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Looks can be deceiving: ecologically similar exotics have different impacts on a native competitor

Claire E. Wainwright^{1,2} · Robert D. Holt³ · Margaret M. Mayfield¹

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Abstract

Exotic species are often predicted to successfully invade when their functional traits differ from species in recipient communities. Many studies have related trait differences among natives and invaders to competitive outcomes. Few studies, however, have tested whether functionally similar invaders have similar competitive impacts on natives. We investigated interactions in communities of a native annual forb Waitzia acuminata (Asteraceae) and two invasive annual grasses that are ecologically similar and co-occur in southwestern Australia. Using a combination of field and laboratory experiments and several performance measures, we assessed impacts of these grasses on W. acuminata. We also examined differences among species in their responses to intraspecific versus interspecific competition, including their frequency dependence. The two similar exotic grasses differed in interaction impacts, with one facilitating and the other suppressing the native. In general, intraspecific competition was stronger than interspecific competition for the native, while evidence of competition was weak for the exotics. These patterns may reflect that W. acuminata does well in these communities due to the combined impacts of stabilization and facilitation, whereas the exotics benefit from limited stabilization (mediated by their weak intraspecific competition) or weak interspecific competition with W. acuminata. We found divergent impacts of the exotic species despite their similar functional traits. We demonstrate that a native species may benefit from interactions with an exotic "benefactor" species, highlighting the potential importance of positive interactions in invaded communities. Our findings underscore the necessity of considering neutral and positive interactions in addition to competition in understanding invasion dynamics in real plant communities.

Keywords Annual plants · Coexistence · Competition · Facilitation · Functional traits

Introduction

Invasions by non-native exotic species have long interested ecologists (Elton 1958; Richardson and Pyšek 2008). The ever-expanding invasion literature is replete with

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- ¹ The Ecology Centre, School of Biological Sciences, The University of Queensland, St Lucia, QLD, Australia
- ² Exponent, Inc., Bellevue, WA, USA
- ³ Department of Biology, University of Florida, Gainesville, FL, USA

descriptions of exotic species displacing native species (Vilà et al. 2011). In many systems, exotic species outcompete native species via resource competition or suppression, which reduces native fitness (e.g., Kueffer et al. 2007; Flory and Clay 2010). These competitive impacts are, however, often exacerbated by an exogenous abiotic disturbance that precedes or accompanies the invasion (e.g., Seabloom et al. 2003) rather than due to intrinsic invader superiority (Daehler 2003). Moreover, in some cases, strong impacts of competition are difficult to discern. Sax and Gaines (2008) for instance observed that on islands, there is scant evidence for exotics competitively excluding natives, and other authors (e.g., reviewed in Fridley et al. 2007) argue that under certain conditions, plant invasion may boost the richness of local communities and regional species pools, without degrading native diversity.

Traits govern how organisms cope with disturbance, competition, and abiotic factors (and the interplay of all these).

Claire E. Wainwright cewain@uw.edu

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 ongoing invasions (Davis et al. 2011; Drenovsky et al. 2012; Lai et al. 2015). 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 communities. For example, many invaders have been found to have high relative growth rates, fecundities, and resource-use efficiencies relative to native species (Funk and Vitousek 2007; Van Kleunen et al. 2010). Non-ordinal trait differences between exotic and native species are also implicated in invasion success [i.e., the "vacant niche" model of invasion (Elton 1958)], such as a unique phenology of the exotic species relative to the native community (Wolkovich and 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 when functional traits relate to invasion success, other studies provide contrary evidence that obvious traits may not be all that informative (Daehler 2003; Leishman et al. 2010). Environmental conditions 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 the influence of context on species interactions. To date, this contextuality has been difficult to predict from functional traits alone. 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 comparing multiple functionally similar invaders.

