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Phenological complementarity, species diversity, and ecosystem function

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Increasing species diversity frequently enhances ecosystem function. Phenological complementarity, the asynchrony of species resource use and growth, may explain how species diversity influences ecosystem function but remains largely untested. We used an early successional plant community containing species with a variety of phenologies to test whether increasing species diversity enhances ecosystem function by increasing phenological complementarity. Over a two-year period, we increased environmental heterogeneity within an abandoned field with variation in disturbance, soil nutrients, water, light availability, and disturbance in 160 permanent plots, and measured percent cover of each plant species three times in each growing season. We did not manipulate species composition directly, and thus diversity and complementarity in each plot were the result of pre-existing conditions and responses of individuals to experimental treatments. Species diversity was measured in two ways, as the total number of species per plot and as the evenness of species abundances. Phenological complementarity was measured as the negative logarithm of the variance ratio. We tested whether the number of plant species per plot, species evenness, and their phenological complementarity in the first year predicted total annual cover in the second year. Total annual cover increased only moderately with number of species and evenness, consistent with studies that randomize species composition among replicate plots. Any effect that species number or evenness had on total annual cover, however, was not due to phenological complementarity. Rather, diversity was unrelated to phenological complementarity. These results indicate that naturally occurring variation in species diversity had little effect on whether phenological complementarity can enhance ecosystem function.

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Experiments that manipulate species diversity frequently show that increasing either the number of species or the evenness of species abundances enhances mean levels of ecosystem function (Naeem et al. 1994, Hooper and Vitousek 1997, McGrady-Steed et al. 1997, Tilman et al. 1997, Symstad et al. 1998, Hector et al. 1999, Petchey et al. 1999, Wilsey and Potvin 2000). Understanding the underlying mechanisms remains an important focus of research (Chapin et al. 2000). Increasing species diversity may enhance ecosystem function by adding complementary species (Tilman et al. 1997a), but few empirical studies have tested this idea (Hooper 1998, Norberg 2000).

Phenological complementarity, the asynchrony of species' growth rates, may enhance ecosystem function when resources are ephemeral (e.g., light, water, nitrogen) and different species peak at different times throughout the growing season (Trenbath 1974, Gulmon et al. 1983, Ewel 1986, Carson and Barrett 1988, Hooper 1998). Most previous work on phenological complementarity in plant communities has focused on factors affecting the evolution (i.e., origin and mainte-

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nance) of complementarity and on coexistence of competitors (Rathcke and Lacey 1985). Here we focus on the consequences of complementarity for ecosystem function. Our goal is to test whether phenological complementarity is the mechanism by which species diversity enhances ecosystem function in an early successional plant assemblage.

We used naturally occurring variation in species composition and diversity in an early successional plant assemblage to examine relationships between diversity, phenological complementarity, and ecosystem function. Phenological patterns in herbaceous plant communities are well known (Rathcke and Lacey 1985) and should provide an ideal model system to demonstrate the effects of phenological complementarity on ecosystem function. Over the two-year period of this study, experimental manipulations of resources created contrasting environmental conditions analogous to larger scale environmental variation, with the potential to improve the generality of our findings (McNaughton 1977, Loreau 1998, Sankaran and McNaughton 1999). We tracked the seasonal responses of all vascular plant species in 160 permanent plots, and quantified relationships between two measures of species diversity (number of species and evenness), phenological complementarity, and total annual cover (analogous to annual net primary productivity). We then tested whether number and evenness of species enhanced ecosystem function, and whether phenological complementarity was the mechanism responsible.

