**Title:** Looks can be deceiving: ecologically similar exotics have opposite impacts on native competitor

**Running head (45 character max.):** Similar exotics have opposite impacts

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**Summary**

* While functional trait differences among native and exotic species have been linked to invasion outcomes, there is substantial variation in the strength of this relationship across natural plant communities. This variation arises because of abiotic and biotic contingencies that determine when trait differences affect invasion success. As a result, interaction outcomes are difficult to predict from functional traits alone. Many studies have tied species’ functional traits to interaction outcomes in communities of natives and a problematic invader. Relatively few studies, however, have examined the contribution of species interactions to variation in invasion impacts of functionally similar invaders.
* Here, we investigated interactions in communities of a native annual forb and two ecologically similar exotic annual grass species that commonly co-occur in semi-arid annual plant communities in southwest Western Australia. Using a combination of field and laboratory experiments and assessment of several performance measures, we studied interaction outcomes on the native species growing in combination with each exotic grass. We also examined differences among all species in their responses to intra- versus interspecific competition, including the magnitude of frequency-dependence of these interactions.
* The two exotic grasses differed substantially in interaction impacts on the native species, with one facilitating and one suppressing the native. In general, intraspecific competition was stronger than interspecific competition for the native, while evidence of intraspecific competition was weak to absent for the two exotics. These patterns may reflect that this native species does well in these invaded communities due to the combined impacts of stabilization and facilitation by some exotics invaders, whereas the exotics both benefit from limited stabilization (mediated by intraspecific competition) or weak competition with common natives species.
* **Synthesis** This study details the complex set of interactions involved in novel annual plant communities. We highlight the divergent impacts two functionally similar exotic grass species have on a common native species in controlled and natural conditions. Our findings highlight the importance of considering neutral and positive interactions between native and exotic species in understanding invasion dynamics in real plant communities.

**Keywords:** annual plants, biotic interactions, coexistence, competition, facilitation, invasion, semi-arid ecosystem

**Introduction**

Invasions by non-native exotic species have long interested ecologists (Elton 1958; Richardson & Pysek 2008). The ever-expanding invasion literature is replete with descriptions of exotic species competitively displacing native species (Levine et al. 2003; Sax & Gaines 2003; Vila & Weiner 2004 and references therein).In many systems, exotic species do out-compete native species via resource competition or suppression, which reduces native fitness (e.g. Dyer & Rice 1999; Brown & Rice 2000; Bakker & Wilson 2001; Kueffer et al. 2007; Flory & Clay 2010). These competitive impacts are, however, often exacerbated by an exogenous abiotic disturbance that precedes or accompanies the invasion (Davis et al. 2000; Seabloom et al. 2003; MacDougall & Turkington 2005) rather than due to intrinsic invader superiority (Daehler 2003).Ecologists have suggested that invasion studies incorporating species’ functional traits as well as origin may yield more useful outcomes for predicting future invasions and improve our ability to prevent further damage to native communities by current invaders (Brown & Sax 2004; Davis et al. 2011; Drenovsky et al. 2012; Lai et al. 2015).

The incorporation of species functional traits into invasion studies over the past decade has yielded important insights into the biological mechanisms underlying ecological resilience, species coexistence, and invasion success. Most studies relating functional traits and demographic performance to invasion outcomes have focused on the absolute trait values of the exotic species or trait distances between the exotic and the native community. For example, many invaders have been found to have high relative growth rates, fecundities, and resource-use efficiencies relative to native species (Funk & Vitousek 2007; Van Kleunen et al. 2010). Non-ordinal trait differences between exotic and native species are also implicated in invasion success (i.e. “vacant niche” model of invasion (Elton 1958)), such as offset exotic phenology relative to the native community (Wolkovich & Cleland 2010) or when exotic species possess vegetative characteristics not commonly found in the native community (e.g., Lloret et al. 2005). Although these are examples of functional traits relating to invasion success, these findings are highly variable, and other studies provide contrary evidence (Daehler 2003; Bellingham et al. 2004; Leishman et al. 2010; Tecco et al. 2010; Davidson et al. 2011). Environmental context and the density of individuals are highly important in determining when differences among native and exotic species are likely to affect invasion outcomes, due in part to effects on species interactions, which are difficult to predict from functional traits alone (Daehler 2003; Von Holle & Simberloff 2005; Tylianakis et al. 2008). Despite this gap in our understanding of the relationship between species functional traits and invasion outcomes, few studies have explicitly examined the contribution of species interactions to variation in invasion impacts using multiple functionally similar invaders.

Given the overwhelming historical focus on the negative direct impacts of exotic species on native species, it is not surprising that evidence for neutral or positive interactions among native and exotic species has only recently started to emerge (Rodriguez 2006). The importance of facilitation, or interactions that confer greater fitness to one or more species in the presence of a “benefactor” species than when the benefactor is absent (reviewed in Callaway 2007), has recently been highlighted and may in fact contribute to observed positive relationships between native and exotic species richness in some systems (Stachowicz 2001; Rodriguez 2006; Shlaepfer et al. 2011). Facilitation has been observed among exotic plant species, i.e. “invasional meltdown” (Simberloff & Von Holle 1999; Jordan et al. 2008), and there are accounts of exotic species facilitated by natives (Maron & Jeffries 1999; Lenz & Facelli 2003; Belnap & Sherrod 2009). There are far fewer published examples of exotic species facilitating native species, especially in terrestrial plant systems. These few cases include examples of exotic species facilitating native recruitment (Kanowski et al. 2008; Elgar et al. 2014) and productivity (Pec & Carlton 2014), or promoting native fitness through environmental engineering, such as increasing soil nutrient levels (Quinos et al. 1998; Knight et al. 2007) or alleviating moisture stress (Titus & Tsuyuzaki 2002). Given that invasion research often intentionally targets problematic exotic species, positive or neutral interactions between native and exotic species may occur more frequently in natural systems than the literature suggests.

