

1 **Title:** Diverse outcomes of species interactions in an invaded annual plant community

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3 **Running head:** Interactions in an invaded annual plant community

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25

26 **Abstract**

27

28 *Aims*

29 Despite acknowledgement that interactions among native and exotic species are important for
30 determining the structure and diversity of novel communities, directed experiments using
31 multiple exotics from the same system are rare. Recent observational studies have highlighted
32 distinct ways that exotic species interface with resident natives across invaded communities.
33 The correlative nature of these studies, however, has provided few details about the
34 mechanisms driving distinct interaction outcomes within the same communities.
35 Our aim was to determine how three exotic annual plant species with distinct relationships
36 with local plant diversity impact the performance of a co-occurring native annual in the York
37 gum-jam woodlands of Western Australia.

38

39 *Methods*

40 We grew species in experimental communities in growth chambers at varying total planting
41 densities to assess how interaction outcomes varied among natives and exotics across a
42 gradient of competition intensity. We measured a variety of performance responses, including
43 survival, biomass, and population-level and individual-level reproductive investment.

44

45 *Important findings*

46 Overall, the effects of interspecific versus intraspecific competition on performance
47 production varied with the identity and density of exotic competitors. The exploitative exotic
48 grass *Bromus madritensis* was dominant in polyculture, whereas the diminutive grass
49 *Pentameris airoides* conferred weak intraspecific competition and interspecific facilitation on
50 native *Waitzia nitida*. The exotic broadleaf forb, *Hypochaeris glabra*, suppressed growth and

51 survival of *W. nitida*, while *W. nitida* had weakly negative, neutral, or positive effects on all
52 exotics. These outcomes highlight the complexity of interactions impacting the diversity,
53 stability and structure of plant communities. As few novel communities contain a single
54 exotic species, understanding the competitive dynamics occurring in diverse novel
55 communities is critical for their conservation and restoration.

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57 *Key Words*

58 annual plants, biotic interactions, competition, invasion, novel ecosystems

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76 **Introduction**

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78 In “novel” plant communities where biological invasions, land use change, and climate
79 change are driving shifts in community diversity and structure, a mechanistic understanding
80 of community-level diversity patterns can provide important insights into how communities
81 are likely to change or persist over the long term (Shea and Chesson 2002; Hobbs et al. 2009;
82 MacDougall et al. 2009; HilleRisLambers et al. 2012). Interactions within and among
83 species are commonly invoked as important determinants of local plant community structure
84 in theoretical and observational studies (e.g. Mouquet et al. 2003; Spasojevic and Suding
85 2012), and are well known to have diverse outcomes, ranging from negative (e.g. Goldberg et
86 al. 2001; Hierro and Callaway 2003; Dangremond et al. 2010) to positive (e.g. Wootton 1994;
87 Callaway et al. 2005; White et al. 2006; Soliveres et al. 2011). Still, experimental evaluation
88 of their realized importance to long-term coexistence and stability of natural plant
89 communities has not kept pace (Siepielski and McPeck 2010).

90

91 Experimental investigation of local scale species interactions can provide important insights
92 into how plant communities persist following environmental change. For example, measuring
93 the impacts of exotic species on native species over small spatial scales is key for
94 determining the contribution of local interaction dynamics to exotic spread and persistence
95 relative to other factors such as abiotic disturbance (MacDougall and Turkington 2005).

96 Much research has been devoted to describing attributes of exotic species that may underlie
97 their success as invaders, including traits and life-history strategies that differ from the native
98 recipient community (Pysek and Richardson 2007; van Kleunen et al. 2010), particularly
99 traits that enable competitive exclusion of native species (Vila and Weiner 2004). There are
100 cases, however, where exotic species that persist in recipient communities are not associated

101 with declines in native species diversity (Levine 2000; Harrison et al. 2006), even at small
102 spatial scales (Lai et al. 2015), though these examples are less frequent than those invoking
103 competitive exclusion.

