Classification: Biological Sciences- Ecology

Plant functional traits and the multidimensional nature of species coexistence

Short title: Functional traits and species coexistence

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Abstract

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 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 quantify how phenotypic differences drive both coexistence and competitive exclusion. Single functional traits were often good predictors of 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 poor predictors of 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.

Significance statement

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. We describe the first test of the assumption that phenotypic differences drive the stabilizing niche differences that promote coexistence. Using advances in ecological theory and detailed experiments, we quantify fitness and niche differences between 102 plant species pairs and relate these differences to 11 functional traits. Individual traits predicted the fitness differences that drive competitive exclusion, but not the stabilizing niche differences that promote coexistence. 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.

/body

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 has several definitions (6), ecological theory specifies that 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 thereby 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 as 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" favor competitive exclusion (14-16). More generally, average fitness differences are those species differences that favor one competitor over the other (2). In principle, many possible relationships between trait differences and coexistence are possible, with differing implications for competitive outcomes. For example, fitness and niche differences could be predicted by non-overlapping 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 niche differentiation between species in communities (18-20).

Although competitive outcomes are determined by the opposing effects of niche differences stabilizing coexistence and fitness differences driving exclusion (2), the extent to which phenotypic differences predict these drivers of coexistence is largely unknown. Prior work has examined the association between species traits and metrics that either aggregate niche and fitness differences (e.g. community membership, competitive dominance, and species abundance; 21, 22, 23), or form components of these quantities (e.g. interaction coefficients, relative yield, and competitive suppression; 24, 25). Only now, with recent developments in coexistence theory (15, 26-29) can we directly evaluate how species traits relate to stabilizing niche differences, average fitness differences, and the dimensionality of species coexistence. Doing so is critical because niche and fitness differences provide the connection between functional trait differences and competitive outcomes.

We conducted a field experiment with 18 annual plant species 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 (30). For our annual plant model, the stabilizing niche differences capture the degree to which intraspecific competition exceeds interspecific competition, while fitness differences reflect a combination of species differences in their seed production and average sensitivity to competition. Species' vital rates and pairwise competitive interactions were quantified by sowing each of the 18 species across a density gradient of itself and each of its seventeen competitors (Figure S1), and quantifying how fecundity declined as a function of increasing neighbor density (31). In addition, we sampled 11 key functional traits (Table 2) for each species, corresponding to variation in leaves, roots, seeds, and whole plant characteristics that are known to describe strategy variation across plant species globally (32-34). We then tested the extent to which these trait differences, representing multiple ecological dimensions, predicted niche and fitness differences between species. Finally, we predict the implications of each trait for coexistence.

For most of the functional traits we sampled, species differences in individual traits were well correlated with the average fitness differences that determine competitive superiority (Figure 1). 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 size; deeper rooting depth), and a more resource-conservative foraging strategy (lower specific leaf area and specific root length). Previous work has

shown that average fitness differences between annual plant competitors can be decomposed into two components: differences between the species in their innate ability to produce seeds (the "demographic component"), and differences in overall sensitivity to both conspecific and heterospecific neighbors (the "competitive response" component) (30). We found that the traits predicting species' fitness differences did so because they were well correlated with differences in the demographic component; only one trait (LDMC) was correlated with the competitive response component (Figure 1, Table S2). This suggests that the influence of traits on competitive dominance in this system arises largely through trait correlations with demographic differences rather than differences in plant-plant interactions.

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 niche differences that we measured in the experiment (Figure 1, Table S2). Despite this finding, 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 (35, 36) 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 multi-trait model was also fit for fitness differences, and the best-fit model included two traits (phenology and leaf size) that were strong predictors of fitness differences in the univariate analyses (BEST analysis, rho = 0.443, p = 0.03).

Because niche differences were only correlated with functional traits in models containing multiple traits (not in univariate analyses), these results reveal that local niche differentiation in the system rests on species differences in multiple ecological dimensions. Two non-mutually exclusive effects may underlie these results. First, different sets of species may be niche differentiated along distinct axes of functional trait variation. For instance, coexistence between some pairs of species may be stabilized by niche differences resulting from contrasting prostrate and erect growth forms, while for others coexistence is stabilized by niche differences related to contrasting fine root foraging strategies (acquisitive vs. resource conservative, as reflected in specific root length). Second, niche differences between these species may require simultaneous differentiation in multiple plant traits (e.g. canopy shape and specific root length), only detectable with the multi-trait model. More detailed studies are needed to distinguish between these two alternatives.

Critically, our results also show that species differences in a single phenotypic trait can have opposing effects on coexistence, contributing to both niche and fitness differences. For example, while higher fitness was associated with later phenology, phenology differences also contributed to niche differences (Table 3, Figure S5). Thus, the greater the phenology difference, the greater the competitive superiority of later phenology competitor (the fitness difference), but also the greater the growth rate advantage when a species drops to low relative abundance (the niche difference).

