Phylogenetic context determines the role of competition in adaptive radiation

Jiaqi Tan¹, Matthew R. Slattery², Xian Yang¹ and Lin Jiang¹

¹School of Biology, Georgia Institute of Technology, Atlanta, GA 30332, USA
²Department of Environmental and Molecular Toxicology, Oregon State University, Corvallis, OR 97330, USA

Understanding ecological mechanisms regulating the evolution of biodiversity is of much interest to ecologists and evolutionary biologists. Adaptive radiation constitutes an important evolutionary process that generates biodiversity. Competition has long been thought to influence adaptive radiation, but the directionality of its effect and associated mechanisms remain ambiguous. Here, we report a rigorous experimental test of the role of competition on adaptive radiation using the rapidly evolving bacterium Pseudomonas fluorescens SBW25 interacting with multiple bacterial species that differed in their phylogenetic distance to the diversifying bacterium. We showed that the inhibitive effect of competitors on the adaptive radiation of P. fluorescens decreased as their phylogenetic distance increased. To explain this phylogenetic dependency of adaptive radiation, we linked the phylogenetic distance between P. fluorescens and its competitors to their niche and competitive fitness differences. Competitive fitness differences, which showed weak phylogenetic signal, reduced P. fluorescens abundance and thus diversification, whereas phylogenetically conserved niche differences promoted diversification. These results demonstrate the context dependency of competitive effects on adaptive radiation, and highlight the importance of past evolutionary history for ongoing evolutionary processes.

1. Introduction

One important evolutionary process that generates biodiversity is adaptive radiation, through which a species lineage diversifies rapidly to occupy available niches within a habitat [1–4]. Often found in insular environments, such as islands [2,5,6] and lakes [7,8], adaptive radiation has been thought to be influenced by two main factors: the availability of ecological niches and the size of ancestral populations [3,9]. Whereas niche availability may affect the selective pressure on the diversifying species, and thus, their establishment [3,9,10], ancestral population size governs the supply of genetic variation, and thus, the potential of diversification. By affecting these two factors, competition—one of the most ubiquitous species interactions—may influence adaptive radiation [11–15]. Several empirical studies [12,16,17] have assessed the role of competition in adaptive radiation. The majority of these studies, however, are based on comparisons of lineages found on islands (where fewer competitors are present) versus those found on the mainland (where more competitors are present) [17–19], or experiments manipulating the presence/absence of intraspecific competitors [14,20,21]. While the findings of observational studies are vulnerable to alternative explanations, experimental studies of intraspecific competition tell us little about how species from evolutionarily more distant lineages affect adaptive radiation. The few experimental tests of the role of interspecific competition, which have either considered a single competitor species [15], or competition from complex natural communities [22], have produced mixed findings. Here, we provide a rigorous experimental test of how competition influences adaptive radiation by allowing the diversifying species to interact with various known intraspecific and interspecific competitors.

In the common scenario where diversifying lineages have the opportunity to interact with different competitors, the strength of competition could vary, with potential consequences for adaptive radiation. In particular, the phylogenetic relationship between the diversifying and competing species may influence
competition, as species traits that determine their interactions are often constrained by their evolutionary histories [23–27]. The variation in these important functional traits across species, however, may translate into differences in species niche and/or competitive fitness, both of which may be important for regulating adaptive radiation [28]. Whereas greater niche difference may reduce niche overlap between diversifying and competing species, supporting larger populations and providing more available niche space for diversification, lower competitive fitness advantage of competing species may also increase the size of diversifying populations, resulting in greater evolutionary potential. Consequently, how phylogenetic distance between the diversifying and competing species relates to competition depends on how species niche and fitness vary across phylogeny [29–31]. For example, in situations where species niches, but not competitive fitness, are phylogenetically conserved, competition may be stronger between more closely related species if it is more strongly influenced by species niche difference than by competitive fitness difference. On the other hand, in situations where only species competitive fitness is phylogenetically conserved, strong competition could occur between distantly related competitors if competition is driven by species competitive fitness difference rather than by niche difference [30]. Applying these ideas to adaptive radiation, we hypothesize that niche and competitive fitness differences together will determine the competitive response of the diversifying lineage, and in turn, its diversification. Furthermore, we hypothesize that how competitors with different phylogenetic distance to the diversifying species affect diversification will depend on the relative strength of their niche and competitive fitness differences and the phylogenetic signal of these differences. We note that experimental tests of these hypotheses, which have not been conducted, will provide important knowledge on the linkage between species past evolutionary histories and contemporary evolution.

