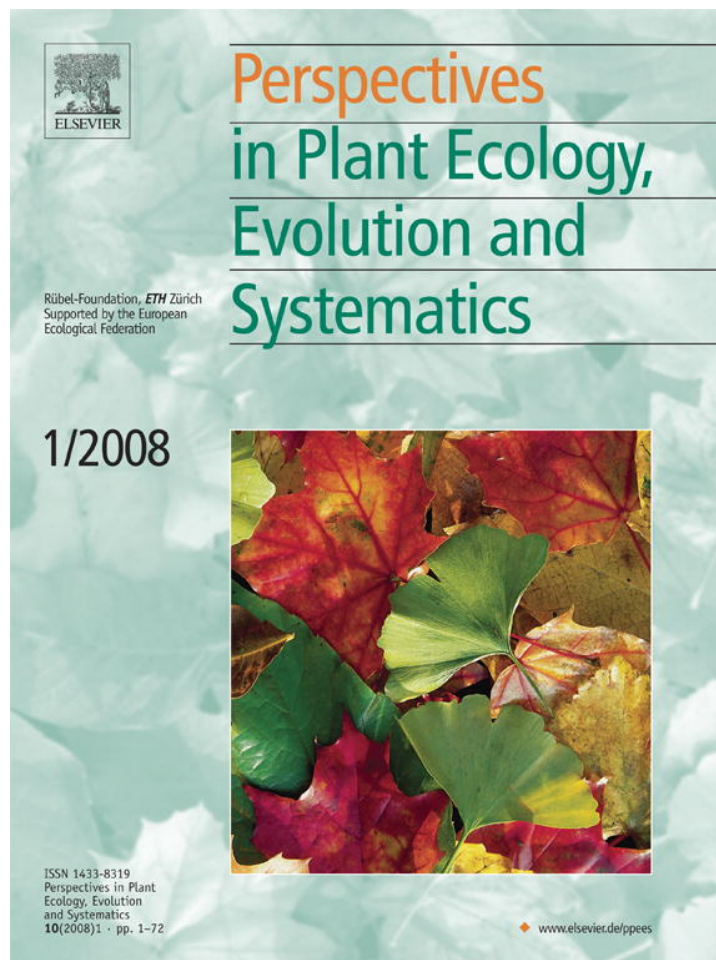


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Does phylogenetic relatedness influence the strength of competition among vascular plants?

James F. Cahill Jr.^{a,*}, Steven W. Kembel^{a,1,2}, Eric G. Lamb^{a,1,3}, Paul A. Keddy^b^a*Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada T6G 2E9*^b*Department of Biological Sciences, Southeastern Louisiana University, Box 10736, Hammond, LA 70402, USA*

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Abstract

A widely assumed but largely untested hypothesis central to ecology and evolutionary biology has been Charles Darwin's suggestion that closely related species will be more ecologically similar, and thus will compete more strongly with each other than they will with more distantly related species. We provide one of the first direct tests of the "competition-relatedness hypothesis" by combining two data sets: the relative competitive ability of 50 vascular plant species competing against 92 competitor species measured in five multi-species experiments, and measures of the phylogenetic relatedness of these species. In contrast to Darwin's assertion, there were weak relationships between the strength of competition and phylogenetic relatedness. Across all species studied, the competition-relatedness relationship was weak and not significant. This overall lack of pattern masked different responses of monocot and eudicot focal (phytometer) species. When monocots served as the focal (phytometer) species, the intensity of competition increased with the phylogenetic distance separating species, while competition decreased with phylogenetic distance for eudicot phytometers. These results were driven by the monocot-eudicot evolutionary split, such that monocots were poor competitors against eudicots, while eudicots are most strongly suppressed by other eudicots. There was no relationship between relatedness and competition for eudicots competing with other eudicots, while monocots did compete more intensely with closely related monocots than with distantly related monocots. Overall, the relationships between competition intensity and relatedness were weak compared to the strong and consistent relationships between competitive ability and functional traits such as plant size that have been reported by other studies. We suggest that Darwin's assertion that competition will be strongest among closely related species is not supported by empirical data, at least for the 142 vascular plant species in this study.

