**Evolutionary history has weak effects on fitness outcomes in an invaded annual plant community in Western Australia**

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**Statement of Authorship**

The research carried out in the course of this investigation and the results presented in this report are, except where acknowledged, the original work of the author, and all research was conducted during the Honours program.

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**Abstract**

As exotic plant species can have negative, neutral, or positive impacts on the resident communities they invade, understanding what is driving this variation is essential to predicting and controlling their impacts. One long-standing hypothesis often used to help explain this variation is the competition-relatedness hypothesis. As it applies to invasion ecology, the competition-relatedness hypothesis predicts that exotic species that share more evolutionary history (i.e. are more phylogenetically related) with neighbours in their invaded communities compete more strongly with them. As empirical support for this hypothesis is mixed, this study investigates whether additional insight from the exotic species’ native ranges may be the key to understanding these complex interactions. Experiments conducted using four exotic annual plant species from an invaded community in southwestern Australia, with a focus on coarse phylogenetic relatedness as a proxy for shared deep evolutionary history, revealed that phylogenetic relatedness had generally weak effects on fitness outcomes in the invaded community. Other factors such as neighbour density and native/exotic status appeared to be potentially more important for these exotic species. In incorporating information from the native range, phylogenetic relatedness of exotics to neighbours in their native communities was neither similar to phylogenetic relatedness to neighbours in the invaded community, nor was it associated with their fitness outcomes, with the exception of one exotic species. As available data were limited in this study, further research is needed to better understand how we can use information from the native range to predict exotic species impacts.

**Introduction**

Plant invasions are a major driver of biodiversity loss and environmental degradation worldwide (Mack et al. 2000). The effects of plant invasions occur at many different scales, ranging from populations to communities, to whole ecosystems (Vila et al. 2011). With the expansion of global trade and an increase in human movement and urbanisation, the rate of species invasion has increased dramatically during the last century with no sign of slowing down (Seebens et al. 2017). Consequently, understanding and predicting which species may successfully invade a community, and the impacts they may have, has become a major goal in invasion ecology. Key to this endeavour is the recognition that the process of “invasion” does not always lead to negative impacts on the resident community. Although exotic species can certainly have these negative effects, those caused by the ‘exploiters’, aligned with the more common term ‘invasive species’, studies suggest that some species, the ‘coexisters’, have either no or even beneficial effects on resident native species (Lai et al. 2015, Wainwright et al. 2017). Understanding why exotic species vary so greatly in the ways they interact with native resident communities is essential to predicting and controlling their impacts.

Central to the many theories for why some exotic species perform better in some locations rather than others, is the concept of a species’ ecological niche. The contemporary definition of a ‘niche’ considers not only a species’ abiotic requirements for persistence and reproduction (i.e. a species’ fundamental niche) (Grinnell 1917, Rosado et al. 2016), but also how they themselves affect the environment, in relation to resource availability, disturbance and biotic interactions (i.e. a species’ realised niche) (Ackerly 2003, Chase and Leibold 2003, Soberón 2007). As contemporary ideas of the niche include both its response to and impact on the abiotic and biotic environment (HilleRisLambers et al. 2012), it is critical we assess both factors when trying to understand variation in invasion success.

In terms of the abiotic environment, the theory of environmental suitability is one well-researched theory for why variation in invasion success can be seen across different taxa and locations. Environmental suitability is the idea that exotic species will perform better in their invaded range if the abiotic conditions are similar, or match those, of their native range (Panetta and Mitchell 1991, Scott and Panetta 1993). In the most straightforward example, a species from a rainforest is unlikely to successfully establish and reproduce if relocated to a desert environment. Although studies have found abiotic matching to be important in determining invasion success (e.g. Dawson et al. 2009), it has been shown that even among species with good matching, invasion success is extremely variable, suggesting other factors are also involved (Williamson 2006, Dawson et al. 2009, Gallien et al. 2015). Notably, other theories of invasion success, such as the enemy release hypothesis (Darwin 1859), increased competitive ability hypothesis (Blossey and Notzold 1995), and the novel weapons hypothesis (Callaway and Aschehoug 2000), highlight the importance of also studying the relationships among organisms (i.e. biotic interactions) in invaded communities.

In terms of the biotic environment, it is well understood that interactions such as competition, mutualism and predation, are all important in defining a species' niche (Belyea and Lancaster 1999, Weiher et al. 2011). Of these different types of biotic interactions, cross-trophic-level interactions have been particularly well-studied in the context of biological invasions (Traveset and Richardson 2014). As such, there is considerable evidence for the importance of the presence of symbiotic microbiota (e.g. Paudel et al. 2014) and functionally similar pollinators (e.g. Parker 1997, Issaly et al. 2020), as well as the absence of enemies (e.g. Colautti et al. 2004) in the invaded range, on invasion success and impact. Although within-trophic interactions, for example plant-plant competition, have been well studied as a mechanism by which exotic species have negative impacts on communities, fewer studies have examined how within-trophic interactions contribute to variation in the outcomes of successful introductions (Northfield et al. 2018). For example, though we have a good understanding that many invasive plant species outcompete native species in invaded regions, we have a limited understanding of how non-invasive “coexister” exotics interact with native species. Our lack of understanding of why certain species compete more strongly or weakly compared to others is a critical gap in invasion ecology theory.

One hypothesis proposed to explain variation in competition strength is the competition-relatedness hypothesis. This hypothesis, usually attributed to Darwin (1859), states that closely related taxa compete more intensely than distantly related taxa, limiting their ability to coexist (Webb et al. 2002). Importantly, this hypothesis assumes that traits important for competitive outcomes, those that impact an individual’s performance (i.e. functional traits), are phylogenetically conserved (Mcgill et al. 2006, Violle et al. 2007, Emerson and Gillespie 2008). Meaning that species that are more closely related, and thus share more evolutionary history, are more similar in the ways they compete for specific resources (Emerson and Gillespie 2008). If they are competing for similar resources, they are unlikely to stably coexist, as per the competitive exclusion principle (Hardin 1960). Decades of studies have explored the competition-relatedness hypothesis, and its value for understanding species interactions, with many studies providing supporting evidence (e.g. Davies 2006, Violle et al. 2011, Allan et al. 2013). Recently, however, with the development of coexistence theory, specifically our understanding of niche and fitness differences (Mayfield and Levine 2010), as well as our recognition that distantly related species can have convergent traits (Drenovsky et al. 2012, Wang et al. 2019), empirical evidence has increasingly challenged this hypothesis.

