Effects of competition on phylogenetic signal and phenotypic plasticity in plant functional traits

Jean H. Burns[1] and Sharon Y. Strauss

Center for Population Biology, University of California, Davis, California 95616 USA

Abstract. Recent studies of communities have examined phylogenetic signal in species' functional traits to infer drivers of community assembly. Phenotypic variation in traits, arising from "constitutive" genetically based variation and from environmental influences on gene expression, or phenotypic plasticity, could affect inferences about community assembly. We found significant trait plasticity in 12 focal species across four species–interaction treatments grown in four soil environments. Phylogenetic signal in traits was present, but was also dependent on species–interactor treatment, suggesting that phenotypic plasticity and plant neighborhood could affect the ability to detect and interpret community phylogenetic patterns of trait variation. Individuals competing with conspecifics expressed significant divergence in specific leaf area (SLA) relative to when they were grown alone. Combined with the observation that competition is stronger between close relatives than between distant relatives in some soils, these results suggest that trait plasticity may be an adaptive response to competition. To test this hypothesis, we examined total biomass in a pot, relative to the predicted biomass of two individuals grown alone, and related pot biomass to phylogenetic distance of the interactor treatment, as well as to divergence in SLA and root:shoot ratio. Within competition treatments, only plastic divergence in root:shoot ratio in one interactor treatment was correlated with increased productivity, and only in one soil type. We also tested whether, across all treatments, divergence in SLA or root:shoot ratio increased pot productivity. We found that "community" productivity was positively influenced both by phylogenetic distance to competitor, as well as by divergence in root:shoot ratio due to both plasticity and constitutive differences. Phenotypic plasticity resulting in trait divergence may increase the ability of plants to coexist and may also decrease phylogenetic signal in community assembly at small spatial scales.

Key words: character displacement; community assembly; community phylogenetics; convergence; phylogenetic signal; phylogeny; plasticity; root:shoot ratio; specific leaf area, SLA; trait divergence.

Introduction

Understanding the roles of environment, interacting species, species traits, and evolutionary history on community assembly patterns has great promise to elucidate general mechanisms influencing coexistence (e.g., Webb et al. 2002, Ackerly 2003, Cavender-Bares et al. 2004, Albert et al. 2010, Clark 2010, Clark et al. 2010, Jung et al. 2010, Kraft and Ackerly 2010). Functional traits are playing an increasingly important role in helping us to understand the mechanisms driving environment–assembly relationships (e.g., Chapin et al. 1993, Cornelissen et al. 2003, Ackerly 2004, Cavender-Bares et al. 2004, Cornwell and Ackerly 2009, Swenson 2009, Hulshof and Swenson 2010). While traits are being used to characterize species and their ecological roles, we also understand that intraspecific variation in traits can contribute greatly to community function and assembly (e.g., Hughes and Stachowicz 2004, Cavender-Bares 2007, Fridley et al. 2007, Lankau 2008, Lankau and Strauss 2008, Fridley and Grime 2010, Jung et al. 2010, Webb et al. 2010), and that this variation has both genetic and environmentally based components. For example, a recent study examining intraspecific variation in specific leaf area (SLA) found that incorporating intraspecific variation increased power to detect a signal of habitat filtering across a flooding gradient (Jung et al. 2010). Intraspecific trait variation is a result of both "constitutive" genetic differences within species and phenotypic plasticity, which may also have a genetic basis. We focus here primarily on phenotypic plasticity in plant functional traits and its influence on coexistence, community productivity, and patterns of phylogenetic signal in traits.

Environmentally influenced plasticity in traits could lessen differences between species, and diminish phylogenetic signal in assembly if, for example, plasticity within a species across environments encompasses much of the trait variation across species in these same

[1] Present address: Department of Biology, Case Western Reserve University, Cleveland, Ohio 44106 USA. E-mail: jbm122@case.edu

environments (Messier et al. 2010). In such cases, a single species could fill the niches of other species (e.g., De Meester et al. 2002). Taken to an extreme, if such dynamics are common, species may be largely ecologically redundant (Hubbell 2001, Siepielski et al. 2010), resulting in processes affecting community assembly potentially determined by plasticity and dispersal, rather than by phylogenetically constrained niches. Moreover, if traits respond plastically to the trait values of competitors, response to competition, too, could obscure phylogenetic signal in traits, especially if competition, rather than abiotic factors, dominates adaptive trait expression and plant performance. Thus, great intraspecific variation in traits could decrease the signal of phylogeny on community assembly. In contrast, even in the presence of environmental variation and competition, constrained trait variation could suggest that species play unique roles in communities, potentially resulting in phylogenetic patterns in community assembly. Thus, understanding to what degree intraspecific trait variation, including that due to phenotypic plasticity, influences the detection of phylogenetic signal in ecologically important traits could provide a greater understanding of processes governing community assembly.

Trait plasticity could respond to biotic factors, as it does to abiotic factors, in ways that mediate coexistence (Pfennig and Murphy 2002, Pfennig and Martin 2009). This has been termed "facultative character displacement" by Pfennig and Murphy (2002, see also Darwin 1859, Brown and Wilson 1956, Grant 1972, Robinson and Wilson 1994), and this plasticity may have both an environmental (competitor) and genetic basis (Scheiner and Lyman 1989). Facultative character displacement, a result of plasticity, is distinguished from "constitutive character displacement" (Pfennig and Murphy 2002), the more traditional view of character displacement in which genetically based changes in traits owing to competitive interactions are expressed consistently through time and across environments.

