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Author(s): Jennifer L. Funk and Amelia A. Wolf

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Testing the trait-based community framework: Do functional traits predict competitive outcomes?

JENNIFER L. FUNK^{1,3} AND AMELIA A. WOLF²

¹*Schmid College of Science and Technology, Chapman University, 1 University Drive, Orange, California 92866 USA*
²*Department of Ecology, Evolution, and Environmental Biology, Columbia University, New York, New York 10027 USA*

Abstract. Plant traits can be used to understand a range of ecological processes, including competition with invasive species. The extent to which native and invasive species are competing via limiting similarity or trait hierarchies has important implications for the management of invaded communities. We screened 47 native species that co-occur with *Festuca perennis*, a dominant invader in California serpentine grassland, for traits pertaining to resource use and acquisition. We then grew *F. perennis* with 10 species spanning a range of functional similarity in pairwise competition trials. Functionally similar species did not have a strong adverse effect on *F. perennis* performance as would be expected by limiting similarity theory. Phylogenetic relatedness, which may integrate a number of functional traits, was also a poor predictor of competitive outcome. Instead, species with high specific root length, low root-to-shoot biomass ratio, and low leaf nitrogen concentration were more effective at suppressing the growth of *F. perennis*. Our results suggest that fitness differences (i.e., trait hierarchies) may be more important than niche differences (i.e., limiting similarity) in structuring competitive outcomes in this system and may be a promising approach for the restoration of invaded systems.

Key words: community assembly; competitive hierarchies; ecological restoration; limiting similarity; phylogenetic diversity; plant invasion; resource acquisition.

INTRODUCTION

Competition is among the most studied processes governing community assembly, with recent work focusing on how trait distributions within communities distinguish the relative importance of competition and other processes, such as environmental filtering (e.g., Suding et al. 2003, Gross et al. 2009, Mayfield and Levine 2010, Kraft et al. 2014). The long-standing theory of limiting similarity states that species with similar trait values will compete more strongly than dissimilar species, leading to niche differences in communities (MacArthur and Levins 1967). However, interspecific trait variation may also reflect fitness differences, meaning that particular trait values confer a competitive advantage resulting in competition hierarchies (Kunstler et al. 2012, Herben and Goldberg 2014, Gross et al. 2015). Whether interspecific trait variation indicates niche or fitness differences within a community has important implications for species coexistence and functional diversity within communities: niche differences tend to promote functional diversity while fitness

differences could limit diversity as species with particular trait values become dominant (Kunstler et al. 2016).

Identifying the processes that regulate species coexistence is essential for managing invaded communities. Many studies have found key trait differences between native and invasive species (e.g., Leishman et al. 2007, Ordonez and Olff 2012, but see Funk et al. 2016); however, it is unclear if this variation translates into niche or fitness differences between these species groups. If limiting similarity is operating in a community, restoration ecologists can strengthen community resistance to invasion by selecting native species that are functionally similar to potential invasive species, thus increasing competition (Funk et al. 2008, Laughlin 2014). While several studies have documented limiting similarity in invaded systems (e.g., Fargione et al. 2003, Turnbull et al. 2005, Emery 2007, Cleland et al. 2013), a recent meta-analysis by Price and Partel (2013) found that the ability of a species to repel functionally similar species was dependent on life form and the type of experiment. Specifically, forbs were able to suppress invasion by functionally similar forbs (no pattern for grasses), but only in synthetic-assembly experiments as opposed to natural communities. While trait-mediated competition hierarchies have been identified in a range of

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³E-mail: jlfunk@chapman.edu

systems (Kunstler et al. 2012, Kraft et al. 2014), few studies have explicitly investigated trait-driven hierarchies in invaded plant communities (Lai et al. 2015). Thus, it remains unclear if managers can optimize invasion resistance by selecting native species that are functionally similar to potential invasive species or natives that possess superior traits.

Following the theory of limiting similarity, we predicted that an invasive species will have lower fitness when grown in the presence of native species with similar resource-use traits. We also examined the relationship between competitive effect (ability to reduce growth of an invader, Goldberg and Landa 1991) and traits to determine if particular trait values confer a competitive advantage. We screened the most common native ($n = 47$) and exotic ($n = 6$) species in a California serpentine grassland for traits pertaining to resource use and acquisition as these traits have been shown to strongly influence community assembly (e.g., Cornwell and Ackerly 2010, Maire et al. 2012, Kraft et al. 2014, Gross et al. 2015). We grew *Festuca perennis*, a widespread weed in the western United States, in competition with 10 species that spanned a range of functional similarity and quantified growth to determine competitive effect and response.