Many studies have investigated invasion success as a function of phylogenetic relatedness to native resident species. With our understanding of the complex nature of relatedness and competitive outcomes, it is not surprising that such studies have found conflicting results. In general, studies focussing on establishment have found that success increases with phylogenetic distance between invaders and native species in the invaded range (Rejmánek 1996, Lockwood et al. 2001, Jiang et al. 2010). However, studies focussing on the spread and impact of exotic species, have been less conclusive (Park and Potter 2013, Tan et al. 2015). Similarly, mixed evidence has been found from studies on community resistance to invasion (Jones et al. 2013, Marx et al. 2016). Accounting for invader phylogenetic similarity to resident communities alone is clearly not sufficient to make strong generalisable conclusions about when and where invasive species succeed or how they impact invaded communities (Gallien and Carboni 2017). One aspect of the relatedness debate that has not been well studied but has been thought to potentially play an important role in determining the variability found in previous studies is the relatedness of the invader to other species in its native range communities, and whether the invader is invading a system with a similar level of relatedness to its native range or not. In much the same way that we look at the abiotic environment and cross-trophic interactions, we can ask: if a species is closely related to its neighbours in its native range (and thus evolved to interact with similar species), does it perform better in communities of closely related individuals in its invaded range? To the best of our knowledge, no studies have investigated this question focussing specifically on exotic plant species (but see Escoriza and Ruhí 2016 for a similar non-plant example).

While phylogenetic relatedness and functional traits can both be measured as proxies to infer the strength of biotic interactions within a community, the benefit of using relatedness rather than traits is that it can tell us about trait differences and shared history between taxa within clades that are both young (terminally rooted) and old (deeply rooted). Phylogenetic relatedness measured at finer scales, for example at the gene or trait level, helps us to understand differences between individuals, populations and closely related “terminal” species. In contrast, phylogenetic relatedness measured at coarser scales, for example, between families or orders, helps us to understand differences between taxa that are deeply conserved and represent clear functional splits (e.g. C3 and C4 pathways). Most studies of plant invasions that account for evolutionary history focus on phylogenetic relatedness measured at finer scales (e.g. Park and Potter 2013, Marx et al. 2016). Here, we instead focus on phylogenetic relatedness measured at coarse scales, as these deep functional differences are widely considered to be important for understanding modern community diversity and function (Futuyma and Agrawal 2009).

Here we investigate the importance of deep evolutionary history on the way four exotic annual plant species interact with residents of their invaded communities in south-west Western Australia. Through a field experiment and investigation of the exotic species’ native range communities, we examined the complex relationship between relatedness and competition, and explored how insight from the native range may be the key to understanding these relationships and their specificity among taxa. Using coarse phylogenetic relatedness as a proxy for shared deep evolutionary history, we address the following questions:

1. How does phylogenetic relatedness of exotic species to neighbours in their invaded communities impact their fitness outcomes?
2. How similar is phylogenetic relatedness of exotic species to neighbours in their native and invaded communities?
3. Is there a relationship between phylogenetic relatedness of exotic species to neighbours in their native communities and fitness outcomes in their invaded communities?

**Methods**

**Field experiment in the invaded range community (Q1)**

*Study site and species*

The field component of this study took place in West Perenjori Nature Reserve (29°28'01.3"S 116°12'21.6"E) in south-west Western Australia. The reserve sits in an extensive agricultural region known as the Avon Wheatbelt: a region that has largely been cleared of native vegetation for wheat and canola agricultural production. The reserve is characterised by an overstorey of York (*Eucalyptus loxophleba* Benth.) and jam (*Acacia acuminata* Benth.) trees with an understorey of hyper diverse winter annual communities as well as some perennial grasses and shrubs. The climate in this system is semi-arid, typical of Mediterranean-type ecosystems, with a mean annual maximum temperature of 28.2°C and mean annual precipitation of 302mm (BOM 2020, site numbers 008296 and 008013, 20-year means). Soils in this system are highly weathered and nutrient poor, particularly in phosphorus (Hopper and Gioia 2004). As this reserve is surrounded by agricultural land, bringing both disturbance and phosphate fertiliser drift, this system is highly invaded, with exotics making up approximately 30 percent of all annual species.

The four focal exotic species chosen for this study included two Poaceae species, *Avena barbata* Pott ex Link and *Pentameris airoides* Nees and two Asteraceae species, *Arctotheca calendula* (L.) Levyns and *Monoculus monstrosus* (Burm.f.) B.Nord. Choosing species from two evolutionarily distinct (deep phylogenetic division) and functionally dissimilar families enabled us to focus on the deeply-rooted evolutionary differences in these species, given limitations in the quality of phylogenies that are possible to construct with the limited information available on species-level phylogenetic relatedness for the relevant species involved. This distinction also allowed us to assess whether our findings are generalisable across large, very distantly related taxonomic groups (monocots and dicots).

The focal exotic species originated from South Africa (*Ar. calendula*, *M. monstrosus* and *P. airoides*) and the Mediterranean (*Av. barbata*). As the abiotic conditions in Western Australia are similar to those in which these species evolved (a Mediterranean climate), these exotic species likely arrived with traits well adapted to the abiotic conditions in this invaded range, making it unlikely that the abiotic environment has major negative impacts on the performance of these species in south-west Western Australia. As previous studies have not, however, compared the biotic communities in the native and exotic Australian ranges of these species, this was an interesting system to specifically explore the importance of coarse evolutionary relatedness to interaction outcomes.

*Experimental design*

Phylogenetic relatedness of interacting species was manipulated within small interaction neighbourhoods in natural assemblages containing each of the focal species in West Perenjori Reserve. Neighbourhoods were assigned one of five treatments, each defined by a range of average phylogenetic distance (i.e. time since divergence) values between neighbouring species and the focal species. These ranges were based on the phylogeny of all annual plant species in the whole community (Appendix S1). Unlike the annual Poaceae species in this system, which are all exotic, there are both native and exotic Asteraceae species. Although all in the same family, the exotic Asteraceae focals are likely to be more distantly related (share less evolutionary history) with the native Asteraceae than to each other, since they originated elsewhere in the world and have only coexisted with the native species since they invaded Australia. To account for this, we set up two separate closely related ‘close’ treatments for the Asteraceae focals (see Table 1). In addition to a ‘control’ treatment, in which the natural assemblage of neighbours was not manipulated, a ‘thinned control’ treatment was set up to account for the effects of density, in which we thinned neighbourhoods to similar densities of the close, intermediate and distant treatments. Replication for each species x treatment combination varied due to the availability of species combinations within natural assemblages across the reserve (see Table 1).

Plots containing one replicate of each treatment were no larger than 4 x 4 m and were spaced at least 10 m apart. Plots were located within four blocks no larger than 200 x 200 m across the reserve. In cases where plots were larger than 2 x 2 m, we split the plot into quadrants, enabling us to test for differences between quadrants during analyses. Subplot interaction neighbourhoods were 15 x 15 cm surrounded by a 10 cm cleared buffer (n=218). Including this buffer ensured that these plants were interacting primarily with others in their neighbourhood. This neighbourhood and buffer size were chosen based on previous research on the annual species in this system that found that reproductive output was impacted only by interactions with neighbouring individuals located within a few centimetres of a focal individual (Martyn, unpublished data). Following the initial setup, treatment neighbourhoods (excluding controls) contained one focal individual with 3-5 neighbours from 1-5 species. However, mortality of neighbours early in the growing season (prior to reproduction) resulted in some treatment plots containing only two neighbours (n=7). New germinants were removed throughout the length of the growing season to ensure treatments were maintained as originally established throughout the full life cycle of the focal plants.

