

Plant functional traits and the multidimensional nature of species coexistence

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Understanding the processes maintaining species diversity is a central problem in ecology, with implications for the conservation and management of ecosystems. Although biologists often assume that trait differences between competitors promote diversity, empirical evidence connecting functional traits to the niche differences that stabilize species coexistence is rare. Obtaining such evidence is critical because traits also underlie the average fitness differences driving competitive exclusion, and this complicates efforts to infer community dynamics from phenotypic patterns. We coupled field-parameterized mathematical models of competition between 102 pairs of annual plants with detailed sampling of leaf, seed, root, and whole-plant functional traits to relate phenotypic differences to stabilizing niche and average fitness differences. Single functional traits were often well correlated with average fitness differences between species, indicating that competitive dominance was associated with late phenology, deep rooting, and several other traits. In contrast, single functional traits were poorly correlated with the stabilizing niche differences that promote coexistence. Niche differences could only be described by combinations of traits, corresponding to differentiation between species in multiple ecological dimensions. In addition, several traits were associated with both fitness differences and stabilizing niche differences. These complex relationships between phenotypic differences and the dynamics of competing species argue against the simple use of single functional traits to infer community assembly processes but lay the groundwork for a theoretically justified trait-based community ecology.

coexistence | functional traits | community assembly | competition

Ecologists have long understood that phenotypic differences between species play an important role in maintaining species diversity within communities (1, 2). Differences in bill shape, body size, or rooting depth are often hypothesized to reduce interspecific relative to intraspecific competition and thereby contribute to the stabilizing niche differences that promote coexistence (3–5). Although the niche describes all aspects of species interactions with their environment (6), in ecological theory developed by Chesson (2) “stabilizing niche differences” between species are those differences that cause intraspecific interactions to be more limiting than interspecific interactions. This gives species a demographic advantage when at low relative abundance (2), which stabilizes coexistence. The expected relationship between trait differences and stabilizing niche differences is the basis for a large body of observational studies that use traits to predict patterns of species co-occurrence and compositional change (3, 7–13). Rigorously testing this relationship is critical because it forms the key pathway by which phenotypic traits influence community assembly, the outcome of biological invasions, species diversity effects on ecosystem function, and the impacts of climate change on community dynamics (5, 8, 12, 13).

Although the literature connecting phenotypic differences to competitive outcomes historically emphasizes stabilizing niche differences, not all phenotypic differences favor coexistence, and this complicates efforts to predict community assembly from trait

patterns. For example, species may differ in traits that influence their ability to draw down shared limiting resources or produce offspring, and the resulting “average fitness differences” [*sensu* Chesson (2)] favor competitive exclusion (14–16). Note that Chesson’s use of the term “fitness” differs from its meaning in evolutionary biology. Average fitness differences in this ecological context are those species differences that favor one competitor over the other regardless of their relative abundance (2) and, like stabilizing niche differences, may be precisely defined for a given mathematical model of species interactions (as we do below). In principle, many possible relationships between trait differences and coexistence are possible, with differing implications for competitive outcomes. For example, fitness and stabilizing niche differences could be correlated with distinct sets of traits (17). Moreover, it may be that niche and fitness differences are best described by multivariate suites of traits, supporting a hypothesis of high-dimensional coexistence between species in communities (18–21).

Although competitive outcomes are determined by the opposing effects of stabilizing niche differences favoring coexistence and fitness differences driving exclusion (2), the extent to which phenotypic differences are related to these drivers of coexistence is largely unknown. Prior work has examined the association between species traits and metrics that either aggregate stabilizing niche and average fitness differences (e.g., community membership, competitive dominance, and species abundance) (22–24) or form components of these quantities (e.g., interaction coefficients, relative yield, and competitive suppression) (25, 26). Only now, with recent developments in coexistence theory (15, 27–30), can we begin to directly evaluate the relationship between species traits and stabilizing niche differences and average fitness differences.

Significance

Biologists have long understood that differences between species in traits such as bill shape or rooting depth can maintain diversity in communities by promoting specialization and reducing competition. Here we test the assumption that phenotypic differences drive the stabilizing niche differences that promote coexistence. Using advances in ecological theory and detailed experiments we quantify average fitness and stabilizing niche differences between 102 plant species pairs and relate these differences to 11 functional traits. Individual traits were correlated with fitness differences that drive competitive exclusion but not stabilizing niche differences that promote coexistence. Stabilizing niche differences could only be described by combinations of traits, representing differentiation in multiple dimensions. This challenges the simplistic use of trait patterns to infer community assembly.

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Doing so is critical because these quantities provide the connection between functional trait differences and competitive outcomes, and thereby offer insight into the functional and phenotypic dimensions that shape species coexistence.