Here, we report an experimental study examining the effect of competition on adaptive radiation, using the rapidly diversifying bacterium *Pseudomonas fluorescens* SBW25 (hereafter SBW25) [21,32–34] as the model organism. In a spatially structured environment (e.g. static microcosms), SBW25 diversifies rapidly and generates a multitude of phenotypes that use different spatial niches. We used multiple environmental bacterial species, which vary in their relatedness to SBW25, as the competitors (figure 1a). We found that competition tended to have an overall negative effect on adaptive radiation. This inhibitive effect of competition, however, decreased with the phylogenetic distance between SBW25 and its competitors. To explain this result, we linked phylogenetic relations of SBW25 and competitors to their competitive fitness and niche, and demonstrated the important roles of competitive fitness and niche differences in regulating the population size and niche availability for the diversification of SBW25.

### 2. Material and methods

#### (a) Bacterial species

We used a smooth morph phenotype colony of *P. fluorescens* SBW25 as the ancestral bacterium [33]. The smooth morph phenotype we used carries a lacZ marker, which makes colonies derived from it exhibit a distinct blue colour on agar with 40 mg l⁻¹ 5-bromo-4-chloro-3-indolyl-β-D-galactopyranoside (X-gal) [21]. Provided with various spatial niche opportunities in static microcosms, smooth morph, which is initially distributed in the broth, diversifies rapidly into multiple specialized phenotypes. Among these phenotypes are the fuzzy spreader, which colonizes the bottom of microcosms, and a variety of wrinkly spreaders, including small-, large-, wheel- and smooth morph-like-wrinkly spreaders, which form biofilm at the air–broth interface. Each SBW25 phenotype has been genetically identified and forms colonies with distinct morphological characteristics on agar (see electronic supplementary material, figure S1) [35]. We can thus distinguish them from each other (p ≥ 0.05).

![Figure 1. The phylogenetic relationship of the bacterium *Pseudomonas fluorescens* SBW25 (short as SBW25) to its competitors *Pseudomonas fluorescens* (PF), *Pseudomonas putida* (PP), *Aerogenes hydrophilia* (AH), *Seratia marcescens* (SER), *Bacillus pumulis* (BP) and *Bacillus cereus* (BC) (a), and SBW25 population density (b) and phenotypic richness (c) in the presence of each individual competitor. The numbers at each node of the phylogenetic tree in panel (a) are the posterior probabilities of node support. Values in panels (b) and (c) are means ± s.e. The significance of differences among the treatments was tested by one-way ANOVA, followed by Tukey’s HSD tests. Treatments sharing the same letter are not different from each other (p ≥ 0.05).](http://rspb.royalsocietypublishing.org/content/journals/10.1098/rspb.2016.2624)
Six common environmental bacteria were used as the competitors of SBW25 (figure 1a). We sequenced the 16S rRNA gene of our study species, including SBW25, and constructed the phylogenetic tree based on the gene sequences (figure 1b). We first aligned these sequences with MAFFT v. 7.316 

