

LETTER

Plant diversity controls arthropod biomass and temporal stability

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Abstract

Understanding the linkages among species diversity, biomass production and stability underlies effective predictions for conservation, agriculture and fisheries. Although these relationships have been well studied for plants and, to a lesser extent, consumers, relationships among plant and consumer diversity, productivity, and temporal stability remain relatively unexplored. We used structural equation models to examine these relationships in a long-term experiment manipulating plant diversity and enumerating the arthropod community response. We found remarkably similar strength and direction of interrelationships among diversity, productivity and temporal stability of consumers and plants. Further, our results suggest that the frequently observed relationships between plant and consumer diversity occur primarily via changes in plant production leading to changed consumer production rather than via plant diversity directly controlling consumer diversity. Our results demonstrate that extinction or invasion of plant species can resonate via biomass and energy flux to control diversity, production and stability of both plant and consumer communities.

Keywords

Biodiversity, diversity–productivity, ecosystem function, insect community, long-term experiment, primary and secondary production., structural equation model.

Ecology Letters (2012) 15: 1457–1464

INTRODUCTION

The species diversity, biomass productivity and temporal stability of an ecological community represent a tightly linked triad of long-enduring interest (Tilman *et al.* 2001; Hector & Hooper 2002; Hooper *et al.* 2005; Tilman *et al.* 2006; Cardinale *et al.* 2012) because mechanistic linkages among the elements of this triad are critical for understanding the consequences of biodiversity loss and for informed management of natural resources and species conservation. Most of the research and debate in this area has focused on plant communities (Cardinale *et al.* 2006; Hector & Bagchi 2007), but we have little understanding of the linkages between the diversity–productivity–stability triads of plants and their consumer communities, particularly outside of the laboratory (Hooper *et al.* 2005; Cardinale *et al.* 2006; Duffy *et al.* 2007). If altered plant diversity leads to predictable changes in production or stability of herbivores and predators, this gap in our understanding is critical, as the production and stability of consumer biomass can influence the value of ecosystem services such as production of extractable resources and can control the detection of long-term trends in natural ecosystems (Hooper *et al.* 2005; Duffy *et al.* 2007; Hector & Bagchi 2007).

Field experiments manipulating plant diversity have primarily focused on quantifying the relationship between plant diversity and primary production (Tilman *et al.* 2001; Cardinale *et al.* 2006), the stability of primary producer biomass (e.g. Frank & McNaughton 1991; Tilman *et al.* 2006), ecosystem outcomes (Hector & Bagchi 2007; Oelmann *et al.* 2011) or more rarely on consumer diversity (Siemann *et al.* 1998; Koricheva *et al.* 2000; Schaffers *et al.* 2008; Haddad *et al.* 2009; Scherber *et al.* 2010). Similarly, studies of consumer diversity and biomass have generally focused on responses within and among consumer guilds, but not responses to changes in plant diversity (Cardinale *et al.* 2006; Duffy *et al.* 2007; but see

Proulx *et al.* 2010). Further, quantification of the temporal stability of consumer biomass (i.e. stability of secondary production) has been limited, to date, to laboratory experiments (McGrady-Steed *et al.* 1997; Petchey *et al.* 1999; Steiner *et al.* 2005) or field observational studies (Halpern *et al.* 2005). Although perturbations that reduce consumer diversity, such as predator extinction, can control ecosystem-level autotroph and heterotroph biomass production and stability (Shurin *et al.* 2002; Borer *et al.* 2005; Halpern *et al.* 2005), and a positive relationship between plant and consumer diversity exists in many ecosystems (e.g. Siemann 1998; Knops *et al.* 1999; Novotny *et al.* 2006; Haddad *et al.* 2009; Jetz *et al.* 2009), studies manipulating autotroph diversity have not clarified whether more diverse plant communities support greater or more temporally stable secondary production.

Using 5 years of species-level arthropod data collected from hundreds of experimental grassland communities of differing plant diversity, we quantify the strength of the pathways connecting the diversity of plant species to the diversity of arthropod species to examine the relative importance of the multiple drivers of consumer diversity and biomass using structural equation models. We focus particular attention on three alternative hypotheses linking plant diversity to consumer diversity and biomass that have strong biological justification.

(1) *Direct effects of plant diversity*: Arthropod diversity is directly constrained by herbivore feeding niches, which are determined by plant diversity (Fig. 1: a→d→e). Thus, increased plant diversity directly increases consumer diversity; arthropod biomass is an outcome, rather than a driver of arthropod diversity (e.g. Siemann 1998; Knops *et al.* 1999; Novotny *et al.* 2006; Schaffers *et al.* 2008; Haddad *et al.* 2009).

