ECOLOGY LETTERS

Ecology Letters, (2014) **17**: 836–844 doi: 10.1111/ele.12289

LETTER

Phylogenetic relatedness and the determinants of competitive outcomes

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Abstract

Recent hypotheses argue that phylogenetic relatedness should predict both the niche differences that stabilise coexistence and the average fitness differences that drive competitive dominance. These still largely untested predictions complicate Darwin's hypothesis that more closely related species less easily coexist, and challenge the use of community phylogenetic patterns to infer competition. We field parameterised models of competitor dynamics with pairs of 18 California annual plant species, and then related species' niche and fitness differences to their phylogenetic distance. Stabilising niche differences were unrelated to phylogenetic distance, while species' average fitness showed phylogenetic structure. This meant that more distant relatives had greater competitive asymmetry, which should favour the coexistence of close relatives. Nonetheless, coexistence proved unrelated to phylogeny, due in part to increasing variance in fitness differences with phylogenetic distance, a previously overlooked property of such relationships. Together, these findings question the expectation that distant relatives should more readily coexist.

Keywords

Annual plants, California grasslands, coexistence, community assembly, competitive responses, demography, fitness, niches, trait conservatism.

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INTRODUCTION

In recent years, ecologists have become increasingly interested in using phylogenetic information to better understand the structure and assembly of communities. At the heart of these approaches is Darwin's hypothesis that competition is more severe between more closely related species. Darwin reasoned that recently diverged species tend to be more similar in traits determining what would come to be known as their ecological niche (Grinnell 1917; Gause 1934; Elton 1946; Hutchinson 1957), and that niche overlap between more closely related taxa would hinder their coexistence (Darwin 1859). Darwin's hypothesis motivated many ecologists in the mid-1900s to use species to genus ratios to infer the intensity of competition in communities (Elton 1946). However, it was not until the ready availability of molecular phylogenies, and the development of the community phylogenetics framework laid out by Webb *et al*. (2002), that the hypothesis gained such a central place in community ecology. In particular, Darwin's hypothesis underlies the common expectation in the community assembly literature that competitive exclusion leaves coexisting species more evenly spaced across the phylogeny than expected by chance sampling from the species pool (Webb *et al*. 2002).

Despite the renewed prominence of the 'competition-relatedness' hypothesis, studies directly quantifying how species' relatedness predicts the outcome of their competition show decidedly mixed results (Maherali & Klironomos 2007; Cahill *et al*. 2008; Jiang *et al*. 2010; Burns & Strauss 2011; Violle *et al*. 2011; Allan *et al*. 2013; Bennett *et al*. 2013; Best *et al*. 2013; Narwani *et al*. 2013; Park & Potter 2013; Fritschie *et al*. 2014). Of course, one potential explanation for the ambiguous nature of the results is the lack of phylogenetic signal in traits structuring competitive outcomes (Losos 2008; Cavender-Bares *et al*. 2009). However, more fundamental problems may exist with the central assumption that increased phylogenetic and trait differences favour coexistence (Mayfield & Levine 2010).

Applying a modern coexistence framework developed by Chesson (2000) to the literature on relatedness and competition, Mayfield & Levine (2010) noted that only some species differences, termed 'stabilising niche differences' favour coexistence, while others, termed 'average fitness differences' favour competitive exclusion. Stabilising niche differences cause intraspecific competition to exceed interspecific competition, and favour coexistence by promoting species that drop to low relative abundance (Adler *et al*. 2007). They can arise when plant species differ in phenology, the resources most limiting growth, and interactions with host-specific pathogens (Liu *et al*. 2012; Godoy & Levine 2014). By contrast, average fitness differences drive competitive exclusion by favouring one competitor over others regardless of their commonness or rarity; in the absence of niche differences, the fitness superior excludes all competitors. Examples include species differences in height in light-limited environments or the ability to deplete a shared limiting soil resource (Harper 1977; Tilman 1987; Ojeda *et al*. 2010).

With stabilising niche differences favouring coexistence and average fitness differences favouring exclusion, the influence of phylogenetic relatedness on the outcome of competition depends on the relative degree to which relatedness predicts niche vs. fitness differences. In one extreme, if relatedness only predicts niche differences between competitors, then more distantly related taxa will more easily coexist, as Darwin hypothesised. At the other extreme, if relatedness only predicts competitive fitness differences, then more distantly related

taxa are less likely to coexist. Thus, the influence of competition on patterns of relatedness is only predictable with a mechanistic understanding of how relatedness reflects the niche and fitness differences that drive competitive outcomes (Mayfield & Levine 2010).

Fortunately, recent advances in coexistence theory by Chesson (2000, 2012; see also Narwani *et al.* 2013; Godoy & Levine 2014) now permit us to directly quantify niche and fitness differences and relate these to phylogenic relatedness. This opportunity, however, brings new empirical challenges. Even if a species' niche and competitive fitness are phylogenetically conserved, the shape of the relationship between niche or fitness differences and phylogenetic distance, as well as the expected pattern of variance in these relationships is unknown. This topic is therefore our first consideration.