Given the overwhelming historical focus on the negative direct impacts of exotic species on native species, it may not be 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 that benefactor is absent (reviewed in Callaway 2007), has recently become a more prominent theme in the literature of invasion biology. Such facilitative effects may in fact contribute to observed positive relationships between native and exotic species richness in some systems (Rodriguez 2006; Schlaepfer et al. 2011). Facilitation has been observed among exotic plant species, i.e., as an ingredient in "invasional meltdown" (Simberloff and Von Holle 1999), and there are accounts of exotic species facilitated by natives (e.g., Lenz and Facelli 2003). 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 and Carlton 2014), or promoting native fitness through environmental engineering, such as increasing soil nutrient levels (Knight et al. 2007) or alleviating moisture stress (Titus and Tsuyuzaki 2002). Given that invasion research often intentionally targets problematic exotic species, positive or neutral interactions between native and exotic species, in which the native species benefits from or is not impacted by exotics, may occur more frequently in natural systems than the literature currently 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 and abundant exotic annual grass species: Aira cupaniana Guss. and Pentameris airoides Nees, Poaceae, which frequently co-occur in semi-arid woodland fragments of southwest Western Australia. Preliminary observations from both field and laboratory studies suggested that W. acuminata survival and/or total biomass are greater when the native forb is growing alongside either of these exotic grass species than when it is grown alone (Wainwright et al. 2017a). 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 intraspecific versus interspecific competition, which is an important desideratum in understanding species coexistence and exclusion (Chesson 2000). We estimated the magnitude of the frequency dependence of these interactions, which is important to gauge, since negative frequency dependence is necessary for the robust coexistence of competing species (Adler et al. 2007).

The specific questions which we ask in this study are: (1) Do functionally similar exotic grasses (*A. cupaniana* and *P. airoides*) have similar impacts on a co-occurring native forb (*W. acuminata*)? (2) What implications do patterns of intraspecific 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 as widely scattered remnants in the agricultural wheatbelt region of southwest Western Australia. The canopy of York gum-jam woodlands is sparse, with understory vegetation comprised of dense annual and perennial forb assemblages, 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-October), and senesce by the onset of the summer dry season.

Waitzia acuminata is an erect herb, occurring in all Australian states with the exception of Tasmania (AVH 2019). Waitzia acuminata is especially common in York gum-jam woodlands at the regional and local (sub-meter) scale $(10.22 \pm 0.43 \text{ individuals per } 0.09 \text{ m}^2; \text{ Dwyer et al.}$ unpublished data). Aira cupaniana is native to the Mediterranean region, though its distribution is now global, and P. airoides is native to South Africa, but now has a widespread Australian distribution (AVH 2019). Both grasses were presumably introduced to the region during periods of agricultural development in the late nineteenth and early twentieth 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 2019). Both species are ubiquitous within woodland fragments across the southwestern agricultural region, and W. acuminata co-occurs commonly with both grass species over regional and local spatial scales. Aira cupaniana and P. airoides occur at similar abundances at local scales in this system $(18.87 \pm 2.50 \text{ and } 21.19 \pm 1.32)$ individuals per 0.09 m², respectively; Dwyer et al. unpublished data). Both A. cupaniana and P. airoides have been termed "coexister" species in this system, because their occurrences are strongly negatively associated with that of robust, invasive exotic annual grasses such as Avena barbata, Bromus madritensis, and Ehrharta longiflora, and positively associated with native species richness (Lai et al. 2015). Moreover, both A. cupaniana and P. airoides display similar functional traits to one another, which differ from those of robust exotic annual grasses, and are commonly referred to as "hairgrasses" or "feathergrasses" due to their quite comparable appearances, with slender, diminutive stature, and similar flowering structures (Fig. 1b, c; Online Appendix Table 1). Both grasses have similarly fine, fibrous root structures, similar SLA, height, phenology, and seed mass compared to other more robust exotic annual grasses in this system (Fig. 1b, c; Online Appendix Fig 1, Table 1). In terms of the basic plant functional traits that have been used in many studies of invasions, it might be reasonable to hypothesize a priori that they should exert comparable impacts upon native species.