Facultative character displacement could result in individuals with greater trait divergence when they co-occur than when they grow alone (Vellend 2006). Alternatively, coexisting individuals across species could converge on an optimal trait value (e.g., Grant 1972, Abrams 1986, Vellend 2006, Fox and Vasseur 2008), if the environment strongly favors specific trait values. Whether species diverge or converge in trait values may be determined by the resource base (Grant 1972, Fox and Vasseur 2008). If there are substitutable resources that can be partitioned (e.g., seeds of different sizes for Galápagos finches), selection may favor divergence (MacArthur and Levins 1967). On the other hand, if there is a single resource needed by all, convergence to best utilize that resource may be the outcome (Abrams 1986, Fox and Vasseur 2008). Evidence exists for both character displacement (divergence in trait values; e.g., Dayan and Simberloff 2005, Davies et al. 2007), as well

as convergence on similar trait values across different taxa in sympatry (Hespenheide 1973, Knouft 2003, Scheffer and van Nes 2006, Matocq and Murphy 2007, Kozak et al. 2009, Mayfield and Levine 2010). For example, Davies et al. (2007) found that sister species in the mammals with greater range overlap also have greater divergence in dentition, consistent with character displacement. Alternatively, character convergence in response to competition has often been a stable outcome of models (e.g., Fox and Vasseur 2008, Abrams 1986); convergence has been reported less frequently than divergence in empirical studies of competition (Hespenheide 1973, Knouft 2003, Scheffer and van Nes 2006, Matocq and Murphy 2007, Kozak et al. 2009, Mayfield and Levine 2010). Adaptive phenotypic plasticity that reduces the strength of competition among interacting individuals (Pfennig and Murphy 2003, Pfennig et al. 2006) could result in trait convergence or divergence among species and could amplify or obscure phylogenetic signal in traits within communities, as traits may change in response to traits of neighboring species or individuals.

In previous experimental work, we found that species competed more intensely with conspecific and congeneric relatives than with confamilial relatives in some soils (Burns and Strauss 2011). In this paper, we analyze patterns of variation in SLA and root : shoot ratio for this same species interaction experiment, and explore the degree to which different soil origins and interactor treatments influenced trait expression and whether trait plasticity in different competitor/soil regimes affected our ability to detect phylogenetic signal in traits. Specifically, we tested whether (1) trait plasticity can alter the signal of phylogeny on traits, resulting in differences in the strength of phylogenetic signal across different environments; (2) species traits are more or less divergent in competition than when grown alone (i.e., whether trait changes are a response to a competitor); and (3) whether plastic trait changes in response to competition are correlated with greater pot biomass for both coexisting individuals, and might thus reflect an adaptive response to competition.

METHODS

Lath house experiment

We conducted an outdoor lath house experiment manipulating soil origin and interacting species for 12 focal species growing at the University of California–Davis Bodega Marine Reserve (BMR), Bodega Bay, California, USA, in five plant families (Rosaceae, Fabaceae, Asteraceae, Polygonaceae, and Juncaceae). These species were grouped into six triplets based on taxonomic ranks, and phylogenetic relationships among focal species were estimated using a maximum-likelihood phylogeny (more methods and species selection details in Burns and Strauss 2011). Each triplet contained two congeners, which were the two focal species, and a third confamilial species (Appendix A:

Table A1; all species present at the BMR). Each focal species was grown in a series of species interaction treatments in which the interactor varied in phylogenetic distance from the focal species. Treatments were: alone, with a conspecific, with a congener, and with a confamilial. Congeners and confamilials were selected at random from the BMR species list (see Burns and Strauss 2011).

Both biotic and abiotic constituents of soils can affect plant performance (Wilson and Tilman 1993, Packer and Clay 2000, Klironomos 2002, Bever 2003, Ehrenfeld et al. 2005, Brandt et al. 2009, Dent and Burslem 2009, te Beest et al. 2009, Weerasinghe et al. 2010). We used whole-field soils collected at BMR from the rhizospheres of the 12 focal species (six pairs of congeners) and their confamilial relatives. Soils under ~10 plants were collected within 10 cm of the soil surface of a target species to obtain biotic components of the soil associated with each species. The species interaction experiment for each focal species (grown alone, with conspecific, congener, or confamilial) was replicated across four soil types: conspecific, congener, confamilial, and potting soils, with 8–10 replicates per treatment (see Burns and Strauss 2011, for additional experimental details). Potting soil was the only soil environment that was identical across all plant species; for example, the "congener" soil treatment was collected from a different species' rhizosphere for each of the focal species. We then measured biomass and functional traits SLA and root : shoot ratio for plants in all soil × interactor combinations. The results for biomass were presented in a previous paper; in short, we found that biomass was lowest in potting-soil treatments and also when plants were competing with conspecifics across all soil types (Burns and Strauss 2011: Fig. S4).

Seeds from mass collections in the field were thoroughly mixed and randomly planted directly into the soil in an outdoor lath house under field growing temperatures and allowed to germinate and grow for three months. Because seeds came from many maternal families randomized across the design, any consistent response by plants to competition or soil treatments we interpret as species-wide phenotypic plasticity in response to treatments. Specific leaf area (SLA) was measured on each individual plant, if the plant was sufficiently large at the time of sampling (at least three leaves); although each soil × competition treatment originally had 6–10 replicates, mortality in some soils and competition treatments meant that replication for each trait measurement ranged from 0 to 10 per treatment per species. SLA was measured from the youngest fully expanded leaf, and was calculated as the area of the leaf divided by its dry mass (Cornelissen et al. 2003). SLA data were, in some cases, less complete than root : shoot ratio data, if plants were too small at the time of sampling to sacrifice a leaf. After three months, plants were harvested, dried, and weighed. The ratio of root dry biomass to shoot dry biomass (root : shoot

ratio) was also calculated, as we expect that such allocation might also be related to competition and coexistence (Cornelissen et al. 2003).