Whether phenology differences ultimately favor or impede coexistence therefore depends on the relative strength of the correlations between phenology differences and niche differences, which favor coexistence, and phenology differences and fitness differences, which drive competitive exclusion. We found that the 12 pairs of species predicted to coexist under our study conditions (that is, where niche differences exceeded fitness differences) had significantly smaller phenology differences than other species pairs (Wilcoxon sign rank test $p < 0.05$, Figure 2). This suggests that phenology differences disfavored coexistence, a result that is consistent with phenology better predicting fitness differences than niche differences, but runs counter to the notion that all trait differences are necessarily stabilizing. A similar result was found for leaf size (Figure 2).

The current study explores trait correlations with the drivers of the competitive interactions between two species. Future research might ask how trait differences affect diffuse, multispecies competition, including intransitive competitive networks. Intransitive competition, which can stabilize coexistence without pair-wise niche differences, most easily arises when competitive dominance in different species pairs is mediated by different limiting factors, such as light versus nutrients (37). Our finding that different traits can individually predict competitive dominance (Figure 1), and that the correlations between these traits were often weak (Table S1) provides a basis for competitive intransitivity in the system.

Our experiment was designed to measure the processes influencing species coexistence in an annual plant community at a neighborhood spatial scale and to relate these processes to species average phenotypic traits across the individuals in the experiment. Additional processes including soil heterogeneity, inter-annual variation in climate, interactions with herbivores and pathogens, and intraspecific trait variation may also enhance or inhibit coexistence (2, 13, 38-40). However, despite the focus of the experiment on the neighborhood spatial scale where niche and fitness differences can be reasonably quantified, our results reveal a surprisingly complex link between phenotypic diversity and competitive outcomes. While multiple phenotypic differences may promote coexistence in some circumstances or for some species pairs, phenotypic differences in widely measured plant traits just as easily promote competitive exclusion, yielding a complex mapping between niche differences, phenotypic differences, and the processes maintaining diversity 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 (34º 40' N, 120º 00'W), 730 meters 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-year

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 200-1000 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 m^2 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 gopher and deer.

Theoretical background for quantifying niche and fitness differences and field parameterization of population models

To quantify the stabilizing niche differences, average fitness differences, 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 (26, 41). This approach has been used elsewhere (30, 31), and is summarized below. Population growth is described as:

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

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 prior to germination in the winter of year t. The germination rate of species i, g_i, reflects the 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:

$$F_i = \frac{\lambda_i}{1 + \alpha_{ii} g_i N_{i,t} + \alpha_{ij} g_j N_{j,t}} \quad (2)$$

The per germinant fecundity of species i in the absence of competition, λ_i, is reduced by the germinated density of conspecifics, $(g_i N_{i,t})$, and heterospecifics $(g_j N_{j,t})$. These neighbor densities are modified by interaction coefficients that describe the per capita effect of species j on species i (α_{ij}). Critically, empirical work in this system supports the functional form of the model (26) and shows that it accurately predicts competitive outcomes between species in the study area (30). These competitive outcomes can be determined by solving equations 1 and 2 for the low density growth rate of each species

when its competitor is at its carrying capacity, and coexistence is inferred if both competitors' low density growth rates are positive.

Using this model of population dynamics between competing species, we then define stabilizing niche differences and average fitness differences between species pairs following earlier studies (27, 30, 31). For the model described by eqns. 1 and 2, previous work (30) shows that niche overlap, ρ, is as follows:

$$\rho = \sqrt{\frac{\alpha_{ij}}{\alpha_{jj}} . \frac{\alpha_{ji}}{\alpha_{ii}}} \qquad (3)$$

Niche overlap therefore reflects the average degree to which species limit conspecific relative to heterospecific competitors. With ρ defining niche overlap between a species pair, the "stabilizing niche difference" is 1-ρ.

In contrast to stabilizing niche differences, average fitness differences drive competitive dominance and exclusion. The average fitness difference between the competitors is $\frac{\kappa_j}{\kappa_i}$, is described (30) as:

$$\frac{\kappa_j}{\kappa_i} = \left(\frac{\eta_j - 1}{\eta_i - 1}\right) \sqrt{\frac{\alpha_{ij}}{\alpha_{jj}} . \frac{\alpha_{ii}}{\alpha_{ji}}}$$

(4)

where

$$\eta_i = \frac{\lambda_i g_i}{1 - (1 - g_i)(s_i)}$$

The greater the ratio, $\frac{\kappa_j}{\kappa_i}$, the greater the fitness advantage of species *j* over *i*. A ratio of 1 indicates equivalent competitive ability. From eqn. 4, it can be seen that competitive dominance can arise though a combination of germination and fecundity advantages $\left(\frac{\eta_j - 1}{\eta_i - 1}\right)$, and lower sensitivity to neighboring competitors $\left(\sqrt{\frac{\alpha_{ij}}{\alpha_{jj}} . \frac{\alpha_{ii}}{\alpha_{ji}}}\right)$. We refer to these two components of average fitness differences as the "demographic ratio" and the "competitive response ratio," respectively.

