

Phylogenetic diversity promotes ecosystem stability

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Abstract. Ecosystem stability in variable environments depends on the diversity of form and function of the constituent species. Species phenotypes and ecologies are the product of evolution, and the evolutionary history represented by co-occurring species has been shown to be an important predictor of ecosystem function. If phylogenetic distance is a surrogate for ecological differences, then greater evolutionary diversity should buffer ecosystems against environmental variation and result in greater ecosystem stability. We calculated both abundance-weighted and unweighted phylogenetic measures of plant community diversity for a long-term biodiversity–ecosystem function experiment at Cedar Creek, Minnesota, USA. We calculated a detrended measure of stability in aboveground biomass production in experimental plots and showed that phylogenetic relatedness explained variation in stability. Our results indicate that communities where species are evenly and distantly related to one another are more stable compared to communities where phylogenetic relationships are more clumped. This result could be explained by a phylogenetic sampling effect, where some lineages show greater stability in productivity compared to other lineages, and greater evolutionary distances reduce the chance of sampling only unstable groups. However, we failed to find evidence for similar stabilities among closely related species. Alternatively, we found evidence that plot biomass variance declined with increasing phylogenetic distances, and greater evolutionary distances may represent species that are ecologically different (phylogenetic complementarity). Accounting for evolutionary relationships can reveal how diversity in form and function may affect stability.

Key words: *biodiversity–ecosystem function; Cedar Creek, Minnesota, USA; ecophylogenetics; ecosystem reliability; niche partitioning; phylogenetic complementarity.*

INTRODUCTION

A central hypothesis of macroevolutionary theory is that rates of speciation depend on ecological opportunity (Jablonski and Bottjer 1991), with the preponderance of species radiations exploiting ecologically “open” niches. Thus, groups of closely related species tend to occupy similar niches (Futuyma 2010, Wiens et al. 2010). This hypothesis suggests that, as environmental conditions and resource availability change, ecological communities composed of species that encompass a broader range of niches (i.e., more distantly related species) would better maintain ecosystem functioning because of the differential species responses to this variation (Tilman 1996, Yachi and Loreau 1999, Hooper et al. 2005, Fox 2010, Hector et al. 2010). Experiments have shown that the stability of ecosystem function increases with greater community diversity: usually measured as species richness (Tilman and Downing 1994, Tilman 1996, Tilman et al. 2006, Hector

et al. 2010). Ecosystem stability has been hypothesized to be affected more by diversity than is ecosystem function (Norberg 2004), and it has been argued that stability is more pertinent for conservation (Srivastava and Vellend 2005). While there have been a multitude of studies published that examine the effect of diversity on function (summarized in Balvanera et al. 2006 and Cardinale et al. 2006), there have been relatively few that examine the stability of ecosystem function (Balvanera et al. 2006), likely because of the amount of time necessary to observe sufficient variation in ecosystem function.

Much of the research on the effect of diversity on ecosystem function and stability has focused on species richness and community composition, and how the distribution of abundances influence ecosystem function has received less attention (Nijs and Roy 2000, Hillebrand et al. 2008). Communities dominated by the best competitor may perform better under a constant, homogeneous environment, but communities with more even abundance distributions should be more stable in the face of environmental variation as there would be less of a lag time for the best suited species to increase in abundance and restore ecosystem function (Norberg 2004, Hillebrand et al. 2008). In a large-scale, multisite

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diversity–ecosystem function experiment, Kirwin and colleagues (2007) showed that species richness affected ecosystem function more strongly in polycultures with high evenness.

The diversity and relative abundances of species should be important only when species differ in niche requirements or their functional contribution to the ecosystem (Nijs and Roy 2000, Mouillot et al. 2005). For example, evenness should matter little for two functionally similar species with high niche overlap (Hooper et al. 2005, Carroll et al. 2011). Conversely, diversity and evenness should strongly affect ecosystem function for combinations of functionally different species with low niche overlap (Carroll et al. 2011). This means that quantifying the relative similarities and differences and the evenness among species is crucial for understanding ecosystem stability.

Quantifying niche and functional differences among multiple species is not straightforward, and instead, phylogenetic diversity may be used as a representation of species similarities and differences (Webb et al. 2002, Cadotte et al. 2008, Cavender-Bares et al. 2009). If phenotypic dissimilarity is correlated with evolutionary divergence times (Felsenstein 1985, Harvey and Pagel 1991), then the simplest models of evolutionary change predict that the more distantly related two species are, the greater likelihood that they differ ecologically. Of course, individual traits may show idiosyncratic patterns and rates of evolution, but overall ecological differentiation, across a suite of traits, is not understood very well. Measures of phylogenetic diversity have been shown for some data sets to better explain variation in community productivity than species richness or functional diversity (Maherali and Klironomos 2007, Cadotte et al. 2008, 2009).