Methods

We conducted this experiment in a forb-dominated successional plant assemblage 15 yr after it was abandoned from agriculture, at the Hutcheson Memorial Forest near New Brunswick, New Jersey, USA (see Carson and Pickett 1990 for site information). This site was dominated by several goldenrod species (*Solidago* sp.), Japanese honeysuckle (*Lonicera japonica*), and a variety of understory forbs. One hundred and sixty 1.0 × 0.5-m plots were laid out in a 10 × 16 array where each plot was separated by at least 2.5 m. Each plot received experimental manipulations in a four way factorial design for two growing seasons (1985–1986). The treatments included fertilizer addition (10-6-4 NPK, applied at 270 kg N ha^{-1} yr^{-1}), water addition (~400 mm yr^{-1}), light addition (by gently tying back the canopy plants within sample plots), and a single early season soil disturbance (1 May 1985 only). To create the disturbance, we used a hand trowel to overturn and expose the soil throughout approximately 70% of each plot to a depth of 10 cm. Our fully crossed design resulted in 16 unique treatment combinations (i.e., fertilizer × water × light × disturbance), with 80 replicates of each level of the main factors, and 10 replicates of each unique combination (see Carson and Pickett 1990 for identical design and treatments in an adjacent younger field). For the purposes of this study, experimental increases in the abiotic heterogeneity of this early successional community created some of environmental heterogeneity observed in other studies (Hector et al. 1999, Sankaran and McNaughton 1999) where heterogeneity was an important random factor.

Ecosystem function – total annual cover

Percent cover is correlated with the ability of plants to acquire light energy, and to reduce light energy available for competing species (Frank and McNaughton 1989, Naeem et al. 1995, Carson and Root 2000). We estimated the percent cover of each species found in each plot in May, July, and September in 1985–1986. The sum of all species cover estimates in each plot typically exceeded 100% at any one sample period because the cover estimate of each species was independent of other species. This approach to percent cover is analogous to the leaf area index (LAI), a commonly used measure of productivity in forests (Waring and Schlesinger 1985). To examine an ongoing ecosystem process rather than a static pattern, we calculated total annual cover (TAC) using a technique to calculate aboveground net primary productivity (ANPP) from biomass samples (Odum 1960, Malone 1968, Carson and Barrett 1988). ANPP of herbaceous plant assemblages is best estimated by sampling biomass multiple times throughout the growing season, and summing the maximum biomass values for each species. Because these estimates of ANPP account for the separate phenologies of each species, this technique provides an accurate assessment of ANPP of an assemblage over its entire growing season (Malone 1968). We calculated total annual cover in an analogous manner: we summed the maximum cover values recorded for each species within each sample plot for each year.

Species diversity

Species composition and diversity were entirely a consequence of pre-existing composition, local extinction, and immigration during the two years of the resource manipulations. This nonrandom loss and gain of species distinguishes this experiment from others where composition is randomized (Naeem et al. 1994, Tilman et al. 1997b, Hooper 1998, Hector et al. 1999). A wide range of metrics are available to quantify species diversity, and most are related (May 1975, Pielou 1977, Gotelli and Graves 1996, Lande 1996). We quantified species diversity in each permanent plot with two contrasting metrics, the total number of species occurring at any time during a single growing season, S, and the evenness of species abundances, E. To calculate evenness, we used Simpson's diversity index, $SDI = 1 - \sum_{i=1}^{S} p^2$, where p is the relative abundance of species i based on the maximum cover value recorded for each species in a given year. Evenness was then calculated as SDI/SDI_{MAX}, where SDI_{MAX} is the maximum value of SDI for a given number of species and occurs when all species have equal abundances. We used evenness based on SDI because it is robust to small sample sizes and is easily interpretable: SDI is the probability that two individuals drawn at random are different species, and it is the variance of species identities (Lande 1996). (Note: analyses using other measures of evenness led to the same qualitative conclusions.)

Phenological complementarity

Species complementarity has been investigated in other community-level contexts, perhaps most notably in attempts to understand diversity–stability relationships (Frost et al. 1995, Tilman et al. 1998). Phenological complementarity may occur whenever resources are limiting and ephemeral (e.g., light, water, nitrogen) (Rathcke and Lacey 1985). We quantified phenological complementarity by modifying the variance ratio used by Frost et al. (1995), where, in our case, phenological complementarity (PC) is

$$PC = -\log_e\left(\mathrm{Var}\left\{\sum_{i=1}^{n} S_i\right\} \Big/ \sum_{i=1}^{n} \mathrm{Var}\{S_i\}\right)$$

