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LETTER

Does species diversity limit productivity in natural grassland communities?

James B. Grace,^{1*} T. Michael Anderson,² Melinda D. Smith,³ Eric Seabloom,⁴ Sandy J. Andelman,⁵ Gayna Meche,⁶ Evan Weiher,⁷ Larry K. Allain,¹ Heli Jutila,⁸ Mahesh Sankaran,⁹ Johannes Knops,¹⁰ Mark Ritchie¹¹ and Michael R. Willig¹²

Abstract

Theoretical analyses and experimental studies of synthesized assemblages indicate that under particular circumstances species diversity can enhance community productivity through niche complementarity. It remains unclear whether this process has important effects in mature natural ecosystems where competitive feedbacks and complex environmental influences affect diversity–productivity relationships. In this study, we evaluated diversity–productivity relationships while statistically controlling for environmental influences in 12 natural grassland ecosystems. Because diversity–productivity relationships are conspicuously nonlinear, we developed a nonlinear structural equation modeling (SEM) methodology to separate the effects of diversity on productivity from the effects of productivity on diversity. Meta-analysis was used to summarize the SEM findings across studies. While competitive effects were readily detected, enhancement of production by diversity was not. These results suggest that the influence of small-scale diversity on productivity in mature natural systems is a weak force, both in absolute terms and relative to the effects of other controls on productivity.

Keywords

Abiotic filtering, biomass production, disturbance, diversity, grasslands, meta-analysis, nonlinear modelling, productivity, richness, structural equation modeling.

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INTRODUCTION

Although much has been written about the importance of biodiversity for ecosystem functioning, there remains a persistent debate about the relevance of the work behind these conclusions to mature natural ecosystems (Aarssen 1997; Huston 1997; Grime 1998; Hector *et al.* 1999; Huston *et al.* 2000; Loreau 2001; Huston & McBride 2002; Srivastava & Vellend 2005; Thompson *et al.* 2005). A key

element in the debate over diversity–production relations is the apparent dichotomy between the conclusions drawn from experimental studies of synthesized assemblages vs. those that emerge from the study of mature natural communities. Most studies of synthesized assemblages have found that increasing diversity contributes to greater and more stable biomass production, at least at low diversity levels (e.g. Tilman *et al.* 2001; Hooper *et al.* 2005; Roscher *et al.* 2005; Spehn *et al.* 2005). In contrast, species reduction

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experiments in natural systems have found production to be rather resilient to declines in diversity (Smith & Knapp 2003; Smith *et al.* 2004; Wardle & Zackrisson 2005; Suding *et al.* 2006), while species addition experiments have shown the key importance of species pools (Foster *et al.* 2004). Other studies have shown that minor species can play a facilitative role (Boeken & Shachak 2006; Polley *et al.* 2006).

Those attempting to synthesize these disparate bodies of information have argued that the information derived from synthesized assemblages and natural communities can be complementary, with each shedding light on somewhat separate realms of system variation (Fridley 2001; Hooper *et al.* 2005; Kahmen *et al.* 2005). Some of the disparities may be resolved by considering the importance of differences in scale (Chase & Leibold 2002). However, there are a variety of reasons why the results from synthesized or early successional communities may not translate to mature natural systems. For example, Yachi & Loreau (2007) have shown that other biotic interactions, such as competition, may reduce the importance of niche complementarity. Also, there is an important difference between showing that a force can operate under constructed circumstances and showing that it is an important force in natural systems. For the former purpose, an experimental demonstration of effect is adequate. For the latter purpose, a consideration of natural ranges of conditions (e.g. Smith & Knapp 2003) and environmental conditioning effects (rather than the elimination of their influences) is needed. It is worth noting that another important contributor to the debate is that some ecologists see enhanced production as a contribution to ecosystem services, and therefore, a justification for preserving biodiversity (e.g. Naeem 2002) whereas others believe that enhanced ecosystem production is in opposition to the preservation of biodiversity, and therefore, an illogical currency by which to measure ecological value (Grime 1997; Fridley 2001; Srivastava & Vellend 2005).

General conclusions that emerge from a consideration of diversity–production relations are that (1) an enhancement of biomass production by diversity can be demonstrated for at least a range of circumstances (low to modest diversities) and (2) quantification of the forces controlling diversity and productivity in natural systems is needed if results are to be related to conservation priorities (Chapin *et al.* 2000; Loreau 2001; Hooper *et al.* 2005; Stevens 2006). As some authors have pointed out (Wardle 2001; Kahmen *et al.* 2005), an expansion of our understanding will in part depend on a reconciliation of experimental with observational data because of the substantial challenges associated with performing controlled experiments involving multiple, simultaneous processes within natural bounds of relevance. In a recent review of the state of our knowledge about biodiversity and ecosystem functioning, Hooper *et al.* (2005)

emphasized that in particular, such a reconciliation will require an integrated consideration of abiotic and biotic controls.