Phylogeny estimation

The phylogeny for species in this experiment, plus additional species to enhance the accuracy of the phylogeny estimation, was estimated based on genes downloaded from GenBank (Burns and Strauss 2011). Four gene regions, rbcL, matK, ITS, and trnL, were aligned and concatenated using MUSCLE version 3.8 (Edgar 2004a, b) and MacClade version 4.08 (Maddison and Maddison 2005), respectively. The resulting supermatrix was analyzed using maximum likelihood (ML) in Garli, version 0.951 (Zwickl 2006), with multiple runs to ensure that the result was not a local optimum. We present results using the single most likely phylogeny with bootstrap proportions from a 100 replicate ML bootstrap analysis (Burns and Strauss 2011: Fig. S1; this phylogeny was also consistent with one generated by Phylomatic, but was more resolved). We used the ML phylogeny to test for phylogenetic signal in species traits, using standard methods (see next section).

Causes of trait variation: phylogenetic signal and effects of interactors

We determined whether the interacting species affected our ability to detect phylogenetic signal among our 12 focal species. We used a randomization test to determine whether there was significant phylogenetic signal for two traits: SLA and root : shoot ratio. These analyses were conducted only for the potting-soil treatment in our experiment because this soil was the only one represented across all triplets (that is, field soil treatments varied with focal species, but potting soil was the same across all species). Complete mortality by some species in certain soil/competition environments meant that we pruned the species tree to explore phylogenetic signal for the same set of taxa across different competition treatments (Fig. 1).

Blomberg's K was used as a metric of phylogenetic signal, where K is calculated as the ratio of the observed phylogenetically correct mean-square error divided by the mean-square error of the data, standardized by the expectation under Brownian motion (Blomberg et al. 2003). We tested for significant phylogenetic signal, relative to a random distribution of the traits observed, given the topology and branch lengths of the ML phylogeny, with 1000 replicates. Analyses were conducted in R (version 2.11.1; SAS Institute 2008).

To examine the degree to which soil type, the presence or relatedness of an interactor, or interactions between these factors contributed to differences in SLA and root : shoot ratio, we first determined whether there was any relationship between plant performance (biomass attained in a treatment) and trait expression. We found that across all treatments and species, there was a significant effect of total plant biomass on SLA. We then
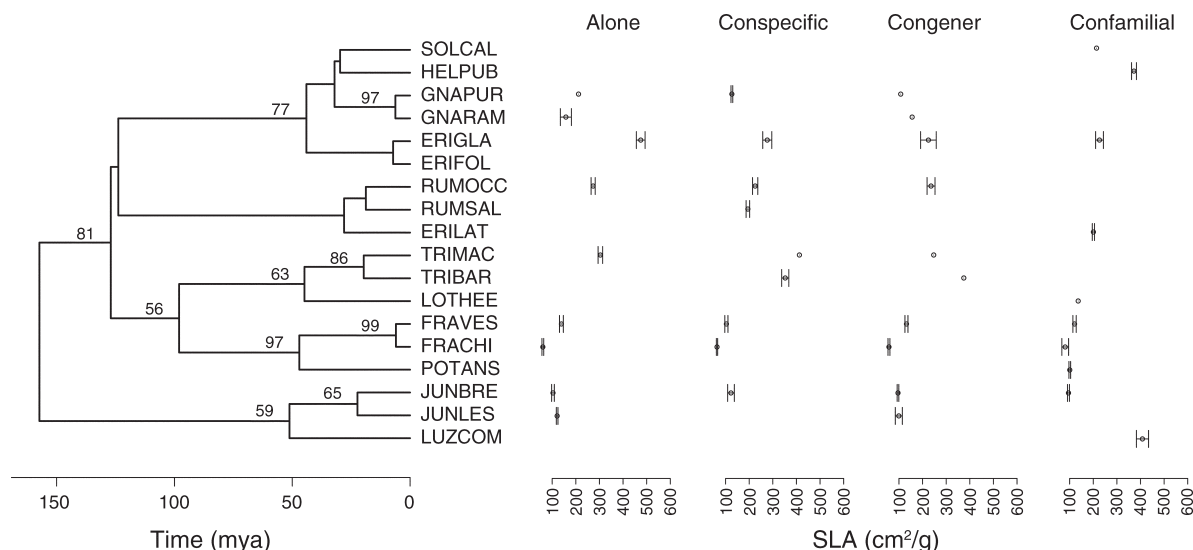
Fig. 1. We tested for phylogenetic signal on traits (e.g., specific leaf area, SLA) across different competition treatments using a randomization test on Blomberg's K, where $K = 0$ corresponds to a random distribution of traits on the phylogeny and $K = 1$ corresponds to Brownian motion evolution of the trait, such that close relatives are more similar than expected by chance. Trait values differed across competitive environments in a way that influenced the phylogenetic signal on those traits (see Table 1). Maximum-likelihood phylogeny with maximum-likelihood (ML) bootstrap values are shown above the branches. Shown are mean trait values ± SE; mya stands for million years ago. Species abbreviations are: SOLCAL, *Solidago californica*; HELPUB, *Helenium puberulum*; GNAPUR, *Gnaphalium purpureum*; GNARAM, *Gnaphalium ramosissimum*; ERIGLA, *Erigeron glaucus*; ERIFOL, *Erigeron foliosus*; RUMOCC, *Rumex occidentalis*; RUMSAL, *Rumex salicifolius*; ERILAT, *Eriogonum latifolium*; TRIMAC, *Trifolium macraei*; TRIBAR, *Trifolium barbigerum*; LOTHEE, *Lotus heermannii*; FRAVES, *Fragaria vesca*; FRACHI, *Fragaria chiloensis*; POTANS, *Potentilla anserina*; JUNBRE, *Juncus breweri*; JUNLES, *Juncus lesueurii*; and LUZCOM, *Luzula comosa*.