where S_i is the percent cover of each species, and $\mathrm{Var}\{\}$ is the sample variance among May, July, and September samples. If all species' peak abundances occur at the same time, then $PC \ll 0$, providing no support for complementarity. If species' peak abundances are randomly or uniformly distributed throughout the growing season, then $PC \geq 0$, providing support for complementarity. In our herbaceous plant assemblage, we expected moderate complementarity ($PC = 0$) because contrasting forces probably set upper and lower limits on variation in species phenologies. The discrete growing season (April–Sept.) should reduce complementarity (i.e., $PC < 0$) because it forces positive covariation among species by constraining the growth and resource use of all herbaceous plant species to the same April–September growing season (Rathcke and Lacey 1985). Alternatively, early successional plant assemblages do contain species with contrasting phenologies (Malone 1968, Carson and Barrett 1988), and since resources (e.g., sunlight, soil moisture, nitrate) are highly ephemeral, even a random temporal distribution of species' abundances ($PC = 0$) would result in complementary resource use.

Measuring the effects of diversity, complementarity, and abiotic factors on ecosystem function

We used forward selection to build a general linear statistical model to explain variation in total annual cover in year two. Using predictor variables measured in year 1 reduces the likelihood that our response variable in year 2 is actually influencing the predictor variables (Tilman and Downing 1994, Huston 1997). Candidate predictor variables included third order polynomial expressions of the continuous variables: phenological complementarity in year 1 (PC), the total number of species per plot in year 1 (S), the evenness of species abundances in year 1 (E). Other candidate predictor variables included each experimental treatment (nitrogen, light, water, disturbance), and all interactions. We added model terms when this resulted in a lower Akaike's information criterion, AIC, corrected for small sample size (Burnham and Anderson 1998). In these analyses, a smaller AIC value indicates a "better" model, that is, a model that makes a more parsimonious tradeoff between explaining as much variation as possible with as little bias as possible. Models with AIC values two or more points worse (in this case larger) than the best model are unlikely to be good descriptors of data (Burnham and Anderson 1998). After our best model was determined, we used type III sums of squares to determine the fraction of the variation in total annual cover explained uniquely by each predictor variable in the model (S-PLUS 2000 1999). We transformed the response (total annual cover, year 2) using the natural logarithm to reduce heteroscedasticity.

Results

Like many early successional plant assemblages (Malone 1968, Carson and Barrett 1988, Mitchley 1988), this site contained species that peaked throughout the growing season (Fig. 1), indicating that phenological complementarity could, in principle, enhance total annual cover. The linear model that provided the best description of these data (i.e., explained the most variation with the least amount of bias) included species number, evenness, and phenological complementarity, as well as several experimental treatments (Table 1). Increases in nitrogen, water, phenological complementarity, number of species, and evenness all led to increases in total annual cover in year two (Fig. 2, Table 2). (The significant decrease in total