To assess fitness outcomes within each interaction neighbourhood we measured reproductive output (as a proxy for fecundity) for each focal individual. For all species except *Ar. calendula*, reproductive output was measured as the number of developed seeds (‘seed count’ hereafter). As *Ar. calendula* seeds disperse quite rapidly, there were many instances where inflorescences had clearly developed seeds but they had dispersed before collection was possible. To account for this, we instead used the number of seed producing inflorescences (‘inflorescence count’ hereafter) as a measure of reproductive output. For the seeds we were able to collect, we found a strong correlation between number of seeds and number of seed producing inflorescences (R2 = 0.85), supporting the use of inflorescence count as a proxy for fecundity in *Ar. calendula.* Neighbour identity and density was recorded for finer scale measurements of phylogenetic relatedness within each treatment category (see below). We also measured several environmental variables which have previously been identified as important for structuring diversity and defining niche space in this system (Dwyer et al. 2015). Canopy cover and soil phosphorus were measured at the relevant plot or quadrant level, and crust presence and litter and woody debris cover were measured at subplot level. Levels of herbivory and pathogen infection were also recorded for each focal plant.

**Investigating the native range communities (Q2+3)**

To better understand the native distribution of each species, we consulted both published literature and global occurrence data. Guided by the Global Index of Vegetation-Plot Databases (Dengler et al. 2011), we contacted database owners in regions where the focal species are native and obtained four separate databases to use in our analyses (see Appendix S3). From these databases we gathered survey data (in the form of species lists) of plant communities from all plots containing our focal species. For *Ar. calendula* and *P. airoides*, we also collected data collected from published literature (see Appendix S3). For consistency, only plots less than or equal to 10 x 10 m were included in the final datasets of each species.

As previously discussed, there are many ways in which you can measure phylogenetic relatedness between species. Molecular-based approaches, looking specifically at similarities in DNA/RNA base pairs for specific genes between species, are particularly important for understanding more recent evolutionary divergences and splits among genera and species. As the focus of this study is on deep evolutionary history, with a focus on family and deeper splits, it is less necessary to use such well resolved phylogenies. Further, due to limited research, well resolved genetic-based terminal phylogenies are simply unavailable for the clades examined in this study. As such, we used time since divergence (‘phylogenetic distance’ hereafter) as a measure of phylogenetic relatedness between pairs of taxa at the family level. This is not an uncommon method in invasion studies looking at phylogenetic-based metrics (e.g. Castro et al. 2014). Although other indices such as net relatedness index (NRI) and nearest taxon index (NTI) (Webb 2000, 2002) could be used in such coarse scale cases, these metrics are based on number of nodes, which is problematic as nodal-distance is highly dependent on a reference phylogeny and is sensitive to variability in clade species richness (Webb 2000). As we are working with thousands of species, simple time since divergence values were deemed more appropriate for this study.

For all species included in our invaded community experimental data and native range data, we attained phylogenetic distance values for each focal-neighbour species’ pair using the Time Tree online database (Kumar et al. 2017). This database combines information from all available published data to give the best estimate of divergence time. Using these values, we calculated average neighbour phylogenetic distance values (‘ANPD’ hereafter) for each plot and focal species. ANPD was the metric used for all non-treatment-based analyses throughout the study (see below).

**Data analysis and statistics**

Statistical analysis was performed in R (R Core Team 2021). To address our three major questions, we conducted several analyses testing four null hypotheses. Due to our knowledge of the complex relationship between relatedness and competitive outcomes, null hypotheses were deemed appropriate here as we expected potentially contrasting effects of relatedness, which is difficult to capture with predictive hypotheses.

For question 1, our experimental design allowed us to quantify relatedness in both a categorical and continuous matter, i.e. through treatments and ANPD values of interactions neighbourhoods. Consequently, we ran two separate analyses testing the following two null hypotheses:

H0 1: There is no effect of relatedness treatment on focal species reproductive output.

H0 2: There is no effect of ANPD on focal species reproductive output.

For null hypothesis 1, the effect of relatedness treatment (i.e. close, intermediate and distant relatedness) was evaluated based on comparison of reproductive output with the control treatments. As we had both unthinned and thinned controls, rejection of the null hypothesis required finding a significant effect of a relatedness treatment with reference to both control treatments. Due to difficulty finding patches where *Av. barbata* and its ‘intermediate’ treatment species existed together (two replicates, Table 1), we excluded the species’ ‘intermediate’ neighbourhoods in the treatment-based analysis for this species (H0 1). These ‘intermediate’ neighbourhoods were, however, included in the ANPD analysis (H0 2) in which specific treatment allocation was unimportant.

For question 2, we tested the following null hypothesis:

H0 3: There is no difference between phylogenetic relatedness of communities in the native and invaded ranges.

Failure to reject this null hypothesis would support our expectation of similar phylogenetic relatedness to neighbours within the native and invaded ranges.

As for question 3, we tested the following null hypothesis:

H0 4: There is no association between ANPD values of the native communities and focal species interaction outcomes in the invaded community.

For null hypotheses 1, 2, and 4, refer to Figure 1 for examples of expected results that would allow us to reject each null hypothesis.

*Invaded community analyses (Q1: H0 1+2)*

For all analyses described below we excluded replicates in which the focal individual was still alive at the point of final seed collection/inflorescence count (n=10). This ensured we were not underestimating reproductive output for any individual that had not yet completed its life cycle.

To test null hypothesis 1, we analysed the effect of treatment on focal species reproductive output using generalized linear mixed effects models with negative-binomial errors and log link function. Models were initially fitted and evaluated with the following random effects: block, plot and quadrant as well as neighbour richness or density (both highly correlated). Due to issues with identification, some interaction neighbourhoods contained new-germinant perennial species, and so to account for this we also fitted models including the presence of perennials as a random effect. The fit of these models was assessed using the Akaike Information Criterion with small sample correction (AICc). ‘Among plot’ as a random intercept appeared to explain important variance and therefore was included in both *Ar. calendula* and *M. monstrosus* treatment-basedmodels*.*

To evaluate treatment effects, we compared model estimates using both thinned control and control treatments as reference groups, both representing a random assortment of species (Table 2). To ensure these treatment replicates represented a random assortment of species we assessed each for its finer scale measure of average neighbour phylogenetic distance (ANPD). Using both visual and computational analyses (see Appendix S2), we excluded outlying plots that were more closely or distantly related than a random assortment of species: one thinned control treatment for each of *A. calendula, M. monstrosus*, and *A. barbata* (Appendix S2: Figure S1).