104

105 Indeed, mounting theoretical and observational evidence has recently challenged the
106 perception that exotic species exert predominantly negative impacts on native species
107 diversity (Melbourne et al. 2007; Davis et al. 2011). For example, in a species-rich,
108 phosphorus-limited annual plant system in Western Australia, Lai et al. (2015) found that
109 exotic species ranged dramatically in their associations with native species richness at
110 neighbourhood scales. Specifically, they found evidence of two distinct “types” of exotics in
111 this system: (1) “exploiters”, which occupied high positions along community trait
112 hierarchies and were negatively associated with native species richness, especially under
113 artificially P-enriched conditions, and (2) “coexisters”, which occupied intermediate positions
114 along trait hierarchies, did not respond (or responded negatively) to P enrichment, and were
115 neutrally or positively associated with native richness (Lai et al. 2015). A third group of
116 exotics had no significant relationships with native richness or P (referred to by Lai et al.
117 (2015) as “other”), which we refer to here as “eccentrics”. Though these findings underscore
118 the growing awareness that not all exotic species have direct negative effects on resident
119 natives (Davis et al. 2011), the mechanisms underlying these varied relationships have yet to
120 be explored experimentally.

121

122 Past experiments designed to quantify the contributions of local scale species interactions to
123 plant diversity maintenance have been criticized for failing to incorporate natural variation in
124 plant densities (Damgaard 2008). These criticisms stem from the potential for nonlinear
125 responses to changes in community density, which occur commonly at small scales in natural

126 systems (Damgaard 2008; but see Levine et al. 2008). The density of individuals in a
127 community, along with species composition, may determine outcomes of competitive
128 interactions that are critical for coexistence. For example, the magnitude of interspecific
129 versus intraspecific competition among annuals may vary with total density depending on the
130 life history stage examined (Leger and Espeland 2010), driving distinct outcomes of these
131 interactions across locations and species combinations.

132

133 Using experimental communities, we varied species composition and density to explore the
134 competitive dynamics of three common exotic and one common native species that regularly
135 co-occur in the York Gum woodlands of southwest Western Australia. Each exotic
136 represents one of the distinct invasion strategies identified in Lai et al. (2015) (exploiters,
137 coexisters, and other/eccentrics) as contributing to different processes that culminate in these
138 diverse novel communities. We start with the prediction that the exotic exploiter species will
139 be competitively dominant when grown with interspecific competitors (native or exotic),
140 exerting particularly strong negative impacts on the native forb species. By contrast, we
141 expect the exotic coexister to have weak interspecific competitive effects on the native
142 species. Finally, given the eccentric exotic species' lack of consistent association with native
143 species in this system (Lai et al. 2015), we expect that it will have weak or intermediate
144 negative impacts on the native forb across the experimental density gradient. The specific
145 questions we ask are:

146

147 1) Do different types of exotic species have predictable responses to intraspecific and
148 interspecific competition based on observed associations with native species diversity in the
149 field?

150 2) How important is plant density in determining competitive outcomes for these distinct
151 species types?

152

153 **Materials and methods**

154

155 *Assembly of experimental communities*

156

157 Experimental communities were made up of winter annual species commonly found in the
158 understory of York gum (*Eucalyptus loxophleba*) – jam (*Acacia acuminata*) woodlands in
159 southwestern Australia. This community type was formerly widespread, but extensive land
160 clearing for the region’s agricultural industry has resulted in fragmentation and degradation
161 of remaining communities, particularly due to invasion by exotic annual grasses and
162 broadleaf weeds (Prober and Wiehl 2011; Prober et al. 2011; Dwyer et al. 2014). Four
163 commonly co-occurring York gum-jam woodland annuals were planted in monocultures,
164 two-species, or three-species mixtures at different densities to assess competitive outcomes
165 among growth forms and origins along a gradient of density. Species were chosen because
166 they are some of the most common native and exotic representatives of their growth form and
167 (for exotics) invader “strategy” in York gum-jam understory annual communities, and
168 because they are commonly observed to co-occur at local scales in natural communities (Lai
169 et al. 2015; Fig S1). The three-species mixture consisted of native slender erect herb *Waitzia*
170 *nitida* (Asteraceae), exotic rosetted herb *Hypochaeris glabra* (Asteraceae; “eccentric”), and
171 robust exotic grass *Bromus madritensis* (Poaceae; “exploiter”), and the two-species mixtures
172 consisted of each constituent species pair (Table S1). We included an additional two-species
173 pair, *W. nitida* and diminutive exotic grass *Pentameris airoides* (Poaceae; “coexister”), to

174 enable comparisons of competitive effects of the two exotic grasses (*P. airoides* and *B.*
175 *madritensis*) which exhibit opposing invasion strategies.