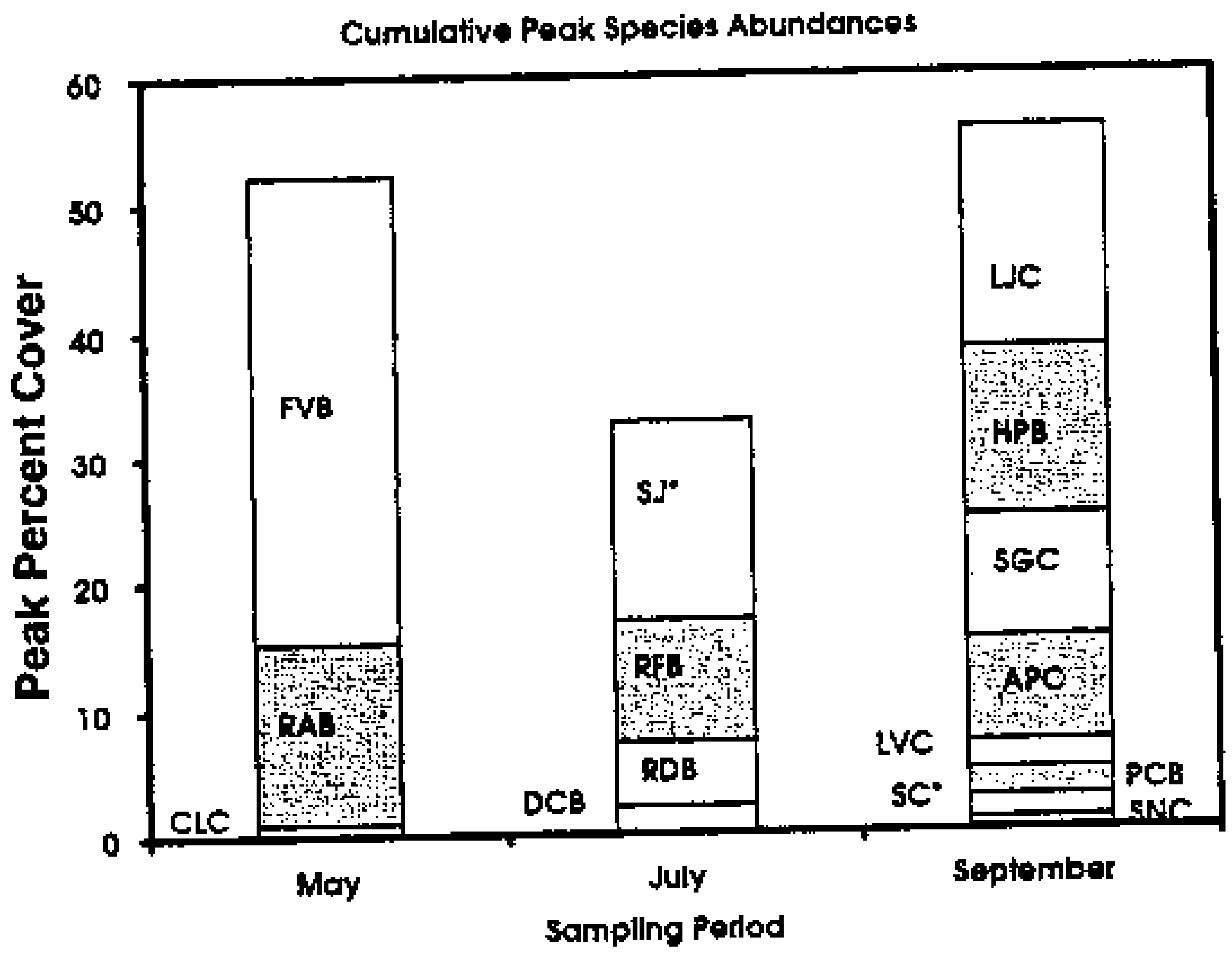

Fig. 1. Species' peak abundances summed across all plots for the 15 most common species in year 2. To test for effects of phenological complementarity on total annual cover, we used a per plot measure that did not sum across plots, and that used all species (see Methods). (Species abbreviations: FVB – *Fragaria virginiana*, SJ* – *Solidago juncea*, LJC – *Lonicera japonica*, HPB – *Hieracium pratense*, RAB – *Rumex acetosella*, SGC – *Euthemia graminifolia*, RFB – *Rubus flagellaria*, APC – *Aster pilosa*, RDB – *Toxicodendron radicans*, LVC – *Linaria vulgaris*, DCB – *Daucus carota*, SC* – *Solidago canadensis*, PCB – *Poa compressa*, SRC – *Solidago rugosa*, CLB – *Chrysanthemum leucanthemum*, SNC – *Solidago nemoralis*). The suffixes B and C refer to basal or canopy growth forms, and * means that both growth forms were found for *S. juncea* and *S. canadensis*.)

annual cover in response to the light amendment [Table 2] was the trivial result of tying back the canopy within the sample plot.) Number of species and evenness, both components of species diversity, together explained 7.4% of the variability in total annual cover. Together, these had roughly half the explanatory power as the experimental water treatments. The positive effects of both species number (Fig. 2B) and evenness (Fig. 2C) on total annual cover appear to plateau, with the greatest effects occurring at fairly low levels of species number and evenness. Phenological complementarity explained only 1.4% of variability in total annual cover. The small size of the effects of species number, evenness, and complementarity did not result from collinearity among these variables because they were not strongly correlated and, separate sequential sums of squares (type I) analyses did not change the results (Venables and Ripley 1999). Neither number of species nor evenness was related to phenological complementarity (Fig. 3).

