A meta-analysis of evolutionary responses in native plants to introduced plant species: does phylogenetic distance play a role?

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Abstract

While there is increasing interest in the evolutionary consequences of species invasions on native plant communities, the connection between the phylogenetic relatedness of invaders and natives, and its evolutionary consequences, has not yet received much attention. One way to examine the role of relatedness on the impact of species invasions is through the use of meta-analytical techniques combined with a phylogenetic framework. I apply this technique and expand on a prior meta-analysis by Oduor (2013), in order to compare how native plant species that either have prior experience coexisting with an invasive (‘experienced’) or do not (‘naïve'), differ in terms of their growth and reproduction in the presence of the invasive for evidence of a phylogenetic signal in their response to plan invasions. My results suggest that the effects of a species invasion on native growth and reproductive traits may be greater when the native and invasive species are distantly related, and/or when the invasive species is allelopathic, but only in the presence on the invader. I also found that the negative effect of competition with an invader on native growth traits tended to be greatest when the native and invasive species were closely related, suggesting that the strength of competition and the evolutionary response of native plants to invasive plants may not be as closely associated as it is often assumed. Overall, my analysis suggests that future studies may benefit from integrating phylogenetic relatedness when exploring native evolutionary responses to invasions, but that considerable work need sot be done to tease apart the roles of relatedness and competition.

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Chapter 1: Introduction and Background

Foreword and general introduction

Species introductions have provided researchers with a fascinating model system for the study of the evolutionary and ecological processes (Desurmont, Herard, and Agrawal, 2012; Franks and Munshi-South, 2014). Species introductions into novel environments can result in rapid adaptive evolution in the introduced species in a short amount of time (Reznick and Ghalambor, 2001). Invasive species, especially plants, which tend to outnumber invasive animal species (Vitousek et al., 1997), are a particular concern due to their ability to disrupt native communities.

There is a growing interest in the role of phylogenetic relationships and community phylogenetic structure as a predictor of invasion success (Violle et al.; Proches et al., 2008; MacDougall, Gilbert, and Levine, 2009; Thuiller et al., 2010; Carboni et al., 2013; Pellock et al., 2013; Bennett, Stotz, and Cahill, 2014; Fridley and Sax, 2014) and impact (Vila, Williamson, and Lonsdale, 2004; Vila and Gimeno, 2007; Morales and Traveset, 2009a; Vila et al., 2011; Vila et al., 2015), and because invasive species have the potential to exert selective pressure on native species there has also been an increasing interest in the evolutionary consequences of invasions on native species (Meiners and Cadenasso, 2005; Lau, 2006; Mealor and Hild, 2006; Carroll, 2007; Vellend et al., 2007; Brewer, 2011; Vila et al., 2011; Mason, French, and Russell, 2012; Lankau, 2013; Oduor, 2013). However, the connection between phylogenetic relationships and the evolutionary consequences of invasions, a natural outgrowth of this field, has not yet received much attention in the literature.

In my thesis, I explore the role of relatedness and competition on the evolutionary effects of plant invasions on native plant species' growth and reproductive traits. In my first chapter I discuss the general background relevant to this field. Since an introduced species can't be expected to have an evolutionary effect on native species without first becoming established, I first discuss some of the factors and frameworks used to understand invasion success. I highlight recent niche-based frameworks which emphasize co-existence theory and competitive outcomes, and explain how phylogenetic relationships are used in various frameworks and why they can potentially function as a context-dependant predictor of invasion success.

In my second chapter I extend the niche-fitness and phylogenetic frameworks for invasion success and hypothesize how phylogenetic relatedness between native and invasive species might generally predict the strength of selection and the evolutionary outcomes for native species. Specifically, in my second chapter I expand on a previous meta-analysis (Oduor, 2013), which found that native plants exhibit an evolutionary trait shift in their growth and reproductive traits in response to interaction with an invader, to see if variation in this effect among studies can be explained by the phylogenetic relatedness between the native and invasive species pairs. I also explore the response to competition in these studies to see if the patterns support the idea of an adaptive response to competition from the invasive, and the idea that the strength of competitive interactions between two species is correlated with their phylogenetic relatedness. In my last chapter I review my findings and discuss future directions. Finally, I include an appendix with additional data and some of the alternative methods which could have been used in the meta-analysis.

Statement of Thesis Contributions

I present my meta-analysis in the style of a scientific publication. With the exception of a few cases where I obtained data directly from the authors, my data was extracted from the published literature. I also used available tree-pruning tools to create my molecular phylogenetic trees, which after some trial and error I believe is the best option (in conjunction with a recent correction of an extensive angiosperm super tree) for authors who don't need extremely refined trees and do not have the experience or data required to build a molecular tree themselves.

Because my meta-analysis builds on an existing review by Oduor (2013), it closely follows the methods described there, and, aside from a few new data points, uses data extracted from the same sources. The Oduor (2013) meta-analysis was chosen as a starting point because the authors collated studies where the designs and data could easily be converted into a suitable effect size to address my question, and outside of this review there are very few studies on plant systems which could be used together in a meta-analysis. While recreating the Odour dataset, I identified a few areas where the methodological decisions could be refined, and I discuss this in my second chapter. In the second half of my analysis I also modify the original calculation of the effect size to estimate the effect of competition treatments on the natives. My use of the dataset is a novel first step into the questions surrounding the role of phylogenetic relationships in the evolutionary effects of invasive plants on native plants.

General factors in invasion success

The question of why some introduced species succeed in becoming established, and why a subset of these species subsequently become invasive, has been addressed from several perspectives. Some perspectives focus on the factors and traits which allow the introduced species to become invasive ('invasiveness'), others on the ecological and community characteristics which allow for invasion ('invasibility'), while still others argue for the integration of both perspectives (Richardson and Pysek, 2006). For example, some studies focus on ecological and community level factors prior to the invasion, such as habitat disturbance (Belote et al., 2008), resource availability (Beckstead and Augspurger, 2004; Ordonez and Olff, 2013; Mattingly and Reynolds, 2014), pre-adaptation or maladaptation to the novel climate or environment (environmental filtering) (Carboni et al., 2013; Ordonez, 2014), and native community structure (Levine, Adler, and Yelenik, 2004; Molinari and D'Antonio, 2014). Others examine more stochastic factors such as the frequency and scale of introduction (Colautti, Grigorovich, and MacIsaac, 2006; Brooks and Jordan, 2013), or more stochastic factors such as the frequency and scale of introduction (Colautti, Grigorovich, and MacIsaac, 2006; Brooks and Jordan, 2013). Many studies emphasize competitive interactions and/or invasive functional traits such as strong dispersal mechanisms, competitive life history traits like high seed set and growth rates, and adaptive phenotypic plasticity (Lee, 2002; Abhilasha and Joshi, 2009; Davidson, Jennions, and Nicotra, 2011). However, support for each of these factors has been mixed and may be highly context dependent; for example, one study found that in monocarpic plants, disturbance and propagule pressure were the strongest predictors for urban woodland invasion at the city level, while competitive traits and ability dominated at the forest level (Golivets, 2014).

Consideration of the ecological and evolutionary interactions between the invader and the local biotic community may improve insight into the context-dependent nature of invasions (Strauss, Webb, and Salamin, 2006). For example, herbivores might host-switch to invasives that lack co-evolved defenses (Bertheau et al., 2010; Cogni, 2010; Andres et al., 2013), while disturbance can favour invasions by freeing up ecological space for colonization (Burns, 2004). Some invasive species can alter soil quality through nitrogen fixation, or release allelopathic root exudates that may directly supress native species' fitness or indirectly alter native-microbial associations (Batten, Scow, and Espeland, 2008; Harnden, MacDougall, and Sikes, 2011; Grove, Haubensak, and Parker, 2012; Aragon et al., 2014; Bansal et al., 2014; Greer et al., 2014), which can in turn alter competitive interactions between native and invasive species and feed back into invasion success (Allcock, 2002; Brewer and Bailey, 2014).

The loss of co-evolutionary relationships, both mutualistic and antagonistic, and subsequent plastic or evolutionary responses in the invasive and the native community may also alter the outcomes of invasion over time (Hallett, 2006; Andonian and Hierro, 2011; Drenovsky et al., 2012; Jones and Gomulkiewicz, 2012). For example, the popular 'evolution of increased competitive ability' (EICA) hypothesis (Blossey and Notzold, 1995) predicts that the escape from specialized natural enemies will favour selection on competitive traits over defensive traits in introduced species, which can increase their invasiveness (Orians and Ward, 2010). While support for this particular hypothesis varies from system to system (Maron et al., 2004; Blumenthal and Hufbauer, 2007; Abhilasha and Joshi, 2009; Doorduin and Vrieling, 2011;

Wang et al., 2011; Felker-Quinn, Schweitzer, and Bailey, 2013), it does seem that evolutionary changes in the introduced species can play a role in the outcomes of invasion, and that adaptive plastic responses can facilitate the colonization of novel or fluctuating environments (Molina-Montenegro et al., 2012; Zhao et al., 2012; Pahl et al., 2013; Fenesi et al., 2014). Lately the evolutionary response of native plant species to invasive plant species has received increased interest (Callaway et al., 2005; Oduor, 2013; Beans and Roach, 2015b, a) and some common garden experiments suggest that these changes could increase the ability of native species to compete with and supress the growth of invasive (Ferrero-Serrano, Hild, and Mealor, 2011; Goergen, Leger, and Espeland, 2011; Sebade, Hild, and Mealor, 2012). However, relatively few studies have examined how these changes affect long-term invasion outcomes or co-evolutionary dynamics.

Phylogenetic relatedness and invasion outcomes

Since closely related species are more likely to be functionally or ecologically similar, the relatedness between species has also been proposed as a predictor of invasiveness (Losos, 2008). In particular, Darwin's naturalization hypothesis proposes a role of relatedness in the successful establishment (or naturalization) of introduced species and their invasiveness (Darwin, 1902; Agrawal et al., 2005; Strauss, Webb, and Salamin, 2006; Cahill Jr et al., 2008; Proches et al., 2008; Hill and Kotanen, 2009; Escobedo, Aranda, and Castro, 2011; Carboni et al., 2013; Park and Potter, 2013; Pellock et al., 2013; Castro et al., 2014; Fridley and Sax, 2014). The hypothesis predicts that decreasing relatedness between an introduced species and its native community, which in a modern framework can be interpreted as an increase in phylogenetic distance, promotes the establishment of introduced species due to greater dissimilarity and reduced competition (Carboni et al., 2013). In other words, it connects niche similarity and the strength of competitive interactions with relatedness, and there has been some support for the role of phylogenetic relatedness in plant invasions. For example, Strauss et al. (2006) showed that California grassland communities where introduced species were less phylogenetically related to the native grass community were more likely to be invasive. Similarly, a recent meta-analysis found that while invasive plants were generally more pollen limited than their native congeners, more phylogenetically novel invaders (defined as a larger phylogenetic branch length to the nearest native neighbour in the community) were less pollen limited, suggesting a link between relatedness and competition for pollinator services between invasive and native plants (Burns et al., 2011).

On the other hand, some studies have found that invasive species tend to be more closely related to species in the native community than expected by chance (Ricotta, Godefroid, and Rocchini, 2010), while others have found no support for Darwin's hypothesis (Escobedo, Aranda, and Castro, 2011; Castro et al., 2014). A recent study suggests that at larger spatial scales, environmental filtering may allow closely related introduced species to become more successful if their similarity to the native species is adaptive in the new environment, but that at smaller scales competition and greater phylogenetic distance are more predictive of success (Carboni et al., 2013), which highlights the difficulty in developing generalized theories to predict plant invasions.

The idea that invasiveness increases with the phylogenetic distance between the introduced species and the native community due to niche differences may not be intuitive since niche differences are typically predicted to facilitate co-existence, not competitive dominance. If the difference between a naturalized introduced species and an invasive one is defined by both its spread and its impact on the native community, then classic niche-based theories would predict that distantly related introduced species are more likely become naturalized (or co-exist) than become invasive and impact native species through competitive dominance. However, in their review of the niche-fitness framework, MacDougall et. al. (2009) posit that niche differences, which favour coexistence, are balanced by fitness differences, which favour competitive dominance. This allows introduced species to coexist with native species and communities when niche differences are sufficiently large, and dominate invasively when fitness differences are large enough to overcome niche differences (Chesson, 2000; MacDougall, Gilbert, and Levine, 2009). Since fitness differences are based on trait differences, and trait differences are thought to increase with phylogenetic distance, this could explain the relationship between distance and invasiveness seen in a few studies (Mayfield and Levine, 2010; Godoy, Kraft, and Levine, 2014). Interestingly, recent work with a field-parameterized model suggests that fitness differences among native and introduced species increases with phylogenetic distance, which could explain how distantly related introduced species can become competitively dominant over natives (Godoy, Kraft, and Levine, 2014). Other factors such as environmental disturbance and filtering, hybridization, and propagule pressure can also affect success (Colautti, Grigorovich, and MacIsaac, 2006) regardless of relatedness, and pair-wise studies of the relationship between distance and competition are mixed (Cahill Jr et al., 2008; Dostal, 2011; Castro et al., 2014; Godoy, Kraft, and Levine, 2014). Overall, the possibility that phylogenetic relatedness can predict invasiveness and fitness differences has interesting implications regarding the role of relatedness on the ecological and evolutionary impacts of invasive plants on native plants.

Impacts of Invasive Plants on Natives

Invasive plant species can have significant direct and indirect impacts on native plant species. These have been extensively reviewed (Vila et al., 2011; Vila et al., 2015) and include reductions in individual native fitness, or more community-oriented impacts such as a reduction in species richness and changes to ecological processes. Resource competition from dominant invasive plant species has frequently been associated with declines in native fitness (Levine et al., 2003), but indirect and disruptive competition can also reduce native plant fitness (Lenz, Moyle-Croft, and Facelli, 2003; White, Wilson, and Clarke, 2006; Beckstead, Meyer, and Augsperger, 2008; Bennett, Thomsen, and Strauss, 2011; Grove, Haubensak, and Parker, 2012; Lau, 2012; Skurski, Rew, and Maxwell, 2014). For example, studies have shown that native species can be affected by indirect alterations to soil microbiota (Pysek et al., 2012), changes in leaf litter decomposition rates (Allison and Vitousek, 2004; Brantley and Young, 2008; Aragon et al., 2014), and alteration of local pollinator networks, although in some cases showy invasives can actually mutualistically increase pollinator visitation to native species by increasing local attraction (Levine et al., 2003; Bartomeus, Vila, and Santamaria, 2008). The physical changes in the structure of the environment, for example in terms of average plant height and light availability, can also alter community-level diversity and structure by selecting against native species which are less adapted to the new condition (Molinari and D'Antonio, 2014).

Long term ecological effects of invasive plant species on natives should eventually lead to an evolutionary response on the part of the native species. For example, invasive species can alter phenotypic selection on native species by competing for pollinators (Beans and Roach, 2015a), and direct competition and/or the presence of allelopathy can select for altered growth patterns and allelopathic resistance (Callaway et al., 2005; Beans and Roach, 2015b). Differences in trait values between remnant native survivors of invasion and naïve populations have been documented in several studies, and could indicate potentially adaptive plastic or evolutionary responses to invasion (reviewed by Oduor 2013). However, in some of these studies there was no detectable difference between the experienced and naïve native species, despite the fact that the invasive was heavily abundant and presumably exerted selection (Oduor, 2013; Lau and Terhorst, 2015). One possible explanation is that these populations lacked sufficient heritable genetic variation in the traits under selection. A review by Berthon (2015) outlines a framework whereby populations which lack genetic variation, but are able to adaptively plastically respond to the invasive, can persist in spite of invasions and may or may not eventually evolve in response to selection from the invasive. To complicate things further, the source of selection must be consistent enough and occur at a high enough to frequency to not be overwhelmed by the rest of the breeding population. If, for example, the introduced species persists only at low densities relative to the native, the low frequency of their interactions may prevent an evolutionary response in the population, despite strong selection on the individuals when an interaction does occur (Jones and Gomulkiewicz, 2012). Stochastic factors such as drift, disturbance resulting in genetic bottle-necks, and gene-flow from un-invaded source populations can also mask selection and prevent adaptive evolution (Oduor, 2013).

Finally, ecological factors can alter the evolutionary response of native species to invasive plant species. Temporal and spatial variation in selective pressure, opposing selection from multiple agents (for example herbivores which may select for defensive traits over competitive traits), and non-additive selection from species interactions can all slow or prevent an evolutionary response to selective pressure and may be fairly common in invaded systems (Lau and Terhorst, 2015). For the most part, studies of evolutionary responses in native plants to invasions suggest that evolutionary responses do occur in the remnant native populations of large invasions, but we do not yet have the ability to predict when and to what extent these responses will occur.

Research Question and System

Here I apply a meta-analysis to investigate the role of phylogenetic relatedness and allelopathy on the competitive and evolutionary effects of invasive plant species on natives. Specifically, I extend a previous meta-analysis which found that native plant species which have persisted through an invasion exhibit higher levels of growth and reproductive traits than naïve natives that had never experienced an invasion (Oduor, 2013). Another recent meta-analysis suggests that there may be a phylogenetic signal in the ecological effects of invasive plants on native plants (Vila et al., 2015), and the invasiveness of introduced species in some systems is correlated with the relatedness between natives and invasives (Strauss, Webb, and Salamin, 2006). To my knowledge, no one has yet conducted a broad-scale synthesis to examine if the relatedness between native and invasive plant species is predictive of the evolutionary response of native plants to invasions.

Meta-analyses are by nature more akin to an observational approach than an experimental one, and as such they are not a robust test of a causal hypothesis (Vetter, 2014). This is particularly important in ecological analysis since there can be so much variance in the study-level factors among systems (Hillebrand, 2001). However, they are still a useful tool for quantitative synthesis and have been used to detect patterns across ecological study systems. For example, meta-analysis has been used quantify in what ways invasive plant species tend to impact ecological processes and native species (Vila et al., 2011; Castro-Diez et al., 2014), how native and invasive plants respond to wildfire (Alba et al., 2015), and what factors generally predict invasiveness (van Kleunen, Weber, and Fischer, 2010; Davidson, Jennions, and Nicotra, 2011). While these types of studies are generally much larger and broader in scope than my own, my analysis does represent a first step into integrating phylogenetic patterns of relatedness and the evolutionary responses of native plants to invasive plants.

Chapter 2: A meta-analysis of the evolutionary impact of invasive plant species on natives: Does phylogenetic relatedness play a role?

Introduction

Questions surrounding the causes and consequences of species introductions have fascinated scientists for centuries, and interest in this field continues to expand with the growing concern over invasive species. Invasive aliens – which are typically defined as introduced species that are so successful in their new range that they dominate local systems and cause ecological and/or economic harm – are a concern around the world (Colautti and MacIsaac, 2004). Invasive alien plant species tend to be well studied, and there have been numerous studies on the factors and/or conditions that promote invasion success (Colautti, Grigorovich, and MacIsaac, 2003; Cadotte, Murray, and Lovett-Doust, 2006; van Kleunen, Weber, and Fischer, 2010) and invasiveness (Strauss, Webb, and Salamin, 2006; Burns et al., 2011; Palacio-Lopez and Gianoli, 2011; Dostal et al., 2013; Keser et al., 2014). There has also been considerable interest in the post-introduction evolutionary consequences of plant invasions; for example, rapid local adaptation has been documented in several invasive species (Novy, Flory, and Hartman, 2013; Turner, Hufbauer, and Rieseberg, 2014; Vandepitte et al., 2014), and the evolutionary background and post-introduction adaptation of introduced species are key components of several hypotheses regarding long-term invasiveness (Bossdorf et al., 2005; Blumenthal and Hufbauer, 2007; Abhilasha and Joshi, 2009; Doorduin and Vrieling, 2011; Felker-Quinn, Schweitzer, and Bailey, 2013). Additionally, because invasive species have the potential to exert strong selective pressure on native species (Lau, 2008), there has been a growing interest in the evolutionary responses of native species to invasions (Meiners and

Cadenasso, 2005; Lau, 2006; Mealor and Hild, 2006; Brewer, 2011; Vila et al., 2011; Mason, French, and Russell, 2012; Lankau, 2013; Oduor, 2013).

Phylogenetically based analyses are increasingly used to understand the causes and consequences of ecological interactions, including species invasions. The frameworks and hypotheses underpinning these types of studies vary, but a core prediction, stemming from the competitive exclusion principle (Hardin, 1960; Chase, 2003), is that if relatedness is positively correlated with niche similarity, then species that are more closely related should compete more strongly for local resources and be less likely to co-exist (Strauss, Webb, and Salamin, 2006; MacDougall, Gilbert, and Levine, 2009; Godoy, Kraft, and Levine, 2014; Ma et al., 2016). Evidence in support of this prediction is mixed in plant systems, with some studies suggesting that closely related species are more similar and/or can compete more strongly (Cahill Jr et al., 2008; Burns and Strauss, 2011) while other studies have found no relationship between relatedness and niche similarity and/or competition (Dostal, 2011; Godoy, Kraft, and Levine, 2014). A natural extension of this prediction for invasion biology is that, provided invasion success is primarily driven by a lack of natural competitors in the introduced species' new range (Richardson and Pysek, 2006; Price and Partel, 2013), then a species introduced to a new community where it lacks close relatives should ultimately become more invasive (Strauss, Webb, and Salamin, 2006).

While there is compelling evidence that the phylogenetic distance between an introduced species and the invaded community is correlated with the ultimate 'invasiveness' of the introduction (Strauss, Webb, and Salamin, 2006; Cadotte, Hamilton, and Murray, 2009; Ricotta, Godefroid, and Rocchini, 2010; Castro-Diez et al., 2014; Ordonez, 2014), there are also exceptions (Ricotta, Godefroid, and Rocchini, 2010; Park and Potter, 2013; Pellock et al., 2013; Ma et al., 2016). A few studies suggest that while competitive interactions are more likely to limit the success of closely related invaders at local scales, at larger regional scales environmental filtering may favour invaders which are more closely related to native species (and thus are better adapted to the local environment) (Ricotta, Godefroid, and Rocchini, 2010; Carboni et al., 2013; Ma et al., 2016). As a further complication, while niche differences may facilitate the successful introduction of potentially invasive non-native species by reducing competition, they do not fully explain the competitive dominance (as opposed to co-existence predicted by niche differences) and the ecological impacts associated with even distantly related invasive species in post-invasion interactions.

Modern niche-fitness frameworks which refine co-existence theory help to guide our understanding of invasiveness and the post-invasion impacts on native species (MacDougall, Gilbert, and Levine, 2009; Godoy, Kraft, and Levine, 2014). In this context niche differences, which are trait differences that reduce intraspecific competition such that a given species competes more with itself than other species, favour the establishment of introduced species through co-existence with natives. The stabilizing effects of niche differences are opposed by fitness (or competitive) differences or traits between the native and invasive species that ultimately favour competitive dominance and the exclusion of either the native or invading species (MacDougall, Gilbert, and Levine, 2009). Examples of fitness traits include clonal growth (Song et al., 2013), greater size, and robust seed production (van Kleunen, Weber, and Fischer, 2010) and could arguably include traits such as allelopathy. These fitness differences may explain why some closely related invaders establish in spite of niche similarity, and why some invaders can have large competitive impacts on distantly related natives (MacDougall, Gilbert, and Levine, 2009). Interestingly, recent research suggests that fitness traits may also exhibit phylogenetic signal; specifically, the difference in fitness between native and invasive species may increase with phylogenetic distance between them (Godoy, Kraft, and Levine, 2014).

There is increasing interest in the ecological impacts of invasive species on native species, and how these fit into existing co-existence and phylogenetic frameworks. For example, one study found that invasive plants closely related to focal native species had a greater negative impact on native plant fitness through competition for pollinators (Morales and Traveset, 2009a). A recent meta-analysis across kingdoms also found that closely related invaders had larger ecological impacts on native species than distantly related species at local scales, which could be explained by stronger niche-based competition from invasive species (Ma et al., 2016). If niche similarity and/or the fitness advantages of the invader do not result in the complete exclusion of a competing native species, then the invasive may exert novel selection on the native species, and create an opportunity for an adaptive evolutionary response in invaded populations. However, to my knowledge no studies have integrated phylogenetic relatedness with both the effects of competitive interactions with invaders on native species and the adaptive responses of the natives.

Hypotheses

I hypothesize that, if phylogenetic relatedness between species is correlated with niche and/or fitness differences, then a) the relatedness between native and invasive species should influence the strength of their competitive interactions, and b) the evolutionary responses of native species to the invasive species should also be correlated with the phylogenetic relatedness of the native and invasive species. However, the direction of the predicted outcomes is dependent on the phylogenetic signal of niche and fitness differences, and their relative roles in the competitive impacts of invasives on native species (Figure 1). My hypothesis focuses on the impacts of direct competition between native and invasive plant species, but invaders may still have indirect impacts on native species that might not have a phylogenetic signal; for example, through soil microbiota changes, allelopathy, and indirect interactions with herbivores and mutualists (Callaway et al., 2004; Lau and Strauss, 2005; Broz, Manter, and Vivanco, 2007; Lau, 2012). It also assumes that evolutionary responses to plant invasions are primarily in response to the competitive interactions between the native and invasive species.