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 (Figure S1). In October 2011, we established 154 rectangular plots separated by landscape fabric to control weeds and fenced to exclude deer and gophers. 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 / m^2 of viable seed, with two replicates per density per species. The 2 g / m^2 plots were 1.5 x 1.7 m and all other

densities were sown into 0.9 x 1.1 m plots. Each plot was divided into 42 subplots (a 6 row by 7 column array) with a buffer of 2.5 cm at the edge of the plot. 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 fecundities as a function of neighbor density. In addition, 10 plots were established with no background species in order to assess focal plant performance in the absence of neighbors. Additional description and discussion of the experimental design can be found elsewhere (31).

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 (34, 42) and are widely sampled within plant communities. At the time of planting, 20 1-m^2 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 / m^2. 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 x 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 5 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 degrees 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 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 sealed plastic bag and stored into a cooler for transport to the laboratory, where they were 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 hours of harvest. Leaves were then dried to constant mass at 60 degrees 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 the WinRhizo software (Regent Instruments, Canada) to determine total fine root length of the subsample. The root samples were then dried to a constant mass at 60 degrees C and weighed.

In addition to the harvesting described above, we selected a second set of 3-8 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 cm 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. As 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 bi-weekly. As differences in fruiting and flowering phenology appeared 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. Finally, we measure seed mass from the combined weight of 500 seeds.

Following the sampling described above, the functional trait measures in Table 2 were calculated following standard protocols (34, 42). Traits were log transformed as needed to improve normality prior to 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 niche and fitness differences quantified in the experiment (e.g. Figure S2). As niche and fitness differences are inherently pairwise measures, we focused on analyses that could account for the non-independence 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 multi-trait comparisons, we conducted a model selection exercise in a Mantel framework by using the BEST routine in the PRIMER software package (35, 36) 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 to 11 functional trait differences and assesses the significance of the best performing model using a permutation test. As the test statistic (Spearman's rho) does not automatically improve with additional variables, no correction (cf. AIC) is needed to compare models with differing numbers of variables.

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 niche difference between them. Stable coexistence within the conditions present in our experiment is predicted when niche differences exceed fitness differences (Figure S3). Using this criterion, we tested whether coexisting pairs differed from non-coexisting pairs with respect to functional traits using a series of Wilcoxon sign-rank tests (Figure S4).

Functional trait variation

Principle components analysis revealed that the primary axis of trait differentiation among our species reflects covariation in traits related to plant size and leaf chemistry (Figure S5). Specifically, the first principle components axis (26% of variation) reflects maximum height, rooting depth, and leaf size (which varies in part due of allometric size constraints) in addition 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 (32), SLA and leaf nitrogen concentration were not strongly correlated in our data, perhaps due to the relatively narrow range of SLA values (123 – 256 cm^2/g) among the annuals in our

study. Additional pairwise correlations are summarized in Table S1. Species differences in principle component axis 1 and 2 scores were good predictors of fitness differences between species (Mantel $p < 0.001$) but not of niche differences (Mantel $p > 0.3$).