176

177 All communities were planted from seed at three density levels: low (21 individuals per pot),
178 medium (51 individuals per pot), or high (81 individuals per pot) in pots with a surface area
179 of 78.5 cm². Each species mixture (n=9) and density (n=3) combination was, on average,
180 replicated three times, for a total of 81 communities at the outset of the experiment, though
181 four pots experienced poor germination and were discarded from all analyses (Table S1). The
182 high density treatment was chosen based on a preliminary pilot study comprising ecologically
183 similar York gum-jam woodland annuals, in which 81 plants per pot created an environment
184 of intense competition among individuals. The low density treatment was chosen based on
185 naturally occurring densities recorded in the field at peak biomass in 2011 (Dwyer et al.
186 2015). Equal proportions of each species were planted in every mixture (ratios of 1:1:1 or
187 1:1) to examine competitive outcomes influenced by density as opposed to relative
188 frequency.

189

190 Seeds were collected from mature plants in several York gum-jam woodland remnants in
191 October 2011 and then underwent a four week dry-after-ripening period at 40°C in a drying
192 oven to alleviate physiological dormancy (important for a number of native Australian forb
193 species; Hoyle et al. 2008). All seeds were then stored in darkness at room temperature until
194 planting. Seed viabilities were assessed according to procedures in the AOSA/SCST
195 Tetrazolium (TZ) handbook (Miller 2010), and were used to estimate the number of seeds
196 needed of each species to reach target densities in each treatment. Soil was obtained from The
197 University of Queensland glasshouse facilities and closely resembled the texture and nutrient
198 content of soil found in York gum-jam woodlands (< 5.0 mg/kg plant-available P; Dwyer et

199 al. 2015). Seeds of component species were mixed evenly and scattered on the soil surface
200 before the first watering. Each pot was hand-watered every four days during the first six
201 weeks and every seven days thereafter (35 mL). Throughout the establishment phase,
202 communities were weeded regularly to maintain prescribed plant densities.

203

204 Experimental communities were grown in two temperature-controlled growth chambers
205 (ThermoFisher Scientific, Adaptis 1000) equipped with fluorescent tubes (c. $650 \mu\text{mol m}^{-2}\text{s}^{-1}$)
206 at The University of Queensland. Pots were randomized between both chambers every week
207 to account for any potential growth chamber or shelf differences. Photoperiod was set to a 12
208 hour cycle, and temperatures ranged from 17.0°C (day) to 7.0°C (night) based on mean
209 winter temperatures typical of the central wheatbelt region in July (BOM 2014) when annual
210 plants typically establish.

211

212 We assessed three components of performance for each of the four focal species across
213 competitor and density combinations: survival, reproductive potential (proportion of plants
214 flowering and flower count as opposed to seed production, as natural pollination mechanisms
215 were absent in growth chambers), and mean biomass per individual. Survival and
216 reproductive potential were recorded for each species in each community at the end of the
217 experiment (c. 120 days). At this time, peak aboveground biomass had been reached and was
218 harvested, separated by species for each community, and oven-dried for three days at 60°C
219 before weighing.

220

221 *Statistical analysis*

222

223 Data analyses were conducted in R (v 3.1.2, R Core Team 2014) using packages lme4 (Bates
224 et al. 2014), and nlme (Pinheiro et al. 2014).

225

226 Species combination and density effects on plant performance were investigated for each
227 species. Density was treated in models as categorical (low, medium, high) when modelling
228 number of flowers per individual, and as a continuous variable when comparing mean
229 biomass per individual, reproductive potential, and survival. Treating density as a continuous
230 variable accounted for instances where target densities were not reached (although equal
231 proportions of each species were still maintained) and therefore comparisons of performance
232 according to discrete density categories among species would not have been valid.