The use of phylogenetic information to explain ecosystem function has, to date, used phylogenetic measures based on presence–absence only, thus ignoring measures that quantify the distribution of evolutionary information in a community or that explicitly incorporate abundances. The first explicit attempt to include species relative abundances into phylogenetic diversity–ecosystem function studies was introduced in a statistical model by Connolly and colleagues (2011). This is, in part, a reflection of the fact that entropic and abundance-weighted phylogenetic diversity measures have been created only very recently (e.g., Hardy and Senterre 2007, Helmus et al. 2007, Allen et al. 2009, Cadotte et al. 2010). There are now metrics available that weight phylogenetic distances by abundance (Helmus et al. 2007) or that are based on the distribution or evenness of evolutionary information in the assemblage (Cadotte et al. 2010). We use both distance-based measures that quantify the distance to other species in the assemblage and entropic measures that evaluate the distribution of evolutionary history based on the distinctiveness of species. For measures that do not include species abundances, “low-diversity” levels would

correspond to community phylogenies that are imbalanced, with numerous closely related species and few distantly related ones. Conversely, “high-diversity” communities would be ones in which species are all equivalently related to one another (Cadotte et al. 2010). Incorporating abundances into these types of metrics changes the interpretation such that highly diverse communities are comprised of evolutionary distinct species that have higher abundances and of species with close relatives having lower abundances. This would be the expectation if distinct species have little niche overlap, while groups of closely related species have high niche overlap and must partition available resources.

In this paper we examine the stability of aboveground biomass, measured as the mean biomass divided by the interannual standard deviation, in a long-term diversity–ecosystem function experiment at Cedar Creek, Minnesota, USA. Specifically, we tested the hypothesis that more phylogenetically diverse assemblages result in biomass productivity that is temporally more stable. Beyond plot-level stability, it is worth studying the covariance and variance of the constituent populations. If the covariance between two species increases, biomass production will be more synchronous, thus lowering stability. If increased phylogenetic distances are correlated with greater community stability and asynchrony between species, then three possible hypotheses may explain why. Hypothesis 1: There may be a phylogenetic nonindependence in species stability. If closely related species share environmental responses and thus have similar variances (Fig. 1a), then sampling from elsewhere in the phylogeny would increase the probability of including a species with different variances (Fig. 1b). This would result in a sampling effect where assemblages of close relatives can have low or high variances depending on their clade. For example, if the species in the clade with black circles in Fig. 1 inherently have low variance, and an assemblage with just these species would have high stability. The converse is true with low phylogenetic diversity (PD) assemblages of species from a high variance clade. According to the measure of stability used here, species with higher average abundances are inherently more stable; thus, they disproportionately drive plot stability. As assemblages include more distantly related species there is a higher probability of including species from stable clades, which would increase average assemblage stability.

Alternatively, including members from different clades in an assemblage can reduce niche overlap or shared environmental sensitivities, resulting in greater stability through lower covariance or lower variance (i.e., phylogenetic complementarity) through two additional mechanisms. Hypothesis 2: Species with reduced niche overlap may have negatively correlated temporal abundances because distantly related species are responding differently to environmental changes (Fig. 1c), producing temporal insurance against environmental