A second objective of this study was to examine if phylogeny predicts competitive outcomes. Phylogenetic differences among native and invasive species are potentially informative if relatedness serves as a proxy for phenotype and, thus, functional traits (Cadotte et al. 2009, Cavender-Bares et al. 2009, Flynn et al. 2011). In this case, phylogenetic information could circumvent the need to collect detailed trait measures to understand invasion and restoration at community and regional levels. To test this, we calculated phylogenetic distance between species in our competition trials to determine its ability to predict competitive outcomes.

METHODS

Study sites

This experiment was conducted in serpentine grassland at Jasper Ridge Biological Preserve and Coyote Ridge in the San Francisco Bay Area, California, USA. Jasper Ridge Biological Preserve is located in San Mateo County, USA (37°24' N, 122°14' W) and Coyote Ridge is located further south in Santa Clara County, California (37°15' N, 121°45' W). Both sites are characterized by Mediterranean climates, with hot, dry summers and cool, wet winters. Mean annual precipitation during the 2009–2010 study period at Jasper Ridge and Coyote Ridge was 761 and 570 mm, respectively, although interannual variation in precipitation is large.

Functional trait survey

We collected functional trait data from 47 native and six exotic species during January to April 2010 (see

Appendix S1: Table S1 for complete species list). We selected common species and excluded species that were so rare that we could not find five replicate individuals. We measured traits corresponding to carbon capture strategy (photosynthetic capacity, leaf mass per unit area), water and nitrogen acquisition and use (water-use efficiency, photosynthetic nitrogen-use efficiency, leaf nitrogen content, root depth, specific root length, root to shoot biomass ratio), and light acquisition and use (light-use efficiency, height). Physiological and chemical analyses were performed on recently mature leaves from five individuals per species.

Photosynthetic rates, transpiration rates, and chlorophyll fluorescence were measured with a LI-6400 portable gas exchange system (LI-COR, Lincoln, Nebraska, USA). All measures were collected between 08:00 and 14:00 with chamber relative humidity between 40% and 60%. Ambient CO₂ concentration, leaf temperature, and irradiance level were held constant at 400 ppm, 25°C, and 2000 μmol photon/s. The effective quantum yield of PSII (Φ PSII) was calculated as $(F_m' - F_s)/F_m'$, where F_s is the fluorescence yield of a light-adapted leaf and F_m' is the maximal fluorescence during a saturating light flash. Water-use efficiency (WUE) was measured as photosynthetic rate divided by transpiration rate.

Following physiological measurements, leaves were harvested, scanned for leaf area, and dried to calculate leaf mass per area (LMA). Total leaf nitrogen (N) concentration was determined with a Costech 4010 Elemental Combustion System (Costech Analytical Technologies, Valencia, California, USA). Photosynthetic nitrogen-use efficiency was calculated as photosynthetic rate divided by leaf N. Plant height was measured from the ground to the tip of vegetative material rather than inflorescences, which can be much taller than leaves in many grassland species. Plants were harvested by digging up the entire root system. Root depth was measured as the depth of the deepest root. A representative subsample of the root system (including absorbing and conducting roots) totaling 60 cm was weighed to determine specific root length (SRL, cm/mg). Above- and belowground biomass was separated, dried, and weighed to determine root to shoot (R:S) biomass ratio.

Functional and phylogenetic similarity

We used principal components analysis (PCA) to identify native species that were similar in water and nutrient use to *Festuca perennis*. Prior to analysis, all traits were log-transformed and standardized using the formula $([\text{trait} - \text{trait mean}]/\text{trait SD})$. We examined correlations among traits and selected five largely independent traits that captured leaf and root function (root depth, LMA, leaf N concentration, photosynthetic rate, and WUE) for 53 species. PC axis 1 explained 41.7% of the variation among species and corresponded with photosynthetic rate and leaf N (Appendix S1: Fig. S1). PC axis 2 explained 21.1% of the variation among species

TABLE 1. Ten species were selected for competition trials with *Festuca perennis* based on their functional similarity with respect to five key functional traits (root depth, leaf mass per area [LMA], leaf N, photosynthetic rate, and water-use efficiency [WUE]).