233

234 The proportion of individuals surviving at 15 weeks, as well as proportion of surviving plants
235 with reproductive potential (having buds or flowers at 14 weeks) were analysed using
236 generalized linear mixed effects models with binomial errors and logit link function, and pot
237 specified as a random effect to account for over-dispersion (Elston et al. 2001). Number of
238 flowers per individual (for *H. glabra* and *W. nitida* only) were analysed using generalized
239 linear mixed effects models with Poisson errors and a log link function, with plant nested
240 within pot as a random effect to account for over-dispersion. Biomass data were ln-
241 transformed to improve normality of residuals and analysed using linear mixed effects
242 models with pot specified as a random effect to account for multiple observations per species
243 within each community. For all models, two-way interactions among fixed effects were
244 explored and removed if not significant

245

246 **Results**

247

248

249 *Survival responses to competition*

250

251 Density-dependence and competitor identity influenced focal species survival to varying
252 degrees (Fig. 1; Table S2). *W. nitida* survival was negatively density dependent in
253 combination with all competitors; however, survival was highest across all densities when it
254 was grown with *P. airoides* (Fig. 1a; Table S2). Exotic forb *H. glabra* survival was
255 particularly sensitive to increasing plant density when grown in mixture with *W. nitida* and *B.*
256 *madritensis* (Fig. 1b; Table S2). By contrast, *B. madritensis* survival was relatively
257 unaffected by inter- or intraspecific competition (Fig. 1c) compared to other species in this
258 experiment, though greater replication may have increased our ability to detect subtle density
259 effects. *B. madritensis* was largely unaffected by either density or the composition of its
260 competitive neighbourhood (Fig. 1c; Table S2). However, *B. madritensis* mortality appeared
261 to increase when grown in high-density mixtures of *W. nitida* and *H. glabra* (Fig. 1c), though
262 this was not significant ($p=0.52$). Conversely, exotic grass *P. airoides* survival decreased
263 when grown densely with *W. nitida*, relative to monocultures of similar density (Fig. 1d;
264 Table S2).

265

266 *Reproductive responses to competition*

267

268 Reproductive potential, measured as the proportion of initial individuals budding or flowering
269 near the end of the experiment, did not mirror species survival responses to competitor
270 identity and density (Table 1). No surviving *W. nitida* individuals invested in reproduction in
271 the presence of *B. madritensis*. A reduced proportion of *W. nitida* individuals invested in
272 reproduction when grown with *H. glabra* ($p<0.001$). By contrast, a greater proportion of

273 surviving *W. nitida* invested in reproduction when grown with *P. airoides* ($p < 0.001$) than in
274 monoculture. However, per capita flower count of *W. nitida* individuals was neither affected
275 by community density nor competitor identity compared to low density monocultures (Table
276 S4). Compared to flowering in monoculture, *H. glabra* displayed significantly reduced
277 reproductive investment when grown with *B. madritensis* (either alone or in three-species
278 mixture with *W. nitida*, Table 1), but increased when grown with *W. nitida* alone ($p = 0.009$).
279 Further analysis of flower count revealed that per capita flower production of *H. glabra*
280 declined in high density communities ($p = 0.01$), as well as communities containing both *B.*
281 *madritensis* and *W. nitida* ($p = 0.01$) compared to low density monocultures (Table S4).
282 Reproductive investment for *P. airoides* was not affected by density in monocultures, but
283 declined when grown in high-density mixtures with *W. nitida* (Table 1). The proportion of
284 surviving *B. madritensis* that invested in reproduction was negatively density dependent
285 overall ($p < 0.001$), and unlike the other focal species was greater in all polycultures than in
286 monoculture (Table 1).

287

288 *Biomass responses to competition*

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290

291 Biomass responses to competition varied among species (Fig 2; Table S3). Biomass of
292 surviving *W. nitida* individuals was not influenced by initial planting density ($p = 0.89$).
293 However, *W. nitida* experienced reduced biomass in all competitor combinations that
294 contained exotic grass *B. madritensis* (*B. madritensis*: $p = 0.008$, *B. madritensis* + *H. glabra*:
295 $p < 0.001$; Fig 2a) compared to monoculture. We note that biomass values for *W. nitida*
296 growing in mixtures containing *B. madritensis* are only available at low densities, as no *W.*
297 *nitida* individuals survived in higher density mixtures. Similarly, *H. glabra* had lower