Here, we examined the effects of biotic interactions on a native annual forb (*Waitzia acuminata* Steetz, Asteraceae) in communities shared with two ecologically similar exotic annual grass species (*Aira cupaniana* Guss. and *Pentameris airoides* Nees, Poaceae), which commonly co-occur in semi-arid woodland fragments of southwest Western Australia. Preliminary observations from both field and laboratory studies suggest that *Waitzia* survival and/or total biomass is greater when growing alongside either of these exotic grass species than when grown alone (Wainwright et al. 2016a). Using a combination of field and laboratory experiments and assessment of several performance measures, we tested for facilitative, competitive and neutral impacts of the exotic grasses on this common native species. We also examined the differences among all three species in their responses to intra- versus interspecific competition and estimated the magnitude of the frequency-dependence of these interactions, which we then discuss in the context of coexistence theory. This study was guided by the following questions: 1) Do functionally similar exotic grasses (specifically *A. cupaniana* and *P. airoides*) have similar impacts on co-occurring native forbs (specifically, *W. acuminata*)? 2) What implications do patterns of intra- versus interspecific interactions have for the potential long-term coexistence of these species in natural communities?

**Materials and methods**

*Study system*

Our three focal species are common in annual understory communities of formerly extensive York gum (*Eucalyptus loxophleba* subsp. *loxophleba*) – jam (*Acacia acuminata*) woodlands, a fragmented semi-arid woodland type that persists in the agricultural wheatbelt region of southwest Western Australia. The canopy of York gum-jam woodlands is sparse, and understory vegetation comprises dense annual and perennial forb assemblages and scattered shrubs and tussock grasses. Typical of Mediterranean-type ecosystems, the annual understory species in this system germinate and grow during the winter-spring rainy season (July to October in this system), and senesce by the onset of the summer dry season.

*W. acuminata* is an erect herb, occurring in all Australian states with the exception of Tasmania (Australia’s Virtual Herbarium). *W. acuminata* is especially common in York gum-jam woodlands at the regional and local (sub-meter) scale (10.22±0.43 individuals per 0.09m2). Both of the exotic annual grasses are commonly referred to as “hairgrasses” due to their slender, diminutive stature and similar flowering structures (Appendix Figure 1). *A. cupaniana* is native to the Mediterranean region, though its distribution is now global, and *P. airoides* is native to South Africa but has a widespread Australian distribution (AVH). Both grasses were presumably introduced to the region during periods of agricultural development in the late 19th and early 20th century (Burvill 1979). Such early introductions are supported by herbarium records dating back to 1893 and 1922 for *P. airoides* and *A. cupaniana*, respectively (Avon Wheatbelt Bioregion, AVH). Both species are now ubiquitous within woodland fragments across the southwestern agricultural region, and *W. acuminata* co-occurs with both grass species over regional and local spatial scales. *A. cupaniana* and *P. airoides* occur at similar abundances at local scales (18.87±2.50 and 21.19±1.32 individuals per 0.09m2, respectively). Both grasses have similarly fine, fibrous root structures (*A. cupaniana*: Virtual Herbarium UIB (2015); *P. airoides*: FAO Grassland Index (2015)), similar SLA (40.26 and 30.32 mm2/mg, respectively), height (150 and 175.5 mm, respectively), and similarly low seed mass (0.02 and 0.05 mg, respectively) (Dwyer et al, unpublished data).

York gum-jam annual communities range in composition from completely exotic-dominated to predominantly native (Dwyer et al. 2015). Communities dominated by exotic species tend to occur in heavily grazed areas and in the absence of grazing along woodland edges adjacent to roads and agricultural fields where robust exotic annual grasses (e.g. *Avena barbata*) and broadleaf weeds (e.g. *Arctotheca calendula*) exploit disturbed conditions (Prober & Wiehl 2011), often to the detriment of native species including *W. acuminata* (Dwyer et al. 2014; Wainwright et al. 2016b). However, in typical woodland interior communities where abiotic conditions are more intact, a different suite of exotic annuals not associated with disturbance tends to dominate the exotic portion of the annual community. Both *A. cupaniana* and *P. airoides* have been termed "coexister" species because their occurrences are strongly negatively associated with that of robust exotic annual grasses and weeds and disturbed soils, and positively associated with native species richness (Lai et al. 2015).

*Field experiments*

The field component of this study took place at Bendering Nature Reserve (32°23’7.88” S, 118°23’5.66”E) and Kunjin Reserve (32 °21’19.31”S, 117 °45’42.32”E) in southwestern Australia during the winter-spring growing season (July – November) of 2013, in the interior of intact York gum-jam woodland areas of these reserves. Bendering and Kunjin Reserves are separated by approximately 65 km and experience similar climatic conditions (mean annual precipitation Bendering: 341 mm, Kunjin: 366 mm (Bureau of Meteorology Station IDs 10583 and 10536, respectively); http://www.bom.gov.au/climate/data/). The component focusing on *W. acuminata* and *A. cupaniana* took place at Bendering Reserve, while the component focusing on *W. acuminata* with *P. airoides* took place at Kunjin Reserve to reflect where both grass species were present in greater relative abundances (*W. acuminata* was common at both reserves). At Bendering Reserve, *W. acuminata* and *A. cupaniana* were both locally abundant and present at varying relative frequencies in natural mixtures. In early August, 2013 ten 30 x 30 cm plots were established using quadrats in areas containing two-species mixtures of *W. acuminata* and *A. cupaniana*. Plots containing monocultures of *W. acuminata* (n=8) were also established at the same site to enable investigation of facilitation and comparisons of the strength of intra versus interspecific competition for *W. acuminata*. Quadrats were located randomly within the experimental site and were separated from one another by at least 1m. All non-focal species were weeded out of the quadrats, though mixtures and monocultures were chosen such that non-focals were absent or present only at low abundances such that only minimal weeding was required. We treated *W. acuminata* as the focal species in this field study and allowed its density to vary between 5 and 25 individuals per quadrat while keeping the density of *A. cupaniana* relatively constant between 120 – 180 individuals per quadrat. These densities are consistent with densities measured in interaction neighborhoods of a variety of species in this system (Mayfield & Stouffer 2017).