(2) *Plant-biomass mediated arthropod diversity*: Plant physical structure directly constrains arthropod diversity via processes such as reduced

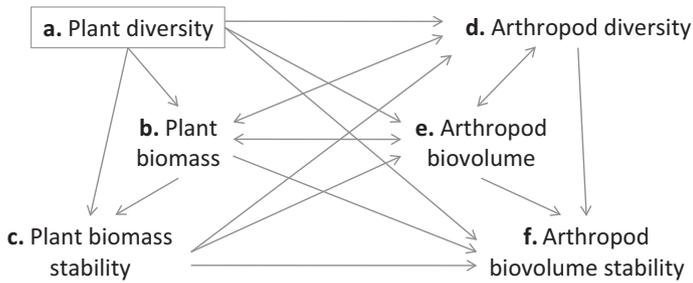


Figure 1 Initial meta-model structure for the structural equation model (SEM) describes the full covariance matrix among plant and arthropod diversity and biomass mean and temporal stability. The box around (a) plant diversity designates the manipulated treatment; all others (b–f) represent responses. Reciprocal links are shown as double-headed arrows.

search efficiency of predators (including birds, spiders and insects) (Fig. 1: $a \rightarrow b \rightarrow d$). Again, in this case, arthropod biomass is an outcome rather than a driver of arthropod diversity (e.g. Landis *et al.* 2000; Finke & Denno 2002).

(3) *Arthropod-biomass mediated diversity*: Plant diversity controls plant production, placing a constraint on total system productivity. Conversion of plant biomass into consumer community biomass, or secondary productivity, then indirectly determines arthropod diversity (Fig. 1: $a \rightarrow b \rightarrow e \rightarrow d$) through an energetic or metabolic pathway (White *et al.* 2007; Ernest *et al.* 2008).

Following tests of these hypotheses, we determine whether the most parsimonious model describing the strength and direction of the relationships among consumer diversity, biomass and temporal variability reflects the relationships among these factors for plants. Further, based on evidence that increasing plant diversity results in increasing temporal stability of plant biomass (Tilman *et al.* 2006; Isbell *et al.* 2009; Hector *et al.* 2010) and insect abundance (Proulx *et al.* 2010), we test whether arthropod biomass also is increasingly stable across a plant diversity gradient and quantify the evidence that asynchrony among arthropod taxa underlies the temporal stability of secondary production (Loreau & de Mazancourt 2008).

METHODS

Plant diversity experiment

In 1993, a field at the Cedar Creek Ecosystem Science Reserve was cleared, divided into 168–13 m × 13 m plots and, in 1994, was seeded with 1, 2, 4, 8 or 16 plant species representing five functional groups (forbs, legumes, woody species and both C3 and C4 grasses). Although relative abundance and production vary through time (e.g. Tilman *et al.* 2006), these plots have been weeded annually to remove the non-planted species. Plant species abundances have been measured annually in these plots, as per cent cover (1996–present) and as biomass (2001–2006).

Arthropod diversity

From 1996 to 2005, arthropods were collected annually at peak plant biomass. Plots were sampled with 25 net sweeps, and all captured individuals were sorted to species or morphospecies and enumerated. In 2005, a randomised subset of 64 plots was sampled across the full range of plant diversity treatments. The final data set

contained 65 534 individuals, representing 15 orders (13 insect orders), and 905 species or morphospecies. In total, 62% of the individuals in the data set were herbivores, 11% predators and 9% parasitoids.

Biovolume estimates

Biovolume, used as a surrogate for arthropod biomass, was estimated for species and morphospecies collected in a nearby field using the average product of the measured length, width and depth for five (or if fewer than five were collected, all) individuals (Siemann *et al.* 1996). Where biovolume was not directly measured for a species collected in the plant diversity plots, we estimated biovolume using the mean biovolume across the closest taxonomic group (genus, family). In cases where the designation was insufficient for matching a taxon name with a taxon biovolume (e.g. no direct biovolume estimates were made for spiders/non-insects, or for Ephemeroptera, Neuroptera or Coleoptera larvae), we estimated biovolume as the mean of the reported size range for the taxon. For all analyses, we removed data for 1169 spiderlings collected in plot 168 in August 2001 because no biovolume estimates existed for these individuals. In total, biovolume was measured or estimated for 91% of individuals (60 530), and across the entire data set, biovolumes ranged from 0.07 mm³ (parasitoid) to 8073 mm³ (dragonfly).

Structural equation model

The relationship between productivity, diversity and stability for plants and consumers arises from a network of dependent direct and indirect relationships (Fig. 1). Structural equation modelling (SEM) is a multivariate method allowing explicit testing of these direct and indirect dependencies; thus, it is well suited to assess the relative support for our hypotheses linking plant diversity to consumer diversity and biomass (Fig. 1). We employ these models in three ways to advance our understanding of the diversity, productivity and stability relationships in our data (Grace 2006). First, we assess the strength of support for the different pathways represented in our three core hypotheses by examining the relative weights of the coefficients on each link in the fitted SEM model. Second, we examine the fit of nested models, to specifically test the importance of each of our hypotheses for explaining the observed data. We infer lack of support for hypotheses that are associated with links that can be removed without causing a significant reduction in the model fit (see Appendix for details). Third, we simplify the model to develop the most parsimonious description of the data. This final parsimonious model provides further insight into the most critical pathways in our meta-model (Fig. 1).