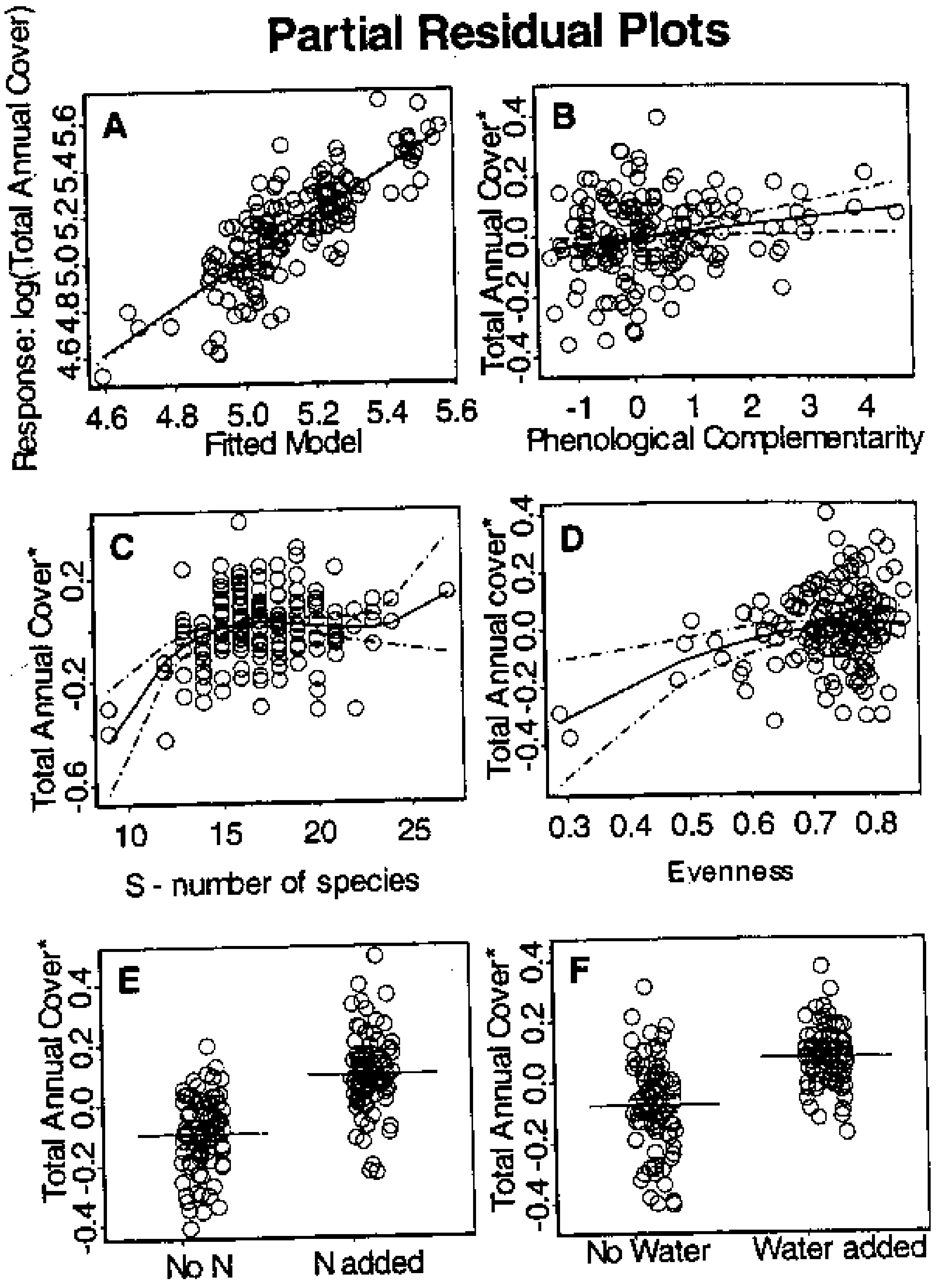

Fig. 2. Relationships between total annual cover in year 2 and all variables in the best model (Tables 1, 2). (A) Transformed total annual cover (year 2) as a function of the best statistical model. The dotted line is the 1:1 relationship. (B–F) Partial residual plots show the effects of each predictor variable (e.g., B-phenological complementarity) and the variation *not* explained by all other predictor variables. * "Total annual cover" in B–F are the partial residuals of transformed total annual cover (i.e., variation not explained by other variables). Horizontal lines in E and F are the treatment means and standard errors.