To assess whether local-scale environmental heterogeneity was responsible for differential performance of *W. acuminata* individuals, we recorded *E. loxophleba* (York gum tree) litter percent cover, *A. acuminata* (jam tree) litter percent cover, total herbaceous litter percent cover, percent soil moisture halfway through the growing season (late September) and percent overhead tree canopy cover for each quadrat. In addition, we collected dry soil from each quadrat at the end of the growing season which was stored in darkness at room temperature in sealed beakers until analysed for nitrate, ammonium, phosphorus, and potassium content. To measure whether N-cycling rates were different between *W. acuminata* monocultures and plots containing *A. cupaniana*, we deployed three anion-exchange membrane (IEM) strips in each quadrat for six weeks during the growing season to estimate nitrate adsorption rates, which were determined according to methods described in Jasrotia & McSwiney (2008) and Vogt (2013). Abundances of *W. acuminata* and *A. cupaniana* were recorded regularly in each quadrat over the course of the growing season. To assess aboveground biomass of *W. acuminata*, all focal individuals were harvested in December 2013 once both species had gone to seed, oven dried at 60˚C for one week and then weighed.

To assess the response of *W. acuminata* to *P. airoides* in the field, 13 *W. acuminata* individuals growing in interaction neighbourhoods consisting solely of *P. airoides* (determined by placing a 10 cm diameter metal ring at ground level around each focal *W. acuminata* individual) were located in a York gum-jam woodland in Kunjin Reserve in August 2013. *W. acuminata* individuals in neighbourhoods containing a background mixture of exotic species were also located to permit comparisons between their effects and those solely due to *P. airoides* on *W. acuminata*. In addition, 15 *W. acuminata* individuals grown in the absence of competition were located by weeding out non-focal species to assess overall effects of interactions with exotic species on *W. acuminata* performance. We did not test differences in N-cycling rates at the scale of these particular interaction neighbourhoods, though IEMs deployed in similar spatially contiguous plots during the 2013 growing season showed no relationship with species composition (Wainwright et al. 2016b). The identities and abundances of all species were recorded in these neighbourhoods, and at peak biomass, the number of flower heads on each *W. acuminata* individual was recorded as a proxy for reproductive investment due to its strong correlation with seed count (r2: 0.51, p < 0.0001; Wainwright et al. unpublished data).

*Growth chamber experiment*

The growth chamber component of this study explored impacts on *W. acuminata* by *A. cupaniana* and *P. airoides* and measured the relative strength of intra vs interspecific competition for all three focal species. *W. acuminata* was grown with either *A. cupaniana* or *P. airoides* in two-species combinations at three relative frequencies (Fig. 1; Appendix Table 1). Monocultures of each species were also planted at each density to directly compare species’ performance measures (survival, productivity, and reproductive investment) with and without interspecific competition at a given intraspecific density.

All of the two-species (*W. acuminata* + grass) communities were planted from seed at a target density of 60 total plants per pot (78.5 cm2 surface area), with the number of each species varying according to the frequency treatment. This density was chosen based on ranges of densities commonly observed in the field (Dwyer et al. 2015). The three species’ relative frequencies (*W. acuminata*: grass ratio) tested were 1:5, 1:1 and 5:1.

Seeds were collected from mature plants in York gum-jam woodland remnants in October 2011 at Bendering Reserve (*W. acuminata* and *A. cupaniana*) and Kunjin Reserve (32 °21’19.31”S, 117 °45’42.32”E); *W. acuminata* and *P. airoides*) and then placed in a drying oven for four weeks at 40°C to after-ripen, which alleviates dormancy of many Australian native forb species (Hoyle et al. 2008). Soil was prepared by The University of Queensland glasshouse facilities to closely resemble the texture and nutrient content of soils in undisturbed York gum-jam woodlands (< 5.0 mg/kg plant-available P; Dwyer et al. 2015), as a 1:3 combination of low-P native potting mix and coarse sand. Seeds of component species were mixed and placed on the soil surface before watering. Each pot was hand-watered every four to five days during the first six weeks of seedling establishment, after which each pot was watered every seven days (35 mL per watering). Throughout the establishment phase, pots were weeded to maintain prescribed plant abundances.

The experimental mixtures were grown in two temperature-controlled growth chambers (ThermoFisher Scientific, Adaptis 1000) containing fluorescent tubes (c. 650 µmol m-2s-1) at The University of Queensland. Pots were randomly shuffled between both chambers every week to account for any potential chamber or shelf effects. Photoperiod was set to a 12 hour cycle, and temperatures ranged from 17.0°C (day) to 7.0°C (night), based on average temperatures in the central wheatbelt region in July (BOM 2014) when annual plants typically establish.

When plants reached peak biomass four months after planting, all pots were harvested and aboveground biomass measured. Aboveground biomass and number of flowers (for *W. acuminata*) was recorded at the individual level, while the proportion of individuals flowering was recorded at the species level in each pot. All variables were recorded at the species level for *A. cupaniana* and *P. airoides* (aboveground biomass was recorded as the mean biomass per individual per pot).

*Statistical analysis*

Analyses were conducted in R v 3.1.2 (R Development Core Team 2014) using packages lme4 (Bates et al. 2014), nlme (Pinheiro et al. 2014), and multcomp (Horthorn et al. 2008).

W. acuminata *performance in the field*

To explore whether abiotic differences among plots may have influenced changes in *W. acuminata* performance measures, several key environmental variables were compared between monoculture and mixture plots using t-tests with Bonferroni corrections for multiple comparisons: ln(nitrate), ln(ammonium), ln(phosphorus), ln(potassium), nitrate adsorption rate, percent soil moisture, and ln(percent tree canopy cover), sqrt(*E. loxophleba* litter percent cover), *A. acuminata* litter percent cover, ln(Herbaceous litter percent cover) were compared at Bendering Reserve, and soil pH and sqrt(percent tree canopy cover) were compared at Kunjin Reserve. Variables were ln- or square-root-transformed as appropriate to improve the normality of their distributions to meet model assumptions.

*W. acuminata* performance measures (survival, biomass per individual, and flower count per individual) from the field component measuring the impacts of *A. cupaniana* were analysed using mixed effects models with community type (mixture with *A. cupaniana* or monoculture) and *W. acuminata* abundance (continuous) and their interaction specified as fixed effects. In all models, the community type x *W. acuminata* abundance interaction term was not significant, and so additive models were used instead.