Given that niche and fitness differences are defined at the species level, and that a species has no differences relative to itself (at zero phylogenetic distance), any relationship between niche or fitness differences and phylogenetic distance between species must pass through the origin. The question is then how fast do these differences accumulate and potentially asymptote with increasing phylogenetic distance. If species' niches and competitive fitness are each conserved (*sensu* Blomberg *et al.* 2003), we expect that on average, niche and fitness differences will be small between sister taxa, and generally increasing with phylogenetic distance (Thuiller *et al.* 2010) (Fig. 1). The pattern of variance in these relationships is also important. Many models of trait evolution predict an increase in trait variance between clade members as phylogenetic distance increases (Paradis 2012), resulting in a pattern where close relatives tend to have similar traits but distant relatives may have similar or divergent traits depending on the course of trait evolution. Therefore, some distant relatives may have substantial niche and fitness differences due to greater evolutionary time for differences to evolve while others may also manifest very low niche and/or fitness differences due to convergence or stasis (Fig. 1 & Appendix S1). As distant relatives are expected to have greater variance in niche and fitness differences than close relatives, many common models of trait evolution actually predict that the drivers of competitive outcomes (niche and fitness differences) should be more variable for distant relatives than close relatives, rather than simply larger, as Darwin proposed for niche differences.

Here, we test how phylogenetic relatedness influences competitive outcomes. We focus on three questions: (1) What is the phylogenetic structure of competitive fitness? (2) How well does phylogenetic distance predict the niche differences that stabilise coexistence and fitness differences that drive competitive exclusion? (3) How can phylogeny's relationship with niche and fitness differences be used to interpret its relationship with competitive outcomes?

We answered these questions by first field parameterising a plant competition model from which the stabilising niche differences, average fitness differences and predicted competitive outcomes were quantified. To parameterise models of pairwise competition between 18 annual California grassland species, we quantified their vital rates (germination, fecundity, seed survival) and interaction coefficients in field plots exposing focal individuals to a density gradient of competitors. We then built a molecular phylogenetic tree, with which we explored the phylogenetic structure of competitive fitness predicted by the parameterised models (Question 1). We then

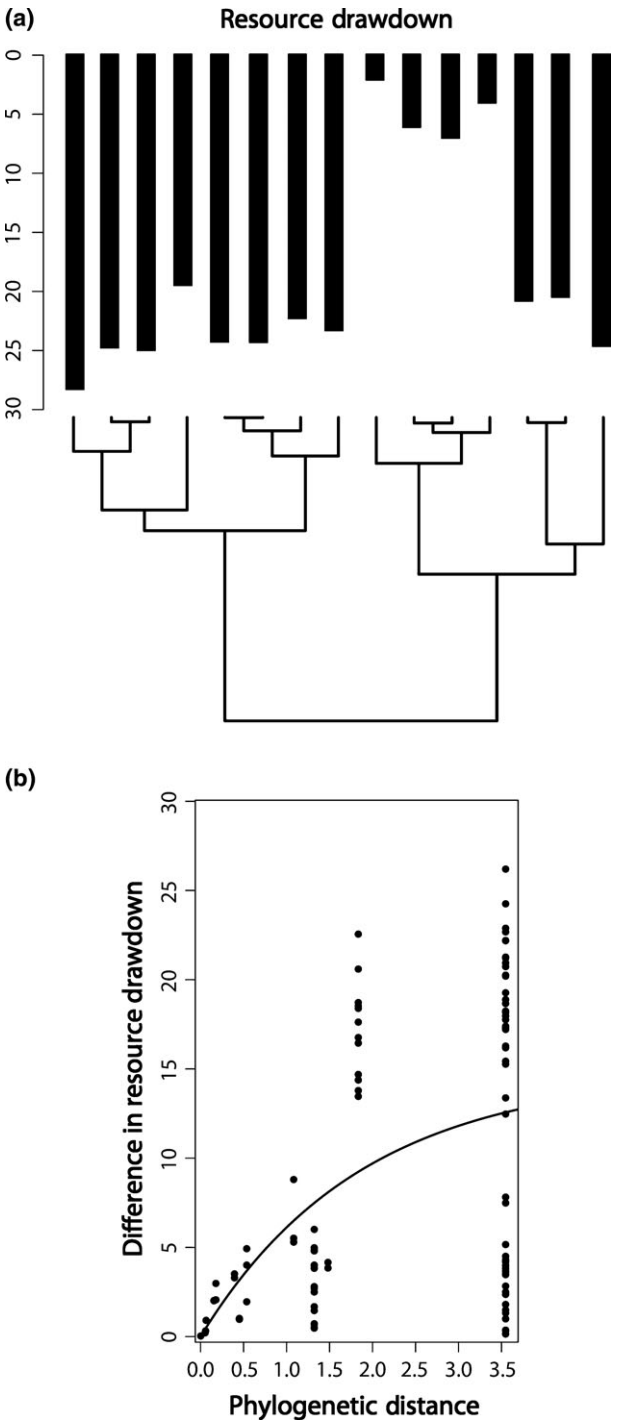

Figure 1 Even when species traits show phylogenetic signal, complex relationships between phylogenetic distance and trait differences can arise. (a) A simulation of a hypothetical phylogeny with a trait, resource drawdown, evolving according to a Brownian model. (b) The relationship between the average trait difference and phylogenetic distance is generally increasing, but also shows increasing variance with decreasing relatedness. If resource uptake were not conserved, closely and distant-related species would show similar trait differences, resulting in a relationship that rapidly asymptotes (as shown in Appendix S1).

related phylogenetic distance to species' pair-wise niche differences and fitness differences (Question 2) and their likelihood of coexistence (Question 3). Our work is novel in quantifying the phylogenetic structure of competitive dominance, in demonstrating the inherently variable relationship of niche and fitness differences with phylogenetic distance, and in evaluating these relationships under field conditions.