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Keywords: Comparative analysis; Competitive effect; Evolution of competitive ability; Phylogeny; Phytometer

*Corresponding author. Tel.: +1 780 492 3792; fax: +1 780 492 9234.

E-mail addresses: jc.cahill@ualberta.ca (J.F. Cahill Jr.), skembel@berkeley.edu (S.W. Kembel), eric.lamb@usask.ca (E.G. Lamb), pkeddy@selu.edu (P.A. Keddy).¹These authors contributed equally to this work.²Current address: Department of Integrative Biology, University of California, Berkeley, CA 94720, USA.³Current address: Department of Soil Science, University of Saskatchewan, Saskatoon, SK, Canada S7N 5A8.

Introduction

As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera. (Darwin, 1859).

The idea that closely related species compete more strongly than more distantly related species is a central tenet of community ecology. This idea, which we term the “competition-relatedness hypothesis”, has been widely discussed by a diversity of researchers (Elton, 1946; Park, 1948; Dayan and Simberloff, 2005), and has been integrated into foundational ecological theories including competitive exclusion (Hardin, 1960), character displacement (Brown and Wilson, 1956) and studies of community taxonomic and phylogenetic structure (Webb et al., 2002). Despite Darwin's idea being at the heart of much of community ecology, it has not been directly tested using a large number of species for nearly 150 years.

Darwin's idea of close relatives competing more strongly than distantly related species is based upon the observation of species being displaced by the invasion of a closely related species (Darwin, 1859). A pattern of phylogenetic overdispersion in community structure (to use modern parlance) would be predicted if close relatives compete intensely, and such a pattern has been documented by numerous studies (Elton, 1946; Maherali and Klironomos, 2007) and interpreted as evidence for the importance of competition among close relatives. However, phylogenetic overdispersion could be caused by a number of mechanisms other than competition (Kraft et al., 2007), such as facilitation by distantly related species (Valiente-Banuet and Verdu, 2007).

An additional aspect of Darwin's assertion is the idea that there is a phylogenetic signal (Blomberg et al., 2003) in the niches and traits of species, and that close relatives are more similar in ‘habits and constitution’. There is some support for this pattern of phylogenetic niche conservatism at broad phylogenetic scales (Prinzing et al., 2001; Wiens and Graham, 2005), although niches and traits can evolve in a convergent or random fashion within many clades (Blomberg et al., 2003; Silvertown et al., 2006), meaning that close relatives are not always the most similar in structure (*sensu* Darwin). As a result, several aspects of Darwin's initial assertion remain unresolved.

One possible reason that Darwin's assertion has not been widely tested is different views among subdisciplines about what is meant by the word ‘competition’. A critical difference between botanical and zoological approaches to the study of competition has been that competition among species in animal communities has generally been inferred based upon the *outcome* of

competition, as measured by changes in the co-occurrences of species (Keddy, 2001; Grime, 2006). This is in contrast to directly measuring the *process* of competition, as is commonly done in plant communities (Keddy, 2001; Grime, 2006). Keddy (2001) makes this point clear when he states, “the term ‘struggle for existence’ should not be seen as synonymous with ‘competition’; this has caused no small amount of confusion, because the term ‘struggle for existence’ is so widely appreciated as the driving force of evolution and speciation. A struggle for existence can include more than just the struggle of organisms with their neighbors for food, or more generally for resources”. It is this view of competition as one of many mechanisms that leads to ‘struggle’ that we use here, and that which suggest Darwin (1859) was referring to when he stated “Not until we reach the extreme confines of life, in the Arctic regions or on the borders of an utter desert, will competition cease.”

Due to the difficulty of measuring the strength of competition between species directly, numerous studies have sought indirect evidence for competition in the taxonomic or phylogenetic structure of ecological communities, assuming that if close relatives are ecologically similar and compete more intensely, they will occur together less frequently than expected by chance, leading to a pattern of taxonomic or phylogenetic overdispersion in ecological communities (Elton, 1946; Harper et al., 1961; Webb et al., 2002).