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 areas heavily grazed by livestock. In the absence of grazing, dominance by exotics is conspicuous along woodland edges adjacent to roads and agricultural fields, where robust exotic annual grasses (e.g., *A. barbata*, *B. madritensis*, and *E. longiflora*) and broadleaf weeds (e.g., *Arctotheca calendula*) exploit disturbed conditions (Prober and Wiehl 2011), often to the detriment of native species including *W. acuminata* (Dwyer et al. 2014; Wainwright et al. 2017b). However, in typical woodland interior



Fig. 1 Focal species selected for the field and growth chamber experiments: **a** native forb *Waitzia acuminata*, **b** exotic annual grass *Pentameris airoides*, **c** exotic annual grass *Aira cupaniana*, and **d** diagram of growth chamber experimental design, where each circle represents a treatment combining the relative frequency and identity of each species (coloured dots) in mixture or monoculture, and each

dot corresponds to ten individuals of the designated species. For trait values, refer to Online Appendix Table 1. Photo credits: *W. acuminata*: author's own; *P. airoides*: Kevin Thiele, *A. cupaniana*: Harry Rose (both CC License 2.0, https://creativecommons.org/licenses/by/2.0/). Colour version of this figure is available online

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, including both *A. cupaniana* and *P. airoides* (Dwyer et al. 2015; Lai et al. 2015), and overall, exotic species are less obviously dominant in these interior sites.

Field experiments and associated statistical analyses

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; https://www. bom.gov.au/climate/data/). Soils are typically highly weathered and derived from the underlying granite bedrock (Beard 1998). The landscape is generally low in elevation (Bendering = approximately 350 m, Kunjin = approximately 310 m), and minimal in topographic relief, with occasional granite outcrops.

The component of this study focusing on W. acuminata and A. cupaniana took place at Bendering Reserve, while the component of the field work focusing on W. acuminata with P. airoides took place at Kunjin Reserve; the study thus encompassed sites where both grass species were present in, respectively, the 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 30×30 cm plots were established using quadrats in areas containing two-species mixtures of W. acuminata and A. cupaniana. Eight 30×30 cm plots containing monocultures of W. acuminata were also established at the same site to provide controls for measuring interactions such as facilitation, and to permit 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 1 m. All non-focal species were weeded out of the quadrats, though mixtures and monocultures were chosen such that non-focals were in any case absent or present only at low abundances (so that only minimal weeding was required). Resulting quadrats contained densities of individuals within the range of those found in unmanipulated communities (Dwyer et al., unpublished data). 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 and 180 individuals per quadrat. These densities are consistent with densities measured in interaction neighborhoods of a variety of species in this system (Mayfield and Stouffer 2017).

To assess the survival of *W. acuminata* in monoculture and in mixtures with *A. cupaniana* in the field, its abundances were recorded regularly in all quadrats over the course of the growing season. To assess the aboveground biomass and the number of inflorescences of *W. acuminata* individuals, all focal individuals were harvested in December 2013 once both species had gone to seed, oven-dried at 60 °C for 1 week, and then weighed, at which time which the number of inflorescences per individual was recorded.

To assess whether local-scale environmental heterogeneity was responsible for differential performance of W. acuminata individuals, we measured site characteristics that on a priori grounds were plausibly important, including litter load, soil moisture and nutrients, and shading. Specifically, 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 and stored the samples in dark conditions at room temperature in sealed beakers; the soil samples were later analysed for nitrate, ammonium, phosphorus, and potassium contents. 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 6 weeks during the growing season to estimate nitrate adsorption rates.

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. Waitzia acuminata individuals in neighbourhoods containing a background mixture of exotic species (ranging between one and three exotic species, also within a 10 cm-diameter neighbourhood) 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 individuals 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.

2017b). The identities and abundances of all species were recorded in these neighbourhoods, and at peak biomass, the number of inflorescences on each *W. acuminata* individual was recorded as a proxy for reproductive investment due to its strong correlation with seed count (r^2 : 0.51, p < 0.0001; Wainwright et al. unpublished data).

All analyses were conducted in R v 3.1.2 (R Core Team 2014) using packages *lme4* (Bates et al. 2015), *nlme* (Pinheiro et al. 2014), and *multcomp* (Hothorn et al. 2008).

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. Variables were ln- or square-root-transformed as appropriate to improve the normality of their distributions to meet model assumptions. 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, and ln(herbaceous litter percent cover) were compared at Bendering Reserve, and soil pH and sqrt(percent tree canopy cover) were compared at Kunjin Reserve.