METHODS

Study site, focal species and phylogeny construction

We conducted our study at the University of California Sedgwick Reserve in northern Santa Barbara County, USA (34° 40′ N, 120° 00′ W), 730 meters above sea level. The climate is Mediterranean with cool, wet winters and hot dry summers. Precipitation totalled 298 mm over the experimental year (October 2011–July 2012), 21% less than the 50-year average.

For our study, we initially selected 22 annual plant species common at the field site but four failed to consistently germinate and were not further considered (Appendix S2). While all species coexist at the scale of the entire reserve, our experiment was designed to evaluate the controls over competitive outcomes at the local scale of species interactions, where mathematical models have been shown to reasonably describe their dynamics (Godoy & Levine 2014). Species were selected to capture a spectrum of relatedness, ranging from closely related congeneric pairs to distantly related species from disparate orders (Appendix S2). Given that deep divergences can overwhelm other signals in phylogenetic community analyses (e.g. Kembel & Hubbell 2006), we focused our experiment on taxa within the eudicots. To estimate phylogenetic relatedness and divergence times between the competing species, we used Bayesian methods (BEAST v.1.7.5) (Drummond *et al*. 2012) incorporating information from four DNA loci compiled from GenBank (http://www.ncbi.nlm.nih.gov/genbank/, last accessed October 2012). We used an uncorrelated lognormal molecular clock and the GTR + I + Γ model for nucleotide substitutions at each locus. Complete construction details for the phylogeny are given in Appendix S3.

Theoretical background for quantifying niche and fitness differences, and predicting competitive outcomes

Our experiment was designed to parameterise a mathematical model from which neighbourhood scale stabilising niche differences, average fitness differences and predicted competitive outcomes could be quantified. Therefore, we first present the model describing the dynamics of competing annual plant populations with a seed bank as follows (Chesson 1990; Levine & HilleRisLambers 2009):

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

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 winter of year t. The germination rate of species i, g_i, is effectively a weighting term for 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 into a function describing how the per germinant fecundity declines with the density of competing germinated individuals in the system.

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

The per germinant fecundity of species i in the absence of competition, λ_i, is reduced by the germinated density of its own, ($g_i N_{i,t}$), and other species ($g_j N_{j,t}$). These germinated densities are multiplied by the interaction coefficients, describing the per capita effect of species j on species i (α_{ij}). Importantly, this model accurately predicts the outcome of competition between annual plants at the neighbourhood scale of species interactions at the study site (Godoy & Levine 2014).

With the dynamics of competition described by this population model, we followed the approach of Chesson (2012) to define the stabilising niche differences and the average fitness differences between each pair of species. This procedure is detailed in Godoy & Levine (2014), the results of which are summarised here.

For the model described by eqns 1 and 2, Godoy & Levine (2014) show that niche overlap, ρ, is the following:

$$\rho = \sqrt{\frac{\alpha_{ij}}{\alpha_{jj}} \cdot \frac{\alpha_{ji}}{\alpha_{ii}}} \tag{3}$$

It reflects the average degree to which species limit individuals of their own species relative to heterospecific competitors. If species much more strongly limit individuals of their own species than individuals of their competitors (α_{jj}, α_{ii}, are much greater than α_{ij}, α_{ji}), then niche overlap will be low, favouring coexistence. On the other hand, if species limit individuals of their own species and those of their competitor equally, niche overlap equals one, making coexistence impossible. With ρ defining niche overlap between a pair of species, their 'stabilising niche difference' is expressed as 1-ρ. For example, two species accessing water from very different soil depths would be expected to have limited niche overlap, and thus a large stabilising niche difference.

In contrast to stabilising niche differences, average fitness differences drive competitive dominance and exclusion. For the annual plant population model in eqns 1 and 2, Godoy & Levine (2014) show that the average fitness difference between the competitors is $\frac{\kappa_j}{\kappa_i}$, where

$$\frac{\kappa_j}{\kappa_i} = \left(\frac{\eta_j - 1}{\eta_i - 1}\right) \sqrt{\frac{\alpha_{ij}}{\alpha_{jj}} \cdot \frac{\alpha_{ii}}{\alpha_{ji}}} \tag{4}$$

and

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

The greater the ratio, $\frac{\kappa_j}{\kappa_i}$, the greater the fitness advantage of species j over i. If the ratio is one, the species are equivalent

competitors. From eqn 4, it can be seen that species gain competitive dominance by a combination of high demographic rates, in what we call the 'demographic ratio', $\left(\frac{\eta_j-1}{\eta_i-1}\right)$, and by low sensitivity to competition, in what we call the 'competitive response ratio' $\left(\sqrt{\frac{\alpha_{ij}}{\alpha_{jj}}}.\frac{\alpha_{ii}}{\alpha_{ji}}\right)$. Specifically, the demographic ratio describes the degree to which species j produces more seeds ($g_j\lambda_j$) per seed loss due to death or germination ($1-(1-g_j)(s_j)$) than species i. The competitive response ratio describes the degree to which species j is less sensitive to competition than species i. Notice that the numerator and denominator differ only in which species is responding to competition, and the arrangement of the interaction coefficients is not the same as with niche overlap (ρ).