We terminated the experiment and destructively sampled each microcosm on day 12. We first mixed the culture in each microcosm by vigorously vortexing the microcosm for 1 min. We acknowledge that some biofilm may not be completely broken apart by this approach, and thus, the population density of wrinkly spreaders may be somewhat underestimated. We then collected the sample from each microcosm, serially diluted the sample with sterilized water, plated the diluted samples on agar with X-gal and incubated the agar plates under 28°C for 3 days. To estimate the abundance of each SBW25 phenotype and competing species, we counted the number of colonies for common and rare strains on separate plates corresponding to different dilution levels (generally 1:10^5 or 1:10^6 dilution for common strains and 1:10^3 dilution for rare strains). To obtain a reliable estimate of SBW25 phenotypic richness (i.e. the number of SBW25 phenotypes present) in each microcosm, we carefully screened the low-dilution (generally 1:10^3 dilution) plates for the presence/absence of each phenotype. To examine the possibility that the variation in sampling effort (the cumulative number of screened colonies on each phenotype) in the rate at which evolution was set equal in every lineage, with the Bayesian method in MrBayes (v. 3.1.2) [43]. One archaeal species was used as the outgroup. Based on the phylogenetic tree, we calculated the phylogenetic distance between SBW25 and each competing bacterial strain by summing the length of intervening branches between them. The diversifying SBW25 and one competitor—P. fluorescens (PF), which was obtained from the Carolina Biological Supply (Burlington, NC), belong to the same species. However, there is significant genetic difference between the two (0.7% in their 16S rRNA sequence). PF did not carry the lacZ marker, and did not diversify within the duration of our experiment.

(b) Experimental protocols

In our experiment, we allowed each competing species to interact with SBW25, and assessed the influence of each of them on the diversification of SBW25. We also set up a control treatment in which competitors of SBW25 were absent (figure 1b,c). Each treatment was replicated six times. The experimental microcosms used in our experiment comprised 25 ml capped test tubes, each containing 6 ml King’s medium B. Prior to the experiment, we plated each bacterial species on agar, randomly selected one colony for each species (one smooth morph colony for SBW25), transferred the selected colonies into test tubes with 6 ml medium, and incubated the cultures under shaking (250 r.p.m) at 28°C overnight. At the beginning of the experiment, we introduced approximately 10^4 individuals of each competing species and SBW25 into their designated microcosms. The microcosms were incubated statically under 28°C for 12 days, which were sufficiently long for the variety of SBW25 phenotypes to emerge [44].

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(c) Quantifying the niche and competitive fitness differences between SBW25 and competitors

We quantified the niche and competitive fitness differences based on the competitive responses of SBW25 and its competitors to each other, following the method of Narwani et al. [31]. We first measured the competitive response of SBW25 to each competing species. We introduced a small number of SBW25 individuals (approx. 10^3 CFU) into competitor-absent microcosms, and into microcosms that had been colonized by a competing species for 24 h, with each treatment replicated three times. We then estimated the population density of SBW25 at hour 0 and 6 in these microcosms with agar plate counts, and calculated the growth rate of SBW25 in the absence (r_meren) and presence (r_poly) of competitors. The competitive response (CR1) of SBW25 to its competitors was calculated as

\[ CR1 = 1 - \frac{r_{poly}}{r_{mono}} \]

Likewise, we measured the growth rate of each competing species when alone and when subject to competition from SBW25, and calculated its competitive response (CR2) to SBW25. All competitive responses, except for those of SBW25 facing Bacillus cereus or Bacillus pumilus, were greater than zero, indicating the presence of competition between SBW25 and the competing species. The competition between SBW25 and B. cereus and between SBW25 and B. pumilus was highly asymmetric (i.e. CR2, but not CR1, is significantly greater than zero in these cases).

Greater niche differences between SBW25 and competitors would result in lower values of both CR1 and CR2, whereas greater competitive fitness differences would lead to greater differences between CR1 and CR2. Therefore, niche and competitive fitness differences of each competing species from SBW25 were calculated [48] as

\[ \text{nichie difference} = 1 - \sqrt{CR1 \cdot CR2} \]

and

\[ \text{competitive fitness difference} = \frac{\sqrt{CR1}}{CR2} \]

Note that competitive fitness differences were expressed as the competitive advantage of competitors over SBW25 in equation (2.3). We also took an alternative approach in estimating the niche and competitive fitness differences between SBW25 and its competitors. In this approach, niche differences were quantified as the differences in bacterial spatial niche preference in three locations (air–broth interface, broth phase and bottom) within the microcosms (see more details in electronic supplementary material, figure S4), and competitive fitness differences were quantified as the differences in bacterial intrinsic growth rates in monocultures. As these approaches produced qualitatively similar results (see electronic supplementary material, figure S4), here we presented those based on competitive responses only.