Although we include the effects of consumers on plants in the full model, our current focus is on pathways supporting consumer diversity and biomass. The combined plant and arthropod data sets, including 5 years of concurrent plant and arthropod diversity and biovolume data for all experimental plots (2001–2005; 64 plots sampled in all years), were used to develop this model. We performed all hypothesis tests on the 4-year data set (168 plots sampled in all years), as well; we report the one qualitative difference we found between these two analyses in the Results. Variables in the model represented means or variances taken across years, such that each plot is described by a single record.

We used likelihood ratios and chi-squared tests to determine if the SEM-predicted variance–covariance matrix differed from the variance and covariance among the observed variables (e.g. plant biomass, arthropod diversity and arthropod biovolume). We then used r^2 values to assess the ability of the model to predict specific variables of interest. Chi-squared tests used a Satorra-Bentler correction (Satorra & Bentler 1994), a robust method recommended for data which might deviate from multivariate normality (Grace 2006). In the final model, the corrected and uncorrected chi-squared values were within 3% of one another (11.34 corrected vs. 11.07 regular χ^2), indicating that small deviations from multivariate normality in these data had little impact on the results. There were not sufficient degrees of freedom to fit the full meta-model with all reciprocal interactions (i.e. Fig. 1). For this reason, our first fitted model does not contain all the links in the full meta-model (Fig. 1). We test the significance of these relationships using a simplified model, which has ample degrees of freedom. To create the simplified model, we removed terms from the full model based on their z and P values with the constraint that the likelihood of the reduced model was not significantly less than the full model, based on likelihood ratio tests, that the reduced model accurately predicted the observed variance–covariance structure of the original variables (i.e. non-significant SEM P -value), and that there was not a large reduction in the ability of the reduced model to predict the endogenous variables (i.e. the r^2 of the endogenous variables was minimally affected). For more details on alternative models and model selection, see Appendix.

We analysed the log of diversity, biomass and stability in these models to linearise the bivariate relationships. Model fits without log transformation were similar to those presented here, but transformed variables provided the best-fitting models for the data. This is consistent with previous treatment of the plant data (e.g. Tilman *et al.* 2001). In addition, previous work on temporal stability of biomass production, spanning longer time frames (1999–2005), detrended biomass before calculating stability but showed that detrending was unnecessary over the shorter time period used in the current analysis (Tilman *et al.* 2006). We examined the effect of detrending arthropod biovolume and obtained similar results, so we present analyses of plot-scale temporal biovolume stability (μ/σ) using the observed data. We further investigated the drivers of temporal stability by quantifying plot-scale order- and family level biovolume synchrony as $\phi_b = \sigma_{bT}^2 / (\sum_{i=1}^s \sigma_{bi}^2)$ (following Loreau & de Mazancourt 2008; Isbell *et al.* 2009), where σ_{bT}^2 represents the total plot-scale arthropod biovolume variance and σ_{bi}^2 represents the plot-scale standard deviation of biovolume for each order or family. Thus, one represents perfect synchrony among taxon groups in temporal biovolume variation, whereas lower values signify increasingly asynchronous responses to plot-scale environments.

We fit models using both measured and rarefied arthropod species richness (following Haddad *et al.* 2009). Rarefaction did not qualitatively alter the results, so we present results based on measured richness. Finally, because the hypotheses could reasonably be tested using either data on herbivores or total arthropod biovolume and diversity, we developed structural equation models using both data sets. The results of these analyses are virtually identical for both data sets (Tables A4 and A5). As we ultimately seek to understand whether changes in plant diversity may lead to predictable changes in production or stability of consumers, we present the results of the total arthropod community analyses.

All analyses were conducted using R (version 2.14; The R Foundation for Statistical Computing); structural equation models were fit using the SEM (version 2.0) package in R.

RESULTS

The bivariate correlations among consumer diversity, net biovolume production and temporal stability were similar in both strength and direction to those of the producers in this experiment (Fig. 2, Table 1). In particular, bivariate correlations showed that, like the plants (Fig. 2a and b, relationships described in detail elsewhere, Tilman *et al.* 2001, 2006), arthropod biovolume increased with arthropod diversity (Fig. 2c, Table 1), and the temporal stability of plot-scale arthropod biovolume increased with increasing arthropod diversity in a plot (Fig. 2d, Table 1).

Bivariate correlations showed strong relationships among plant and arthropod factors, as well. Plot-scale arthropod biovolume was correlated with both arthropod diversity (Fig. 2c, Table 1) and total abundance (Table 1); however, while total arthropod biovolume and diversity both increased with plant diversity (Table 1, Fig. 3a) and biomass (Table 1, Fig. 3b and d), total arthropod abundance was correlated with plant diversity ($r^2 = 0.25$, $P = 0.047$) but was independent of plot-scale plant biomass (Table 1). Similarly, arthropod biovolume stability was positively correlated with both arthropod and plant diversity and biomass (Fig. 2d and Table 1).