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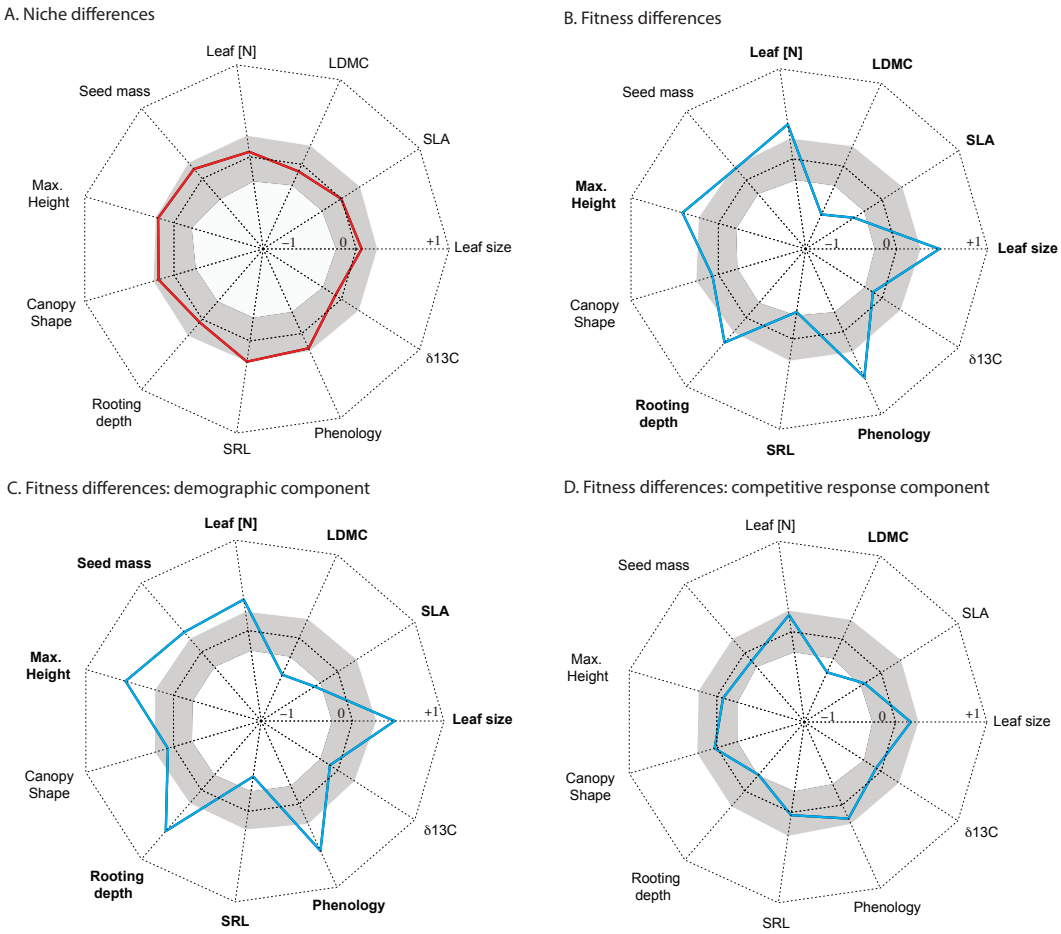
Figure legends

Figure 1. Functional trait correlates of fitness (A) and niche (B) differences among 18 annual plants. As fitness and niche differences are pairwise measures, correlations are calculated with mantel tests. Panels C and D show trait correlations with the two components of fitness differences, the demographic components and the competitive response component. Colored lines show correlations calculated from the mantel test, ranging from -1 at the center of the plot to 1 at the margin. Central band of grey denotes the central 95% of null correlation values from the mantel permutations. See Table 2 for trait abbreviations. Results in bold are significant following Benjamini-Hochberg correction for multiple comparisons (Table S2).

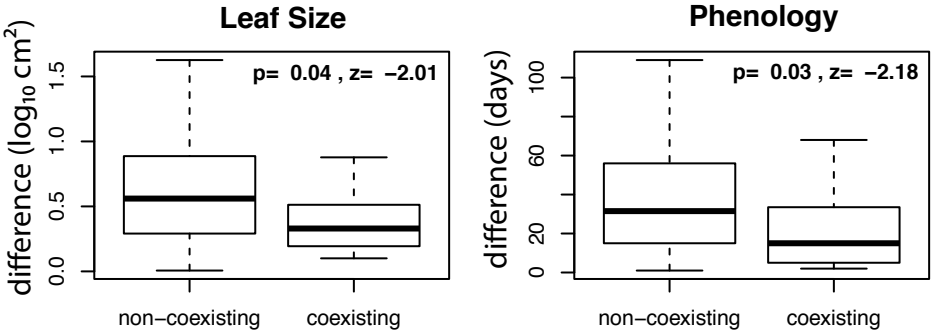
Figure 2. Trait differences between species pairs predicted to coexist (where stabilizing niche differences exceed fitness differences). Pairs predicted to coexist are significantly more similar in leaf size and phenology (Wilcoxon sign rank test $p < 0.05$) than species pairs where fitness differences exceed niche differences; all other trait differences are *n.s.*

1 Figure 1


A. Niche differences
Leaf [N]
LDMC
SLA
Leaf size
δ13C
Phenology
SRL
Rooting depth
Canopy Shape
Max. Height
Seed mass
−1
0
+1
B. Fitness differences
C. Fitness differences: demographic component
D. Fitness differences: competitive response component

2

1 Figure 2


Leaf Size
difference (log_{10} cm^2)
0.0
0.5
1.0
1.5
p= 0.04 , z= −2.01
non−coexisting
coexisting
Phenology
difference (days)
0
20
60
100
p= 0.03 , z= −2.18
non−coexisting
coexisting

2

3

Table 1: Species used in the experiment.

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

Table 2: Functional traits sampled in this study.

Organ	Trait	Units
leaf	Leaf size	cm2
	Specific leaf area (SLA)	g/cm2
	Leaf nitrogen concentration	mg/g
	Leaf dry matter content (LDMC)	mg/g
seed	Seed mass	g
root	Rooting depth	cm
	Specific root length (SRL)	m/g
whole plant	Maximum height	cm
	Canopy shape index	dimensionless
	Phenology (peak fruiting)	day of year
	Carbon isotope composition	δ13C

Table 3: Results from BEST model selection procedure for explaining niche (A) and fitness (B) differences using combinations of functional traits. Tables detail the traits selected in each of the 3 best-fit models, with spearman's rho given for each model. The significance of the best model is assessed using a permutation test. Traits in bold are selected in the best-fit model.

