

LETTER

Plant diversity and the stability of foodwebs

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Abstract

Insect outbreaks in forest and agriculture monocultures led Charles Elton to propose, a half-century ago, that higher plant diversity stabilized animal foodweb dynamics in natural ecosystems. We tested this hypothesis by studying arthropod community dynamics in a long-term experimental manipulation of grassland plant species diversity. Over the course of a decade, we found that higher plant diversity increased the stability (i.e. lowered year-to-year variability) of a diverse (>700 species) arthropod community across trophic levels. As the number of plant species increased, the stability of both herbivore and predator species richness and of total herbivore abundance increased. The underlying mechanisms driving these diversity–stability relationships were plant diversity, via effects on primary productivity and plant community stability, and portfolio effects. Taken together, our results show that higher plant diversity provides more temporally consistent food and habitat resources to arthropod foodwebs. Consequently, actively managing for high plant diversity may have stronger than expected benefits for increasing animal diversity and controlling pest outbreaks.

Keywords

Arthropods, biodiversity, consumers, herbivores, insects, long term, plant diversity, predators, stability, trophic structure.

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INTRODUCTION

For a half-century, ecologists have debated whether the diversity of species maintains the stability of ecosystems (MacArthur 1955; Elton 1958; Woodwell & Smith 1969; May 1974; Pimm 1991; McCann 2000). The ‘diversity–stability hypothesis’ gained early acceptance based on its relevance to conservation and agriculture, including observations that monocultures in agricultural systems are prone to pest outbreaks and simpler island systems are more susceptible to species invasions (Elton 1958; Andow 1991). Controversy arose when modelling efforts posited that diversity can actually reduce, rather than increase, the stability within an ecosystem (May 1974; McCann 2000; Gross *et al.* 2009). This spawned a flurry of theoretical and experimental research on diversity–stability relationships, and an increasing number of experimental studies indicate that diversity leads to stability in plant communities, with few exceptions (King & Pimm 1983; Tilman & Downing 1994; Lehman & Tilman 2000; Cottingham *et al.* 2001; Pfisterer & Schmid 2002; Tilman *et al.* 2006b; van Ruijven & Berendse 2007; Valone & Schutzenhofer 2007; Isbell *et al.* 2009; Hector *et al.* 2010).

What remains unclear is whether, as Elton (1958) originally proposed, plant diversity also stabilizes the diverse, multitrophic populations and communities that plants support (Hurd *et al.* 1971; McCann 2000). Foodweb stability is thought to depend on trophic interactions, including the degree of consumer feeding specialization, or foodweb connectivity (McCann *et al.* 1998; McCann 2000; Turchin 2003; Murdoch *et al.* 2005; Rooney *et al.* 2006; Jiang & Pu 2009). Plant diversity could affect foodweb connectivity in a variety of ways (May 1974; McCann *et al.* 1998; Gross *et al.* 2009; O’Gorman & Emmerson 2009). Higher plant diversity increases plant productivity and predator abundance (Tilman *et al.* 2006a; Haddad *et al.* 2009), which increases the amount of energy transfer among interacting species and thus increases foodweb connectivity. Yet, plant diversity increases consumer diversity and habitat structure, which increases the number of potential interactions as well as the potential for prey escape from predation, thus decreasing foodweb connectivity (McCann 2000; McCann *et al.* 2005). Empirical studies of foodweb stability have been limited primarily to aquatic microcosms and have yielded mixed results (McGrady-Steed & Morin 2000; Petchey 2000; Kolasa & Li 2003; Steiner *et al.* 2006; Vogt *et al.* 2006; Jiang & Pu 2009). No long-term studies of diverse animal communities have tested whether plant diversity stabilizes foodwebs.

We provide long-term empirical evidence that the stabilizing effects of greater plant diversity on community properties extend to the higher trophic levels that plants support. We specifically address three questions in studies of a diverse arthropod community: (1) Does plant diversity increase the temporal stability of herbivore populations and communities? (2) What are the mechanisms by which plant diversity affects consumer stability? and (3) Do the effects of plant diversity on consumer stability differ at herbivore and predator trophic levels?