We conducted a field experiment with 18 annual plant species (Table 1) in a California grassland to field-parameterize mathematical models of competition, with which we quantified the stabilizing niche differences, average fitness differences, and predicted competitive outcomes for 102 species pairs (31). As detailed in *Materials and Methods* and in prior work (31), with our annual plant competition model the stabilizing niche difference $(1 - \rho)$ proves to be the following (28, 31, 32):

$$(1 - \rho) = 1 - \sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{jj}\alpha_{ii}}}, \quad [1]$$

where α_{ij} describes the per capita effect of species j on species i . The stabilizing niche difference therefore reflects the degree to which intraspecific competition (in the denominator) exceeds interspecific competition (in the numerator).

The average fitness difference between the competitors is κ_j/κ_i and is expressed (31) as

$$\frac{\kappa_j}{\kappa_i} = \left(\frac{\eta_j - 1}{\eta_i - 1} \right) \sqrt{\frac{\alpha_{ij}\alpha_{ii}}{\alpha_{jj}\alpha_{ji}}}, \quad [2]$$

where η_i describes the seeds produced per seed lost from the seed bank for plant species i (explained in *Materials and Methods*). The greater the ratio, κ_j/κ_i , the greater the fitness advantage of species j over i , and the faster species j excludes i in the absence of stabilizing niche differences. We refer to the two components of average fitness differences as the “demographic ratio” $((\eta_j - 1)/(\eta_i - 1))$ and “competitive response ratio” $[\sqrt{(\alpha_{ij}\alpha_{ii})/(\alpha_{jj}\alpha_{ji})}]$. This latter term describes the degree to which species i is more sensitive to intra- and interspecific competition than species j . See *Materials and Methods* for more details on the model.

To parameterize these expressions, species’ vital rates and pairwise competitive interactions were quantified after sowing each of the 18 species across a density gradient of itself and each of its 17 competitors (Fig. S1) and quantifying how fecundity declined as a function of increasing neighbor density (32). In addition, we sampled 11 key functional traits (Table 2 and Table S1) for each species, corresponding to variation in leaves, roots, seeds, and whole-plant characteristics that are known to describe

Table 2. Functional traits sampled in this study

Organ	Trait	Units
Leaf	Leaf area	cm ²
	SLA	g/cm ²
	Leaf nitrogen concentration	mg/g
	Leaf dry matter content (LDMC)	mg/g
Seed	Seed mass	g
Root	Rooting depth	cm
	SRL	m/g
Whole plant	Maximum height	cm
	Canopy shape index	Dimensionless
	Phenology (peak fruiting)	Day of year
	Carbon isotope composition	δ13C

strategy variation across plant species globally (33–35). We then tested the extent to which these trait differences, representing multiple ecological dimensions, were correlated with stabilizing niche differences $(1 - \rho)$ and average fitness differences (κ_j/κ_i) between species pairs in our study. Finally, we tested how trait differences related to the predicted outcome of competition.

For most of the functional traits we sampled, species differences in individual traits were well correlated with the average fitness differences (κ_j/κ_i) that determine competitive superiority (Fig. 1 and Fig. S2). Competitive superiority (that is, having higher average fitness than a competitor) was positively correlated with later phenology, larger potential size (larger maximum height and leaf area and deeper rooting depth), and a more resource-conservative foraging strategy (lower specific leaf area and specific root length).

Counter to the common use of trait differences as proxies for stabilizing niche differences (4, 8, 13), no single functional trait difference was correlated with the substantial variation in stabilizing niche differences $(1 - \rho)$ that we measured in the experiment (Fig. 1A and Table S2). Despite this finding, these niche differences were well described by a model containing multiple traits (Table 3) including specific root length, seed size, canopy shape, maximum height, and phenology. A model selection routine (36, 37) selected this five-trait model as the best descriptor of niche differences (BEST analysis, $\rho = 0.408$, $P = 0.03$) out of all possible combinations of the traits sampled.