Species	Life form	Code	Euclidean distance	Effect of <i>F. perennis</i> on competitor biomass		Effect of competitor on <i>F. perennis</i> biomass	
				Decline (%)	<i>t</i>	Decline (%)	<i>t</i>
<i>Bromus hordeaceus</i>	annual grass	brho	0.22	18.2	2.47*	39.5	-2.44*
<i>Layia platyglossa</i>	annual herb	lapl	0.30	35.9	3.12**	20.8	-1.74
<i>Stipa pulchra</i>	perennial grass	stpu	0.45	2.2	0.85	12.8	-0.94
<i>Microseris douglasii</i>	annual herb	mido	0.55	15.0	0.09	18.1	-1.50
<i>Melica californica</i>	perennial grass	meca	0.63	56.1	2.99**	-8.5	0.45
<i>Agoseris heterophylla</i>	annual herb	aghe	0.70	28.0	0.99	25.6	-1.64
<i>Festuca microstachys</i>	annual grass	femi	1.99	31.6	3.86**	50.3	-4.28**
<i>Lasthenia californica</i>	annual herb	laca	2.66	72.8	3.71**	30.8	-2.65*
<i>Plantago erecta</i>	annual herb	pler	2.70	40.9	4.62**	17.8	-1.09
<i>Elymus multisetus</i>	perennial grass	elmu	2.79	40.9	2.76*	3.4	-0.23

Notes: Species are listed in order of decreasing similarity (lower Euclidean distance is more functionally similar). One invasive species (*B. hordeaceus*) was included in the experiment. *Festuca perennis* suppressed the growth (percentage of reduction in biomass) of six competitors. In contrast, *F. perennis* biomass was reduced by only three of 10 competitors. * $P < 0.05$, ** $P < 0.01$ (df = 8 for all analyses).

and corresponded with LMA and root depth. Euclidean distances were calculated between each species and the focal invader, *F. perennis*, using the first two principal components (Appendix S1: Table S1). Ten competitors spanning a range of functional similarity were selected based on these distances, seed availability, and germination rate (Table 1; Appendix S1: Supplemental Methods).

Competition experiment

Species were grown in monoculture (20 individuals per pot) or with *F. perennis* (10 individuals and 10 *F. perennis* individuals) at approximate plant density in the field (~2,500 plants/m²; J. Funk, unpublished data). There were five replicate pots per treatment (monoculture or mixed) per species. In October 2011, seeds were sown in serpentine soil in small pots (0.5 L) corresponding to monoculture and mixed treatments and grown in a greenhouse. In December 2011, plants were transferred to larger pots (1 m length, 10 cm diameter) in a field environment at Jasper Ridge. All pots contained autoclaved serpentine soil collected from a road cut at Coyote Ridge. Soil moisture in the pots was monitored with a HOBO node soil moisture sensor (W-SMC; Onset Computer Corporation, Bourne, Massachusetts, USA) and maintained at field moisture (averaged 23.3% volumetric water content over the course of the experiment).

Plants were harvested at two time points corresponding to peak biomass. At each harvest, three monoculture pots of *F. perennis* were harvested for comparison. Plants in mixed cultures were sorted to species and aboveground biomass was dried at 60°C for 72 h and weighed. Total aboveground biomass was divided by the number of individual plants to yield an average aboveground plant mass

per treatment. Given the rocky nature of the soil, the small diameter of the tubes, and the fragile roots of several species, we were unable to extract whole root systems; thus, we were unable to collect belowground trait data. The effect of native species on *F. perennis* performance was assessed by comparing average plant mass of *F. perennis* in mixed cultures to average plant mass in *F. perennis* monocultures. The effect of *F. perennis* on native species performance was assessed by comparing average plant mass of native species in mixed cultures to average plant mass in native species monocultures. Differences in average plant mass between mixed cultures and monocultures were evaluated with *t* tests for each species.

In order to examine the effects of relatedness on competitive outcomes, we constructed a community phylogeny for the 11 species included in this study (see Appendix S1: Supplemental Methods). To determine the relative predictive power of functional and phylogenetic metrics on competitive outcomes, we correlated functional and phylogenetic distances with competitive outcomes using species means. In addition, we tested for phylogenetic signal for each trait used in this study (see Appendix S1: Supplemental Methods). All PCA, *t* test, and correlation analyses were conducted in R (version 3.2.0; R Development Team 2015).

RESULTS

Functional similarity, as assessed by Euclidean distance in functional trait space, was not correlated with a species' competitive response (biomass reduction of the competitor by *Festuca perennis*, $R^2 = 0.33$, $P = 0.08$) or competitive effect (biomass reduction of *F. perennis* by the competitor, $R^2 = 0.00$, $P = 0.88$). Similarly, phylogenetic distance was not correlated with competitive effect

TABLE 2. Correlations (r) between plant traits and the percentage of biomass decline in *Festuca perennis* (competitive effect) and competitors (competitive response) when grown in competition.