used a phylogenetic generalized least-squares (PGLS; Martins and Hansen 1997) model to explore variation in expression of SLA and root : shoot ratio as a function of: focal species competition treatment (conspecific, congener, confamilial), soil type (conspecific, congener, confamilial, potting), all appropriate interactions, and with total biomass as a covariate in the model. PGLS models include phylogeny as a variance–covariance matrix in the error structure of the model (Martins and Hansen 1997). Individuals within species were treated as polytomies, with branch lengths within species assigned an arbitrarily small value of 0.0001 (sensu Ruber and Adams 2001; and D. C. Adams, *personal communication*). We determined the optimal model of evolution, amongst Brownian, Grafen, and Ornstein-Uhlenbeck (OU) models, using AIC_c, and created the variance–covariance matrix using the optimal model (Burnham and Anderson 2002, Paradis et al. 2004). We then compared a model with and without phylogeny, again using AIC_c to choose the most probable model, to avoid over-parameterizing the model if including the phylogeny was unnecessary (Burnham and Anderson 2002). We then selected the optimal model amongst possible combinations of predictor variables (see Appendix A) as the model minimizing AIC_c (Burnham and Anderson 2002), under the constraint that models with all interactions were often inestimable owing to mortality in some soil–interactor combinations. We included total biomass as a covariate in these models to learn

whether aspects of soil and competition treatments, above and beyond their effects on overall plant performance (biomass), affected trait expression, and we repeated the analyses without the total biomass covariate. A significant effect of treatment (i.e., soil source and/or interacting species) on our response variables (SLA and root : shoot ratio) indicates a role of environment in trait expression; in other words, phenotypic plasticity. SLA was square-root-transformed, and root : shoot ratio was natural-log-transformed to meet distributional assumptions. Analyses were conducted in R (version 2.11.0; Paradis et al. 2004).

Evidence for trait divergence in response to interactors

Trait divergence, or convergence, between interactors could mediate coexistence. In our previous study, we found that competitive intensity, measured as relative interaction intensity, RII, calculated as (biomass in competition − biomass alone)/(biomass in competition + biomass alone) (see Armas et al. 2004), depended on both soil origin and identity of interactor (Burns and Strauss 2011). Here, we assessed whether traits responded plastically to this competition and whether such variation was potentially adaptive. We estimated trait divergence when each species was grown alone in a particular soil type, and then asked how much traits changed when the same species were grown in competition in the same soil.

Several factors might result in changes in trait divergence across the experiment. If trait values are phylogenetically conserved, then as phylogenetic distance to an interactor increases, so will trait divergence, a result indicating conserved genetically based differences across species. Second, if competition is strong and the focal species is strongly suppressed by the interactor, then this reduced biomass might cause divergence in SLA simply as an epiphenomenon of competition, because SLA was significantly correlated with biomass. Divergence in this case could be an outcome of competition, but may not be an adaptive plastic response that reduces competition. Third, adaptive phenotypic plasticity might increase divergence (or convergence) of traits in response to competition between individuals increasing resource partitioning and fitness. The challenge is to discriminate between adaptive trait changes and changes that might happen as a by-product of competition but that are not adaptive.

First we asked whether there was trait divergence or convergence within pots between interacting individuals, and then we assessed whether there was evidence that this variation was adaptive. To measure trait divergence, we compared the absolute value of differences in SLA and root : shoot ratio for conspecifics or congeners when growing alone vs. when they were in competition in the same soils. To estimate expected trait divergence based on trait variation when plants were grown alone, trait values of individuals grown alone were paired at random within species and soil treatments, and the absolute values of the difference of their traits was calculated for each randomized pair, for k pairs, analogous to a bootstrap with replacement.

We predicted that, if individuals respond to competition by diverging in their trait expression, then the difference in trait expression will be larger with competition than for the same species grown alone in the same soil environment. To compare trait divergence alone vs. in competition, we compared divergence across competition and soil treatments using the same model selection criteria described in the previous section. Because confamilials were never grown alone, we could only test for plastic trait divergence in conspecific and congener competition treatments.

Next, we asked whether trait divergence as a result of plasticity could be adaptive; we tested whether greater trait divergence was positively correlated with total biomass attained summed across both interactors within the same pot. We calculated the relativized total biomass per pot as the sum of the biomass for each species, standardized by the mean biomass alone for that species, in each soil treatment. Relativized biomass per pot was calculated as follows:

$$\text{Relativized total biomass per pot} = \left(\frac{B_{1w}}{B_{1a}}\right) + \left(\frac{B_{2w}}{B_{2a}}\right).$$

where B_{1w} is the biomass of species (or individual) 1 with an interactor, and B_{1a} is the biomass of species 1 alone in the same soil. For conspecific competition, the denominators are the same. Thus, the relativized total biomass per pot is a measure of the productivity in that pot, relative to what we expect for those species based on biomass achieved when they grew alone in that same soil. We predicted that if trait divergence enhances productivity, there should be a positive relationship between trait divergence and the relativized total biomass per pot; such a positive relationship would be consistent with adaptive trait divergence. Optimal models were selected using AIC_c (Burnham and Anderson 2002) using PGLS (Martins and Hansen 1997) following the same procedure outlined in the previous section (R Statistics, version 2.11.1; Paradis et al. 2004, R Development Core Team 2008). Because phylogenetic distance between interactors is also a possible source of "constitutive" trait divergence, we conducted analyses for each competitor treatment separately to estimate just the effects of plasticity on pot productivity.