To directly test the hypothesis that phylogenetic relatedness and the strength of competition are correlated, it is essential to have direct measurements of competition, rather than simply patterns of species occurrence, which may be affected by numerous processes other than competition (Adler et al., 2007; Kraft et al., 2007). A handful of studies have directly tested whether competition is stronger amongst closely related individuals within a species (Cheplick and Kane, 2004), stronger among congeners versus members of different genera (Resetarits, 1995), or have measured competition intensity within and among functional groups (Johansson and Keddy, 1991).

Previous efforts to address this question have been limited by the difficulty of conducting competition experiments involving large numbers of species. The number of treatments needed to conduct pairwise tests of competitive interactions among N species is $N(N-1)/2$. As a result, a modest comparative study of 10 species would require 45 treatments, and a more reasonable comparative study with 50 species would require 1225 treatments.

One solution to the problem of comparing competitive abilities among large numbers of species, while keeping the experimental design within reason, is to deliberately simplify the experimental design (Keddy, 2001). Instead of including all possible pairwise combinations, all the species of interest are grown in competition with one, or a few, common comparison species (the ‘phytometer’ species) (Gaudet and Keddy, 1988). In such a design,

competition is measured as a species' ability to intercept resources and suppress the growth of the phytometer, relative to the growth of the phytometer alone (Goldberg, 1990, 1996; Keddy, 2001). This approach measures competitive effect, not response (sensu Goldberg, 1990). There is substantial evidence to suggest that competitive hierarchies are concordant in plants and, although phytometer identity can influence the absolute strength of competition, it does not influence the ranking of competitive effects among test species (Keddy and Shipley, 1989; Shipley, 1993; Goldberg, 1996).

By combining measures of competitive ability (Table 1; Gaudet and Keddy, 1995; Rösch et al., 1997a; Keddy et al., 1998, 2000, 2002) with phylogenetic distances among species based on molecular phylogenies including those species, we are able to provide the first comparative test involving large numbers of species of the question: 'Is competition stronger among more closely related species than among more distantly related species?'

Materials and methods

Data collection

Data were collected from previously published comparative studies of plant competition. A literature

search on the ISI Web of Science in March 2006, using terms such as "competitive hierarchy" and "competitive effect" was used to identify potential studies. Additional studies were identified through the reference lists of the potential studies. Due to the comparative nature of the question we are testing, we established several stringent study selection criteria. (1) The study must have been published in a peer reviewed journal. (2) The study must include a minimum of five unique combinations of species grown in competition, along with data on the phytometer's growth in the absence of any competition. (3) The study must have used an additive, rather than replacement series design, as these alternative designs measure very different aspects of plant competition (Keddy, 2001).

These criteria resulted in five suitable studies (Gaudet and Keddy, 1995; Rösch et al., 1997a; Keddy et al., 1998, 2000, 2002), each of which reported the competitive effect of a number of plant species on phytometers in pot experiments. Study details are presented in Table 1. Together these datasets included 50 phytometer and 126 competitor species (Fig. 1 and Online Supplemental Table 1). Since some species were used as both phytometers and competitors, the dataset included a total of 142 species in 419 unique phytometer–competitor species combinations. This is a large number of data points, and should provide for a robust test of the

Table 1. Summary of studies used as data sources in this paper. Note that not all possible target–competitor combinations were used in some studies or were not reported due to mortality in all replicates

