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**1Title: Competition reverses the response of shrub seedling mortality
2and growth along a soil moisture gradient**

3

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23**Running head:** Competitive dynamics vary with rainfall

24**Summary:**

251. Predicting species responses to climate change involves understanding
26both the direct effects of environmental change, as well as indirect effects
27mediated by altered interspecific interactions. Indirect effects may be
28particularly important for understanding native species responses in systems
29invaded by highly competitive exotic species. For instance, Mediterranean
30climate regions are predicted to experience more frequent drought, and are
31increasingly invaded by exotic annual plants. For native shrubs in these
32regions, seedling establishment is episodic, and associated with high rainfall
33years. However, exotic annual plants also often increase in abundance with
34high rainfall, suggesting competition from exotic annual species could alter
35the relationship between rainfall and shrub seedling establishment. Theories
36such as the stress-gradient hypothesis predict competition intensity should
37increase with resource supply, but there have been few evaluations of
38competitive interactions across experimental gradients of soil moisture
39availability.

402. Here we examined how competition from an exotic annual influenced
41native shrub establishment, across an experimental soil moisture gradient.
42Seedlings of two native shrub species (*Encelia californica* and *Eriogonum*
43*fasciculatum*) were grown with and without an exotic grass competitor
44(*Avena fatua*) across eight water availability levels, and monitored for growth
45and survival. These species are common and abundant in the Mediterranean

46climate region of coastal Southern California, where climate change
47projections include long-term drought for the coming decades.
483. Without competition, shrub seedlings achieved higher growth and survival
49at high water availability levels. However, when grown in competition with
50the exotic grass, shrub seedlings had higher growth and/or survival under
51relatively dry conditions, suggesting competition can modify and even
52reverse species responses to changing rainfall patterns, compared to
53predictions made in the absence of competitors. The exotic grass strongly
54reduced soil nitrate and water availability when it was planted with the
55native shrub seedlings, and the exotic grass responded with positive but
56saturating growth with increasing levels of water addition.
57Synthesis. This experiment demonstrates that competition from invasive
58species can alter native species responses to climate change; consistent with
59ecological theories predicting a positive association between the supply of
60limiting resources and the intensity of competition.

61

62**Key-words:** *Avena fatua*, coastal sage scrub, drought tolerance, *Encelia*
63*californica*, *Eriogonum fasciculatum*, global change ecology, invasion,
64Mediterranean-type ecosystems, plant-plant interactions

65 **Introduction**

66 As the impacts of climate change become ever more apparent,
67 ecologists are being called upon to use ecological theory to forecast species
68 responses (Bellard et al. 2012), and predict ramifications for communities
69 and ecosystems (Smith, Knapp & Collins 2009). Predictions of future shifts in
70 biodiversity need to include not only direct responses to shifting climate, but
71 also indirect effects mediated through shifting species interactions (Suttle,
72 Thomsen & Power 2007; Tylianakis et al. 2008; Kleinhesselink & Adler 2015;
73 Alexander et al. 2016). For instance, invasions by exotic species threaten
74 biodiversity worldwide (Butchart et al. 2010), and have been shown to
75 reduce native diversity especially at local scales (Powell, Chase & Knight
76 2011). Invasive plants also have the potential to alter resident species
77 responses to climate change. Water is a key limiting resource for plant
78 growth, and many mid-latitude areas are expected to experience reductions
79 in precipitation with future climate change, in concert with greater
80 interannual variability in precipitation in many regions (Collins et al. 2013).

81 Native versus exotic species may vary in their ability to capitalize on
82 pulses of soil moisture and to tolerate drought, resulting in the potential for
83 shifting community composition as a result of future precipitation changes
84 (Weltzin et al. 2003). Exotic species have often been hypothesized to benefit
85 disproportionately over native species in response to climate change (Dukes
86 & Mooney 1999), potentially because exotic species have broader climate
87 tolerances than native species (Goodwin, McAllister & Fahrig 1999; Qian &

88Ricklefs 2006). Or, invading species could benefit from climate change by
89having greater phenotypic plasticity than native species (Davidson, Jennions
90& Nicotra 2011), a key adaptation to variable environmental conditions.
91Recent meta-analyses suggest exotic species benefit more than native
92species from high soil moisture (Sorte et al. 2013; Liu et al. 2017), but with
93significant variation in both native and exotic species responses to variation
94in water availability.

