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**Phylogenetically novel species are more successful due to high competitive ability at local
and regional spatial scales**

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Senior Honors Thesis

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ABSTRACT

While few introduced exotic species become invasive, this small number of species poses serious threats to biodiversity, ecosystem function, and recreation, leading ecologists to study why certain species become invasive and why certain communities are prone to invasions. Several leading hypotheses seek to explain invasiveness, including the Enemy Release Hypothesis, the trait superiority hypothesis, and the Biotic Resistance Hypothesis, but none are consistently supported in the literature. We suggest that the lack of uniting hypothesis is a result of the inability to put multiple proposed mechanisms in the same framework, and suggest for a uniting framework Darwin's Naturalization Hypothesis along with a mechanistic approach and a view of multiple spatial scales. We address this by conducting an experimental study seeking the response of the effect of a competitor reduction treatment to phylogenetic novelty for native and invasive species over local and regional scales. We address (1) whether phylogenetic novelty correlates with high competitive ability, (2) if and how this relationship differs when novelty is assessed at regional versus local spatial scales, and (3) how this mechanism differs between native and invasive species. We find a significant negative correlation between phylogenetic novelty and effect of competitor reduction at both spatial scales tested, indicating that novel species are better competitors, though the relationship is driven mostly by native rather than invasive species. Our results increase our understanding of Darwin's Naturalization Hypothesis because we are the first to show that novel species are more successful due to increased competitive ability. These results are consistent with many other studies that find a correlation between phylogenetic novelty and spread of invasive species, tapping competition as an important mechanism in invasion.

INTRODUCTION

The rapid spread of exotic species in our globalized society poses serious threats to biodiversity, ecosystem function, and recreation. Invasive exotic species are now considered to be the greatest global threat to biodiversity, after habitat loss (Wilcove 1998, Powell et al 2013). The total economic cost of these species in the US alone has been estimated at 120 billion dollars annually (Pimentel 2005). While many exotic species are introduced into new habitats, only about 10% are able to establish in their new environment, and only about 10% of those established will spread rapidly and become invasive (Williamson and Fitter 1996). Given the huge impact of this small number of species, two major goals of ecological research are to discover why certain species become invasive while others do not, and why certain communities are prone to invasions while others are not.

Two of the most prominent hypotheses that address why certain plants become invasive are enemy release and trait superiority. The Enemy Release Hypothesis posits that exotic species leave their specialist enemies behind when they expand into a new range (Keane and Crawley 2002, Liu and Stiling 2006). Thus they receive less pressure from specialist enemies than the native species in the communities they invade. While generalist enemies may attack them, these enemies attack all species similarly, so exotic species suffer less damage overall than their native competitors. This advantage allows them to outperform native species. Alternatively, the trait superiority hypothesis proposes that invasive species have superior traits to the native species in the range they are invading (Van Kleunen et al. 2010, Kolar and Lodge 2001). The advantage may come in many forms, for instance allelopathy which is the chemical suppression of other nearby vegetation, or the ability to fix nitrogen at faster rates (e.g., Vitousek and Walker 1989). However, studies investigating these two hypotheses have found mixed results, and no single

hypothesis so far proposed is consistent with all plant invasions. Sometimes, invasive plants receive lower levels of enemy damage than native plants and exotic non-invasive plants (e.g. Mitchell and Power, 2003), while other times invasive plants have similar levels of damage or even more damage (e.g. Agrawal and Kotanen 2003, Funk and Throop 2010). Similarly invasive plants may sometimes have traits that differ from those of native plants and exotic non-invasive plants, while other times traits appear to explain little about invasiveness (Pysek and Richardson 2007).

It has long been thought that diverse ecological communities should resist invasion by exotic species. The Biotic Resistance Hypothesis posits that communities with more species are more resistant to biological invasion because they use more niche space, leaving less room for potential invaders (Elton 1958). However, the relationship between biodiversity and invasibility remains unclear. Some studies show that increasing biodiversity decreases invasibility (e.g. Maron and Marler 2007) while others show that more diverse habitats contain more exotic species (e.g. Stohlgren et al 2003).