We developed a SEM to examine the relative importance of pathways by which altered plant diversity can control consumer diversity and secondary production (Fig. 1). We used this SEM to examine the support for our three hypotheses about drivers of arthropod diversity (Appendix Table A1). Removal of the link between plant diversity and arthropod diversity (H1, Fig. 1: a→d) still fit the observed data ($\chi^2 = 2.271$; d.f. = 2; $P = 0.321$) and did not differ from a model including this link, based on a likelihood ratio test ($P = 0.087$), thus providing no support for this hypothesis. Although removal of the link between plant biomass and arthropod diversity (H2, Fig. 1: b→d) fit the observed data ($\chi^2 = 5.237$; d.f. = 2; $P = 0.073$), removal of this link produced a model significantly poorer than the full model (likelihood ratio $P = 0.007$). This is the only hypothesis for which the results depended on the subset of data analysed: using the 4-year data set with greater replication, removal of this link resulted in a model that fit the data ($\chi^2 = 3.288$; d.f. = 2; $P = 0.193$), and was similar to the full model (likelihood ratio $P = 0.075$). Thus, the evidence for the importance of biomass in directly constraining arthropod diversity is moderate, but inconclusive. In contrast, removal of the link between plant biomass and arthropod biovolume (H3, Fig. 1: b→e) produced a model that did not fit the observed data ($\chi^2 = 14.108$; d.f. = 2; $P = 0.001$) and was much poorer than the full model (likelihood ratio $P < 0.001$), providing strong support for this hypothesis. Further, removing the link between arthropod biovolume and arthropod diversity (H3, Fig. 1: e→d) also produced a model that did not fit the observed data ($\chi^2 = 28.904$; d.f. = 2; $P < 0.001$) and was much poorer than the full model (likelihood ratio $P < 0.001$), providing further evidence in strong support of this hypothesis.

The reduced SEM showed surprising concordance in the magnitude and direction of relationships among arthropod diversity, biovolume and temporal variation with those of plants (Fig. 3; details of model reduction in Appendix). Experimental plots with higher plant diversity produced more biomass (standardised regression coeffi-

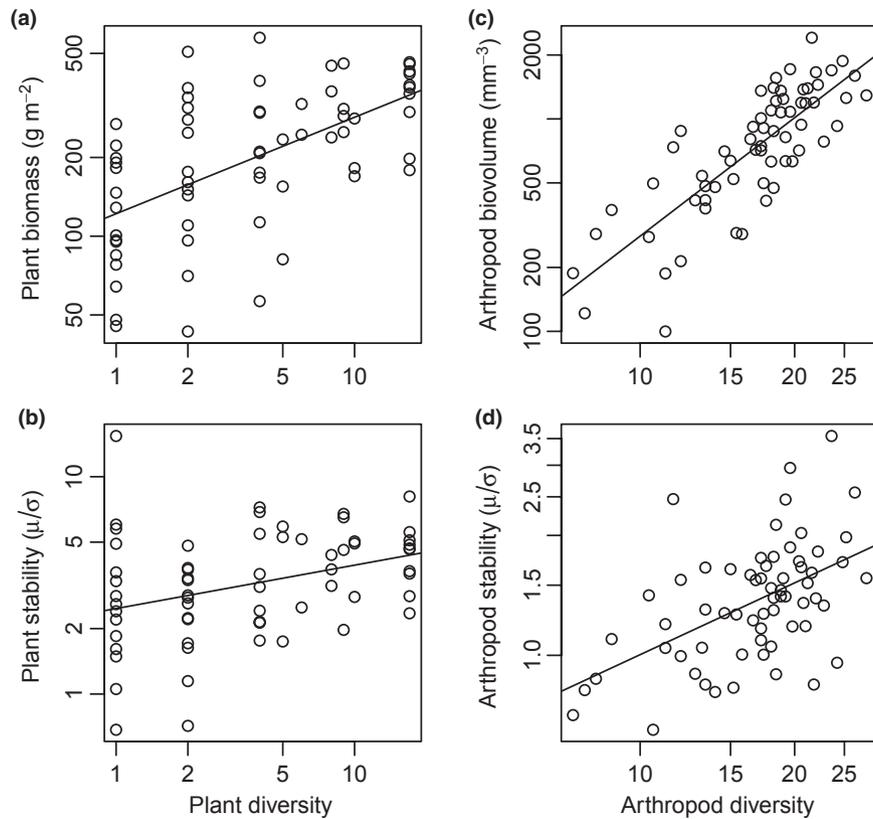


Figure 2 Bivariate correlations among plot-scale diversity, biomass and temporal stability for arthropods (c, d) are strongly concordant with those reported for plants (a, b). See Table 1 for correlation values and significance.