Waitzia acuminata performance measures (survival, biomass per individual, and inflorescence 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 mixedeffects model with binomial errors and logit link function. Plot was included as a random effect. Waitzia acuminata biomass responses were In-transformed and modelled using linear mixed-effects models with plot specified as a random effect to account for multiple observations per plot. W. acuminata inflorescence 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 overdispersion where appropriate (Elston et al. 2001). Both biomass and inflorescence 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.

To measure the impacts of *P. airoides* on *W. acuminata* in the field, inflorescence 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. Plant density was included as a covariate to account for differences in species' abundances in interaction neighbourhoods.

Growth chamber experiment and associated statistical analyses

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. *Waitzia acuminata* was grown with either *A. cupaniana* or *P. airoides* in twospecies combinations at three relative frequencies (Fig. 1d; Online Appendix Table 2). 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 (Fig. 1d; Online Appendix Table 2). Treatments and replicates are detailed in Online Appendix Table 2.

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 (W. acuminata and P. airoides) and then placed in a drying oven for 4 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 4-5 days during the first 6 weeks of seedling establishment, after which each pot was watered every 7 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. $650 \mu mol m^{-2} s^{-1}$) 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-h 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 4 months after planting, all pots were harvested and aboveground biomass measured. Aboveground biomass and number of inflorescences (for *W. acuminata*) were 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).

To statistically analyse the 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 inflorescences 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) (Fig. 1d). 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 three species combinations (W. acuminata, W. acuminata + A. cupaniana, and W. acumi*nata* + *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 inflorescences produced (*W. acuminata* only) across a range of species' relative frequencies in a community. *Pentameris 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 (a continuous variable). Survival, flowering probability, and inflorescence count were all modelled using error structures as described above. Mean biomass per plant was square-root transformed instead of In-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; see Online 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

Environmental variables

No significant differences were detected in environmental variables between mixture and monoculture plots at either reserve (Appendix Table 4).

Effect of A. cupaniana and P. airoides on W. acuminata in the field

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 inflorescences produced per surviving individual declined significantly with increasing conspecific density (biomass: p = 0.02, number of inflorescences: p = 0.005; Table 1; Fig. 2b, c). Though biomass and inflorescence count visually appeared to modestly increase in the highest density plots, quadratic terms were not significant (data not shown).

By contrast, inflorescence production for *W. acuminata* individuals declined significantly in diverse exotic neighbourhoods (estimate: -1.88, SE: 0.58, z: -3.23, p=0.001)

Table 1Effects of the presenceof A. cupaniana and conspecificdensity on various metricsof performance (survival,In-transformed biomass (g), andnumber of inflorescences) ofW. acuminata in the field usinglinear mixed-effect models

	Response of W. acuminata					
	Proportion surviving	Biomass per individual	Inflorescence count per flowering indi- vidual			
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			

Values indicate mixed-effects model coefficients and SEs in parentheses. Variance estimates are reported within and among plots, which were specified as a random effect. Asterisks denote level of significance (* $p \le 0.05$, **p < 0.01, ***p < 0.001)



Fig. 2 Performance of W. acuminata whilst growing in monoculture, in mixture A. cupaniana, or in the presence of P. airoides in the field: a proportion surviving, **b** aboveground biomass (g) per individual, c number of inflorescences per individual by conspecific abundance (x axis), d the number of inflorescences per W. acuminata individual growing without competitors ("Solo (none)"), in exotic neighbourhoods of only P. airoides, and in diverse exotic neighbourhoods ("Other exotics"). Solid line = monoculture, dashed line = in mixture with A. cupaniana. For analytical results, refer to Table 1

as well as neighbourhoods composed of *P. airoides* only (estimate: -2.32, SE: 0.67, z = -3.50, p = 0.0005) compared to solo individuals grown in the absence of competition. This pattern was not further affected by the density of competitors in plots (estimate: 0.17, SE: 0.09, z = -0.10, p = 0.09).

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

At low conspecific abundances, *W. acuminata* survival was reduced only when *P. airoides* was also present (p=0.007; Table 2; Fig. 3a).