Briefly, Figure 1 indicates that because niche differences should be negatively correlated with the strength of competition between invasives and natives, and positively correlated with phylogenetic distance, then closely related invaders should compete more strongly with natives and exert more selective pressure on them. Fitness differences that favour a closely related invader should result in the strongest competitive impact on natives due to competition from both niche overlap and the fitness advantage of the invader (Ma et al., 2016), but even small fitness differences can allow the invader to establish and exclude the native. Since niche differences promote co-existence by reducing competition between species, slight fitness differences that favour the invader should generally only result in a small competitive impact when niche differences are large (co-existence); however, very large fitness differences may still allow for a strong competitive impact even when niche differences are large by overcoming the stabilizing effect of niche differences.

If the fitness differences relevant to invasiveness are not correlated with phylogenetic distance, or if they have a negative correlation with distance, then across multiple species and cases there should be a negative trend between phylogenetic distance and the competitive impact of established invasives on natives (Ma et al., 2016), resulting in stronger selection on the native when the invader is closely related. If native species respond to this selection via niche differentiation (to avoid competition) or by becoming more competitive (reducing fitness differences), then the strength of this response should also be negatively correlated with phylogenetic distance. However, if fitness differences do have a positive phylogenetic signal (Godoy, Kraft, and Levine, 2014), and both niche and fitness differences are equally predictive of competitive outcomes, there may not be a detectible correlation between phylogenetic distance and competition or an evolutionary response. Finally, if fitness differences have a positive phylogenetic signal and are a stronger determinant of competitive outcomes between native and invasive species than niche similarity, there may be a positive correlation between distance and the effects of competition (Godoy, Kraft, and Levine, 2014).

To explore these hypotheses, I updated the data analyzed in a meta-analysis by Oduor (2013) and conducted a meta-analysis with relatedness as a moderator variable (Borenstein et al., 2009e; Vetter, 2014). The results of the meta-analysis by Oduor (2013) indicate that, under common conditions, ‘experienced’ native plant populations (i.e., those with a history of coexistence with an invasive plant species) exhibit greater growth and reproductive trait values relative to ‘naïve’ populations (i.e., those with no history with the invasive species). If the native populations adapted to the invasive by becoming more competitive, which reduces fitness differences, then the differences in growth and reproductive traits could represent an evolutionary response to invasion. However, if the native species were to primarily respond by avoiding competition (such as through niche differentiation or tolerance) then these trait differences would only reflect fitness components that could arise from changes in the traits that determine niche overlap or tolerance. In addition, these differences could be attributable to plasticity, or adaptation to other abiotic or biotic differences between the naïve and experienced environments. Since it was not possible to differentiate between niche and fitness traits or responses with the dataset, a potential evolutionary response to invasion can only be indirectly inferred through the factorial competition treatments present in the studies, as described below and in Figure 2. Therefore, while this meta-analysis is by nature correlational and more akin to an observational study (Vetter, 2014), I believe the analysis will highlight the importance of considering phylogenetic relationships when studying the evolutionary consequences of biological invasions.

Predictions and study design

Most of the studies included factorial competition treatments with the invasive, and since my hypothesis is grounded on the assumption of an evolutionary response to competitive interactions with the invasive which vary with their relatedness, I predicted that naïve and experienced plants would differ in their response to competitive planting treatments. Specifically, I predicted that experienced plants should be less impacted by competition than naïve plants in general (suggesting an adaptive response to the invasive), and that the magnitude of this response would be correlated with phylogenetic distance, such that the effect of competition on naïve plants would be greatest when they are closely related to the invasive— unless fitness differences across the species pairs are correlated with phylogenetic distance, in which case distantly related invasives may have an equal or greater impact on naïve natives. If the experienced natives have adapted to strong competition from the invader then they should be less impacted by competition with the invader, resulting in a weaker relationship between relatedness and the effect of competition.

I also predicted that the effect of experience with the invasive on growth and reproductive traits would be correlated with relatedness. Specifically, that the effect of experience would follow the same phylogenetic direction as the effect of competition, such that natives which experienced the strongest competition from an invasive would have the greatest difference between their experienced and naïve populations. If this trend is present in the absence of competition from the invasive, it could reflect an evolutionary response in the measured growth and reproductive traits to the invasive and/or some other difference between the native environments. Since the traits used in the analysis can also be considered a proxy for performance or fitness then the effect of experience should be greater under competition with the invasive if the native species adaptively responds to the invasive through an evolutionary trait shift or phenotypic plasticity. As a final caveat, if the effect of experience is only significant under competition, and not in the absence of the invasive, this could suggest that an unmeasured adaptive evolutionary or plastic response (such as niche differentiation) is being reflected in the greater performance/fitness of the experienced plants under competition. If the effect varies with relatedness, then it would suggest that this unmeasured response is correlated with phylogenetic distance.

1

Methods

Data-collection

Effect sizes were compiled following the methodology outlined in Oduor (2013). Briefly, Oduor (2013) selected studies which directly compared differences in growth and reproductive traits for naïve and experienced native plant populations, where naïve is defined as populations without a history of interaction with an invader, and experienced is defined as native populations that have previous experience with the invasive. There was no minimum number of generations of invasion specified, but the majority of the studies did report an invasion period of at least 20 years or a range from 25 to 75 years. Since the invasive species in question were very dominant, the native species were often remnant survivors expected to be under strong selection (Oduor, 2013). Studies that explored multi-species assemblages were not included, and each study included in the analysis is associated with a specific native species paired with a specific invasive species.

The data required to calculate effect sizes were extracted from the papers reported in Oduor (2013). Additional searches using the key terms from the original study (i.e., (invasive plant OR invader plant OR exotic plant OR alien plant OR invasive weed) AND (natural selection* OR evolutionary response* OR native plant resistance* OR native plant tolerance* OR native plant adaptation*)) and a citation search on the selected studies were also conducted to identify new studies published after 2013 on Web of Science, Google Scholar, and Scopus. Only one additional study was identified and included in the analysis using this method.

In two studies (Grondahl and Ehlers, 2008; Jensen and Ehlers, 2010) included in Oduor (2013), I discovered that the species identified as the invasive, *Thymus pulegioides,* is actually native to the region of study, and was therefore incorrectly identified as an invasive by Odour (2013). However, like many of the non-native invasive species in that study this species is allelopathic and has a tendency to dominate local ground-cover (Jensen and Ehlers, 2010). Presumably these similarities to non-native invasive species justified its inclusion, and I therefore included one of the two *Thymus* studies used by Oduor (2013) in my analysis. The second study (Grondahl and Ehlers, 2008), which I ultimately excluded, used a 'naïve' population that co-existed with a *Thymus* phenotype expressing a different allelopathic chemical than the experienced population. I deemed this study too dissimilar from the definition of naïve populations used in the other studies. Additionally, one set of competition-treatment results from another study (Ferrero-Serrano, Hild, and Mealor, 2011), was excluded because it did not seem to fit the terms of inclusion that Oduor (2013) set out. In my opinion, the experienced populations were not adequately experienced with that particular species, because the authors tested the response of the experienced native to competition with a novel invasive species, and not the co-occurring invasive it was actually experienced with.

Information about each study and the data used to calculate effect sizes were then entered into an Access (Microsoft, 2013) database. The study authors, native-invasive species pair studied, growth and/and reproductive trait names, study variables (i.e., study design type, additional experimental treatments, location), sample sizes, and the reported means or summary statistics for each trait were all recorded. If the required data were only presented in figures they were extracted using ImageJ (Schneider, Rasband, and Eliceiri, 2012). If critical data were missing from the study or a reasonable estimation of the mean or sample size could not be made, then the data were requested from the primary author (*N* = 3). If the sample sizes for the reported means or summary statistics were not directly reported, and the authors could not be reached to clarify, the sample sizes were conservatively estimated from descriptions in the text and/or degrees of freedom. Raw data provided by the primary authors of three studies were used in the analysis, and these raw data included information on a native species (*Galeopsis speciosa*) that was not included in the Oduor (2013) study.

Effect sizes

The effect sizes for each study were calculated as Hedges *g*, which is a standardized measure of the difference between the means of two groups (Vetter, 2014). If the means and standard deviations (or standard error) were reported in a study, Hedges *g* was calculated as follows (Vetter, 2014):

$$g = \left(\frac{\bar{X}_t - \bar{X}_c}{s}\right)$$

$$s = \sqrt{\frac{(n_t - 1)SD_t^2 + (n_c - 1)SD_c^2}{n_t + n_c - 2}}$$

With variance:

$$v_g = \left(\frac{n_t + n_c}{n * n_c}\right) + \left(\frac{g^2}{2 * (n_t + n_c)}\right)$$

Where the subscripts *t* and *c* denote the treatment (experienced) and control (naïve) groups, *s* is the pooled standard deviation, *SD* is the standard deviation of the sample mean, and *n* is the sample size. If the means and standard deviations were not available, Hedges *g* was calculated using summary statistics according to the formulas outlined in Vetter (2014) when possible. Additionally, Hedges *g* was also used to quantify the response of naïve and experienced plants to competition from the invasive in studies that included a factorial competition treatment. The competitive response was calculated using the treatment (competitive planting) group and the associated control group for each study, resulting in two separate effect sizes per study: the competitive response of naïve plants, and the competitive response of experienced plants.

Studies and pooled effect sizes

A meta-analysis is typically conducted across studies using one effect size for each study, but in many cases it is possible to extract multiple effect sizes from a given research paper (Vetter, 2014). In some cases these effect sizes are from independent subgroups within the study and it may be appropriate treat them as independent ‘studies’, while in other cases combining them is more appropriate (Borenstein et al., 2009d). Several studies in the database reported results for a given invasive species in association with multiple native species, and since the variation in effect size between each native-invasive pair within a paper is of interest for my analysis, each of these pairs were considered to be independent “studies” with their own respective effect sizes (Oduor, 2013). For example, a study could have reported results of invasive species “1” with native species “a” and “b”, resulting in independent studies “1a” and “1b” (Oduor, 2013).

However, multiple native species were not the only source of multiple effect sizes. Other sources included multiple traits measured on the same set of plants, multiple treatments (e.g., nutrient/light levels, competitive planting with the invasive), replicate population means reported separately, and traits measured at multiple time points. Multiple effect sizes measured from the same group of plants are not independent and ideally should not be treated as separate studies (Vetter, 2014). However, even multiple experiments may be problematic due to the use of clones or full sibling families, and over-representation of one population within one research group. Several methods for handling dependencies within the dataset have been proposed over the years (Borenstein et al., 2009c, b, a; Lajeunesse, 2011; Vetter, 2014), so when multiple effect sizes could be extracted from the same species pair within a study I proceeded as follows:

1) If the means for separate replicate populations were reported the combined weighted mean and standard deviation were used to calculate the pooled effect size. This helped maintain consistency with the studies that reported overall means across replicates (Borenstein et al., 2009d).
2) If the studies reported multiple traits measured on the same set of samples an effect size was calculated for each trait and pooled using an inverse-variance weighted average, which is adjusted for the correlation between traits, in the MAd R-package (Borenstein et al., 2009b; Lajeunesse, 2011; Vetter, 2014). Since the correlation between the measured traits was not always provided, the correlation coefficient was assumed to be $r = 1$ which is the most conservative option (Borenstein et al., 2009b). Two sub-categories were created for pooling: growth traits (e.g., biomass, root biomass, tiller number, leaf number) and reproductive traits (e.g., seed number, inflorescence number, flowering date). Since pooling effect sizes from different traits could mask trait-specific effects the most commonly measured trait, total biomass, was also used in a separate analysis without effect size pooling.

3) If the study reported the results of multiple experiments or treatments such as competitive planting, nutrient or light treatments levels, herbivory, or other significant differences the following methods were used:
    a. The multiple effect sizes were averaged using individual random-effects meta-analysis to generate a single weighted overall effect size for each unique species pair within a paper, effectively treating them as nested subgroups with separate variance estimates (Vetter, 2014). However, for one analysis the experiments/treatments were pooled within two levels of competition treatment (yes or no) for use in the interaction models (figure 1). A more refined method, which would help account for the similarity within these nested groups, involves multi-level modelling in R with the uncombined effect sizes; however, I was not confident in my use of these models since my attempts to view the profile plots used to check for proper model parametrization resulted in error messages.
    b. The multiple effect sizes were considered to be independent studies. This was the method used by Oduor (2013) and was included for consistency with the Oduor study. For the competitive response analysis the effect sizes for the naïve and experienced populations were also treated as independent studies since they were drawn from different populations, the number of naïve and experienced studies were balanced, and the goal of the analysis was to explore potential differences between the naïve and experienced groups.

Phylogenetic distance

To see if the effect of experience with the invasive species, and the response to competition with the invasive, varied with how closely related the native and invasive were, I included an estimate of the phylogenetic distance between the native and invasive species for each study as a moderator variable in my analysis. However, because the majority of the species pairs used in my analysis were clustered at the extreme ends of the range of phylogenetic distance I also used con-familial status (whether or not the native and invasive were in the same family) as a categorical (binary) proxy for relatedness in separate models. To calculate the phylogenetic distance between the native and invasive species in each study, a backbone phylogenetic tree of angiosperms was generated using the S.Phylomaker package in R (Qian and Jin, 2015) to prune the Qian and Jin (2015) correction of the Zanne et al. (2013) mega-tree (Zanne et al., 2013; Zanne et al., 2014; Qian and Jin, 2015). The Zanne et al. (2013) tree is a fossil (39 fossils) time-scale molecular tree built from 7 gene regions (*atpB*, ITS, *matK, rbcL, trnL-F,* 18S rDNA, and 26SrDNA*)*. It encompasses 31,749 land plants and contains most of the species used in the analysis. The corrected tree, known as the PhytoPhylo megatree, resolves some of the errors and outdated nomenclature present in the original Zanne et al. (2013) mega-tree. The super-tree method, which typically results in a backbone tree resolved at the family level with species attached as polytomies, and when used with the PhytoPhylo tree can be a robust and suitable proxy for trees resolved at the species level in ecological studies (Qian and Zhang, 2016).

Before producing the tree in S.Phylomaker, the species names reported in the study database were resolved according to The Plant List standard (2013) by cross referencing the names used in the individual studies with accepted synonyms in The Plant List. I then compared the lists of potential synonyms against the species used in the mega-tree, and the species list that produced the most matches with the tree was used to create a pruned backbone tree of the species used in my analysis. Specifically, the S.Phylomaker package was used in R to prune the PhytoPhylo mega-tree to the matching species from my analysis, and species not present in the original backbone were assigned to their parent taxa as polytomies (Qian and Jin, 2015). Their branch-lengths were estimated using the method outlined in the bladj function in Phylocom (Webb, Ackerly, and Kembel, 2008; Qian and Jin, 2015), which sets unknown branch lengths by evenly placing undated nodes between known dated nodes and between dated nodes and terminal ends. The pair-wise phylogenetic distances (in units of time according to the branch length distance between tree tips) between the species were then calculated from the final tree using the cophenetic.phylo function in the 'ape' R package (Paradis, Claude, and Strimmer, 2004), and the distance between the native and invasive species pair in each study was included as a study level variable.

Analysis

I used a combination of random-effects meta-analysis and mixed-effects meta-regressions with moderator variables to explore the overall effect of experience and competition on native plant growth and reproduction, and to see if the variance in the effects between studies could be explained by the relatedness between the native and invasive species, the inclusion of competition treatments (when analysing the effect of experience), experience (when analysing the effect of competition), and the allelopathic status of the invasive species. The allelopathic status of the invasive was included because several of the invasive species were allelopathic (as described by the study authors) and allelopathy could alter the strength of competition on native species and select for resistance (Callaway et al., 2005; Mealor and Hild, 2006; Dostal, 2011).

Unlike a fixed-effects model, which assumes that the true effect size for each study is the same (or is the same within groups if the models include a moderator variable) and any differences are due to sampling error, the random-effect model allows for each study to have a different true effect size, and the between-studies variation (tau^2) is added to the variance of each study's effect size (Vetter, 2014). Since I expected there to be differences in the effect sizes due to study-level differences and the use of different species, I chose to use random-effects models for my analysis. I used mixed effects models for the meta-regressions which included moderator variables because, although I expected that these variables would explain some of the variation between studies there are still many differences between the studies that could result in true differences not explained by simple one or two-factor models (the random component) (Vetter, 2014).

I chose to present my results using models with a restricted maximum likelihood estimator for tau^2, which is the default option in the "Metafor" R package. However, for comparison the results were also generated using a method-of-moments method (which does not assume a normal distribution of the effect sizes) (Viechtbauer, 2010; Vetter, 2014), and because of the small sample size I also tested the models using the Knapp-Hurtang adjustment (which leads to a more conservative estimate of significance when sample sizes are small) (Viechtbauer, 2010; Vetter, 2014) and I made note of when a model was no longer significant using one of these alternative methods. These analyses were conducted using a combination of the R packages

Metafor (Viechtbauer, 2010) and MAd (Hoyt, 2014), and a program called OpenMee (Viechtbauer, 2010; Dietz et al., 2016).

Since there were methodological differences in how I gathered my data and treated multiple effects sizes relative to Odour's (2013) analysis, I first performed a basic random-effects meta-analysis (Vetter, 2014) to determine if my updated dataset still corroborated Oduor's (2013) findings that, on average, experienced populations had greater growth and reproductive traits than their naïve counterparts. This basic analysis also allowed me to determine if there was heterogeneity in the effect of experience between studies. If Q, which is a weighted sum of squares that measures the dispersion of the study effect sizes around their mean, is significant, then there is true variance in the effect size that is not explained by the model; in which case, an overall effect size predicted by the model should be interpreted cautiously and it is worth looking for moderators that explain the variation in the study effects (Vetter, 2014).

To explore whether the variation in the effect of experience with an invasive on the growth and reproductive traits of the native species could be explained by the relatedness between the species, I performed a restricted maximum likelihood random-effects meta-regression (Vetter, 2014), which included the phylogenetic distance (or con-familial status as a discrete proxy for relatedness due to the lack of data-points in the mid-range for phylogenetic distance) between the native and invasive species as a moderator variable. Several studies also included a competitive planting treatment with the invasive species; additionally, many of the invasive species were allelopathic, which could alter the impact of the invasive on the native and select for resistance. To address the potential effect of competition treatments and of allelopathy on the effect of experience (separate from relatedness) I used meta-regression models with the following subgroups of studies as moderator variables:

a) Competition vs. no competition treatment

b) Presence vs. absence of allelopathy in the invasive

In their analysis, Oduor (2013) concluded that the overall difference in trait size between naïve and experienced plants did not differ between studies with and without a competition treatment; however, if the relatedness between species is predictive of selection on the native species, a simple sub-group analysis may not capture an adaptive response to competition from the invader. Since I hypothesized that competitive interactions play a role in the relationship between relatedness and the response to invasion by native species, I included the interaction between competition treatments and the other factors (relatedness and allelopathy) in separate meta-regression models. Finally, to explore the competitive response of experienced and naïve plants, the analyses were repeated using an effect size reflecting the difference between the competition treatment and control groups, and instead of competition I included the level of experience in the models.

Results

When multiple treatments and time points were treated as independent studies there were a total of 68 studies for all traits pooled: 60 studies for growth traits, 37 studies for reproductive traits, and 36 studies for total biomass alone. The majority of studies (*N* = 44) included an allelopathic invasive, as determined by the species descriptions in the study introductions and the presence of multiple (>3) studies supporting the allelopathic status, and the number of studies that did or did not include a competition treatment was similar (*N* = 32 and 36, respectively). There were no studies in which the invasive was both non-allelopathic and in a different family than the native species. When multiple treatments and time points per study were averaged to produce a single effect size per species pair per paper, there was a total of 27 studies for all traits, 26 for growth traits, 14 for reproductive traits, and 14 for total biomass. In some cases, the sample sizes for competition treatments and studies with an allelopathic invasive were uneven. For the sample sizes for all combinations of the family, allelopathy, and competition subgroups, see Tables A2 through A6 (Appendix 1).

Meta-analysis

When multiple treatments and time-points were included as independent studies I found a positive overall effect of experience with the invasive on the size of combined growth and reproductive traits (Table 2: overall effect size = 0.3982, SE = 0.0489), which suggests that experienced plants have greater trait values than naïve plants. This result corroborates the larger effect on combined growth and reproductive traits in the experienced plants group reported by Oduor (2013). However, when I analyzed reproductive traits alone, experienced plants did not differ significantly from the naïve plants (Table 2). Experienced plants were significantly larger for growth traits alone and for biomass alone, but this difference was smaller than when all of the traits were combined. When multiple treatments and time points were averaged prior to the analysis, the results were essentially the same (Table 2). There was a significant amount of heterogeneity in the effect of experience among studies, which suggests that there are true differences among studies that might be explained by study-level variables. The amount of true heterogeneity (represented as I^2 , which is the percentage of the variance in the effect sizes that is not due to sampling error alone) was small and had a large uncertainty (reflected in the 95% confidence interval) for biomass and for all traits when the treatments were not combined, which makes it difficult to infer whether the variance is due to true heterogeneity among studies or sampling error (Table 2).

Moderator analysis

The tests of competition, allelopathy, and relatedness as potential variables to explain the heterogeneous effect of experience with an invasive on native growth and reproductive traits found mixed results. When multiple treatments were considered as independent I found no difference in the mean effect of experience on trait size among studies with and without a competition treatment for any combination of traits (see Appendix 1 Table A18: p-value > 0.05), and the model did not explain any of the heterogeneity in the effect of experience between studies.

For all combinations of traits, the effect of experience was larger when the native and invasive species were in different families (Table 3; Figure 5). This difference was reflected in the distance model, with the effect of experience on the size of growth and reproductive traits increasing if they are in different families (Table 3; Figure 6). Phylogenetic distance explained less of the variation in the effect of experience than family (8.2% vs 13.77%, 8.5% vs 12%, and 1.6% vs 18.8% for all traits, growth traits, and reproductive traits). Phylogenetic distance did not explain any of the heterogeneity in the effect sizes for biomass and there was no difference in the mean effect size between species pairs that were and were not in the same family for biomass (Table 3).

The presence of allelopathy in the invasive explained some of the heterogeneity in the size of the effect for all traits (Q_m = 10.4759, p = 0.0012), growth traits (Q_m= 5.8472, p = 0.0156), and reproductive traits (Table 3: Q_m = 8.8334, p = 0.003) with the estimated effect of experience moderately increasing by 0.397, 0.36, and 0.55, respectively, in studies where the invasive species was allelopathic. Since the intercept terms of the models were close to zero, the results suggest that experienced plants tended to have greater growth and reproductive traits relative to the naïve plants when the invasive was allelopathic, but not when the invasive lacked allelopathy (Table 3; Figure 5). However, there was still a significant amount of unexplained between-study heterogeneity within the levels of allelopathy (Table3; Table A18) and the model for allelopathy explained less than 20% of the heterogeneity in the effect size across studies.

When the effect sizes from multiple treatments (including competition) and time points were averaged into a single effect size per study prior to the analysis, the effect of experience did still seem to be larger for reproductive traits, but again, only when the invasive was allelopathic (Table 5). However, the number of studies for this test was very small (N = 7 for each subgroup). Additionally, there were no longer any significant differences in the effect of experience for allelopathy, distance, or family membership for all other trait combinations.

Interaction models

The basic moderator analysis suggests that there is no difference in the mean effect of experience on native plant traits between studies with and without competition treatments. However, when multiple treatments were treated as independent studies I detected an interaction between competition and phylogenetic distance for all traits combined (estimate for interaction coefficient = 0.0016, SE = 0.007, $p < 0.05$; $Q_m = 10.62$, $p = 0.0165$) as well as for growth traits alone (Table 4; Figure 8), which suggests that the effect of experience varies with phylogenetic distance, but that this trend also varies with the presence or absence of the invasive. Specifically, the effect of experience increased with phylogenetic distance when the invasive was present, but not when it was absent but the slope of the relationship was very small (Figure 8: regression coefficient for all traits = 0.0016 ± 0.0005, $p = 0.0014$; growth traits = 0.0017 ± 0.0006, $p = 0.0015$). These interaction models accounted for 14.25% and 16.35% of the heterogeneity in the effect of experience on plant traits, respectively (Table 4), and the model was not significant for reproductive traits.

In terms of the discrete proxy for relatedness, con-familiarity, the effect of experience was smaller for reproductive traits when the native and invasive species were in the same family and when the natives were grown alone, and the effect was larger for growth traits when the species were in the same family and grown with the invasive (Table 4; Figure 7). The effect of experience on growth traits among studies was also larger when the invasive was allelopathic and the plants were grown in competition, but not when they were grown alone. The effect on reproductive traits was also larger when the invasive was allelopathic and when the native plants were grown alone (Table 4; Figure 7).

Finally, when multiple treatments were combined (except for competition treatments, resulting in two effect sizes per study if there was a competition treatment) prior to the analysis, there was still a significant interaction between phylogenetic distance and competition for the effect of experience on growth and reproductive traits (Table 6; Figure 9). The effect of experience on plant traits increased slightly with distance when there was a competition treatment, but distance did not explain any of the variation in the effect of experience in the absence of competition (Table 6; Figure 9). For all traits and growth traits the effect of experience was larger for allelopathic invasives in the presence of competition, but for reproductive traits the effect was larger for allelopathic invasives in the absence of competition (Table 6: $p < 0.05$). There was a significant interaction between family and competition for growth traits and the effect of experience was larger when the species were in different families, but only for studies with a competition treatment (Table 6; Figure 9). However, the number of studies for growth traits was extremely small when divided according to competition and allelopathy or competition and family (e.g., $N < 6$ in some cases, see appendix 1 Table A15).