To test null hypothesis 2, we followed the same methods for testing null hypothesis 1 but using treatment-independent ANPD values as the explanatory variable. This allowed us to capture relatedness values from within the control and thinned control plots originally ignored in the treatment-based analysis. Removing the intricacies of the ‘close 1’ and ‘close 2’ treatments for Asteraceae focals enabled us to test for the effects of relatedness independent of identity per se. As we had abundance values for each neighbour species, we were able to calculate ANPD values both including and excluding abundance, resulting in two separate models per focal species (Table 3). As with the treatment-based analyses, ‘among plot’ was included as a random intercept in both *Ar. calendula* and *M. monstrosus* ANPD-basedmodels. Additionally, ‘neighbour density within plot’ was included as a random slope in the models for *Av. barbata*.

*Native range analyses (Q2+3: H0 3+4)*

Based on the species lists collected from the native ranges we calculated ANPD values for all herbaceous species in each plot. As we did not have abundance data for each species, ANPD for each plot was calculated excluding abundance. Beyond mean and minimum/maximum values, to better describe the range of ANPD values calculated from native range plots, we constructed density plots. This allowed us to understand the distribution of values across the entire possible 0-160 million year range.

As survey data from the native communities were based on plots of different sizes from different locations, and contained different amounts of information on species, we conducted several preliminary assessments of the survey data. Firstly, we assessed the distribution of ANPD values based on plot size and location. For all focal species, plot size did not have a large effect on the distribution of ANPD values. This was similar for plot location, excluding *Av. barbata*, where there were slight differences between datasets from different countries, with a maximum difference in country ANPD means of 39 million years. Secondly, we assessed differences in the distribution of native range ANPD when including or excluding exotic species. As some of the exotic species present in these plots may have only recently established in that location, it is possible that they were not present in the selective environment of the focal exotic species’ native populations before they invaded Australia. Finally, as species lists contained individuals identified to the genus or family level, for which we could not discern details on growth habit (herb/shrub etc.) or native/exotic status, we also compared ANPD value distributions including or excluding these unknowns. Including exotic and unknown species did not affect native range ANPD distributions for all focal species, therefore, results presented here are based on analyses including all species (natives, exotics and unknowns).

To test null hypothesis 3, we assessed whether phylogenetic relatedness values in the invaded community - the location of the field experiment - matched phylogenetic relatedness in the native communities of each focal species. To measure phylogenetic relatedness in the invaded community, we calculated focal specific ANPD of all known annual plant species in West Perenjori Nature Reserve (see Appendix S1). For each species we then simply examined where this ANPD value sat within the distribution of ANPD values from native range plots.

To test null hypothesis 4, we assessed whether there was an association between native range phylogenetic relatedness and focal species interaction outcomes in the invaded community. To do this we looked at whether there was any ‘matching’ between the distribution of native range ANPD values and reproductive output as a function of abundance-independent ANPD from the invaded community experimental plots (Q1: H0 2) (e.g. in Figure 1C). Although we were unable to attain performance measures of the focal species in the native range plots, directly comparing interaction outcomes between native and invaded communities would be a valuable future study.

**Results**

**The effect of relatedness treatment on focal species reproductive output (Q1: H0 1)**

Relatedness treatment had generally weak effects on focal species reproductive output. For all species, there were clear differences between group model estimates, in magnitude, direction and statistical significance, when control and thinned control treatments were used as reference groups (Table 2).

*Ar. calendula:* Focal reproductive output in the ‘close 1’ treatment (those with exotic Asteraceae neighbours) was significantly higher than in the control treatment (p=0.03) but did not differ significantly from the thinned control treatment (Table 2). Reproductive output was also significantly different between the two control treatments (p=0.02), with lower inflorescence count in the control treatment compared to the thinned control treatment (Table 2).

*M. monstrosus*: Only focal individuals in the ‘close 2’ treatment (those with native Asteraceae neighbours) had significantly lower reproductive output than those in the thinned control treatment (p=0.01, Table 2). Similarly, although not statistically significant (p=0.2), focals in ‘close 2’ treatment had lower reproductive output than focals in the control treatment (large and negative coefficients, Table 2). Although not significant, reproductive output in the ‘close 1’ treatment was higher than in both control treatments (positive and relatively large coefficients, Table 2).

*P. airoides*: Focal reproductive output was lowest in the ‘close’ treatment compared to the controls, however this was only significant when compared to the control treatment (Table 2, p=0.04). Reproductive output in the ‘distant’ treatment, although not significant, was positive and large compared to either control treatments (Table 2).

*A. barbata*: There was no significant effect of treatment on focal reproductive output (Table 2). However, although not significant, reproductive output appeared lower for focals in the control treatment compared to the thinned control treatment (a large and negative coefficient, p=0.09, Table 2).

**The effect of ANPD on focal species reproductive output (Q1: H0 2)**

Although species specific, ANPD had generally weak effects on focal species reproductive output (Table 3). For all species, there were no differences between significance values for models of ANPD when calculated either including or excluding neighbour species abundances (Table 3). For both *M. monstrosus and Av. barbata,* ANPD did not significantly affect reproductive output, with model coefficients of almost 0 (Table 3, Figure 2B(ii) and 2D(ii)). Although a similar non-significant relationship was found for *Ar. calendula,* model coefficients were negative and slightly larger with almost significant p-values (p=0.09 and p=0.07, including and excluding abundances respectively, Figure 2A(ii)). For *P. airoides*, an increase in ANPD was significantly associated with an increase in focal reproductive output (Table 3, Figure 2C(ii)).

**The similarity of ANPD between the native and invaded range communities (Q2: H0 3)**

ANPD between the native and invaded range communities were generally quite different. The ANPD for West Perenjori Reserve (the invaded community) was 63 million years for the Asteraceae focals (*Ar. calendula* and *M. monstrosus)* and 147 million years for the Poaceae focals (*P. airoides* and *Av. barbata)*. For all species, ANPD values from the invaded community sat outside (*Ar. calendula*, *M. monstrosus* and *P. airoides)* or just on the edge (95th percentile, *Av. barbata*) of the ANPD distribution from plots in the native range (Figure 2A-D(i)). The differences between mean native range ANPD and invaded community ANPD was greatest for the two Asteraceae focals, with invaded community ANPD sitting at 37 million years lower than their mean native range ANPD values of 100 million years (Figure 2A-D(i)). In contrast, ANPD for the Poaceae focals was 34 and 17 million years higher in the invaded community than the mean native range ANPD values of 113 and 130 million years for *Av. barbata* and *P. airoides,* respectively.