Table 1. Model selection for explaining variation in total annual cover in year 2 (TAC2). Models with AIC values larger by two or more points (δ AIC) are unlikely to describe the data as accurately as the best model (Burnham and Anderson 1998). The number of parameters listed below includes both the intercept and the error variance, as well as terms listed under "Models". (*PC* – phenological complementarity, *S* – total number of species per plot, *E* – evenness of species abundances, *N* – nitrogen amendments, *L* – canopy tie-backs, *W* – water amendments).

Models	No. of parameters	AIC	δ AIC (Candidate – Best)	R^2_{TOTAL}
Best model:				
$\log(\text{TAC2}) \sim PC+S+S^2+S^3+E+E^2+N+L+W+N{:}L+W{:}L$	13	–177.1	0.0	0.66
Other logical candidate models:				
$\log(\text{TAC2}) \sim S+S^2+S^3+E+E^2+N+L+W+N{:}L+W{:}L$	12	–173.5	3.6	0.65
$\log(\text{TAC2}) \sim PC+S+S^2+S^3+N+L+W+N{:}L+W{:}L$	11	–170.8	6.2	0.64
$\log(\text{TAC2}) \sim PC+E+E^2+N+L+W+N{:}L+W{:}L$	10	–164.5	12.6	0.62

Table 2. Unique effects (type III sums of squares) on total annual cover of each factor and covariate in the best model. (*PC* – phenological complementarity, *S* – total number of species per plot, *E* – evenness of species abundances per plot).

Source	df	SS	%SS explained	*P*
Nitrogen	1	1.439	21.0%	<0.0001
Light	1	1.148	16.8%	<0.0001
Water	1	0.895	13.0%	<0.0001
Light: Nitrogen	1	0.049	0.7%	0.0970
Light: Water	1	0.096	1.4%	0.0210
PC	1	0.096	1.4%	0.0207
$S+S^2+S^3$	3	0.331	4.8%	0.0005
$E+E^2$	2	0.179	2.6%	0.0075
Residuals	148	2.850	38.1%	

Discussion

We found no evidence that phenological complementarity was the mechanism responsible for the observed positive relationships between number of species, evenness, and total annual cover. Increasing diversity (numbers or evenness) did not enhance phenological complementarity, and phenological complementarity explained little of the variation in total annual cover. This may not be surprising because other studies have shown that ecosystem function responds to diversity most dramatically at very low diversity (e.g., 0–8 species) (Tilman et al. 1997b, Hooper 1998, Hector et al. 1999), and in our study each plot had at least eight species. Natural variation in phenological complementarity may not suffice, and in particular, may not include low enough levels, to properly test its importance in influencing ecosystem function. Indeed, phenological complementarity may be critical to the maintenance of ecosystem function in this assemblage, but sufficient complementarity may be achieved at low levels of diversity. In very species-poor assemblages, increasing diversity might enhance phenological complementarity and lead to greater observed effects of complementarity. Direct manipulations of species phenologies would test this hypothesis. Our results indicate, however, that at the moderately high levels of diversity and complementarity observed throughout our sample plots, diversity was unrelated to phenological complementarity, and complementarity was only weakly related to total annual cover.