Most analyses of diversity–production relationships for mature natural ecosystems have relied on univariate methods (ANOVA, regression) (Waide *et al.* 1999; Gross *et al.* 2000; Mittelbach *et al.* 2001; Thompson *et al.* 2005) and have not controlled for confounding environmental effects or considered reciprocal interactions between diversity and production. A few investigations have examined more complex models involving abiotic and biotic influences on species diversity (Grace & Pugsek 1997; Weiher 2003; Harrison *et al.* 2006), but such models have not sought to address the potential impact of diversity on productivity in natural systems. Recently, Kahmen *et al.* (2005) failed to find effects of diversity on production in mature montane vegetation using linear multivariate modelling. However, the generally nonlinear nature of diversity–productivity relationships raises questions about the findings from such studies.

The potential for multivariate modelling to reveal signals in data that better represent the multiplicity of processes operating in natural systems is increasingly being understood by ecologists (Shipley 2000; Grace 2006). The application of such methods to complex ecological situations continues to be limited by important technical issues, such as our ability to model nonlinear effects in a way that allows them to be directly compared with linear effects. Bivariate diversity–productivity relationships are conspicuously nonlinear, suggesting a need for nonlinear modelling approaches that will not be biased against detecting nonlinear effects. In this paper, we first describe a general model for examining interactions between diversity and productivity that controls for environmental influences. We then develop a nonlinear modelling approach by extending the conventional structural equation modeling (SEM) framework through a modification of the LISREL equations. We present the results from our analyses of mature natural grasslands. Finally, we combine our SEM results using the additional technique of meta-analysis (Gurevitch *et al.* 2001) for the added benefit of allowing us a rigorous method for drawing overall conclusions.

A NONLINEAR, MULTIVARIATE, MODELLING APPROACH

From a multivariate perspective, it is understood that relationships between system properties can be masked, altered, or generated by the effects of correlated environmental effects (here we mean ‘environment’ in its most general sense). A degree of statistical control for such correlated effects can be achieved via measurement and incorporation into analyses (as a result, we have some

confidence that smoking tobacco causes cancer despite the fact that a controlled experimental study has never been conducted). For the purposes of this paper, we have sought to fit data to the model shown in Fig. 1. In this model, we follow the lead of most other investigators by representing diversity using species richness and community productivity using biomass production. This model recognizes that both richness and production can be jointly influenced by complexes of environmental factors (shown as hexagons in Fig. 1). A distinction between abiotic influences and those classified as disturbances is represented in the model both because of theoretical interest and because of the statistical value of having multiple environmental factors in the model (which increases the potential for model identification, a fundamental requirement for successful estimation). In this model we seek to control for the effects of abiotic and disturbance factors (paths 1–4) so as to quantify the effects that production can have on richness (e.g. via competition or facilitation, path 5) and the effects that richness can have on production (e.g. via niche complementarity, path 6). Environmental effects (e.g. abiotic factors and disturbances) can either be correlated or uncorrelated in this model. Any of the paths shown may represent nonlinear influences.

In Appendix S1, we describe in more detail the mathematical basis for the nonlinear modelling approach used in our analyses. Basically, there are three major problems that must be solved simultaneously to arrive at a nonlinear modelling formulation that would be appropriate to our modelling effort. First, we require an approach that is

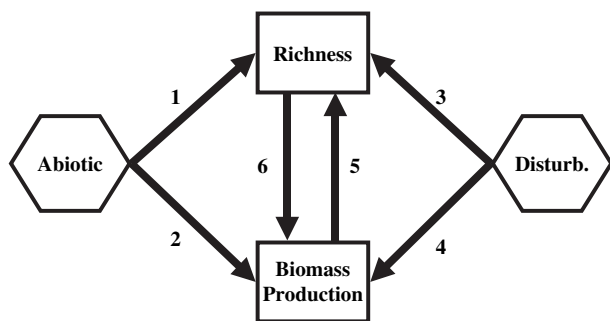


Figure 1 Multivariate statistical model used to evaluate data from 12 grassland studies. Path 1 represents the effects of abiotic conditions on richness operating independent of those mediated indirectly through biomass production. Path 2 represents the net effect of abiotic conditions on production. Path 3 represents the disturbance history on richness. Path 4 represents the change in production associated with disturbance history. Path 5 represents the combined effects of competitive exclusion, competitive inhibition, and facilitation, while path 6 represents the influences of niche complementarity as well as any other effects of richness on production (e.g. facilitation).