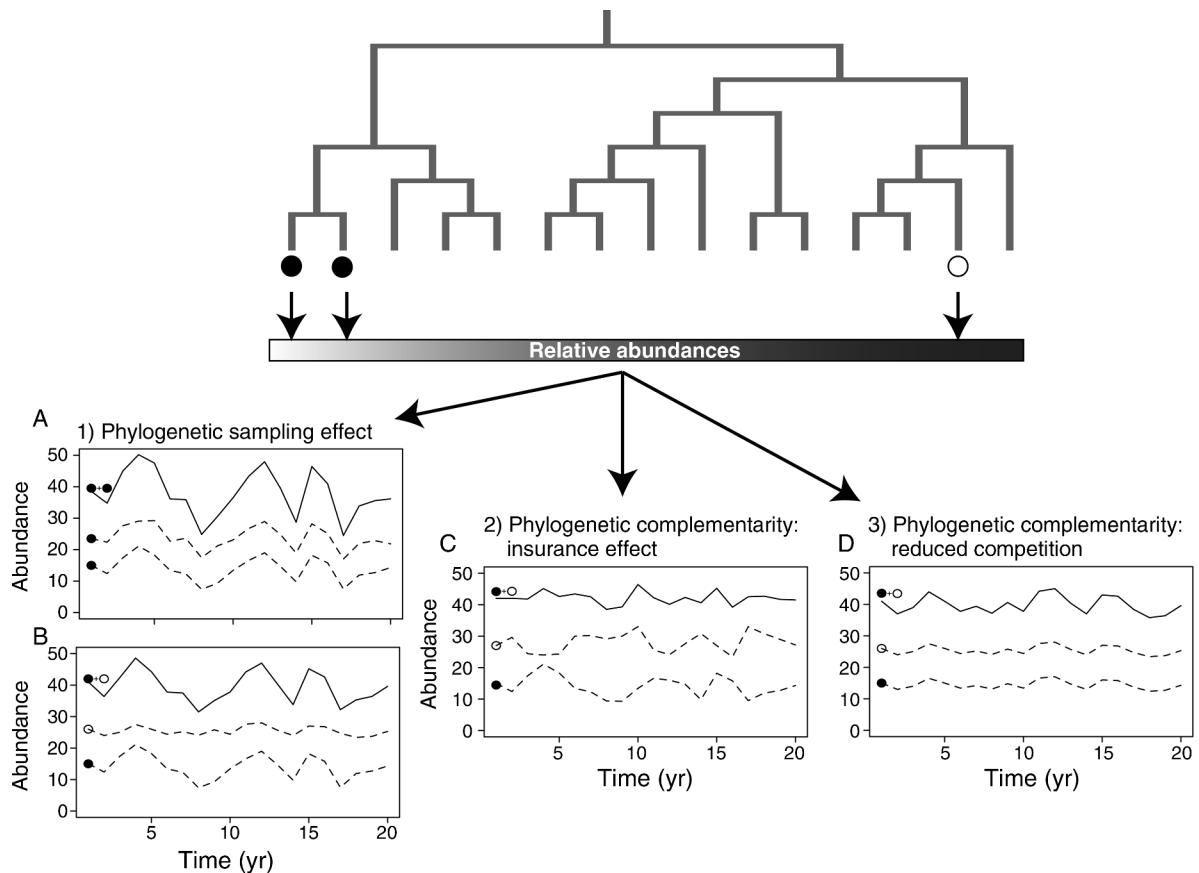


FIG. 1. A hypothetical phylogeny and simulated species abundance fluctuations showing how hypothesized mechanisms would influence community dynamics. (A) For the phylogenetic sampling effect (1), closely related species (solid circles) could show correlated responses to environmental variation due to shared tolerances and both be highly variable, resulting in a highly variable community. (B) A distantly related species (single open circle) is not expected to have correlated responses and may result in a more stable community. There are two potential mechanisms for niche complementarity. The first mechanism is reduced competition with increasing phylogenetic distance (2). (C) At its extreme, distantly related noninteracting species (solid + open circle) will have idiosyncratic responses to environmental fluctuations, and the community may appear more stable, while closely related species may be competing strongly and amplifying oscillations while competitive hierarchies switch with changing environments. (D) Finally, with the phylogenetic insurance hypothesis (3), distantly related species may have very different responses to environmental fluctuations, and coexistence in time means that communities are more stable because species replace the functioning of other species when the environment changes. Shown are the individual population dynamics (dashed lines) and the combined two-species community dynamics (solid lines).

variation (Yachi and Loreau 1999, Lehman and Tilman 2000, Hector et al. 2010). Here, species replace one another in dominance, better maintaining community function. Hypothesis 3: Alternatively, distantly related species combinations could result in individual species having lower variances because competition is reduced or that positive interactions are stronger than negative ones, so that variances are primarily responding to environmental variation and not shifts in competitive superiority. Strong interactions have been shown to reduce community stability (see May 1972, but compare with Ives et al. 1999). If closely related species compete more intensely, small environmental fluctuations could alter competitive hierarchies, amplifying variances (i.e., if a species declines due to stressful environmental conditions at the same time when another species

becomes competitively superior, it will show more of a rapid decline than if it had been alone; Fig. 1d). For hypothesis 2, biomass production would show asynchronous fluctuations across multiple species, especially for distantly related species, and thus, community stability is a product of species asynchrony (Fig. 1c; Lehman and Tilman 2000). If species have reduced interactions (hypothesis 3), their fluctuations need not be asynchronous for the community to be relatively stable. Finally, we examined these hypotheses using measures of phylogenetic diversity that use presence-absence or abundance weighting (shown as a transition between the phylogeny and the dynamics in Fig. 1). Abundance-weighted measures may better explain stability by discounting the phylogenetic contribution of consistently rare species.

METHODS

Study site

In 1994, 13×13 m plots were seeded with 1, 2, 4, 8, or 16 grassland savanna species at Cedar Creek Natural History Area, Minnesota, USA. Species were randomly chosen from a pool of 20 species that included four C_3 grasses, C_4 grasses, legumes, nonlegume herbaceous forbs, and two woody species: *Achillea millefolium*, *Pascopyrum smithii*, *Amorpha canescens*, *Andropogon gerardii*, *Asclepias tuberosa*, *Dalea candida*, *D. purpurea*, *Elymus canadensis*, *Koeleria cristata*, *Lespedeza capitata*, *Liatris aspera*, *Lupinus perennis*, *Monarda fistulosa*, *Oligoneuron rigidum*, *Quercus ellipsoidalis*, *Q. macrocarpa*, *Panicum virgatum*, *Poa pratensis*, *Schizachyrium scoparium*, and *Sorghastrum nutans*. At each level of diversity, 28–35 replicates were established, and plot composition was maintained by manually weeding and annual burns (full details are available online, and in Tilman et al. 1997, Knops et al. 1999).⁵

Productivity was estimated by clipping, drying, and weighing aboveground biomass in four 0.1×3.0 m strips per plot. Biomass was sampled annually from 1996 to 2010. All plots were annually burned. A few plots that consistently did not burn are excluded. Woody species (*Quercus ellipsoidalis* and *Q. macrocarpa*) contributed little to productivity, and were rarely encountered by clipped strips, but when present, they mostly consisted of woody nonliving biomass that had accumulated over many years, and so they were excluded from the calculations. In 2001–2008 and in 2010, for each plot, biomass from one strip was sorted by individual species and weighed. Data from this experiment (e120) are available through the Cedar Creek Long Term Ecological Research (LTER) website.⁶

Monthly snowfall, precipitation, and maximum and minimum temperature for the duration of the experiment were obtained from Minnesota Climatology Working Group of the State Climatology Office for the Cedar weather station (latitude, 45.31288; longitude, 93.28832; available online).⁷

Phylogeny construction

We used the phylogeny produced in a previous publication (Cadotte et al. 2009). Briefly, GenBank (Benson et al. 2005) was queried for four gene sequences (*matK*, *rbcl*, *ITS1*, and *5.8s*) for 31 species used in two experiments at Cedar Creek, and two representatives of early-diverging angiosperm lineages as outgroup species, *Amborella trichopoda* and *Magnolia grandiflora*. Fourteen species were represented by at least one gene in GenBank. For the remaining species, we used gene sequences from a congeneric relative not included in these experiments. All sequences were aligned using

MUSCLE (Edgar 2004). A maximum-likelihood phylogeny was estimated using the PHYML algorithm with a BIONJ starting tree (Guindon and Gascuel 2003, Anisimova and Gascuel 2006). The maximum-likelihood tree is available in Cadotte et al. (2009). A single species that lacked any genetic data, *Rudbeckia hirta*, was added as a polytomy with *Liatris aspera* and *Coreopsis palmata* because they are all considered members of the Asterioideae subfamily.