A. Niche differences

model rank	rho	N traits	traits
1	0.408 (p = 0.031)	5	**specific root length, canopy shape, max. height, phenology, seed mass**
2	0.403	6	**specific root length, canopy shape, max. height, phenology, seed mass,** leaf [N]
3	0.389	5	**specific root length, canopy shape, max. height, phenology**, leaf [N]

B. Fitness differences

model rank	rho	N traits	traits
1	0.443 (p = 0.035)	3	**leaf size, canopy shape, phenology**
2	0.441	4	**leaf size, canopy shape, phenology,** SLA
3	0.430	5	**leaf size, canopy shape, phenology,** SLA, seed mass

Supporting information

Table S1: Pairwise functional trait correlations (pearson's r).

	Leaf size	SLA	LDMC	Seed mass	Max. Height	SRL	Canopy shape	Rooting depth	Phenology	Leaf [N]
SLA	-0.09									
LDMC	-0.64	0.01								
Seed mass	-0.06	0.21	0.30							
Max. Height	0.54	-0.18	-0.36	0.00						
SRL	-0.09	0.53	-0.16	-0.12	-0.11					
Canopy shape	-0.34	-0.11	0.34	0.37	-0.54	0.00				
Rooting depth	0.23	0.04	0.04	0.47	0.51	-0.03	0.14			
Phenology	0.07	-0.46	-0.40	-0.32	-0.05	-0.42	-0.02	-0.12		
Leaf [N]	0.24	0.20	-0.39	-0.09	0.01	-0.14	-0.04	-0.08	0.23	
δ13C	-0.23	-0.70	0.38	-0.10	-0.10	-0.42	0.20	-0.24	0.13	-0.29

Table S2: Correlations between trait differences and coexistence parameters, with results from Mantel tests. Values in bold correspond to tests that are significant at $\alpha = 0.05$ following the Benjamini & Hochberg correction for multiple comparisons.

trait	Niche difference	p	Fitness difference	p
Leaf size	0.059	0.676	**0.469**	**< 0.001**
SLA	-0.003	0.942	**-0.367**	**0.008**
LDMC	-0.084	0.476	**-0.584**	**< 0.001**
Leaf [N]	0.055	0.734	**0.383**	**0.006**
Seed mass	0.137	0.346	0.172	0.112
Max. Height	0.178	0.102	**0.411**	**< 0.001**
Canopy Shape	0.172	0.146	0.066	0.598
Rooting depth	0.044	0.832	**0.361**	**< 0.001**
SRL	0.225	0.058	**-0.300**	**0.022**
Phenology	0.174	0.144	**0.552**	**< 0.001**
δ13C	-0.077	0.502	-0.122	0.354

trait	Demographic response difference	p	Competitive response difference	p
Leaf size	**0.461**	**< 0.001**	0.166	0.192
SLA	**-0.303**	**0.012**	-0.216	0.094
LDMC	**-0.443**	**0.002**	**-0.402**	**0.002**
Leaf [N]	**0.343**	**0.004**	0.185	0.122
Seed mass	**0.287**	**0.006**	-0.117	0.282
Max. Height	**0.547**	**< 0.001**	-0.071	0.518
Canopy Shape	0.064	0.63	0.025	0.872
Rooting depth	**0.594**	**< 0.001**	-0.234	0.046
SRL	**-0.386**	**0.002**	0.031	0.82
Phenology	**0.563**	**< 0.001**	0.164	0.196
δ13C	-0.105	0.336	-0.066	0.492