By contrast, *W. acuminata* biomass per individual was not different between monoculture and two-species communities

	Response of W. acuminata					
	Proportion surviving	Biomass per individual	Proportion flowering	Inflorescence count per flowering indi- vidual		
Low W. acuminata density						
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 es	timates)					
Among pot	1.18	< 0.0001	< 0.0001	< 0.0001		
Within pot	NA	1.17	NA	0.61		
Medium W. acuminata densit	у					
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 (variance es	timates)					
Among pot	0.19	< 0.0001	0.12	0.12		
Within pot	NA	1.42	NA	0.61		
High W. acuminata density						
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 (variance es	timates)					
Among pot	1.65	0.06	0.08	0.23		
Within pot	NA	1.80	NA	0.05		

 Table 2
 Effects of the presence of A. cupaniana and P. airoides on various performance metrics (survival, In-transformed biomass (g), proportion flowering, and number of inflorescences) of W. acuminata in growth chambers using linear mixed-effects models

Values indicate mixed-effects model coefficients and SEs in parentheses from the separate models conducted for *W. acuminata* at low, medium, or high densities (10, 30, and 50 W. *acuminata* individuals, respectively). Variance estimates are reported within and among pots, which were specified as a random effect. Asterisks denote level of significance (* $p \le 0.05$, **p < 0.01, ***p < 0.001)

containing either grass species at any abundance (Table 2; Fig. 3b). However, direct *post hoc* pairwise comparisons revealed that at high conspecific abundances, *W. acuminata* individuals were significantly larger when *A. cupaniana* was also present (estimate: 0.64, SE: 0.27, adjusted p = 0.04).

The proportion of *W. acuminata* survivors flowering was significantly lower at high conspecific abundances when *P. airoides* was present relative to when *A. cupaniana* was present or neither grass was present (Table 2; Fig. 3c; p = 0.02), but was otherwise unaffected.

Of the *W. acuminata* individuals that flowered, the number of inflorescences produced per individual was significantly lower at low conspecific abundances when *P. airoides* was present than in monoculture or in mixture with *A. cupaniana* (p=0.02; Table 2; Fig. 3d).

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

Survival was not significantly related to relative frequency for any species (Table 3; Fig. 4a), but frequency dependence

was evident in other performance measures to varying degrees.

Waitzia acuminata individual aboveground biomass (averaged per pot) declined as its relative frequency increased in communities also containing *A. cupaniana* (p < 0.0001; Table 3; Fig. 4b). This density-dependent biomass effect was not evident when *W. acuminata* was grown with *P. airoides* (Table 3; Fig. 4b), although *W. acuminata* biomass was, on average, lower when growing with *P. airoides* than with *A. cupaniana* (p = 0.02; Online 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

Fig. 3 Performance of W. acuminata in monoculture (black circles), in mixture with A. cupaniana (grey triangles), and in mixture with P. airoides (light grey squares) by conspecific abundance category (10, 30, or 50 individuals), including: mean \pm SE, **a** proportion of individuals surviving, b aboveground biomass (g) per plant, c proportion of surviving individuals flowering, and d the number of inflorescences per flowering individual. Letters denote significant differences among species combinations within a given W. acuminata abundance category (x axis). For analytical results, refer to Table 2

was found for *W. acuminata* inflorescence 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 seemingly functionally similar exotic annual grass species interact in distinct ways with a common native forb. These differences are evident both in the field as well as in controlled growth chamber conditions. For W. acuminata, the balance between intra- versus interspecific impacts shifted according to its density, the identity of competitors, and the metric of performance. Our results underscore the potential for seemingly similar exotic competitors to mediate density dependence in native species 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. Our results also suggest that one should be cautious in making inferences using trait-based approaches. There is surely some difference between these species in traits that account for their divergent impacts, but this difference is not captured in the morphological and life-history variables that are easily discerned and typically used in traitbased approaches in invasion biology.

Diverse impacts of exotic grasses in the field

In the field, interactions between *W. acuminata* and *A. cupaniana* were largely neutral or positive, whereas 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. These findings were robust across a range of *W. acuminata* abundances in both reserves. We acknowledge that field interactions between *W. acuminata* and each focal exotic grass were observed at different sites. These sites, however, are relatively close in proximity and are environmentally similar. Furthermore, interactions were not modified by differences in within-site environmental conditions at either site.