The proportion of *W. acuminata* individuals surviving in the field was modelled as a function of treatment (mixture with *A. cupaniana* or monoculture) in a generalized mixed effects model with binomial errors and logit link function. Plot was included as a random effect. *W. acuminata* biomass responses were ln-transformed and modelled using linear mixed effects models with plot specified as a random effect to account for multiple observations per plot. *W. acuminata* flower counts per plant were modelled using a generalized linear mixed effects model with Poisson errors and log link function. Plot was included as a random effect, and plant within plot was also included to account for over dispersion where appropriate (Elston et al. 2001). Both biomass and flower count models were fitted with the addition of a quadratic term to account for nonlinear responses upon visual inspection of response data, and were dropped when non-significant.

In the field study, measuring the impacts of *P. airoides* on *W. acuminata*, flower count per *W. acuminata* individual was modelled as a function of competitor identity (*P. airoides* or “other exotics) compared to solo plants using a generalized linear mixed effects model with Poisson errors and log link function, and plot specified as a random effect and plant nested within plot to account for overdispersion. Plant density was included as a covariate to account for differences in species’ abundances in interaction neighbourhoods.

W. acuminata *performance in growth chambers*

To investigate effects of *A. cupaniana* or *P. airoides* on *W. acuminata* in growth chambers, we compared *W. acuminata* performance measures (survival, individual plant biomass, proportion of surviving individuals flowering, and the number of flowers per flowering individual) with and without the grass species present while holding *W. acuminata* density constant. To avoid confounding the effects of grass presence with its relative abundance, these response variables were modelled within each *W. acuminata* abundance category separately (10, 30, or 50 *W. acuminata* individuals) as grass abundances varied with *W. acuminata* abundance to maintain overall community densities (Fig. 1). In other words, this analysis allowed investigation of general differences in *W. acuminata* performance measures due to addition of grass across a range of conspecific abundances. Responses were analysed using mixed effects models where fixed effects included identity of competing individuals (*W. acuminata* if monoculture, and *A. cupaniana* or *P. airoides* if two-species mixture). Community (pot) was specified as a random effect to account for multiple observations (individuals) per pot. *Post-hoc* Tukey tests of differences among all 3 species combinations (*W. acuminata*, *W. acuminata + A. cupaniana*, and *W. acuminata + P. airoides*) were then conducted on all responses.

The various responses in the growth chamber experiment were modelled using the same transformations and error structures as described for the field experiment (e.g. binomial errors for survival). Flowering of surviving plants was treated as a binary response and modelled as for binary survival responses.

To determine the relative impacts of intra vs interspecific interactions on focal species performance, we analysed survival, mean biomass per individual (as grass biomass was measured at the species level per pot), proportion flowering, and number of flowers produced (*W. acuminata* only) across a range of species’ relative frequencies in a community. *P. airoides* monocultures only reached 50 instead of the targeted 60 individuals, so relative frequency = 1.0 for this species reflects a density of 50 rather than 60 individuals. Because both community types containing *W. acuminata* as a focal species shared the same data where *W. acuminata* relative frequency was equal to 1.0, separate models were run for *W. acuminata* with each grass competitor.

Response variables were modelled as a function of species’ relative frequencies (continuous). Survival, flowering probability and flower number were all modelled using error structures as described above. Mean biomass per plant was square-root transformed instead of ln-transformed because the latter over-corrected the skew in this response variable. Again, pot was specified as a random effect where required to account for multiple observations per pot and for overdispersion (Poisson model).

To enable direct comparisons of *W. acuminata* performance measures in neighbourhoods of *P. airoides* versus *A. cupaniana*, we also modelled these responses without the shared data (i.e. excluding pots with *W. acuminata* relative frequencies of 1.0; Appendix Table 3). For these models the fixed effects were competitor identity (*P. airoides* or *A. cupaniana*), relative frequency of *W. acuminata*, and their interaction.

**Results**

W. acuminata *survival, productivity, and reproductive investment in the field*

No significant differences were detected in environmental variables between mixture and monoculture plots at either reserve (Appendix Table 2). Survival of *W. acuminata* from seedling to adult was significantly greater for *W. acuminata* individuals growing in the presence of *A. cupaniana* than those found in monoculture across all conspecific densities (p=0.01; Table 1; Fig. 2a). All surviving *W. acuminata* plants flowered. The aboveground biomass and the number of flowers produced per surviving individual declined significantly with increasing conspecific density (biomass: p=0.02, number of flowers: p=0.005; Table 1; Fig. 2b, c). Though biomass and flower count visually appeared to modestly increase in the highest density plots, quadratic terms were not significant (data not shown). Individual flower production for *W. acuminata* individuals declined significantly in diverse exotic neighbourhoods (estimate: -1.07, SE: 0.38, z: -2.86, p=0.004) as well as neighbourhoods consisting of *P. airoides* only (estimate: -1.42, SE: 0.59, z=-2.39, p=0.02) compared to individuals grown in the absence of competition. This pattern was not further affected by the density of competitors in plots (estimate: -0.02, SE: 0.09, z=-0.19, p=0.85).

*Effect of* A. cupaniana *and* P. airoides *on* W. acuminata *in growth chamber*

At low conspecific abundances, W*. acuminata* survival was reduced only when in mixture with *P. airoides* (p=0.007; Table 2; Fig. 3a). In contrast to survival, however, *W. acuminata* biomass per individual was no different between monoculture and communities with either grass species added at any abundance (Table 2; Fig. 3b), though direct *post-hoc* pairwise comparisons revealed that at high abundances, *W. acuminata* individuals were significantly larger than in monoculture when *A. cupaniana* was present (estimate: 0.64 , SE: 0.27, adjusted p=0.04). The proportion of *W. acuminata* survivors flowering was significantly lower at high conspecific abundance with *P. airoides* present (Table 2; Fig. 3c; p=0.02) but was otherwise unaffected. Of the *W. acuminata* individuals that flowered, the number of flowers produced per individual was significantly lower at low conspecific abundance when *P. airoides* was added (p=0.02; Table 2; Fig. 3d).