298 biomass per individual in both mixtures containing *B. madritensis* (*B. madritensis*: $p < 0.001$,
299 *W. nitida* + *B. madritensis*: $p < 0.001$; Fig. 2b) than in monoculture. Unlike *W. nitida*, the
300 individual biomass of *H. glabra* and *B. madritensis* plants declined with increasing densities
301 across all competitor combinations (all $p < 0.001$; Fig. 2c). For *B. madritensis*, intraspecific
302 competition reduced biomass per individual more than interspecific competition (Fig. 2c;
303 Table S3). For *P. airoides*, neither planting density nor growing with *W. nitida* significantly
304 influenced biomass of surviving individuals relative to monoculture (Density: $p = 0.69$, *W.*
305 *nitida*: $p = 0.12$), although the inability to detect relationships among these variables may have
306 been due to low replication (Fig. 2d).

307

308 **Discussion**

309

310 Changes in the identity of species in competition mixes were generally more important than
311 plant density for determining the relative strength of intra- versus interspecific competition.
312 Across the four species, we observed a competitive hierarchy consistent with our initial
313 predictions. The “exploiter” exotic grass *B. madritensis* was the competitive dominant,
314 followed by the “eccentric” exotic forb *H. glabra*, the native *W. nitida*, and the “coexister”
315 exotic *P. airoides*, which only had neutral or positive effects on *W. nitida*. Our study provides
316 clear evidence of distinct competitive strategies and impacts of successful exotic species from
317 the same novel community. Such details are important for gaining a holistic understanding of
318 how invaded communities maintain large persistent populations of native species despite
319 extensive invasion.

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324 Exotic “exploiter” *B. madritensis*

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326 Consistent with our initial predictions, among the three focal species for which all 1-, 2- and
327 3-way combinations were tested (*B. madritensis*, *H. glabra*, and *W. nitida*), we found a
328 competitive hierarchy topped by *B. madritensis*. It is possible that *W. nitida* may be able to
329 locally persist in the presence of *B. madritensis* or *H. glabra* provided that their field
330 densities remain lower than those investigated in this experiment. In local patches where *B.*
331 *madritensis* densities are naturally low, abiotic factors not tested in this experiment may
332 contribute to invasion resistance (Prober and Wiehl 2011). Natural densities, however, are
333 often as high as or higher than those used in this study, especially in disturbed and P-enriched
334 areas (Dwyer et al. 2015). Thus, stable coexistence of these species is unlikely in natural
335 assemblages, with the potential exception of areas in which low-nutrient microsites are far
336 more common than P-enriched or disturbed microsites.

337

338 *B. madritensis*' consistently high survival in this experiment is not surprising given how
339 successful the species is in most of its introduced range (IUCN/SSC Invasive Species
340 Specialist Group 2005). Like many other exotic annual grasses, *B. madritensis* may grow and
341 establish more rapidly than natives (DeFalco et al. 2003) and naturally forms dense swards
342 (Salo 2004), which may confer an advantage over native forbs such as *W. nitida*. Though not
343 explicitly tested here, this advantage may be mediated by competition for light (Dwyer et al.
344 2015), water, and nutrients (D'Antonio and Vitousek 1992). Furthermore, in natural systems
345 *B. madritensis* has the potential to promote positive feedbacks through alteration of
346 disturbance regimes, particularly fire (D'Antonio and Vitousek 1992; Brooks 1999; Brooks
347 2000). *B. madritensis* was not, however, immune to intraspecific competition. The species

348 invested less in reproduction and individuals were smaller on average in high-density
349 treatments, consistent with other studies of this species (Wu and Jain 1979) and its congeners
350 (Lowe et al. 2003; Vasquez et al. 2008). Given *B. madritensis* ' widespread success as an
351 invader, it seems that its high survival is sufficient to offset density-dependent declines in
352 biomass and reproductive output, at least in its invaded ranges. While the average size of *B.*
353 *madritensis* individuals was reduced by crowding, individuals were still larger on average
354 and more likely to invest in reproduction when grown in mixed stands than in monoculture.
355 Overall, this suggests that *B. madritensis* was more negatively impacted by intraspecific than
356 interspecific competition, though the absolute effects of either form of competition were
357 small relative to those observed for other species in this study.