flexible and general in its approximation of nonlinear relationships. To accomplish this, we used an expanded polynomial approach in which higher order transformations were included in the model. Second, because nonlinear interactions between production and richness are internal (endogenous) to the model, we required an approach in which the interactions between the terms included for nonlinear modelling with the other variables in the model were controlled. This was handled using a system of appropriate correlated errors. Third, a significant problem with nonlinear modelling relates to interpretability. As Heise (1972) first articulated, the individual coefficients in polynomial regressions are largely uninterpretable and certainly not directly comparable to the coefficients associated with linear relationships. One way to solve this problem is through the use of composite variables that capture the collective effects of the set of coefficients associated with the polynomials. We applied the methods developed in Grace & Bollen (2007) for composite modelling to the problem of representing nonlinear effects, resulting in the development of nonlinear coefficients that are directly comparable to the coefficients representing linear effects in the model. Again, more detail is provided in the online Appendix S1.

Returning to the model to be solved for this study, there are four important implications of the graphical representation in Fig. 1: (1) it implies a non-recursive specification because of the reciprocal pathways between richness and production, (2) it contains composite variables ('abiotic' and 'disturb') that potentially represent collections of variables, (3) it represents a snapshot expectation based on underlying dynamic processes, and (4) it represents a family of possible models depending on the coefficients estimated for the numbered pathways. Elaborating on these points: (1) Non-recursive models possess several properties of importance. One is that they represent a static feedback process that summarizes an implied time sequence of events. Another is that solution procedures are required for such models that accommodate the inherent non-independence of errors for the variables included in the loop (in this case, richness and production). Yet another is that results obtained from the analysis of such models represent an estimated equilibrium among the feedback processes. (2) While underlying processes are dynamic, the data available to us are not sufficient for estimating a dynamic SEM. Because of this, an interpretational consistency between pattern and process must be assumed. Such a consistency depends on a correlation between current measures of system states and those that existed at the times when influences occurred. This is, in effect, a quasi-equilibrium assumption that applies to many forms of data analysis. (3) By describing the graphical representation in Fig. 1 as a family of models, we make reference to the fact that the results of our analysis

may indicate that the data support a model that is some simplification of Fig. 1.

Field data

A substantial number of data sets were examined for inclusion in this study as part of a multicampus course involving six universities that participated in the Knowledge Network for Biocomplexity Project conducted at the National Center for Ecological Analysis and Synthesis (Andelman *et al.* 2004). A requirement to be included in this analysis, beyond the measurement of richness and biomass production, was that data sets must include measurements of environmental factors that could be referenced to each plot. Also, sites recently disturbed in a major way (e.g. by agricultural tillage within the past few years) were excluded, as were very small data sets (fewer than 20 independent plots). Plot sizes ranged from 0.5×0.5 to 10×10 m² for the various studies. Data sets that relied on larger plots were excluded because the magnitude of within-plot heterogeneity was deemed to be too great for comparability to results from smaller plots. It should be noted that for the analyses conducted in this paper, plots and sample spans were not required to be identical nor did we attempt to scale the data to the same level because we based comparisons among sites on internally standardized coefficients.

For this investigation, we confined our attention to data sets whose samples were contained within a landscape or smaller span. While a consideration of this spatial scale leaves unanswered questions relating to regional variations in diversity, the data analysed here are of the type most commonly examined in studies addressing theories of niche complementarity and competition. The reliance on small-plot data also has the desirable property of reducing complications posed by having large amounts of undescribed spatial heterogeneity within large plots. For simplicity and for consistency with most other studies of this topic, we used species richness (number of species) as a focal measure of diversity (though we recognize that richness and diversity are not strictly synonymous). Also for consistency across data sets and because of its relevance to our model, we used estimated annual biomass production as our measure of productivity. Using these criteria, we were able to obtain 12 appropriate data sets that contained both measures of richness and production as well as reasonably good measures of environmental conditions (Table 1). These studies included prairies, meadows, wetlands and other grasslands from a variety of regions of the world and included a total of 1339 individual plots. Environmental variables were classified as being either abiotic influences or disturbance influences. We recognize that the distinction between these two classes of factors is not always unambiguous; however, for consistency we always included

herbivory, fire and mowing as disturbances, and soil and physical characteristics as abiotic factors.

Statistical evaluations

The model shown in Fig. 1 was evaluated separately for each community. Prior to fitting SEMs, we screened for a minimal set of indicators of abiotic and disturbance effects on richness and biomass production. Stepwise procedures were used to select from a parsimonious set of predictors (including higher-order transformations) to avoid inflating the estimated importance of environmental factors by overfitting using a large numbers of predictors. In actuality, for most studies only a few environmental variables were available for analysis (Table 1), reducing the potential for overfitting.