Finally, to incorporate both "constitutive" trait divergence related to phylogenetic distance of the interactor in addition to "facultative" trait divergence owing to plastic responses to competitors, we included all treatments in a single analysis exploring the relationship between trait divergence and relativized pot productivity. This analysis examined the combined explanatory power of phylogenetic distance to the interactor and trait divergence on pot productivity. Model selection was again done using AIC_c (Burnham and Anderson 2002) with standard least-squares restricted maximum likelihood (REML) to determine the amount of variation in "community" productivity explained by interactor treatment and trait divergence; variables were natural-log-transformed (JMP, version 8.0.1; SAS Institute 2009). PGLS was not used for this analysis because the response is a function of multiple species (the two in the pot), and the amount of variance explained (coefficient of determination) was of interest. Trait divergences were natural-log-transformed for all analyses.

RESULTS

Is there phylogenetic signal in functional traits and is it affected by the competitor treatment?

The traits measured here exhibited phylogenetic signal (Fig. 1; Appendix B: Fig. B1), and the degree of phylogenetic signal in species' traits (in potting soil) was dependent on the species–interactor treatment (Table 1, Fig. 1). Close relatives were more similar to one another in root : shoot ratio (phylogenetically clustered) than expected by chance, but this phylogenetic signal was detected only when plants were competing with conspecifics or with congeners (Table 1), which are the most stressful competition treatments based on biomass attained by plants (Burns and Strauss 2011: Fig. S4). When plants competed with confamilials, the least stressful competition treatment based on biomass,

TABLE 1. Tests for phylogenetic signal on specific leaf area (SLA) and root:shoot ratio in the potting-soil treatment.

| | Grown alone | | | Grown with competition | | | | | | | | |
| | | | | With conspecific | | | With congener | | | With confamilial | | |
Trait and comparison	N	K	P	N	K	P	N	K	P	N	K	P
SLA												
Alone vs. conspecific	7	0.08	0.79	7	0.02	0.99						
Alone vs. congener	9	0.09	0.82				9	0.02	0.98			
Root:shoot ratio												
Alone vs. conspecific	9	0.73	0.11	9	1.02	**0.05**						
Alone vs. congener	10	0.55	0.13				10	1.12	**0.04**			
Alone vs. confamilial	7	0.18	0.43							7	0.76	0.07

Notes: Each competition treatment was compared to the alone treatment with identical taxon sampling, to control for differences in taxon sampling across competitor treatments (comparisons with identical taxon sampling across each row; Fig. 1; thus, we have multiple tests of phylogenetic signal when grown alone). Power was insufficient to test for phylogenetic signal on SLA in the confamilial treatment compared with the alone treatment ($N = 4$ when we include only identical taxa in both treatments; Fig. 1). We present Blomberg's K, where $K = 1$ indicates perfect Brownian motion evolution and values less than 1 indicate conservatism less than Brownian (Blomberg et al. 2003), given the topology and branch lengths of the maximum-likelihood (ML) phylogeny, with 1000 replicates.

we could detect no phylogenetic signal (Table 1), and there was also no detection of phylogenetic signal when plants were grown alone and attained greatest biomass (Fig. 1; Burns and Strauss 2011: Fig. S4). This result suggests that phylogenetic constraints are expressed more strongly in stressful than benign competition environments.

Is there significant plasticity across soil and species interactor treatments?

Because seeds were randomly assigned to experimental treatments, significant effects of treatments on trait expression were interpreted as plastic responses of a species to soil and competitor environments. SLA was significantly negatively related to total plant biomass across treatments (Table 2, Fig. 2). Total plant biomass explained >60% of the variation in SLA, but there was no strong interaction between soil type or competitor in the slope of this relationship ($0.10 < P < 0.12$). Given that the expression of SLA and root:shoot ratio were influenced by overall plant performance, we included total biomass in our model selection process to determine whether other factors, above and beyond differences in biomass, could explain patterns of plasticity in SLA and root:shoot ratio (Appendix A).

We found that soil, the interactor treatment, and their interaction influenced the expression of SLA (Table 2; Appendix B: Figs. B2 and B3), above and beyond the effects of plant performance. Models without total biomass as a covariate yielded the same patterns of significance in effects (Appendix A: Table A2). The patterns of trait plasticity were idiosyncratic across species, with some species exhibiting higher SLA in conspecific and others in heterospecific soils (Appendix A: Table A2 and Appendix B: Fig. B2). Root:shoot ratio was also plastic with respect to soil type, but, surprisingly, not with respect to interactor treatment (Table 2); as for SLA, interspecific variation also explained significant amounts of variance in root:shoot ratio (Appendix B: Fig. B3). One of the reasons for idiosyncratic responses across species to competitor treatments might lie in the relative value of traits of the two interactors. For example, if the SLA of one congener is larger than the other's, one species might

TABLE 2. SLA and root:shoot ratio in 12 focal species, as a function of soil treatments, and interactor treatments in the lath house experiment in a phylogenetic generalized least-squares analysis (PGLS).

Source	Numerator df	Denominator df	F	P
SLA				
Total biomass	1	915	190.04	<0.0001
Species	11	915	3.98	<0.0001
Soil type	3	915	80.12	<0.0001
Interactor	3	915	110.51	<0.0001
Soil type × interactor	9	915	2.52	0.008
Root:shoot ratio				
Total biomass	1	1024	3.32	0.07
Species	11	1024	67.36	<0.0001
Soil type	3	1024	71.24	<0.0001