METHODS

We studied arthropod population and community dynamics for 11 years in the Cedar Creek Ecosystem Science Reserve biodiversity experiment. The diversity of plant species was manipulated by planting 1, 2, 4, 8, or 16 plant species drawn from a pool of 18 plant species in 168 13 × 13 m plots. The experiment was initiated in 1994, and data collection on consumers began in 1996. Plots have been maintained by weeding three to four times annually to remove unwanted plant species. More detailed methods about the experimental design and maintenance are available elsewhere (Tilman *et al.* 2001; Haddad *et al.* 2009).

Arthropods were sampled in 163 plots from 1996 to 2006. We sampled 112 238 individuals of 733 arthropod species from 1996 to 2006 (Fig. 1), a period that included wide variation in environmental conditions such as temperature and precipitation (Tilman *et al.* 2006b). Plots were sampled with a sweep net 38 cm in diameter, sweeping the net just above ground level through the vegetation 25 times in each plot, with each sweep being *c.* 2 m in length. Although sweeping does not sample all arthropod groups, our work has shown that arthropod responses to plant diversity are similar using sweep or vacuum samples (Siemann *et al.* 1998; Haddad *et al.* 2001). All samples were taken on 1 day year⁻¹ in August at the time that plots have highest levels of standing biomass. Sampling one time per year has been shown to be sufficient, yielding results consistent with those obtained with more frequent sampling (Haddad *et al.* 2001). All arthropods were sorted, identified to species or morphospecies, and counted. Additionally, all arthropod species were separated into trophic levels (herbivores, predators, parasitoids, detritivores, and omnivores), and herbivores were classified as specialists or generalists (Haddad *et al.* 2009). In this study, we focus on the dominant trophic groups, herbivores, predators, and parasitoids, which make up >80% of the number of species and individuals. And, because of their similar responses to our treatments, we pooled predators and parasitoids for community-level analyses (Haddad *et al.* 2009). Because arthropod abundances were unusually high as plots were establishing in 1996 and 1997, we excluded these years from analysis (doing so did not qualitatively change our results, nor did restricting our analysis to only 2000–2006 when the plots were most mature).

Dispute over biodiversity–stability relationships can result from ambiguous definitions of stability (Pimm 1991; Ives & Carpenter 2007). We focus our analysis on a standard measure of stability used in numerous ecological studies, temporal stability, measured as the inverse coefficient of variation (cv^{-1}) within plots across years (Pimm 1991; Tilman *et al.* 2006b; Ives & Carpenter 2007). CV , equal to the standard deviation divided by the mean, is a scale-independent measure of variability; thus cv^{-1} is a measure of stability. At the arthropod population level, we tested the effects of plant diversity on population size and its temporal variation (Andow 1991). At the arthropod community level, we evaluated fluctuations in both the number of arthropod species observed (‘species richness’) and their summed abundance across all species within a plot (‘total abundance’).

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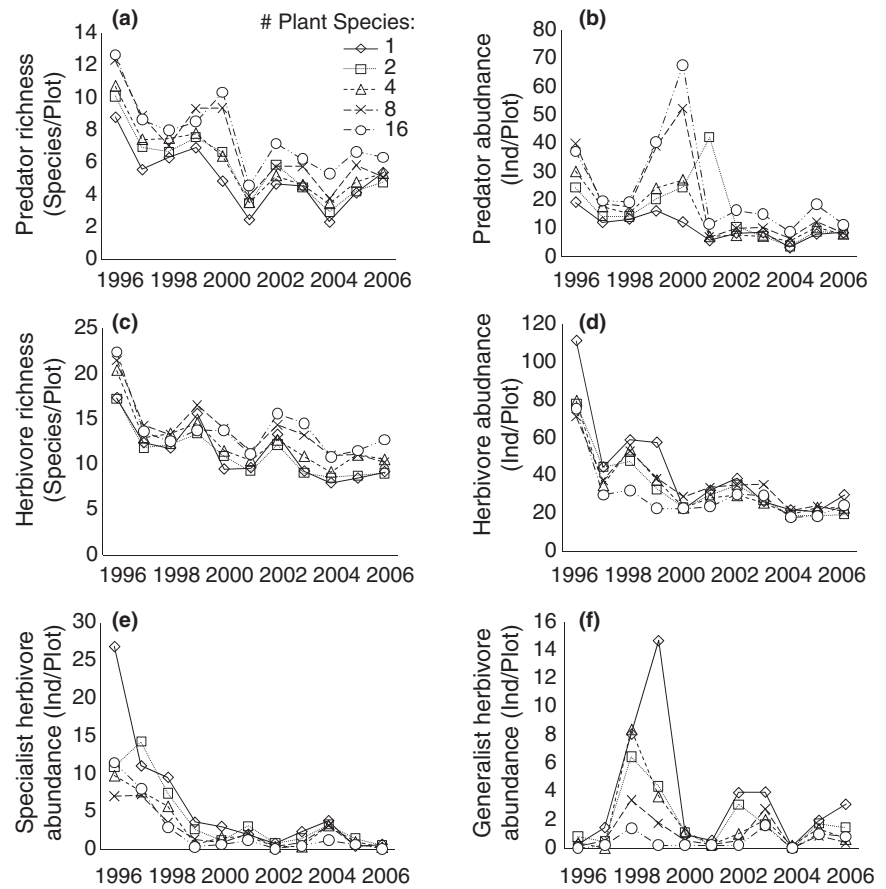