Phylogenetic diversity measures

There is now a plethora of metrics that quantify phylogenetic diversity (e.g., Webb et al. 2002, Hardy and Senterre 2007, Helmus et al. 2007, Cadotte et al. 2010, Kembel et al. 2010), and although we examined several in our analyses (see Appendix A), we detail only a few here. Phylogenetic diversity can be measured in a number of different ways, with a common measure being PD, defined as the sum of the phylogenetic branch lengths represented by a set of co-occurring species (Faith 1992, Cadotte et al. 2008). Since both the number of species in a sample and the phylogenetic topology affect PD values, other measures attempt to account for topology. The mean nearest taxon distance (MNTD) is the average of the shortest phylogenetic distance for each species to its closest relative in the assemblage (Webb et al. 2002, Kembel et al. 2010). Mean pairwise distance (MPD) is the average of all phylogenetic distances connecting species together in a sample (Webb et al. 2002, Kembel et al. 2010). Finally, we used an entropic measure of phylogenetic diversity (H_{ed}) that is based on the relative distribution of evolutionary distinctiveness in a community (Cadotte et al. 2010), where evolutionary distinctiveness is measured as the amount of a species' evolutionary history that is not shared with other species (see Isaac et al. 2007, Redding et al. 2008). H_{ed} can be thought of as a measure of the distribution of evolutionary information in a community, with high H_{ed} values corresponding to communities where species are equivalently related to one another and low values correspond to an imbalanced phylogeny (Cadotte et al. 2010).

The four measures of phylogenetic diversity (PD, MNTD, MPD, and H_{ed}) are all calculated on community composition, but do not take abundances into account. In addition to the four metrics, we also used abundance-weighted versions of MNTD, MPD, and H_{ed} . For both MNTD and MPD, the phylogenetic distances used to calculate the means are weighted as

$$\frac{\sum_{i=1}^{S_p} (m_i \cdot n_i)}{\sum_{i=1}^{S_p} n_i}$$

where S_p is the number of species in plot p , m_i is the minimum or mean phylogenetic distance to other

⁵ <http://www.cedarcreek.umn.edu/research/exper/e120/>

⁶ <http://www.cedarcreek.umn.edu/research/data/>

⁷ <http://climate.umn.edu/>

community members (for MNTD and MPD, respectively), and n_i is the abundance of species i . We denote the abundance-weighted versions as $MNTD_{ab}$ and MPD_{ab} , and we will refer to the measures based on presence-absence as $MNTD_{pa}$ and MPD_{pa} . The abundance-weighted version of H_{ed} (H_{aed}) scales evolutionary distinctiveness of a species by its relative abundance such that diverse communities are those where abundance is proportional to evolutionary distinctiveness, with distinct species having high abundance and those with many close relatives having lower abundance (Cadotte et al. 2010). These diversity measures were chosen because they have abundance-weighted versions and are minimally correlated with PD and their abundance-weighted counterparts (see Appendix B). All diversity metrics were calculated at the plot level.

Our measure of abundance is each species' biomass from the 0.1×3 m strip, and we standardized species biomass by total strip biomass. This was done because strip biomass is correlated with estimated plot biomass ($r = 0.846$, $P < 0.001$), and this could introduce spurious correlations between the abundance-weighted metrics and plot productivity. Thus we used relative abundances, where the sum of abundances in a plot equals 100.

We used two R packages to calculate these metrics: Picante (Kembel et al. 2010) for $MNTD_{pa}$, $MNTD_{ab}$, MPD_{pa} , and MPD_{ab} ; and *ecoPD* (Cadotte et al. 2010) for PD, H_{ed} , and H_{aed} .

Statistical analyses

Since only the data from 2001 to 2010 (excluding 2009) contain biomass estimates for individual species, we confined our analyses to these years, thus allowing us to directly compare presence-absence metrics to abundance-weighted ones. Further, we analyzed the effect of diversity on ecosystem function using diversity measures from the initial sown composition, as well as the realized diversity based on the actual composition in plots during the time frame analyzed. All metrics were correlated against time to determine if there was a trend in diversity over time. There were not any apparent time lags from cross-correlation analyses. We also examined whether the temporal correlations were influenced by plant richness treatment.

To determine if variation in biomass production was driven by environmental variation, we used mixed-effects models with precipitation, snow accumulation, and maximum and minimum temperatures as fixed effects, plot nested within year as a random effect, and biomass produced as the dependent variable. We examined the average productivity and stability. For average productivity, we regressed it against the various diversity metrics and compared their relative explanatory value using Akaike weights (Johnson and Omland 2004). The mean of the diversity metrics across time in a plot was used. For the best predictor variable, we examined how the explanatory variable performed (looking at Akaike information criterion [AIC]) for

each year. To quantify the stability of biomass production across time for each plot, we divided the mean plot biomass (μ) by a temporally detrended standard deviation (σ_d). This ratio is the inverse of the coefficient of variation (e.g., Tilman et al. 2006, Hector et al. 2010). Detrending was done by calculating the standard deviation for the residuals from a linear regression of plot biomass on the logarithm of year, which provided a better error distribution and fit the data better (Tilman et al. 2006).