A multitrait model was also fit for fitness differences (κ_j/κ_i) , and the best-fit model included two traits (phenology and leaf area) that were strong correlates of fitness differences in univariate analyses (Fig. 1) as well as canopy shape (a measure of investment in vertical vs. lateral growth; Table 3, BEST analysis, $\rho = 0.443$, $P = 0.03$). The inclusion of this last trait indicated that species with greater investment in lateral spread tended to have higher average fitness. Univariate correlations between each functional trait and the two components of the average fitness difference, the demographic ratio $[(\eta_j - 1)/(\eta_i - 1)]$ (Fig. 1C) and competitive response ratio $[\sqrt{(\alpha_{ij}\alpha_{ii})/(\alpha_{jj}\alpha_{ji})}]$ (Fig. 1D), suggested that functional traits were a better predictor of the demographic ratio. However, the individual traits are not independent (Fig. S3 and Table S1), and when we conducted multivariate BEST analyses we failed to find a significant combination of traits that was well correlated with either of the two fitness difference components (Table 3, BEST analysis, $P > 0.1$). Given that the product of these two components, the average fitness difference (κ_j/κ_i) , was well described by a multitrait model, our results indicate that weak relationships between plant traits and species’ demography and response to competition can nevertheless combine to render a significant relationship with average fitness differences.

Because stabilizing niche differences were only correlated with functional traits in models containing multiple traits (not in univariate analyses), these results reveal that neighborhood-scale stabilizing niche differences in the system result from species

Table 1. Species used in the experiment

Species	Code	Family
<i>Agoseris heterophylla</i>	AGHE	Asteraceae
<i>Agoseris retrorsa</i>	AGRE	Asteraceae
<i>Amsinckia menziesii</i>	AMME	Boraginaceae
<i>Anagallis arvensis</i>	ANAR	Myrsinaceae
<i>Centaurea melitensis</i>	CEME	Asteraceae
<i>Clarkia purpurea</i>	CLPU	Onagraceae
<i>Erodium botrys</i>	ERBO	Geraniaceae
<i>Erodium cicutarium</i>	ERCI	Geraniaceae
<i>Euphorbia peplus</i>	EUPE	Euphorbiaceae
<i>Geranium carolinianum</i>	GECA	Geraniaceae
<i>Hemizonia congesta</i> ssp. <i>luzulifolia</i>	HECO	Asteraceae
<i>Lasthenia californica</i>	LACA	Asteraceae
<i>Lotus purshianus</i>	LOPU	Fabaceae
<i>Lotus wrangelianus</i>	LOWR	Fabaceae
<i>Medicago polymorpha</i>	MEPO	Fabaceae
<i>Navarretia atractylodes</i>	NAAT	Polemoniaceae
<i>Plantago erecta</i>	PLER	Plantaginaceae
<i>Salvia columbariae</i>	SACA	Lamiaceae

in widely measured plant traits just as easily promote competitive exclusion, yielding a complex mapping between stabilizing niche differences, phenotypic differences, and the processes determining competitive outcomes in ecological communities. These complex relationships argue against the simple use of single traits to infer community assembly processes but lay the foundation for a theoretically robust trait-based community ecology.

Materials and Methods

Study Location and Species Selection. Our experiment was conducted at the University of California Sedgwick Reserve in Santa Barbara County, USA (34° 40' N, 120° 00' W), 730 m above sea level. The climate is Mediterranean with cool, wet winters and hot, dry summers. Precipitation totaled 298 mm over the experimental year (October 2011–July 2012), 21% less than the 50-y average. We selected 18 common annual plant species from within the reserve for use in the experiment (Table 1). The species are drawn from 10 different families within the eudicots and capture a wide range of functional trait variation within the constraints of the Mediterranean climate annual plant lifestyle. Four additional species were selected at the start of the experiment but failed to establish at sufficient density in the experimental treatments and are not discussed further. Seeds for the experiment were collected from 200 to 1,000 mother plants in the spring and summer of 2011, mixed across mother plants, and subsampled to determine species average seed mass, a functional trait in our study (Table 2). We competed all possible heterospecific and conspecific pairs of the 18 species against each other within a 500-m² area that had been previously cleared of all vegetation (the design is presented in the next section). Soils within the plot are finely textured serpentine soils, and the area was fenced to exclude gophers and deer.

Theoretical Background for Quantifying Niche and Fitness Differences and Field Parameterization of Population Models. To quantify the stabilizing niche differences (Eq. 1), average fitness differences (Eq. 2), and predicted competitive outcomes between species pairs we specified a mathematical model that captures the dynamics of competing annual plant populations with a seed bank (27, 40). This approach has been used elsewhere (31, 32) and is summarized below. Population growth is described as

$$\frac{N_{i,t+1}}{N_{i,t}} = (1 - g_i)s_i + g_i F_i, \quad [3]$$

where $N_{i,t+1}/N_{i,t}$ is the per capita population growth rate and $N_{i,t}$ is the number of seeds of species i in the soil before germination in the winter of year t . The germination rate of species i , g_i , weights an average of two different growth rates: s_i , the annual survival of ungerminated seed in the soil, and F_i , the viable seeds produced per germinated individual. F_i can be expanded to describe the relationship between per germinant fecundity and the density of competing germinated individuals in the system:

$$F_i = \frac{\lambda_i}{1 + \alpha_{ij}g_jN_{j,t} + \alpha_{ij}g_jN_{j,t}}. \quad [4]$$