Figure 1 Effects of plant diversity on arthropod population and community dynamics over a 11-year time series. Mean per plot predator and parasitoid (a) species richness and (b) total abundance (summed across species within a plot); herbivore (c) species richness and (d) total abundance; and abundances of (e) a specialist herbivore, *Aphis* sp. and (f) a generalist herbivore, *Lygus lineolaris*. Data presented are those used in the stability analysis shown in Fig. 2.

In our analysis of population stability, abundances for each plot were detrended by regressing abundances against year before calculating standard deviation of detrended abundances. Detrending removed variation caused by long-term directional change in arthropod abundances that could be attributed to plot establishment or other factors (and, analysis of stability on untransformed abundance data did not qualitatively change our conclusions). For each plot, cv^{-1} was then calculated as the actual mean divided by the detrended standard deviation. This measure of stability was then used as the dependent variable in linear regression, and independent variables included the number of planted species, the number of plant functional groups, the actual number of plant species, plant Shannon–Weiner index, which accounts for relative abundances of each plant species, and mean plant biomass (see Table S2 in Supporting Information). For herbivores, we included the temporal stability of community biomass or, for specialists restricted to a plant genus or family, of biomass of their host plants. We also included the ratio of total predator : herbivore abundance summed over the entire study duration in the analysis as a measure of trophic control on herbivore population stability.

We note that, because of plant diversity’s strong effects that have been demonstrated previously, many of the plant community variables are intercorrelated (Table S2). The ‘best model’ was thus determined by the forward addition of variables, starting with the variable that yielded the highest r^2 in univariate regression, and systematically adding variables to determine the significant factors in multiple regression. In most cases, there was only one significant factor in a model, and there were never more than two significant factors in multiple regression. We did not formally evaluate the statistical significance of differences in selected predictors across different response variables, because our predictors represent concurrent pathways by which plant species richness can impact arthropod stability, and these pathways are difficult to tease apart with our data. Although we recognize limitations in our ability to distinguish the effects of these correlated factors, responses are ultimately, directly or indirectly, related to manipulated levels of plant species richness, and we present the best models to further inform potential mechanisms.

We tested the effects of plant diversity on temporal stability of the most common arthropod populations individually, including species that were sampled at least 600 times throughout the time series when their abundances were pooled across plots and years, and were also found in more than 400 plots*years. For each analysis, we included only those plots with five or more individuals (that is, at least one individual in

more than half of the years). Because of these restrictions, analyses of population responses focused on a different subset of plots for each species (Table 1) and we were unable to test directly for differences in responses among species. Our restrictions resulted in the analysis of 12 abundant herbivorous insect species (of which 7 were specialists) and 7 abundant predator and parasitoid species. Specialists were defined through knowledge from the field and/or the literature as herbivores that consumed a single species, genus, or family of plants (Haddad *et al.* 2009).

Because most species were rare and could not be analysed individually as described above, we also tested for the effects of plant diversity on the temporal stability in abundances of the total number of individuals in each plot, summed across all species within a trophic group. Dependent variables for total abundances were the same as in the analysis of individual populations. In addition, we tested whether the temporal stability in abundance of herbivores or predators and parasitoids was related to the temporal stability in abundance of predators and parasitoids or herbivores.