95 Climate change induced drought may also alter competitive
96interactions between native and exotic species. Species interactions such as
97competition are often shaped by resource availability (Tilman 1982), and
98numerous observational studies have demonstrated complex shifts in
99species interactions along gradients of aridity and soil moisture (Maestre,
100Valladares & Reynolds 2005; Padilla & Pugnaire 2006). The influence of
101environmental context on species interactions has long been a focus of
102ecological theory. Classically, Grime (1973) predicted that dominant species
103were more likely to competitively exclude subdominant species as
104productivity of the environment increased. Similarly, the stress gradient
105hypothesis asserts that species interactions often shift in strength or even
106direction along environmental gradients, with less intense competition in
107environments that are stressful and/or have low resource availability
108(Bertness & Callaway 1994; Maestre et al. 2009). In contrast, resource-ratio
109theory predicts that competition will be consistently important across
110environmental gradients (Tilman 1988). Although many experimental and

111observational studies have evaluated these theories in relation to overall
112community productivity (reviewed by Goldberg et al. 1999; Rees 2013), few
113experimental studies have evaluated variation in species interactions along
114gradients of soil moisture (but see Pickett & Bazzaz 1978; Kadmon 1995).

115 Several lines of evidence suggest that plant growth should respond in
116a non-linear fashion along moisture gradients. First, classic predictions
117suggest plant growth will increase with precipitation until reaching a
118saturation point (Lieth 1975), after which point another resource or resources
119may become limiting or co-limiting (Liebig 1842; van der Ploeg, Bohm &
120Kirkham 1999; Harpole et al. 2011). Optimal allocation theory (Thornley
1211972; Bloom, Chapin & Mooney 1985; Wilson 1988) predicts that plants will
122allocate a greater portion of biomass to roots when below-ground resources
123are limiting (e.g. water or nutrients) and to above-ground structures when
124light is limiting (Gleeson & Tilman 1992; Poorter et al. 2012). Shifting
125allocation to non-photosynthetic tissues below-ground could also contribute
126to a positive saturating water-productivity relationship if nutrients become
127limiting at high levels of soil moisture (e.g. co-limitation, Hooper & Johnson
1281999). Models demonstrate that variation among species in their height
129(Goldberg et al. 2017), biomass (Rees 2013), or resource uptake rates
130(Everard et al. 2010), can also cause non-linear competition intensities along
131resource gradients. Studies that quantify these non-linear environment-
132performance relationships could greatly aid in the ability of ecologists to

133predict how species are likely to respond to changing environmental
134conditions (Austin & Smith 1989).

135 Drought is expected to be a significant component of climate change in
136mid-latitude regions (Collins et al. 2013), including many Mediterranean -
137type ecosystems (MTEs) worldwide. These semi-arid ecosystems harbor
138exceptional biodiversity, which is under threat from climate change
139(Underwood et al. 2009). For example, the California Floristic Province along
140the western coast of North America is predicted to be a regional climate
141change "hot spot" in the coming decades (Diffenbaugh & Giorgi 2012),
142largely due to shifts in the amount and temporal variability of precipitation.
143The region is expected to experience increasingly persistent drought in the
144coming decades (Seager et al. 2007), in concert with higher interannual
145variability in rainfall (Yoon et al. 2015). Hence, plant species in this region
146may experience both extremes of drought or deluge from year to year.

147 Despite the importance of soil moisture for community composition
148and ecosystem functionality in Mediterranean systems (Lavorel et al. 1998),
149the impacts of shifting rainfall regimes for species interactions - especially
150during initial establishment periods - are poorly understood. Globally, the
151impact of climate change on initial life stages is seen as a key knowledge
152gap (Parmesan & Hanley 2015). The MTEs of Southern California are
153historically shrub dominated (Cleland, Funk & Allen 2016; Parker, Pratt &
154Keeley 2016). For perennial species, including shrubs, seedling
155establishment is a critical demographic stage determining species