Notes: SLA was square-root-transformed, and root:shoot and total biomass were natural-log-transformed to meet assumptions of analysis. See Appendix A: Table A2 for model selection.
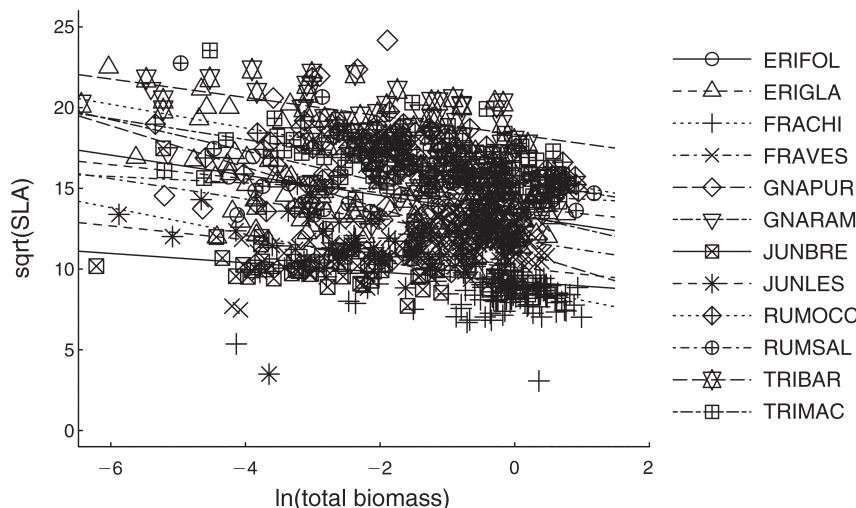
FIG. 2. Measured across the whole experiment, specific leaf area scaled negatively with total biomass (originally measured in grams) across the 12 focal species (see Table 2). See Fig. 1 for key to species abbreviations.

respond to congener competition by shifting to a larger SLA, while the other shifts to a smaller SLA, yielding character divergence, but no consistent effects of competing with a congener on mean SLA. Changes in SLA in potmates may also come about from above-ground competition that could shade, or increase moisture in the microclimate of, the smaller competitor. Such effects could explain the negative relationship between plant size and SLA (Fig. 2).

What are the patterns of trait divergence?

We asked whether individuals responded to the species–interactor treatments by diverging in trait expression, where we measured trait divergence within a pot relative to traits expressed by each species growing alone in the same soil treatment. We did not have sufficient power to test for interactions in models of SLA divergence (Appendix A: Table A3). We found that divergence in SLA was a function of relatedness to the interacting species, as well as of total biomass (Table 3). Effects of interactor treatment on divergence in SLA were significant both in the presence and absence of total plant biomass as a covariate in the model, suggesting that some mechanism in addition to simply plant size was driving trait divergence (Table 3; Appendix A: Table A3).

After controlling for phylogeny using PGLS, divergence in SLA was greater between conspecific potmates than when conspecifics were grown alone (Table 3, Fig. 3), consistent with phenotypic plasticity contributing to trait divergence between competitors; unlike with conspecifics, divergence in SLA between congeneric potmates did not differ significantly from when congeners were grown alone (Table 3, Fig. 3), despite the fact that congeners competed as strongly as conspecifics in terms of biomass attained in this experiment (Burns and Strauss 2011: Fig. S4).

Divergence in root:shoot ratio between interactors varied by species, soil treatment, and interactor (Table 3). In the interactor treatment averaged over all soils, divergence in root:shoot ratio was higher for conspecific potmates than when conspecifics were grown alone (Table 3, Fig. 3). As with SLA, there was no significant divergence in root:shoot ratio when congeners were potmates relative to when they were grown alone (Table 3).

To test whether plastic changes in traits in potmates could be adaptive, we asked whether trait divergence between individuals within pots was correlated with overall greater pot productivity. Plastic responses were signifi-

TABLE 3. Test for effects of treatments on trait divergence in competition across 12 focal species, tested on the absolute value of the difference in traits between individuals in a pot, using a PGLS model with divergences natural-log-transformed, and with natural-log-transformed total biomass as a covariate.

Trait and source	Numerator df	F	P
Divergence in SLA			
Total biomass	1	9.72	0.002
Interactor	2	10.08	0.0001
Contrast			
Alone vs. conspecific	1	24.65	<0.0001
Alone vs. congener	1	3.74	0.06
Divergence in root:shoot ratio			
Species	10	5.04	<0.0001
Soil type	3	16.22	<0.0001
Interactor	2	24.12	<0.0001
Contrast			
Alone vs. conspecific	1	14.26	<0.0001
Alone vs. congener	1	2.89	0.09

Notes: To illustrate the difference in predictions across soil type, soil type was included in the contrasts for both divergence in SLA (denominator df = 213) and root:shoot ratio (denominator df = 186). We show the most probable model, based on lowest AIC_c (Appendix A: Table A3).

cantly related to pot productivity only for root : shoot ratio in the confamilial treatment (Table 4).

When trait divergence was considered across all treatments, including the combined effects of plasticity and fixed differences between species, the suite of four best models always included species, phylogenetic distance between competitors, divergence in root : shoot ratio, and divergence in SLA, which was negatively related to pot productivity (Appendix A: Table A5). Thus, pots that were the most productive, based on expected productivity of the same species grown alone in the same soil, had competitors that were phylogenetically more distantly related, with divergent root : shoot ratios, but with relatively more convergent SLA (Table 5).

Overall, we found evidence that expression of functional traits was plastic in these species, changing with soil, competitive regime, or both. Moreover, there was also phylogenetic signal in trait expression, though the ability to detect this signal depended on the competitor treatment, suggesting a role for community composition in the expression of phylogenetic signal in trait expression in the field.

DISCUSSION

There is growing evidence that intraspecific trait variation can contribute to coexistence (e.g., Lankau and Strauss 2008, Ashton et al. 2010, Clark et al. 2010, Jung et al. 2010). The contributions of both phylogenetic signal and phenotypic plasticity to patterns of trait divergence have implications for coexistence theory and contribute to ideas about limiting similarity (e.g., MacArthur and Levins 1967) and niche segregation (e.g., Grime 1974, Anten and Hirose 1999, Davies 2001). Divergence between species as a result of trait plasticity could enhance species' ability to coexist (Pfennig et al. 2006), though there are relatively few nonbehavioral empirical examples (but see, e.g., Nobel 1997, Ashton et al. 2010, and references in Pfennig and Pfennig 2010), and especially few in plants.