One reason that no uniting hypothesis explains all plant invasions may be because most studies consider only a single hypothesis, when in fact multiple mechanisms addressed in these hypotheses are at work (Lowry et al 2013). A prospective uniting hypothesis would place both species-based hypotheses like the Enemy Release Hypothesis and the superior traits hypothesis, with community-based hypotheses like the Biotic Resistance Hypothesis into the same framework.

One framework that helps integrate the two perspectives is Darwin's Naturalization Hypothesis, proposed back in 1859, which suggests that novel species should be more invasive than less novel species (Darwin 1859). Under this hypothesis, a species with traits allowing for

high competitive ability will be more invasive, but only if this trait is not already present in the target community. In this way, the hypothesis addresses simultaneously elements of the species-based invasion hypotheses and of the community-based invasion hypotheses. While the connection to multiple invasion hypotheses is promising, Darwin's Naturalization Hypothesis has also seen both support and contradiction. Many studies have sought a connection between phylogenetic novelty and invasiveness, but the results are mixed (Strauss et al 2006, Diez et al 2008, Thuiller et al 2010). However, most studies consider only a single spatial scale, namely the phylogenetic novelty of a species compared to species in a large geographic region (e.g. Strauss et al 2006). At large spatial scales, environmental filtering might play a more important role than competition in determining which exotic species are successful (Pearse et al. 2013). Few studies consider the local scale, which is the scale most appropriate to test whether higher competitive abilities of exotic species result from their novel traits (but see Lim et al 2014). To fully understand Darwin's Naturalization Hypothesis, we must investigate novelty at multiple spatial scales.

Understanding the relationship between novelty and competitive ability has applicability beyond understanding biological invasions, and might explain why some native species become common in a community while other remain rare. Research considering the role of novelty for both exotic and native species will help clarify whether some exotic species become invasive for the same reasons some native species become common. Such research could also provide predictive power for which species might become invasive in the future. Many studies use native and invasive congeners to evaluate hypotheses about species invasion because such pairings control for evolutionary history (e.g. Kolb and Alpert 2003, Burns 2006). However we will use

con-familial species to achieve a wider range of phylogenetic distance between our native and invasive species while still controlling for evolutionary history.

In order to synthesize the hypotheses for what causes plant invasions, this study will address (1) whether phylogenetic novelty correlates with high competitive ability, (2) if and how this relationship differs when novelty is assessed at regional versus local spatial scales, and (3) how this mechanism differs between native and invasive species.

METHODS

Study Area

Our study was conducted at the Tyson Research Center, an 800-hectare site that is dedicated to ecological research. Owned by Washington University in St. Louis, the site is situated 35 kilometers southwest of the city of Saint Louis, Missouri. The area is dominated by oak-hickory forest, and interspersed with smaller grasslands, glades, old fields, and human-disturbed open areas. The climate is temperate, with uniform average precipitation over the course of the year.

Study Species

Study species were chosen based on their prevalence in the study area, and their phylogenetic diversity. Native species chosen were generally common in the area so that they would be comparable to successful exotic species. Exotic and native species pairs within each family were similar in their growth habit and preferred habitat. The study species are summarized in Table 1.

Site Preparation

Plots for native species were established during the spring of 2014. Plots for exotic species were established earlier during the spring and summer of 2013-2014, since these species' plots were also part of a related study at Tyson Research Center relating phylogenetic novelty of invasive species to their population growth rate. Once an appropriate population of each focal species was identified, the plot size was determined such that each plot had at least 4 individuals and not more than 20 individuals (See Table 1 for plot size used for each species). Individual plots were established as squares on the ground with iron rebar installed at each corner. For each species, at least 15 plots were established, (more plots were established if necessary to achieve adequate sample size of each stage class), and the focal species within plots were thinned if the density was too high. Plots were randomly assigned via a random number generator to one of three treatments: competitor reduction, herbivore reduction, and control, however this study will focus only on the competitor reduction and the control treatment.