156distribution and abundance (Grubb 1977). Low soil moisture limits seedling
157survival (Fenner 1987; Harrington 1991) and semi-arid ecosystems (such as
158this MTE) often have pulses of shrub establishment in years of high rainfall
159(Nicholls 1991; Brown, Valone & Curtin 1997; DeSimone & Zedler 1999;
160reviewed in Holmgren et al. 2006). The MTE region of California is
161increasingly invaded by exotic annual species (Eliason & Allen 1997;
162Seabloom et al. 2006), as are other MTEs globally (Funk et al. 2016). Exotic
163annual grasses in particular are projected to benefit from the rising
164temperatures associated with climate change (Sandel & Dangremond 2012),
165and often increase in abundance following high rainfall years (Hobbs &
166Mooney 1991; Keeley, Fotheringham & Baer-Keeley 2005; Ashbacher &
167Cleland 2015). High growth of exotic annual species could competitively
168suppress native shrub seedlings in high rainfall years, thereby preventing
169shrub recruitment (Eliason & Allen 1997; Seifan, Tielborger & Kadmon 2010).
170Hence in this system and others worldwide, the response of native species to
171combined invasion and shifts in precipitation regime is not well understood
172(Vilà et al. 2007; Bradley et al. 2010).

173 Here we experimentally evaluated how rainfall quantity and
174competition by an exotic annual grass interacted to influence the growth and
175survival of native shrub seedlings. We grew these species under eight levels
176of water addition to enable us to discern between linear and curvilinear
177relationships between soil moisture and species performance. We
178hypothesized that native shrub seedlings grown alone would display a

179positive, saturating relationship between growth and soil moisture
180availability. However, we expected that the focal exotic grass would benefit
181disproportionately from high soil water availability, resulting in competitive
182suppression of shrub seedlings under high rainfall scenarios, and hence a
183reversal of the shrubs' responses observed in the absence of competition.
184

185**Materials and methods**

186 The experiment was conducted in a greenhouse at the University of
187California, San Diego Biology Field Station (32N 53' 7", -117W 13' 48") from
188February to April 2009. Although short-term, this corresponds to the length
189of the growing season documented for the herbaceous community, as well
190as for peak shrub growth, in coastal sage scrub vegetation (Cleland, Funk &
191Allen 2016). Air was continuously circulated with large greenhouse fans, with
192no temperature control, so the plants experienced realistic growing season
193temperatures. The study focused on two native shrub species that are
194widespread and abundant in coastal sage scrub communities - *Encelia*
195*californica* (Asteraceae, common name "coast sunflower") and *Eriogonum*
196*fasciculatum* (Polygonaceae, common name "California buckwheat"). Both
197species are commonly utilized in restoration efforts (Bowler 2000; Padgett,
198Kee & Allen 2000), where competition from exotic annual grasses often limits
199restoration success (Cox & Allen 2008). We planted the native shrubs as
200seedlings either with or without competition from *Avena fatua*, a widespread
201exotic annual grass invader in coastal sage scrub and other California

202ecosystems (D'Antonio et al. 2007). The focal shrub species and exotic
203herbaceous species both germinate in the late fall with the onset of the
204winter rainy season in this MTE (Padgett, Kee & Allen 2000; Wainwright,
205Wolkovich & Cleland 2012).

206 Seedlings of each shrub species (one per pot) were grown from seed
207(RECON Native Plants, San Diego, California) and transplanted into 5-liter
208pots (17 x 17 cm square, 30 cm deep, Stuewe & Sons) containing
209unamended sandy loam topsoil harvested from a local coastal sage scrub
210site (Agriservices, Vista, California). Holes allowed excess water to drain out
211from the bottom of the pots. Seedlings were between 2 and 3 cm tall at the
212time of transplant, and pots were simultaneously seeded with or without *A.*
213*fatua* (40 seeds per pot with an approximate 75% germination rate,
214germination occurred within one week of planting). Pots were arranged in
215three blocks. Each block contained eight replicates of all treatments: each of
216the focal shrub species grown with or without competition, at each of the
217eight levels of watering, resulting in 268 pots per block, and a total of 768
218pots. The experiment had high levels of replication to facilitate discerning
219between linear and curvilinear relationships between biomass and watering
220level. Blocks were rotated once during the experiment.