**The association between native range ANPD and focal species interaction outcomes in the invaded community (Q3: H0 4)**

Although species specific, there was generally a weak association between native range ANPD and focal species interaction outcomes. For *Ar. calendula, M. monstrosus* and *Av. barbata* there was no association between native range ANPD values and interaction outcomes (Figure 2 A, B and D). Contrastingly, the distribution of ANPD values from native range plots matched interaction outcomes for *P. airoides*. That is, reproductive output for *P. airoides* in the invaded Western Australia site was higher at ANPD values similar to those observed in this species’ native range, specifically, in plots where neighbours were distantly related (Figure 2C).

**Discussion**

Although species specific, the overall findings of this study suggest that there is limited evidence for an effect of phylogenetic relatedness on exotic species fitness outcomes in the invaded annual plant community of West Perenjori Reserve. In incorporating information from the native range, we found that phylogenetic relatedness of exotics species to neighbours in their native communities was neither similar to phylogenetic relatedness to neighbours in the invaded community, nor was it associated with their fitness outcomes in the invaded community, with the exception of one focal species.

**How does phylogenetic relatedness of exotic species to neighbours in their invaded communities impact their fitness outcomes?**

From the treatment-based analysis we found a lack of significant treatment effects on reproductive output compared to both control and thinned control treatments, and therefore we were unable to reject null hypothesis 1 for all species. Although we removed outlying control plots, that were either too close or too distantly related compared to a random assortment of species in the system, it is important to recognise that even a random assortment of species from any natural system has a phylogenetic signal. This is particularly relevant for the annual plant system chosen for this experiment, which is dominated by dicots. This means that for monocot and dicot focals, a natural assortment of species in this system is going to be more distantly and closely related, respectively, than a random assortment of species. Consequently, results from treatment-based analyses cannot be used in isolation when drawing conclusions about the effects of deep phylogenetic relatedness on the outcome of species interactions. A benefit of our analytical approach is that our ANPD analysis removed this treatment group effect and simply used relatedness on a continuous scale, dissolving any structure to the data created by our experimental design that was reliant on naturally assembled communities. In combining information from both analyses, the specific significant effects found within the treatment-based analysis help us to understand some of the patterns we see in our ANPD-based analysis, potentially unveiling other important factors that drive interaction outcomes for these species and in general.

For *Ar. calendula*, although negative, the effect of ANPD on reproductive output, both including and excluding abundance, was not statistically significant (Table 3, Figure 2A(ii)). As such, we failed to reject null hypothesis 2 for this species. Although focal plants in the ‘close 1’ treatment (those with exotic Asteraceae neighbours) had significantly higher reproductive outputs than those in the control treatment, potentially driving the slightly higher reproductive output we see for low ANPD values (Figure 2A(ii)), focal plants in that same treatment had similar reproductive outputs to those in the thinned control treatment (model coefficient of almost 0, Table 2). All other treatment coefficients were highly variable between control and thinned control reference groups (Table 2). Further, focal plants from the control treatment had significantly lower reproductive outputs than those in the thinned control treatment (Table 2). These differences in reproductive outcomes between control treatments, that differ primarily in their densities, suggest that there is a density effect for this species that is independent of phylogenetic signal. As past studies of plant interactions in other systems have found evidence of this density effect (e.g. Zhang and Tielbörge 2020), further study should investigate its importance in driving interaction outcomes for *Ar. calendula*.

For *M. monstrosus*, there was no significant effect of ANPD on reproductive output, meaning we failed to reject null hypothesis 2 (Table 3, Figure 2B(ii). The differing results between ‘close 1’ and ‘close 2’ treatments for this species (Table 2) suggest that neighbour identity, in the sense of native or exotic status, rather than relatedness, potentially drives interaction outcomes for this species. It is possible that *M. monstrosus* is competing more strongly with invaded range residents that are native compared to exotic. Similar evidence of this differential response has been shown for other exotic species. For example, the negative effect of smooth brome (*Bromus inermis*) on species richness in its invaded communities was found to be higher for native resident species compared to exotics (Stotz et al. 2017 and see Gooden et al. 2009, Bernard‐Verdier and Hulme 2015). However, the mechanism behind this differential response remains largely unknown (Stotz et al. 2017). Further investigation into the interaction response of *M. monstrosus* with other natives and exotics, outside of the Asteraceae family, could reveal similar differential patterns, a result that is likely important for understanding how to effectively manage this exotic species.

For *P. airoides*, the effect of ANPD on reproductive output was significant, allowing us to reject null hypothesis 2 (Table 3, Figure 2C(ii)). For this species, we found lower reproductive output in neighbourhoods of closely related species, and therefore conclude that neighbour phylogenetic relatedness does impact interaction outcomes for *P. airoides*. Although these results are consistent with the competition-relatedness hypothesis, that species more closely related compete more strongly (Webb et al. 2002), further examination of functional traits within relevant species combinations are needed to be confident about this conclusion. Without further analysis, other mechanisms could also explain the observed relationship. For instance, if we were to find that important functional traits are phylogenetically convergent, an outcome in which distantly related species occur together more frequently could be explained by habitat filtering rather than competitive exclusion of functionally similar, closely related species (Webb 2002, Cavender-Bares et al. 2004).

For *Av. barbata*, there was no significant effect of ANPD or relatedness treatment on reproductive output, meaning we failed to reject null hypothesis 2. These results indicate that factors other than relatedness are likely important for this species. The almost statistically significant differences in reproductive output between the two control treatments, that differ primarily in their densities, suggest that there may be a density effect for this species. Such a density effect may explain why density included as a random effect did explain important variation in ANPD-based models for *Av. barbata* (variance=0.21). Further study should investigate the importance of density in driving interaction outcomes for this species.

Across the four species we observed variable effects of coarse phylogenetic relatedness on fitness outcomes. Our findings are consistent with both studies that have found a positive relationship between fitness outcomes and relatedness (as with *P. airoides,* e.g. Allan et al. 2013, Park and Potter 2013) and studies that have found no relationship (as with the other three focal species, e.g. Cahill et al. 2008, Bennett et al. 2013). In terms of comparing results between and within monocot and dicot groups, we found no pattern between species. This lack of pattern conflicts with existing literature with some studies finding different responses between monocot and dicot focals (e.g. Cahill et al. 2008). However, as we only analysed two species from each group, repeating our experiment with more species would be needed to determine the generalisability of our results.

**How similar is phylogenetic relatedness of exotic species to neighbours in their native and invaded communities?**

Phylogenetic relatedness to communities in the native range was overall quite different than that in the invaded WA community, with ANPD from West Perenjori Reserve falling either outside or on the very edge of native range ANPD distributions for all species (Figure 2A-D(i)). As such we rejected null hypothesis 3 for all species. These results suggest that both Asteraceae and Poaceae focals came from native locations likely containing more distantly related monocots (i.e. grasses) than West Perenjori Reserve. Although these results indicate a lack of similarity between exotic species-specific phylogenetic relatedness to native and invaded plant communities, it is critical we interpret such results considering some of the limitations often prevalent in these large scale, data dependent studies.