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

	Response					
	Proportion surviving	Mean biomass per individual	Proportion flowering	Inflorescence count per flowering indi- vidual		
W. acuminata (with A. cup	paniana)					
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 (varianc	e estimates)					
Among pot	1.04	0.001	0.18	0.05		
Within pot	NA	NA	NA	0.71		
W. acuminata (with P. air	oides)					
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 (varianc	e estimates)					
Among pot	0.12	0.005	0.46	0.08		
Within pot	NA	NA	NA	0.65		
A. cupaniana (with W. act	uminata)					
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 (varianc estimates)	e	- 0.04 (0.59)				
Among pot	2.88	0.0009	0.27			
Within pot	NA	NA	NA			
P. airoides (with W. acum	inata)					
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 (varianc	e estimates)					
Among pot	7.12	0.0025	0.39			
Within pot	NA	NA	NA			

Table 3 Effect of relative frequency (ranging from 0.18 in two-species mixture to 1.0 in monoculture) of *W. acuminata, A. cupaniana,* and *P. airoides* on performance metrics (survival, sqrt-transformed

mean biomass per individual (g), proportion flowering, and number of inflorescences) in growth chambers using mixed-effects models

Values indicate mixed-effects model coefficients and SEs in parentheses. Variance estimates are reported within and among pots, which were specified as a random effect. Asterisks denote level of significance (* $p \le 0.05$, **p < 0.01, ***p < 0.001)

potentially facilitate W. acuminata through indirect positive plant-soil feedbacks (reviewed in Callaway 2007). 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). In addition, while not investigated in this study, the importance of positive higher order interactions (i.e., non-additive effects of interactions between co-occurring, non-focal individuals) has recently been quantified in this system, including among individuals of Aira species and W. acuminata, indicating that they may be involved in facilitative outcomes (Mayfield and Stouffer 2017). Finally, nutrient cycling rates may differ in soils beneath patches of annual grasses compared to soils characteristic of native communities where annual grasses have not occurred historically. For example, Pec and Carlton (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. Waitzia acuminata has a later phenology than A. cupaniana, so it is possible that senescence of A. cupaniana individuals may be beneficial to W. acuminata during its active growth phase by providing a nutrient pulse. Aira cupaniana litter is less persistent than that of other higher biomass common exotic annual grasses (e.g., A. barbata, B. madritensis, and E. longiflora) and native herbaceous species in this system (pers. obs.). Thus, A. cupaniana could potentially serve as a phenologically pulsed nutrient source for W. acuminata individuals (Facelli and Pickett 1991). We did test for differences in nutrient levels and cycling rates between mixtures and monocultures in the field, and found no detectable differences among experimental mixtures, so have no direct evidence for this intriguing possible modality of facilitation.

Fig. 4 Species performance measures of **a** proportion surviving, b mean biomass per individual (g), c proportion of survivors flowering, and d the number of inflorescences per flowering individual of W. acuminata (points transparent and sqrt-transformed for visibility). Species responses are plotted by their relative frequencies in a community of 60 individuals, where W. acuminata (with A. cupaniana) = black dashed/triangle, W. acuminata (with *P. airoides*)=black solid/ circle, A. cupaniana (with. W. acuminata) = grey dashed/triangle, and P. airoides (with W. acuminata) = light grey solid/ circle. Both lines for W. acuminata share the same data points at relative frequency = 1.0. All points have been jittered horizontally for visibility. For analytical results, refer to Table 3 and Online Appendix Table 3

Diverse impacts of exotic grasses in growth chambers

As in the field, the grasses exerted different impacts on W. acuminata in growth chambers. We observed facilitation of W. acuminata by A. cupaniana in the absence of any obvious stressors in growth chamber communities, suggesting that facilitation is not just mediated via the alleviation of strong abiotic stressors. Further research is needed to elucidate the mechanistic underpinnings of this observed facilitation. The fact that this interaction was found in a laboratory setting indicates that this relationship may to a degree occur independently of environmental variation in the field. For example, although the growth chamber experiment did not take place in field-collected soils, there could conceivably be vertical transmission of microbes on seed surfaces, so a microbial component of the facilitative interaction cannot be entirely discounted. The potential role of microbes in mediating changes to plant community structure following invasion has been established (Wolfe and Klironomos 2005), and that could be playing a role in our system. While the potential for microbes to improve coexistence potential among plant species has been noted (Miki et al. 2010), most documented microbially mediated effects of exotic species on native species have been negative or neutral (e.g., Batten et al. 2008; Jordan et al. 2008).