We found variation in phylogenetic signal across treatments, suggesting that detection of community phylogenetic patterns of trait variation may depend on intraspecific trait variability, as well as the community context in which traits are measured. We tended to find greater phylogenetic signal in traits when environments were more stressful, that is, when the environment supported overall lower plant biomass. In this experiment, lowest biomass occurred when plants competed with conspecifics in potting soils. Conversely, there was an absence of phylogenetic signal in traits in the treatments where plants were largest (growing alone or with confamilials). Thus, more stressful environments could reveal greater constraints and result in greater expression of phylogenetic signal in traits (cf. Cavender-Bares et al. 2006, Swenson and Enquist 2009).

This large amount of phenotypic plasticity in plant functional traits is consistent with other studies (Cav-
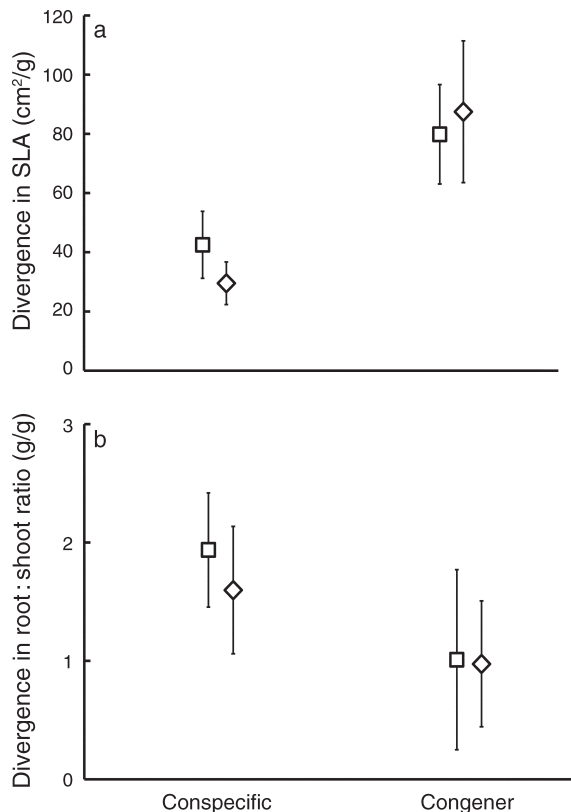

FIG. 3. (a) Divergence in SLA was greater when plants were grown with conspecifics than when grown alone (see Table 3), and (b) divergence in root : shoot ratio was greater when grown with conspecifics than when grown alone (see Table 3). Raw means ± SE; analyses incorporated phylogeny in the error structure of the phylogenetic generalized least-squares (PGLS) model, so standard errors do not reflect model errors. Squares indicate divergences with competitors; diamonds are comparable alone estimates of divergence.

ender-Bares et al. 2006, Swenson and Enquist 2009); trait values were strongly influenced by soil type and the identity of the interacting species (Table 2). A large proportion of the variation in SLA, a commonly measured trait, was explained by plant biomass, which we know from earlier analyses is, in turn, explained by species identity, soil environment, and species interactor treatment (Burns and Strauss 2011). Thus, SLA expression responds strongly and plastically to both competitor and soil environments, again consistent with other studies. We did not control for genotype across treatments in this study, and some of the within-species variation could be genetic variation; however, seeds were placed randomly across the treatments, therefore systematic effects of the environment are the result of plasticity in trait expression. Plasticity in SLA and root : shoot ratio were related to interactor treatment, with greater divergence when individuals were grown with conspecifics than when they were grown alone.

To explore whether divergence in traits was adaptive in competition, we first asked whether, *within* each

TABLE 4. Test for potential adaptive value of trait divergence due to plasticity.

Potential predictor and source	Numerator df	Denominator df	F	P
Divergence in SLA†				
Conspecific competitor				
Species	10	124	36.60	<0.0001
Soil type	3	124	8.70	<0.0001
Congener competitor				
Species	5	51	0.58	0.71
Soil type	3	51	4.81	0.005
Confamilial competitor				
Species	1	14	3.52	0.08
Soil type	1	14	0.53	0.48
Divergence in root:shoot ratio				
Conspecific competitor				
Species	9	113	0.002	1.00
Soil type	3	113	10.50	<0.0001
Congener competitor				
Species	5	49	0.47	0.79
Soil type	3	49	6.35	0.001
Confamilial competitor				
Species	1	8	12.37	0.008
Divergence in root:shoot ratio	**1**	**8**	**7.51**	**0.03**
Soil type	1	8	0.56	0.48
Species × divergence	1	8	0.05	0.82
Soil × divergence	1	8	0.99	0.35
Species × soil	1	8	1.22	0.30
Species × soil × divergence	1	8	0.002	0.97

Notes: We asked whether the relativized total biomass per pot was a function of trait divergence, species, soil type, or their interactions. Analyses were conducted separately for each competition treatment to ensure that effects were due to plasticity, not to taxonomic signal on trait divergence (i.e., confamilials are likely to be more different in their trait divergence than congeners). Models with the lowest AIC_c are presented (Appendix A: Table A4). Trait divergence was positively related to total biomass per pot only for root:shoot ratio in the confamilial treatment (indicated by bold type).

† Divergence in SLA was not a significant predictor of total per pot biomass (Appendix A: Table A4).

interactor treatment, plasticity in trait divergence was associated with greater overall pot productivity. Pot productivity was measured as the fraction of biomass attained relative to the sum of the biomass that each species attained alone in the same soil. We found that divergence in root:shoot ratio between confamilial competitors within a pot increased overall pot productivity (Table 4, Fig. 4); there were no significant effects on pot productivity of divergence with other interactors,

but numbers of species in these comparisons were smaller. There was no evidence for benefits of divergence in SLA on pot productivity.