Parameter	Competitive effect	Competitive response
Root:Shoot	-0.89**	-0.45
Leaf N	-0.74*	-0.07
Root depth	-0.58	-0.16
Plant height	-0.53	-0.02
Photosynthetic rate	-0.43	-0.21
Nitrogen-use efficiency	-0.36	-0.05
Seed mass	-0.12	-0.68*
Light-use efficiency	0.15	0.39
Water-use efficiency	0.20	-0.26
LMA	0.24	0.05
Specific root length	0.83**	0.02

Note: The traits are ordered from strong negative correlation to strong positive correlation with the percentage of decline in *F. perennis*. * $P < 0.05$, ** $P < 0.01$.

across multiple measures (taxonomic $R^2 = 0.08$, $P = 0.42$; maximum likelihood $R^2 = 0.00$, $P = 0.99$; Bayes $R^2 = 0.01$, $P = 0.83$).

While most competitors experienced reduced biomass when grown with *F. perennis* in mixed cultures, *F. perennis* biomass was reduced by only three of 10 competitors and increased when grown in competition with *Melica californica*, a native perennial grass (Table 1; Appendix S1: Fig. S2). Three traits were positively (SRL) or negatively (R:S, leaf N) correlated with competitive effect (Table 2, Fig. 1). However, these traits did not correlate with competitive response. Instead, larger-seeded species experienced smaller biomass reduction when grown in competition with *F. perennis* (Table 2). All trait correlations are presented in Appendix S1: Table S3. Of

the four traits correlated with competitive outcomes, only leaf N concentration showed a phylogenetic signal (Appendix S1: Table S4).

DISCUSSION

Our results from a paired competition experiment based on functional similarity with a dominant invasive grass species provide no support for limiting similarity. In contrast to expectations, functionally similar competitors did not perform better than functionally dissimilar species in the presence of *Festuca perennis* (competitive response), nor did they have an adverse effect on *F. perennis* performance (competitive effect). Instead, our results are consistent with the idea that particular trait values conferred higher competitive ability against *F. perennis*. Species with a strong competitive effect on *F. perennis* had high SRL, low R:S, and low leaf N. These three traits were strongly correlated with each other (Appendix S1: Table S3). The only trait that was significantly correlated with competitive response was seed mass: larger-seeded competitors experienced lower biomass declines when grown with *F. perennis*. While resources afforded to large-seeded species may buffer them against competition with *F. perennis* (Moles and Westoby 2006), seed mass was not correlated with any other trait in this study and, thus, does not appear to fit into a successful “strategy” in invaded serpentine grassland.

High SRL allows species to efficiently take up nutrients and water without a significant biomass investment (Cornelissen et al. 2003) and our finding that the best competitors with *F. perennis* had high SRL supports our initial prediction that these species are competing for belowground resources. High allocation to roots (e.g., R:S and root mass fraction) is often negatively correlated with SRL reflecting a trade-off between deep root systems requiring thicker roots and shallow root systems