| Study | # Target–competitor species pairs ^a | Experimental design |
|-------------------------|--|---|
| Gaudet and Keddy (1995) | 54 | 41 competitor species and 2 target species. 4 competitor individuals (single ramets collected in the field) planted around a single target plant (grown from seed) in 11 pots. 5 replicates per species combination; total biomass harvested after 1 growing season. |
| Rösch et al. (1997a) | 39 | 10 competitor species and 4 target species. 1 competitor and 1 target individual grown from seed in 11 pots. 5 replicates per species combination; aboveground biomass harvested after 17 weeks. Both high and low nutrient treatments were included in this experiment; competitive effects from the high nutrient treatments are used here. |
| Keddy et al. (1998) | 247 | 7 competitor species and 48 target species. Dense swards of each competitor species established from seed and grown for three years in 101 pots. 1 target individual (45 species single ramets collected in the field and 3 species grown from seed) was planted into the center of each sward. 1 replicate per species combination; aboveground target biomass harvested after 1 growing season. |
| Keddy et al. (2000) | 26 | 26 competitor species and 1 target species. 3 competitor individuals (single ramets collected in the field) around a single target plant (grown from seed) in 1 litre pots. 5 replicates per species; aboveground biomass harvested after 1 growing season. Both high and low nutrient treatments were included in this experiment; competitive effects from the high nutrient treatments are used here. |
| Keddy et al. (2002) | 63 | 63 competitor species and 1 target species. 3 competitor individuals (single ramets collected in the field) around a single target plant (grown from seed) in 1 litre pots. Five replicates per pot; total biomass measured after 1 growing season. Both unstressed and stressed (smaller pots, reduced water and nutrients) treatments were included in this experiment; competitive effects measured in the unstressed treatment are used here. |

^aTen species pairs were replicated in more than one study (Gaudet and Keddy 1995–Keddy et al. 1998: 2 pairs; Gaudet and Keddy 1995–Keddy et al. 2000: 5 pairs; Keddy et al. 1998–Keddy et al. 2000: 3 pairs). In all cases the average *z*-scores of the replicated pairs were used in this analysis.