221 Beginning February 20th, pots were hand watered twice per week at
222eight watering levels: 200, 250, 300, 350, 400, 450, 500 or 550 ml. These
223amounts were chosen to replicate the range of soil moisture observed in the
224nearest coastal sage scrub site in the U.S. Climate Reference Network (Bell

225 et al. 2013; Diamond et al. 2013). Our treatments encompassed the range of
226 soil moistures documented during the growing season in soils to 5 cm depth
227 (compare values in Table S1 and Fig. 1a). Soil water content was measured
228 weekly, integrated from the surface to a depth of 7.5 cm with a Spectrum
229 Field Scout TDR 100 portable volumetric soil moisture meter (Aurora, IL).
230 Data were averaged across weeks to yield an average soil moisture value
231 per pot.

232 Plant available inorganic nitrogen at the peak of the growing season
233 was measured in pots planted with *E. californica* using anion and cation (AMI-
234 7001, CMI-7000, Membranes International Inc.) ion exchange membranes
235 (Subler, Blair & Edwards 1995). Pots with *E. fasciculatum* were not measured
236 for inorganic nitrogen availability due to time constraints. Ion exchange
237 membrane (IEM) stakes were constructed by first cutting larger sheets into
238 1.0 cm x 5.0 cm strips, and then gluing the strips onto plastic greenhouse
239 stakes (1.5 cm x 15.5 cm) with epoxy based glue. The IEMs were soaked in
240 5M KCl overnight and then rinsed thoroughly in deionized water prior to
241 placement in soil. Two IEM stakes (one anion, one cation) were placed
242 vertically in the pots on April 22nd. After 5 days of incubation the IEM stakes
243 were removed and rinsed with deionized water to remove excess dirt and
244 debris. After cleaning each membrane was placed in a test tube with 20 mL
245 of 2M KCl, and shaken for two hours. Extracts were analyzed for nitrate
246 (Doane & Horwáth 2003) and ammonium (Weatherburn 1967) on a Multiscan
247 FC spectrophotometer. Ammonium captured on the ion exchange resins was

248too close to the detection limit to be reliable, so only data for nitrate
249availability are presented. The short deployment time (5 days) was meant to
250prevent saturation of the ion exchange membrane sites, but a longer
251deployment time would have been needed to measure ammonium, which
252has lower concentrations than nitrate in coastal sage scrub soils (Vourlitis et
253al. 2007).

254 Above- and below-ground biomass were harvested 10 weeks after
255planting, at the time of peak *A. fatua* biomass, and when this exotic species
256had begun to senesce in the lowest soil moisture treatments. The entire soil
257contents of each pot were passed through a 4 mm sieve, with roots collected
258and rinsed free of soil to measure belowground biomass. All biomass was
259dried at 40° C until reaching constant weight. Roots could not be sorted to
260species level in the competition pots, therefore only pots containing a single
261species were used for analyses of below-ground production and allocation.
262The original experimental design did not include treatments with *A. fatua*
263grown alone. However, due to shrub seedling mortality there was a subset of
264pots with zero above-ground biomass of the native shrub measured at the
265end of the experiment. We used this subset of pots when the focal species
266was *E. fasciculatum*, since seedling mortality was constant across watering
267treatments, allowing for a consistent sample size to estimate below-ground
268allocation by *A. fatua*. While a small amount of shrub root biomass could
269remain from the dead seedling, this quantity was not likely to influence our
270estimate of *A. fatua* root biomass for two reasons. First, at the time of the

271biomass harvest dead seedlings were pulled out of the pot, including roots.
272Second, the final above-ground biomass of surviving shrub seedlings in the
273competition treatment was generally less than 1 gram (see Figure 2 b and c);
274accordingly, we would also expect very low levels of root biomass for shrub
275seedlings in the competition treatment.

276 Statistical analyses were performed separately for the two focal shrub
277species, in R v 3.0.2 (R Core Team 2016). Above- and below-ground biomass
278production, soil moisture, and nitrate availability measures were evaluated
279with linear mixed models using the lmer routine from the package lme4
280(Bates et al. 2015b), with maximum likelihood estimation. Block was
281included as a random factor, and water-addition amount (continuous
282variable) and competition (factor) were included as fixed factors, including
283their interactions. To evaluate whether quadratic, as opposed to linear,
284models better fit the data, we compared the models with only water and
285competition as factors to models including a squared term for water, and
286interactions. The fixed effects in the linear model were a nested set of the
287terms in the quadratic model, and hence model fits were compared using
288likelihood ratio tests (Lewis, Butler & Gilbert 2011). If there was not a
289significant difference in the fit of the two models, the simpler model was
290reported. Analyses evaluating the growth and allocation patterns of *A. fatua*
291did not include competition as a predictor variable, but otherwise followed
292the same procedures as for data analysis of the focal native shrubs.
293Similarly, analyses of below-ground biomass were conducted separately for

294each species in monoculture, and hence competition was not included in the
295models.