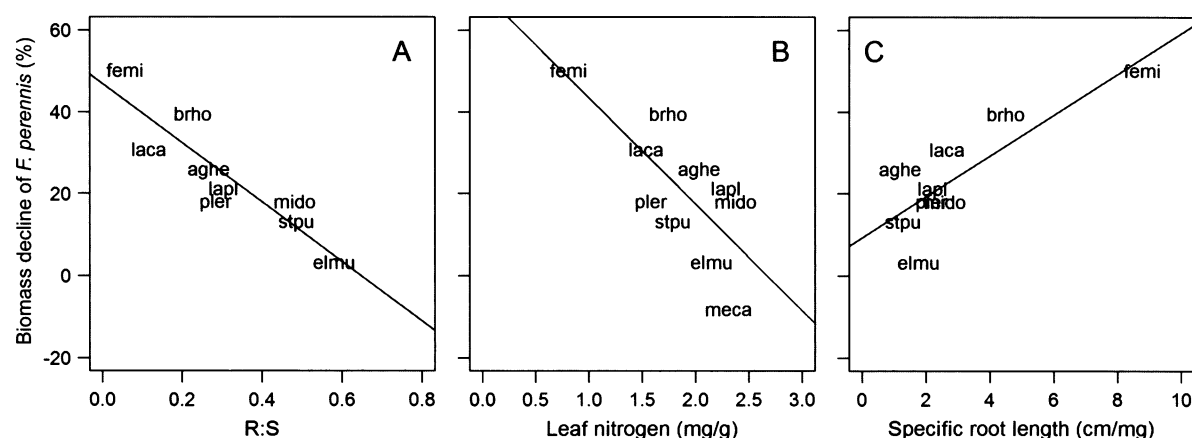


FIG. 1. The relationship between competitive effect (*Festuca perennis* biomass decline) and (A) root-to-shoot biomass ratio (R:S; $r = -0.89$, $P = 0.001$), (B) leaf nitrogen content ($r = -0.74$, $P = 0.015$), and (C) specific root length ($r = 0.83$, $P = 0.005$). Species codes are provided in Table 1. We were unable to collect root data for *Melica californica* (meca); thus, this species is absent from panels A and C.

comprised of thinner roots (e.g., Larson and Funk 2016). The three species with highest competitive effect (*Bromus hordeaceus*, *Festuca microstachys*, *Lasthenia californica*) had shallow roots (3–7.5 cm), low R:S, and high SRL. Interestingly, high SRL did not translate into higher leaf N; these traits were negatively correlated across species ($r = -0.77$; Appendix S1: Table S3). Species with high SRL may have diluted leaf N to increase productivity, which has been observed in other systems (e.g., Chapin 1980, Walters and Reich 1989, Funk et al. 2007). However, it is doubtful that aboveground production was high enough to shade out *F. perennis*. Height was not a good predictor of competition with *F. perennis* as several natives with short stature (e.g., *Agoseris heterophylla*, *L. californica*, *Microseris douglasii*) performed relatively well in competition with this species. Thus, we conclude that plants primarily competed for belowground resources in the top soil layer, as many of the best competitors had shallow roots with high SRL.

Within a particular vegetation community, such as California serpentine grassland, the traits that confer a competitive advantage will vary spatially and temporally. In a serpentine grassland site in central California, Kraft et al. (2015) found that competitively superior species displayed a different set of traits than found in our study, including late phenology, large size (height, leaf area, root depth), and conservative foraging strategies (high LMA, low SRL). One explanation for the discrepancy between studies is that fitness differences vary across communities based on the species present (e.g., dominant invasive species); the study by Kraft et al. (2015) focused on forbs while our study included a mix of grasses and forbs. Furthermore, previous studies in this community type have noted that fitness differences can vary within a site based on environmental variation associated with different soil patches (Reynolds et al. 1997). Competitive traits may also vary strongly within the growing season and across years as resource availability changes (e.g., Goldberg 1996, Keddy et al. 2000, Gremer et al. 2013). For example, interannual variation in rainfall can be high in California grassland systems (Hobbs et al. 2007); thus, traits conferring drought tolerance might be important one year, while traits that optimize light or nutrient acquisition might be important the next.

Despite the fact that the congener *F. microstachys* was the best competitor with *F. perennis*, phylogenetic relatedness was not a good predictor of competition. The “competition-relatedness hypothesis” states that closely related species are functionally similar and compete more strongly with each other than with more distantly related taxa (e.g., Cahill et al. 2008). Mayfield and Levine (2010) questioned the premise of this hypothesis and suggested that competitive exclusion among closely related species will depend on the strength of niche (i.e., limiting similarity) vs. fitness (i.e., competitive hierarchy) differences. Results from our competition experiment suggest that trait differences among species in this system may be more aligned with a competitive hierarchy rather than

limiting similarity; thus, it makes sense that phylogenetic relatedness may be a poor predictor of competitive outcomes. Additionally, while there is often a phylogenetic signal in plant traits (Ackerly 2009), empirical studies have demonstrated that phylogenetic and functional trait diversity may not be correlated (Maire et al. 2012, Ordonez 2014) and if traits are highly plastic we might not expect relatedness to be a good predictor of functional similarity. Indeed, while half of the traits we measured had significant phylogenetic signal, three of the four traits that correlated with competitive outcomes against *F. perennis* were not phylogenetically linked (Appendix S1: Table S4). While the phylogenetic diversity represented in our study was not particularly low in the context of ecological restoration, which can involve a small number of species, half of our 10 species were from Poaceae. Thus, with the caveat of low phylogenetic diversity, our results support the idea that phylogeny alone may not strongly predict community assembly processes and may not be a suitable replacement for trait data in projects seeking native competitors for invasive species.

In conclusion, while further studies are needed to understand how fitness and niche differentiation influence community assembly and how this varies across systems (e.g., low vs. high productivity sites), our results suggest that managers should consider screening for traits that convey fitness differences and planting or seeding these species in invaded sites.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecs.1484/supinfo>