Estimation and model fitting were performed using the software Mplus (Muthén & Muthén 2006). Maximum likelihood solution procedures were used for all data sets for consistency. Nonlinear relationships were evaluated through the inclusion of polynomial terms and the performance of single-degree-of-freedom chi-square tests. Only where higher-order terms were found to contribute significantly were they retained in models.

We subsequently performed meta-analyses of the individual SEM results for each community with the MetaWin software (Rosenberg *et al.* 2000). Effect strengths were calculated based on standardized path coefficients. The decision to base the meta-analysis on standardized path coefficients was based on their comparability, the fact that the coefficients themselves are relatively insensitive to sample size, and the relevance to SEM's regression-parameter underpinnings. Standardized path coefficients from the SEMs were converted effect size estimates using Fisher's z -transformation. Weighting was used where the weights were the reciprocal of the sample variance, thus, giving us cumulative effect size estimates. A random model without structure was chosen for the analysis. Bootstrapping was used to estimate 95% confidence intervals. Because the effects of abiotic conditions were not expected to have consistent coefficient signs across studies (because measured properties varied widely), for the paths associated with abiotic conditions we analysed the absolute values of the coefficients. Analyses of heterogeneity were conducted using chi-square tests to judge significance.

RESULTS

Bivariate patterns

For 10 of the 12 studies, a non-random bivariate relationship was observed between richness and biomass production (Fig. 2). The two sites for which no significant bivariate relationship were observed included the Tanzanian grass-

Table 1 Descriptive information about data included in analyses*

| Site | Community types | Diversity range, spp/plot | Plot size | Ave. biomass production, g m ⁻² year ⁻¹ | Bio. prod. range, g m ⁻² year ⁻¹ | # | Abiotic predictors† | Disturbance predictors |
|----------------------------|---------------------------|---------------------------|-------------|---|--|-----|---|---|
| Utah montane grassland | Shortgrass steppe | 3–10 | 0.8 × 1 m | 168 | 41–360 | 27 | Bio. prod. = f(C:N, bulk density) richness = f(elevation zone) | Bio. prod. = f(grazing treatment) richness = f(grazing treatment) ns‡ |
| Tanzanian grasslands | Tropical grasslands | 5–12 | 1 × 1 m | 524 | 216–830 | 29 | Bio. prod. = f(elevation, precipitation, inorganic N) richness = f(organic, C:N, Ca) | Bio. prod. = f(grazing) richness = f(grazing) ns |
| Minnesota prairie | Tallgrass prairie | 6–18 | 4 × 2 m | 243 | 70–415 | 24 | richness = f(bulk density) | Bio. prod. = f(burn history) richness = f(burn history) |
| Kansas prairie | Tallgrass prairie | 20–59 | 10 m-diam. | 295 | 167–487 | 72 | Bio. prod. = f(elevation, soil moist.) richness = f(elevation, soil NH ₄) | Bio. prod. = f(burn history) richness = f(burn history) |
| Mississippi prairie | Tallgrass prairie | 3–24 | 0.5 × 0.5 m | 162 | 98–516 | 99 | Bio. prod. = f(organic, Ca, canopy§) richness = f(organic, Ca) | No disturbance measures were available |
| Louisiana prairie | Tallgrass prairie | 3–15 | 0.5 × 0.5 m | 486 | 195–850 | 107 | Bio. prod. = f(Zn, Ca, Mg, silt) richness = f(elevation, Mg, Mn) | Bio. prod. = f(animal digging) ns richness = f(animal digging) ns |
| Indian tropical savanna | Tropical grassland | 3–20 | 1 × 1 m | 440 | 35–1355 | 40 | Bio. prod. = f(Mn, Co) | Bio. prod. = f(grazing) ns richness = f(grazing) ns |
| Wisconsin prairie | Tallgrass prairie | 4–22 | 0.5 × 0.5 m | 296 | 15–1433 | 168 | richness = f(clay) Bio. prod. = f(clay, silt, soil moisture, K) | richness = f(grazing, droppings) Bio. prod. = f(burn history) ns richness = f(burn history) |
| Finnish meadows | Mixedgrass meadows | 1–25 | 1 × 1 m | 268 | 20–1788 | 354 | richness = f(sand, organic) richness = f(elevation, soil type) | Bio. prod. = f(grazing) ns richness = f(grazing) |
| Texas grasslands | Coastal tallgrass prairie | 9–38 | 10 × 10 m | 1328 | 382–3374 | 54 | flooding duration, soil type) Bio. prod. = f(cation exchange capacity) | Bio. prod. = f(burn history, haying) richness = f(burn history, haying) |
| Louisiana coastal wetlands | Fresh to saline marshes | 0–17 | 1 × 1 m | 1562 | 0.4–4014 | 190 | richness = f(salinity, Mn, P, NO ₃ , silt) Bio. prod. = f(elevation, salinity) | Bio. prod. = f(grazing, scouring) richness = f(grazing, scouring) ns |
| Louisiana riverine marsh | Fresh to saline marshes | 2–19 | 1 × 1 m | 1443 | 182–4395 | 175 | salinity, N, organic) Bio. prod. = f(elevation, salinity regime) richness = f(elevation, salinity, salinity regime) | Bio. prod. = f(grazing, scouring) richness = f(grazing, scouring) |