Confounded moderators

Allelopathy and family membership were highly correlated (correlation coefficient = -0.8312094) (i.e., all species pairs where the invasive was in the same family as the native had an allelopathic invasive). Not surprisingly, allelopathy and distance showed the same pattern (correlation coefficient = 0.807194). In a subset of studies where the native and invasive species were in the same family there was no longer a significant difference in the effect of experience between the levels of allelopathy (difference in mean effect size = 0.303, SE = 0.21, $Q_m = 2$, $p = 0.1562$), and among allelopathic invaders there was no difference in effect based on family membership (difference in mean effect size = 0.1097, SE = 0.21, Qm = 0.28, $p = 0.6$). A regression model including both allelopathy and family did not have any significant terms, although the omnibus test of the model itself was significant ($Q_m = 10.59$, $p = 0.005$), which suggests at least one of the terms explain some of the variance in the effect of experience, and the entire model explained ~ 15.8% of that variation (or heterogeneity). A regression including distance and allelopathy was significant and explained 15.84% of the heterogeneity in the effect sizes ($Q_m = 10.4220$, $p = 0.0055$); however, only the model estimate for allelopathy was significant (model coefficient = 0.4503, SE = 0.2061, $p = 0.0289$; Q_m for allelopathy alone = 4.77, $p = 0.0289$), suggesting that only allelopathy explained the variation in the effect of experience.

Competitive Response

When prior experience with the invasive was ignored, there was a significant negative overall effect of competitive planting with the invasive on the native trait values when all trait combinations were considered, and when biomass was considered alone (Table 7). The overall effect size for the competitive response on all traits combined, growth traits in isolation, and biomass in isolation was negative, indicating that the plants exhibited lower trait values when grown with the invasive. For all traits combined, there was a significant amount of heterogeneity in the effect of competition among studies; however, the estimate for the percentage of the variance attributable to true heterogeneity had a large confidence interval for reproductive traits ($I^2 = 68.78$, CI = 39.59 - 86.84), making it difficult to distinguish between true differences and error sampling variance.

There was no difference between experienced and naïve plants ($p > 0.05$) in terms of the effect of competition with the invasive species on their reproductive and growth traits

(Table 9). Across both experience levels, the models for phylogenetic distance and same-family membership explained 19% and 12% of the heterogeneity in the magnitude of the effect of competition across studies, respectively, for all traits. There was a small positive influence of phylogenetic distance on the effect of competition on native species' combined growth and reproductive traits which, given that native species which are closely related to the invasive experienced a large decrease in their traits when under competition, suggests that the negative effect of competition with the invasive decreases with distance. This is supported by the same-family model, which suggests that the negative effect of competition on the native species' combined growth and reproductive traits is greater when the native and invasive species are in the same family (Figure 11: regression coefficient for distance = 0.0016, SE = 0.0005, $p = 0.0028$; coefficient for same-family (yes) = -0.4587, SE = 0.1881, $p = 0.0148$). For growth traits across both experience levels, distance, same-family membership and allelopathy explained 55%, 35%, and 20% of the heterogeneity in the effect of competition, respectively. Increasing distance, being in different families, and having an allelopathic invasive reduced the negative effect of competition on growth traits across experience levels (Table 8: coefficient for distance = 0.0029, SE = 0.0006, $p < 0.001$; coefficient for same family (yes) = -0.7659, SE = 0.2156, $p = 0.004$; coefficient for allelopathy (yes) =0.6598, SE = 0.2480, p=0.0078). Distance and same family membership were also significant predictors for biomass across studies and explained 41% and 13% of the heterogeneity, respectively, among studies, but there were only two studies in the "same family" subgroup and there were relatively few studies with closely related pairs (Figure 10).

The influence of distance, family membership, and allelopathy on the effect of competition on the native species' traits also varied slightly with the native's experience level (Table 9 and Table A21; Figure 12). However, there was no evidence of an interaction between experience level and distance, allelopathy, or family membership ($p > 0.05$ for the interaction term for all traits). Studies with same-family species pairs exhibited a marginally smaller effect size for all traits when the plants were experienced, but not when they were naïve, and the estimated effect size for experienced plants increased slightly with distance (Table 9; Figure 12). Studies with same-family species pairs exhibited a stronger effect of competition on growth traits, the negative effect of competition was slightly reduced with phylogenetic distance regardless of experience level, and the negative effect of competition on experienced plant's growth traits was smaller when the invasive was allelopathic (Table 9; Figure 12). There were very few studies available for reproductive traits and biomass for this analysis and there were no significant predictors for these traits.

Finally, when distance and allelopathy were both included in the model (ignoring experience), increasing distance still had a positive influence on the effect of competition (model coefficient for distance = 0.0023, SE = 0.0009, $p = 0.0162$ for all traits). However, allelopathy no longer significantly influenced the effect of competition on growth traits when distance was included in the model, and a model including family and allelopathy had no significant model estimates, which makes it difficult to determine if one, both, or neither of these factors can explain the variance in the effect of competition on native species' traits.

Discussion

The competitive differences between invasive and native species have been explored as a factor in invasion success, but they may also be important to our understanding of the evolutionary response of natives to invaders (Gioria and Osborne, 2014). In this study, I demonstrated that the phylogenetic relationship between an introduced species and its invaded community may influence the ecological and evolutionary impact of an invasive on native species. I predicted that the variation in the effect of invasive plants on native plant species' growth and reproductive traits would be explained by the relatedness between the native and invasive species. I also explored whether the allelopathic status of the invasive species would predict its impact; both factors have been hypothesized to explain the strength and direction of the competitive interactions between native and invasive species (Cahill Jr et al., 2008; Dostal, 2011; Lankau, 2012; Jones, Nuismer, and Gomulkiewicz, 2013). Finally, I predicted that naïve and experienced native plants would differ in terms of their response to competition with the invasive, and that variation in this effect would be explained by relatedness. Through meta-analysis I found that, in general, experienced plants expressed slightly higher levels of growth and reproductive traits in the presence of an invasive, relative to naïve plants, particularly when the native and invasive species were more distantly related. When I compared studies with and without a competitive planting treatment, the direction between relatedness and the effect of experience on native growth traits was only significant if the native plants were grown with the invasive (i.e. the difference between experienced plants grown under competition and naïve plants grown under competition was significant), which could suggest a difference in their plastic response to competition, evolved tolerance, or competitive ability. I also found that the effect of experience on native growth and reproductive traits was greater in studies with an allelopathic invasive, although this association was only significant in studies where the native naïve and experienced plants were grown with the invasive, and there was a confound between relatedness and allelopathic status. I found no difference between experienced and naïve plants in terms of the overall effect of competition on growth and reproductive traits. However, I found that the growth of natives was less impacted by competition with the invasive when they were more distantly related, that allelopathic invasives had a smaller effect on native growth and reproductive traits than non-allelopathic invasives (potentially because of the confound with relatedness), and that the influence of relatedness and allelopathy is only slightly less pronounced for experienced relative to naïve plants. Therefore, it would seem that a stronger competitive impact on the native species did not result in a stronger evolutionary or plastic response (as estimated by the difference in growth and reproductive traits between experienced and naïve plants) to the invasion, which does not match my initial predictions.

In general, the effects of both experience and competition were more pronounced when using a categorical metric for relatedness (i.e., same family membership) than when using the continuous phylogenetic distance between the native and invasive species. This could be because the distribution of species pairs was largely clustered at the extreme ends of the distance scale, and using con-familiarity as the cut-off point for relatedness eliminated noise from the few points in the mid-range. An experimental study of the interactions between native and invasive plant species found that the competition by an invasive was greater for closely related (albeit and the con-generic level) natives than distantly related (non con-familial) natives, but that phylogenetic distance itself was not a strong predictor (Feng and van Kleunen, 2016), so it may be the case that a coarser measure of relatedness is more appropriate when comparing species pairs that range from congeners to species that are unrelated at the family level, or when using roughly resolved phylogenies.

Niche-fitness frameworks

My results support the idea that phylogenetic relatedness can predict the post-invasion ecological impacts of an invasive plant species on natives. Darwin's naturalization hypothesis predicts that introduced species should more easily establish ('naturalize') if they are distantly related to native species, because greater phylogenetic distance should be correlated with reduced [niche] similarity (Darwin, 1902), but in theory this should generally result in less competition between the two species and thus a smaller impact on natives in the absence of large fitness differences. Since my analysis is concerned with already established invasive species and their impacts, then under classic niche based frameworks like Darwin's I would expect greater competition on native species from more closely related invasive plants (Macdougall *et al.*, 2009; Wan *et al.*, 2009; Gioria e Osborne, 2014; Godoy *et al.*, 2014). This was the trend I observed when I examined the effect of competition on native species, but the minimal difference in this pattern between the naïve and experienced subgroups suggests that the experienced plants were generally not more tolerant of competition from the invasive.

Frameworks which combine niche and fitness-difference frameworks to expand on co-existence theory suggest that fitness differences, which are trait differences that facilitate competitive dominance between two interacting species irrespective of the stabilizing niche differences that may favour co- existence (Chesson, 2000), may allow introduced species to exclude distantly related species (Chesson, 2000; MacDougall, Gilbert, and Levine, 2009). A few recent studies have suggested that fitness differences may increase with the phylogenetic distance between species (Godoy, Kraft, and Levine, 2014; Germain, Weir, and Gilbert, 2016) and that, in particular between allopatric species (Germain, Weir, and Gilbert, 2016), niche differences may not be as strongly correlated with phylogenetic distance as once assumed (Godoy, Kraft, and Levine, 2014). In allopatric species, such as the case of invasives, this could lead to the expectation of reduced co-existence when the invasive is closely related to the native. My results regarding the effect of experience might support this notion at first glance, since they suggest that the effect of experience is greater when the natives and invasives are distantly related, which could indicate an evolutionary response to the invasive. However, this pattern only occurred when the natives were under competition, which suggests that either an unmeasured trait differs between the experienced and naïve populations (and the measured growth and reproductive traits are a fitness component) or that the experienced plants have a greater plastic response to the invasive. Additionally, my results regarding the actual effect of competition seemingly contradict this idea since the effect of competition was stronger when the species were more closely related. Therefore, it seems likely that some other factor is at play with regards to the evolutionary effect of plant invasions in these studies.

Competition subset

The most obvious candidate for the disparity between the effect of competition and the effect of experience would be that not all studies were represented in the competition analysis, since they either lacked a factorial competition treatment or I was unable to pull the appropriate data from the results. In the analysis using the combined effect sizes, two studies lacked a competition treatments and 6 studies lacked a competition free control. Within these studies four invasives (*R. repens, B. tectorum, C. stoebe, and A. petiolata)* and four natives (*S. airoides, S. comata, E. multisetus, and P. pumila)* are represented, and with three exceptions these studies have large effect sizes for distantly related pairs and small effect sizes for the closely related pairs. Excluding these studies from the analysis of the effect of experience results in a non-significant trend for relatedness, so there may be some other factor within these studies which drives the response. Since the association between relatedness and the effect of experience was fairly weak in my study, it could simply be that the opposing influence of competition between more closely related species was not the main driver of this plastic or evolutionary response (Godoy, Kraft, and Levine, 2014) and that other biotic and abiotic factors may mediate selection on the native species and its response to invasives (Lau and Terhorst, 2015).

Phenotypic plasticity

Plasticity is an intriguing possibility that could explain the mixed results in both my dataset and studies of competition and relatedness in plant invasions (Cahill Jr et al., 2008; Dostal, 2011; Castro et al., 2014; Godoy, Kraft, and Levine, 2014; Godoy and Levine, 2014). One study of adaptive plastic trait responses (measured as the root-to-shoot ratio and surface leaf area) to competition in a community assembly context found that in some treatments, plants grown with distantly related competitors had greater biomass than those with closely related competitors. They also found that, generally, the plants had an adaptive plastic response to competition and soil treatments which was expressed as divergence in their root to shoot ratios. The authors suggest that both plastic (or facultative) trait divergence and the divergence in traits due to phylogenetic distance may offset the effects of competition and facilitate co-existence, but that plasticity could mask phylogenetic trait signals in a community context (Burns and Strauss, 2012). The majority of the traits used in my analysis are more similar to a productivity metric (e.g., biomass) than functional traits (which may be more predictive of niche or fitness differences), so while my results do corroborate a relationship between distance and the competitive effect of the invasive, at least for the species and systems used in my analysis, I cannot clearly infer the presence of an adaptive plastic response. However, the difference between experienced and naive plants in my dataset was greatest when they were distantly related to the invasive and under competition—if this were to be a function of an adaptive plastic response instead of an evolutionary response it could in part explain why the effect of competition was weakest when the native and invasive species were distantly related. It would be interesting to see if trait plasticity could account for some of the unexplained variation in the effect of competition and experience.

Other factors affecting evolutionary responses

Other factors can influence the strength of selection and the adaptive response (or lack thereof) in the native, whether due to competition with the invasive or because of other biotic and environmental influences which impose selection on the invasive or act as barriers to adaptation (Lau, 2012; Lau and Terhorst, 2015). For example, environmental disturbance and habitat-level differences could alter the frequency and outcomes of competitive interactions with the invasive (Huston, 2004; Molinari and D'Antonio, 2014), while invasion stage and intensity (Theoharides and Dukes, 2007; Pellock et al., 2013; Gioria and Osborne, 2014) and the scale of the analysis (Proches et al., 2008; Cadotte, Hamilton, and Murray, 2009) can alter the relative importance and direction of phylogenetic relatedness as a predictor of invasiveness. It may be the case that these may alter the competitive interactions and native response to invasions. In addition, several studies suggest that the invasives themselves undergo rapid adaptation in their new range that may allow them to become more competitive (Blumenthal and Hufbauer, 2007; Dlugosch and Parker, 2008; Abhilasha and Joshi, 2009; Barney, Whitlow, and DiTommaso, 2009; Buswell, Moles, and Hartley, 2011), which opens up the possibility of co-evolutionary feedbacks that might vary depending on the time since the invasion. It is also worth noting that a large study which tested the correlation between distance and the strength of competition found weak support for a linear relationship, because the competitive dominance of eudicots over monocots influenced the patterns of relatedness and competition (Cahill Jr et al., 2008F). When the focal and competing species in the study were monocots they found that competition decreased with phylogenetic distance, and that eudicots tended to be superior competitors to monocots. When eudicots competed with other eudicots they did not detect a phylogenetic signal. Therefore, while the patterns of relatedness with respect to the competitive effects of invasive plants on native plants may not be straightforward, it does seem that phylogenetic relatedness can be a context-dependent predictor of these effects.

In addition, factors such as a lack of heritable genetic variation in the traits under selection, low frequencies of species interactions, weak selection, stochastic factors such as gene flow, and non-additive selection from other species can inhibit also adaptation in native species (Berthon, 2015; Lau and Terhorst, 2015). For example, it could be that the species in my analysis under the strongest competition are so suppressed that they have low interaction frequencies with the invader or may become bottle-necked to the point that they lack the genetic variation to adapt to the invasive. The majority of the native species in my analysis that were closely related to the invasive were also wind-pollinated grasses, which could have high gene flow that might counter the effects of selection from strong direct competition (Ellstrand, 2014). Finally, complex eco-evolutionary interactions such as plant-soil feedback (Deck, Muir, and Strauss, 2013), co-evolutionary relationships (Lankau, 2012), and herbivore and pollinator mediated selection (Russell et al., 2007; Moron et al., 2009; Lau, 2012; Oduor et al., 2013; Beans and Roach, 2015a) may also play a role in altering the invasion outcomes and the ecological and evolutionary effects of invasive species on natives. Given the complexity of the interactions and factors which can alter native responses to invasions, future studies and syntheses of the evolutionary responses of native plants to invasive plants would benefit from consideration of both community-level interactions and pair-wise competitive interactions, and in particular the indirect interactions which could alter selective pressure or competitive outcomes, to help to build on existing frameworks and predict the outcomes of invasions.

Allelopathy confound

Allelopathy could account for some of the variation in the effect of experience on native growth and reproductive traits since it may be a factor in invasion success and the outcome of competition between native and invasive plant species (Hierro and Callaway, 2003; Dostal, 2011; Lankau, 2011, 2012; Gioria and Osborne, 2014). Allelopathy, which is usually considered to be an indirect form of competition, can enhance selective pressure via competitive interactions and the alteration of the local environment (Levine et al., 2003; Callaway et al., 2005; Mealor and Hild, 2006; Dostal, 2011; Gioria and Osborne, 2014). However, the effects of allelopathy may be difficult to separate from the effects of resource competition, which is driven by fitness traits and/or niche overlap (review by Gioria and Osborne, 2014), and studies report mixed results regarding selection on natives from invasive allelopathy (Ridenour and Callaway, 2001; Renne et al., 2004; Mealor and Hild, 2006; Qin et al., 2007; Corbin and D'Antonio, 2010; Bennett, Thomsen, and Strauss, 2011; Dostal, 2011; Gioria and Osborne, 2014; Greer et al., 2014; Uddin et al., 2014).

However, relatedness and allelopathy were confounded in my dataset: all of the studies where the natives and invasive were in the same family also had an allelopathic invasive. This made it difficult to disentangle the effects of allelopathy and relatedness, potentially explaining why allelopathic invasives had a less competitive effect on natives than the non-allelopathic species. This confound seems to occur because, of the two non-allelopathic invasives in the studies, the grass *B. tectorum* was exclusively paired with native grasses that had a small phylogenetic distance between them. Likewise, the herbaceous Medicago polymorpha was also paired with a native in the same family with a small phylogenetic distance. Since the majority of invasive species and grasses, and grasses can also be allelopathic (Greer et al., 2014), I believe this confound is a coincidence of the species selection by the original authors. Regardless, both allelopathy and relatedness are interesting possibilities in the context of the evolutionary effects of plant invasions and competitive interactions with native plants.

Methodological considerations

It should be noted that the strongest support for relatedness as a moderating factor came from the dataset based entirely on Oduor's (2013) methods which, in my opinion, had some issues of non-independence due to the treatment of experimental groups of siblings and clones, and multiple time-points, as independent studies. When I attempted to account for this dependence by averaging these studies, relatedness was not a significant predictor of the effect of experience except for in the studies with a competition treatment. This could be attributable to the removal of skew from the over-representation of a set of influential families, or the averaging out of a particularly influential data point, but it also reduced the sample size, and reduced the variance of the average effect size, which could result in the loss of informative data (Vetter, 2014). However, even in the reduced dataset, relatedness still explained some of the variation in the effect of experience in the studies with a competition treatment. It could be that competition is a key factor, but since the sample size becomes quite small when divided by competition treatment, caution is warranted. There were also slight differences in the magnitude and significance of some of the effects depending on which plant traits (e.g., all, growth, or reproductive) were under consideration. Since invasions may not impose selection on different plant traits equally, especially since other factors such as herbivore or pollinator-mediated selection, disturbance, soil-feedbacks, the time since invasion, and niche overlap can influence the strength and outcomes of selection (Cipollini and Hurley, 2008; Lau, 2008; Lankau, 2012, 2013; Beans and Roach, 2015a, b; Ferguson et al., 2015; Lau and Terhorst, 2015), it seems probable that which traits were reported by each study and pooled within those categories could influence the results. Unfortunately, the differences between studies in which traits were reported, and the small sample sizes, make it difficult to justify analyzing each trait separately and necessitated pooling them. It would be interesting to see the effect of experience on a per-trait basis, but more data would be needed. Ultimately, because of the sensitivity of the results to the traits used and the manipulation of a subset of the studies, these results should be cautiously interpreted as a potential trend that warrants further exploration.

Conclusion

Meta-analysis can help consolidate contrasting hypotheses and create broader and more general frameworks for understanding invasions (Koricheva and Gurevitch, 2014), but it relies on sufficient background studies and data. There was considerable repetition among species in the studies I used, and the species were highly clustered phylogenetically. A wider range of native-invasive species pairs (from a phylogenetic perspective), and in particular a greater phylogenetic distribution of native species, would be helpful for future studies of this type. Binning the studies according to whether the native and invasive were in the same family helped, but even so there was considerable scatter in the effect sizes not explained by the moderators used in my analysis.

Prior to my analysis there had been little investigation into the question of whether the relatedness between native and invasive plants species plays a role in the evolutionary impacts of invasions on native species. My findings encompass a range of systems and suggest that there could be intriguing relationships between relatedness (and/or allelopathy in the invasive species) and evolutionary trait changes in native growth and reproductive traits. I also found patterns suggesting that distantly related species tend to compete less strongly than closely related species. My findings highlight the importance of considering the evolutionary relationships between native and invading plant species when evaluating the ecological and evolutionary impacts of invasions, and the need to extend current invasion frameworks to not just encompass the causes of invasions, but also the consequences and the factors which influence these outcomes.

Tables and Figures

Introduction

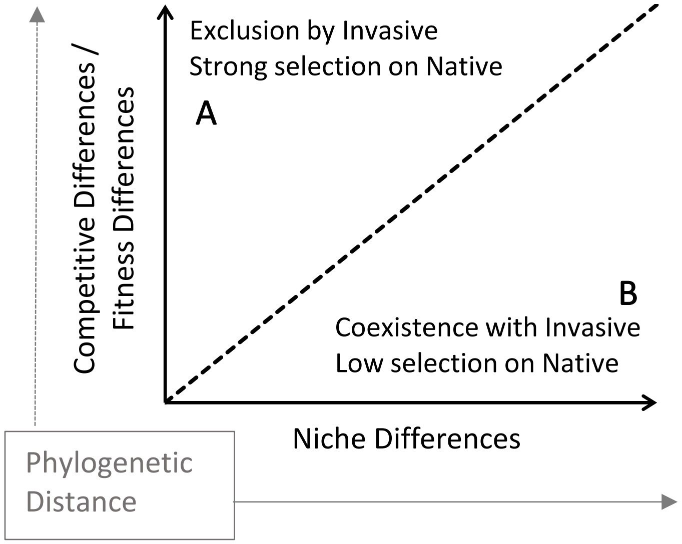

Figure 1. The niche-fitness framework in the context of phylogenetic relatedness and how these translate into selection on native species in pair-wise interactions with invaders. Niche differences between interacting species favour co-existence by reducing competition for partitionable resources between the species, or alternatively cause a species to limit itself more than others at high densities. Fitness differences, which promote competitive asymmetry, favour the competitive dominance of one species and can result in the exclusion of the other. While niche differences have long been hypothesized to increase with phylogenetic distance, only recently has there been some evidence to support the idea that fitness differences between competing species may also increase with phylogenetic distance (Godoy, Kraft, and Levine, 2014). The framework will be discussed in the context of an invader which is not excluded by the native: A) When niche differences are small and fitness differences are large (and favour the invader), the invader can successfully establish and may exclude the native due to the strong competition from both niche similarity and the general fitness advantage. This can lead to strong selection on natives to either become more competitive (reducing the fitness differences) or to avoid competition through niche differentiation (increasing niche differences). A larger competitive asymmetry requires a larger niche difference to offset it, and conversely smaller niche differences require less competitive asymmetry to exclude the native. B) When niche differences are large they favour co-existence and the invader can establish, but competition and selective pressure on the native is reduced unless the invader possesses a fitness advantage or has an indirect impact on the native (e.g through allelopathy, changes in soil microbiota, pollinator or herbivore interactions). As niche differences increase larger fitness differences are required for invaders to exclude the naïve species and have a large impact. If both niche and fitness differences are positively correlated with phylogenetic distance, with equal slopes and an equal increase (fitness differences) or decrease (niche differences) in competition between two species, they will mask each other's phylogenetic signal. If phylogenetic distance is not positively correlated with fitness differences (or is weakly correlated) there should be a general pattern of stronger competition and selection on native species when invaders are closely related, because exclusion becomes more probable when smaller fitness differences are required to overcome the stabilizing niche differences (larger exclusion area on the graph). Figure adapted and altered from (MacDougall, Gilbert, and Levine, 2009).

Competition

Experience	No	Yes		
No	**A** Naïve natives grown alone	**B** Naïve natives grown with invasive	**B-A**	Initial effect of competition on native fitness outcomes (Does the invader impact the naïve native?)
Yes	**C** Experienced natives grown alone	**D** Experienced natives grown with invasive	**C-D**	Effect of competition on native fitness outcomes post-invasion (Does the invader impact the experienced native?)
	A - C	**B-D**		
	Effect of past exposure to invader (Are experienced plant's growth and reproductive traits different from naïve plants when the invader is absent?)	Effect of past exposure, while under competition with the invasive (Are experienced and naïve traits different when under competition from the invasive)		

(A-C) vs (B-D)	May differ due to a plastic response to competition or an evolutionary response (e.g if A-C < B-D experienced plants perform better relative to naïve plants when under competition from the invasive, suggesting an adaptive plastic response or an adaptive evolutionary response that increases the experienced plants' tolerance to the invasive)
(B - A) vs (C- D)	Expected to differ if experienced plants have adapted to competition from the invasive or if naïve and experienced plants differ in their plastic response to competition (if the absolute value of A-B < C-D experienced plants perform better than naïve plants under competition with the invasive)

Figure 2. The factorial design of the studies used in the analysis, the comparisons (effect sizes) derived from the studies, and what these comparisons describe in the context of phylogenetic relatedness and my hypothesis. Each cell (A, B, C, D) describes the characteristics of the population means used in the effect size. (A-C) indicates that the effect size was the mean standardizes difference between populations A and C for a given study. In the competition treatments the studies used clones or seed families from the same populations as the control group. If (B-A) varies with phylogenetic distance, suggesting that the competitive impacts of the invasive varies with phylogenetic distance, and if natives respond evolutionarily and adaptively to this competition, then (A-C) and/or (B-D) should also vary with distance in the same direction as (B-A).