296 The root mass fraction (RMF) was calculated as the proportion of total
297biomass (above- + below- ground) comprised by roots (Reich 2002). This
298continuous variable was bounded by 0 and 1 hence we assumed a beta-
299distribution (Bolker 2008), and RMF was analyzed using a generalized linear
300mixed model in the glmmADMB package (Skaug et al. 2012), using the same
301model terms already described. We checked for overdispersion in the
302resulting model residuals using the method and code presented by Valdivia
303et al. (2014), and found there was not significant overdispersion.

304 Survival of the native shrub seedlings was a binary variable (yes/no)
305and hence was first analyzed using a generalized linear model assuming a
306binomial distribution and a logit link function, again in the glmmADMB
307package. However, models for *E. californica* did not converge, a common
308occurrence in generalized linear mixed models with a low number of levels
309for random effects (our design had only three blocks), or when these models
310are overparameterized (Bates et al. 2015a). Hence, survival was instead
311analyzed using a general linear model specifying a binomial distribution
312where block was included as a fixed (instead of random) effect.

313 Factor significance for all tests was evaluated with Type II tests using
314the Anova function in the car package (Fox & Weisberg 2011). Wald chi-
315square statistics are presented for both the generalized linear models and
316general linear models.

317

318 **Results**

319 *Soil moisture and nitrate responses*

320 Soil moisture increased with increasing levels of water addition, as best
321 described by a curvilinear model containing a quadratic term, and differed
322 between competition treatments (Fig. 1a, Table 1). With *E. californica* grown
323 alone, volumetric soil moisture saturated around 25% at the 400 ml water
324 treatment. In treatments with *E. californica* grown with the competitor *A.*
325 *fatua*, soil moisture was lower and less variable across all watering
326 treatments, remaining relatively constant between 11-14% moisture. In pots
327 planted with *E. fasciculatum* both alone and in competition, soil moisture
328 remained constant at watering levels of 200 – 450 ml. However, at the
329 highest watering levels, soil moisture in pots with *E. fasciculatum* grown
330 alone continued to increase, while the competition treatment's soil moisture
331 rate of increase slowed.

332 Soil nitrate availability was significantly lower when *E. californica* was
333 grown in competition with *A. fatua* than when grown alone, and declined with
334 increasing water addition, best described by a curvilinear relationship (Fig.
335 1b). As a result, there were significant higher order interaction terms (Table
336 1). In pots planted with *A. fatua*, nitrate availability reached a low of 0.05
337 ppm per membrane around the 400 ml watering regime, and remained at
338 this level under higher watering regimes. In pots without *A. fatua*, nitrate

339availability peaked around 0.12 ppm per membrane, between the 250 – 350
340ml watering treatments.

341

342 *Shrub seedling survival*

343 For both focal species, seedling survival declined in the competition
344treatment, and the response to water treatment varied depending on
345whether the seedling was grown alone or in competition (competition ×
346water interaction, Table 1, Fig. 2). Grown alone, *E. californica* had nearly
347100% survival, and survival was not effected by watering treatment (Fig. 2a).
348In competition, survival of *E. californica* initially declined steeply but then
349leveled off with increasing water (Fig. 2b). In contrast, *E. fasciculatum*
350survival increased with increasing water addition when grown alone (Fig 2c),
351but survival declined with increasing water addition when in competition (Fig.
3522d). The survival responses of *E. fasciculatum* were best described by a
353linear model, without the quadratic term. As described in the Methods, block
354was included as a fixed effect for this analysis and was marginally significant
355(*E. californica* $p = 0.06$, *E. fasciculatum* $p = 0.08$).