Finally, we analysed the stability of arthropod diversity by trophic group, defined as the temporal variability in the number of herbivore or predator and parasitoid species. As there was no trend in species richness over time, data on species richness were not detrended. Dependent variables in the analysis of stability of diversity were the same as in the analysis of individual populations. In addition, we tested whether the temporal stability in species richness of herbivores or predators and parasitoids was related to the temporal stability in abundance of predators and parasitoids or herbivores.

We evaluated five potential mechanisms that could account for increased stability of herbivore communities at higher plant diversity: overyielding of herbivore abundance, decreasing covariance among herbivore populations, the ‘portfolio effect’, predator ‘top-down’ control, and host-plant effects (Tilman 1999). Overyielding could explain increased herbivore stability if, as plant diversity increased, herbivore abundances increased more rapidly than variation in their abundances (Hector *et al.* 2010). Covariances among population fluctuations are driven by species’ (dis)similar responses to environmental perturbations and by interspecific interactions (e.g., competition), and reduced covariance indicates higher temporal stability. To determine the contribution of covariance to explanation of diversity–stability relationships, we regressed the ratio of (summed variance of individual species)/(variance of the entire community), where (variance of the entire community) = (summed variance of individual species + covariance of individual species), against plant species richness. The portfolio effect can stabilize community dynamics by averaging the fluctuations of multiple independently

Table 1 Factors affecting the stability of 19 common arthropod populations, where *n* refers to the number of plots that contained the species, 'Factor' refers to significant independent variables in regression, 'Response' refers to the direction of the responses, and 'Effects of plant diversity on arthropod abundance' refers to the relationship between those variables in repeated-measures ANOVA across all years (Table S1)

Species	<i>n</i>	Factor	Response	r^2	<i>P</i>	Effects of plant diversity on arthropod abundance
Specialist herbivores						
<i>Aphis</i> sp.	114	Plant biomass (ln)	–	0.26	0.001	–
<i>Olella</i> sp.	125	Plant biomass	–	0.03	0.03	–
<i>Oxycnema</i> sp.	141	No. plant species	–	0.05	0.004	Lowest abundance at 2 plant sp
<i>Nysius niger</i>	43	cv^{-1} <i>E. canadensis</i>	+	0.11	0.02	–
<i>Macrostelus fascifrons</i>	90	No. plant species (ln)	–	0.21	0.001	–
		cv^{-1} Asters	+		0.03	
<i>Nesoteles neglectus</i>	87	n.s.				Highest abundance at 2 plant sp.
<i>Trigonotylus coelestialium</i>	47	Plant biomass (ln)	–	0.13	0.008	–
Generalist herbivores						
<i>Empoasca fabae</i>	51	No. plant sp. (observed)	+	0.18	0.001	n.s.
<i>Cicadellid</i> sp.	119	n.s.				Highest abundance at 2 plant sp.
<i>Lygus lineolaris</i>	57	n.s.				–
<i>Eudria inimica</i>	97	n.s.				n.s.
<i>Scaphytopius acutus</i>	60	n.s.				Highest abundance at 4 plant sp.
Predators and parasitoids						
<i>Tetrastichus</i> sp.	146	No. plant species (ln)	+	0.04	0.009	+
<i>Orius insidiosus</i>	92	n.s.				Highest abundance at 8 plant sp.
<i>Arachnid</i> sp.	61	n.s.				n.s.
<i>Medeterus</i> sp.	102	Plant biomass (ln)	–	0.08	0.003	Highest abundance at 2 plant sp.
<i>Encyrtid</i> sp.	72	n.s.				–
<i>Nabis americana</i>	79	n.s.				+
<i>Metaphidippus</i> spp.	66	n.s.				Highest abundance at 8 plant sp.

Factors included the experimental number of plant species, plant biomass, stability of individual plant species for specialists (measured as cv^{-1}), number of observed plant species, the ratio of predator : prey abundances, and the stability of predator and parasitoid abundances.

varying arthropod populations (Tilman 1999). We quantified the portfolio effect by fitting a power-law relationship ($s^2 = cm^z$, where s^2 is the variance, m the mean, and c and z are constants) between species mean and variance for the 12 most abundant herbivore species. Finally, top-down and host-plant effects could be evaluated based on the results of regression analysis described above.