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362 *Exotic "coexister" P. airoides*

363 In contrast to *B. madritensis*, neither biomass nor reproductive investment of the diminutive
364 exotic grass *P. airoides* changed significantly across the intraspecific density gradient
365 explored in our experiment. Mortality, however, was similarly low in the highest density
366 monocultures of this species, particularly when compared to mixtures of similar density
367 containing native *W. nitida*. Positive intraspecific interactions have been demonstrated in
368 both annual (e.g. Levine and HilleRisLambers 2009; Leger and Espeland 2010) and perennial
369 species (e.g. Fajardo and McIntire 2011) and often result from the amelioration of
370 environmental stresses outweighing the competitive effects of intraspecific aggregation.
371 Environmental stress gradients were not imposed in this study, but it is possible that soils

372 beneath denser *P. airoides* communities may have been more mesic due to reduced
373 evaporation at the soil surface (Callaway 2007).
374
375 Interestingly, for all densities of *W. nitida*, survival was higher when additional *P. airoides*
376 plants were present in mixtures, suggesting that *P. airoides* may facilitate some natives in this
377 system. Recently, more emphasis has been placed on the role that positive interactions play in
378 structuring plant communities (Brooker et al. 2008). The potential role of *P. airoides* as a
379 facilitator has not been previously documented to our knowledge. Field surveys spanning the
380 York gum-jam woodland range indicate that *P. airoides* and *Aira cupaniana*, a functionally
381 similar exotic grass in this system, are positively associated with native species richness both
382 at regional and local scales (Lai et al. 2015). Further studies of *P. airoides* (and *Aira* species)
383 in combination with more native species are needed to draw general conclusions about the
384 potential importance of these exotics in maintaining native diversity in these communities.
385
386
387 *Exotic “eccentric” H. glabra and native forb W. nitida*
388 Overall, both forbs, whether native or exotic, displayed higher intraspecific density-
389 dependent mortality than the exotic annual grasses. which demonstrated negligible self-
390 thinning. By contrast, *W. nitida* exhibited strong contest competition (Crawley 1990),
391 resulting in taller (but not more massive) survivors under intense intraspecific competition
392 (pers. obs.) potentially indicating compensatory growth, consistent with previous suggestions
393 that competition for light may be key in regulating competitive outcomes for forbs in this
394 system, particularly under moist, P-enriched conditions (Dwyer et al. 2015).
395

396 This potential for self-limitation is reflected in observed patterns of co-occurrence over local
397 scales in the field based on natural species abundances. *W. nitida* is a widespread species
398 positively associated with native annual plant species richness in York gum-jam woodlands
399 (Lai et al. 2015). Like many annuals native to semi-arid systems, the abundance of *W. nitida*
400 is potentially co-regulated by biotic interactions and seed dormancy mechanisms which
401 buffer the effects of interannual climate variation (Chesson 2000). *H. glabra*, while also fairly
402 ubiquitous in York gum-jam woodlands, is unlike many other exotic annuals in this system in
403 that it is not associated with soil eutrophication, nor is it associated with reduced species
404 richness (Lai et al. 2015). Because it does not show evidence of dormancy or seedbank
405 formation (Baker and O'Dowd 1982), we suspect that additional density-dependent processes
406 such as herbivory may be involved in regulating its abundance in the field.

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413 *Conclusion*

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415 Here, we have documented a range of interaction dynamics that are entirely consistent with
416 the invasion outcomes and diversity patterns observed in natural York gum annual
417 communities. There are clearly myriad potential outcomes of interactions among different
418 species over small scales, depending both on species-specific attributes and the density of the
419 community.

420

421 Rather than focusing on the outcomes of one type of interaction using species pairs, we
422 revealed a diverse suite of interaction outcomes in monocultures, pairs, and three-species
423 mixtures. Our results suggest that neutral and positive interactions between exotics and
424 natives may be more prevalent than is currently appreciated. Further, this study provides
425 insight into the diverse processes relevant to the assembly of communities comprising native
426 and exotic species. Future research should be directed towards clarifying the importance of
427 these interactions relative to other processes in promoting the stability of complex novel
428 communities.