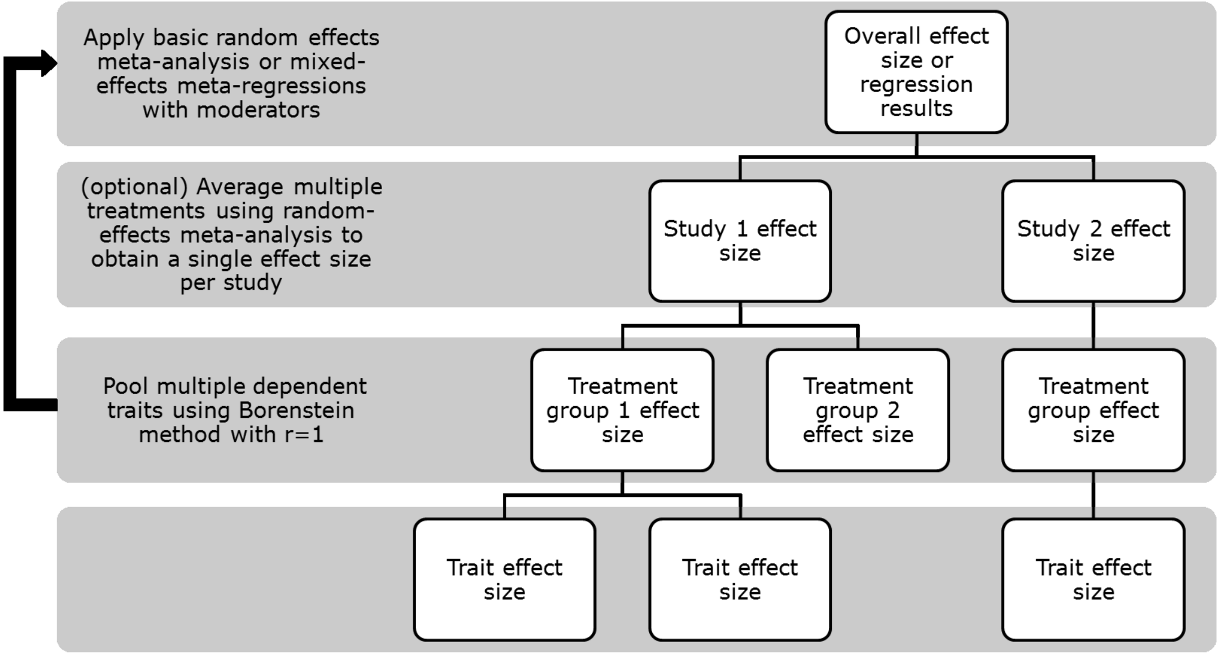

Figure 3. A representation of the nested multi-level nature of the study effect sizes used in the analysis, and how they were combined. In the analysis where multiple treatments were considered to be independent, the treatment group effect sizes were not averaged prior to the analysis (represented by the arrow bypassing that stage).

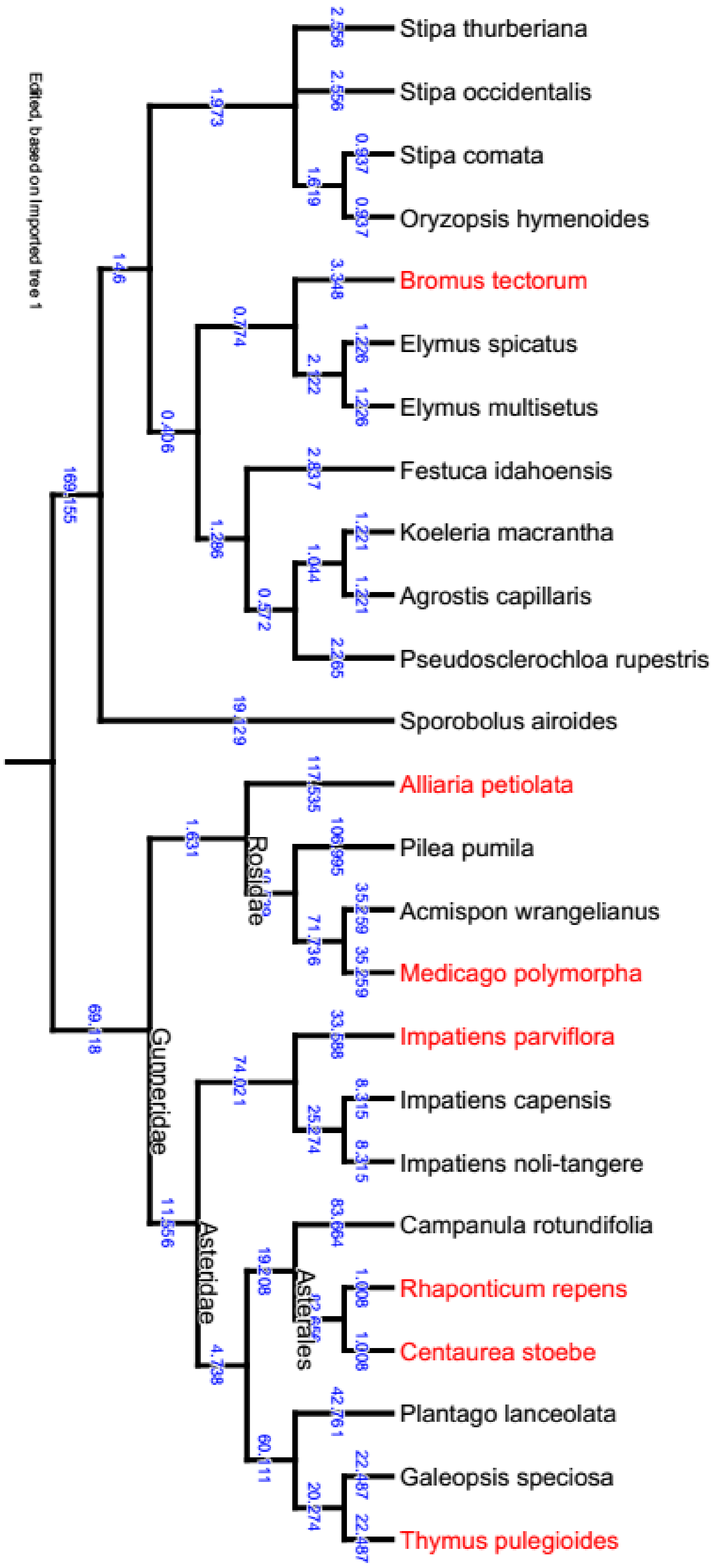

Figure 4. The phylogenetic tree of the native and invasive (red) species included in the study. Branch lengths are represented in blue.

Table 1. The native and invasive species pairs used in the analysis and the associated publications that the effect sizes were drawn from. Synonyms for species names that were used by the original author are presented in round brackets, and family is presented in square brackets.

Invasive species	Native species	Distance between species (Mya)	Study
Alliaria petiolata [Brassicaceae]	*Impatiens capensis* [Balsaminaceae]	238.331	(Cipollini and Hurley, 2008)
Bromus tectorum [Poaceae]	*Elymus multisetus* [Poaceae]	6.69695	(Goergen et al., 2011) (Leger, 2008) (Rowe and Leger, 2011)
	Oryzopsis hymenoides (Achnatherum hymenoides) [Poaceae]	9.05782	(Goergen et al., 2011)
	Pseudosclerochloa rupestris (Poa secunda) [Poaceae]	8.24585	(Goergen et al., 2011)
	Stipa comata (Hesperostipa comata) [Poaceae]	9.05781	(Goergen et al., 2011)
	Stipa thurberiana (Achnatherum thurberianum) [Poaceae]	9.05781	(Goergen et al., 2011)
Centaurea stoebe (Centaurea maculosa) [Asteraceae]	*Elymus spicatus (Agropyron spicatum)* [Poaceae]	376.5665	(Lesica and Atthowe, 2007) (Callaway et al., 2005)
	Festcua idahoensis [Poaceae]	376.5665	(Callaway et al., 2005)
	Koeleria micrantha [Poaceae]	376.5665	(Callaway et al., 2005)
	Pseudosclerochloa rupestris (Poa sandbergii) [Poaceae]	376.5665	(Callaway et al., 2005)
	Stipa occidentalis [Poaceae]	376.5665	(Callaway et al., 2005)
Impatiens parviflora [Balsaminaceae]	*Galeopsis speciose* [Lamiaceae]	215.219	(Dostal et al., 2012)
	Impatiens noli-tangere [Balsaminaceae]	67.17685	(Dostal et al., 2012)
Medicago polymorpha [Fabaceae]	*Acmispon wrangelianus (Lotus wrangelianus)* [Fabaceae]	9.05781	(Lau, 2006)
Rhaponticum repens [Asteraceae]	*Sporobolus airoides* [Poaceae]	376.5665	(Sebade et al., 2012) (Ferrero-Serrano et al., 2011) (Bergum et al., 2012)
	Stipa comata (Hesperostipa comata) [Poaceae]	376.5665	(Ferrero-Serrano et al., 2011) (Mealor and Hild, 2007) (Mealor and Hild, 2007)
Thymus pulegioides [Lamiaceae]	*Agrostis capillaris* [Poaceae]	376.5665	(Jensen and Ehlers, 2010)
	Campanula rotundifolla [Campanulaceae]	205.743	(Jensen and Ehlers, 2010)
	Plantago lanceolate [Plantaginaceae]	85.52188	(Jensen and Ehlers, 2010)

Results: Tables

Table 2. The overall effect size estimates (Hedges g, the difference between experienced and naïve populations for growth and/or reproductive traits) and heterogeneity statistics for all traits, pooled growth traits, and pooled reproductive traits. Multiple treatments and time points within a study were treated as independent. Standard errors are presented in round brackets and the 95% confidence intervals in square brackets. All estimates were also significant using the KNHA adjustment and the DL estimator.

	Effect Size			Heterogeneity			
Traits	**Estimate**	**p**	df	**Tau^2**	**Q**	**p**	**I^2 (%)**
Treatments and time points independent							
All	**0.24(0.06**)	0.0001	67	0.2(0.0467)	276.27	<0.001	78.92[71.36,86.6]
Growth	**0.27(0.07)**	<0.001	59	0.21(0.05)	258.64	<0.001	78.36[69.07,85.73]
Reproductive	0.18(0.118)	0.12	36	0.45(0.12)	238.84	<0.001	90.75[86.35,95.11]
Biomass	**0.31(0.078)**	1e-04	35	0.14(0.05)	101.78	<0.001	65.58[47.22,80.67]
Treatments and time points pooled							
All	**0.314(0.09)**	0.001	26	0.18(0.067)	109.42	<0.001	83.87[71.96,92.36]
Growth	**0.35(0.11)**	0.001	25	0.23(0.08)	127.97	<0.001	84.55[73.05,92.03]
Reproductive	-0.08(0.18)	0.65	13	0.36(0.17)	96.89	<0.001	93.44[87.88,98.54]
Biomass	**0.231(0.1)**	0.025	13	0.09(0.05)	39.66	2e-04	66.86[31.77,88.32]

Table 3. The regression models for the effect of experience with the invasive (Hedge's g, the difference between experienced and naïve native populations). The phylogenetic distance between native-invasive pairs, whether or not the invasive was allelopathic, and same family membership (between the native and invasive pairs) were used as moderators for three trait combinations. Multiple time points and treatments were treated as independent studies. Standard errors are presented in round brackets and the 95% confidence intervals in square brackets.

	Phylogenetic Distance			Allelopathy			Same Family		
	1	2	3	1	2	3	1	2	3
Intercept	***0.086****** ***(0.06)***	0.081 (0.11)	0.042 (0.16)	-0.008 (0.097)	0.005 (0.13)	-0.18 (0.16)	***0.41****** ***(0.082)***	***0.38*** ***(0.09)******	***0.56*** ***(0.17)*****
Phylogenetic Distance	***0.0009**** ***(0.0004)***	***0.0009*** ***(0.0004)****	0.001 (0.001)						
Allelopathy				***0.40***** ***(0.12)***	***0.36*** ***(0.15)****	***0.64*** ***(0.21)*****			
Same Family							***-0.28*** ***(0.14)****	***-0.28*** ***(0.14)****	***-0.62*** ***(0.22)*****
R^2	8.12	8.40	1.60	17.50	11.88	20.43	13.71	7.27	18.84
Tau^2	0.180	0.196	0.443	0.167	0.188	0.358	0.174	0.198	0.365
Tau^2SE	0.040	0.050	0.121	0.041	0.049	0.100	0.042	0.051	0.102
QM	5.33	4.73	1.71	10.46	5.84	8.83	8.44	4.06	7.91
df	66	58	35	66	58	35	66	58	35
QMp	***0.021***	***0.030***	0.191	**0.001**	**0.016**	**0.003**	**0.004**	**0.044**	**0.005**
QE	260.53	243.69	234.14	243.08	231.48	206.88	251.01	243.21	209.90
QEp	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
H^2	4.41	4.28	10.47	4.06	4.17	8.73	4.21	4.33	8.90
I^2	77.32	76.61	90.45	75.38	76.03	88.54	76.23	76.90	88.77
k	68	60	37	68	60	37	68	60	37

Model coefficient significance: $^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

For QMp: * means that p<0.05 with DL only, *italics* means p<0.05 with KNHA adjustment

Table 4. The interaction regression models (REML) for the effect of experience with the invasive (Hedge's d, the difference between experienced and naïve native populations). Multiple time points and treatments were treated as independent studies. The following models are presented: Competition treatment * Phylogenetic distance (interaction model); Competition treatment * Allelopathic invasive (interaction model); Competition treatment * Same family (yes, no, between native and invasive species) for all traits (1), growth traits (2), and reproductive traits (3). For the categorical variables (competition treatment, allelopathy, and family) "no" was set as the reference variable (dummy coded as 0). Standard errors are presented in round brackets and the 95% confidence intervals in square brackets.

	Phylogenetic Distance x Competition			**Allelopathy x Competition**			**Same Family x Competition**		
	1	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
Intercept	0.237 (0.13)	0.087 (0.148)	***0.286*** ***(0.119)****	0.258 (0.156)	0.179 (0.199)	0.199 (0.121)	-0.0260 (0.2070)	-0.3349 (0.2104)	***0.5542*** ***(0.2241)****
Competition	-0.28 (0.18)	-0.32 (0.21)	0.17 (0.33)	-0.17 (0.2)	-0.29 (0.26)	0.39 (0.33)	0.22 (0.16)	***0.33*** ***(0.17)****	0.007 (0.36)
Distance	***-0.00*** ***(0.0006)***[1]	***-0.0001*** ***(0.0006)***[1]	0.0013 (0.0013)						
Distance*Competition	***0.0016*** ***(0.0007)****	***0.002*** ***(0.0008)****	0.0002 (0.002)						
Allelopathy				***0.22*** ***(0.18)***[1]	***0.07*** ***(0.23)***[1]	***0.79*** ***(0.28)*****			
Competition*Allelopathy				0.33 (0.25)	0.53 (0.30)	-0.37 (0.45)			
Same Family							***-0.12*** ***(0.17)***[1]	***0.08*** ***(0.19)***[1]	***-0.72*** ***(0.29)****
Competition*Family							-0.44 (0.24)	***-0.68*** ***(0.27)****	0.27 (0.46)
QM	10.26	10.42	2.23	12.37	9.74	10.05	12.17	11.29	8.5
QMp	***0.02***	***0.015***	0.53	***0.01***	***0.021***	***0.02***	***0.01***	***0.01***	***0.04***
R^2	14.2	16.4	0	17.4	15.1	17.7	17.1	17.7	14.5
Tau^2	0.17	0.18	0.47	0.17	0.18	0.37	0.17	0.18	0.38
QE	234.35	206.73	226.04	232.6	212.25	200.4	231.69	205.76	204.66
QEp	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
k	68	60	37	68	60	37	68	60	37
H^2	4.13	3.93	10.85	4.02	4.02	8.84	4.04	3.91	9.22
I^2	75.81	74.57	90.78	75.13	75.12	88.69	75.23	74.4	89.15
Tau^{2}SE	0.04	0.05	0.13	0.04	0.05	0.11	0.04	0.05	0.11
df	64	56	33	64	56	33	64	56	33

Model coefficient significance: $^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

For QMp: ***** means that $p<0.05$ with DL only, *italics* means $p<0.05$ with KNHA adjustment

[1] Significant when competition = yes is set as the reference value

Table 5. The regression models for the effect of experience with the invasive (Hedge's d, the difference between experienced and naïve native populations) with pooled treatments (including competition). The phylogenetic distance between native-invasive pairs, if the invasive was allelopathic, and same family membership (between the native and invasive pairs) were used as moderators for: (1) all traits combined, (2) growth traits, (3) reproductive traits, (4) total biomass. Competition treatments, time points, and other multiple treatments for a given native-invasive pair within a study were averaged prior to the analysis. For models where competition treatments were not pooled (but all other treatments are pooled) see the appendix.

	Phylogenetic Distance				**Allelopathy**			**Same Family**		
	1	**2**	**3**	**4**	**1**	**2**	**3**	**1**	**2**	**3**
Intercept	0.14 (0.16)	0.14 (0.19)	-0.312 (0.22)	0.036 (0.22)	0.073 (0.17)	0.13 (0.21)	-0.42 (0.22)	***0.42*** ***(0.11)******	***0.43*** ***(0.13)******	0.30 (0.26)
Distance	0.0008 (0.0006)	0.0009 (0.0007)	0.002 (0.001)	0.0008 (0.0007)						
Allelopathy					0.34 (0.20)	0.29 (0.24)	***0.70 **** ***(0.31)***			
Same Family								-0.32 (0.20)	-0.27 (0.23)	-0.63 (0.34)
R^2	3.55	2.90	14.43	0.00	6.97	1.50	26.34	5.61	0.94	13.33
Tau^2	0.172	0.223	0.312	0.088	0.166	0.226	0.268	0.169	0.227	0.316
Tau^2SE	0.066	0.0831	0.1522	0.0596	0.0642	0.0841	0.1334	0.065	0.0845	0.1538
QM	1.85	1.82	2.65	1.08	2.76	1.45	5.18	2.60	1.39	3.52
df	25	24	12	12	25	24	12	25	24	12
QMp	0.173	0.177	0.104	0.298	0.097	0.228	***0.023****	0.107	0.238	0.061
QE	106.96	123.90	90.63	36.00	101.45	122.41	75.45	104.98	124.35	86.04
QEp	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
H^2	5.78	6.21	12.27	3.00	5.62	6.32	10.74	5.63	6.25	12.29
I^2	82.70	83.90	91.85	66.70	82.21	84.17	90.69	82.24	84.01	91.86
k	27	26	14	14	27	26	14	27	26	14

Model coefficient significance: $^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

For QMp: * with no **bold** means that p<0.05 with DL only, *italics* means p<0.05 with KNHA adjustment

Table 6. The interaction regression models (REML) for the effect of experience with the invasive (Hedge's d, the difference between experienced and naïve native populations), with multiple treatments pooled. Results are presented for (1) all traits, (2) growth traits, and (3) reproductive traits. The models include the interaction between competition treatments and the following moderators: the phylogenetic distance between the native and invasive, whether or not the invasive is allelopathic, and whether or not the native and invasive are in the same family. Multiple timepoints and treatments per species pair per study were averaged within competition treatments (yes and/or no) prior to the analysis.

	Phylogenetic Distance x Competition			Allelopathy x Competition			Same Family x Competition		
	1	2	3	1	2	3	1	2	3
Intercept	0.20 (0.17)	0.11 (0.19)	-0.11 (0.34)	0.0411 (0.19)	0.07 (0.21)	-0.46 (0.32)	***0.29 (0.14)****	0.1954 (0.14)	0.64 (0.38)
Competition	-0.10 (0.24)	0.0129 (0.26)	0.27 (0.58)	0.02 (0.26)	0.038 (0.30)	0.47 (0.58)	0.25 (0.18)	***0.38 (0.19)****	-0.12 (0.54)
Distance	***0.0001 (0.0007)***^{1}	***0.0003 (0.0007)***^{1}	0.001 (0.002)						
Distance*Competition	0.001 (0.0009)	0.001 (0.0010)	-0.0002 (0.003)						
Allelopathy				***0.2602 (0.2284)***^{1}	0.14 (0.25)	***1.04 (0.47)****			
Competition*Allelopathy				0.1911 (0.3157)	0.29 (0.35)	-0.56 (0.76)			
Same Family							***-0.2002 (0.22)***^{1}	***-0.06 (0.24)***^{1}	***-1.0140 (0.4902)****
Competition*Family							-0.2703 (0.30)	-0.41 (0.33)	0.55 (0.75)
QMp	0.127	0.065	0.782	0.075	0.096	0.107	0.064	0.068	0.135
R^2	9.5	13.39	0	12.1	10.84	13.52	13.02	12.83	11.36
Tau^2	0.177	0.183	0.852	0.172	0.189	0.656	0.170	0.184	0.672
QE	150.10	150.40	205.24	151.65	154.94	172.15	150.63	152.73	182.57
QEp	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
k	46	44	22	46	44	22	46	44	22
H^2	4.28	4.03	20.77	4.25	4.16	16.98	4.13	4.02	16.84
QM	5.71	7.24	1.08	6.92	6.35	6.09	7.28	7.12	5.57
I^2	76.63	75.19	95.19	76.49	75.99	94.11	75.81	75.15	94.06
Tau^2SE	0.054	0.058	0.306	0.053	0.059	0.240	0.053	0.058	0.245
df	42	40	18	42	40	18	42	40	18

Model coefficient significance: $^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

For QMp: * means that p<0.05 with DL only, *italics* means p<0.05 with KNHA adjustment

[1] Significant when competition = yes is set as the reference value

Table 7. The overall effect of competition with the invasive (Hedges *g,* the difference between native populations with competitive planting treatments and the control) across native species' experience level with the invasive species for all traits, growth traits, reproductive traits, and biomass. Multiple treatments (other than competition) and time points were averaged prior to the analysis.

	Effect Size			Heterogeneity			
Traits	**Estimate**	**p**	df	**Tau²**	**Q**	**p**	**I² (%)**
All	-0.72(0.1)	<0.0001	37	0.27(0.1)	206.5	<0.0001	81.97[72.3,90.19]
Growth	-0.89(0.12)	<0.0001	35	0.44(0.13)	189.79	<0.0001	84.36[76.54,91.69]
Reproductive	0.34(0.1)	9.00E-04	15	0.11(0.06)	45.58	1.00E-04	68.78[39.59,86.84]
Biomass	-0.69(0.18)	2.00E-04	25	0.78(0.25)	230.59	<0.0001	89.76[83.2,94.85]

Table 8. The regression models for the effect of competition with the invasive (Hedges *g*, the difference between native populations with competitive planting treatments and the control) on native growth and reproductive traits, ignoring level of experience with the invasive. Results are presented for (1) all, (2) growth, and (3) reproductive traits. The phylogenetic distance between native-invasive pairs, whether or not the invasive was allelopathic, and same family membership (between the native and invasive pairs) were used as moderators for three trait combinations. For the categorical variables "no" was set as the reference variable (dummy coded as 0). The effect sizes for naïve and experienced plants were kept separate but multiple treatments were combined. Standard errors are presented in brackets.

	Phylogenetic Distance			**Allelopathy**			**Same Family**			**Experience**		
	1	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	2	3
Intercept	-1.0341 (0.1399)***	-1.4819 (0.1492)***	0.4072 (0.1527)**	-0.9712 (0.1656)***	-1.3563 (0.2100)***	0.4645 (0.1617)**	-0.5335 (0.1182)***	-0.6136 (0.1272)***	0.3434 (0.1604)*	***-0.86*** ***(0.14)******	-1.06 (0.17)***	***-0.93*** ***(0.26)******
Distance	0.0016 (0.0005)**	0.0029 (0.0006)***	-0.0007 (0.0012)									
Allelopathy				0.3805 (0.2024)	0.6598 (0.2480)**	-0.2053 (0.2084)						
Same Family							-0.4587 (0.1881)*	-0.7659 (0.2156)***	0.0015 (0.2153)			
Experience										0.29 (0.19)	0.35 (0.24)	0.46 (0.37)
R^2	19.2343	55.0926	0	4.3536	20.2366	3.9926	12.8135	35.8475	0	3.13	2.7	1.8
Tau^2	0.2159	0.1961	0.1151	0.2556	0.3484	0.1058	0.233	0.2802	0.1219	0.26	0.42	0.76
Tau^2SE	0.0706	0.0703	0.0656	0.0804	0.1083	0.0621	0.0748	0.0914	0.0684	0.081	0.13	0.07
QM	8.9095	26.1359	0.3358	3.5337	7.079	0.9701	5.9435	12.6147	0.0001	2.25	2.1	1.56
df	36	34	14	36	34	14	36	34	14	36	34	24
QMp	0.0028	0	0.5622	0.0601	0.0078	0.3247	0.0148	0.0004	0.9943	0.13	0.15	0.21
QE	204.2205	106.3924	43.1142	204.2669	156.5523	39.4623	205.2143	121.7632	45.4696	200.5555	184.121	223.7707
QEp	0	0	0.0001	0	0	0.0003	0	0	0	<0.0001	<0.0001	<0.0001
H^2	4.5851	3.4033	3.269	5.182	5.2701	3.0838	4.8553	4.4263	3.3885	5.25	6.21	3.28
I^2	78.1901	70.6171	69.4095	80.7024	81.0252	67.5721	79.404	77.4079	70.4883	80.97	83.89	69.55
k	38	36	16	38	36	16	38	36	16	38	36	16

Model coefficient significance: $^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

For QMp: ***** means that p<0.05 with DL only, *italics* means p<0.05 with KNHA adjustment

Table 9. The interaction regression models for the effect of competition with the invasive (Hedges *g,* the difference between native populations with competitive planting treatments and the control) on native growth and reproductive traits. Results are presented for the following models: Experience * Distance (interaction model); Experience * Allelopathic invasive (yes, no) (interaction model); and Experience * Same Family (yes, no for naïve and experienced pairs) for (1) all traits, (2) growth traits and (3) biomass. For the categorical variables "no" was set as the reference variable (dummy coded as 0). Standard errors are presented in brackets. Multiple effect sizes due to treatments other than competition (e.g nutrient levels) were pooled within experience level for a given species pair within a study. Interaction models with k<20 are not presented. Models 3 and 4 were not presented for biomass because there were no non-allelopathic studies and only 2 same family studies.