RESULTS AND DISCUSSION

For herbivore populations, we found that the effects of plant diversity on population stability depended on the degree of herbivore feeding specialization. We analysed the 12 most abundant herbivore species, a collection that accounted for 24% of total arthropod abundance and included several agriculturally important pests. We found that the population stability of six of seven specialist herbivores was reduced with increasing plant diversity or factors correlated with higher plant diversity, such as higher plant biomass or lower population stability of individual host-plant species (Fig. 2c; Table 1). Conversely, plant diversity never reduced the stability of populations of generalist herbivore species (Fig. 2f; Table 1), and for one generalist species, population stability increased with increasing plant species diversity (Table 1).

In contrast to patterns at the population level, we found that plant diversity increased herbivore stability at the community level. As plant diversity increased from 1 to 16 plant species, the temporal stability of total herbivore abundance increased by 43% ($n = 163$, $r^2 = 0.06$, $P = 0.002$; Fig. 2d), and the stability in herbivore species richness increased by 24% (log scale, $n = 163$, $r^2 = 0.07$, $P = 0.001$; Fig. 2c). Similar to what has been observed for the plant community in this experiment (Tilman *et al.* 2006b), higher plant diversity resulted in the destabilization of specialist herbivore populations, but the stabilization of the entire herbivore community.

In our evaluation of potential mechanisms by which increased plant diversity stabilized herbivore communities, overyielding could be eliminated because total herbivore abundances decreased with increasing plant species richness (Haddad *et al.* 2009). Average species covariance was positive at all levels of plant diversity, yet the contribution of species covariance to total community variance decreased as plant species richness increased ($n = 163$, $r^2 = 0.04$, $P < 0.01$). Because competition among diverse herbivores is expected to be weak, the most likely explanation for this decrease is less similar responses to environmental variation across herbivore species.

In the analysis of power-law relationships, we estimated $z = 1.72$ ($n = 1079$, $r^2 = 0.78$). Under idealized conditions, if the mean and variance of individual herbivore species are related by a power law with $z > 1$, then statistical averaging (the so-called portfolio effect) will increase the stability of herbivore communities as herbivore species richness increases (Doak *et al.* 1998; Tilman *et al.* 1998). Further, statistical averaging predicted by this power-law relationship is robust to effects of plant species

richness on herbivore abundances and to correlations in fluctuations among herbivore species (Doak *et al.* 1998). Because plant diversity and herbivore diversity are positively related, our estimate of $z = 1.72$ suggests that portfolio effects are partially responsible for the observed relationship between plant diversity and herbivore community stability.

We considered how plant diversity may influence herbivore community stability via 'top-down' control by predators and parasitoids. In particular, the ratio of predator-to-herbivore abundance has previously been observed to increase threefold from the least to most plant-diverse plots (right side of Fig. 2; Haddad *et al.* 2009). In no case was this factor, nor the stability of predator and parasitoid abundances, statistically significant in models of herbivore population or community stability. This provided further support that stabilizing effects on herbivores are primarily bottom up (see below). However, more detailed empirical work is needed in this and other systems comparing the relative importance of plant vs. predator communities on herbivore population stability before generalizations can be made.

Finally, we found that plant diversity was the primary mechanism explaining patterns of herbivore stability in this study (Table 1) through increased productivity and stability of the host plants themselves (Tilman *et al.* 2006a,b). As plant diversity increased from 1 to 16 species, plant productivity increased by 238%, and plant community stability increased by more than 50% (right side of Fig. 2; Tilman *et al.* 2006a,b). In the best statistical model, the stability of total herbivore abundance was positively related to plant diversity (Shannon–Weiner index) and to the temporal stability of plant biomass ($n = 163$; $r^2 = 0.14$, $P = 0.001$). Over the 11-year duration of our study, high plant diversity resulted in more consistent food and habitat resources available to herbivores. Concomitantly, the stability of individual plant species decreased (Tilman *et al.* 2006b), thereby decreasing the stability of specific plant populations required by specialist herbivore species (Table 1). Thus, we conclude that diversity–stability relationships among herbivores are best explained by a combination of host-plant effects, decreased covariances in herbivore abundances, and portfolio effects.