*References providing additional information about the data sets are as follows: Grazed and Ungrazed Finnish meadows – J. B. Grace and H. Jutila, *Oikos*, 85, 398–408 (1999); Indian tropical savanna – M. Sankaran, *Disturbance, Diversity and Community Dynamics in a south Indian Savanna-Grassland Ecosystem*, PhD Thesis, Syracuse, University, Syracuse, NY, USA (2001); Kansas tallgrass prairie – Smith et al., unpublished data; Louisiana coastal marsh – J. B. Grace and G. R. Guntenspergen, *Ecotone*, 6, 381–391 (1999); Louisiana tallgrass prairie – J. B. Grace, L. K. Allain and C. Allen, *Journal of Vegetation Science*, 11, 443–452 (2000); Louisiana-Mississippi marsh – J. B. Grace and B. H. Pugesek, *American Naturalist*, 149, 436–460 (1997); Minnesota tallgrass prairie – J. Knops, *Oecologia*, 150, 477–483 (2006); Mississippi blackland prairie – E. Weiher, S. Forbes, T. Schauwecker and J. B. Grace, *Oikos*, 106, 151–157 (2004); Texas coastal grasslands – J. B. Grace, L. K. Allain, H. Q. Baldwin, A. G. Billock, W. R. Eddleman, A. M. Given, C. W. Jeske and R. Moss, *USGS Open-File Report 2005-1287*, 40 pp. (2005); Utah montane grassland – E. S. Bakker, M. E. Ritchie, H. Olff, D. G. Milchunas and J. M. H. Knops, *Ecology Letters*, 9, 780–788 (2006); Wisconsin tallgrass prairie – E. Weiher, *Oikos*, 101, 311–316 (2003); Tanzanian grasslands – T. M. Anderson, M. E. Ritchie, E. Mayemba, S. Eby, J. B. Grace, and S. J. McNaughton, *American Naturalist* (in press).

† = f() is to be read, 'was found to be a function of...'

‡ ns = deemed non-significant.

§ Note that for this analysis, the presence of a tree canopy (shadow effect) was treated as an abiotic condition for simplicity.