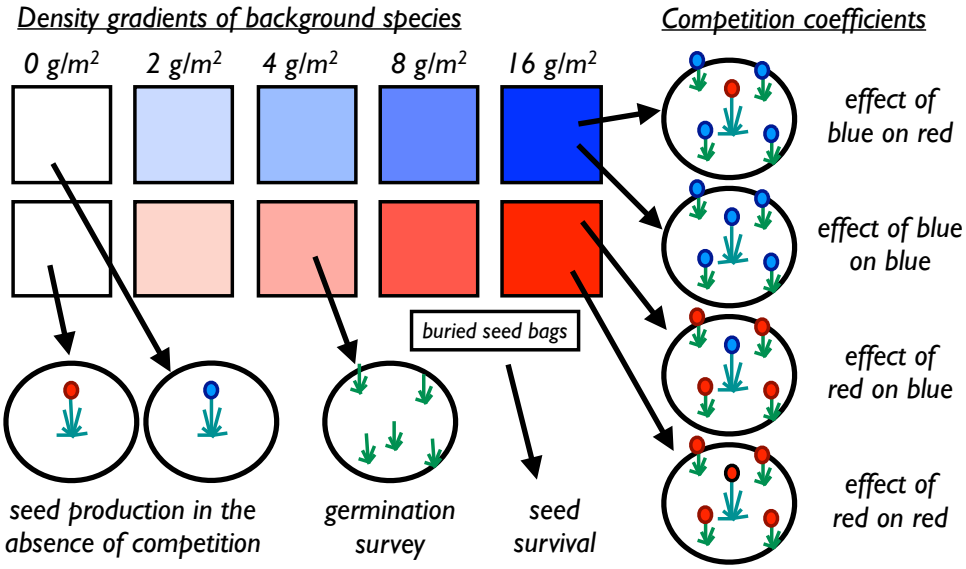


Figure S1: Schematic of parameter estimation from the experiment. Each species (here, "red" and "blue") is sown in a density gradient and focal individuals of all species are planted into these plots. Germination of the background species is measured early in the year. Seed survival is measured from buried seed bags. Seed production at low density and competition coefficients are measured from seed production of focal plants at each neighbor density. These parameters are then combined to estimate niche and fitness differences for each species pair.

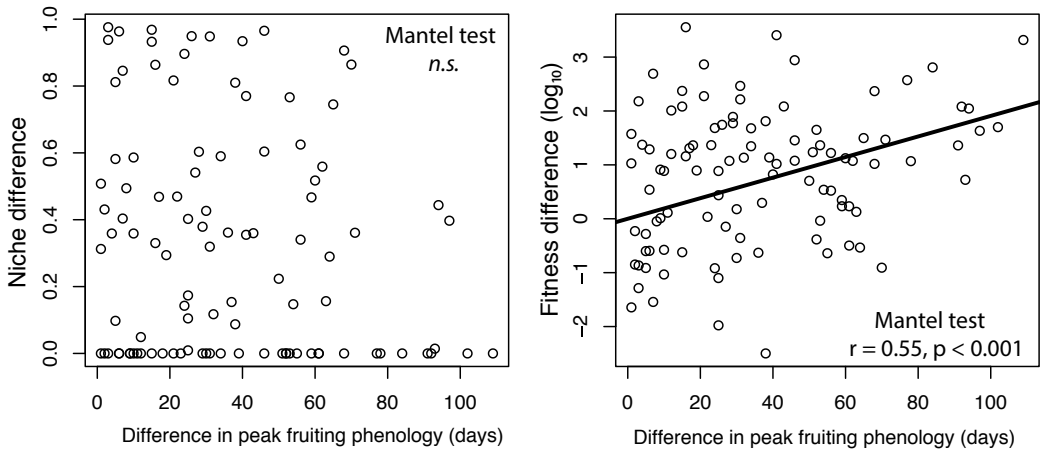


Figure S2: An example of the correlation between trait differences and niche and fitness differences for species pairs in the experiment, in the case of phenology.