We were also interested in patterns of variability for single species. We tested whether variability in biomass differed for species using a Levene's test. We tested whether phylogenetic sampling or complementarity has a role in explaining phylogenetic diversity-stability relationships. To examine the phylogenetic sampling effect, we used Blomberg's K (Blomberg et al. 2003) to test for a phylogenetic signal in single species' mean stabilities ($\mu_i/\sigma_{d,i}$). We assessed the significance of the K values by randomly shuffling mean stability values among species 1000 times and calculated 95% confidence intervals. For complementarity, we were interested in the relative magnitude of species variances and covariances in plots, where a high covariance indicates species synchrony and high variance, asynchrony (Fox 2010, Proulx et al. 2010). We calculated an index of asynchrony (v) as the ratio between species variances to total plot variation in biomass values (B) across S species in a plot:

$$v = \frac{\sum_{i=1}^S \text{var}(B_i)}{\sum_{i=1}^S \text{var}(B_i) + \sum_{i=1}^S \sum_{j \neq i} \text{cov}(B_i, B_j)}$$

Akaike weights were used to regress v against the different diversity metrics and compared using. All analyses were run using R version 2.9.1 (R Development Core Team 2009).

RESULTS

While previous analyses have shown that variation in biomass production was best explained by phylogenetic diversity (Cadotte et al. 2008, 2009), they did not examine how abundance-weighted measures perform, or how the explanatory value changes over time. We examined how various measures of species and phylogenetic diversity explain variation in average plot biomass production (full list of variables compared is available in Appendix A). The single best explanatory variable is the abundance-weighted mean pairwise distance (MPD_{ab} ; Akaike weight [AW] = 0.999, $P < 0.0001$, $R^2 = 0.541$; Fig. 2A). We examined the explanatory ability of MPD_{ab} for each year and found that AIC values generally decline with time (Fig. 2B), indicating increasing explanatory value with time (the

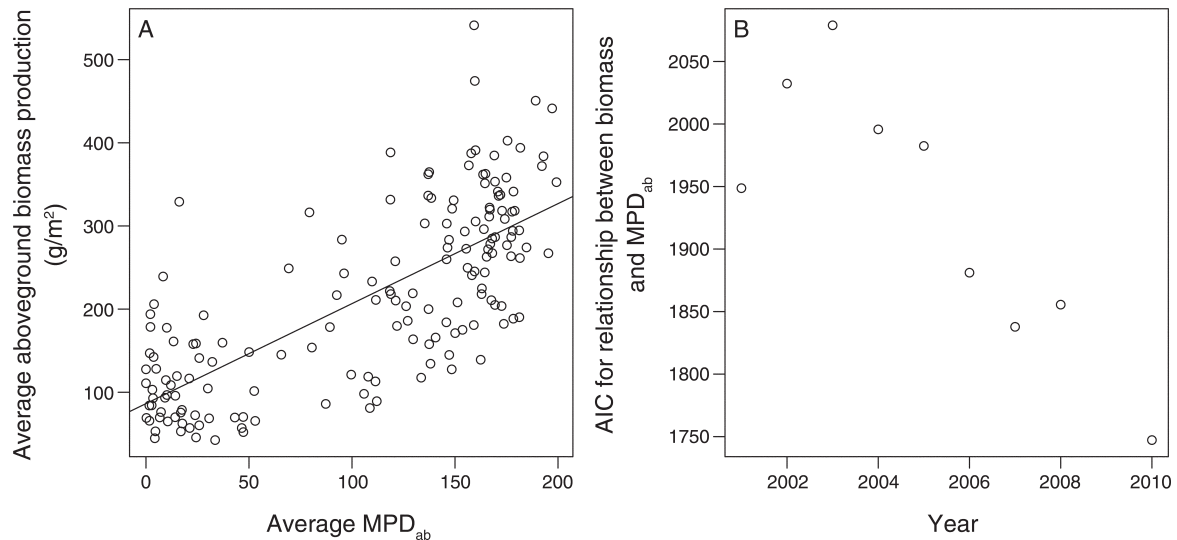


FIG. 2. (A) Plot aboveground biomass production increases with abundance-weighted mean pairwise distance (MPD), both averaged across 2001–2010. (B) The relative explanatory value of abundance-weighted MPD (MPD_{ab}) increases (decreasing Akaike information criterion [AIC]) with time. In each year, MPD was a highly significant predictor of biomass ($P < 0.0001$).

highest AIC corresponds to $R^2 = 0.345$ and the lowest was 0.489 in 2010).

Beyond the amount of biomass production, ecosystem stability is an important aspect of ecosystem function. After an initial increase, productivity has been variable through time (Fig. 3). Maximum productivity has been more variable than the minimum. This variability is explained, in part, by local weather conditions. Using mixed-effects models with fixed effects as precipitation, snow accumulation, and maximum and minimum temperatures, with plot nested within year as a random effect, precipitation alone was the most parsimonious model explaining variation in biomass production (AIC = 28 368, coefficient = 0.562, 95% CI = 0.478–0.641, $P < 0.0001$).