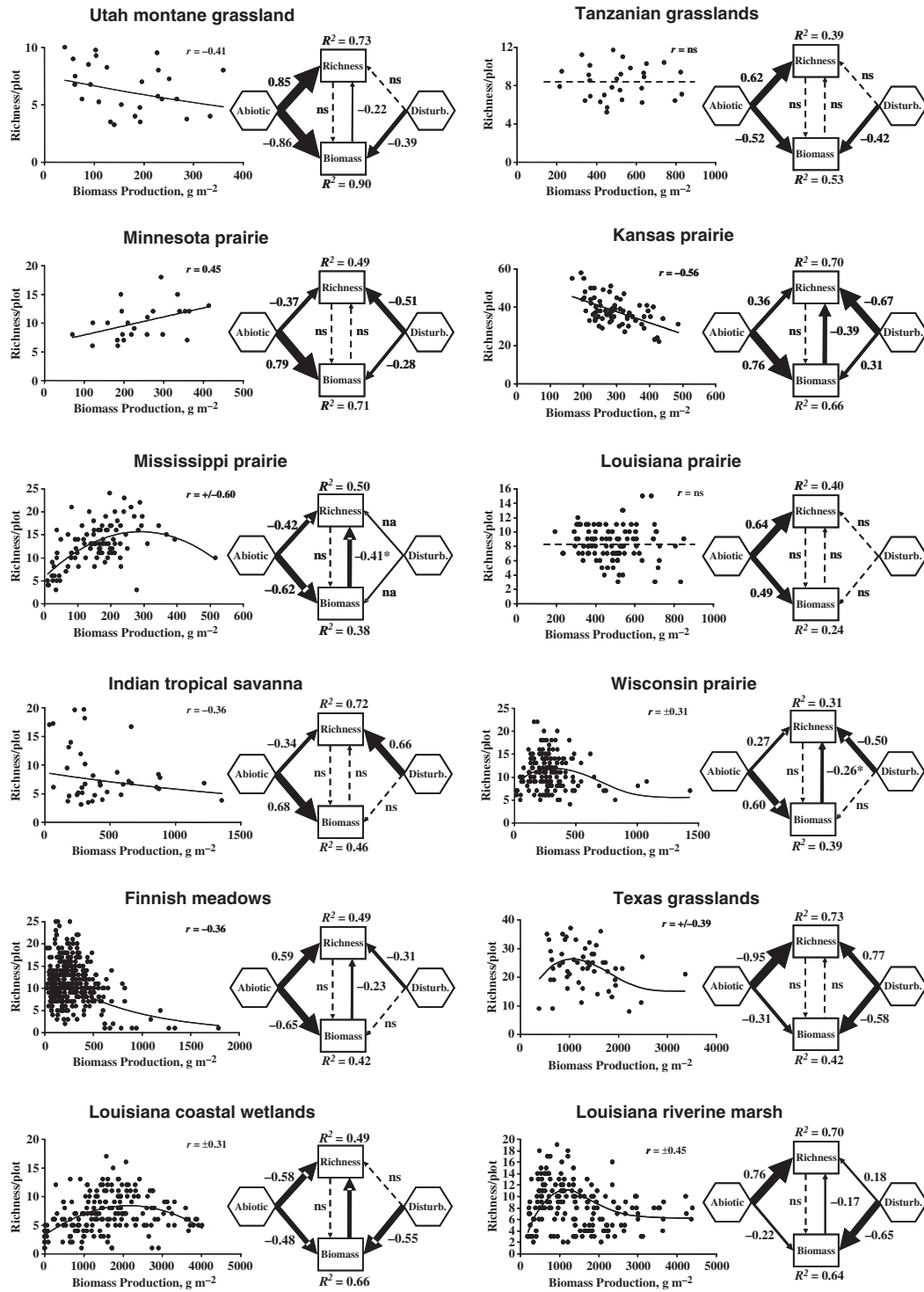


Figure 2 Bivariate and multivariate relationships involving richness and biomass production. Sites are arranged by maximum production (from lowest to highest). Strength of bivariate relationships are represented by the correlations between biomass production and species richness per plot (r). For multivariate model results (in diagrams to the right of bivariate plots), standardized coefficients are reported. Nonlinear effects are represented by coefficients followed by an asterisk. For the Mississippi prairie, there were no measures of recent disturbances. na, not applicable; ns = non-significant.

lands (one of the least productive sites) and the Louisiana prairie (a moderate productivity site). For four of the sites where a significant pattern was found, a negative monotonic relationship was detected. These included the Utah montane grassland, the Kansas prairie, the Finnish meadows, and the Indian tropical savanna. While the first three of these were highly productive sites, the fourth (Utah) was not. Importantly, three of the sites contained plots that were very low in production and still retained high richness values (all except the Kansas site, which possessed no low productivity plots).

Six of the sites were found to have a positive segment to the relationship, with five of the six being unimodal (having both positive and negative segments). Those with unimodal patterns included the Louisiana coastal wetlands, the Louisiana riverine marsh, the Mississippi prairie, the Texas grasslands, and the Wisconsin prairie. The Mississippi prairie relationship was predominately positive, with only a few points on the right side of the peak, while the other sites with a unimodal patterns possessed numerous plots on both sides of the apparent peak. Only one site, the Minnesota prairie, was found to demonstrate a purely positive relationship between richness and production. This site was among the least productive, though in actuality, it bore some resemblance to the Mississippi prairie except for the few plots from the Mississippi site in which richness declined at higher production levels.

Structural equation modeling results – abiotic and disturbance effects

The paths from abiotic conditions to richness and biomass production in the SEM results (Fig. 2) were significant for all sites. Associations between richness and abiotic conditions ranged from modestly strong (e.g. Wisconsin prairie, $\gamma = 0.27$) to extremely strong (e.g. Texas grasslands, $\gamma = -0.95$). Signs of these path coefficients were not consistent; however, we do not place any particular interpretation on this because they would not be expected to be consistent given that environmental conditions were not measured in consistent fashions at different sites (for example, at one site increased elevation might represent less flooding stress and more favourable conditions for growth while at another site it might represent decreased nutrient supply). In contrast, disturbance effects on richness and production were less consistently strong. For some sites, recent disturbances had little measurable effect (e.g. the Louisiana prairie, $\gamma = \text{ns}$ for both), whereas for others (e.g. Texas grasslands, $\gamma = 0.77$ for richness and $\gamma = -0.58$ for production), impacts were conspicuous. With regard to the particular environmental and disturbance factors found to be important, all results are based on statistically significant contributions to the SE models. Additional details about the individual environmental variables that were important can be found in Table 1.