*All species responses to intra vs interspecific neighbourhoods in growth chambers*

Survival was not related to relative frequency for any species (Table 3; Fig. 4a), but frequency-dependence was evident in other performance measures to varying degrees.

*W. acuminata* individual aboveground biomass (averaged per pot) declined as its relative frequency increased in communities containing *A. cupaniana* (p<0.0001; Table 3; Fig. 4b). By contrast, *P. airoides* exerted stronger interspecific competition on *W. acuminata* biomass (p=0.02; Appendix Table 3). Neither grass species’ mean biomass per plant was significantly related to its relative frequency (Table 3; Fig. 4b).

The proportion of *A. cupaniana* individuals that flowered was unaffected by its relative frequency in mixture. A positive relationship was found, however, between the proportion of *P. airoides* individuals flowering and relative frequency (p=0.02; Table 3; Fig. 4c). The proportion of surviving *W. acuminata* that flowered declined significantly as its relative frequency increased, but only in communities containing *A. cupaniana* (p=0.03; Table 3; Fig. 4c). A similar relationship was found for *W. acuminata* flower counts per plant, which declined with increasing relative frequency in communities containing *A. cupaniana* (p=0.002; Table 3; Fig. 4d).

**Discussion**

Our findings reveal that two functionally similar exotic annual grass species interact in distinct ways with a common native forb. Interactions between *W. acuminata* and *A. cupaniana* were neutral or positive and interactions between *W. acuminata* and *P. airoides* were neutral or competitive, implying that invaders with similar growth forms, abundances, and traits do not necessarily have similar impacts on resident species. The balance between intra and interspecific effects on *W. acuminata* shifted according to density, competitor identity, and metric of performance. Both grasses responded neutrally or positively to increasing conspecific abundance, which may promote their invasiveness. Our results underscore the potential for similar exotic competitors to mediate native density dependence in distinct ways. Overall, the prevalence and contingencies of positive interactions between native and exotic species merit further attention when assessing invasion impacts on native communities.

*Interactions with* A. cupaniana *and* P. airoides *in the field*

In the field, we found that *W. acuminata* survival was significantly greater in plots containing the exotic annual grass *A. cupaniana.* *W. acuminata* biomass and flower production were impacted less by the presence of *A. cupaniana* than by conspecifics, suggesting that the effects of intraspecific competition are stronger than interspecific interactions for *W. acuminata* productivity and reproductive investment when growing in mixture with *A. cupaniana*. By contrast, the effects of *P. airoides*, as well as multispecies exotic communities, on *W. acuminata* flower production were negative. This indicates that interspecific competitive effects of *P. airoides* are greater than that of *A. cupaniana* in natural communities despite their morphological similarity. This trend was robust across a range of *W. acuminata* abundances, indicating that the positive effect of *A. cupaniana* was not strongly contingent on the intensity of conspecific competition in the field. The generality of this interaction should be investigated further by determining whether *A. cupaniana* similarly affects other co-occurring native and exotic species, or if its effects are unique to *W. acuminata*. Additionally, the consequences of this facilitation should be evaluated relative to co-occurring species at the population and community level.

Positive interactions between exotic *A. cupaniana* and native *W. acuminata* could arise through a number of mechanisms, such as plant-soil feedbacks. Preliminary observations suggest that *W. acuminata* does not regularly form mycorrhizal mutualisms (A. Nance, pers. comm.), though facultative mycorrhizal associations or benefits from other microorganisms in soils beneath *A. cupaniana* could potentially facilitate *W. acuminata* through indirect positive plant-soil feedbacks (reviewed in Callaway 2007). In addition, nutrient cycling rates may also differ in soils beneath patches of annual grasses from soils characteristic of native communities where annual grasses have not occurred historically (Hobbie 1992). For example, Pec (2014) found that the survival of a native annual forb in a California coastal sage scrub community was potentially facilitated by the senescence of co-occurring exotic annual grasses. *W. acuminata* has a later phenology than *A. cupaniana*, so it is possible that senescence of *A. cupaniana* individuals may have been beneficial to *W. acuminata* during its active growth phase by providing a nutrient pulse. *A. cupaniana* litter is less persistent than that of other higher biomass common exotic annual grasses and native herbaceous species in this system (pers. obs.). Thus, *A. cupaniana* could potentially serve as a nutrient source for *W. acuminata* individuals (Facelli & Pickett 1991), though we tested for differences in nutrient levels between mixtures and monocultures in the field at the end of the growing season only (Appendix 1). Alternatively, greater relative humidity and reduced temperatures experienced in denser plant neighbourhoods in this system (Wainwright, unpublished data) may have facilitated *W. acuminata* via reduced evaporation at the soil surface (Callaway 2007). Positive higher-order interactions among individuals of *A. cupaniana* and *W. acuminata* may also have driven facilitative outcomes (Mayfield & Stouffer 2017), though these were not investigated in this study.

*Diverse impacts of exotic grasses in growth chambers*

In growth chambers, *A. cupaniana* had a neutral or positive effect on *W. acuminata* performance measures across a range of relative abundances. Surviving *W. acuminata* individuals were significantly larger when *A. cupaniana* was present at high conspecific densities than without, indicative of growth facilitation at high density. These results support the overall trend of neutral or positive interactions between these two species in the field, although *A. cupaniana* impacted different performance measures in the growth chamber than in the field (production as opposed to survival), potentially because environmental conditions were less stressful in growth chambers than in the field. It is possible, however, that reduced evaporation associated with higher plant densities operated in the growth chamber as well as the field. The fact that this interaction was found in a laboratory setting indicates that this relationship may occur independently of environmental variation in the field. It also limits the likelihood of microbe- mediated facilitation, as growth chamber soils were sterile.