	Phylogenetic Distance x Experience			**Allelopathy x Experience**		**Family x Experience**	
	1	2	3	1	2	1	2
Intercept	***-1.11*** ***(0.2)******	-1.58 (0.21)***	***-2.47*** ***(0.58)******	***-1.07*** ***(0.24)******	-1.43 (0.3)***	***-0.71*** ***(0.17)******	-0.86 (0.18)***
Experience	0.16 (0.28)	0.2 (0.29)	0.72 (0.81)	0.2 (0.33)	0.15 (0.42)	0.38 (0.24)	0.48 (0.25)
Distance	***0.0013*** ***(0.0008)***[1]	***0.0025*** ***(0.0008)*****[1]	***0.005*** ***(0.002)*****[1]				
Distance*Experience	0.0007 (0.001)	0.0007 (0.001)	-0.0009 (0.003)				
Allelopathy				***0.31*** ***(0.29)***[1]	0.52 (0.35)		
Experience*Allelopathy				0.13 (0.41)	0.28 (0.5)		
Same Family: yes						***-0.34*** ***(0.27)***[1]	***-0.56*** ***(0.3)***[1]
Experience*Same Family						-0.24 (0.37)	-0.4 (0.42)
R^2	20.9	57.9	41.1	4.3	20.6	14.3	39.1
Tau^2	0.21	0.18	0.46	0.26	0.35	0.23	0.27
Qm	11.99	31.21	16.59	5.93	9.81	8.86	16.88
df	34	32	22	34	32	34	32
QMp	___0.007**___	***<0.0001***	___0.001**___	0.12	***0.02***	___0.03*___	***0.0007***
QE	195.3229	96.7043	113.4931	197.8889	151.0267	196.431	110.83
QEp	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Model coefficient significance: $^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

For QMp: ***** means that p<0.05 with DL only, *italics* means p<0.05 with KNHA adjustment

[1] Significant when competition = yes is set as the reference value

Results: Figures

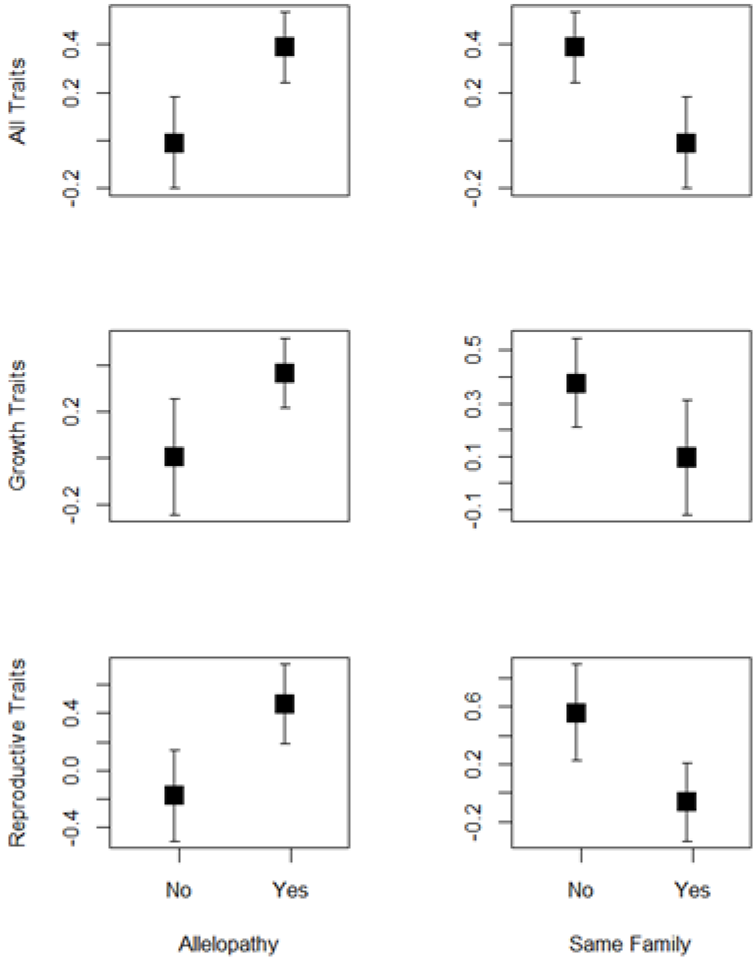

Figure 5. The estimated effect sizes (Hedges *g*, the difference between experienced and naïve plants) and 95% confidence intervals from the regressions of all traits combined (top), growth traits (middle), and reproductive traits (bottom) with the presence of allelopathy in the invasive (left) and whether or not the native and invasive were in the same family (right) as the moderator variables. All tests of the moderators were significant (Qm $p < 0.05$). Multiple treatments and time points were treated as independent studies

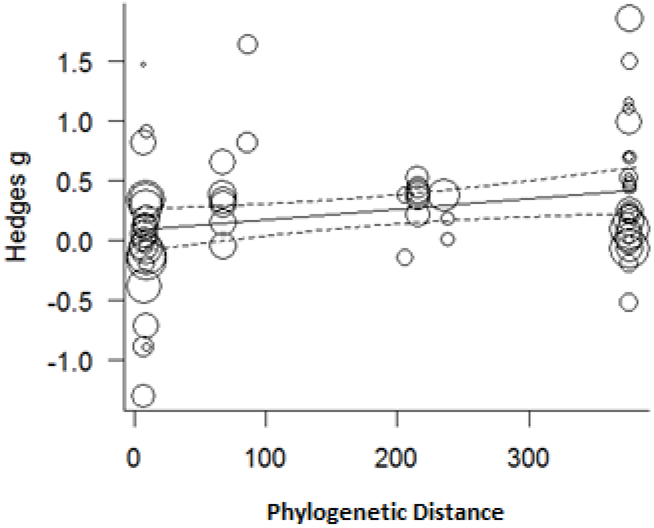

Figure 6. The regression of Hedges *g* (the difference between experienced and naïve native plant populations) against the phylogenetic distance between the native and invasive species, for all pooled traits. The 95% confidence interval is shown as dashed lines. The individual study effect sizes are plotted as circles with their size proportional to their weights in the regression. Multiple treatments and time points were treated as independent studies. Model co-efficient for distance = 0.0009, Qm=5.35, p=0.0297, R^2=8.21%.

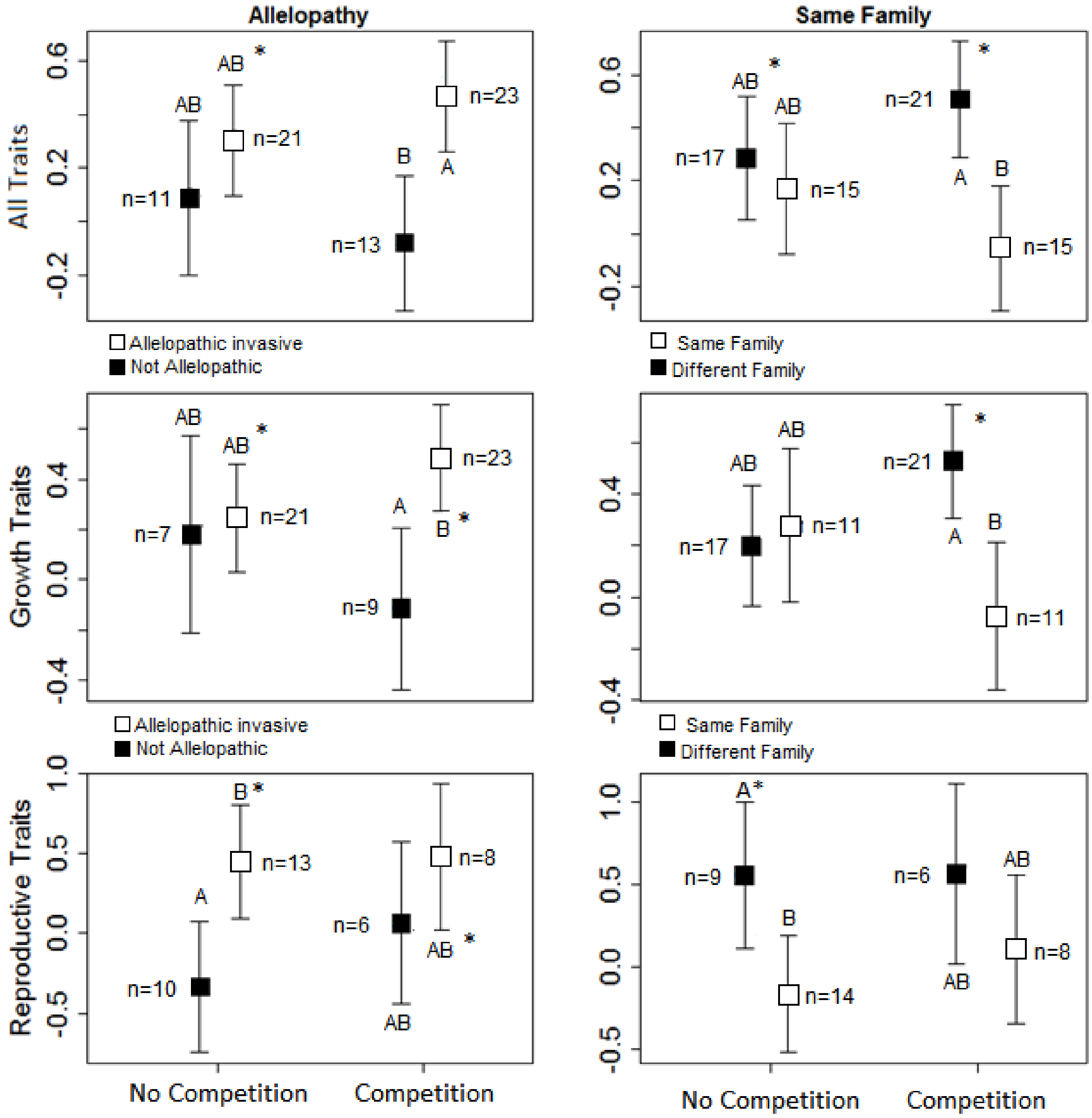

Figure 7. The mean effect size estimates (Hedges *g*) and 95% confidence intervals from the family by competition (right) and allelopathy by competition (left) regressions for all traits combined (top), growth traits (middle), and reproductive traits (bottom). For allelopathy and family, matching letters indicate significant differences between the estimated effect size for a given combination of factors (p<0.05) and effect sizes with * are significantly different from 0. The x axis indicates if the studies did or did not plant the native with the invasive. Same family indicates if the native and invasive species were or were not in the same family for all graphs on the right side, and allelopathy indicates if the invasive species was or was not allelopathic for all graphs on the left side. Multiple treatments and time points were considered to be independent.

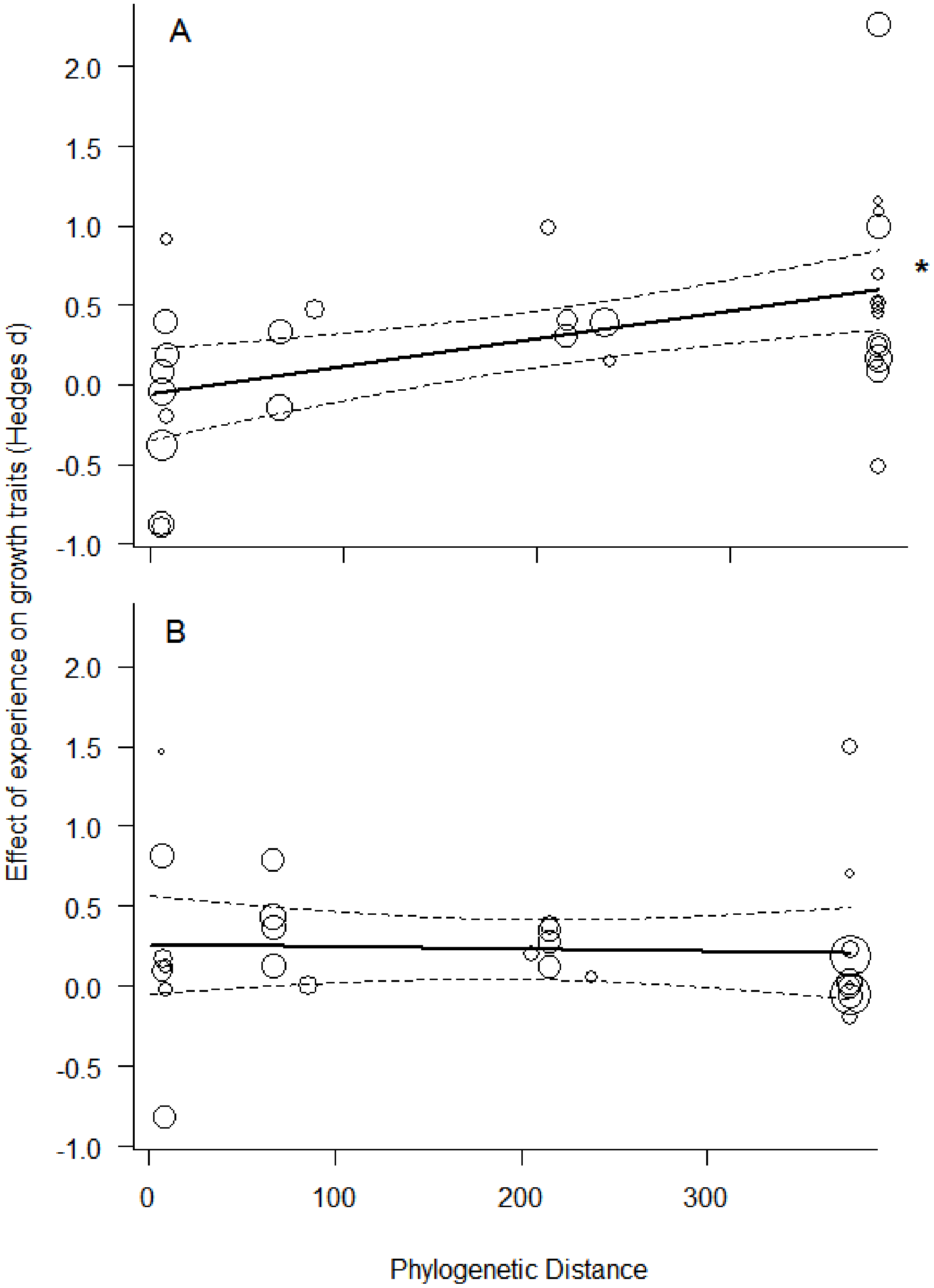

Figure 8. The regression of the effect size against distance with (A, top panel) and without competition (B, bottom panel) for growth traits. Solid lines are the effect sizes estimated from the regression including distance, competition, and the interaction term of distance*competition as moderators. Confidence intervals are presented as dashed lines. The individual study effect sizes used in the model are presented as circles with their size proportional to their weight. * indicates a significant estimate. Multiple effect sizes were treated as independent.

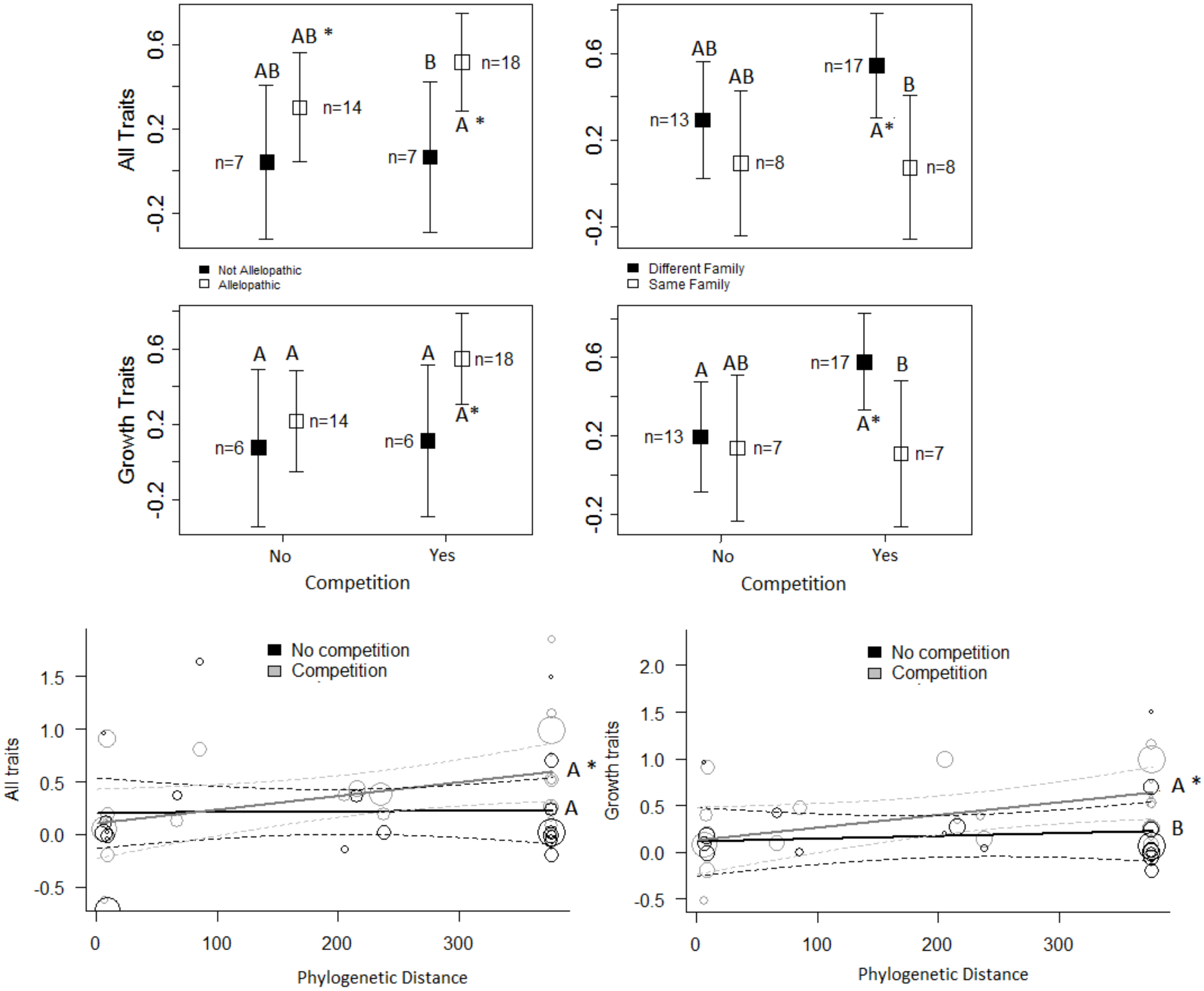

Figure 9. The mean effect size estimates (Hedges *g*) and 95% confidence intervals predicted by the family by competition (right) and allelopathy by competition (left) regressions for all traits combined (top) and growth traits (middle). For allelopathy and family, matching letters indicate significant differences between the estimated effect size for a given combination of factors (p<0.05) and effect sizes with * are significantly different from 0. The x axis indicates if the studies did or did not plant the native with the invasive. Same family indicates if the native and invasive species were or were not in the same family for all graphs on the right side, and allelopathy indicates if the invasive species was or was not allelopathic for all graphs on the left side. The distance by competition regressions for growth traits (bottom left) and all traits (bottom right) are also show with the 95% confidence intervals represented by the dash lines. Multiple treatments and time points were averaged before the analysis.

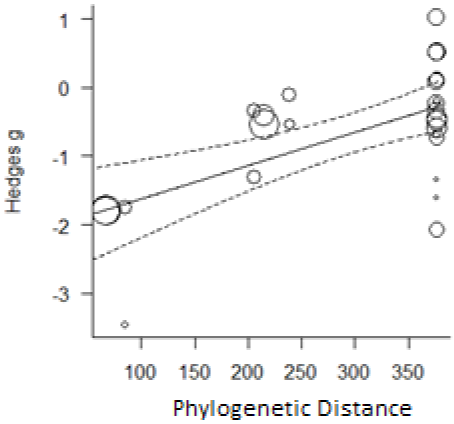

Figure 10. The phylogenetic distance regression (REML) for the competitive response (Hedges *g*, the difference between plants grown with the invasive and control plants grown alone) for total biomass across both levels of experience. Individual studies are presented as circles which are proportional to their weights. Model coefficient for distance = 0.0049, SE = 0.0013, p=0.0002, Qm=0.0002, R2=41.23%, k=26.

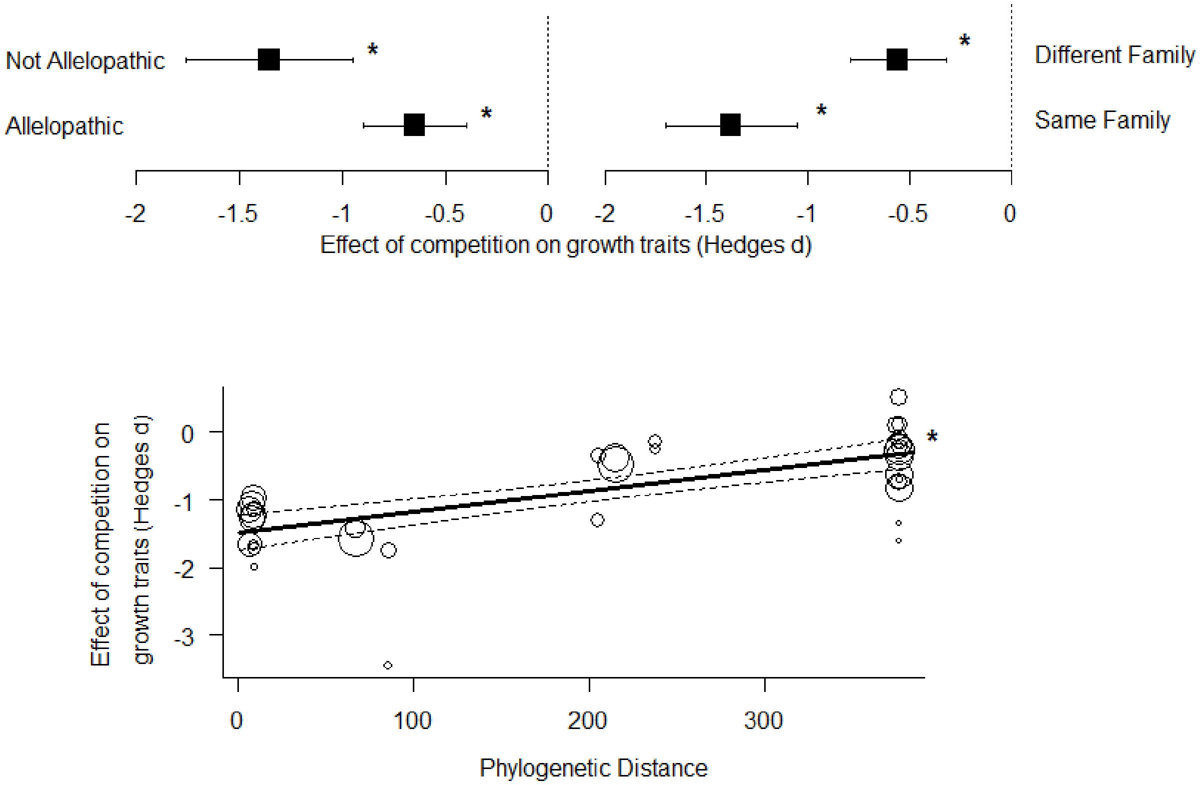

Figure 11. The mean effect size estimates (Hedges *g,* the difference between competition treatment and control) and the 95% confidence intervals predicted by the allelopathy (top left), family (top right), and distance (bottom) regression models for native growth traits. Effect sizes with * are significantly different from 0. Because the differences between naïve and experience studies were so slight models which do not include experience level as a variable are shown. Competition treatment indicates if the invasive was present in the native plots in a factorial design. Same family indicates if the native and invasive species were or were not in the same family, and distance is the phylogenetic distance between the native and invasive species for each study. All models were significant. Multiple treatments and time points were averaged before the analysis.