To quantify each species' fitness against all other competitors, we also quantified κ_i as an absolute quantity (rather than part of a ratio) by assuming that niche differences are zero and that species i's competitive response, r_i is a species trait (explained in Appendix S4). We could fit r_i with a simpler model than one allowing for interaction coefficients specific to each species pair (fitting all pairwise α_{ij}'s), which allowed us to estimate some interaction coefficients missing from the pairwise analyses (Appendix S4).

Coexistence requires both species to invade when rare (Chesson 2012). This condition is satisfied when (Godoy & Levine 2014):

$$\rho < \frac{\kappa_j}{\kappa_i} < \frac{1}{\rho} \tag{5}$$

Therefore, competitors can coexist when large niche differences (little niche overlap) overcome large average fitness differences, or at the other extreme, when weak niche differences stabilise the interaction between competitors with similar fitness. We used this condition (or equivalently, the invasion growth rates) to predict the outcome of competition between all species pairs once the models were fully parameterised.

A competition experiment to obtain species' vital rates and competition coefficients

We conducted an experiment to parameterise models of pairwise competition between the 18 focal species finally considered with estimates of species' germination fractions (g_i), per germinant fecundities in the absence of neighbours (λ_i), seed survival in the soil (s_i) and all pairwise interaction coefficients (α_{ij}). In October 2011, we established 176 rectangular plots separated by landscape fabric to control weeds in a 500 m^2 area of finely textured serpentine soils previously cleared of all vegetation, and fenced to exclude deer and gophers. The overall design involved sowing each species as focal individuals into a density gradient of each competitor species (including itself). To create this gradient, we randomly assigned each plot to a single species at a competitor density of 2, 4, 8, or 16 g/m^2 of viable seed, and we sowed two replicate plots per density per species. The 2 g/m^2 plots were 1.5 × 1.7 m and all other densities were sown into 0.9 × 1.1 m plots. We then divided each plot into 42 subplots (a six row by seven column array) with a buffer zone from the plot edge of 2.5 cm. Each species was then sown with five viable seeds to establish 'focal' individuals at the centre of two subplots per plot, and these were subsequently thinned to a single focal species' germinant. In plots with a seed density of 2 g/m^2, the distance between focal individuals was 24 cm, whereas in plots with a higher seed density (and thus smaller plants), the distance between focal individuals was 14 cm in 0.9167 m^2. In addition, to assess species' demographic performance in the absence of neighbours, we sowed focal individuals of all species into ten 4 m^2 plots with no neighbours (> 32 cm between plants). Appendix S5 provides a schematic and outline of the experimental design.

All seeds were sown into the experiment in November 2011 prior to the first major rains of the winter. These seeds were collected on the reserve the prior spring and summer from 200 to 1000 mature mother plants per species. To ensure reasonable germination, we supplemented two early storms, one in December 2011 and one in January 2012, with an additional 60 mm of water per storm event, applied with sprinklers. Season-long 'rainfall' was increased by the supplementation but it remained near the 50-year average.

We quantified the germination of viable seeds (g_i) by counting the number of germinants in six of the aforementioned plots per species (density from 4 to 16 g/m^2). The total number of germinants was divided by the total number of viable seeds sown, and this fraction was averaged across plots for inclusion as the species' germination in the model.

To assess species' per germinant fecundities in the absence of neighbours (λ_i), and the per capita effect of each species on itself and their competitors (the interaction coefficients), we measured the seed production per germinant (F_i) of all focal individuals in the 176 plots (weighing the total mass of seeds produced, dividing through by seed weight, and correcting for viability). To quantify the competitive environment of each focal plant, we counted the number of competitor individuals within a 7-cm radius in early spring after germination.

At the completion of the experiment, we used maximum likelihood methods to fit both λ_i, and α_{ij} (bounded to be positive) according to the function:

$$F_i = \frac{\lambda_i}{1+\sum_j \alpha_{ij} N_{j,t}}$$

$N_{j,t}$ was the number of germinated competitor individuals of species j surrounding focal individuals of species i. For each target species i, we fit a separate model jointly evaluating its response to individuals of all other species and itself. This approach fits a single per germinant fecundity in the absence of competition, λ_i for each species i. To obtain the seed bank survival (s_i) in eqn 1, we followed the methods of Godoy & Levine (2014), burying seeds from November 2011 to August 2012.

Analysing the relationship between phylogeny and competition

With the empirically estimated vital rates and interaction coefficients, we tested for phylogenetic signal in species' competi-

tive ability (Question 1) quantified in two ways. First, we estimated species 'average fitness', and its demographic and competitive response components, by field parameterising eqn S2 (Appendix S4), which follows from eqn 4. This approach necessarily generates a fully transitive competitive hierarchy as would arise if all species compete for a single limiting resource (Appendix S4). Second, we ranked competitors by simulating the fully parameterised annual plant population model (eqns 1 and 2) with all 18 species. The competitor that excluded all others was given the highest rank, and then the simulation was run again without that competitor. This process was repeated until all species were ranked, and coexisting species were given a tied rank score. We then used Blomberg's K, Pagel's λ, and Moran's I, to test the phylogenetic signal of these various measures of competitive ability (details in Appendix S3). We used three different metrics because in general, phylogenetic metrics lack power with small phylogenies including those with < 20 taxa.