Though we found evidence of facilitation in field and growth chamber communities, caution should be exercised when attempting to relate local-scale positive and neutral pairwise interactions to effects on whole communities. The long-term trajectory of positive interactions and their implications for community structure are likely complex and depend on factors occurring over larger spatial and temporal scales than were measured in this study. In particular, it has been suggested that invasive plants may promote extinction in native plant communities not by competitive exclusion, but by reducing the size of native refugia and disrupting native metapopulation connectivity, processes which may occur over long timescales and may be masked by current trends of native persistence (Gilbert & Levine 2013). Small-scale microsite conditions may also differentially favour certain species and alter the strength of interactions between native and exotic species, though we note that results were retained in laboratory settings, suggesting that they are robust to local environmental conditions. While two-species mixtures certainly occur naturally in this plant community at the scale examined in this study, they do not always interact in isolation. Additionally, temporal environmental heterogeneity could alter these dynamics. Specifically, interannual variation in rainfall can affect the type and strength of interactions in herbaceous plant communities over time through changes in species relative and absolute abundances (Hobbs & Mooney 1991) and phenologies (Quevedo-Robledo et al. 2010). Additionally, the frequency and magnitude of species interactions, as well as the performance measures affected, may change with environmental stress in complex ways (Tielborger & Kadmon 2000). If interactions between these native and exotic species are mediated by environmental stress, their outcome may ultimately depend on whether the stress is resource-based (i.e. water stress) or non-resource based (i.e. temperature stress; Maestre et al. 2009), though we observed facilitation in the absent of obvious stressors in this study. Further experimentation in a variety of systems is required to assess the prevalence and contingencies of positive interactions as a mechanism promoting the coexistence of native and exotic species in diverse invaded communities.

*Species responses to intra vs interspecific competition*

The only occurrence of negative frequency-dependence in mixture was for *W. acuminata* biomass and reproductive investment, which both declined with increasing conspecific frequency in mixtures with *A. cupaniana*. These results indicate that intra- rather than interspecific interactions determine *W. acuminata* productivity in this mixture, corroborating observations of these species in the field. Conversely, interspecific competition was more evident in mixtures with *P. airoides*, where dischordant performance responses were evident. At high densities, despite *W. acuminata* individuals attaining higher biomass, reproductive output was reduced compared to individuals in monoculture or growing with *A. cupaniana*. This suggests that *W. acuminata* may not increase from rarity in a neighbourhood of *P. airoides* as rapidly as in a neighbourhood of *A. cupaniana*. In natural communities, however, environmental heterogeneity may buffer *W. acuminata* from intense competition with *P. airoides* in certain microsites (Melbourne et al. 2007).

Both grasses showed neutral or positive relationships between performance measures and their relative frequency in mixture. Despite being relatively abundant in York gum woodland understories, both species are positively associated with native species richness and are not associated with elevated soil P (indicative of anthropogenic eutrophication in this system; Lai et al. 2015), suggesting that factors other than P-enrichment may contribute to their persistence and ubiquitous distribution in predominantly native species-rich communities. Though neither *P. airoides* nor *A. cupaniana* are associated with disturbed conditions, high propagule pressure may potentially contribute to their invasion success (Holle & Simberloff 2005) through production of large quantities of non-dormant, readily germinable seed compared to native species in this system (Lai et al. 2015; Wainwright & Erickson unpublished data). A combination of insensitivity to interspecific competition, neutral or positive density dependence, and relatively high fecundities may underlie the invasion success of these species.

*Conclusions*

This study presents multiple lines of evidence of a native plant species benefiting from interactions with an exotic “benefactor” species. Positive interactions of this nature have rarely been documented, despite their potential prevalence in invaded plant communities. The results of this study imply that under certain conditions, these interactions may promote coexistence between native and exotic species in invaded plant communities.

Our findings underscore the need for approaches to understanding invaded plant communities that are more inclusive of variable species interactions and the ways they may respond to further environmental change. Recently, exotic dominance has been highlighted as a better option than species richness for assessing the extent and condition of invaded plant communities (Seabloom et al. 2013). Our results suggest that even the relative abundances of exotic species may not accurately predict their impact on native species or the function of communities post-invasion. The impacts of invasion cannot be easily predicted or generalized, even when comparing the impacts of very similar exotic species.

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**Data accessibility**

DRYAD entry doi: xxxxxxx (TBD depending on acceptance)

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**Table 1** Coefficients and (SEs) from mixed-effects models of *W. acuminata* performance measures in the field when growing with or without *A. cupaniana*. Asterisks denote level of significance (\*: p≤0.05, \*\*: p<0.01, \*\*\*: p<0.001).

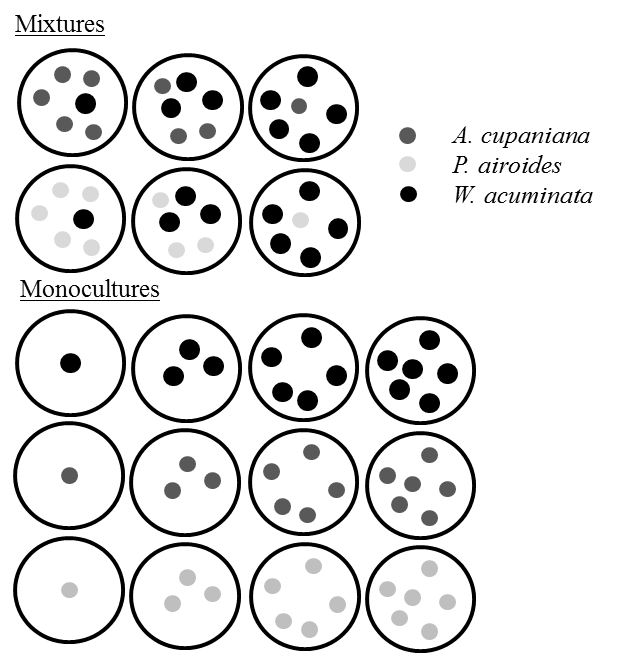
|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed effects** | **Response of *W. acuminata*** | | |
| Proportion individuals surviving | ln(Biomass per individual (g)) | Flower count per flowering individual |
| Intercept (Monoculture) | 0.38 (0.52) | -0.07 (0.34) | 3.41 (0.27)\*\*\* |
| *A. cupaniana* present | 0.88 (0.34)\* | -0.38 (0.25) | -0.17 (0.20) |
| Conspecific density | 0.02 (0.03) | -0.06 (0.02)\* | -0.05 (0.02)\*\* |
| **Random effects (variance estimates):** |  |  |  |
| Among plot | 0.05 | 0.20 | 0.11 |
| Within plot | NA | 0.75 | 0.41 |

**Table 2** Coefficients and (SEs) from mixed effects models of *W. acuminata* performance measures in growth chambers when growing with or without *A. cupaniana* or *P. airoides*. Separate models were conducted for *W. acuminata* at low, medium, or high abundances (10, 30, and 50 *W. acuminata* individuals respectively). Asterisks denote level of significance (\*: p≤0.05, \*\*: p<0.01, \*\*\*: p<0.001).

