Plant diversity controls arthropod biomass and temporal stability

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.

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→b→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→b→e→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 mm$^3$ (parasitoid) to 8073 mm$^3$ (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), 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 (\( \mu/\sigma \)) using the observed data. We further investigated the drivers of temporal stability by quantifying plot-scale order- and family level biovolume synchrony as \( \phi_i = \sigma^2_{\text{ar}}/(\sum_{j=1}^m \sigma_{bi})^2 \) (following Loreau & de Mazancourt 2008; Isbell et al. 2009), where \( \sigma^2_{\text{ar}} \) represents the total plot-scale arthropod biovolume variance and \( \sigma_{bi} \) 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\( \rightarrow \)d) still fit the observed data (\( \chi^2 = 2.271; \text{d.f.} = 2; P = 0.321 \)) 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\( \rightarrow \)d) fit the observed data (\( \chi^2 = 5.237; \text{d.f.} = 2; P = 0.073 \)), 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 (\( \chi^2 = 3.288; \text{d.f.} = 2; P = 0.193 \)), 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\( \rightarrow \)c) produced a model that did not fit the observed data (\( \chi^2 = 14.108; \text{d.f.} = 2; P = 0.001 \)) 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: c\( \rightarrow \)d) also produced a model that did not fit the observed data (\( \chi^2 = 28.904; \text{d.f.} = 2; P < 0.001 \)) 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-
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 arthropods, 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_T^2, r = 0.42, P < 0.001), but a more rapid increase in the variance of summed taxon-level biovolume [(Σ_i=1^n σ_i)^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 biomass.

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)

<table>
<thead>
<tr>
<th></th>
<th>Plant biomass</th>
<th>Plant stability</th>
<th>Arthropod diversity</th>
<th>Arthropod biovolume</th>
<th>Arthropod stability</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Plant diversity</strong></td>
<td>0.516</td>
<td>&lt;0.001</td>
<td>0.532</td>
<td>&lt;0.001</td>
<td>0.369</td>
</tr>
<tr>
<td><strong>Plant biomass</strong></td>
<td>0.082</td>
<td>0.520</td>
<td>0.437</td>
<td>&lt;0.001</td>
<td>0.258</td>
</tr>
<tr>
<td><strong>Plant stability</strong></td>
<td>0.092</td>
<td>0.471</td>
<td>0.089</td>
<td>0.485</td>
<td>0.147</td>
</tr>
<tr>
<td><strong>Arthropod diversity</strong></td>
<td>0.751</td>
<td>&lt;0.001</td>
<td>0.463</td>
<td>&lt;0.001</td>
<td>0.463</td>
</tr>
<tr>
<td><strong>Arthropod biovolume</strong></td>
<td>0.132</td>
<td>0.299</td>
<td>0.047</td>
<td>0.715</td>
<td>0.542</td>
</tr>
<tr>
<td><strong>Arthropod abundance</strong></td>
<td>0.831</td>
<td>&lt;0.001</td>
<td>0.355</td>
<td>0.004</td>
<td></td>
</tr>
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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 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 ($\chi^2 = 11.34, \text{d.f.} = 9, P = 0.25$), 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 arthropod diversity (also see Appendix).

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
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; Scheber 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; Scheber 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-

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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 productivity (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 of arthropod species (White et al. 2008). By contrast, community assembly. 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 pathway by which plant and consumer diversity, productivity and stability triads will be synchronised across trophic levels.

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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.

REFERENCES


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