Given that this variation in biomass production exists, we then asked how species and phylogenetic diversity explain biomass production stability. There were not any strong overall trends in diversity change over time. None of the variables considered in this analysis were significantly correlated with time ($P > 0.05$): richness ($r = -0.223$; SD = 0.427), PD ($r = -0.207$, SD = 0.446), $MNTD_{pa}$ ($r = 0.251$, SD = 0.466), $MNTD_{ab}$ ($r = 0.168$, SD = 0.469), MPD_{pa} ($r = 0.010$, SD = 0.520), MPD_{ab} ($r = -0.050$, SD = 0.518), H_{ed} ($r = -0.256$, SD = 0.431), and H_{aed} ($r = 0.152$, SD = 0.466). Even though neither mean species nor phylogenetic diversity systematically changed over time, changes in diversity were related to planted richness. Specifically, several measures were likely to show declines in high richness treatments (16 species), including realized richness ($P < 0.0001$), PD ($P < 0.0001$), H_{ed} ($P < 0.0001$), MPD ($P < 0.001$), and MPD_{ab} ($P < 0.0001$). Conversely, MNTD increased the most in the high richness plots ($P = 0.0004$). However,

change in biomass production through time for a plot was not related to richness treatment ($P = 0.91$).

Ecosystem stability, as measured by μ/σ_d was significantly related to most of the diversity measures (Appendix A). Stability increased with increasing H_{ed} , realized richness, H_{aed} , planted richness, PD, MPD_{ab} , $MNTD_{pa}$, and $MNTD_{ab}$, but not MPD_{pa} (Table 1). H_{ed} best explained variation in stability (Table 1, Fig. 4), and multivariable models were found not to be more efficacious according to AIC. The two best multivariable models ($H_{ed} + H_{aed}$ and realized richness + H_{aed}) had AIC values (AIC = 450 for both) larger than the single model with H_{ed} (AIC = 448).

That phylogenetic relationships explain variation in ecosystem stability could be caused by several mechanisms. First, there could be a phylogenetic sampling effect such that species exhibiting higher stability are closely related to other stable species, and vice versa for unstable species (hypothesis 1). Species do show variation in stability (Appendix C) with overall significant differences in stability (Levene's $F_{17,1802} = 6.576$, $P < 0.0001$). However, mean stability does not show a phylogenetic signal using Blomberg's K ($K_{observed} = 0.361$, $K_{null} = 0.255$ (95% CI = 0.104–0.452). Mantel tests correlating variances with phylogenetic distances within individual plots also did not show a significant relationship ($P > 0.05$). Therefore, the fact that increased phylogenetic distances correspond to increased stability is not because of a propensity to include clades with more stable species.

The phylogenetic insurance hypothesis (hypothesis 2) predicts that the relationship between phylogenetic diversity and ecosystem stability is from greater distances between co-occurring species that result in

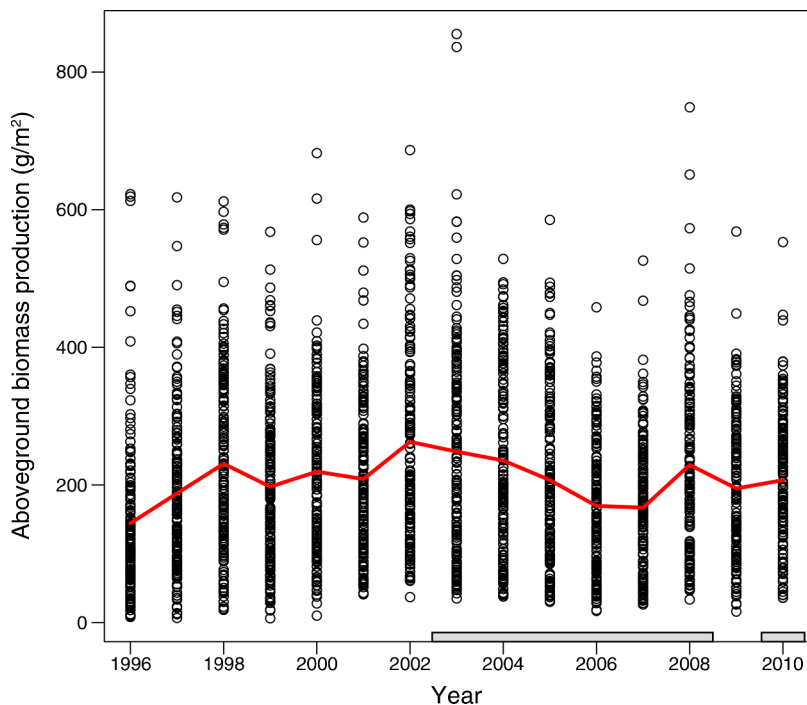


FIG. 3. Aboveground biomass production from each plot throughout the duration of the experiment. The red solid line reflects mean productivity, and the shaded bars along the bottom axis indicate years when individual abundances were available.

emergent stability through greater asynchrony (v) in the individual temporal dynamics of species. We examined how the degree of asynchrony was explained by the various diversity metrics. The best model explaining variation in v was a quadratic MPD_{ab} ($AW = 0.927$, $R^2 = 0.375$), with a generally declining relationship (Fig. 5). Despite the appearance that v peaks at intermediate MPD_{ab} values, this was not supported by a Mitchell-Olds-Shaw test (Mitchell-Olds and Shaw 1987). Our measure of asynchrony was slightly negatively correlated

with stability ($r = -0.18$, $P = 0.02$), mainly because closely related species were more likely to have correlated abundances through time than distantly related ones (Mantel $r = 0.04$, $P = 0.012$).