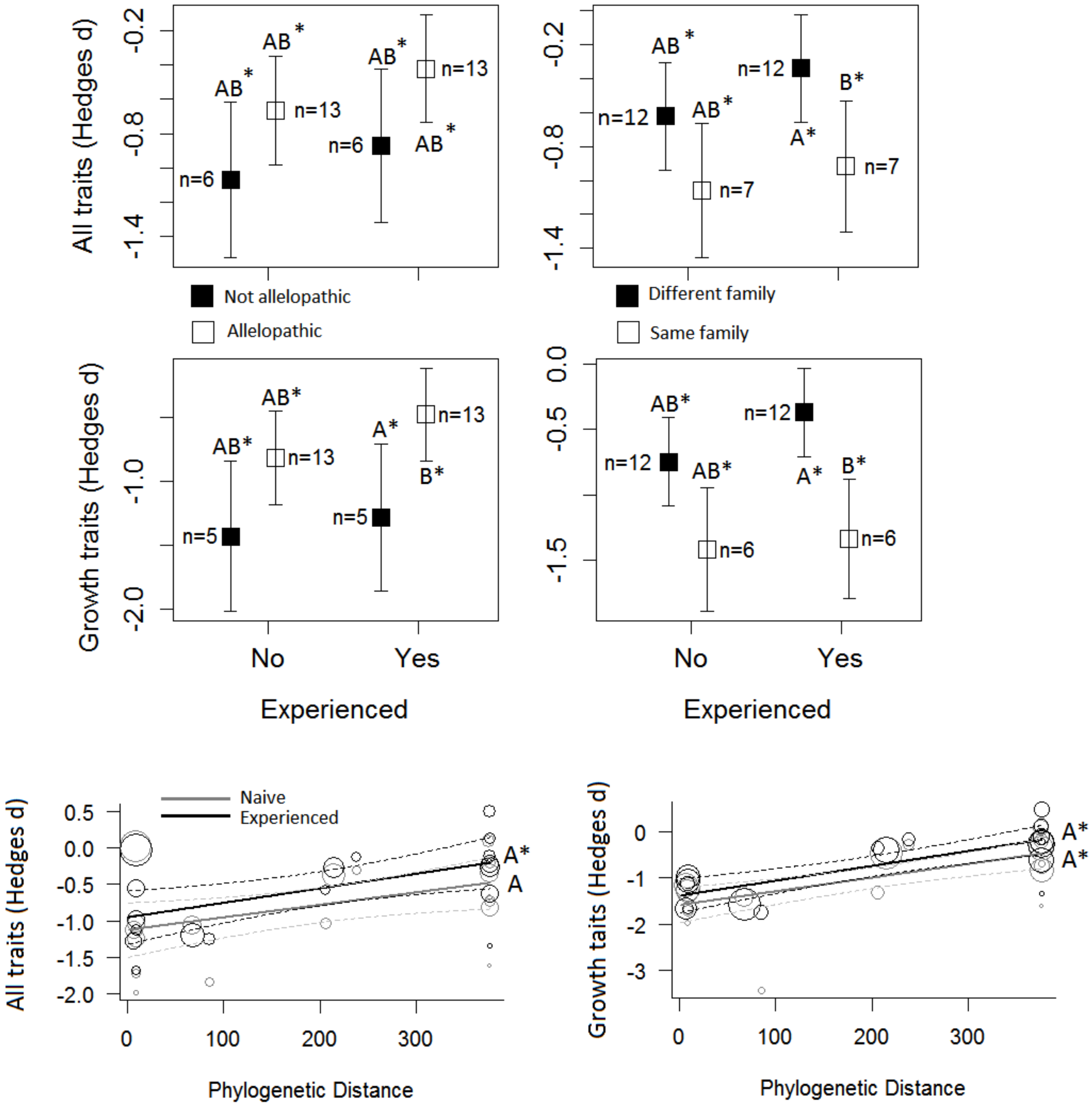

Figure 12. Effect size estimates for experience level crossed with either distance (bottom 2 panels), allelopathy (left), or whether or not the invasive and native are in the same family (right) for all traits (top) and growth traits (middle). For the distance regression the 95% confidence intervals are presented as dashed lines and * indicates that the regression coefficient for that factor combination is significant. For allelopathy and family, matching letters indicate significant differences between the estimated effect size for a given combination of factors (p<0.05) and effect sizes with * are significantly different from 0. Error bars represent the 95% confidence interval. Individual studies are presented as circles which are proportional to their weights. For allelopathy and family all of the individual estimates were significantly greater than 0 (p<0.05). The models for distance and same family were significant

Chapter 3: Discussion and future directions

In my thesis, I tested whether the phylogenetic relatedness between a native and invasive plant species could explain the magnitude of any evolutionary consequences of the plant invasion~~s~~ on a native plant. In my first chapter I discussed the frameworks used to understand invasion success, and emphasized how niche based frameworks and phylogenetic relationships might predict various patterns of invasion success. In my second chapter I build on these frameworks, and ask whether the phylogenetic relatedness between native and invasive and native plant species can explain the effect of invasion history on evolutionary consequences for native traits. Since allelopathy can reduce native fitness and growth, and some studies suggest that native plants may develop resistance to invasive allelochemicals (Callaway et al., 2005; Lankau, 2012), I also asked whether allelopathy in the invasive could explain this effect. Finally, I examined a subset of studies with factorial competitive planting treatments to see if the changes in native traits might be adaptive.

My analysis suggests that phylogenetic relationships and allelopathy may explain some of the ecological and evolutionary effects of plant invasions under specific contexts, and highlights the complexity of using meta-analysis to address questions in evolutionary ecology. In general, distantly related native and invasive species, and allelopathic invasives, were weakly associated with a larger evolutionary effect of invasion history on native growth and reproductive traits. However, when the studies were divided into those with and without a competitive planting treatment with the invasive, the association was only significant in studies where the natives were grown in the presence of the invasive. Since the effect is the difference in trait values between experienced and naïve plants this could suggest an adaptive evolutionary or plastic response in the experienced plants to competition when the invasive is allelopathic and/or distantly related to the native. While is difficult to evaluate if a response is adaptive using meta-analysis (Leimu and Fischer, 2008), there was little evidence that the experienced and naïve plants generally differed in their response to competition, although I did find differences in the competitive response between experienced and naïve plants with distance, and native species which were distantly related to the invasive were generally less affected by competition, which suggests that the larger growth and reproductive traits seen in experienced plants that are distantly related to the invasive (or when the invasive is allelopathic) reflects an adaptive response to competition. In my discussion, I pointed out that my results are sensitive to the methodological choices used to manipulate the data, and which traits were measured, and so should be interpreted with some caution. There are also a multitude of factors which could disrupt, alter, or mask evolutionary responses, such as the indirect herbivore-mediated selection that negated adaptation to the invasive in one of the studies used in the analysis (Lau, 2006). Unfortunately, the scope of my analysis and the availability of data did not allow me to control for these factors. The results from my analysis paint a complicated picture and additional studies are needed to elucidate the patterns seen in these studies.

Future directions

Phylogenetic relationships may play an important role in understanding the causes and consequences of plant invasions, but additional manipulative and observational studies across a range of systems are needed to clarify under what context phylogeny is correlated with invasion outcomes. For example, the relatedness between invasive species and the recipient community may be able to predict invasiveness, but this effect may depend on spatial and phylogenetic scale, the stage of the invasion (Cadotte, Hamilton, and Murray, 2009; Godoy, Kraft, and Levine, 2014), ecological impact (Morales and Traveset, 2009b; Vila et al., 2015), and/or community assembly and phylogenetic structure (since community phylogenetic diversity may influence invasiveness and invasibility) (Cadotte, Hamilton, and Murray, 2009; Carboni et al., 2013; Bennett, Stotz, and Cahill, 2014; Carvallo et al., 2014). However, the relative importance of phylogenetic distance between an interacting native and invasive species, or invasives and the native community as a whole, are relatively unexplored in the context of native evolutionary responses. In light of the potential for phylogenetic distance to predict differential fitness between interacting species (Godoy, Kraft, and Levine, 2014), developing the theoretical connection between phylogenetic relatedness and niche-fitness frameworks could provide valuable context in predicting the effects of phylogenetic distance on coexistence, competitive dominance, and ultimately the evolutionary impacts of plant invasions.

Assessing the role of relatedness in the evolutionary consequences of invasions is an intriguing idea. However, studies that focus on the ecological and/or evolutionary effects of a species introduction may be somewhat limited if they restrict themselves to singular traits within a population or species and don’t encompass the ecological and evolutionary interactions between the invader and the local biotic community which can alter evolutionary outcomes (Strauss, Webb, and Salamin, 2006). Comprehensive studies which consider both the traits of introduced species and the broader context of the community are needed to develop a more generalized understanding of the ecological and evolutionary impacts of species introductions. As our knowledge of the causes and consequences of species’ invasions grows, we can continue to move toward the development of unifying frameworks to better predict outcomes. While this process can be difficult due to the variation in the ecological and evolutionary factors at play among systems, as more studies are conducted across a range of systems meta-analysis can be a useful tool to identify factors which explain variation between systems and inform future empirical studies.

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Appendix

Study details

Resolved species names

Table A10. The original and resolved list of species names used in the analysis. Species names were resolved according to TPL (The Plant List) using the Taxonomic Name Resolution Service.

Original Species Name	TPL Resolved List
Acroptilon repens	*Rhaponticum repens*
Alliaria petiolata	*Alliaria petiolata*
Centaurea maculosa	*Centaurea maculosa*
Impatiens parviflora	*Impatiens parviflora*
Cirsium arvense	*Cirsium arvense*
Bromus tectorum	*Bromus tectorum*
Medicago polymorpha	*Medicago polymorpha*
Sporobolus airoides	*Sporobolus airoides*
Impatiens capensis	*Impatiens capensis*
Festuca idahoensis	*Festuca idahoensis*
Pseudoroegneria spicata	*Elymus spicatus*
Koeleria macrantha	*Koeleria macrantha*
Stipa occidentalis	*Stipa occidentalis*
Poa secunda	*Pseudosclerochloa rupestris*
Impatiens noli-tangere	*Impatiens noli-tangere*
Hesperostipa comata	*Stipa comata*
Achnatherum hymenoides	*Oryzopsis hymenoides*
Elymus multisetus	*Elymus multisetus*
Achnatherum thurberianum	*Stipa thurberiana*
Lotus wrangelianus	*Lotus wrangelianus*
Agrostis capillaris	*Agrostis capillaris*
Campanula rotundifolia	*Campanula rotundifolia*
Thymus pulegioides	*Thymus pulegioides*
Achillea millefolium	*Achillea millefolium*
Plantago lanceolata	*Plantago lanceolata*

Table A11. Publication identification codes (accession code) for the papers that the studies were drawn from.

Accession Code	Author
1	Bergum et al., 2012
2	Cipollini et al., 2008
3	Callaway et al., 2005
4	Dostal et al., 2012
5	Ferrero-Serrano et al., 2011
6	Goergen et al., 2011
7	Lau et al., 2006
8	Mealor and Hild, 2007
9	Leger, 2008
10	Lesica and Atthowe, 2007
11	Sebade et al., 2012
12	Rowe and Leger, 2011
15	Jensen and Ehlers, 2010
16	Lankau, 2012

Studies with multiple treatments as independent

Table A12. The native and invasive species pairs used in the analysis with the total numbers of studies included for each combination of traits. Multiple experiments and timepoints per species pair per publication were treated as independent studies.

Pair	All	Growth	Reprod	Biomass
Rhaponticum repens & Sporobolus airoides	7	7	3	2
Centaurea stoebe & Festcua idahoensis	2	2	0	2
Centaurea stoebe & Elymus spicatus	4	4	0	4
Centaurea stoebe & Stipa occidentalis	2	2	0	2
Centaurea stoebe & Koeleria micrantha	2	2	0	2
Impatiens parviflora & Impatiens noli-tangere	6	6	6	6
Rhaponticum repens & Stipa comata	4	4	0	2
Bromus tectorum & Stipa comata	2	2	1	0
Bromus tectorum & Oryzopsis hymenoides	2	2	1	0
Bromus tectorum & Elymus multisetus	8	8	3	2
Bromus tectorum & Stipa thurberiana	2	2	1	0
Medicago polymorpha & Acmispon wrangelianus	8	0	8	0
Thymus pulegioides & Agrostis capillaris	2	2	0	2
Thymus pulegioides & Campanula rotundifolla	2	2	2	2
Thymus pulegioides & Plantago lanceolata	2	2	2	2
Alliaria petiolate & Impatiens apensis	2	2	2	2
Bromus tectorum & Pseudosclerochloa rupestris	2	2	2	0
Centaurea stoebe & Pseudosclerochloa rupestris	2	2	0	0
Impatiens parviflora & Galeopsis speciosa	6	6	6	6
Alliaria petiolate & Pilia pumila	1	1	0	0
Total Studies	68	60	37	36

Table A13. The number of studies (when multiple treatments and timepoints were treated as independent studies) for each combination of pooled traits (all, growth, reproductive, and total biomass) and for each combination of 3 categorical (yes/no) moderators. The moderators are the presence or absence of a competition treatment, whether or not the native and invasive species were in the same family, and whether or not the invasive was allelopathic.

Competition	**n**	**n**	**y**	**y**
Allelopathy	**n**	**y**	**n**	**y**
All	11	21	13	23
Biomass	0	18	2	16
Growth	7	21	9	23
Reprod	10	13	6	8
Competition	**n**	**n**	**y**	**y**
Same Family	**n**	**y**	**n**	**y**
All	17	15	21	15
Biomass	14	4	14	4
Growth	17	11	21	11
Reprod	9	14	6	8
Same Family	**n**	**n**	**y**	**y**
Allelopathy	**n**	**y**	**n**	**y**
All	0	38	24	6
Biomass	0	28	2	6
Growth	0	38	16	6
Reprod	0	15	16	6

Studies with treatments and time points combined

Table A14. The list of native and invasive species pairs and the total numbers of studies for each combination of traits when multiple experiments/pair/paper were combined into a single study.

			Traits	
Pair	**All**	**Biomass**	**Growth**	**Reprod**
Alliaria petiolate & Impatiens capensis	1	1	1	1
Bromus tectorum & Elymus multisetus	3	1	3	2
Bromus tectorum & Oryzopsis hymenoides	1		1	1
Bromus tectorum & Pseudosclerochloa rupestris	1		1	1
Bromus tectorum & Stipa comata	1		1	1
Bromus tectorum & Stipa thurberiana	1		1	1
Centaurea stoebe & Elymus spicatus	2		2	
Centaurea stoebe & Festcua idahoensis	1		1	
Centaurea stoebe & Koeleria micrantha	1		1	
Centaurea stoebe & Pseudosclerochloa rupestris	1		1	
Centaurea stoebe & Stipa occidentalis	1		1	
Impatiens parviflora & Galeopsis speciosa	1	1	1	1
Impatiens parviflora & Impatiens noli-tangere	1	1	1	1
Medicago polymorpha & Acmispon wrangelianus	1			1
Rhaponticum repens & Sporobolus airoides	4	1	4	2
Rhaponticum repens & Stipa comata	2	1	2	
Thymus pulegioides & Agrostis capillaris	1	1	1	
Thymus pulegioides & Campanula rotundifolla	1	1	1	1
Thymus pulegioides & Plantago lanceolata	1	1	1	1
Alliaria petiolate & Pilia pumila	1		1	
Centaurea stoebe & Festcua idahoensis		1		
Centaurea stoebe & Elymus spicatus		2		
Centaurea stoebe & Stipa occidentalis		1		
Centaurea stoebe & Koeleria micrantha		1		
Total Studies	**27**	**14**	**26**	**14**

Table A15. The number of studies when multiple treatments were combined into a single study for each combination of pooled traits and for each combination of 2 categorical (yes/no) moderators. The moderators are whether or not the native and invasive species were in the same family, and whether or not the invasive was allelopathic.

Competition	**n**	**n**	**y**	**y**
Allelopathy	**n**	**y**	**n**	**y**
All	7	14	7	18
Growth	6	14	6	18
Reproductive	7	6	3	6
Biomass	0	12	1	13
Competition	**n**	**n**	**y**	**y**
Same Family	**n**	**y**	**n**	**y**
All	13	8	17	8
Growth	13	7	17	7
Reproductive	5	8	5	4
Biomass	11	1	12	2
Same Family	**n**	**n**	**y**	**y**
Allelopathy	**n**	**y**	**n**	**y**
All	0	14	30	2
Growth	0	12	30	2
Reproductive	0	10	10	2
Biomass	0	1	23	2
Same Family Total	**9**	**8**	**8**	**1**
Different Family Total	**18**	**18**	**6**	**12**
Allelopathic Total	**19**	**19**	**7**	**13**
Not Allelopathic Total	**8**	**7**	**7**	**1**

Competitive response

Table A16. The list of native and invasive species pairs and the total numbers of studies for each combination of traits when multiple experiments and timepoints were combined into a single study.

Pair	All	Growth	Reproductive	Biomass
Alliaria petiolate & Impatiens capensis	2	2	2	2
Bromus tectorum & Elymus multisetus	2	2	2	
Bromus tectorum & Oryzopsis hymenoides	2	2		
Bromus tectorum & Poa secunda		2	2	
Bromus tectorum & Stipa comata	2	2		
Bromus tectorum & Stipa thurberiana	2	2		
Centaurea stoebe & Festcua idahoensis	2			2
Centaurea stoebe & Elymus spicatus	2	2		2
Centaurea stoebe & Koeleria micrantha	2	2		
Centaurea stoebe & Pseudosclerochloa rupestris	2	2		2
Centaurea stoebe & Stipa occidentalis	2	2		2
Impatiens parviflora & Galeopsis speciosa	2	2	2	2
Impatiens parviflora & Impatiens noli-tangere	2	2	2	2
Medicago polymorpha & Lotus wrangelianus			2	
Rhaponticum repens & Hesperostipa comata				2
Rhaponticum repens & Sporobolus airoides				2
Rhapontocum repens & Sporobolus airoides	2	2		
Rhapontocum repens & Stipa comata	2	2		
Thymus pulegiodes & Agrostis capillaris	2	2		2
Thymus pulegiodes & Campanula rotundifolla	2	2	2	2
Thymus pulegiodes & Plantago lanceolata	2	2	2	2
Medicago polymorpha & Acmispon wrangelianus	2			
Bromus tectorum & Pseudosclerochloa rupestris	2			
Total	**38**	**36**	**16**	**26**

Table A17. The number of studies (when multiple treatments and timepoints were combined into a single study) for each combination of pooled traits (all, growth, reproductive, and total biomass) and for each combination of 2 categorical (yes/no) moderators. The moderators are whether or not the native and invasive species were in the same family, and whether or not the invasive was allelopathic.

Experienced	**n**	**n**	**y**	**y**
Same Family	**n**	**y**	**n**	**y**
all	12	7	12	7
growth	12	6	12	6
reproductive	4	4	4	4
biomass	12	1	12	1

Experienced	**n**	**n**	**y**	**y**
Allelopathy	**n**	**y**	**n**	**y**
all	6	13	6	13
growth	5	13	5	13
reproductive	3	5	3	5
biomass		13		13

Results

Full model outputs

Table A18. Classic subgroup meta- analysis for the difference in phenotypic trait values between naïve and experienced plants (Hedges g). Multiple treatments and time points were considered independent studies.

							Heterogeneity			
Subgroup	**Traits**	**Subgroup**	**k**	**Effect Size**	**S.E**	**p-value**	**Q**	**df**	**p**	**I^2**
Competition	**All**	n	32	0.23	0.087	0.008	103.002	31	0	70%
		y	36	0.25	0.082	0.002	173.089	35	0	80%
		Overall	68	0.24	0.06	0	276.267	67	0	76%
		Within					276.0913	66	0	
		Between					0.0264	1	0.8709	
	Growth	n	28	0.23	0.1	0.02	69.298	27	0	61%
		y	32	0.31	0.094	0.001	188.038	31	0	84%
		Overall	60	0.27	0.069	0	258.638	59	0	77%
		Within					257.3363	58	0	
		Between					0.289	1	0.5909	
	Reproductive	n	23	0.12	0.12	0.318	199.863	22	0	89%
		y	14	0.29	0.151	0.056	37.057	13	0	65%
		Overall	37	0.19	0.094	0.049	238.845	36	0	85%
		Within					236.9198	35	0	
		Between					0.761	1	0.383	
	Biomass	n	18	0.34	0.11	0.002	28.033	17	0.045	39%
		y	18	0.28	0.11	0.012	70.819	17	0	76%
		Overall	36	0.31	0.078	0	101.782	35	0	66%
		Within					98.8526	34	0	
		Between					0.1377	1	0.7106	
Allelopathy	**All**	n	24	-0.01	0.093	0.926	99.662	23	0	77%
		y	44	0.39	0.071	0	143.421	43	0	70%
		Overall	68	0.24	0.056	0	276.267	67	0	76%
		Within					243.0822	66	0	
		Between					11.4425	1	7.00E-04	
	Growth	n	16	0	0.126	0.977	74.792	15	0	80%
		y	44	0.37	0.076	0	156.692	43	0	73%
		Overall	60	0.27	0.065	0	258.638	59	0	77%
		Within					231.4843	58	0	
		Between					6.13	1	0.0133	
	Reproductive	n	16	-0.16	0.133	0.231	66.658	15	0	77%
		y	21	0.46	0.118	0	140.218	20	0	86%
		Overall	37	0.19	0.088	0.034	238.845	36	0	85%
		Within					206.8761	35	0	
		Between					12.1133	1	5.00E-04	
	Biomass	n	2	-0.46	0.264	0.084	0.382	1	0.536	0%
		y	34	0.36	0.071	0	75.674	33	0	56%
		Overall	36	0.3	0.069	0	101.782	35	0	66%
		Within					76.056	34	0	
		Between					8.8382	1	0.0029	
	All	n	38	0.4	0.079	0	137.543	37	0	73%
		y	30	0.06	0.084	0.51	113.473	29	0	74%

Same family		Overall	68	0.24	0.057	0	276.267	67	0	76%
		Within					251.0158	66	0	
		Between					9.233	1	0.0024	
	Growth	n	38	0.38	0.085	0	146.889	37	0	75%
		y	22	0.1	0.108	0.373	96.322	21	0	78%
		Overall	60	0.27	0.067	0	258.638	59	0	77%
		Within					243.2104	58	0	
		Between					4.1998	1	0.0404	
	Reproductive	n	15	0.55	0.142	0	136.612	14	0	90%
		y	22	-0.05	0.114	0.668	73.29	21	0	71%
		Overall	37	0.19	0.089	0.035	238.845	36	0	85%
		Within					209.902	35	0	
		Between					11.0051	1	9.00E-04	
	Biomass	n	28	0.35	0.091	0	60.498	27	0	55%
		y	8	0.18	0.153	0.236	38.358	7	0	82%
		Overall	36	0.31	0.078	0	101.782	35	0	66%
		Within					98.8554	34	0	
		Between					0.917	1	0.3383	

Treatments and time points combined

Table A19. The regression models for the effect of experience with the invasive (Hedge's g, the difference between experienced and naïve native populations) with multiple treatments (except competition) pooled. The phylogenetic distance between native-invasive pairs, whether or not the invasive was allelopathic, and same family membership (between the

native and invasive pairs) were used as moderators for: (1) all traits combined, (2) growth traits, (3) reproductive traits, (4) biomass . Competition treatments, time points, and other multiple treatments for a given native-invasive pair within a study were averaged prior to the analysis. For full model outputs see appendix 1 (Table A19).

	Phylogenetic Distance				Allelopathy			Same Family		
	1	**2**	**3**	**4**	**1**	**2**	**3**	**1**	**2**	**3**
Intercept	0.150 (0.12)	0.12 (0.13)	-0.018 (0.26)	0.102 (0.21)	0.053 (0.13)	0.095 (0.15)	-0.32 (0.2579)	***0.435*** ***(0.09)******	***0.41*** ***(0.097)******	***0.58*** ***(0.26)****
Distance	0.0007 (0.0005)	0.0009 (0.0005)	0.001 (0.002)	0.0009 (0.0007)						
Allelopathy					***0.37*** ***(0.16)****	0.305 (0.18)	***0.84*** ***(0.35)****			
Same Family								***-0.35*** ***(0.15)****	-0.29 (0.17)	***-0.81*** ***(0.35)****
R^2	4.88	6.93	0.00	2.83	12.94	6.38	20.73	12.35	5.74	18.41
Tau^2	0.186	0.197	0.770	0.145	0.170	0.198	0.601	0.171	0.199	0.619
Tau^2SE	0.055	0.059	0.264	0.066	0.051	0.060	0.210	0.052	0.060	0.215
QM	2.63	3.33	0.78	1.54	5.47	2.96	5.83	5.38	2.89	5.18
df	44	42	20	24	44	42	20	44	42	20
QMp	0.105	0.068	0.377	0.227	***0.019***	0.085	***0.016***	***0.020***	0.089	***0.023***
QE	176.14	175.70	213.25	76.17	164.27	172.35	180.50	169.33	177.00	188.05
QEp	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
H^2	4.61	4.35	20.07	3.23	4.33	4.38	16.46	4.32	4.37	16.63
I^2	78.29	77.00	95.02	69.08	76.88	77.19	93.92	76.84	77.14	93.99
k	46	44	22	26	46	44	22	46	44	22

Table A20. The interaction regression models (REML) for the for the effect of experience with the invasive (Hedge's g, the difference between experienced and naïve native populations). The following models are presented: (1) Competition treatment (yes, no); (2) Competition * Phylogenetic Distance (interaction model); (3) Competition* Allelopathic invasive (yes, no) (interaction model); (4) Competition * Same Family (yes, no, for naïve and experienced pairs). For the categorical variables "no" was set as the reference variable (dummy coded as 0). Multiple time points and treatments were combined prior to the analysis. Standard errors are presented in round brackets and the 95% confidence intervals in square brackets.