(d) Data analysis

To assess the effect of competitors on SBW25 population size, we conducted one-way ANOVA, followed by Tukey’s honest significance test (HSD) tests, with the competitors (seven classes, including the control) as the class variable, and SBW25 population density as the dependent variable. To improve data normality, we log-transformed (log_{10}(y + 1)) population density data prior to the
Figure 2. The relationship between SBW25–competitor phylogenetic distance and niche difference (a), and the relationship between SBW25–competitor phylogenetic distance and competitive fitness (b). Data are plotted with regression lines. Niche and competitive fitness difference values were averaged across replicates.

Table 1. Summary of multiple regression analyses. SBW25 population density and phenotypic richness were related to SBW25–competitor phylogenetic distance, niche and competitive fitness differences by multiple linear and Poisson regression models, respectively. Test statistics of the linear regression model are t-values for variables and F-value for the model, and those of the Poisson regression model are Wald $\chi^2$ values for variables and likelihood ratio $\chi^2$ value for the model.

<table>
<thead>
<tr>
<th>response variable (n = 36)</th>
<th>source of variance</th>
<th>test statistic</th>
<th>p-value</th>
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<td>niche difference</td>
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<td>model</td>
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<tr>
<td>phenotypic richness (Poisson)</td>
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Analysis. Because the phenotypic richness data were discrete and followed a Poisson distribution (goodness-of-fit test: $\chi^2 = 27.964$, $p = 0.520$), we examined the effect of different competitors on SBW25 phenotypic richness in a generalized linear model (GLIM) with Poisson distribution, followed by Tukey’s HSD tests. We tested the relationship between SBW25–competitor phylogenetic distance and their niche and competitive fitness differences using simple linear regressions. Multiple linear and Poisson regressions were performed to assess the overall effects of SBW25–competitor phylogenetic distance and their niche and competitive fitness differences on SBW25 population size and phenotypic richness, respectively. Separate simple linear and Poisson regressions were used to test for the effects of each predictor variable on SBW25 population size and phenotypic richness, respectively. We also examined the relationship between SBW25 population density and phenotypic richness with Poisson regression. All statistical analyses were performed in R v. 3.2.2 [49]. Tukey’s HSD tests for GLIM were performed with the ‘glht’ function in the ‘multcomp’ package [50], the rarefaction curves were generated with the ‘rarecurve’ function in the ‘vegan’ package [51] and the asymptotic phenotypic richness was calculated with the ‘iNext’ function in the ‘iNext’ package [47,52].

3. Results
The effects exerted by different competitors on the population density of SBW25 varied significantly (figure 1b; one-way ANOVA: $F_{6,35} = 10.379$, $p < 0.001$). SBW25 population density was reduced by two of the six competitors (i.e. P. fluorescens (PF) and Serratia marcescens; Tukey’s HSD, $p < 0.05$), but not by the other four competitors. Likewise, the competitors differed in their effects on SBW25 phenotypic richness (figure 1c; Poisson GLIM: Wald $\chi^2 = 58.141$, d.f. = 6, $p < 0.001$), which was reduced by three competitors (i.e. P. fluorescens (PF), Aeromonas hydrophilia and S. marcescens; Tukey’s HSD, $p < 0.05$).

Linear regression showed that the niche difference between SBW25 and its competitors increased with their phylogenetic distance (figure 2a; $R^2 = 0.816$, $p = 0.014$), indicating significant phylogenetic signal of species niches. In contrast, the competitive fitness difference between SBW25 and its competitors was not related to their phylogenetic distance (figure 2b; $R^2 = 0.210$, $p = 0.360$).

Multiple regressions revealed that only competitive fitness difference, not phylogenetic distance or niche differences, had strong influence on SBW25 population density, whereas all the three variables were found significant for SBW25 phenotypic richness (table 1). Simple regressions confirmed these results (figure 3). SBW25 population density declined with increasing competitive fitness difference, but was unaffected by phylogenetic distance or niche difference (figure 3a,c,e). On the other hand, SBW25 phenotypic richness increased as phylogenetic distance and niche difference increased, but declined as competitive fitness difference increased (figure 3b,d,f).
In addition, we found that SBW25 phenotypic richness was positively related to its population density (figure 4; Poisson regression: pseudo-$R^2 = 0.724$, $p < 0.001$). This positive relationship between SBW25 phenotypic richness and population density remained, even after the data from microcosms in which SBW25 was driven to extinction (i.e. its population size was zero) were excluded (pseudo-$R^2 = 0.449$, $p < 0.001$).