TABLE 1. Explanatory ability of the nine diversity metrics on stability of annual biomass production.

| Variable | AIC | AW† | R^2 | P |
|--------------------------|-----|--------|-------|--------|
| H_{ed} | 448 | 0.839 | 0.19 | <0.001 |
| Richness _{real} | 454 | 0.061 | 0.16 | <0.001 |
| H_{aed} | 459 | 0.004 | 0.14 | <0.001 |
| Richness _{int} | 462 | 0.001 | 0.12 | <0.001 |
| PD | 463 | <0.001 | 0.12 | <0.001 |
| MPD_{ab} | 464 | <0.001 | 0.11 | <0.001 |
| $MNTD_{pa}$ | 465 | <0.001 | 0.11 | <0.001 |
| $MNTD_{ab}$ | 467 | <0.001 | 0.10 | <0.001 |
| MPD_{pa} | 484 | <0.001 | <0.01 | 0.952 |

Note: Abbreviations are: H_{ed} , entropic phylogenetic diversity; Richness_{real}, realized richness; H_{aed} , abundance-weighted H_{ed} ; Richness_{int}, initial richness; PD, phylogenetic diversity; MPD_{ab} , abundance-weighted mean pairwise distance; $MNTD_{pa}$, presence-absence mean nearest taxon distance; $MNTD_{ab}$, abundance-weighted mean nearest taxon distance; and MPD_{pa} , presence-absence mean pairwise distance.

† Akaike weights (AW) calculated from a larger set of candidate models (see Appendix A).

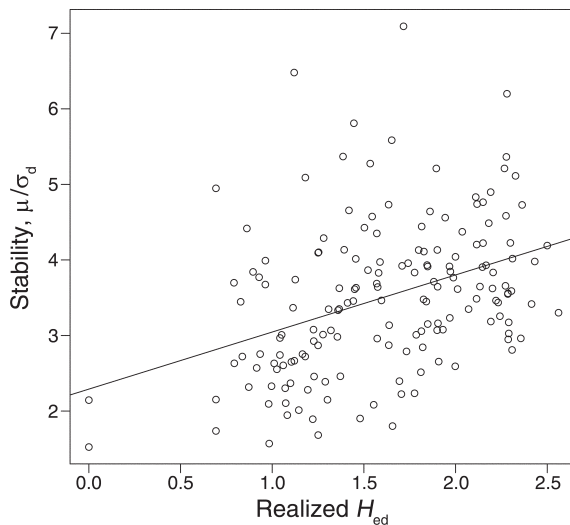


FIG. 4. Ecosystem stability (μ/σ_d , where μ is mean plot biomass and σ_d is temporally detrended standard deviation) from 2001 to 2010 increased with increasing average plot realized H_{ed} . H_{ed} can be thought of as a measure of the distribution of evolutionary information in a community, with high H_{ed} values corresponding to communities where species are all equivalently related, and low values reflect imbalanced community phylogenies.

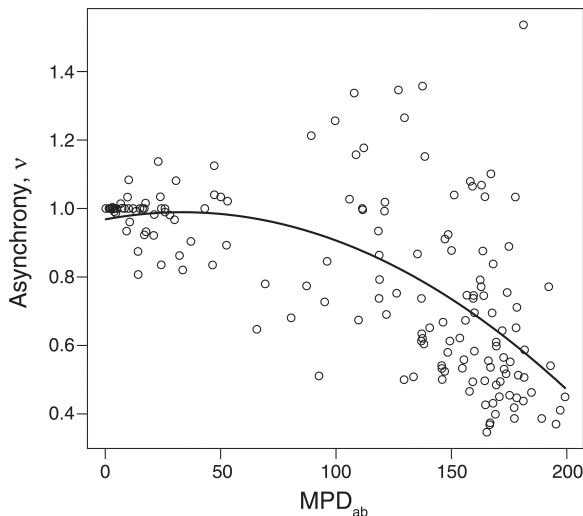


FIG. 5. The degree of species' asynchrony in a plot (v) generally declines with increasing abundance-weighted MPD.

Importantly, the covariance between species within plots was not correlated with the phylogenetic distance separating them, based on a Mantel test ($r = -0.01$, $P = 0.54$). The single-species variances within plots were not related to the phylogenetic distance to the closest relative ($r = -0.01$, $P = 0.63$), although most values were close to zero. However, extremely high variances were found only in species planted with close relatives (Fig. 6), consistent with hypothesis 3.

DISCUSSION

Ecosystems are dynamic, and understanding which aspects of diversity best explain different measures of ecosystem function is critical if scientists are going to inform policy and management initiatives. Earlier analyses of the results of this experiment showed that the number of species and their functional traits explained productivity and stability (Tilman et al. 2001, 2006). Here we show that the evolutionary relationships among co-occurring species explain more of the variation in ecosystem function and stability than species richness. Previous research has shown that the importance of complementarity increases with time (Cardinale et al. 2007), so the strength of the biodiversity–ecosystem function relationship gets stronger through time. Thus, experimental manipulations must be observed over multiple years to accurately observe patterns. If phylogenetic measures represent the potential for species to use resources in complementary ways, then these measures should also better explain variation in biomass production through time. We found that abundance-weighted mean pairwise phylogenetic distance, MPD_{ab} , became better at explaining variation in plot productivity through time.

