturb.herbiv	~~	ClimateOnProd	-0.032	0.160	-0.197	0.844
SiteSoilFert	~~	ClimateOnProd	-0.515	0.118	-4.381	0.000

```
PLOT-SCALE RESULTS

  Number of observations                          1126
  Estimator                                     Robust
  Minimum Function Test Statistic               21.907
  Degrees of freedom                                16
  P-value (Chi-square)                           0.146
  Scaling correction factor                      6.990
    for the Satorra-Bentler correction

Parameter estimates:
  Standard Errors                           Robust.sem
                   Estimate  Std.err  Z-value  P(>|z|)
Regressions:
  PlotRich ~
    SiteRich          0.650    0.058   11.163    0.000
    PlotShade        -0.839    0.157   -5.361    0.000
    PlotSoilSuit      0.999    0.182    5.475    0.000
  PlotShade ~
    PlotBiomass       0.142    0.023    6.267    0.000
    SoilWithShade*    1.000    0.392    2.550    0.011
  PlotBiomass ~
    SiteBiomass       1.018    0.018   57.436    0.000
    PlotProd          0.001    0.023    0.045    0.964
  PlotProd ~
    SiteProd          1.012    0.014   72.971    0.000
    PlotRich          0.025    0.009    2.660    0.008

Complete List of Correlations:
            lhs op            rhs est.std    se       z pvalue
   PlotBiomass ~~      PlotProd   0.868 0.034 25.379  0.000
      SiteRich ~~  PlotSoilSuit  -0.030 0.145 -0.207  0.836
      SiteRich ~~ SoilWithShade  -0.111 0.140 -0.790  0.429
      SiteRich ~~   SiteBiomass  -0.170 0.174 -0.976  0.329
      SiteRich ~~      SiteProd  -0.099 0.183 -0.541  0.589
  PlotSoilSuit ~~ SoilWithShade   0.792 0.060 13.134  0.000
  PlotSoilSuit ~~   SiteBiomass   0.314 0.184  1.705  0.088
  PlotSoilSuit ~~      SiteProd   0.519 0.101  5.121  0.000
 SoilWithShade ~~   SiteBiomass   0.217 0.172  1.264  0.206
 SoilWithShade ~~      SiteProd   0.413 0.113  3.638  0.000
   SiteBiomass ~~      SiteProd   0.841 0.062 13.634  0.000

* statistical control for covariate effect
```

S4. Additional Details about Structural Equation Model Results and Interpretations

As discussed above, since Soil Fertility and Soil Suitability were developed as composite indices, the best way to judge their interpretive content is through loadings (post hoc correlations), as in principal components analysis[210]. Our site-level soil suitability index was correlated with several soil properties, though most strongly with soil texture (r=0.73). Our site-level soil fertility index was most strongly related to soil P (r=0.62) and to pH (r=-0.61). At the plot level, the Soil Suitability index was a nonlinear function of soil N, suggesting some optimal level for species richness. Soil fertility variations at the plot-level were constructed as a combination of N, P, and C. However, the relationship to residual plot productivity was not judged to be significant, and thus, is not interpretable.

The sole climate explanatory variable for increasing richness at the site-level was mean annual precipitation during warmest quarter (thus this effect was not a composite effect and can be interpreted in a straightforward manner). Surprisingly, productivity in this sample of sites was most strongly related to warm, dry conditions based on the loadings (correlation with potential evapotranspiration = -0.84). The climatic influences on productivity and richness were not positively correlated in this case as one might have anticipated (r = -0.191). Again, more detail on the process of composite construction can be found in the Supplementary Information file containing the computer script.

The results from evaluations of model dimensionality are summarized in Extended Data Table 3. The primary criteria used to judge the consequences of eliminating variables from models (i.e., reducing model dimensionality) included (a) poor model fit, i.e., model misspecification), (b) a loss of detectable signal for one or more pathways in other parts of the model (summarized in Extended Data Table 3), and (c) reduced variance explanation in the model. The logic behind these criterion was that the historical debate over productivity – richness relations is first and foremost about what processes are sufficiently important in natural systems to have detectable effects. If, for example, removing heterogeneity from the model causes us to no longer detect the effects of disturbance on richness, it implies our model is too simplistic to approximate the data-generating processes.

It is worth elaborating here on certain of the findings. Perhaps of most interest is the finding that productivity leads to declines in richness while richness leads to increases in productivity. This appears to be a classic +/- feedback, which is of the stabilizing type. We would expect that stabilized systems would tend to resist change, as increases in richness would ultimately lead to increased competition and decreased productivity would lead ultimately to increased richness and productivity enhancements. The role of other critical drivers in the system will undoubtedly influence how this will work and further study, both empirical and theoretical, is warranted.

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