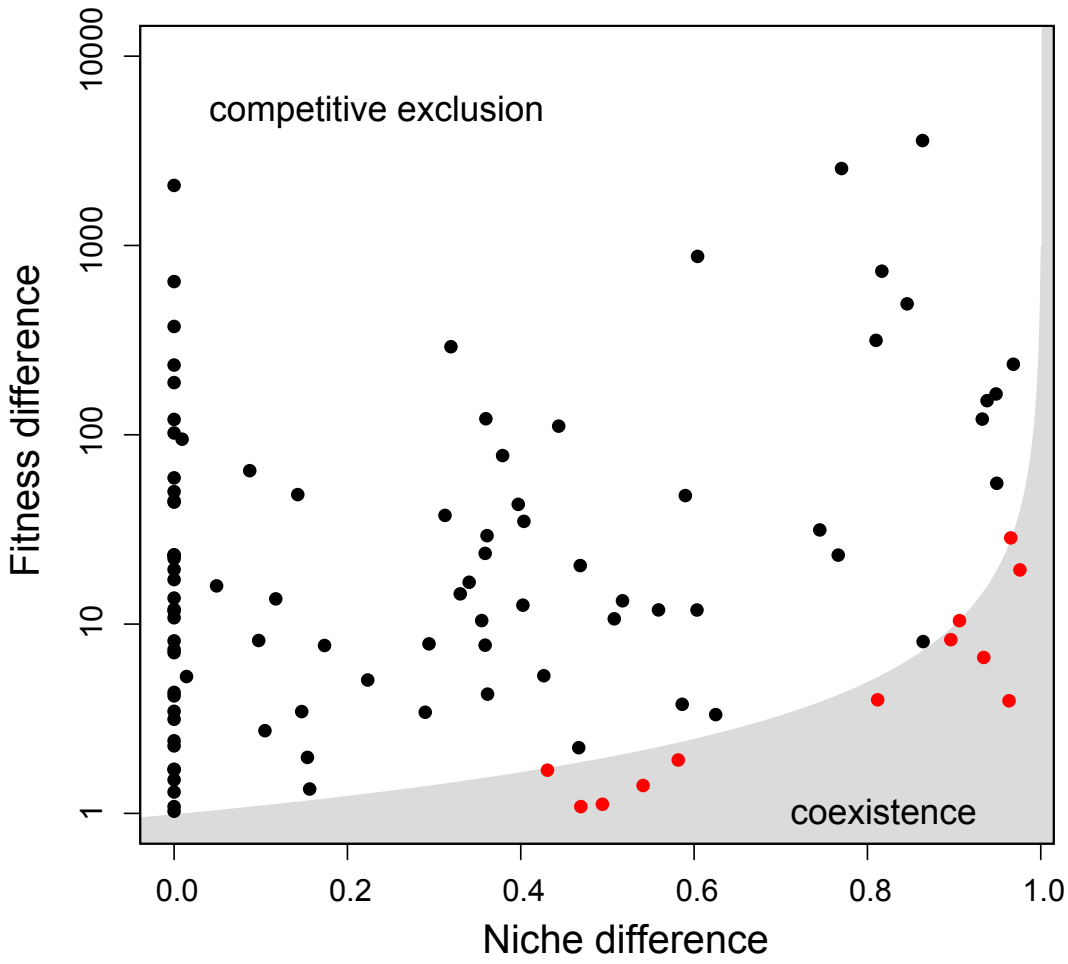


Figure S3: Fitness and niche differences for the species pairs in the experiment. Each point represents a unique pair of species. The shaded grey area represents the area where niche differences exceed fitness differences and coexistences is predicted to occur. Twelve species pairs fall in this zone- in all other cases fitness differences exceed niche differences and one species is predicted to exclude the other eventually.