Further, our results reveal that assemblages that contain more phylogenetic diversity (measured as H_{ed})

tend to be more stable than less diverse plots. Previous studies have reported that stability may be a product of the dynamics of the dominant species (Polley et al. 2007, Grman et al. 2010, Sanderson 2010), which is undoubtedly true, but our analyses reveal that plots with more evolutionarily distinct species are more stable, regardless of the abundance distribution (e.g., H_{ed} is a better explanation of stability than the abundance-weighted H_{aed}). Interestingly, patterns of average biomass production and asynchrony, which is a pairwise attribute, were better explained by measures that incorporate relative abundances.

There are three hypotheses that explain potentially increasing stability in phylogenetically more diverse plots: first is that there is phylogenetic nonindependence in species stability (hypothesis 1: phylogenetic sampling effect); secondly, greater phylogenetic distances in an assemblage reflect complementary fluctuations because of niche differences (hypothesis 2: insurance effect); and thirdly, through weaker interactions among distant relatives (hypothesis 3). We failed to find evidence for an evolutionary sampling effect. Conversely, we found a negative relationship between the level of plot asynchrony and phylogenetic distance, as well as a negative relationship between a species variance and the phylogenetic distance to the closest relative in the plot, whereas covariance did not show any systematic relationship to pairwise distance. The expectation of the insurance hypothesis was that greater plot stability was produced by greater asynchrony, as a species replaces another's functional importance when it declines (Isbell et al. 2009, Hector et al. 2010). However, our results indicate that more phylogenetically diverse plots actually show greater synchrony, but due to reduced variance (i.e., the numerator in Eq. 2). While

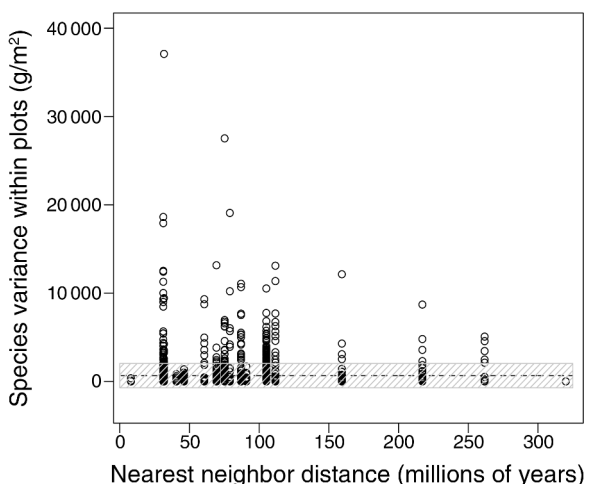


FIG. 6. Individual species variance within plots and the phylogenetic distance to its closest relative. The dashed line and hatched area represent the mean variance and standard deviation, which is not significantly different than zero.

covariance was unrelated to phylogenetic distances, there was extremely high variance observed in some assemblages with closely related species, but not in assemblages with distant relatives, supporting hypothesis 3. This final result requires additional experimental verification since extreme variances were observed only in the nearest neighbor distances with many observations (e.g., many grass to forb comparisons), with very few high nearest neighbor distances.

However, an alternative to competition per se and not explicitly tested in these analyses, is that distantly related species are more likely to participate in facilitative interactions (Verdu et al. 2009). Assemblages with facilitative interactions should be more stable since facilitation is known to be especially important at buffering populations against stressful environmental conditions that would normally reduce fitness (Maestre et al. 2009). Further, biomass production should be higher in assemblages with facilitative interactions since species benefiting from facilitation should attain higher abundances than when alone.

Our power to detect phylogenetic influences on species temporal variance was limited by three aspects of our analysis. First, this experiment was not explicitly designed to test hypotheses about the influence of community phylogenetic structure on ecosystem processes. The assemblages used in this study contain few extremely closely related taxa (i.e., congeneric pairs), meaning that mean pairwise distances were skewed towards having longer phylogenetic distances. Further, in a phylogenetically informed experimental design, one should also have phylogenetic distances replicated in different clades; for example, multiple pairs of close relatives. Fig. 6 further highlights this concern, where the nearest neighbor distances in diverse assemblages simply cluster into family-level distances. The second analytical limitation was that we examined the influence of pairwise distances on species variability; the reality is that, in speciose communities, multiple species interact. Perhaps neither nearest neighbor distances nor mean pairwise distances adequately capture the complex interactions among multiple co-occurring species. A final limitation is through the use of our measure of stability, which changes with the mean and standard deviation (SD) of biomass produced. Randomly distributed SD and an increasing mean would still result in higher stability, but the exact mechanism would be unclear. Analyses of stability must also be accompanied by analyses of species variances and covariances.

CONCLUSIONS

Phylogenetic diversity has an important influence on ecosystem function. The effect of phylogenetic diversity on aboveground productivity increased through time and was also associated with greater ecosystem stability. This effect was not due to a phylogenetic sampling effect, where certain groups of close relatives are inherently more variable than others. Rather, it appears

that species in more phylogenetically diverse plots show more stability, presumably because they utilize unshared resources or are benefiting from facilitative interactions.

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SUPPLEMENTAL MATERIAL

Appendix A

AIC values for variable selection (*Ecological Archives* E093-187-A1).

Appendix B

Correlations among diversity metrics (*Ecological Archives* E093-187-A2).

Appendix C

Individual species variances (*Ecological Archives* E093-187-A3).