356

357 *Above-ground biomass responses*

358 Above-ground biomass of both shrub species was significantly
359suppressed by competition, but the response to watering treatment
360depended on competitive context (Fig. 2, Table 1). In the absence of
361competition, shrub biomass increased in a positive, saturating relationship

362with increasing water supply (Fig. 2 a,c). In contrast, when grown with *A.*
363*fatua*, shrub biomass had either a negative or non-significant relationship
364with increasing watering supply (Fig. 2b,d). The two focal shrub species
365varied, however, in the magnitude of these responses.

366 Grown alone, *E. fasciculatum* biomass responded more positively to
367high water addition than *E. californica*, increasing nearly ten-fold in biomass
368production from the 200 ml watering treatment to the 450 ml water
369treatment (average of 3.16 g to 12.99 g, Fig. 2a). In contrast, *E. californica*
370biomass only experienced a two-fold increase from the least to most
371productive treatments (average of 1.67 g at 200 ml to 3.51 g at the 350 ml
372treatment), and an earlier point of biomass saturation (Fig. 2a). When grown
373with *A. fatua*, *E. fasciculatum* was more strongly competitively suppressed
374than *E. californica*. In the presence of the competitor, *E. fasciculatum*
375seedlings had a mean above-ground biomass production of 0.02 g, and did
376not vary significantly with watering treatment (Fig 2d). In contrast, *E.*
377*californica* seedling biomass averaged 0.56 grams at the lowest level of
378watering when grown with *A. fatua*, and declined more than 10-fold as water
379addition increased, to an average of 0.04 g above 400 ml of water addition
380(Fig 2b).

381 Biomass production of the exotic grass, *A. fatua*, had a strongly
382positive, though saturating, growth response to increasing water treatments
383(Fig. 2 b,c, Table 1). This represents a steeper response slope for increased
384biomass production with greater water availability than was observed for

385 either of the focal shrub species when they were grown alone (Fig. 2 a,b).
386 The amount of *A. fatua* biomass on a per area basis ($\sim 170 - 700 \text{ g/m}^2$) was
387 similar to estimates of herbaceous biomass production at field sites
388 dominated by exotic annual grasses. For instance, unmanipulated plots
389 associated with the Nutrient Network in southern California observed
390 between 100 and 500 g/m^2 of herbaceous biomass across five years which
391 varied in annual rainfall (e.g. Elliott Chaparral Reserve, Sedgewick Reserve,
392 in (Fay et al. 2015)).

393

394 *Below-ground biomass and fractional root allocation*

395 Belowground production increased with watering treatment (Table 2)
396 for both shrub species and for *A. fatua* (Fig. 3a). The RMF of *E. californica*
397 biomass was less sensitive to watering treatment and remained nearly
398 constant at 25%. In contrast, the RMF of both *E. fasciculatum* and *A. fatua*
399 declined with increasing watering treatment until reaching a saturation point
400 at the 450 ml water treatment (Fig. 3b). For root production, the quadratic
401 model fits were not significantly better than the linear models (Table 2). For
402 RMF, the quadratic models fit better than the linear models (Table 2).

403

404 **Discussion**

405 The findings of this study demonstrate that interactions with
406 competitors can alter species' responses to changing environmental
407 conditions. Grown alone, high water availability increased aboveground

408 biomass of both focal shrub species, and *E. fasciculatum* had increased
409 survival, consistent with previous work showing the importance of high soil
410 moisture for shrub establishment in this system (Kummerow, Ellis & Mills
411 1985; DeSimone & Zedler 1999). Conversely, in competition with an invasive
412 grass, shrubs were nearly competitively excluded at high levels of water
413 addition. Instead, both species had greater survival at low levels of water
414 availability, and seedlings of *E. californica* were more than ten times larger
415 at low than high levels of water availability.