***Models significant using the DerSimonian-Laird estimator ** Models significant using the Knapp and Hartung adjustment**

Traits	Model	Moderator	Estimate	SE	Z	p	Tau^2	R^2	Q	p	Q	p
All	Competition	Intercept	0.2155	0.1127	1.9123	0.0558	0.194246	0.93	1.2302	0.2674	176.4489	<0.001
		Competition	0.1699	0.1532	1.1092	0.2674						
All	Distance * Competition	Intercept	0.2029	0.1708	1.1885	0.2346	0.176929	9.76	5.7565	0.1241	150.6158	<0.001
		Distance	1.00E-04	7.00E-04	0.0892	0.9289						
		Competition	-0.1011	0.2394	-0.4222	0.6728						
		Distance*Competition	0.0012	9.00E-04	1.3731	0.1697						
All	Allelopathy*Competition	Intercept	0.0411	0.1865	0.2203	0.8256	0.172017	12.27	6.9567	0.0733	152.5936	<0.001
		Allelopathy	0.0241	0.2614	0.0923	0.9265						
		Competition	0.2601	0.2285	1.1384	0.255						
		Allelopathy*Competition	0.1923	0.3158	0.6091	0.5425						
All	Same Family* Competition	Intercept	0.2938	0.1382	2.1256	0.0335	0.17016	9.76	7.3183	0.0624	151.384	<0.001
		Same Family	0.2524	0.1843	1.3697	0.1708						
		Competition	-0.2002	0.2194	-0.9125	0.3615						
		Same Family*Competition	-0.2716	0.3026	-0.8974	0.3695						
Growth	Competition	Intercept	0.1751	0.118	1.4838	0.1379	0.201693	4.95	2.6564	0.1031	176.7243	<0.001
		Competition	0.2607	0.16	1.6298	0.1031						
Growth	Distance*Competition	Intercept	0.113	0.1867	0.6053	0.545	0.183279	13.63	7.2918	0.0632	150.7894	<0.001
		Distance	3.00E-04	7.00E-04	0.4155	0.6778						
		Competition	0.0126	0.2611	0.0484	0.9614						
		Distance*Competition	0.0011	0.001	1.1082	0.2678						
Growth	Allelopathy*Competition	Intercept	0.0748	0.2128	0.3515	0.7252	0.188819	11.02	6.3822	0.0944	155.7225	<0.001
		Allelopathy	0.0384	0.2967	0.1293	0.8971						
		Competition	0.1412	0.2531	0.5579	0.5769						
		Allelopathy*Competition	0.2943	0.349	0.8431	0.3992						
Growth	Same Family*Competition	Intercept	0.1954	0.1424	1.372	0.1701	0.18456	13.63	7.1617	0.0669	153.3965	<0.001
		Same Family	0.383	0.1898	2.0179	0.0436						
		Competition	-0.0586	0.2383	-0.246	0.8057						
		Same Family*Competition	-0.4103	0.3292	-1.2464	0.2126						
		Same Family	0.4993	0.3522	1.4176	0.1563						
		Competition	-0.3711	0.3181	-1.1668	0.2433						
		Same Family*Competition	-0.1015	0.4687	-0.2165	0.8286						

Competitive response: Treatments pooled

Table A21. The regression models (REML) for distance, allelopathy in the invasive, and whether or not the native and invasive were in the same family. Regressions were run separately for naïve plants and experienced plants. Effect sizes (Hedges g) were calculated using the difference between competition treatments and controls for naïve and experienced plants (effect sizes for naïve and experienced plants were kept separate). Models term estimates (with standard error in

brackets) and outputs are presented for all pooled traits, pooled growth traits, and total biomass. Multiple effect sizes due to treatments other than competition (e.g nutrient levels) were pooled within experience level for a given species pair within a study. Only significant models are presented, but each model was run for each subset of plants for each type of trait.

	All		**Growth**				**Biomass**	
Experience	**Y**	**Y**	**Y**	**N**	**Y**	**Y**	**Y**	**N**
Intercpt	***-0.9454 (0.1771)******	***-0.3431 (0.1534)****	***-1.3852 (0.1620)******	***-1.6133 (0.2529)******	***-1.2814 (0.2652)******	***-0.3698 (0.1403)*****	***-1.7803 (0.3945)******	***-2.5065 (0.7071)******
Distance	***0.0019 (0.0007)*****		***0.0032 (0.0006)******	***0.0026 (0.0009)*****			***0.0045 (0.0013)******	***0.0054 (0.0023)****
Allelopathy					***0.7921 (0.3133)****			
Same Family		***-0.5685 (0.2421)****				***-0.9691 (0.2344)******		
R^2	31.85	23.73	76	36.26	29.38	63.3	61.8	31.54
Tau^2	0.1653	0.185	0.0906	0.3082	0.2665	0.1385	0.1845	0.735
Tau^{2}SE	0.0837	0.0909	0.0614	0.1459	0.1262	0.0795	0.1232	0.3642
QM	7.6782	5.512	26.9204	7.6287	6.3925	17.086	12.7486	5.7649
df	17	17	16	16	16	16	11	11
QMp	***0.0056***	***0.0189***	***<0.001***	***0.0057***	***0.0115***	***<0.0010***	***0.0004***	***0.0163***
QE	88.3654	89.578	35.6335	61.0708	75.814	41.2118	31.471	82.022
QEp	0	0	0.0033	0	0	0.0005	0.0009	0
H^2	3.6846	3.9846	2.1655	4.4639	4.4417	2.771	2.8739	8.6934
I^2	72.8603	74.9031	53.8213	77.5982	77.4863	63.9124	65.2044	88.497
k	19	19	18	18	18	18	13	13

Model estimates: ***p < 0.001, **p < 0.01, *p < 0.05

QMp: **bold** (no *) p<0.05 with DL only, *italics* p<0.05 with KNHA adjustment

Forest Plots

Effect of Competition

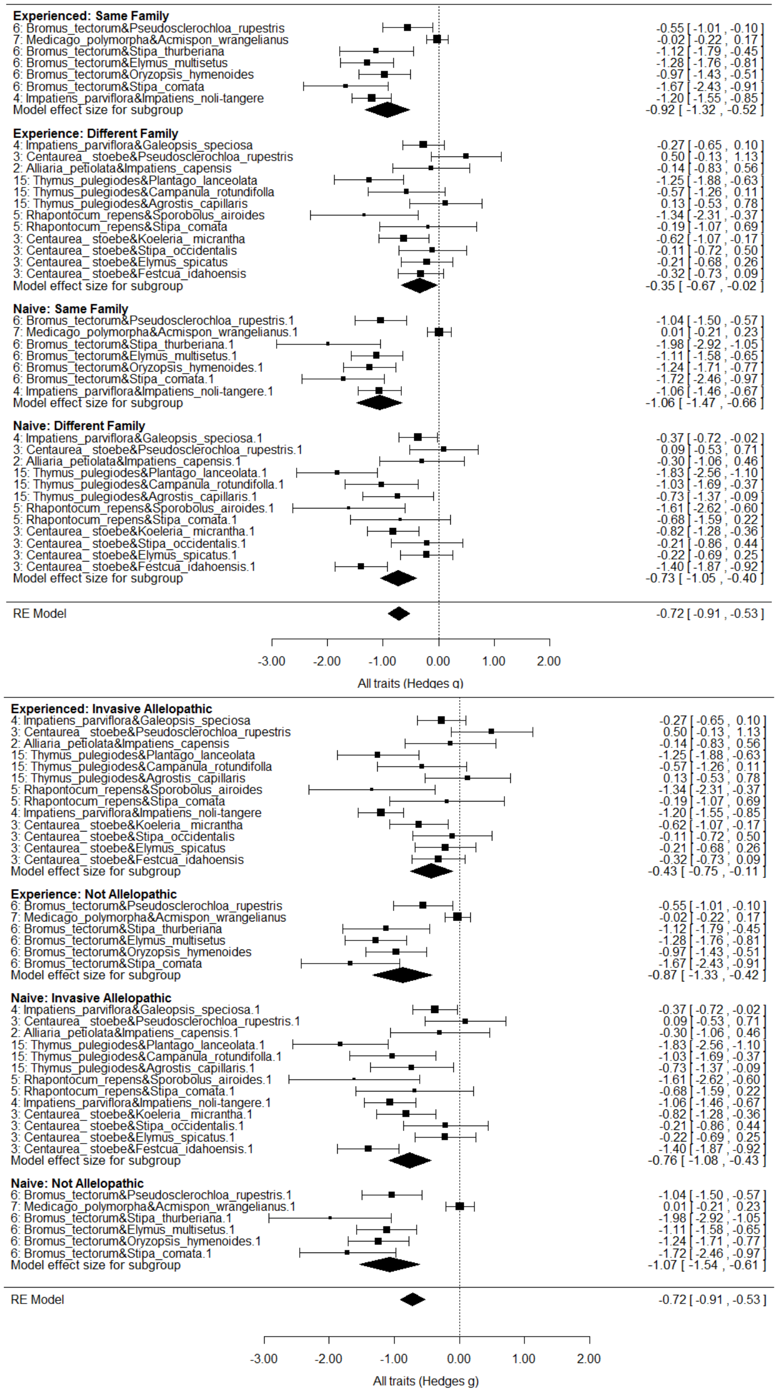


Figure A13. Forest plot of the effect of competition (Hedges g, the difference between populations planted with the invasive and populations planted without the invasive) for all traits combined. The subgroup diamonds represent the effect size estimated by the model for a random study, drawn from the same universe as this population of studies, with those traits (e.g allelopathy, experience).

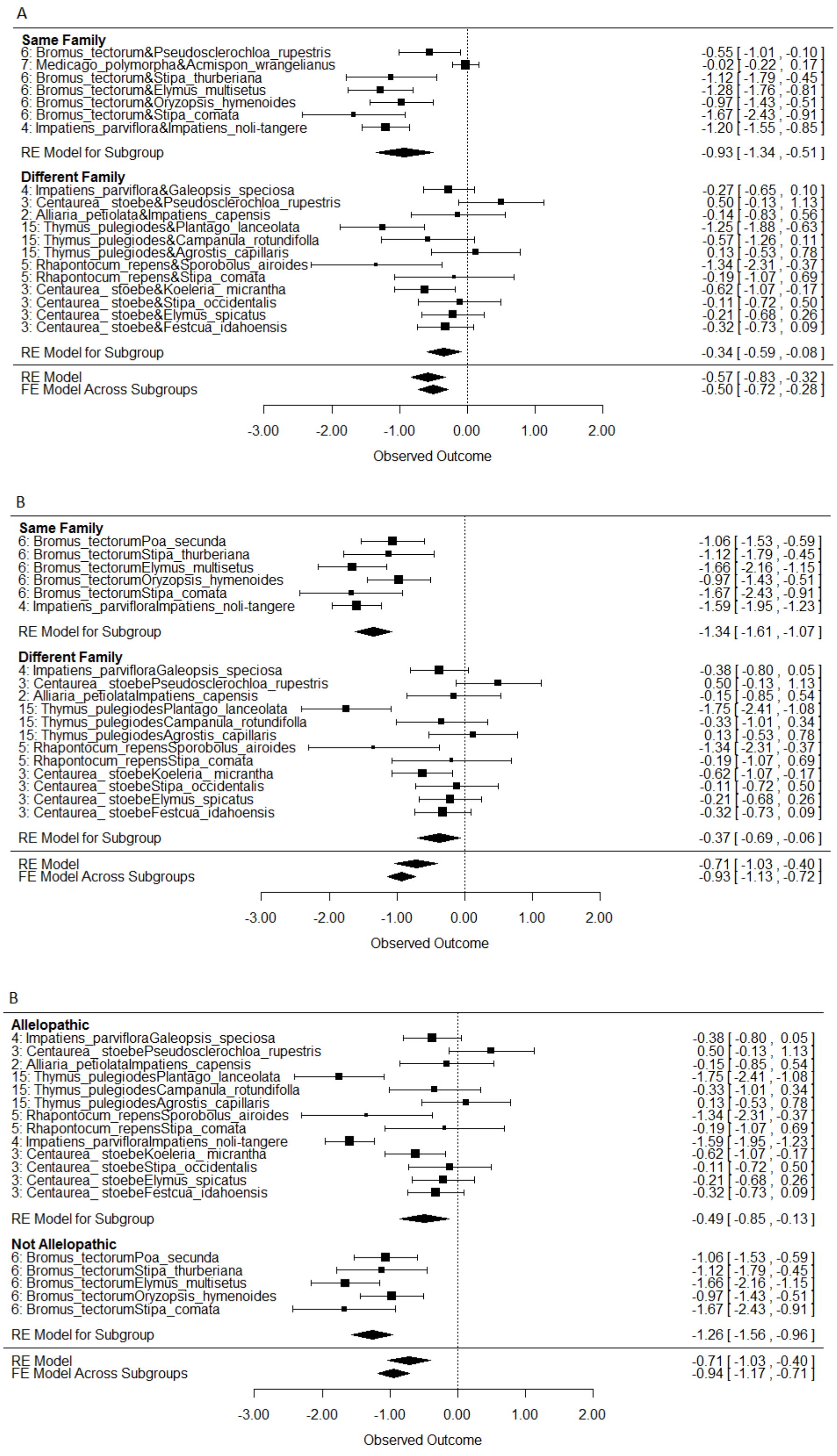


Figure A14. Forest plots for the effect of competition on (A) and growth traits (B) for populations with are experienced with the invasive. Study effect sizes are separated by the presence of allelopathy in the invasive, and whether or not the invasive and native are in the same family.

All studies by allelopathy

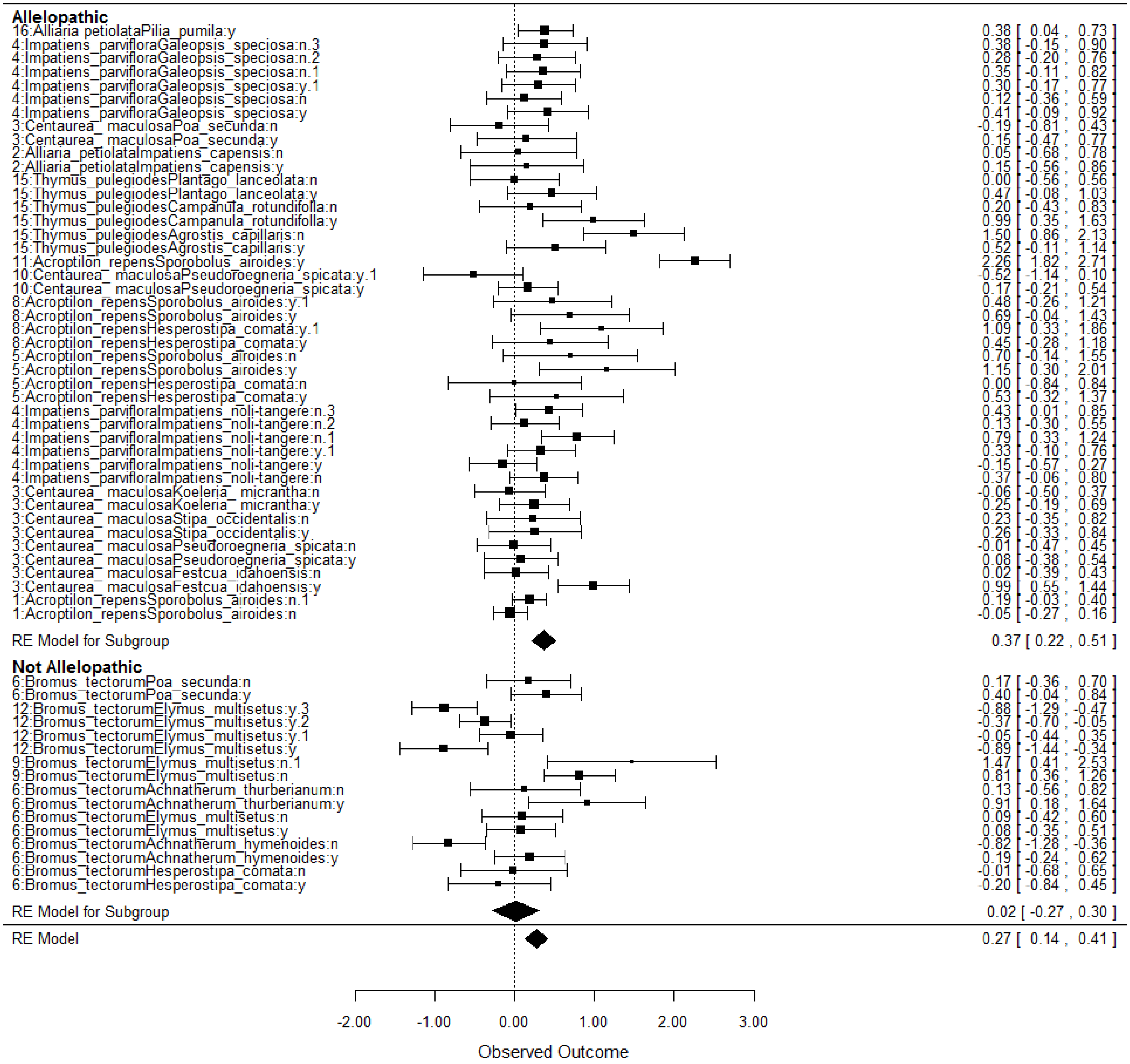
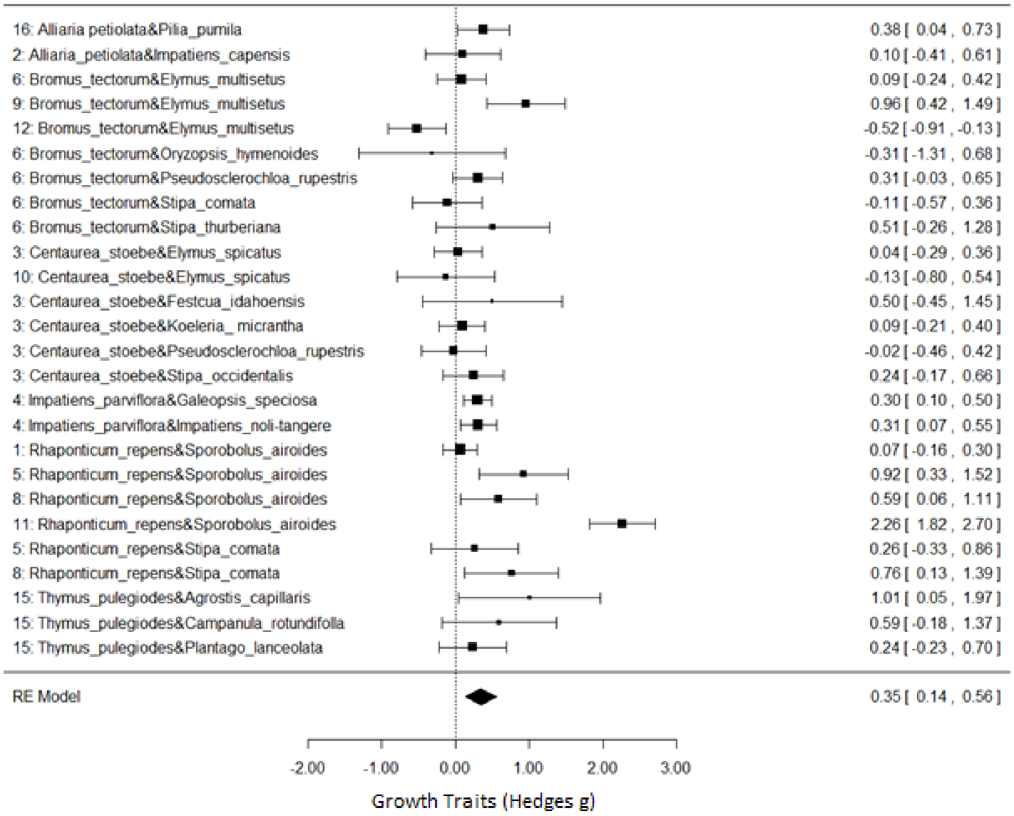
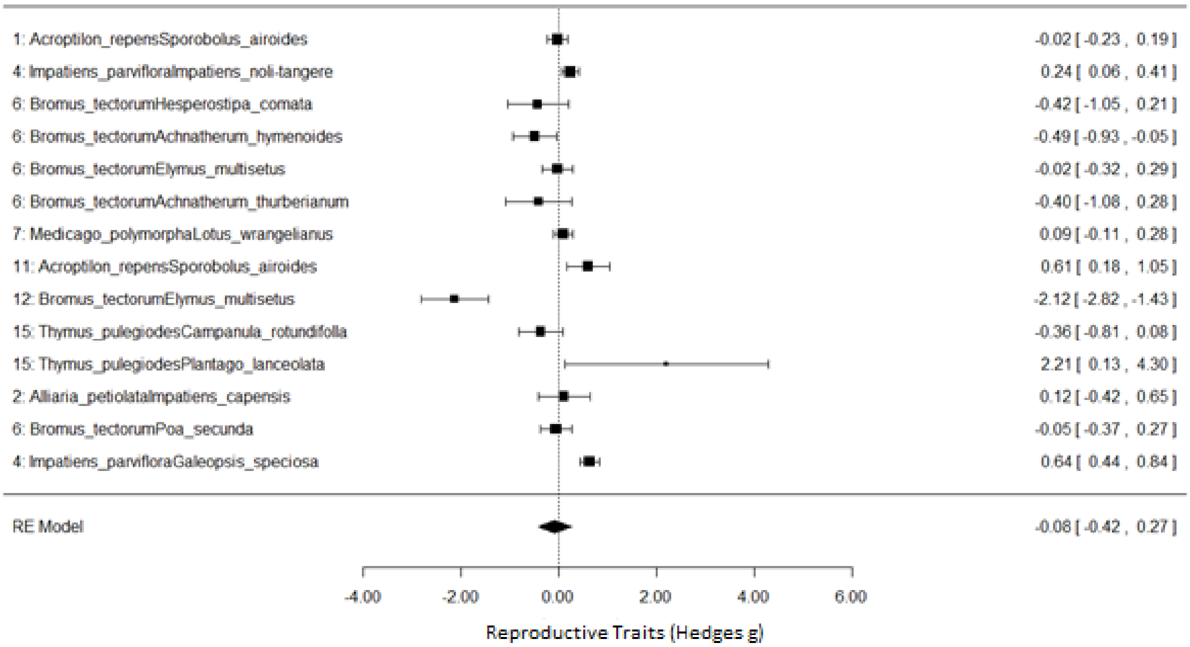


Figure A15. Forest plot of the effect sizes for all traits (Hedges *g*, the difference between experienced and naïve plants) for each study with the presence of an allelopathic invasive as subgroups. Multiple treatments per study were not averaged into a single effect size. Studies are labelled on the left with the accession code (publication identity) followed by the invasive species, the native species, whether or not the native was planted with the invasive (y/n), and an arbitrary number to ensure that multiple treatments had a unique label. Squares represent individual effect sizes, scaled to represent their weight in the analysis, with 90% confidence interval bars. Overall effect sizes (from a REML meta-regression including allelopathy as a moderator) for each subgroup, and the overall effect size ignoring allelopathy are presented as diamonds, with the center placed at the overall effect size and the left and right ends encompassing the 95% confidence interval.