Though we found evidence of local facilitation, caution should be exercised when attempting to relate local-scale positive and neutral pairwise interactions to effects at the landscape scale and 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, which may be masked by current trends in native persistence (Gilbert and Levine 2013). Small-scale microsite conditions may also differentially favour certain species and alter the strength of interactions between native and exotic species. However, we note that in our study, comparable results were retained in laboratory settings, suggesting that the mechanisms at play are robust to variation in local environmental conditions. While two-species mixtures occur naturally in York gum-jam woodlands at the scale examined in this study, local sites are often more diverse than our experimental plots. Moreover, 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 and phenologies (Quevedo-Robledo et al. 2010). In addition, the frequency and magnitude of species interactions, as well as the performance measures affected, may change with environmental stress in complex and poorly understood ways.

Species responses to intraspecific vs interspecific competition

Density dependence in W. acuminata clearly depends on its interspecific milieu. The only occurrence of negative frequency dependence in a species mixture in the growth chamber was for W. acuminata biomass and reproductive investment, which both declined with increasing conspecific frequency in mixtures with A. cupaniana. These results indicate that intraspecific rather than interspecific interactions determine W. acuminata productivity in this mixture. Conversely, interspecific competition was more evident in mixtures with P. airoides, where discordant performance responses were evident. At high densities, despite W. acumi*nata* individuals attaining higher biomass, reproductive output was reduced compared to individuals in monoculture or when 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, making exclusion less likely.

In contrast to W. acuminata, both grasses showed neutral or positive relationships between performance measures and their relative frequency in mixture. Despite being relatively abundant in York gum-jam 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 these predominantly native annual plant communities. Though neither P. airoides nor A. cupaniana are associated with disturbed conditions, high propagule pressure may contribute to their invasion success (Holle and Simberloff 2005) through production of large quantities of non-dormant, readily germinable seed, compared to the rate of viable non-dormant seed production by native species in this system (Lai et al. 2015; Wainwright and Erickson unpublished data). Thus, a combination of insensitivity to interspecific competition, neutral or even positive density dependence, and relatively

high fecundities may underlie the invasion success of these species.

Conclusions

Here, we present multiple lines of evidence suggesting that a native plant species benefits from interactions with an exotic "benefactor" species. Positive interactions of this nature have been documented much less often than negative interactions, despite their potential prevalence in invaded plant communities. The results of this study also suggest that under certain conditions, positive interactions may promote coexistence between native and exotic species in natural plant communities. Furthermore, comparable effects were not observed for a second, seemingly quite similar exotic species. Another result from our study is that one impact of interspecific interactions might be a modification in the strength of intraspecific density dependence in a focal species. Intraspecific density dependence is a fundamental driver of plant population dynamics, yet how such density dependence is influenced by interspecific interactions has been rarely examined. Our findings suggest that this topic warrants more focused scrutiny across taxa and ecosystems.

Our findings underscore the need for approaches to understanding invaded plant communities that are more inclusive of variable species interactions and the ways which they may respond to further environmental change. Recently, exotic dominance has been highlighted as a better option than species richness for assessing the 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, in part because interactions can be positive as well as negative. Moreover, our study provides an example of why the impacts of invasion cannot be easily predicted or generalized, given our demonstration of the disparate impacts of very similar exotic species.

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Author contribution statement All authors conceived the ideas underlying the study. The experiments were designed primarily by CW and MM with input from RH. CW collected the data with input from RH and analysed the data with input from MM. CW wrote the manuscript with substantial input from RH and MM. **Data availability** The data sets generated and/or analysed during the current study are available in the figshare repository, https://doi.org/10.6084/m9.figshare.8316515.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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