We next used the field parameters to calculate the niche differences (eqn 3), fitness differences (eqn 4), and predicted outcome of competition (evaluating the invasion growth rates) between each pair of species (eqn 5). With these measures, we regressed species' niche and fitness differences against their phylogenetic distance (in Mya) obtained from the phylogeny (Question 2). To accomplish this, we first performed Mantel tests to evaluate whether the relationships were statistically significant. Second and independent of the Mantel tests, we fit several non-linear curves to specifically estimate the shape of the relationship, because bounds to phenotypic space within a clade can result in asymptotic relationships between phylogenetic distance and trait difference. We only considered non-linear functions that pass through the origin because both niche and fitness differences equal zero between members of the same species. The alternative, a linear curve with a non-zero y-intercept would violate our theoretical framework. The function $y = a(1 - e^{-bx})$, which ranges from linear to asymptotic proved best (Appendix S6). The fitness differences analysed here assume a single limiting factor within each pair (but not for all 18 species), and thus different pairs can compete for different resources.

Finally, in cases where data only allowed us to fit three of the four interaction coefficients necessary for estimating the niche and fitness differences, we used the interaction coefficient produced by the product of the responding species' competitive response (r) and the effecting species competitive effect (e) for the missing coefficient (Appendix S4). Because we have no *a priori* hypotheses for how phylogeny predicts positive feedbacks, in the 15% of pairs where the interspecific effects exceeded intraspecific effects, the stabilising niche difference was set to zero (complete niche overlap) for subsequent analyses. Similar results for the relationship between phylogeny and niche differences were obtained when these cases were removed altogether (Appendix S6). Last, we used a permutation test and a bootstrap analysis to evaluate how phylogenetic distance related to the likelihood of coexistence between species pairs (Question 3), as predicted by the parameterised mutual invasion condition (eqn 5, details in 'Results'). All analyses were conducted in R (version 2.13.2) (R Development Core Team 2013).

RESULTS

Phylogenetic structure of competitive ability

We found that species' competitive ability as measured by either their competitive rank in simulations or their average fitness showed phylogenetic structure (Fig. 2). The better ranked competitors in simulation and those with the highest average fitness (κ) were clustered within the Asteraceae and its sister node, including *Plantago erecta* (Plantaginaceae) and *Salvia columbariae* (Lamiaceae). Meanwhile, the poorest competitors were the two members of the Geraniaceae (*Geranium carolinianum, Erodium botrys*) (Fig. 2). When we decomposed species' average fitness into its demographic (η) and the competitive response (r) components, we found that both show significant phylogenetic signal using one of three metrics (Fig. 2).

Relationships between phylogenetic distance and stabilising niche and fitness differences

Overall, we found that more distantly related competitors had significantly greater competitive asymmetries than close relatives (Fig. 3a), though the relationship was not strong. Furthermore, we found that phylogenetic distance was a better predictor of species differences in their sensitivity to competition (Fig. 3c) than their demographic productivity (the number of seeds produced per seed lost, Fig. 3b), though both contributed to the weak but significant correlation between phylogenetic distance and competitive dominance. As predicted, we found increasing variance in fitness differences and its components with increasing phylogenetic distance (Fig. 3, studentised Breusch–Pagan test = 4.96, $P = 0.026$). This means that while large average fitness differences were more likely to be found between distantly related taxa, many pairs of distantly related taxa show small fitness differences.

In contrast to average fitness differences, stabilising niche differences showed no significant relationship with phylogenetic distance (Fig. 4), despite the fact that our species pairs ranged in estimated divergence times from 50 to 320 million years. Given that species have no niche difference from themselves, we can infer that niche differences between these annual plants approach their asymptotic value in < 50 million years, although the shape of this rise cannot be determined from our species pairs (Fig. 4). Similar asymptotic relationships between phylogenetic distance and niche differences were observed with other non-linear functions (Appendix S6). Consistent with our lack of evidence for increasing niche differences with phylogenetic distance, and by inference no phylogenetic structure to species niches in this coexistence context, variance in niche differences did not increase with phylogenetic distance (studentised Breusch–Pagan test = 0.54, $P = 0.462$).

Does phylogenic relatedness predict competitive outcomes?

Using the criteria for coexistence in eqn 5, we calculated the niche difference necessary to stabilise coexistence between species pairs of varying phylogenetic distance, based on their predicted average fitness difference (the line in Fig. 3a). We found that over the range of relatedness between our species pairs, the