The per germinant fecundity of species i in the absence of competition, λ_i , is reduced by the germinated density of conspecifics, ($g_iN_{i,t}$), and heterospecifics, ($g_jN_{j,t}$). These neighbor densities are modified by interaction coefficients that describe the per capita effect of species j on species i (α_{ij}). With this model, the number of seeds produced per seed lost from the seed bank due to death or germination (in the absence of neighbors), a critical term in the average fitness difference in Eq. 2, is (31)

$$\eta_i = \frac{\lambda_i g_i}{1 - (1 - g_i)(s_i)}. \quad [5]$$

Critically, empirical work in this system supports the functional form of the model in Eqs. 3 and 4 (27) and shows that it accurately predicts competitive outcomes between species in the study area (31).

Using this model of population dynamics between competing species, we then define stabilizing niche differences (Eq. 1) and average fitness differences (Eq. 2) between species pairs following earlier studies (28, 31, 32). For the model described by Eqs. 3 and 4, the niche overlap, ρ , is $\sqrt{(\alpha_{ij}\alpha_{ji})/(\alpha_{jj}\alpha_{ii})}$, and $1 - \rho$ becomes the stabilizing niche difference. The average fitness difference between the competitors is κ_j/κ_i , as explained in ref. 31 and as presented in Eq. 2. Following earlier work (31, 32), the condition for coexistence (mutual invasibility) can be expressed as $\rho < \kappa_i/\kappa_j$, where species j is the fitness superior.

These models were parameterized with estimates of species' germination fractions, per germinant fecundities in the absence of neighbors, seed

survival in the soil, and all pairwise interaction coefficients using experimentally assembled plant communities (Fig. S1). In October 2011 we established 154 rectangular plots separated by landscape fabric to control weeds. The design involved sowing each species as focal individuals into a density gradient of each potential competitor (including conspecifics). We randomly assigned each plot to be sown with one of the 18 species at a density of 2, 4, 8, or 16 g/m² of viable seed, with two replicates per density per species. The 2-g/m² plots were 1.5 × 1.7 m and all other densities were sown into 0.9 × 1.1-m plots. Each plot was divided into 42 subplots (a six row by seven column array) with a buffer of 2.5 cm at the edge of the plot. The equivalent of five viable seeds of one species were then sown into a subplot to establish a focal individual at the center, with two subplots sown per species per plot. After germination these were thinned to one focal individual per subplot. The experimental plots were used to assess germination rates as well as species' per germinant fecundity as a function of neighbor density. In addition, 10 plots were established with no background species to assess focal plant performance in the absence of neighbors. Additional description and discussion of the experimental design can be found elsewhere (32).

Sampling of Functional Traits. We selected 11 plant functional traits to measure on each species in the experiment (Table 2). These traits are known to capture ecologically important variation in leaves, roots, seeds, and whole-plant function across plant species worldwide (35, 41) and are widely sampled within plant communities. At the time of planting, 20 1-m² plots were established interspersed with the competition plots for the sole purpose of destructive trait sampling. Each plot was sown with a mixture of species from the experiment at a total density of 8 g/m². At peak biomass, 40–50 mature individuals from across the trait plots and the experiment were selected for height measurements, used to estimate maximum height within the conditions found in our experiment as the 95th quantile of the distribution of measured heights. Using the trait plots, 8–15 individuals were selected for harvest of aboveground tissues, and from those 8 individuals were selected to have a sample of the root system harvested in a 10 × 10-cm soil core for measurement of fine roots. Low germination for two species (ANAR and ERBO; see Table 1 for species codes) limited harvesting to five individuals per species.

At harvest we first measured the height and canopy shape of each species. The lateral spread of the canopy from the main axis, as viewed from above, was measured at the farthest point from the main axis and at 90° clockwise from this point. The two measurements of lateral extent were averaged, and canopy shape was quantified as the ratio of lateral extent to height. This yields an index that ranges from close to 0 for a plant with primarily erect, vertical growth (such as CLPU) to >> 1 for low, prostrate growth forms (such as LOWR and MEPO). Next, the entire aboveground portion of each plant was placed into a moistened paper towel within a sealed plastic bag and stored in a cooler for transport to the laboratory, where it was kept in dark, refrigerated conditions. Three leaves were selected from each plant, blotted dry, weighed, and then imaged on a flatbed scanner at 600 dpi to determine fresh leaf area. All fresh leaves were processed within 5 h of harvest. Leaves were then dried to constant mass at 60 °C, weighed to determine dry mass, and subsequently bulked by species and ground to a fine powder for nitrogen and carbon isotope analysis by the Center for Stable Isotope Biogeochemistry at the University of California, Berkeley.