As with any study using survey data from multiple sources and locations, careful consideration must be given to the specific sampling methods used and the scale at which that sampling occurred. Data available and used in this study was based on plant communities surveyed at three separate scales. The invaded community ANPD values were calculated based on a list of species across the entire reserve (>2km2), native range community ANPD values were calculated based on plots ranging from 0.5 to 100m2 and ANPD values for experimental neighbourhoods were calculated based on plots approximately 0.02m2 in size. What is particularly concerning about this variability is that several studies have shown that community phylogenetic patterns are strongly spatially dependent (Jin et al. 2020). It is frequently observed that neighbouring individuals tend to be distantly related at smaller spatial scales (e.g. directly surrounding a focal individual), but closely related at larger spatial scales, with evidence of phylogenetic clustering at these larger scales (Cavender-Bares et al. 2006, Swenson et al. 2007, Parmentier et al. 2014).

With the composition of species changing from smaller to larger scales, the value of ANPD calculated based on a focal species is likely going to be different whether it is including the plants immediately surrounding it, or 5 metres away from it. Consequently, our interpretation of the association between native range ANPD and invaded community fitness outcomes (see below) is most valuable when calculating ANPD on the same spatial scale. The same thing can be said regarding using a species list from across the entire reserve to calculate a general invaded community ANPD. Given our understanding of environmental niches, it is unlikely that our focal exotic species are interacting with all of the species in the reserve. Ideally, we would be able to sample the native range and invaded communities at similar scales to those in the experimental neighbourhoods. To ensure that the entire range of neighbouring species the focal species is interacting with is detected, it is crucial that this finer scale sampling occurs across the entire location and that species lists are averaged across sampling plots. Although such spatial biases were unavoidable for this particular study, due to limitations in data availability, it is critical that future studies investigating differences in biotic communities between the native and invaded range, use data collected at similar spatial scales, or at least take any differences into consideration when drawing their conclusions.

Although we often know the general region of the world where a species is native, for example, the Mediterranean, without extensive genetic sampling we are usually unable to define the exact region and origin, and from which population, an exotic species originated. Consequently, it is common practice to sample across the entire native range, ensuring that the native source population is likely well represented within the broad regional survey (e.g. Escoriza and Ruhí 2016). This method is unlikely to be problematic for species with very small native ranges, for example the cape provinces of South Africa for both Asteraceae focals as well as *P. airoides*. However, for species such as *Av. barbata*, whose native range description includes several countries, it is difficult to conclude that sampling throughout that entire range is providing data that is a reasonable estimate of the native source population from which this exotic species population originated. Beyond simple geographical distance, it is possible that slight differences in microclimates could be driving some of the differences we see in species compositions and therefore ANPD across the native range. Evidence of variation in the distribution of ANPD values for *Av. barbata* in each native country (maximum mean difference of 39 million years) further highlights this. Not knowing the exact source location limits how we can use native range information to understand biotic interactions and invasion impacts in the invaded range.

In much the same way there is variation in biotic communities across the native range, there is also variation in the communities an exotic species is interacting with across its invaded range. In this study, we measured ANPD and its effects on fitness outcomes for each species in a single reserve. ANPD in this region of the invaded range appeared quite different to that of the native range, however this may not be the case for other locations. Given the likely variability in climatic conditions, soil properties and levels of disturbance across a species' entire invaded range (often across multiple continents), you would expect to find differences between the communities an exotic species resides in. As the extent to which we could investigate the questions addressed in this study was limited (one location), exploring phylogenetic relatedness patterns across the entirety of the invaded range may provide additional valuable insight into why exotic species vary so greatly in the ways they interact with and impact resident communities.

**Is there a relationship between phylogenetic relatedness of exotic species to neighbours in their native communities and fitness outcomes in their invaded communities?**

Our results provide weak evidence for an effect of phylogenetic relatedness of exotics to neighbours in their native communities on their fitness outcomes in the invaded community. As we did not see a significant effect of coarse phylogenetic relatedness on fitness outcomes for *Ar. calendula, M. monstrosus* and *Av. barbata*, this third question pertained only to *P. airoides*.

For *P. airoides*, reproductive output was highest at large ANPD values (i.e. distantly related) (Figure 2C(ii)). As the distribution of ANPD values from the native range is left skewed, meaning most ANPD values were quite high, there does appear to be evidence of “matching” between the native range and exotic species interaction outcomes. It is possible that as this species has come from a biotic community dominated by distantly related species, it achieves higher fitness when competing with neighbours that are also distantly related. However, as we know this interaction outcome is consistent with the competition-relatedness hypothesis, it is difficult to conclude whether this effect was due to similarities between the native and invaded communities, or due simply to competitive exclusion (and lower focal plant fitness) in closely related neighbourhoods. In other words, does this species perform better in distantly related neighbourhoods in its invaded range because it originated in distantly related communities (and therefore evolved to interact with distantly related neighbours), or does this species perform better in distantly related neighbourhoods simply because it is functionally dissimilar to distantly related neighbours (irrelevant to its native communities). As mentioned previously, further research examining functional traits between species pairs is needed to fully understand the observed pattern for this species.

**Conclusion**

The competition-relatedness hypothesis, as it applies to invasion ecology, predicts that exotic species that share more evolutionary history (i.e. are more phylogenetically related) with neighbours in their invaded range compete more strongly with them. In investigating this hypothesis for four exotic annual plant species, with a focus on phylogenetic relatedness measured at coarse scales, we found weak but mixed evidence. Further, using information on phylogenetic relatedness of exotic species to their native range communities provided limited insight into invaded range interaction outcomes. Beyond the competition-relatedness hypothesis, future research focussed on incorporating information from the native range may uncover important factors that help explain why exotic species vary so greatly in the ways they interact with native resident communities. In addition to improving our fundamental understanding of invasion dynamics, such research may also improve our ability to predict and manage the impacts of exotic species on the earth’s biodiversity.

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**Figures and Tables**

**Table 1: The range of average neighbour phylogenetic distance values and focal species-specific replication for each relatedness treatment.** For Asteraceae focals, close treatments 1 and 2 refer to neighbourhoods containing only exotic and native neighbours, respectively. Values of replication indicate those included in final analyses.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Treatment | | Average neighbour phylogenetic distance (myr) | Number of replicates per focal species | | | |
| *Arctotheca calendula* | *Monoculus*  *monstrosus* | *Pentameris airoides* | *Avena*  *barbata* |
| Close | Close Poaceae | 10.9-50 | - | - | 10 | 11 |
| Close 1 Asteraceae  (exotics) | 31-39 | 10 | 10 | - | - |
| Close 2 Asteraceae  (natives) | 38.2-39 | 9 | 9 | - | - |
| Intermediate | | 62-117 | 9 | 10 | 6 | 2 |
| Distant | | 160 | 9 | 10 | 10 | 12 |
| Control | | NA | 10 | 10 | 10 | 12 |
| Thinned control | | NA | 10 | 10 | 9 | 10 |

Myr, million years.