Treatments

For the competitor reduction treatment, the aboveground portion of all plants that were in the plots, other than the study species, was removed. The biomass removed was collected and dried to provide a record of the amount of competition faced by the focal species. A border a quarter as long as the length of one of the plot's sides was maintained free of competitors to avoid any edge effects. Competitor biomass was removed every other week during the growing season, or more often if competing plants grew back quickly. In forested plots, only competitors in the understory that were below breast height were removed since removing trees would have fundamentally changed the habitat type. The plants in the control plots were un-manipulated.

Demography Data Collection

Early in the season (May or June) of 2014 or in some cases 2013, initial plant size and stage was collected for each individual (methods for each species in Table 2). Individuals were mapped using a grid system so that they could be relocated later in the season. Later in the season, between July and September, data were collected on the second measure of plant fitness (Table 2). All data was matched to the individual so as to record individual growth over the course of a single season. The one species that was an exception to the single-season rule was *Lonicera maackii*, for which the first and second measure of plant size were taken in July 2013-July 2014. Effect sizes of the competitor reduction treatment were calculated by dividing the average growth of individuals in the competitor reduction treatment by the average growth of individuals in the control treatment. However, due to the intense deer herbivory on *Cirsium discolor* biased towards the competitive removal treatment, this species and the invasive thistle species, *Carduus nutans* were analyzed differently. Their growth was plotted against their level of herbivory for each treatment, and the ratio of their intercepts was taken to be the effect size. The intercepts represent the estimated growth rate individuals would have in each treatment in the absence of herbivory.

Herbivory Data Collection

Data on the herbivory level of each plant was collected and used as a covariate in cases in which herbivory differed significantly between the competitor reduction and control treatments. For each individual herbivory level was estimated at the end of the season at the same time late season demographic data was collected. Each leaf of each individual was visually scored for

percent insect herbivory using a categorical scale with nine categories (0, 1-5, 6-10, 11-25, 26-50, 51-70, 71-80, 81-90, 91-100). The total average herbivory was calculated as the average of the mean values in each category weighted by the number of leaves in each category. For *Cirsium discolor*, which received significant deer herbivory, percent herbivory caused by deer was also estimated on for each plant. The total herbivory for this species was found to be the sum of the percent deer herbivory on the whole plant and the insect herbivory multiplied by the percent of the plant remaining after the deer herbivory.

Community Data Collection

We collected data on the local community of each species to use in our phylogenetic analysis at the local scale. During the months of June and July, data was taken on the presence and abundance of species that co-occur in study plots with each focal species. For each focal species, every co-occurring plant within the marked plots was identified to species. Trees with canopies completely above breast-height were omitted. For each co-occurring plant species, its percent cover in each plot was estimated visually. Species that had a very small percent cover were recorded as having 1 percent cover.

Phylogenetic data

To build a phylogeny for angiosperms at the Tyson Research Center and for each local community for each focal species, we used the super-tree of Soltis *et al.* (2011) as a phylogenetic constraint and source of dating information and phyloGenerator and willard packages in R 3.1.2 (Pearse and Purvis 2013). Several measures of phylogenetic novelty were calculated for each species, using phylogenetic distance in units of branch length. These included the distance to the

closest relative at the Tyson Research Center, the average distance to each species in the local community, the average distance to each species in the local community weighted by percent cover, the distance to the closest relative in the local community, and also repeated the previous measures while excluding exotic species.