Structural equation modeling results – interactions between richness and biomass production

Structural equation modeling results indicated that in 5 of the 12 sites examined, neither an effect of richness on production nor an effect of production on richness could be detected. The sites for which this pattern was found included the Tanzanian grasslands, Minnesota prairie, Louisiana prairie, Indian tropical savanna, and Texas grasslands. The seven remaining sites all showed effects of production on richness; for three of those seven (Mississippi prairie, Wisconsin prairie and Louisiana coastal wetlands), the effects of production on richness were nonlinear. For two of these cases (Mississippi and Louisiana), the nonlinear effect of production on richness was fit by a second-order polynomial. For the Wisconsin prairie, a linear and third-order term were required. For all sites with nonlinear effects, the predominant effect was negative (meaning that the net effect was a decrease). For the remaining sites where effects of production on richness were detected (Utah montane grassland, Kansas prairie, Wisconsin prairie, Finnish meadows and Louisiana riverine marsh) those effects were simple linear ones. Effect strengths measured for the effects of production on richness varied from as low as -0.17 (Louisiana riverine marsh) to as high as -0.41 (Mississippi prairie). It can be noted that for all sites evidencing a significant effect of production on richness, the bivariate relationship between these two variables included a negative slope. However, the reverse was not the case. For two sites (Indian tropical savanna and Texas grasslands), a negative bivariate slope between production and richness was observed, though no multivariate effect of production on richness was detected.

Meta-analysis results

Meta-analysis (Table 2) allowed for the estimation of effect sizes for the paths in the multivariate models across sites (summarized in Fig. 3). Effect sizes for abiotic influences on production and richness were significant in all cases and the averages across the study were found to be 0.70 and 0.73. The relationships between production and disturbance were significantly different from zero in 7 of the 12 cases (Such tallies are not used for significance testing). The meta-analysis supported a finding of a significant effect of disturbance on production across the study (-0.26). In contrast, relationships between richness and disturbance were divided nearly equally between positive and negative in the site-specific studies and showed no consistent pattern across studies (0.01). A consistent effect of production on richness was supported by the meta-analysis (-0.19). Interpretation of this result was complicated slightly by the fact that three of the studies showed nonlinear effects

Table 2 Summary of results from meta-analysis of model paths, including average effect sizes (detransformed), bootstrapped 95% confidence intervals (CIs) and measures of data heterogeneity (QT) and its significance for the six paths in the statistical multivariate model (Fig. 3) for all sites.

| Pathway | Effect size | CIs | QT | <i>p</i> | df |
|---------|-------------|----------------|------|----------|----|
| A → R | 0.73* | 0.49 to 1.05 | 17.1 | 0.10 | 11 |
| A → B | 0.70* | 0.56 to 0.85 | 11.8 | 0.38 | 11 |
| D → R | 0.01 | -0.33 to 0.35 | 14.8 | 0.14 | 10 |
| D → B | -0.26* | -0.51 to -0.01 | 7.8 | 0.64 | 10 |
| B → R | -0.19* | -0.35 to -0.03 | 13.3 | 0.27 | 11 |
| R → B | -0.03 | -0.12 to 0.06 | 9.8 | 0.54 | 11 |

*Found to be consistently different from zero over all studies.

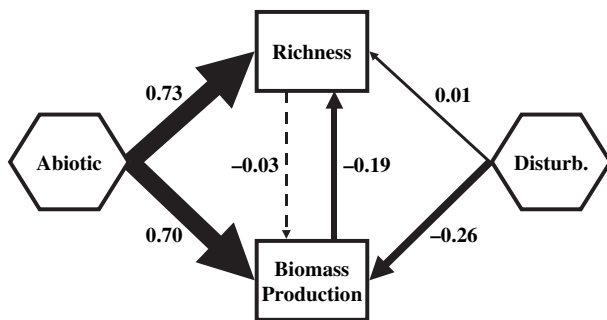


Figure 3 Summary of meta-analysis results (for more detail see Table 2). Shown are average effect sizes as standardized path coefficients.

and it was not possible to estimate the independent contributions of the contributing terms. Still, the total information available indicated negative effects of production on richness across studies, though the individual effects ranged from moderately strong to undetectable. There was no indication of a positive path from richness to production in any of the cases. This was true despite the fact that positive bivariate relationships between the two variables (including unimodal relationships, which included a positive phase) were common (found in 6 of 12 studies). Meta-analysis results indicated an average effect size of -0.03 (ranging between -0.12 and 0.06), thereby providing no evidence supporting the positive relationship predicted by theory.