429

430 **Supplementary Data:** Photos of focal species, species combination descriptions, and
431 detailed model results from mixed effects models of species survival and biomass responses
432 are available online as a supplement to this manuscript.

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578 **Table 1** Model coefficients and (SEs) from mixed effects models of focal species
 579 reproductive investment (proportion of initial plants budding or flowering) at 14 weeks in
 580 different competitor combinations by initial planting densities. The intercept values relate to
 581 performance in monoculture (growing with intraspecifics). A dash corresponds to instances
 582 when the focal species combination did not occur, “NS” corresponds to cases where no
 583 interaction terms were significant and a simpler additive model was used, and “NA”
 584 corresponds to cases where interactions could not be estimated from the data. Asterisks
 585 denote level of significance (*: $p \leq 0.05$; **: $p < 0.01$; ***: $p < 0.001$).

Fixed effects	Focal species			
	<i>B. madritensis</i> (<i>exploiter</i>)	<i>H. glabra</i> (<i>eccentric</i>)	<i>P. airoides</i> (<i>coexister</i>)	<i>W. nitida</i> (<i>native</i>)
Intercept (intraspecifics)	-2.93 (0.82)***	-0.35 (0.31)	-0.40 (0.44)	-0.38 (0.28)
Total plant density	-0.05 (0.01)***	-0.02 (0.005)***	-0.004 (0.008)	-0.03 (0.006)***
Competitor combination: (interspecifics)				

<i>B. madritensis</i>	-	-2.81 (0.63)***	-	NA (0)
<i>B. madritensis</i> + <i>H. glabra</i>	-	-	-	NA (0)
<i>H. glabra</i>	3.01 (0.87)***	-	-	-1.87 (0.56)***
<i>P. airoides</i>	-	-	-	1.13 (0.28)***
<i>W. nitida</i>	1.65 (0.93).	0.67 (0.26)**	0.73 (0.79)	-
<i>W. nitida</i> + <i>B. madritensis</i>	-	-1.67 (0.47)***	-	-
<i>W. nitida</i> + <i>H. glabra</i>	2.54 (0.88)**	-	-	-
Competitor combination ×				
Density interactions:				
<i>B. madritensis</i> + <i>H. glabra</i> : Density	NS	NS	-	NS
<i>H. glabra</i> : Density	NS	NS	-	NS
<i>P. airoides</i> : Density	NS	NS	-	NS
<i>W. nitida</i> : Density	NS	NS	0.04 (0.02)**	NS
<i>W. nitida</i> + <i>B. madritensis</i> : Density	NS	NS	-	NS
<i>W. nitida</i> + <i>H. glabra</i> : Density	NS	NS	-	NS
Random effects				
Among pot variance	1.04	0.10	0.26	0.06

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613 **Figure captions**

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616 **Fig. 1** Proportion of individuals surviving by total density of individuals in a community for

617 a) *W. nitida*, b) *H. glabra*, c) *B. madritensis*, and d) *P. airoides*. Lines correspond to the

618 different competitor combinations as follows: Intraspecifics = black solid, *B. madritensis* =

619 black long dash and open circle, *H. glabra* = light gray solid, *P. airoides* = gray long dash

620 and open circle, *W. nitida* = solid gray, *B. madritensis* + *H. glabra* = gray short dash and

621 triangle, *B. madritensis* + *W. nitida* = light gray short dash and triangle, *H. glabra* + *W.*

622 *nitida* = black short dash and triangle. Points have been jittered for visibility (amount =
623 0.025).

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625 **Fig. 2** Mean biomass per individual by total density of individuals in a community for a) *W.*
626 *nitida*, b) *H. glabra*, c) *B. madritensis*, and d) *P. airoides*. Lines correspond to the different
627 competitor combinations as follows: Intraspecifics = black solid, *B. madritensis* = black long
628 dash and open circle, *H. glabra* = light gray solid, *P. airoides* = gray long dash and open
629 circle, *W. nitida* = solid gray, *B. madritensis* + *H. glabra* = gray short dash and triangle, *B.*
630 *madritensis* + *W. nitida* = light gray short dash and triangle, *H. glabra* + *W. nitida* = black
631 short dash and triangle

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