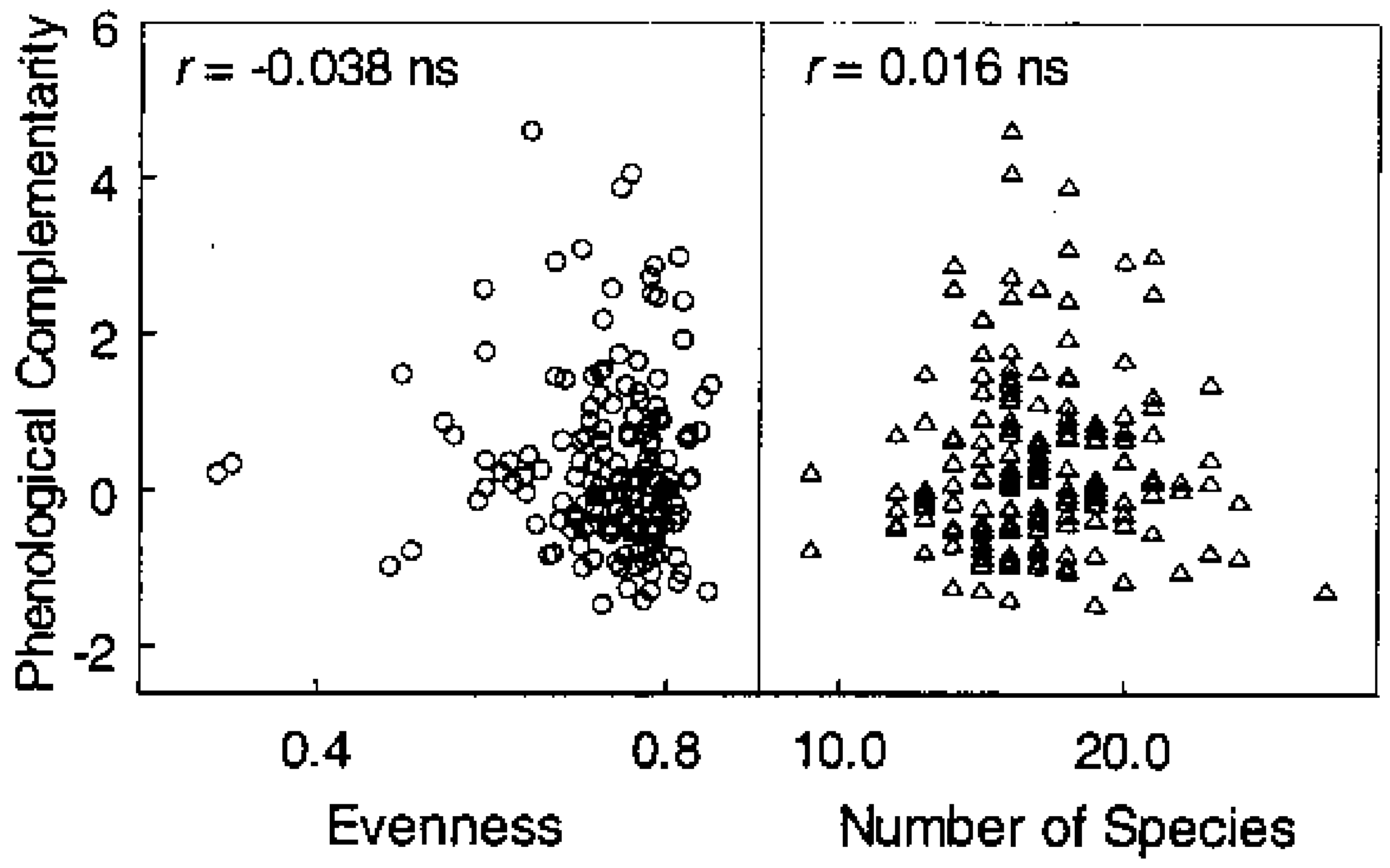

Fig. 3. Relations between phenological complementarity and two measures of species diversity, evenness of species abundances and number of species.

Studies such as this one that use naturally occurring, nonrandom species assemblages complement studies that randomize diversity and composition among replicates. They are complementary because using nonrandom assemblages assesses the relative importance of diversity in controlling ecosystem function in extant communities (Phillippi 1993, Wardle et al. 1997, Hodgson et al. 1998, Sankaran and McNaughton 1999). In our study, nonrandom processes such as establishment, competition, and local adaptation (Linhart and Grant 1996) undoubtedly helped structure local neighborhood composition. Our results corroborate the more highly controlled studies that also find relatively small, but persistent effects of species diversity on ecosystem function, regardless of the large influence of other abiotic factors (Hector et al. 1999). Greater understanding of how diversity and complementarity influence ecosystem function will require experiments that allow nonrandom processes to determine composition. The resulting species combinations, assembled independently of the factors that created them, would then allow direct experimental tests of the roles of diversity and complementarity in natural systems (Petchey 2000).

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