4. Discussion

Competition is widely considered as a key ecological factor, influencing adaptive radiation [3]. A number of experimental studies [20–22,53] have compared adaptive radiation in the presence and absence of competitors, and found that competition, either from different phenotypes of the same species or different species, frequently reduced diversification. No [15] or a positive [20] effect of competition on diversification has also been reported. However, we know little about how phylogenetic context, as the outcome of past evolutionary history, influences adaptive radiation. Our study explored the situation in which the diversifying species faces various competitors differing in their phylogenetic distance to the diversifying species, a scenario that is likely to occur in nature, and reported three notable findings (summarized in figure 5). First, diversification varied with phylogenetic distance between the competing and diversifying species, characterizing the context dependency of the impacts of competition on adaptive radiation (figure 3b). Second, the phylogenetically conserved niche difference affected adaptive radiation without changing the population size of the diversifying species (figure 3c, d), pointing to the importance of niche
availability for adaptive radiation. Third, the competitive fitness difference between the diversifying species and competitors, while not phylogenetically conserved, was the only factor regulating the population size of the diversifying species (figure 3d), with ensuing consequences for adaptive radiation (figure 3f). We discuss these findings in more detail below.

We hypothesized that knowledge of factors regulating the strength of interactions between diversifying and competing species was important for predicting adaptive radiation. The positive effect of phylogenetic distance on diversification observed in our experiment (table 1 and figure 3) provided direct support for this hypothesis. One possible scenario where this result could arise is that phylogenetically more closely related species are more similar in their niches, but not competitive fitness, and thus, compete more strongly. This scenario likely played out in our experiment where difference in niches, including those related to species spatial distribution (i.e. spatial niches), was phylogenetically conserved, but difference in competitive fitness was not (figure 2). The strong phylogenetic signal of niche indicates that its availability for the diversifying species would decrease as the phylogenetic distance between the diversifying and competing species decreased. Note, however, that the reduction in niche availability suppressed diversification, without altering population size of the diversifying species (figure 3c,d and electronic supplementary material, figure S4). These results therefore provided strong support for the importance of niche pre-emption as a potentially important mechanism for competition to reduce adaptive radiation [20–22,53].

In our experiment, the competitive fitness of competing species, though not phylogenetically conserved, was the only significant predictor of SBW25 population size (table 1 and figure 3e). The observed negative effect of competition on SBW25 population size was further transmitted onto a negative effect on diversification (figure 3f), through the dependence of SBW25 diversification on its population size (figure 4). In particular, the higher competitive fitness of two species, A. hydrophila and S. marcescens (figure 2b), led to lower SBW25 abundance and possibly more rapid niche occupation, resulting in lower levels of diversification (figure 1c). Similar results were also reported by Bailey et al. [20], who found a negative relationship between the fitness of SBW25’s intraspecific competitors and its diversification. Importantly, when their effects were considered together in a multiple regression, phylogenetic distance, niche and competitive fitness differences remained significant predictors of SBW25 phenotypic richness (table 1). This result suggests the importance of taking both phylogenetically conserved and non-conserved traits, including niche and competitive ability differences, into consideration for making predictions under the phylogenetic context.

Our results show that the population size of the diversifying lineages is the key transmitter of the effect of competitive fitness difference on adaptive radiation. The positive association between SBW25 population size and diversification found in our study (figure 4) provided strong support for the reduction of population size as an important mechanism through which adaptive radiation is inhibited. Similar relationships between population size and diversification have been reported in studies involving SBW25 [37,38] and other diversifying lineages [54,55]. Small population size tends to discourage adaptive radiation for several reasons. First, small population size means reduced intraspecific competition, translating into weak disruptive selection [56]. Second, even given constant per capita mutation rates, small ancestral populations would produce fewer mutants than large ones [57]. Third, cooperation that may create novel niches is less likely to occur in smaller populations. In our experiment, biofilm formation that requires cooperation may be reduced in small P. fluorescens populations, with a negative effect on the emergence of new WS phenotypes [35,53].