Treatments combined





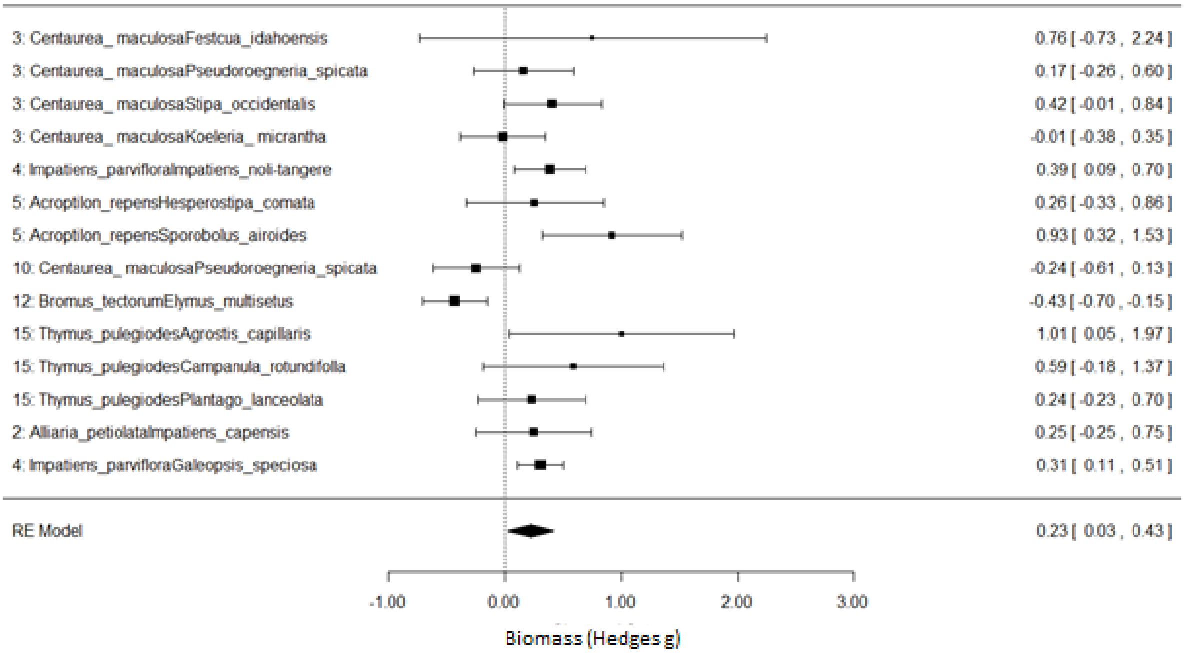
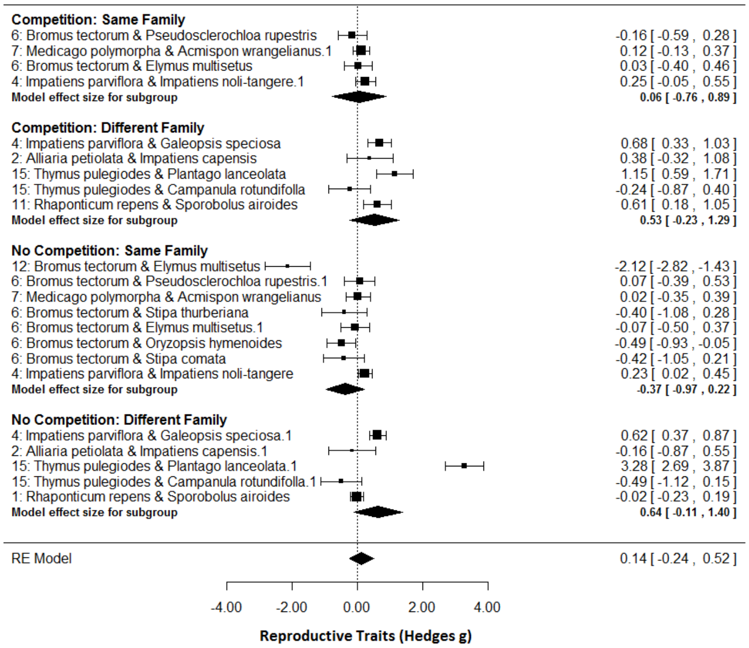


Figure A16 Forest plots of the difference between experienced and naïve plants (Hedges g) for phenotypic traits. Growth traits (top), reproductive traits (middle), and biomass (bottom) are presented. Competition treatments, timepoints, and other treatments for a given native-invasive pair within a study were pooled using separate random effects meta-analysis for each study. Publication identification codes and the native-invasive pair for each study are indicated. Squares represent the effect size for each study with standard errors, while the diamond represents the overall effect size across studies with the edges of the diamond indicating the 95% confidence interval. Means and 95% confidence intervals are indicated on the far right for each study.



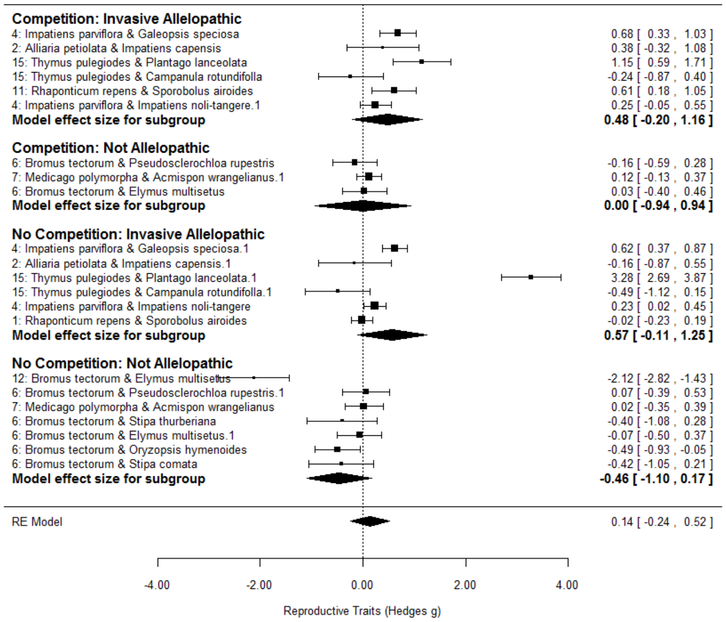
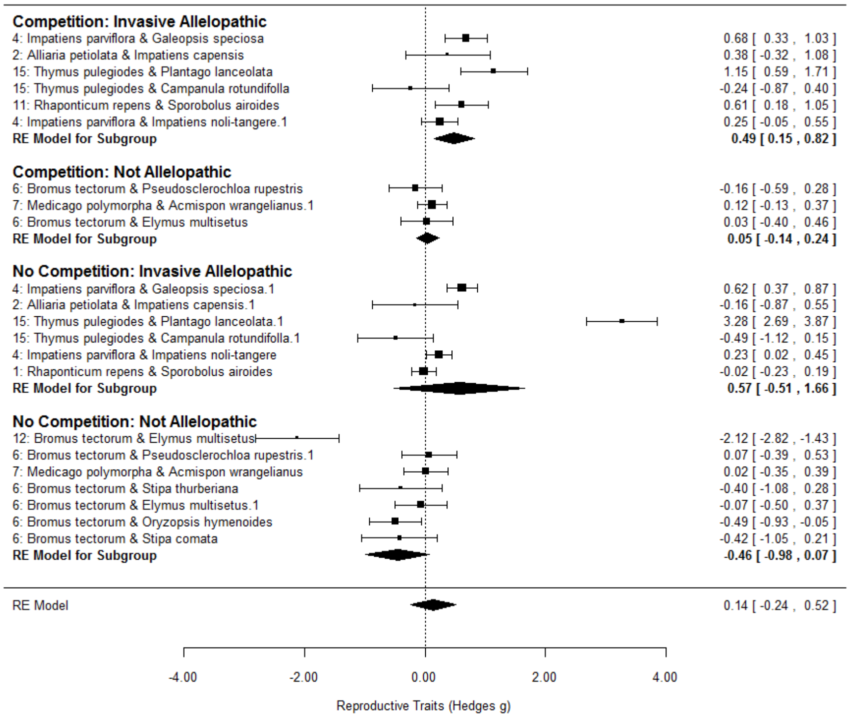


Figure A17. Forest plots of the effect of experience on native growth and reproductive traits (Hedges *g*, the difference between experienced and naïve plants) for each study. Multiple treatments per study were averaged into a single effect size. Studies are labelled on the left with the accession code (publication identity) followed by the invasive species and the native species, and an arbitrary number to ensure unique label. Squares represent individual effect sizes, scaled to represent their weight in the analysis, with 90% confidence interval bars. The estimated effect sizes (from a REML meta-regression including an interaction term with competition for the presence of allelopathy and same-family membership) for each subgroup, and the overall effect size ignoring the moderators, are presented as diamonds with the center placed at the overall effect size and the left and right ends encompassing the 95% confidence interval.



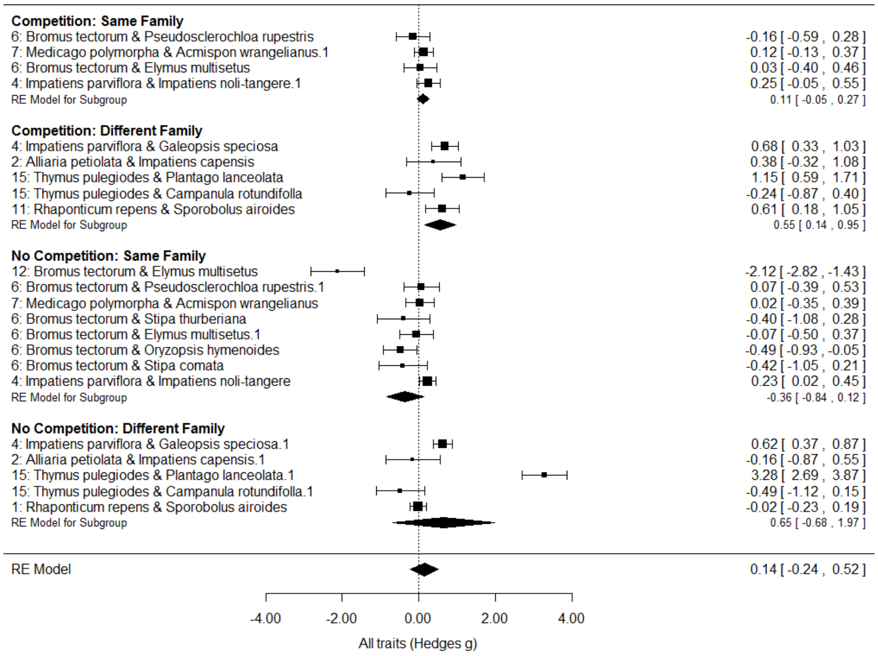


Figure A18. Forest plots of the effect of experience on native growth and reproductive traits (Hedges *g*, the difference between experienced and naïve plants) for each study. Multiple treatments per study were averaged into a single effect size. Studies are labelled on the left with the accession code (publication identity) followed by the invasive species and the native species, and an arbitrary number to ensure unique label. Squares represent individual effect sizes, scaled to represent their weight in the analysis, with 90% confidence interval bars. *The overall effect sizes for each subgroup are calculated from individual random effects meta-analysis on each subgroup*. The overall effect sizes are presented as diamonds with the center placed at the overall effect size and the left and right ends encompassing the 95% confidence interval.

Funnel plots

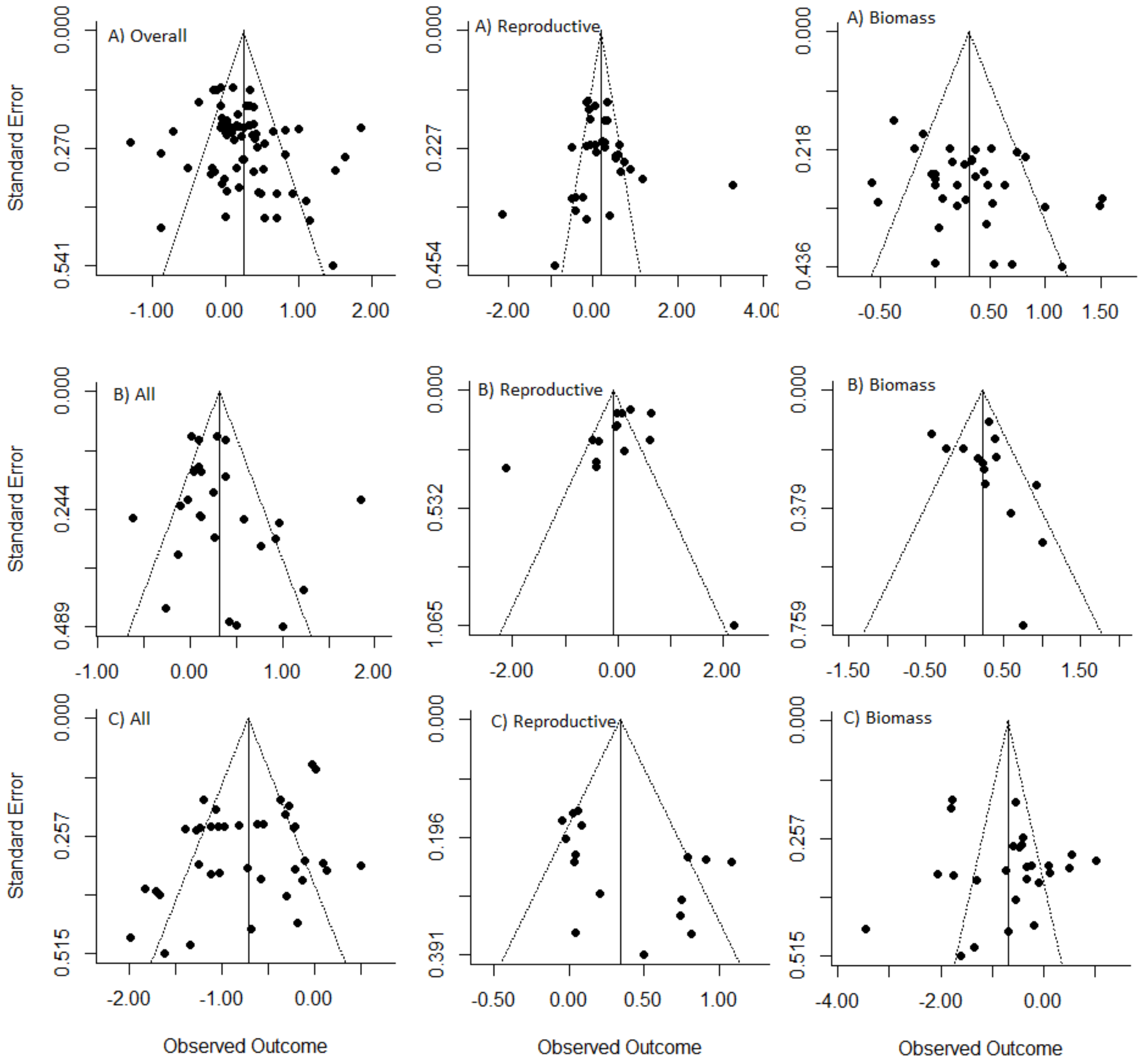


Figure A19. Funnel plots for A) All traits when treatments are not combined, B) All traits when treatments are combined, and C) All traits for the competitive response with all traits combined. Funnel plots may not be a good indicator for publication when there is a significant amount of heterogeneity between studies (Vetter, 2014).

Methodological Variations

Multi-level Models

In my main analysis I dealt with multiple experiments and timepoints for the same native-invasive pair within a paper by averaging them into a single effect size (using a random effects meta-analysis before the actual analysis). However, another method involves the use of multi-level models which apply random effects at the level of some grouping variable- that is to say, studies in different groups are treated as independent, but those within the same group are given the same random-effects variance component. I also use this method can also be used to try and account for the potential similarity between studies which share a native species.

Table A22. Multi-level model results with random effects at the level of the native-invasive pair within a paper (therefore, multiple experiments and timepoints for that pair within a paper are grouped). for all traits. Multiple measurements on the same plants were still combined prior to analysis.

Intrcpt	0.3483***	0.1535	0.0705	0.4506***
	(0.1025)	(0.1548)	(0.1630)	(0.1124)
Distance		0.0008		
		(0.0006)		
Allelopathy: Y			0.3699	
			(0.1958)	
SameFamily: Y				-0.3531
				(0.1900)
QM	11.5497	1.9987	3.5702	3.4525
df	59.0000	66.0000	66.0000	66.0000
QMp	0.0007	0.1574	0.0588	0.0632
QE	258.6380	260.5321	243.0822	251.0158
QEp	0.0000	0.0000	0.0000	0.0000
sigma2	0.2326	0.1963	0.1818	0.1834
k	60.0000	68.0000	68.0000	68.0000

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

Statistical models

Table A23. Multi-level interaction model results with random effects at the level of the native-invasive pair within a paper (therefore, multiple experiments and timepoints for that pair within a paper are grouped) for all traits. Multiple measurements on the same plants were still combined prior to analysis

	Competition	**Distance**	**Allelopathy**	**SameFamily**
Intrcpt	0.2709 (0.1019)**	0.1528 (0.1568)	0.0098 (0.1716)	0.3383 (0.1263)**
Competition:Y	0.1029 (0.0656)	0.0045 (0.0873)	0.1137 (0.0947)	0.1892 (0.1036)
Distance		0.0004 (0.0006)		
Competition*Distance		0.0007 (0.0004)		
Allelopathy:Y			0.3792 (0.2099)	
Competition*Allelopathy			-0.0238 (0.1312)	
SameFamily:Y				-0.2616 (0.2012)
Competition*SameFamily				-0.1495 (0.1337)
Qm	2.4601	7.2130	5.9515	7.1301
df	66.0000	64.0000	64.0000	64.0000
QMp	0.1168	0.0654	0.1140	0.0679
QE	276.0913	234.3470	232.5961	231.6929
QEp	0.0000	0.0000	0.0000	0.0000
sigma2	0.2050	0.1825	0.1841	0.1760
k	68.0000	68.0000	68.0000	68.0000

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

Statistical models

When random effects were applied at the level of the individual naïtive-invasive pairs in each publication (thus applying random effects to to account for multiple treatments per study), the influence of phylogenetic distance on the effect of experience was slightly larger in studies with a competitive planting treatment (difference in model estimates = -0.0007, SE = 0.0003, p = 0.024), and this also held for native-invasive species which were in the same family (difference = 0.411, SE = 0.1959, p = 0.0358). The trend with family held for growth traits, but not distance, and there was a significant overall difference between studies with and without a competition treatment (Table A23). For reproductive traits, both allelopathic invasives and same family membership predicted a larger effect of experience when natives were planted with the invasive, although allelopathy also predicted a larger effect size in the absence of a competition treatment (

Table A26).

Table A24. Multi-level model results with random effects at the level of the native-invasive pair within a paper (therefore, multiple experiments and timepoints for that pair within a paper are grouped) for growth traits. Multiple measurements on the same plants were still combined prior to analysis.

	Model 1	**Model 2**	**Model 3**	**Model 4**
Intrcpt	0.3483^{***}	0.1287	0.1151	0.4436^{***}
	(0.1025)	(0.1723)	(0.1917)	(0.1217)
Distance		0.0010		
		(0.0006)		
Allelopathy: Y			0.3200	
			(0.2249)	
SameFamily: Y				-0.3023
				(0.2159)
QM	11.5497	2.4213	2.0247	1.9592
df	59.0000	58.0000	58.0000	58.0000
QMp	0.0007	0.1197	0.1548	0.1616
QE	258.6380	243.6940	231.4843	243.2104
QEp	0.0000	0.0000	0.0000	0.0000
sigma2	0.2326	0.2184	0.2211	0.2224

k	60.0000	60.0000	60.0000	60.0000

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

Table A25. Multi-level interaction model results with random effects at the level of the native-invasive pair within a paper (therefore, multiple experiments and timepoints for that pair within a paper are grouped) for growth traits. Multiple measurements on the same plants were still combined prior to analysis

	Competition	**Distance**	**Allelopathy**	**SameFamily**
Intrcpt	0.2450 (0.1117)*	0.1022 (0.1800)	-0.0453 (0.2150)	0.2711 (0.1325)*
Competition:Y	0.1824 (0.0798)*	0.0552 (0.1282)	0.2993 (0.1654)^{1}	0.2902 (0.1038)**
Distance		0.0006 (0.0007)		
Competition*Distance		0.0006 (0.0005)		
Allelopathy:Y			0.3975 (0.2518)	
Competition*Allelopathy			-0.1542 (0.1888)	
SameFamily:Y				-0.1411 (0.2261)
Competition*SameFamily				-0.2700 (0.1617)
Qm	5.2284	9.0929	7.7528	9.9505
df	58.0000	56.0000	56.0000	56.0000
QMp	0.0222	0.0281	0.0514	0.0190
QE	257.3363	206.7268	212.2453	205.7632
QEp	0.0000	0.0000	0.0000	0.0000
sigma2	0.2309	0.2034	0.2321	0.2042
k	60.0000	60.0000	60.0000	60.0000

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

1 significant model term when competition (yes) is set at reference value

Table A26. Multi-level interaction model results with random effects at the level of the native-invasive pair within a paper (therefore, multiple experiments and timepoints for that pair within a paper are grouped) reproductive traits. Multiple measurements on the same plants were still combined prior to analysis

	Experience	**Distance**	**Allelopathy**	**SameFamily**
Intercept	0.0262 (0.2369)	-0.1820 (0.3150)	-0.4599 (0.2942)	0.6201 (0.3298)
Experience:Y	-0.0133 (0.0796)	-0.0360 (0.1004)	0.0447 (0.1034)	-0.2008 (0.1663)
Distance		0.0017 (0.0018)		
Experience*Distance		0.0003 (0.0010)		
Allelopathy:Y			0.9894 (0.4142)*	
Distance*Allelopathy			-0.1482 (0.1618)	
SameFamily:Y				-0.9880 (0.4340)*
Experience*SameFamily				0.2391 (0.1894)
Qm	0.0280	1.2235	6.0542	5.9340
df	35.0000	33.0000	33.0000	33.0000
QMp	0.8671	0.7474	0.1090	0.1149
QE	236.9198	226.0369	200.4020	204.6579
QEp	0.0000	0.0000	0.0000	0.0000
sigma2	0.7277	0.7348	0.5399	0.5782
k	37.0000	37.0000	37.0000	37.0000

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

Statistical models

Multi-level models for the native species

In one section of the analysis I presented the results for when all multiple treatments (including competition treatments) were pooled. However, a considerable amount of studies shared the same native species. To try and account for this, I applied random effects at the level of the native species identity for the multivariate model. The results are as shown:

Table A27. Regression models for the effect of experience on reproductive traits. Multiple experiments were uncombined. The multi-level model uses native species identity as the grouping variable.

	Model 1	**Model 2**	**Model 3**	**Model 4**
Intercept	0.1184	0.0108	-0.2566	0.5334
	(0.2090)	(0.2871)	(0.2662)	(0.2915)
Distance		0.0010		
		(0.0018)		
Allelopathy: Y			0.7382*	
			(0.3721)	
SameFamily: Y				-0.7132
				(0.3833)
QM	0.3212	0.3207	3.9365	3.4627
df	36.0000	35.0000	35.0000	35.0000
QMp	0.5709	0.5712	0.0473	0.0628
QE	238.8446	234.1402	206.8761	209.9020
QEp	0.0000	0.0000	0.0000	0.0000
sigma2	0.4837	0.5216	0.3754	0.3901
k	37.0000	37.0000	37.0000	37.0000

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

Statistical models

Table A28. Interaction regression models for the effect of experience on reproductive traits. Multiple experiments were uncombined. The multi-level model uses native species identity as the grouping variable.

	Experience	Distance	Allelopathy	SameFamily
Intercept	0.0912 (0.2085)	0.0096 (0.2877)	-0.2872 (0.2655)	0.5099 (0.2944)
Experience:Y	0.0823 (0.0755)	-0.0195 (0.0949)	0.1113 (0.1024)	0.0583 (0.1385)
Distance		0.0007 (0.0018)		
Experience*Distance		0.0011 (0.0006)		
Allelopathy:Y			0.7514 (0.3724)*	
Distance*Allelopathy			-0.0670 (0.1514)	
SameFamily:Y				-0.7151 (0.3851)
Experience*SameFamily				0.0316 (0.1651)
Qm	1.1900	4.5714	5.3431	4.6943
df	35.0000	33.0000	33.0000	33.0000
QMp	0.2753	0.2060	0.1483	0.1956
QE	236.9198	226.0369	200.4020	204.6579
QEp	0.0000	0.0000	0.0000	0.0000
sigma2	0.4737	0.5187	0.3681	0.3833
k	37.0000	37.0000	37.0000	37.0000

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

Competition treatment subset

The results presented here are for the subset of studies which included a factorial competition treatment. The effect size was the difference between experience and naïve plants.

Treatments not pooled

Table A29. Meta-regression results for the effect of experience on all native plant traits for a subset of studies which included a factorial competition treatment. Multiple treatments were kept as independent studies.

	Overall	Distance	Allelopathy	Family
Intrcpt	0.2646^{***}	0.2229	0.2459	0.4510^{***}
	(0.0578)	(0.1193)	(0.1513)	(0.0934)
Distance		0.0006		
		(0.0005)		
Allelopathy: Y			0.1426	
			(0.1765)	
SameFamily: Y				-0.2594
				(0.1471)
R^2		14.1300	0.0000	30.5400
Tau^2	0.0704	0.0364	0.0453	0.0295
Tau^2SE	0.0309	0.0362	0.0395	0.0337
QM		1.8207	0.6529	3.1123
df		18.0000	18.0000	18.0000
QMp		0.1772	0.4191	0.0777
QE	86.0054	27.7051	29.7278	26.0445
QEp	0.0001	0.0667	0.0402	0.0987
H^2	1.9984	1.5033	1.6250	1.4062
I^2	49.9608	33.4779	38.4606	28.8888
k	44.0000	20.0000	20.0000	20.0000

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

Statistical models

Table A30. Interaction meta-regression for the effect of experience on all traits for a subset of studies which included a factorial competition treatment. Multiple treatments were kept as independent studies.

	Experience	**Distance**	**Allelopathy**	**SameFamily**
Intrcpt	0.1641 (0.0899)	0.0637 (0.1486)	-0.1250 (0.1755)	0.1968 (0.1130)
Experience:Y	0.1937 (0.1267)	0.1681 (0.2075)	0.3747 (0.2433)	0.2605 (0.1602)
Distance		0.0005 (0.0006)		
Experience*Distance		0.0001 (0.0008)		
Allelopathy:Y			0.3822 (0.2021)	
Distance*Allelopathy			-0.2378 (0.2817)	
SameFamily:Y				-0.0887 (0.1859)
Experience*SameFamily				-0.1692 (0.2608)
R^2	5.3600	3.6000	16.7200	6.0500
Tau^2	0.0811	0.0826	0.0714	0.0805
Qm	2.3392	4.2774	6.5978	4.5624
df	38.0000	36.0000	36.0000	36.0000
QMp	0.1262	0.2330	0.0859	0.2068
QE	80.0219	76.1736	70.9437	75.1293
QEp	0.0001	0.0001	0.0005	0.0001
k	40.0000	40.0000	40.0000	40.0000

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

Statistical models