Table 1 Bivariate correlation matrix and significance for plant and arthropod community measures. For these comparisons, values are untransformed; the 5-year data set was used to calculate all correlations (d.f. = 62)

	Plant biomass		Plant stability		Arthropod diversity		Arthropod biovolume		Arthropod stability	
	Corr.	<i>P</i>	Corr.	<i>P</i>	Corr.	<i>P</i>	Corr.	<i>P</i>	Corr.	<i>P</i>
Plant diversity	0.516	<0.001	0.216	0.087	0.532	<0.001	0.596	<0.001	0.369	0.003
Plant biomass			0.082	0.520	0.437	<0.001	0.668	<0.001	0.258	0.039
Plant stability					0.092	0.471	0.089	0.485	0.147	0.245
Arthropod diversity							0.751	<0.001	0.463	<0.001
Arthropod biovolume									0.434	<0.001
Arthropod abundance	0.132	0.299	0.047	0.715	0.831	<0.001	0.542	<0.001	0.355	0.004

cient = 0.57). Increased arthropod diversity also resulted in greater biovolume (0.35); however, the reciprocal effect of arthropod biovolume on diversity was nearly twice as strong (0.62). Thus, for both plants and arthropods, increased diversity increases productivity, but arthropod productivity even more strongly controlled diversity in this experiment, as predicted by H3. Similarly, increased plant diversity led to increased temporal stability of plant biomass (0.35); although only plant diversity was manipulated, the relationship between diversity and temporal stability was even stronger for consumers (0.52). Interestingly, after accounting for the partial correlations among diversity, biomass and temporal stability of biomass for both plants and consumers, the direct paths linking biomass to temporal stability for both plants and arthropods were non-significant ($P > 0.05$).

We examined whether increasing community-wide asynchrony of arthropod taxa biovolume led to the observed arthropod diversity–stability trends (Loreau & de Mazancourt 2008). Across 5 years,

standardised community-wide synchrony declined with increasing order- and family level arthropod diversity in plots ($r = -0.34$, $P = 0.006$ for order-level data). This trend was driven by an increase in the total plot-scale biovolume variance (σ_{bT}^2 , $r = 0.42$, $P < 0.001$), but a more rapid increase in the variance of summed taxon-level biovolume [$(\sum_{i=1}^S \sigma_{bi})^2$, $r = 0.69$, $P < 0.001$], resulting in a net decline in community-wide synchrony, and increased temporal stability, with increased arthropod diversity.

In addition, the reduced model showed a very strong link from plants to arthropods via biomass production, but no reciprocal effect of arthropod diversity or biovolume on plant biomass (Fig. 3c; Table 2). As changes in plot-scale biovolume can reflect changes in arthropod abundance or composition (or both), we further examined the correlations between plant biomass and arthropod mean abundance and mean size (Fig. 4). These relationships suggest that the mean size of arthropod species increases with plant