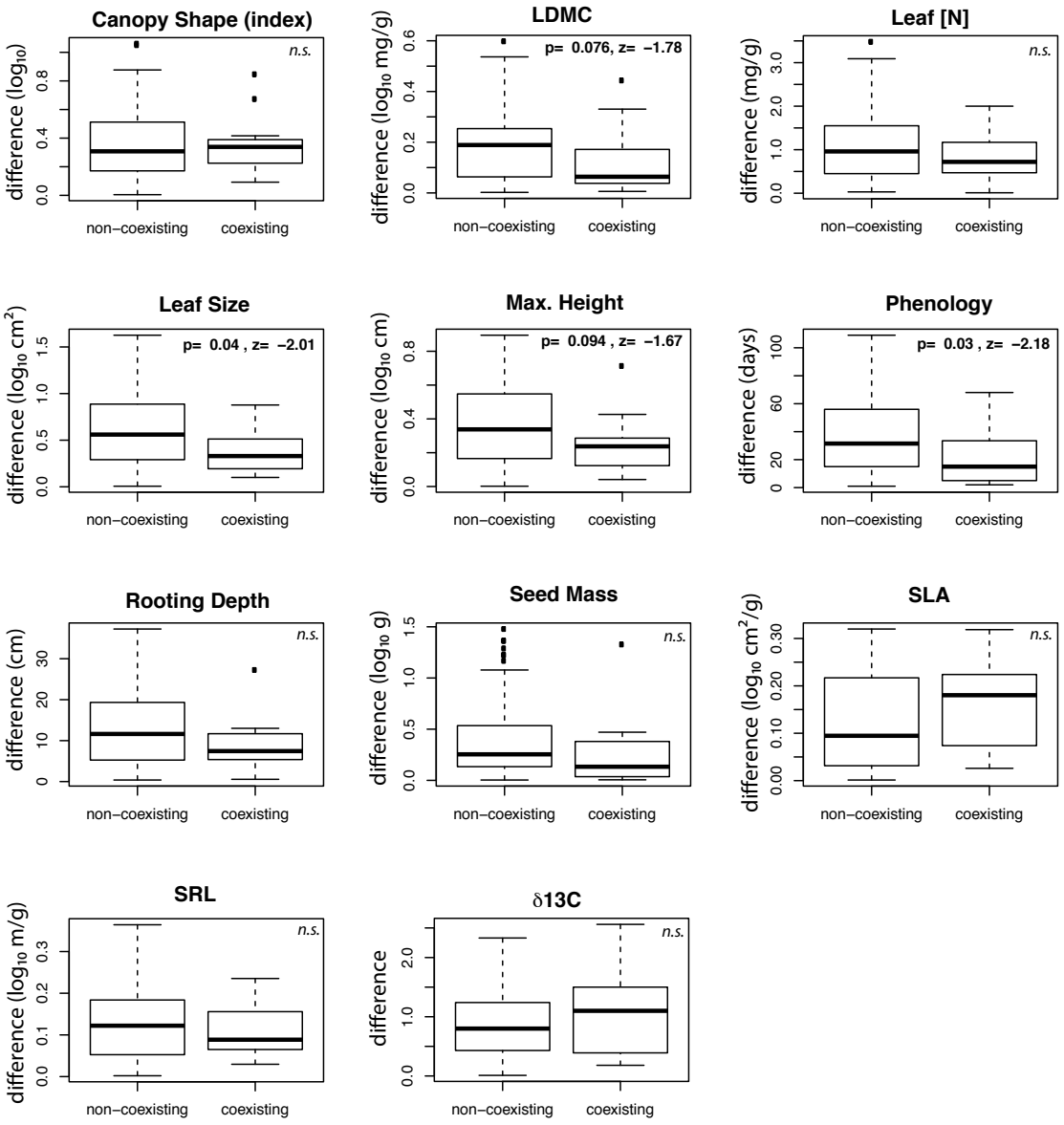


Figure S4: Trait differences between pairs of species that are predicted to coexist in contrast with differences between pairs not predicted to coexist long term. Test statistics correspond to a two-tailed Wilcoxon test implemented in the R package 'coin.' Pairs predicted to coexist are significantly more similar in leaf size and phenology ($p < 0.05$) and tend to have more similar LDMC and Maximum Height ($p < 0.1$) than pairs that are not predicted to coexist long term.

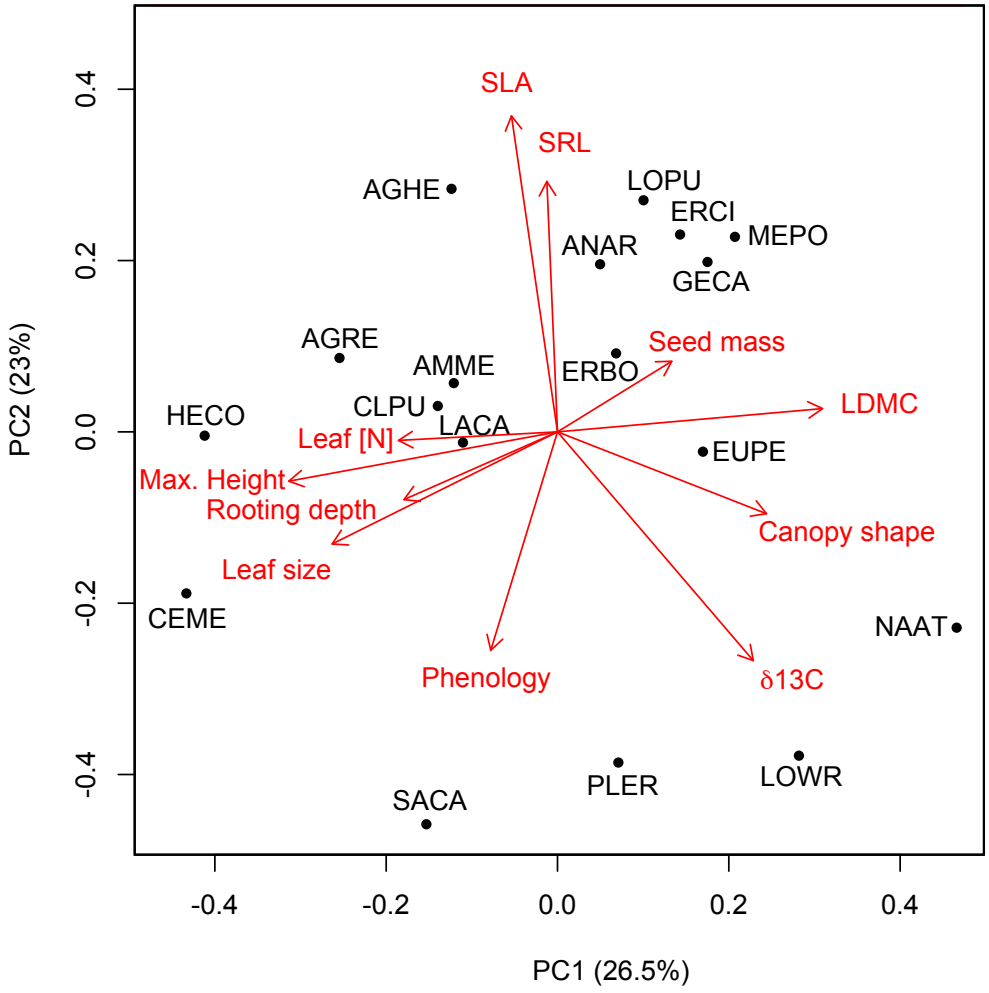


Figure S5: Principle components analysis of trait differences between species in the experiment. For species codes see Table 1, for trait abbreviations see Table 2.