**Chart

Description automatically generated**

**Figure 1: Conceptual expectation of results that would allow us to reject the null hypotheses.** A) For null hypothesis 1, showing higher fitness when competing with phylogenetically dissimilar neighbours (i.e. those is the distant treatment) compared to a random assortment of neighbouring species (e.g. those in the control treatment). B) For null hypothesis 2, showing increasing fitness as a function of increasing average neighbour phylogenetic distance (ANPD). C) For null hypothesis 4, showing two cases (species A and B) of an association between (ii) fitness outcomes as a function of ANPD within experimental plots and (i) the distribution of ANPD values from native range plots (represented as a density plot). Myr, million years.

**Table 2: Effects of phylogenetic relatedness treatments on focal species reproductive output using generalised linear models.** Values indicate model coefficients and (SEs) with reference to either the control or thinned control experimental treatments. Where applicable, variance estimates are reported among plots, which was specified as a random effect. For Asteraceae focals, close treatments 1 and 2 refer to neighbourhoods containing only exotic and native neighbours, respectively. Asterisks denote level of significance (\*p ≤ 0.05, \*\*p < 0.01, \*\*\*p < 0.001).

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  | | Focal species | | | | | |
| *Arctotheca calendula* | *Monoculus monstrosus* | | *Pentameris*  *airoides* | | *Avena*  *barbata* |
| Response variable | | | | | | | |
|  | | Inflorescence count | | Seed count | Seed count | Seed count | |
| Random effects | | | | | | | |
| Among plot | | 0.08 | | 0.75 | - | - | |
| Fixed effects: Reference group = Control | | | | | | | |
| Intercept | | 1.51 (0.21) \*\*\* | | 2.35 (0.46) \*\*\* | 6.28 (0.32) \*\*\* | 3.11 (0.16) \*\*\* | |
| Thinned control | | 0.58 (0.26) \* | | 0.46 (0.54) | -0.27 (0.47) | 0.43 (0.25) | |
| Close | Close 1 (exotics) | 0.54 (0.25) \* | | 0.68 (0.53) | -0.96 (0.46) \* | 0.17 (0.24) | |
| Close 2 (natives) | 0.24 (0.27) | | -0.71 (0.55) |
| Intermediate | | -0.09 (0.28) | | 0.04 (0.52) | -0.77 (0.53) | - | |
| Distant | | 0.11 (0.27) | | 0.03 (0.52) | 0.40 (0.46) | 0.28 (0.23) | |
| Fixed effects: Reference group = Thinned control | | | | | | | |
| Intercept | | 2.09 (0.20) \*\*\* | | 2.81 (0.47) \*\*\* | 6.01(0.34) \*\*\* | 3.53 (0.19) | |
| Control | | -0.58 (0.26) \* | | -0.46 (0.54) | 0.27 (0.47) | -0.43 (0.25) | |
| Close | Close 1 (exotics) | -0.03 (0.24) | | 0.22 (0.52) | -0.67 (0.47) | -0.25 (0.25) | |
| Close 2 (natives) | -0.34 (0.26) | | -1.12 (0.55) \* |
| Intermediate | | -0.66 (0.27) \* | | -0.42 (0.53) | -0.50 (0.54) | - | |
| Distant | | -0.47 (0.26) | | -0.43 (0.52) | 0.67 (0.47) | -0.14 (0.25) | |

All models used a negative binomial distribution and log link function.

**Table 3: Effects of average neighbour phylogenetic distance (including and excluding species’ abundances) on focal species reproductive output using generalised linear models.** Values indicate model coefficients and (SEs) for average neighbour phylogenetic distance values calculated to the family level either including or excluding species’ abundances (separate models). Where applicable, variance estimates are reported for the random effects of among plot and neighbour density within plot. Asterisks denote level of significance (\*p ≤ 0.05, \*\*p < 0.01, \*\*\*p < 0.001).

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Focal species | | | | | |
| *Arctotheca calendula* | *Monoculus monstrosus* | | *Pentameris*  *airoides* | | *Avena*  *barbata* |
| Response variable | | | | | | |
|  | Inflorescence count | Seed count | | Seed count | | Seed count |
| Including species’ abundances | | | | | | |
| Fixed effects: | | | | | | |
| Average neighbour  phylogenetic distance | -0.14 (0.08) | -0.001 (0.15) | 0.46 (0.17) \*\* | | -0.01 (0.07) | |
| Random effects: | | | | | | |
| Among plot | 0.09 | 0.67 | | - | | - |
| Neighbour density within plot | - | - | | - | | 0.21 |
| Excluding species’ abundances | | | | | | |
| Fixed effects: | | | | | | |
| Average neighbour  phylogenetic distance | -0.15 (0.08) | -0.03 (0.15) | | 0.01 (0.003) \*\* | | -0.01 (0.06) |
| Random effects: | | | | | | |
| Among plot | 0.08 | 0.66 | | - | | - |
| Neighbour density within plot | - | - | | - | | 0.21 |

All models used a negative binomial distribution and log link function.