Final Data Analysis

We used a randomization test in R 3.1.2 to determine the significance of the relationship between phylogenetic novelty and effect size of the competitive reduction treatment. This randomization test was used in addition to a simple linear regression because the effect size for each species had its own independent, asymmetric error bars. For each treatment for each species, we recorded the number of individuals within that treatment. Then, we drew a random population of the same size from that treatment pool with replacement. We calculated the random effect size for this treatment using the same method as described and tabulated in the *Demography Data Collection* section which differed as tabulated in Table 2. We then used linear regression to test for a relationship between the effect size of competition and each measure of phylogenetic novelty, and recorded the slope associated with the linear model. This randomization process was repeated 5000 times, and a set of randomly generated slopes was collected. These results were then compared to the linear regression of true effect size as related to a measure of phylogenetic novelty. The proportion of random slopes with the opposite sign from the true slope was interpreted as the probability that the slope we found had a negative sign by chance alone. The linear regression of true effect size as related to a measure of phylogenetic novelty was also used to find the adjusted R-squared value, which indicates how much variation in the data can be explained by the linear relationship.

RESULTS

The effect size of the competitive removal treatment decreased with phylogenetic novelty; this relationship was true for measures of phylogenetic novelty at both spatial scales, measures that were unweighted and weighted by local species abundance, and measures that only considered the closest relative in the local community (Figure 1, Table 3). This means that more novel species perform similarly under differing levels of competition, so competition is not affecting them as much as phylogenetically less novel species. This implies that these more novel species are overall better competitors than less novel species compared to species with which they co-occur. The measure of phylogenetic distance that considered the nearest neighbor at the scale of the research center explained the most variance in the effect size of competition, and was very significant in our nonparametric randomization analysis ($r^2 = 0.2842$, $p_{\text{regression}} = 0.06491$, $p_{\text{randomization}} = 0.0042$, Table 3). However, the native and invasive species showed different patterns in the relationship between the effect size of competition and phylogenetic distance. Exotic species had relatively high effect sizes for competition, but no relationship between the effect size of competition and phylogenetic distance whereas native species showed a negative trend between the effect size of competition and phylogenetic distance (Figures 2 and 3). There was no relationship observed between the amount of biomass removed and the effect size ($p=0.8047$).

DISCUSSION

To examine whether phylogenetic novelty correlates with high competitive ability, we determined the effect of a competitor reduction treatment for a native and an exotic species from each of 5 plant families. When considered all together, we observed that increased phylogenetic novelty correlates with decreased effect of competitor reduction treatment. This indicates that more phylogenetically novel species are already better competitors compared to other co-occurring species, and therefore do not respond as strongly to competitor reduction. However, some of the small effect sizes we observed may be due to the relatively short time between the establishment of treatments and the collection of demographic data.

In the future, we can address the short time scale of our study by using response of population growth rate λ requiring us to maintain our experimental treatments for at least one year, and equalizing any bias that some species might have towards competition or growth in a certain season.

Our results are consistent with many other studies that have reported that there is a correlation between plant success and phylogenetic novelty, though these studies typically examine exotic species only (e.g. Rejmanek 1996, Lockwood et al 2001, Ricciardi and Atkinson 2004, Lambdon and Hulme 2006, Carboni et al 2013, but see Daehler 2001, Lim et al 2014). However our study is the first study to experimentally manipulate competition in the field and correlate the effect size to phylogenetic novelty. Thus, we are the first to show that novel species are more successful due to competitive ability. Though the studies differ in methodology, our results are similar to a greenhouse experiment that found native species to perform better when grown with distant rather than with close relatives in field soils (Burns and Strauss 2011).

We initially expected that the relationship we found between phylogenetic novelty and competitive ability might differ between a local scale versus a regional scale. While there is some quantitative difference in this relationship at these two scales, the same qualitative trend is seen for the regional and local scale. One reason for this may be that our regional scale, which is our 800 hectare research station, is not a large enough an area to see a qualitative difference in trend. Perhaps analyzing an even larger area, such as all of Missouri, would lead to a stronger environmental filtering effect whereby less novel species are more successful due to their lack of ability to survive in a certain environment.