DISCUSSION

What is most conspicuous in the results of this study is that we were not able to detect a positive effect of species richness on biomass production for any of the individual sites. For some sites this result is not surprising. For example, the data for the Kansas prairie contained no low-production, low-richness plots. Examination of the bivariate

relationship showed only a negative relationship between richness and production of the sort one would expect to reflect strong and persistent competitive effects of production on richness. Such was not the case for several other sites. For example, both the Louisiana coastal wetlands and the Louisiana riverine marsh showed a positive relationship between richness and production through at least a portion of the range of the data. The analyses performed in this study have the potential to extract a positive signal from richness to production if a measurable effect has taken place (verified in simulation studies; Grace, unpublished data). More surprising among the findings is that for both the Minnesota and Mississippi prairies, where the relationships of richness to production were strongly positive and monotonic or nearly so, there was no indication of an effect of richness on production. Rather, for the Minnesota site, the bivariate relationship appears to be driven by a convergence of forces (soil and fire effects). For the Mississippi site, the bivariate pattern appears to result from convergent abiotic effects plus a complex influence of production on richness.

Evidence for influences of production on richness was conspicuous. The SEM results imply that negative effects of production on richness were common in these systems. However, it is also clear that such negative effects, which we cautiously interpret as resulting from competitive exclusion, do not dominate in the control of species richness (see also S.D. Wilson, unpublished data). For three of the sites, Mississippi prairie, Wisconsin prairie and Louisiana coastal wetlands, the nonlinear path from production to richness implies that some positive process may have also been operating (while not shown in the figures, a nonlinear pathway involves multiple terms and each implies a separate process). There is experimental and observational evidence to suggest that such an effect might represent facilitation of richness, such as through shading and protection of young seedlings, but it could also be abiotic ameliorations or enhancements of the rhizosphere community (Bertness & Callaway 1994; Goldberg *et al.* 2001; Molofsky & Bever 2002).

Not surprisingly, biomass production was found to strongly and consistently vary with abiotic conditions. Disturbance also consistently reduced production in these sites. In principle, negative effects of disturbance on biomass production indirectly promote species richness by relaxing competitive pressure (estimated indirect effect = $-0.26 \times -0.19 = +0.05$). We found a consistently strong influence of abiotic conditions on richness independent from indirect effects mediated through abiotic influences on production. We interpret the direct pathway from abiotic factors to richness as environmental filtering. Environmental filtering of species richness at large spatial scales and extents is well documented (e.g. Hawkins *et al.* 2003; Currie *et al.* 2004) and can be shown

to operate at fine scales as well (Gough *et al.* 1994; Grace 1999). Less anticipated was the lack of consistent effects of disturbance on richness. We interpret these results to imply that mortality and species loss was modest in most of the systems studied (or that recovery was rapid). Because the analyses control for the indirect effect of disturbance on richness mediated through biomass production, they support the interpretation of positive paths from disturbance to richness (found in Indian savanna, Louisiana riverine marsh and Texas grasslands) as indications of some kind of storage effect whereby sites with a substantial history of disturbance have higher levels of richness than do other sites.

In conclusion, while there has been much written about the importance of niche complementarity as a mechanism for promoting production, our results (along with others, Smith & Knapp 2003; Smith *et al.* 2004; Kahmen *et al.* 2005; Wardle & Zackrisson 2005; Suding *et al.* 2006) suggest that the importance of such processes cannot be extrapolated from studies of synthesized assemblages to mature natural ecosystems. There are various reasons why this lack of extrapolation might occur. First, it is known based on theoretical grounds that competitive interactions can reduce the effects of niche complementarity (Yachi & Loreau 2007) and we would expect that the effects of competition would be more evident in mature systems than in synthesized mixtures. Clearly detectable competitive influences were observed in 7 of the 12 systems examined. Second, experimental studies of the sort conducted to examine the influence of species number on production create artificial conditions that may not be relevant to natural systems. We should not automatically expect that effects shown by such experiments will be sufficiently important to be detectable in mature natural communities where myriad factors influence biomass production. As in physics where it is important to distinguish strong forces from weak forces to understand quantum dynamics, in ecology a similar distinction should be made if research findings are to be relevant to conservation priorities.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 The structural equation modeling approach used to examine nonlinear, nonrecursive relationships.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2007.01058.x>

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