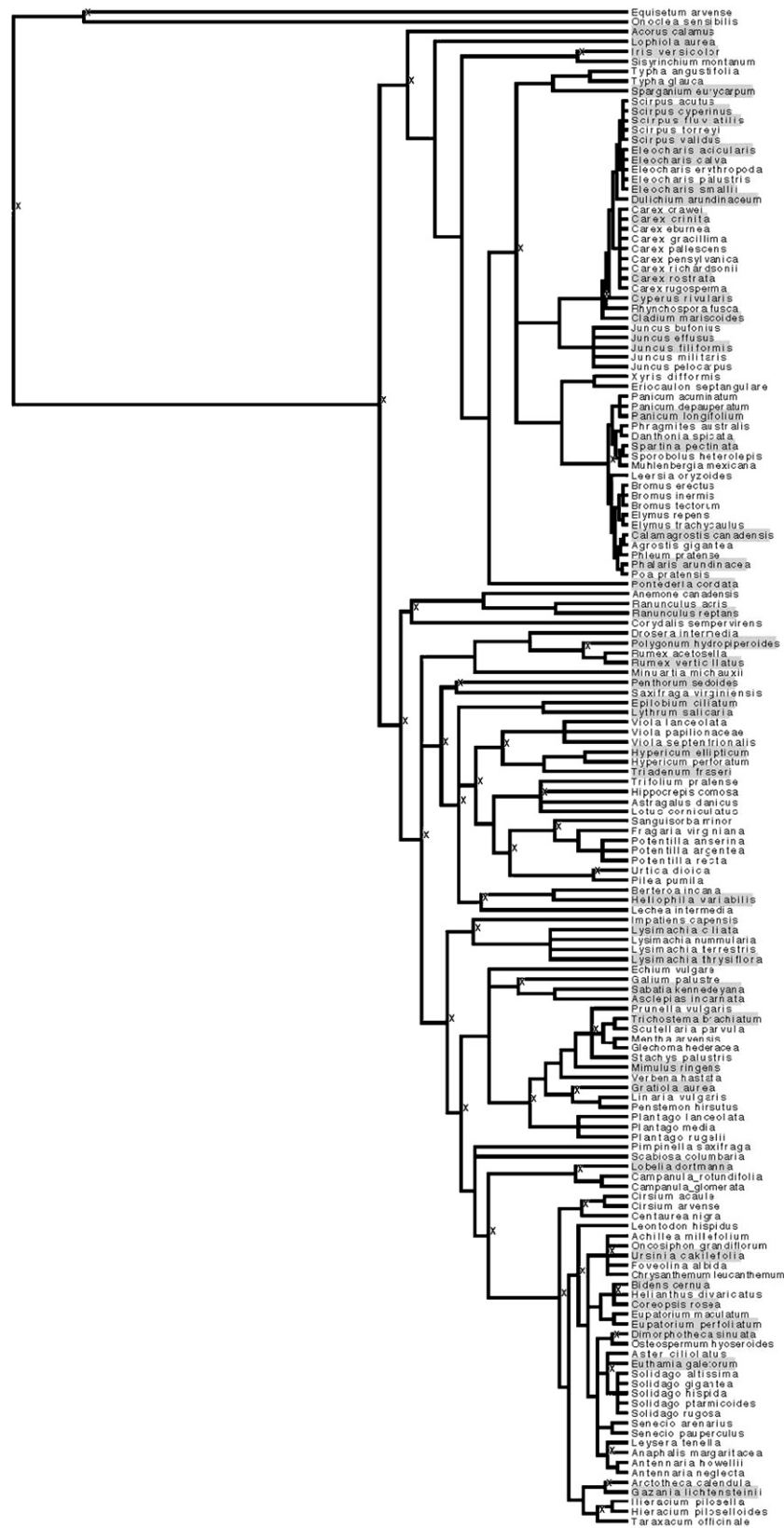


Fig. 1. Hypothesized phylogenetic relationships among all species included in this study. Nodes labeled with an X had their age fixed based on clade age estimates reported by Wikstrom et al. (2001) and Pryer et al. (2004). Species shaded gray were used as phytometers in at least one study.

competition-relatedness hypothesis. No effort was made to restrict this test to only native or introduced species.

The studies used were all pot experiments where a single phytometer plant was grown both alone and in competition with one or more individual of the competitor species. In all cases, we report competitive effect as the percentage reduction in phytometer biomass when grown with the competitor compared to phytometer biomass when grown alone. Experimental conditions differed between the studies, but in general the experiments were conducted in non-stressful conditions with abundant water and nutrients, and lasted for one growing season. Several of these studies included both high and low resource and stress treatments, but due to insufficient numbers of species combinations from the low resource treatments, all analyses in this paper are based on plants grown in high-resource conditions.

The species used were largely herbaceous species of wetland (Gaudet and Keddy, 1995; Keddy et al., 1998, 2000), old field, rock barren, and alvar (Keddy et al., 2002) habitats in northeastern North America, and an arid ephemeral community from Namaqualand, South Africa (Rösch et al., 1997a). These species belong to the major angiosperm clades, and include many representatives from large families including the Asteraceae, Poaceae, and Cyperaceae, as well as from families including the Liliaceae, Xyridaceae, Violaceae and Droseraceae (Fig. 1). Several large genera had multiple species represented including *Scirpus* (five species), *Eleocharis* (five species), *Carex* (nine species), *Juncus* (five species), and *Solidago* (five species). The wetland plants occupy habitats that are dominated by herbaceous species and often have strong nutrient gradients and fluctuating water levels (Gaudet and Keddy, 1995). Although the location of wetlands may change during glacial periods, wetland habitats are widespread and there are good reasons to assume that these species have interacted for millions of years in both glaciated and non-glaciated areas (Keddy, 2000). Old fields are more recent habitats in North America, although some of the species that occur in these conditions may have naturally occupied adjoining savannas and alvars, which have always been a prominent feature of the North American vegetation (Anderson et al., 1999). The Namaqualand species are members of an annual ephemeral community that rapidly develops in the spring of years with extensive winter rainfall (Rösch et al., 1997a, b).

We obtained a phylogenetic hypothesis for the 142 species included in this study using Phylomatic (Webb and Donoghue, 2004), a tree assembly toolkit and database. The backbone of the resulting tree was based on an expert interpretation (Stevens, 2006) of the APG II (Angiosperm Phylogeny Group, 2003) phylogenetic classification of flowering plant orders and families.