When we separate the native species from the invasive species in our study, we see a more negative relationship between phylogenetic novelty and effect of competitor reduction in native species than invasive species. One reason for this may have been the presence of *Cirsium discolor* on the side of the native species. *C. discolor* was strongly affected by the competitor reduction treatment and also had low phylogenetic novelty due to its native congener *Cirsium altissimum*, and its co-occurrence with several other species of Asteraceae which are common in its prairie habitat. If this species were to be removed from the analysis, the native species and the invasive species would have more similar relationships between novelty and competitive ability. Another reason for the difference between trends in response to competitor reduction in native and invasive species may be our small sample size, and the fact that no extremely novel invasive species are included in our sample. We are unable to determine whether a very novel invasive species would perhaps have a negative effect size due to competitor reduction, as was true with some of the native species. In the future, we would like to add more species to the study.

Another explanation for why the invasive species all have similar and positive effect sizes may be because they have all adapted to a disturbance based growth strategy. There is often

a tradeoff between colonization ability and competitive ability whereby the traits that make species good colonizers (e.g., small seeds) are the same ones that make them poor competitors in benign (undisturbed) environments (Hastings 1980, Nee and May 1992, Tilman 1994, Calcagno et al 2006). These species might perform well for a window in time when newly disturbed habitats become available, but then have their fitness dramatically affected by competition as other species colonize and grow on these habitats. It is possible that we observed the latter half of this process for all of our exotic species since we located places where these species were already established in significant numbers, rather than as they were colonizing new areas.

Our research advances our understanding of Darwin's Naturalization Hypothesis by considering both native and exotic species in the same study, directly measuring the importance of competition, and considering phylogenetic novelty at multiple spatial scales. Native species showed wider variation in their effect size of competition, with some species showing extreme benefits of competitor reduction treatments and other species seeming to benefit from the presence of their interspecies neighbors. Further, the effect of competition of native species decreased with the novelty of the species at both local and regional spatial scales. The exotic species in our study all showed strong effects of competitive removal treatments, suggesting that resident flora are strongly affecting the fitness of these species and perhaps restricting their distribution to more disturbed habitats.

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TABLES AND FIGURES

Family	Exotic species	Native Species	Plot size
Lamiaceae	<i>Perilla frutescens</i>	<i>Teucrium canadense</i>	½m X ½m
Asteraceae	<i>Carduus nutans</i>	<i>Cirsium discolor</i>	1m X 1m
Rosaceae	<i>Potentilla recta</i>	<i>Geum canadense</i>	½m X ½m
Caprifoliaceae	<i>Lonicera maackii</i>	<i>Symphoricarpos orbiculata</i>	2m X 2m
Fabaceae	<i>Lespedeza cuneata</i>	<i>Desmodium perplexum</i>	Exotic: ½m X ½m Native: 1m X 1m

Table 1: Basic information on selected study species.

Species	Native/ Exotic status	Early Season size measurement	Late Season Fitness measurement	Growth metric
<i>Perilla frutescens</i>	Exotic	Height	Number of fruits	Number of fruits / Height
<i>Teucrium canadense</i>	Native	Height	Number of fruits	Number of fruits / Height
<i>Carduus nutans</i>	Exotic	Number of leaves for non-reproductive individuals	Number of leaves for non-reproductive individuals	Late season leaf number / Early season leaf number
<i>Cirsium discolor</i>	Native	Number of leaves for non-reproductive individuals	Number of leaves for non-reproductive individuals	Late season leaf number / Early season leaf number
<i>Lonicera maackii</i>	Exotic	Height for non-reproductive individuals	Height for non-reproductive individuals	Later year height – Earlier year height
<i>Symphoricarpos orbiculata</i>	Native	Canopy volume	Number of fruits	Number of fruits / Canopy volume
<i>Lespedeza cuneata</i>	Exotic	Height	Height if reproductive	Late season height / Early season height
<i>Desmodium perplexum</i>	Native	Height	Height	Late season height / Early season height
<i>Potentilla recta</i>	Exotic	Number of leaves	Number of fruits	Number of fruits / Number of leaves
<i>Geum canadense</i>	Native	Number of leaves	Number of fruits	Number of fruits / Number of leaves

Table 2- Species-specific information on demographic data collected.