The second approach was to ask whether trait divergence in interactors increased pot productivity across all treatments. This measure includes both trait plasticity and constitutive differences between species, and thus includes greater trait variation. We found that divergent root:shoot ratios and convergent SLA be-

TABLE 5. Test for community productivity consequences of phylogenetic distance and trait divergence, with relativized total pot biomass as a measure of productivity. Relativized biomass removed mean effects of species' biomass from the analysis.

Source	Numerator df	Denominator df	F	P
Phylogenetic distance	1	7	6.74	0.04
Divergence in root:shoot ratio	1	259	11.92	<0.01
Divergence in SLA	1	246	6.94	<0.01
Soil type	3	11	0.10	0.96

Notes: The model with the lowest AIC_c is presented and includes random effects species, species × soil, and species × phylogenetic distance (random effects not shown); see Table A5 in Appendix A for alternative models with low AIC_c and Table A6 in Appendix A for the full a priori model. A significant phylogenetic distance effect indicates that the relatedness of competitors has an effect on overall pot productivity, where more distantly related interactors result in greater pot productivity. Model-adjusted $R^2 = 0.44$.

tween interactors were associated with greater total pot productivity, as was phylogenetic distance to the interactor (see also Burns and Strauss 2011).

Our results suggest that trait plasticity could enhance patterns of coexistence: Habitat filtering may favor initial establishment of close relatives (e.g., Burns and Strauss 2011), and trait plasticity may allow future coexistence through niche partitioning (see also Lusk et al. 2008). Alternatively, like rapid adaptation of founding populations (De Meester et al. 2002), significant amounts of phenotypic plasticity, as we found here, could result in a priority effect that fills the available niche space and prevents subsequent colonization, potentially decreasing the invasibility of the habitat. The high degree of trait plasticity observed here, and elsewhere (e.g., Messier et al. 2010), could decrease phylogenetic signal on the niche, potentially resulting in a weaker signal of phylogeny on community assembly in cases where plasticity plays an important role in assembly (Jung et al. 2010). Kraft and Ackerly (2010) showed that trait and phylogenetic patterns in a tropical tree community were similar across most, but not all spatial scales, with trait data exhibiting more evidence of niche partitioning than phylogenetic relatedness patterns at small spatial scales. Phenotypic plasticity and facultative character divergence in response to species interactions with neighbors could potentially explain the lack of concordance between phylogenetic signal and trait signal at these smaller spatial scales.

Finally, the relationship between trait divergence and total pot biomass has implications for ecosystem functioning (Table 5). Phylogenetic distance between competitors correlates with productivity, consistent with results of whole-community experiments (Cadotte et al. 2009). Constitutive trait divergence, reflected in relatedness to competitor, and facultative trait divergence via phenotypic plasticity both contributed to community productivity, potentially by decreasing the strength of competition. Thus, combining information about within-species variance (both intraspecific genetic variation and intraspecific trait plasticity) with interspecific variation and phylogenetic distances may increase our ability to explain ecosystem functioning.

We suggest that phenotypic plasticity could play an important role in species coexistence, community assembly, and patterns of phylogenetic signal. Moreover, plasticity in response to species–interactor treatments affected our ability to detect phylogenetic signal on traits, which has important implications for understanding community assembly studies, particularly those that use phylogenetic signal on species traits and community phylogenetic dispersion to infer mechanisms of community assembly. We demonstrated that phenotypic plasticity results in trait divergence patterns that could mediate species coexistence and affect community productivity. A caveat to our study is that small numbers of species, and in some cases, small numbers of surviving individuals in some of our soil/competitor
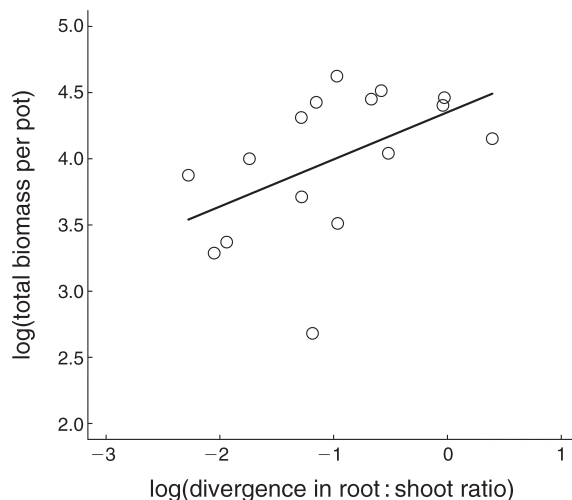

FIG. 4. In the confamilial competition treatment, the relativized total pot biomass was greater when divergence between potmates in root : shoot ratio was greater (see Table 4). Note the log scale; measurements were originally made in grams of roots per grams of shoots.

treatments, may limit our ability to understand how important these effects are in obscuring phylogenetic signal. In addition, the phylogenetic scale of any study could influence the relative importance of intraspecific trait variation. Because many comparative studies are conducted at the family level or below, intraspecific trait variation, including phenotypic plasticity, could play a large role in these studies. Studies combining phylogenetic analysis with information on intraspecific trait variability will create new opportunities to determine mechanisms involved in plant community assembly, species coexistence, and community productivity.

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SUPPLEMENTAL MATERIAL

Appendix A

Tables with additional methods and analysis including descriptions of focal species, model selection criteria, and a priori model for pot productivity (*Ecological Archives* E093-181-A1).

Appendix B

Supplementary figures including phylogenetic signal on traits and trait means across treatments (*Ecological Archives* E093-181-A2).