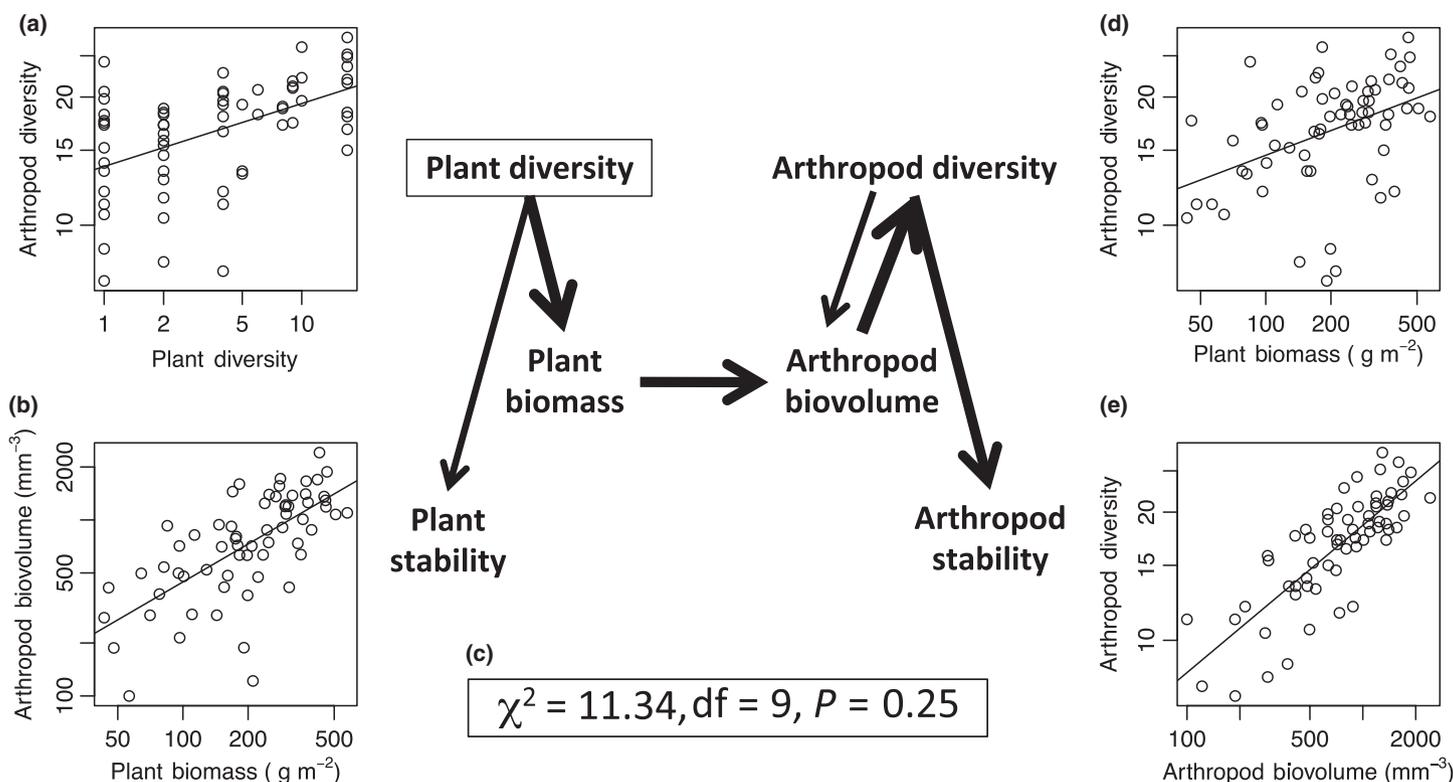


Figure 3 Although bivariate plots show positive correlations between plant and arthropod measures (panels a, b, d, e; correlation values in Table 1), the strongest structural equation model (SEM) pathway from plant to consumer diversity after accounting for partial correlations is via autotroph and heterotroph productivity (panel c). (a) shows the bivariate plant and arthropod diversity correlation (H1). (b) and (e) show correlations from plant biomass via arthropod biovolume to arthropod diversity (H3). (d) shows the plant biomass and consumer diversity correlation (H2). The bivariate correlations for the within-guild relationships in Fig. 3c are shown in Fig. 2. The full structural equation model considered all links (Fig. 1); the Appendix details the model reduction procedure. Line thickness is proportional to each SEM-estimated regression coefficient (Table 2). Model fit metrics (panel c) indicate that this model cannot be rejected as an explanation of covariance in the data set.

biomass production, whereas there is no significant relationship between plot-scale plant biomass and arthropod abundance. However, in spite of the strong relationship between plant biomass and arthropod biovolume, there was no link from plant stability to

Table 2 Final simplified structural equation model depicted in Fig. 3c: raw and standardised coefficients for the most parsimonious model that does not differ from the full model with the addition of a significant link between arthropod richness and arthropod biovolume (Table A3). The model provided a good fit to the observed covariance matrix (Model A1; $\chi^2 = 11.34$; d.f. = 9; $P = 0.253$). The r^2 values for the endogenous variables are as follows: plant biomass (0.32), plant stability (0.12), arthropod richness (0.61), arthropod biovolume (0.72) and arthropod stability (0.27)

Parameter	Estimate	SE	z	P	Standardised estimate
Plant diversity to plant biomass	0.369	0.056	6.598	0.000	0.568
Plant diversity to plant stability	0.200	0.067	2.987	0.003	0.345
Plant biomass to arthropod biovolume (H3a)	0.558	0.085	6.548	0.000	0.527
Arthropod biovolume to arthropod diversity (H3b)	0.269	0.047	5.764	0.000	0.623
Arthropod diversity to arthropod biovolume	0.819	0.317	2.584	0.010	0.354
Arthropod diversity to arthropod stability	0.598	0.104	5.730	0.000	0.517

arthropod stability (Fig. 3c, Table 2), suggesting that temporal stability for both plants and arthropods is more strongly controlled by their own diversity than by extrinsic factors that would lead to plant–arthropod covariation.

The final SEM provides a good fit to the observed covariance matrix ($\chi^2 = 11.34$, d.f. = 9, $P = 0.25$), and although there is no direct link between plant diversity and arthropod diversity, this model accounts for a substantial proportion of the variation in arthropod diversity ($r^2 = 0.61$). Interestingly, the SEM describes substantially more of variability in arthropod biovolume ($r^2 = 0.72$) and arthropod stability ($r^2 = 0.27$) compared with plant biomass ($r^2 = 0.32$) and plant stability ($r^2 = 0.12$). Notably, we find no support in our hypothesis tests or model reduction for a direct link between plant diversity and arthropod diversity (also see Appendix). Thus, our results suggest that the primary driver of relationships between plant diversity and consumer diversity (Fig. 3a) that have been observed in many studies likely occur via changes in primary production leading to changed secondary production, that is, arthropod biovolume (Fig. 3b).