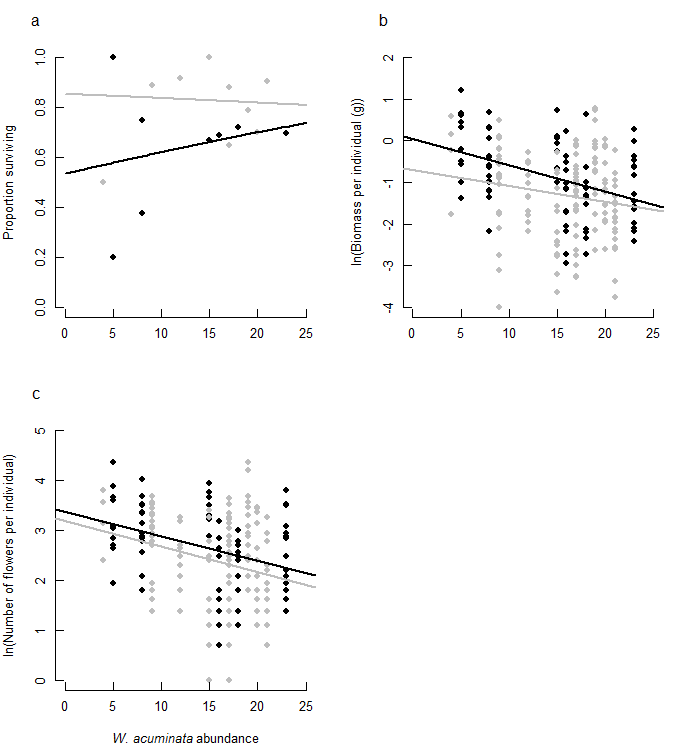
|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **Response of *W. acuminata*** | | | |
| Proportion individuals surviving | ln(Biomass per individual (g)) | Proportion individuals flowering | Flower count per flowering individual |
| **Model: Low *W. acuminata* abundance** |  |  |  |  |
| Fixed effects: |  |  |  |  |
| Intercept (monoculture) | 2.54 (0.94)\*\* | -2.35 (0.19) \*\*\* | 0.38 (0.36) | 1.55 (0.21)\*\*\* |
| *A. cupaniana* present | -1.27 (1.07) | 0.07 (0.26) | 0.35 (0.50) | -0.18 (0.28) |
| *P.airoides* present | -3.34 (1.23)\*\* | -0.76 (0.48) | -0.38 (0.79) | -1.51 (0.64)\* |
| Random effects (variance estimates): |  |  |  |  |
| Among pot | 1.18 | <0.0001 | <0.0001 | <0.0001 |
| Within pot | NA | 1.17 | NA | 0.61 |
| **Model: Medium *W. acuminata* abundance** |  |  |  |  |
| Fixed effects: |  |  |  |  |
| Intercept (monoculture) | 0.79 (0.27)\*\* | -3.06 (0.14)\*\*\* | 0.36 (0.29) | 1.25 (0.22)\*\*\* |
| *A. cupaniana* present | -0.20 (0.36) | 0.05 (0.18) | -0.49 (0.37) | -0.01 (0.29) |
| *P. airoides* present | -0.69 (0.43) | -0.04 (0.22) | -0.65 (0.46) | -0.16 (0.38) |
| Random effects (variances estimates): |  |  |  |  |
| Among pot | 0.19 | <0.0001 | 0.12 | 0.12 |
| Within pot | NA | 1.42 | NA | 0.61 |
| **Model: High *W. acuminata* abundance** |  |  |  |  |
| Fixed effects: |  |  |  |  |
| Intercept (monoculture) | 0.31 (0.76) | -3.98 (0.20)\*\*\* | -0.29 (0.27) | 0.81 (0.20)\*\*\* |
| *A. cupaniana* present | 0.62 (1.03) | 0.65 (0.27) | 0.12 (0.36) | 0.23 (0.26) |
| *P. airoides* present | -0.56 (1.52) | 0.89 (0.43) | -2.04 (0.84)\* | -0.95 (0.75) |
| Random effects (variances estimates): |  |  |  |  |
| Among pot | 1.65 | 0.06 | 0.08 | 0.23 |
| Within pot | NA | 1.80 | NA | 0.05 |

**Table 3** Coefficients and (SEs) from mixed effects models of focal species performance (proportion surviving, mean individual biomass, proportion flowering, and number of flowers for flowering *W. acuminata*) in the growth chamber experiment by relative frequency (ranging from 0.18 in 2-species mixture to 1.0 in monoculture). Asterisks denote level of significance (\*: p≤0.05, \*\*: p<0.01, \*\*\*: p<0.001).