Measure of Novelty	Regression adjusted r ² -value	Regression p-value	Randomization p-value
Distance to closest relative at Tyson	0.2842	0.06491	0.0042
Distance to closest native relative at Tyson	0.2689	0.07153	0.032
Average pairwise distance to all local species	0.1837	0.1201	0.0566
Average pairwise distance to native local species	0.1939	0.1131	0.0512
Average pairwise distance to all local species weighted by percent cover	-0.0009411	0.3485	0.0648
Average pairwise distance to native local species weighted by percent cover	0.04111	0.2729	0.0592
Distance to closest local relative	-0.1165	0.8118	0.4248
Distance to closest native local relative	0.06191	0.2423	0.0642

Table 3- Summary of linear regression results for each measure of phylogenetic novelty tested. R-squared values are adjusted r-squared values, regression p-values are associated with the linear model for effect size as related to phylogenetic novelty, and randomized p-values are the number of randomized slopes that were greater than zero over the total number of randomized trials (N=5000).

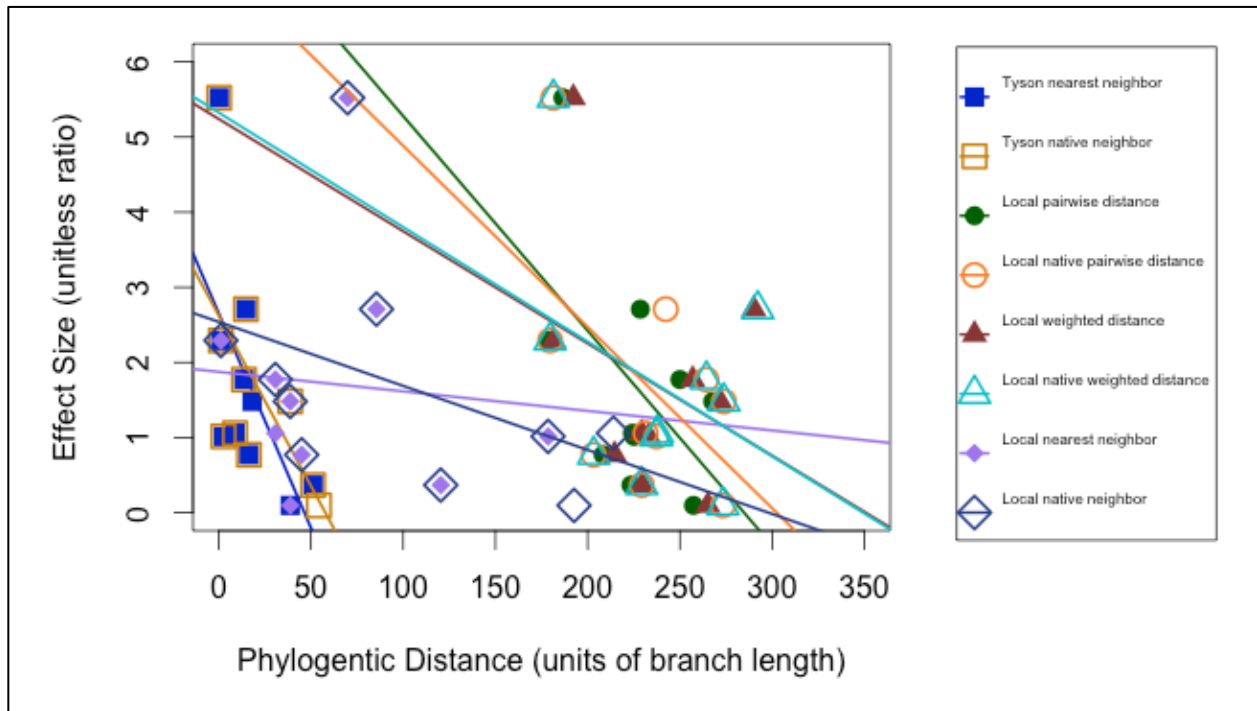


Figure 1: Increased phylogenetic distance was related to decreased effect when removing competitors for all measures of phylogenetic distance calculated. Nearest neighbor means the distance to the most closely related species, native neighbor is the nearest neighbor among only native species. Pairwise distance is the average distance to all other species present, and native pairwise neighbor is the pairwise distance to only native species. Weighted distance is the pairwise distance, except weighted by percent cover, and native weighted distance is the weighted distance when considering only native species. R-squared values shown are the adjusted r-squared values.

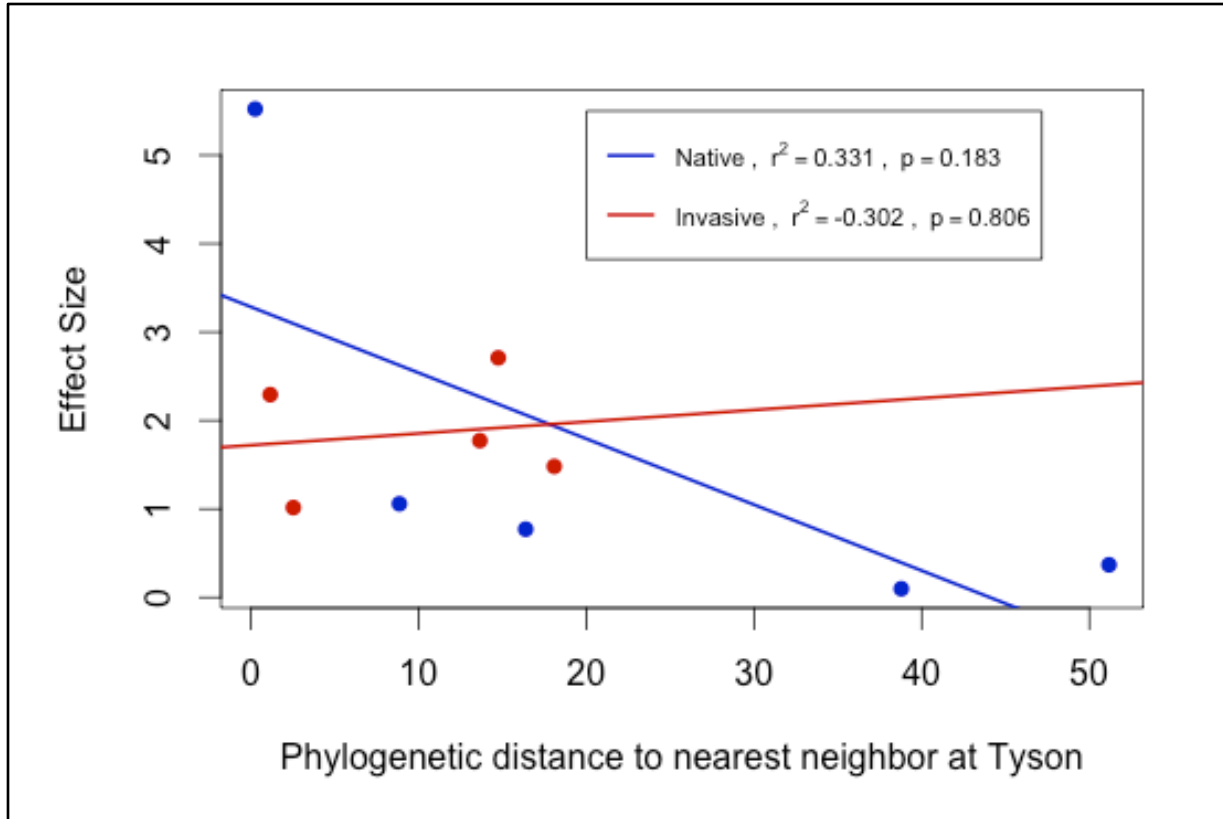


Figure 2: The negative relationship between phylogenetic distance and effect size is present only for native species at the scale of Tyson Research Center.