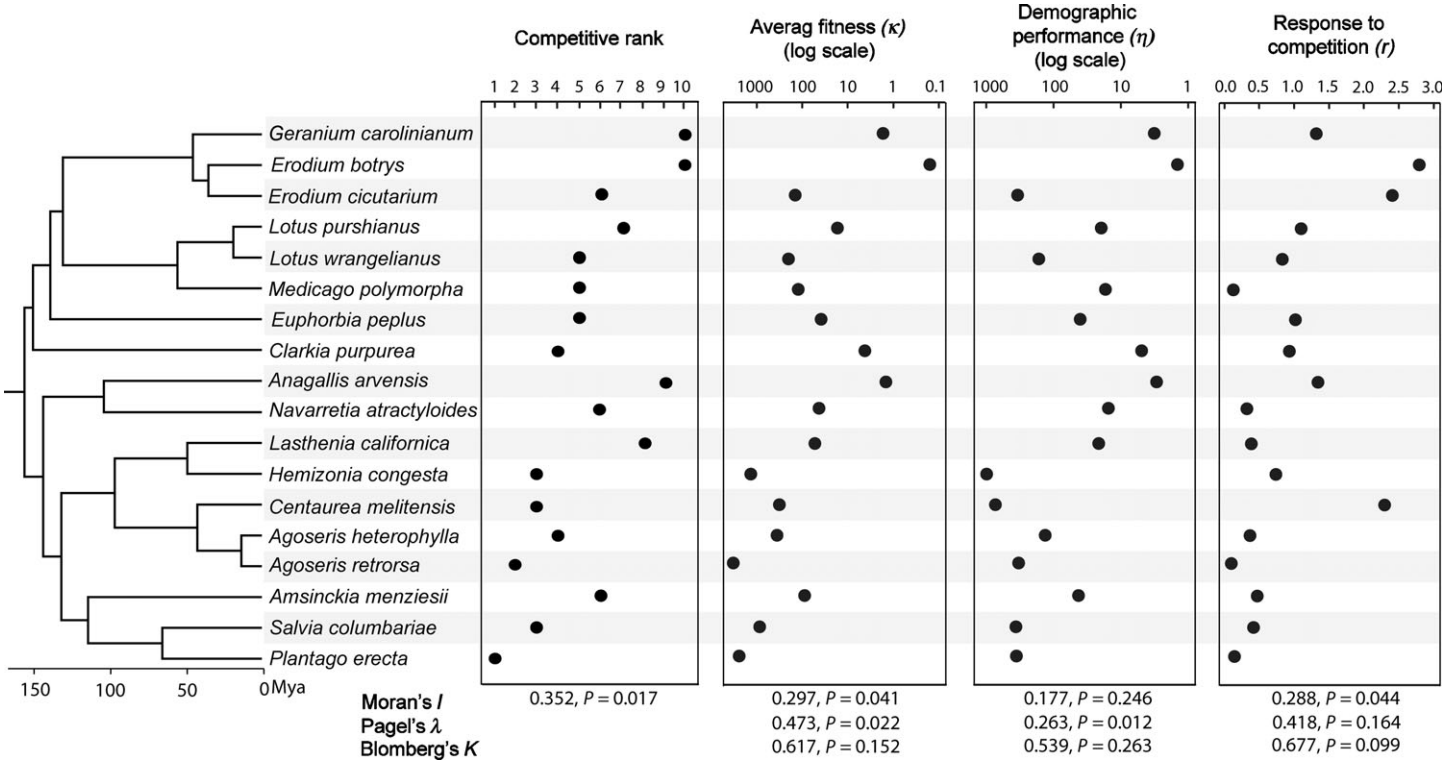

Figure 2 Phylogeny of the 18 annual plant species, their competitive rank from simulations, and theoretically derived measures of average fitness (κ) and its two components, demographic performance (η) and response to competition (r). Shown at the bottom are statistical measures of phylogenetic signal for all four measures of competitive ability. Node bootstrap support for the phylogeny is provided in the Appendix S3.

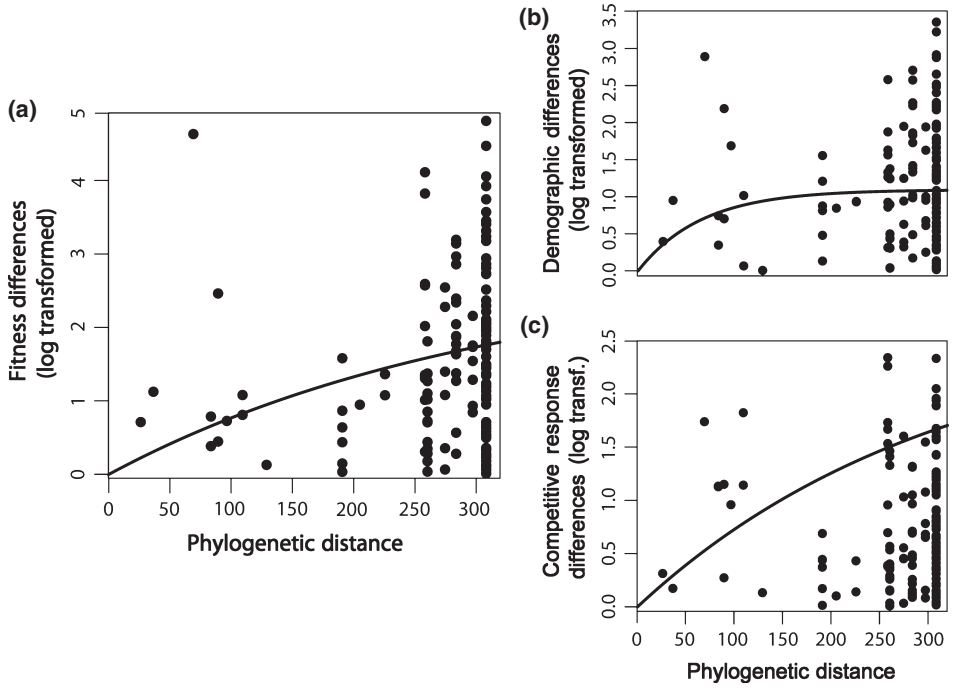

Figure 3 Relationship between species phylogenetic distance (in millions of years) and their (a) average fitness differences and its two components: (b) demographic differences and (c) competitive response differences. Lines show the best fit non-linear curve from Appendix S6. The statistical significance of the relationships between species' phylogenetic distance and their (a) fitness difference (r = 0.17, $P = 0.018$), (b) demographic difference (r = 0.10, $P = 0.092$) and (c) competitive response difference (r = 0.19, $P = 0.013$) comes from separate Mantel tests that properly account for the lack of independence among species pairs but assume linearity and are not fixed through the origin. Note the log transformation of the fitness differences, which were absolute valued before plotting.