Our results offer clear support that increasing plant diversity controls herbivore diversity and dynamics in this grassland ecosystem. The lowest levels of plant diversity had 43% more herbivore individuals summed across the study period (Haddad *et al.* 2009), and low diversity treatments had significantly higher abundances of specialist agricultural pests like aphids and northern false chinch bugs (*Nysius niger*; Tables 1 and S1). Moreover, at lower levels of plant diversity, total herbivore abundances fluctuated more over time. Thus, the loss of plant diversity has the potential to alter the important ecosystem service of controlling herbivore outbreaks. For specialist herbivore species, the biological control conferred by higher plant diversity reduced abundances, but increased variability, of individual species (Tables 1 and S1). Increasing sampling frequency to multiple times throughout a growing season and accounting for

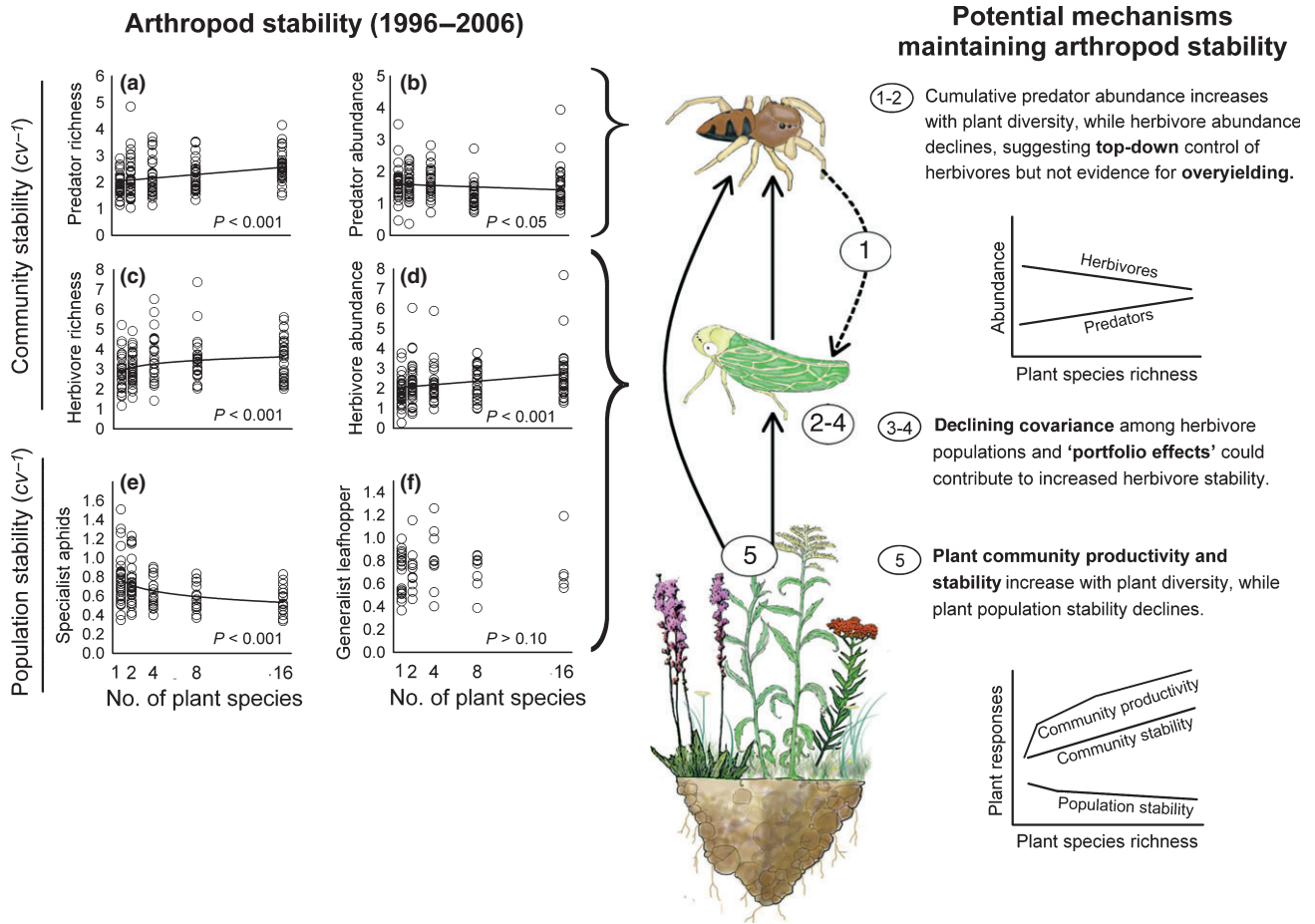


Figure 2 Effects of plant species richness on arthropod population and community stability. Higher plant diversity (a) increases predator and parasitoid (abbreviated ‘Predator’) community stability for species richness; (b) reduces predator and parasitoid community stability for total abundance; (c,d) increases herbivore community stability for species richness and total abundance; (e) reduces population stability of most herbivore specialists, including *Aphis* spp.; and (f) has no negative effect on the stability of most herbivore generalists, including *Lygus lineolaris*. Temporal stability was measured as cv^{-1} at the population and community levels. Potential mechanisms (right panels) show the results of this and prior studies that inform arthropod responses in this study, including that plant diversity (1) increases predator abundances and potential for trophic control of herbivores (Haddad *et al.* 2009); (2) reduces herbivore abundances and thus eliminates the possibility of overyielding (Haddad *et al.* 2009); (3, 4) reduces species covariances and enhances portfolio effects (this study); and (5) decreases plant population stability (Tilman *et al.* 2006b), increases plant community biomass (Tilman *et al.* 2001), and increases the stability of plant community biomass (Tilman *et al.* 2006b).

spatial dynamics beyond the plot scale could help account for some of the unexplained variation in arthropod community dynamics over time (Haddad *et al.* 2001).