Within-family phylogenetic relationships were further resolved based on data from various published molecular phylogenies (Poaceae (Salamin et al., 2002), Asteraceae (Bremer, 1994), Cyperaceae (Roalson et al., 2001), Rosaceae (Eriksson et al., 2003), Fabaceae (Doyle et al., 1997), Lamiales (Olmstead et al., 2001; Walker et al., 2004), Scrophulariaceae (Olmstead et al., 2001). Branch lengths for the phylogeny were obtained using the BLADJ module of Phylocom version 3.40 software (Webb et al., 2006), which fixed the age of 41 internal nodes based on published clade age estimates (Wikstrom et al., 2001; Pryer et al., 2004). Undated internal nodes in the phylogeny were spaced evenly between dated nodes to minimize tree-wide variance in branch length.

Data analysis

Given the existence of numerous studies of competition, each of which used one or more phytometer species with a varying number of competitor species, we employed a meta-analytic framework to measure the overall evidence for a relationship between the strength of competition and phylogenetic distance. Meta-analyses incorporate variation in observed correlations and sample sizes among different data sources when calculating the average correlation or 'effect size' across all data sources (MetaWin, 1997). Since the strength of a relationship between competition and relatedness could vary depending on the phytometer species used, we treated each phytometer's competition-relatedness correlation as a data point in a meta-analysis. For each phytometer, we calculated the Spearman rank correlation between the competitive effect of each competitor species and the phylogenetic distance separating that species from the phytometer. The use of Spearman correlations was necessary due to non-normal distributions of competition intensities and phylogenetic branch lengths separating species.

Phytometers differed in the number of competitor species used to calculate the competition-relatedness correlation. To account for this, we treated each phytometer's correlation between competition and relatedness as the effect size in a meta-analysis while the number of competitor species against which a particular phytometer grew was used as the sample size. We used MetaWin (1997) to calculate the mean effect size across all phytometers, equivalent to the mean correlation between competition and phylogenetic relatedness, taking into account variation in the number of different species each phytometer competed against.

This statistical approach provides a clear test of the effects of phylogenetic distance on competitive effect between two species. However, it does not allow us to determine what other factors, such as differences in

plant size, are associated with the observed variation in competitive effect among species pairs. Unfortunately, because the studies were conducted under different growth conditions, it is impossible to make meaningful comparisons of plant traits (e.g. size) across studies. As a result, we are unable to determine whether any phylogenetic-competition relationship becomes stronger, or more muted, after controlling for size (or other trait differences) among competing species.

Inspection of the overall meta-analysis results indicated that the sign of the correlation between competition and relatedness appeared to differ depending on whether phytometers were monocots or eudicots. We first re-analyzed the data using a random effects model with the class of the phytometer as a grouping variable and effect size as the response variable. To further explore relationships among monocots and among eudicots, we re-analyzed the data for monocot phytometers competing against only monocot competitor species, and for eudicot phytometers competing against only eudicot competitor species. It was not possible to estimate the correlation between competition and relatedness for eudicot phytometers competing against monocot competitors or for monocot phytometers competing against eudicot competitors, since all pairs of species in these two groups are equally distantly related through their most recent common ancestor.

Results

In general, there was a weak, but non-significant, tendency for plant species to compete more intensely with their close relatives. Across all phytometer species and studies, the average correlation between competition intensity and the phylogenetic distance separating species was negative, but the effect size was very small and overlapped with zero (Mean competition-relatedness correlation = -0.13 , $N = 50$, 95% CI: -0.31 to 0.04) (Fig. 2). In addition to the meta-analysis presented here, we have analyzed these data a number of different ways, including (1) treating every study (rather than each phytometer) as different data points, and (2) pooling all data together and using a regression to determine if there was an overall relationship between competition and phylogenetic distance. The answer from all three approaches has been consistent: there is a tendency for a slight negative relationship between phylogenetic distance and competition, though the effect size is low. Whether the actual statistic is non-significant, such as in the current analyses, or significant (as found in one of the two prior analyses), is not important. Regardless of statistical significance, there is no strong effect of relatedness on the strength of competition between species.