Figure 4. The relationship between SBW25 population density and phenotypic richness as revealed by Poisson regressions. The solid line indicates the relationship when all the data were considered. The dashed line indicates the relationship when data from the microcosms in which SBW25 was driven to extinction, and therefore, its phenotypic richness was automatically zero were excluded. Note that the density data were recorded as colony forming units (CFU) per ml and log10 (x + 1)-transformed. Jitters were vertically added to overlapping data points to make them visible.

Figure 5. A schematic diagram summarizes the effects of phylogenetic distance, niche and competitive fitness differences between the diversifying and competing species on the population size and adaptive radiation of the diversifying species. The significant positive and negative relationships found in our experiment are indicated by the red and blue arrows, respectively, while the non-significant relationships are indicated by the grey dashed lines. (Online version in colour.)
Darwin's phylogenetic-limiting similarity hypothesis suggests the increased likelihood of coexistence between more distantly related species, based on the premise that closely related species tend to be similar in their niches and thus compete strongly [23]. While having received some experimental support [24–26,58], this hypothesis has been challenged recently [29–31,59–61]. By linking the modern species coexistence theory, which emphasizes the importance of both species niche and competitive fitness differences [28], to phylogenetic divergence among species, Mayfield & Levine [30] suggested that the pattern predicted by the phylogenetic-limiting similarity hypothesis is just one of several possible scenarios that could play out in competitive communities. Mayfield & Levine [30] made their suggestion by considering the variation in the phylogenetic signal of species niche and competitive fitness. Ecologists have just begun to apply this framework to empirical systems. For example, Narwani et al. [31] reported that neither niche nor competitive fitness differences among green freshwater algae were phylogenetically conserved, and consequently, species phylogenetic relationships did not predict competitive outcomes. Godoy et al. [29], on the other hand, found that phylogenetic distance predicted the competitive fitness difference, but not niche difference, among the annual plant species they studied in California. The increased variance in competitive fitness difference with increasing phylogenetic distance, however, led to a non-significant effect of phylogeny on competitive outcomes in their study. Applying Mayfield & Levine’s [30] framework to adaptive radiation under competition, we found that increasing species phylogenetic distance increased species niche difference, but not competitive fitness difference, and that species phylogenetic distance significantly affected diversification. Note that the existing microbial studies have frequently detected significant phylogenetic signal for species niches [24–26,58], despite the various possible scenarios of how phylogenetic distance might also be related to their competitive fitness [29–31]. One interesting question is thus whether there is some fundamental difference between microorganisms and macroorganisms in their niche and competitive fitness distribution patterns across phylogeny. Obviously, the limited number of empirical studies precludes a general conclusion, emphasizing the need for more studies on this topic across various organisms.

Our study shows that the phylogenetic distance between the radiating lineage and competitors has an appreciable influence on adaptive radiation, demonstrating a linkage between species evolutionary histories and contemporary evolution. Mechanistically, the observed phylogenetic distance effect on adaptive radiation arises from phylogenetically conserved species niche difference, which influences niche availability in the habitat, and non-conserved species competitive fitness difference, which influences population size of the radiating lineage (figure 5). These results thus illustrate the importance of knowledge on the distribution of niche and competitive fitness differences across species phylogeny for better understanding patterns of adaptive radiation. More generally, such knowledge will help us evaluate the extent to which information on species phylogenetic relationships is useful for understanding mechanisms of community assembly, as originally hypothesized by Darwin [23].

Data accessibility. Experimental data are published in the Dryad Digital Repository (http://datadryad.org/review?doi=10.5061/dryad.7n4f3). Phylogenetic data are available in TreeBASE (accession number S19320).

Authors’ contributions. J.T. and L.J. designed the study; J.T. and M.R.S. performed the experiment; J.T., X.Y. and L.J. analysed the data and wrote the paper.

Competing interests. The authors have no competing interests.

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