The effects of plant diversity on higher trophic levels have the potential to dampen with increasing distance up the food chain. Yet, we found that responses of predator and parasitoid species richness to plant diversity were consistent with responses of herbivore species richness. As plant diversity increased, the stability of predator and parasitoid species richness increased by 33% (Fig. 2a; $n = 163$, $r^2 = 0.09$, $P = 0.001$), potentially as a result of higher habitat structure and herbivore diversity (McCann *et al.* 2005; Haddad *et al.* 2009). We found that predator and parasitoid abundance responses were more variable. For the seven most abundant predator and parasitoid species, stability increased with increasing plant diversity for one species, decreased with increasing plant biomass for another species, and had no effect on the remaining five species (Table 1). The stability of total predator and parasitoid abundance showed a slight negative response to the number of plant species (log scale, $n = 163$, $r^2 = 0.02$, $P = 0.03$; Fig. 2b), and it responded similarly to plant functional group richness ($r^2 = 0.04$, $P = 0.008$). This reduced stability of predator abundance at higher plant diversity might reflect the inherent oscillatory nature of predator–prey interactions (Turchin 2003). We found positive covariance for predators that was unaffected by plant diversity. This may indicate similar response to environmental variation across species or to synchronous oscillations in response to interactions with prey.

Our results reveal that plant species diversity has effects that propagate up the foodweb, affecting the trophic stability from plants to predators. Congruent with theory (May 1974; McCann *et al.* 1998; McCann 2000; Gross *et al.* 2009), as foodweb complexity increased and as interspecific interactions were likely less tightly coupled, the stability of species richness increased at herbivore, predator, and parasitoid trophic levels. As Elton (1958) suggested, we found that plant diversity increased community stability both by reducing herbivore population abundances and by reducing the

variability in total herbivore abundances and diversity. Plant diversity thus provides a key ecosystem service by reducing insect outbreak potential defined both in terms of herbivore population and community abundance and herbivore community variability over time. This service can be enhanced through landscape management for biodiversity, such as in conservation or restoration of natural areas in agricultural landscapes and diverse plantings for biofuels production (Tscharntke *et al.* 2005; Losey & Vaughan 2006; Landis *et al.* 2008; Isaacs *et al.* 2009). More broadly, our work suggests that biodiversity conservation or restoration at the producer trophic level contributes to the maintenance of diversity, function, and stability of entire foodwebs.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Effects of plant diversity on abundances of the most abundant arthropod species found in the experiment.

Table S2 Correlation among factors used in the analysis.

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