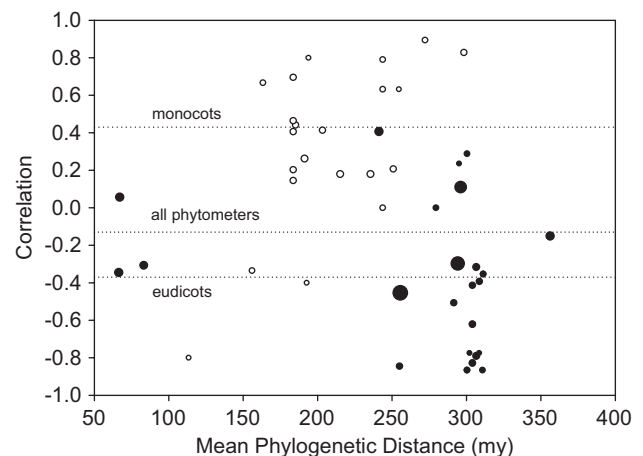


Fig. 2. Correlation (Spearman's rho) between competitive effect and mean phylogenetic distance for each phytometer. The y-value of each data point represents the correlation coefficient between the strength of competition and the phylogenetic distance of each of the competitor species, for one phytometer species. The x-value of each data point represents the average phylogenetic distance between a given phytometer and all of the species against which it competed. The use of this x-axis is for visualization only to show that different phytometers varied greatly in the average relatedness of their competitors. Symbol sizes are proportional to sample size. Filled circles are eudicot phytometers, and open circles are monocot phytometers. Reference lines represent the mean effect size for all phytometers, monocot phytometers, and eudicot phytometers.

Underlying the lack of overall effect were differences among taxa within the study (Online Supplemental Table 1). There was a significant difference in the mean correlation between phylogenetic distance and competition for monocot and eudicot phytometers ($P < 0.001$; random effects model). Monocot phytometers competed most intensely with their distant relatives (mean effect size (95% CI) = 0.43 (0.15 – 0.71)), but eudicot phytometers competed most intensely with close relatives (Mean effect size (95% CI) = -0.37 (-0.52 to -0.23)). These results appear driven primarily by differences in competitive ability among monocots (whose distant relatives were the more competitive eudicots) and eudicots (whose close relatives were other competitive eudicots). When analyzed based only upon within-clade competition, monocot phytometers competed more intensely with closely related monocots (mean effect size = -1.00 , $N = 13$, 95% CI: -1.59 to -0.40), while eudicots showed no significant relationship between competition and phylogenetic distance (mean effect size = -0.15 , $N = 8$, 95% CI: -0.59 to 0.29).

Discussion

Overall, these results provide limited support for Darwin's assertion that closely related species will

compete more strongly than more distantly related species (Fig. 2; Darwin, 1859). The finding that species have the potential to compete strongly regardless of their relatedness is consistent with the view that competition is strong and widespread among plant species (Aarssen and Epp, 1990; Goldberg and Barton, 1992; Gurevitch et al., 1992; Keddy, 2001). It is interesting to note that the relatively weak competition-relatedness correlations we found are similar to those that would be predicted if competition has been a persistent and strong selective force, leading toward niche differentiation and character displacement over evolutionary time (Connell, 1980). This however is an extremely difficult hypothesis to test, and is most often assumed (Connell, 1990; Keddy, 2001). This particular study is unable to differentiate whether the minor decrease in competition with increased phylogenetic distance is due to niche differentiation and character displacement or due to evolutionary changes unrelated to competition. Alternatively, it is not significant and not meaningful. To answer such questions will require a better understanding of both the microevolutionary consequences of competition among plants (Miller, 1995) and the macroevolutionary history of the evolution of traits related to plant competitive ability (Gaudet and Keddy, 1988).