DISCUSSION

Our analyses demonstrate substantial concordance between the diversity, production and temporal variability triad of plants and consumers, suggesting that data on changes in primary producer diversity may provide significant information about the consumers

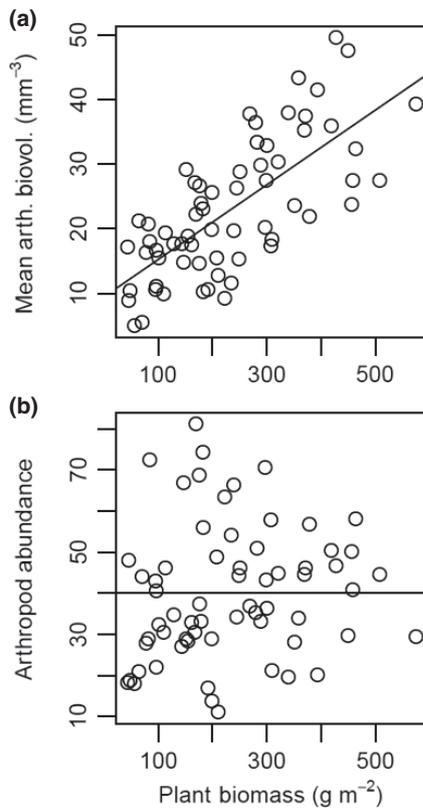


Figure 4 Bivariate correlations between plant biomass and the two components of plot-scale arthropod biovolume, (a) arthropod mean size ($r = 0.72$, $P < 0.001$) and (b) arthropod abundance ($r = 0.13$, $P = 0.299$), demonstrate that the mean size of arthropod species in plots increases with plot-scale plant biomass

they support. Furthermore, we found that the strongest link between plant and arthropod diversity is mediated by plant and consumer biomass (i.e. *arthropod-biomass mediated diversity*). In contrast, there was no support for a direct link from plant diversity to arthropod diversity (i.e. *direct effects of diversity*) and inconclusive support for a weak link from plant biomass to arthropod diversity (i.e. *plant-biomass mediated diversity*). Further, we found that, like plants, arthropod diversity has an independent role in constraining both arthropod productivity and the stability of arthropod production. Finally, we clarified that arthropod stability increases with arthropod diversity because of increased asynchrony among taxa.

Previous work supports the generality of each of the linkages in this biomass-mediated model. For example, there is strong theoretical support for the direct effects of changes in plant diversity controlling plant production through the effects of both species sampling and functional complementarity (Hooper *et al.* 2005). Further, while observed productivity–diversity relationships are highly heterogeneous along natural gradients (Adler *et al.* 2011), experiments that manipulate diversity, thereby providing insights into changes predicted from species extinction or invasion, show a consistent increase in productivity with diversity (Cardinale *et al.* 2009, 2012). Primary production is consistently associated with consumer diversity, as well (Landis *et al.* 2000; Borer *et al.* 2007; Scherber *et al.* 2010). However, our results suggest that the direct effect of plant production on consumer diversity, when significant, is a minor effect compared with the indirect effect via secondary production. Although there are clearly cases where increased autotroph biomass production is not

reflected in increased consumer biomass (Gruner 2004; Borer *et al.* 2006), there is significant empirical support for the intertrophic links between primary and secondary production (Hillebrand *et al.* 2009). Our concurrent examination of plant and consumer diversity and biomass in response to experimentally manipulated diversity provides novel insights into the relationships among these previous findings, suggesting that plant diversity perturbations such as invasion or extinction can resonate within and across trophic levels to control the diversity, production and stability of entire communities.

In this experimental manipulation of plant diversity, the reciprocal effect of productivity on diversity cannot be quantified for plants (Tilman *et al.* 2001); however, for arthropods where both of these factors varied, our model suggests that their reciprocal effects are independently important in describing the arthropod community response to manipulated plant diversity. Our results for arthropods resonate with the ‘multivariate productivity–diversity (MPD) hypothesis’ proposed to unify our understanding of the multiple drivers and outcomes of both productivity and diversity for autotrophs (Cardinale *et al.* 2009). In particular, Cardinale *et al.*’s model (2009), generalised to the arthropods in this study, suggests that the productivity of the local plant environment may simultaneously limit total arthropod biomass and the fraction of arthropod species that coexist within a plot, while the diversity of arthropod species in a plot also may limit total arthropod biomass via complementarity of resource use. Thus, our work contributes to the growing awareness of the multivariate causal interactions controlling both diversity and productivity in ecological communities (Grace *et al.* 2007; Gross & Cardinale 2007; Cardinale *et al.* 2009; Adler *et al.* 2011), and suggests that relationships like those described for plants similarly constrain consumer diversity and productivity.

Although the patterns that emerge from this integrated multivariate analysis are unique, the groundwork for understanding these relationships has been laid by extensive examination of bivariate relationships arising from experiments in this system and others. Where plant diversity is experimentally manipulated, there is generally a positive relationship between diversity and biomass productivity (Tilman *et al.* 2001; Hector & Bagchi 2007) as well as diversity and temporal stability (Tilman *et al.* 2006). Insect diversity also has been shown to increase with manipulated plant diversity (Siemann *et al.* 1998; Haddad *et al.* 2009) and plant productivity (Siemann *et al.* 1998). Although ours is the first study to examine the temporal stability of secondary biomass production, work in similar ecosystems at this site has demonstrated an increase in arthropod diversity (Siemann *et al.* 1998) and plot-scale arthropod biovolume (Haddad *et al.* 2000) with nitrogen fertilisation. Our analyses shed new light on this earlier work, suggesting that perturbations to the ecosystem that lead to changed primary productivity, such as changes in plant diversity or fertilisation, will control arthropod diversity primarily via an energetic pathway rather than directly via diversity of feeding niches.