Fine root samples in soil cores were placed into sealed bags in a cooler at harvest and kept in refrigeration until they could be processed within 12–36 h. Root samples were gently washed over a 0.5-mm sieve to remove soils, and a sample of the washed root system of each focal plant was transferred to ethanol for later analysis, taking care to remove roots from other individuals. For analysis, a small subsample of fine roots (<2 mm in diameter) was floated in water, arranged to minimize overlap and scanned at 600 dpi using WinRhizo software (Regent Instruments) to determine total fine root length of the subsample. The root samples were then dried to a constant mass at 60 °C and weighed.

In addition to the harvesting described above, we selected a second set of three to eight individuals per species for root system excavation to estimate rooting depth. Sample size was again limited by poor germination for some species. Soil was carefully removed alongside the main root system a few centimeters at a time until no further roots from the focal plant were apparent, and this depth recorded. More precise measurements from techniques using soil corers or root augers were not possible at the site because of the very shallow rooting depth of many of the species in the experiment and the abundance of rocks and clay aggregates in the soil. Because this method may miss fine roots extending below the point of excavation it likely offers a conservative underestimate of the rooting depth of each species.

Finally, we monitored the fruiting and flowering phenology of the species in the experiment biweekly. Because differences in fruiting and flowering phenology seemed to be well correlated across species in the study we used date of peak fruiting as a measure of gross phenological differences between species. We defined peak fruiting as the date when developing fruits outnumbered flowers on >50% of the reproductive individuals in a species in the experiment.

Following the sampling described above, the functional trait measures in Table 2 were calculated following standard protocols (35, 41). Traits were log-transformed as needed to improve normality before analysis. Trait measurements were averaged across individuals to arrive at species-level trait averages used in analyses.

Analyses. We tested for correlations between functional trait differences and the stabilizing niche and average fitness differences quantified with parameters from the experiment (e.g., Fig. S2). Because niche and fitness differences are inherently pairwise measures, we focused on analyses that could account for the nonindependence present in pairwise comparison data (e.g., 18 species in all pairwise combinations result in 153 possible heterospecific interactions). At the end of the experiment we had sufficient data to fit models for 102 of 153 potential species pairs. For univariate comparisons we used Mantel tests, with the Benjamini and Hochberg correction for multiple comparisons. For multitrait comparisons we conducted a model selection exercise in a Mantel framework by using the BEST routine in the PRIMER software package (36, 37) to identify the combination of trait differences that best described fitness and niche differences. The BEST routine calculates Spearman's rho for all combinations of 1–11 functional trait differences and assesses the significance of the best-performing model using a permutation test. Because the test statistic (Spearman's rho) does not automatically improve with additional variables, no correction (e.g., Akaike information criterion) is needed to compare models with differing numbers of variables. Our analyses focused on testing linear relationships between trait differences and both fitness and niche differences, because an examination of the data did not indicate that nonlinear relationships would be

well supported (e.g., Fig. S2). However, more complex relationships may exist in other datasets.

We then evaluated the predicted outcome of competitive interaction between pairs of species in the experiment by comparing the magnitude of the estimated fitness and stabilizing niche difference between them. Stable coexistence based on interactions at the scale of our experiment is predicted when $\rho < \kappa_i/\kappa_j$, where species j is the fitness superior (Fig. 2). Using this criterion, we tested whether coexisting pairs differed from noncoexisting pairs with respect to functional traits using a series of Wilcoxon signed-rank tests (Fig. 3 and Fig. S4).

Functional Trait Variation. Principal components analysis revealed that the primary axis of trait differentiation among our species reflects covariation in traits related to plant size and leaf chemistry (Fig. S3). Specifically, the first principal components axis (26% of variation) reflects maximum height, rooting depth, and leaf area (which varies in part due to allometric size constraints) in addition to leaf nitrogen and dry matter content. Specific leaf area (SLA) and specific root length (SRL) were tightly associated, suggesting a coordination between above- and belowground foraging strategies. In contrast to many global studies (33), SLA and leaf nitrogen concentration were not strongly correlated in our data, perhaps owing to the relatively narrow range of SLA values (123–256 cm²/g) among the annuals in our study. Additional pairwise correlations are summarized in Table S1. Species differences in principal component axis 1 and 2 scores were well correlated with fitness differences between species (Mantel $P < 0.001$) but not with niche differences (Mantel $P > 0.3$).

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