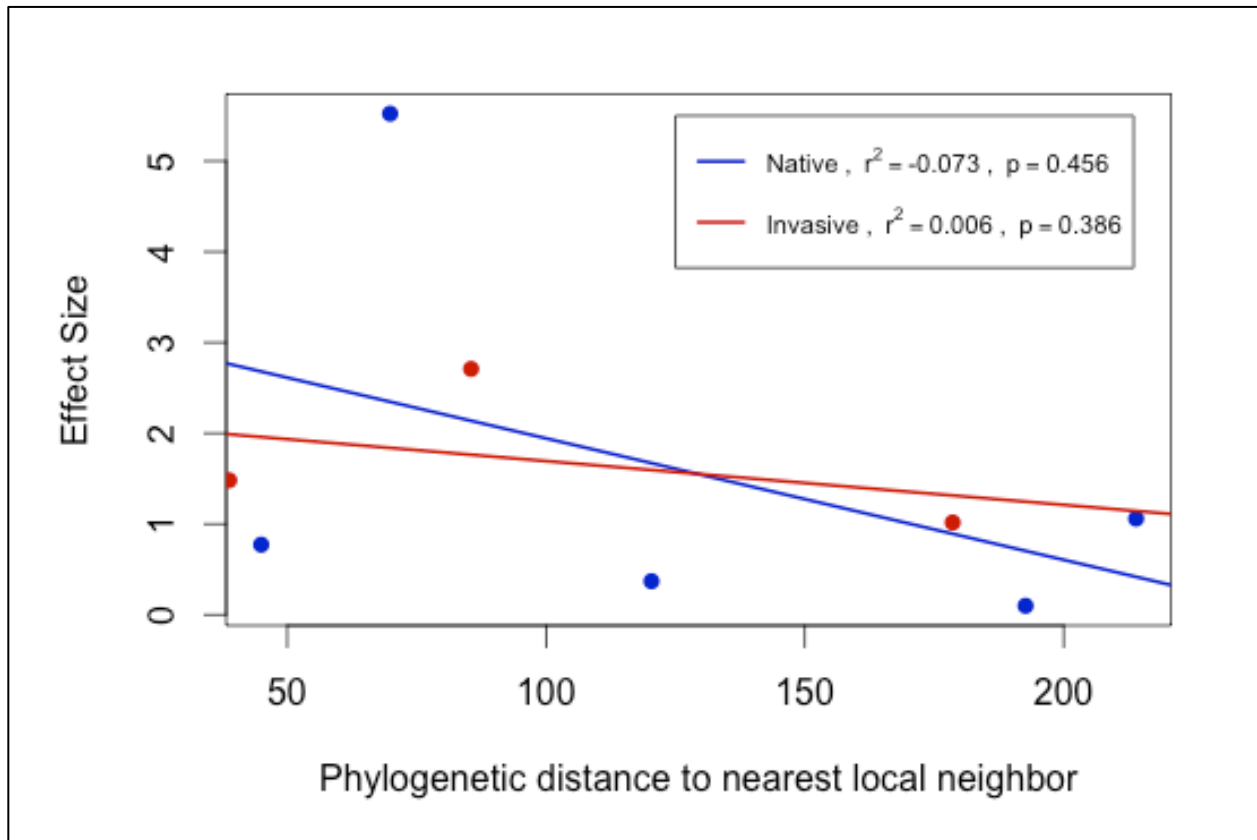


Figure 3: The negative relationship between phylogenetic distance and effect size is present for both native and invasive species for 3 out of 6 of the measures of phylogenetic novelty at the local scale.