The diversity of available niches is generally assumed to cause the observed correlations between plant and arthropod diversity (e.g. Schaffers *et al.* 2008; Haddad *et al.* 2009; Scherber *et al.* 2010); however, the strength of specialisation and resource partitioning by insect herbivores, thought to underlie much of the relationship between plant diversity and insect diversity, may not be as strong as is often assumed (Wertheim *et al.* 2000; Novotny *et al.* 2006). Changes in diversity affect both the structure and function of communities, and increased diversity consistently results in increased bio-

mass production for plants, animals, and microbes (e.g. Cardinale *et al.* 2006; Stachowicz *et al.* 2007). In spite of this well-described relationship, consumer diversity is most commonly examined as a function of producer diversity, rarely accounting for the concurrent effects of producer diversity on primary production (e.g. Knops *et al.* 1999; Novotny *et al.* 2006; Haddad *et al.* 2009; Jetz *et al.* 2009). Our work here shows that these bivariate relationships are strongly mediated through the effect of plant diversity on primary productivity. Where primary production has been manipulated and measured, it can be very important in controlling consumer diversity (Siemann 1998; Haddad *et al.* 2000). Interestingly, in a fertilisation study, where plant diversity declined but primary production increased, arthropod diversity also increased (Siemann 1998), reinforcing the centrality of plant production, rather than plant diversity, in constraining arthropod diversity. In addition, we find no support in our data for this relationship arising via greater accumulation of mobile arthropods on high biomass plots: the strong correlation of plant biomass with arthropod size but non-significant relationship with arthropod abundance suggests that the effect of plant biomass on consumer biomass is driven by turnover of arthropod species favouring larger taxa in more productive plots. Thus, relationships commonly found between plant and consumer diversity appear to be driven indirectly via primary production with minimal contribution, if any, from niche diversity. Although this result may seem intuitive, ours is one of the first studies to demonstrate that total plot productivity, determined by plant diversity, has little direct control over arthropod diversity, but rather sets a limit on the production of arthropod biomass that serves as an energetic or metabolic baseline constraining the number of arthropod species (White *et al.* 2007; Ernest *et al.* 2008).

Declines in species diversity can lead to declines in temporal stability of biomass production for producers (e.g. Frank & McNaughton 1991; Tilman *et al.* 2006) as well as diversity, abundance or biomass of consumers (Neutel *et al.* 2002; Worm *et al.* 2006; Shurin *et al.* 2007; Proulx *et al.* 2010). Mathematical descriptions demonstrate that the relationship between species diversity and the temporal stability of biomass production operate similarly for autotroph and consumer diversity (Cardinale *et al.* 2006; Duffy *et al.* 2007). Our results show the surprising outcome that changes in plant diversity can lead to an even greater effect on temporal stability for consumers than for plants (Tilman *et al.* 2006) via strongly increased asynchrony among taxon groups with increasing plant diversity, as has been observed in plant communities (Hector *et al.* 2010). Consumer diversity can control the stability of biomass production within and among trophic levels, as well; predator removal or extinction, for example, can indirectly control both herbivore and plant stability (Halpern *et al.* 2005). The analyses presented here extend this understanding to demonstrate that whole-community effects of diversity can originate with changes in plant diversity, controlling species synchrony and the stability of biomass production for both plant and consumer communities.

Humans have been a singularly effective force in moving species among biogeographic regions and restructuring local and regional community composition. We often examine the effects of altered biodiversity within a focal group. Given our observation of tight coupling among productivity, diversity and stability across trophic levels, our results indicate that anthropogenic alterations of plant diversity can lead to biomass, diversity and stability responses that are mirrored across trophic levels. Our results suggest that the flux of biomass and energy among trophic levels may be a primary path-

way by which plant and consumer diversity, productivity and stability triads will be synchronised across trophic levels.

ACKNOWLEDGEMENTS

These analyses would not have been possible without the extensive work of John Haarstad (1946–2008) who performed all of the arthropod collection and identification for this study. Because these analyses were conceived after his death, he is not named as an author, but his many contributions are gratefully acknowledged. In addition, the authors thank Evan Siemann for his data set on Cedar Creek arthropod biovolume, which also was instrumental in these analyses. Special thanks to Drew Kerkhoff for his insights. The manuscript also benefitted substantially from the suggestions of three anonymous referees. This work was funded, in part, by the University of Minnesota and NSF grant DEB-0620652 supporting the Cedar Creek LTER.

AUTHORSHIP

EB conceived the analyses and completed the arthropod biovolume data set, DT conceived the original experimental design and directed data collection and curation, and EB and ES performed all analyses. EB wrote the first draft of the manuscript, and all authors contributed to revisions.

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Editor, Vojtech Novotny

Manuscript received 27 March 2012

First decision made 23 April 2012

Second decision made 8 August 2012

Manuscript accepted 22 August 2012