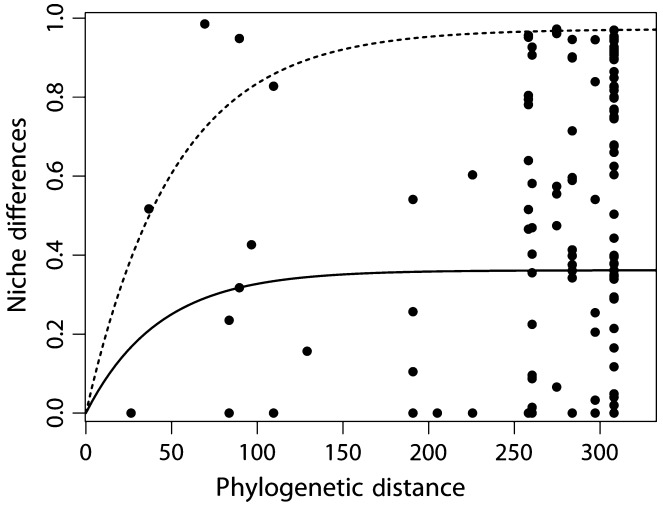

Figure 4 The relationship between stabilising niche differences and phylogenetic distance (in millions of years) for pairs of annual plant species in our experiment (solid line). The dashed line shows the strength of the niche difference necessary to stabilise the interaction between species of varying relatedness based on the relationship between relatedness and average fitness differences in Fig. 3a. Non-significant Mantel test results (r = 0.04, $P = 0.307$) and the rapidly asymptotic nature of the non-linear fit both support the lack of a relationship between niche differences and phylogenetic distance over the range of relatedness found among our species pairs.

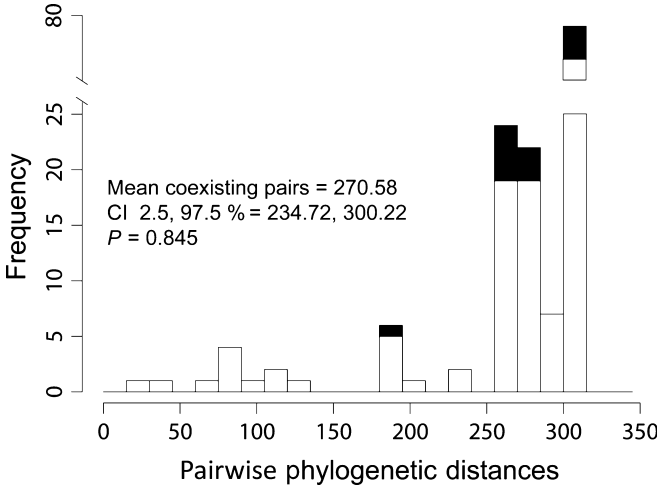

Figure 5 The twelve pairs of species predicted to coexist from parameterised models (shown in black) show phylogenetic distance that is consistent with 12 random draws from the pool of species pairs. Pair ages are given in Mya. Note the break in the *y*-axis.

predicted niche difference was generally less than that required for coexistence given the fitness differences (Fig. 4, the solid line lies below the dashed line). Moreover, the shortfall was greatest at the largest phylogenetic distances, as would be predicted with effects of phylogeny on fitness differences but not niche differences. For example, niche differences after 75 Mya of separation averaged 0.3. This is sufficient to stabilise competition between species with a fitness difference of *c*. 1.5, yet average fitness differences were 5 at 100 Mya and 25 at 250 Mya respectively. With more closely related species exhibiting a smaller gap between the observed and required niche differences, one would predict greater coexistence between more closely related species than distant relatives.

However, we found that the 12 pairs of species predicted to coexist from the parameterised models were not significantly more closely related than would be expected by chance according to a permutation test drawing 12 random species pairs 999 times from the 153 total pairs in the experiment. Similarly, a bootstrap analysis showed that the mean phylogenetic distance of the 12 pairs predicted to coexist fell well within the 95% confidence interval of phylogenetic distance for the randomly drawn pairs (Fig. 5). Of course, the fraction of species pairs that were predicted to coexist was quite small, so one explanation for our negative result is that we lacked enough coexisting pairs to test the influence of relatedness on this outcome. However, even when we relaxed the coexistence criterion from $\rho < \frac{\kappa_i}{\kappa_j}$ (where species *j* is the better competitor), to $0.9\rho < \frac{\kappa_i}{\kappa_j}$, which generated 18 pairs of coexisting species, we still found no significant effect of phylogenetic distance on likelihood of coexistence (mean phylogenetic distance coexisting pairs = 259.9 Mya, CI (2.5–97.5%) = 241.43–297.09, $P = 0.327$).

DISCUSSION

It has been over 150 years since Darwin proposed that greater niche overlap between more closely related species should hinder their coexistence. However, the opportunity to rigorously evaluate this hypothesis has only recently arisen with theoretical advances in coexistence research by Chesson (2000, 2012) and the ready availability of phylogenies. In this study, we found no evidence that evolutionary relatedness predicts the niche differences that stabilise coexistence between pairs of 18 annual plant species in California. By contrast, relatedness did predict species average fitness differences, which determine competitive dominance. The strongest competitors were phylogenetically clustered around the Asteraceae and its sister clade containing the Lamiaceae and Plantaginaceae (Fig. 2). Species distantly related to this group of superior competitors were up to three times more sensitive to competition and sometimes made three orders of magnitude fewer seeds per seed lost than their superiors (Fig. 2). These results provide some of the first empirical support for recent hypotheses that species' average fitness can show phylogenetic signal, causing increasing competitive asymmetry with phylogenetic distance (Mayfield & Levine 2010; HilleRisLambers *et al*. 2012).