Chart, line chart

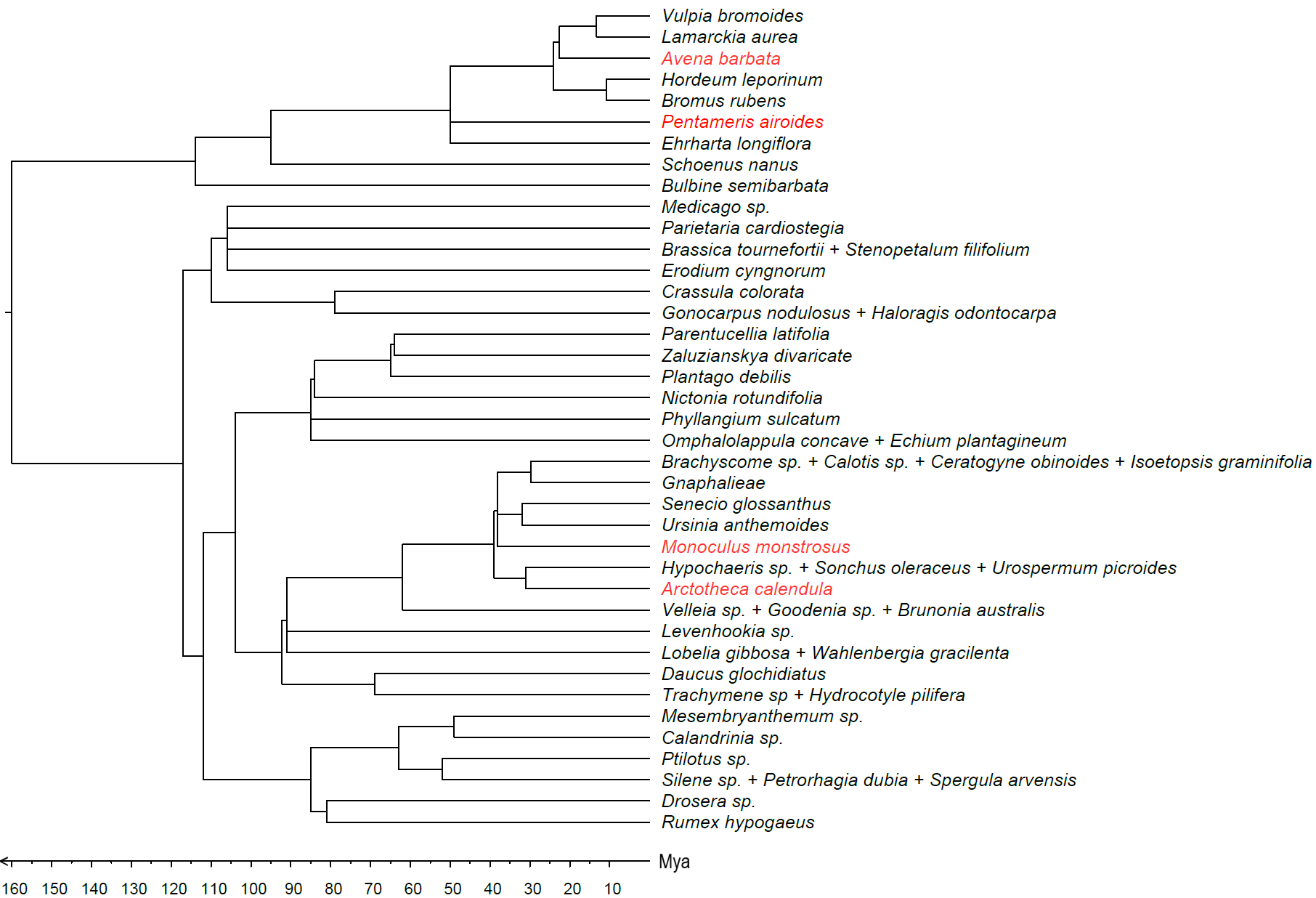
Description automatically generated

**Figure 2:** For each focal species A) *Arctotheca calendula*, B) *Monoculus monstrosus*, C) *Pentameris airoides* and D) *Avena barbata*, panels present (i) the distribution of average neighbour phylogenetic distance (ANPD) values calculated from surveyed plots in the native range (represented using a density plot) and (ii) reproductive performance (species specific) as a function of ANPD. All values of ANPD included here were calculated to the family level excluding neighbour species abundances. Dotted black lines in panels (i) represent focal specific ANPD values for West Perenjori Nature Reserve (the invaded range community). Grey shading in panels (ii) represents 95% confidence levels. Myr, million years.

**Supporting Information**

**Appendix S1:**

***Phylogenetic relationships between all annual plant species in the invaded community***



**Figure S1: Unresolved time-tree of all known annual plant species in West Perenjori Nature Reserve, Western Australia**. Focal species of the study are indicated in red. Divergence times between taxa pairs used to generate the tree were estimated using the Time Tree online database (Kumar et al. 2017). Mya, million years ago.

**Appendix S2:**

***Control plot testing***

To ensure the control and thinned control treatment replicates represented a random assortment of species we assessed each for its finer scale measure of average neighbour phylogenetic distance (ANPD), calculated to the family level. Experimental plot ANPD values were compared to the range of ANPD values from surveyed plots randomly sampled 100 times for plot specific densities and averaged. The survey data used for each species was based on surveys of 30 x 30 cm plots in West Perenjori and Kunjin Nature Reserves, Western Australia, in 2011 (see Dwyer et al. 2015). Outlier plots were excluded from the treatment-based analysis if they were noticeably different from others in the same treatment (visual assessment) and if they sat outside of the range of both ANPD values (including and excluding abundance) for each plot (computational assessment) (see Figure S1).

Diagram

Description automatically generated

**Figure S1:** **Results from testing for outlying control and thinned control experimental plots using values of average neighbour phylogenetic distance (ANPD) calculated to the family level both including and excluding abundance for each focal species.** Experimental plot ANPD values (blue or red) are overlaid on top of boxplots of ANPD values from the survey plots. Plots with points coloured red were identified as outliers (see Appendix S2 for details). Missing plot values indicate the data were excluded prior to testing. Myr, million years.

**Appendix S3:**

***Information on data collected from the native range communities***

**Table S1: Information on data from the native range plots for each focal species.**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Focal species | | | |
| *Arctotheca*  *calendula* | *Monoculus monstrosus* | *Pentameris*  *airoides* | *Avena*  *barbata* |
| Total plots | 43 | 113 | 28 | 954 |
| Survey time period | 1988-2019 | 2008-2018 | 1988-2008 | 1957-2017 |
| Plot sizes | 5 x 5 m (26 plots)  10 x 10 m(17 plots) | 5 x 5 m (44 plots)  10 x 10 m(69 plots) | 10 x 10 m | 0.7 x 0.7 m –  10 x 10 m |
| Plot locations | Northern and  Western Cape,  South Africa | Northern and  Western Cape,  South Africa | Western Cape,  South Africa | Spain, Italy, Portugal, Greece, France, Albania |
| Mean ANPD  (min-max) | 100 (70-146) | 100 (71-126) | 130 (81-146) | 113 (0-160) |
| Mean species richness  (min-max) | 25 (14-41) | 24 (10-47) | 22 (9-32) | 26 (1-96) |
| Included databases | BIOTA | BIOTA | BIOTA | SIVIM, VDCNP, VDHI |

Mean, minimum and maximum values for average neighbour phylogenetic distance (ANPD) and species richness were calculated including all herbaceous species (natives, exotics, and those with unknown growth habits). All databases were identified using the Global Index of Vegetation-Plot Databases (Dengler et al. 2011). For *Ar. calendula* and *P. airoides*, we also collected data from published literature (Joubert and Moll 1992).

BIOTA: Biodiversity Monitoring Transect Analysis in Africa (email contact: [Ute.Schmiedel@uni-hamburg.de](mailto:Ute.Schmiedel@uni-hamburg.de))

SIVIM: Iberian and Macaronesian Vegetation Information System (email contact: [xfont@ub.edu](mailto:xfont@ub.edu))

VDCNP: Vegetation Database of the Cilento National Park (email contact: [leonardo.rosati@unibas.it](mailto:leonardo.rosati@unibas.it))

VDHI: Vegetation Database Habitat of Italy (email contact: [michele.desanctis@uniroma1.it](mailto:michele.desanctis@uniroma1.it))