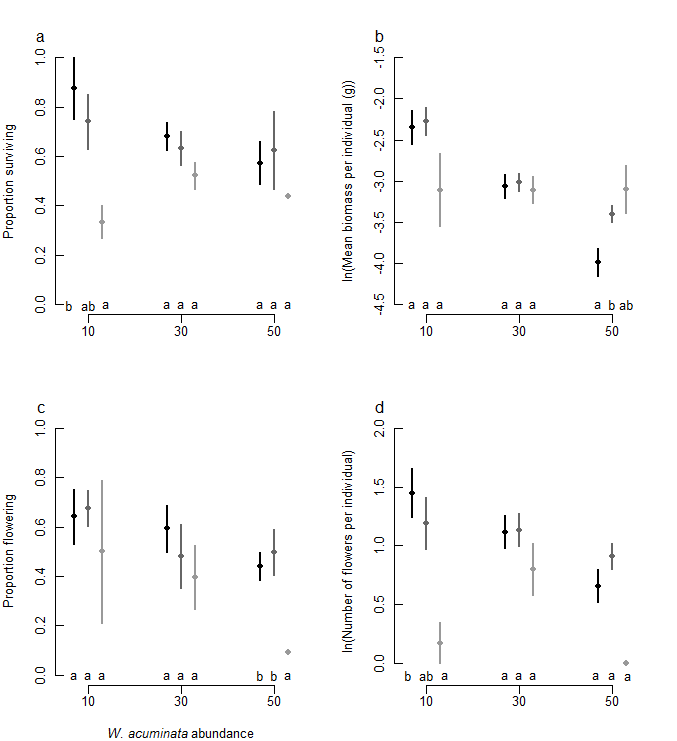
|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **Response** | | | |
|  | Proportion individuals surviving | Biomass per individual (g) | Proportion individuals flowering | Flower count per flowering individual |
| **Model: *W. acuminata* (with *A. cupaniana)*** |  |  |  |  |
| Fixed effects: |  |  |  |  |
| Intercept | 1.29 (0.60)\* | 0.40 (0.02)\*\*\* | 0.66 (0.39) | 1.67 (0.21)\*\*\* |
| Relative frequency | -0.92 (0.86) | -0.16 (0.03)\*\*\* | -1.10 (0.52)\* | -0.93 (0.30)\*\* |
| Random effects (variance estimates): |  |  |  |  |
| Among pot | 1.04 | 0.001 | 0.18 | 0.05 |
| Within pot | NA | NA | NA | 0.71 |
| **Model: *W. acuminata* (with *P. airoides)*** |  |  |  |  |
| Fixed effects: |  |  |  |  |
| Intercept | -0.57 (0.43) | 0.26 (0.05)\*\*\* | 1.02 (1.03) | 0.98 (0.45)\* |
| Relative frequency | 0.79 (0.53) | 0.02(0.07) | -3.40 (1.93) | -0.34 (0.55) |
| Random effects (variance estimates): |  |  |  |  |
| Among pot | 0.12 | 0.005 | 0.46 | 0.08 |
| Within pot | NA | NA | NA | 0.65 |
| **Model: *A. cupaniana (with W. acuminata)*** |  |  |  |  |
| Fixed effects: |  |  |  |  |
| Intercept | 1.84 (1.08) | 0.17 (0.02)\*\*\* | 0.24 (0.43) |  |
| Relative frequency | 1.48 (1.56) | -0.04 (0.02) | -0.04 (0.59) |  |
| Random effects (variance estimates): |  | -0.04 (0.59) |  |  |
| Among pot | 2.88 | 0.0009 | 0.27 |  |
| Within pot | NA | NA | NA |  |
| **Model: *P. airoides (with W. acuminata)*** |  |  |  |  |
| Fixed effects: |  |  |  |  |
| Intercept | 1.40 (2.65) | 0.11 (0.05)\* | -2.87 (1.10)\*\* |  |
| Relative frequency | 1.37 (2.65) | 0.10 (0.63) | 2.98 (1.30)\* |  |
| Random effects (variance estimates): |  |  |  |  |
| Among pot | 7.12 | 0.0025 | 0.39 |  |
| Within pot | NA | NA | NA |  |



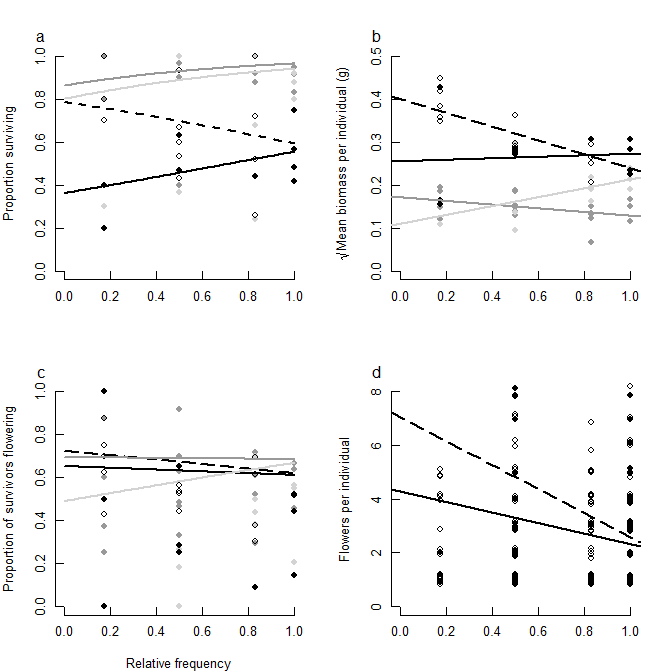
**Fig. 1** Diagram of growth chamber experimental design. Each circle represents a treatment combining the relative frequency and identity of each species (coloured dots) in mixture or monoculture. Each dot corresponds to 10 individuals of the designated species.



**Fig. 2** a) Proportion of *W. acuminata* individuals surviving, (b) aboveground biomass per individual, and (c) flower count per individual by conspecific abundance (x-axis) whilst growing in the presence of *A. cupaniana* (grey) or in monoculture (black) in the field.

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**Fig. 3** *W. acuminata* (a) proportion of individuals surviving, (b) aboveground biomass per plant, (c) proportion of surviving individuals flowering, and (d) flower count per flowering individual by conspecific abundance category (10, 30, or 50 individuals) in monoculture (black), in mixture with *A*. *cupaniana* (grey), and in mixture with *P. airoides* (light grey). Letters denote significant differences among species combinations within a given *W. acuminata* abundance category (x-axis).



**Fig. 4** Species performance measures of (a) the proportion of individuals surviving, (b) mean biomass per individual, (c) proportion of survivors flowering, and (d) flower count per flowering individual (*W. acuminata* only). Species responses are plotted by their relative frequencies in a community of 60 individuals, where *W. acuminata* (with *A. cupaniana*) = black dashed/open point, *W. acuminata* (with *P. airoides*) = black solid, *A. cupaniana* (with. *W. acuminata*) = grey, and *P. airoides* (with *W. acuminata*) = light grey. Both lines for *W. acuminata* share the same data points at relative frequency= 1.0.