A hypothesis with inherent variability

With fitness differences increasing with phylogenetic distance, and no influence of phylogeny on stabilising niche differences, we expected coexistence to be more common between more closely related taxa (Mayfield & Levine 2010), the opposite of Darwin's hypothesis. However, we found that species pairs predicted to coexist from our models were of no lesser phylo-

genetic distance than pairs randomly selected from the pool (Fig. 5).

This finding emerges partly from the limited number of species pairs in the experiment, and partly from the high degree of scatter in the relationship between phylogenetic distance and competitive dominance, which arises from two sources. First, there may be weak phylogenetic structure to the traits driving competitive dominance. Second, variable relationships are inherent to hypotheses based on a correlation between phylogenetic distance and a trait difference, even for traits showing strong phylogenetic structure. Indeed, we observed phylogenetic signal in species' competitive fitness and increasing variance in fitness differences with phylogenetic distance (Fig. 3); more distantly related taxa had on average greater fitness differences, although several distantly related taxa still had small average fitness differences between them. This variability was enough to allow some distantly related species to coexist, suggesting that the outcome of competition can be more variable for distant than close relatives. For example, even if on average, both niche and fitness differences increase with phylogenetic distance, the increasing variance in these relationships means that only distant relatives are likely combine large competitive asymmetries with small niche differences (rapid competitive exclusion), or large niche differences with small competitive asymmetries (highly stable coexistence). Overall, our results suggest that increasing variance in niche or fitness differences with phylogenetic distance may play a central role in determining the phylogenetic relatedness of coexisting species.

Scale and other limitations

Stabilising niche differences and average fitness differences between species depend on the spatial and temporal scale of study. Our study was specifically designed to evaluate these quantities at the local scale of species interactions, the scale that is the most feasible for experiments. However, coexistence and the outcome of competition may depend on species differences in how they respond to spatial environmental heterogeneity occurring at scales greater than our study plots (Chesson 2000). In fact, the phylogenetic structure to competitive dominance at our experimental site can potentially drive stabilising niche differences at larger scales in a spatially heterogeneous landscape. This would arise if different clades were competitively favoured in different locations. For example, members of the Asteraceae and its sister clade were competitively favoured within our experimental plot (Fig. 2), but species from other clades that co-occur at the larger scale of Sedgwick reserve might be favoured on drier, rockier soils unexplored in this study. Prior observational work has shown that species with contrasting phenotypes from disparate clades show site-specific competitive or demographic advantages (Lloret *et al.* 2005; Diez *et al.* 2008; Burns & Strauss 2011). Phylogenetic structure to species responses to temporal variability or between year soil feedbacks (Mills & Bever 1998) can similarly underlie a relationship between phylogeny and coexistence at longer time scales than our study.

Our approach of fitting competition models to experimental data is an important advance over prior studies of the competition-relatedness hypothesis, because it directly evaluates the relationship between phylogeny and stabilising niche differences, which lies at the heart of Darwin's hypothesis (but see Narwani *et al.* 2013). Our model is flexible, allowing, for example, different pairs of species to compete for different limiting factors, although it does have key assumptions (beyond the scale issue of the prior paragraph). Importantly, it assumes additive effects of all competing species, something difficult to empirically evaluate. Doing so in future work, however, brings the opportunity to test how relatedness predicts competitive outcomes under diffuse competition, an interesting avenue for future studies.

CONCLUSIONS

Our results have demonstrated two reasons that Darwin's hypothesis concerning coexistence and relatedness may be overly simplistic. First, because phylogeny can predict species' average fitness differences, as shown here, and these counter any potential relationship between evolutionary relatedness and stabilising niche differences, there is no clear expectation for how relatedness predicts the outcome of competition. Second, because the stabilising niche differences and fitness differences that actually determine the outcome of competition are expected to increase in variance with phylogenetic distance, we should expect greater variance in competitive outcomes; more rapid exclusion and more stable coexistence with phylogenetic distance. Together, these insights should give further pause to investigators using phylogenetic patterns to infer competitive relationships, even when niche and/or fitness traits are phylogenetically conserved.

ACKNOWLEDGEMENTS

Lindsey Rice helped with field work. Janneke Hille Ris Lambers helped with the R code for fitting the competition coefficients. Peter Chesson showed us how to obtain expressions for stabilising niche differences and average fitness differences for the annual plant model. Peter Adler, Jake Alexander, Monique de Jager, Sabine Güsewell, Nicky Lustenhouwer, Anita Narwani and Tanja Stadler provided comments on the manuscript. O.G acknowledges postdoctoral financial support provided by the Spanish Ministry for Education and Science and Fulbright Commission (FU-2009-0039). J.M.L. acknowledges support from the Packard Foundation, and NSF grant DEB 0743365.

AUTHORSHIP

All authors designed the study. OG and NJBK conducted fieldwork. OG built the molecular phylogeny. NJBK estimated the competition coefficients. OG and NJBK analysed the results. OG and JML wrote the first draft of the manuscript and NJBK contributed substantially to revisions.

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Editor, Jerome Chave
Manuscript received 6 January 2014
First decision made 11 February 2014
Manuscript accepted 2 April 2014