Although, not significant, there was a weak negative relationship between relatedness and competition (Fig. 2). The relatively small effect size could be due to a variety of factors. First, as in any meta-analysis, methodological differences among the studies may have obscured underlying patterns. A second explanation could be that the plant traits related to competitive ability are not necessarily evolutionarily conserved, and thus phylogenetic history may not be particularly important in determining the strength and outcome of competitive interactions. For example, several studies have found plant height and other functional traits to be tightly correlated with competitive ability (Mitchley and Grubb, 1986; Gaudet and Keddy, 1988; Rösch et al., 1997b). Among some of the species included in this study, Gaudet and Keddy (1988) found that biomass alone could explain 63% of the variation in competitive ability among species with traits such as height and canopy characteristics explaining much of the remaining variation. Thus, knowledge of ecological traits may be more valuable than phylogenetic information if we wish to predict and understand the competitive ability of a given species. However, to determine the relative importance of phylogeny and plant traits in determining the strength of competition requires additional information about the morphology and physiology of the species used in the study, which was not available for all of the studies used here. Because competition can play an important role in structuring plant communities (Tilman, 1988; Grime, 2001; Keddy, 2001), resolution of

this issue is critical to improving our understanding of the evolutionary ecology of natural communities.

Differences in competitive effect between monocots and eudicots (Fig. 2) suggest fundamental differences in functional ecology related to competition in these two clades. Within each clade the intensity of competition was consistent, but eudicots were much better competitors against monocot phytometers than monocots were against eudicot phytometers. There are numerous differences in functional traits (e.g. morphological, physiological, and ecological) that could contribute to the stronger competitive effects of eudicots on monocots. For example, meristems positioned near the shoot tips and secondary growth producing woody stems are important eudicot traits associated with large size, a trait itself tightly associated with high competitive ability (Gaudet and Keddy 1988; Rösch et al., 1997b). Belowground trait differences between monocots and eudicots that could lead to greater eudicot competitive ability are less clear. Eudicots often forage more precisely at smaller spatial scales than monocots (Kembel and Cahill, 2005); more precise nutrient foraging may confer a competitive advantage when rooting volumes are limited.

One limitation of this study is that data were obtained exclusively from plants grown under fertile conditions. As a result, competition for light was likely the dominant form of competition. It is unclear whether the same results would be obtained under lower nutrient conditions where root competition would likely be much more intense (Grime, 1977; Casper and Jackson, 1997; Keddy, 2001), or where they may have been non-additive interactions between above- and belowground competition (Cahill, 1999). There is experimental evidence to support both sides of the argument, as shifts in competitive hierarchies among a few species have been observed following changes in resource availability and disturbance (e.g. Rice and Menke, 1985; Wilson and Tilman, 1995; Suding and Goldberg, 2001), while larger comparative studies have generally found that hierarchies are relatively stable between environments (Rösch et al., 1997a; Keddy et al., 1994, 1998, 2000, 2002).

Darwin's original hypothesis focused on the ecological similarity of and competition between congeners. We did not specifically test the strength of competition between congeneric species, but our use of molecular phylogenetic information and fossil age estimates to measure relatedness allowed us to test for more general relationships between relatedness and competition. Although the analyses here are the largest tests to date of this long-standing assumption, we note that our analyses were conducted on a narrow range of species, raising questions about the generality of our findings. We limited our analysis to vascular plants, but in Darwin's initial presentation of his assertion he

provided examples of charlock (a mustard), cockroaches, thrush, swallows, and rats, clearly indicating he believed this to be a widespread phenomenon that could influence species from diverse lineages. We did not use a random selection of vascular plants, but the species included a broad array of families and genera, and occurred in several different habitats.

In summary, this study provides little support for Darwin's assertion that closely related species will compete more strongly than more distantly related species. The wide variation in interaction strength among distantly related species was partly driven by the pattern of strong competitive effects of eudicots on monocots but only weak effects of monocots on eudicots. The different competitive effects of species from these two clades suggest that there are fundamental differences in their functional ecology related to competition. Relatedness was weakly related to competitive ability, and it is likely that much more variation in competitive ability can be explained by functional traits than by phylogenetic history.

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Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.ppees.2007.10.001](https://doi.org/10.1016/j.ppees.2007.10.001)

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