416 Some field studies have similarly found greater competitive intensities
417 with increasing site fertility (e.g. Wilson & Keddy 1986), but others have
418 found constant levels of competitive intensity across soil fertility gradients
419 (Wilson & Tilman 1991; Peltzer, Wilson & Gerry 1998), and a meta-analysis of
420 competition experiments found that average competitive intensity as
421 measured by biomass actually declined with increasing productivity of the
422 habitat (assumed to correlate with high resource supply), while competitive
423 intensity measured by survival increased positively with productivity
424 (Goldberg et al. 1999). Some of these disparate findings can be explained by
425 differences in metrics and their interpretation (Grace 1991). To clarify,
426 Welden & Slauson (1986) proposed a distinction between the importance
427 and intensity of competition, where importance is defined through
428 comparison with the relative influences of other factors (stress, disturbance)
429 while intensity refers specifically to the reduction in performance due to the
430 presence of neighbors. Using this framework to interpret the results of this

431study, competition was more important than water limitation, because
432competition suppressed native shrub seedling biomass to a greater degree
433than soil moisture stress, and because the exotic grasses competitively
434suppressed the native shrub seedlings at all points along the soil moisture
435gradient. However, competitive intensity was lowest under low soil moisture,
436when biomass of the exotic grass competitor was suppressed by soil
437moisture limitation.

438 Globally invasive species have statistically higher growth rates than
439non-invasive species (van Kleunen, Weber & Fischer 2010), and also more
440traits associated with high water demand (Cavaleri & Sack 2010). Hence,
441exotic species often expected to benefit disproportionately over native
442species from high soil moisture (e.g. Daehler 2003). However, a large meta-
443analysis found that while exotic species tended to be favored under
444enhanced rainfall, and native species under drought, the trend was non-
445significant and characterized by substantial variation (Sorte et al. 2013). The
446results of the present study, and others, suggest that some of this variation
447may be explained by competitive context. Consistent with our findings,
448experiments in both Northern California grasslands (Eskelinen & Harrison
4492015a) and Mongolian steppe (Liancourt et al. 2013), found native species
450only benefited from enhanced rainfall in the absence of competitors. Other
451experiments, however, have found that added precipitation had little
452influence on the relative abundances of native versus exotic species (Pfeifer-
453Meister et al. 2016), found variation among native species in their response

454to competition and increasing rainfall (Levine, McEachern & Cowan 2010), or
455that native species' growth was similarly suppressed by exotic competitors
456regardless of water supply (Maron & Marler 2008).

457 Many other aspects of the environment likely modify the influence of
458neighbors on species responses to variation in water availability. For
459instance, Richardson et al. (2012) found that competition from exotic species
460suppressed native cover in northern sites (cooler, wetter), but facilitated
461native cover in southern sites (drier, warmer). Similarly, in arid sites grasses
462have been shown to facilitate shrub establishment (Mazzola et al. 2011). One
463mechanism by which grasses could facilitate shrub establishment in dry sites
464is by reducing herbivory on seedlings (Soliveres et al. 2011). Soil depth has
465important influences on the total water holding capacity of soil accessible by
466roots, and influences the identity of interacting species along soil depth
467gradients (Bernard-Verdier et al. 2012). Indeed, variation in the identity of
468interacting species is one of the most important factors influencing
469competitive intensity (Goldberg et al. 1999); hence, progress in predicting
470variation in competitive intensity along environmental gradients will require
471a greater understanding of how species traits interact with resource supply
472to influence competitive outcomes.

473 While both shrub species in this experiment showed greater biomass
474accumulation with increasing water availability when grown alone, and
475strong declines when grown in competition, the functional form of these
476relationships differed. In particular, when in competition with the exotic

477annual grass, *E. californica* achieved higher biomass at low soil moisture
478levels, while *E. fasciculatum* was competitively suppressed to a similar
479magnitude at all soil moisture levels. Variation between the two focal shrub
480species in their responses to water availability and competition from exotic
481species could be explained by a trade-off between stress tolerance and
482competitive ability (Liancourt, Callaway & Michalet 2005). *E. californica* is
483restricted to cooler coastal areas while *E. fasciculatum* is distributed along
484the coast and into more arid inland areas (S2), suggesting that *E.*
485*fasciculatum* can tolerate a greater range of moisture stress. In keeping with
486the predicted trade-off in stress tolerance and competitive ability, *E.*
487*fasciculatum* was also competitively suppressed to a greater degree than *E.*
488*californica* when grown with the exotic grass competitor. However, our
489estimates of survival do not support this hypothesis, because *E. fasciculatum*
490survival declined at low soil moisture, while *E. californica* had nearly %100
491survival regardless of water treatment.

492 Alternatively, these differing responses to soil moisture and
493competition are potentially explained by different nutrient demand and
494strategies for drought adaptation in the two species. *E. californica* is a
495drought deciduous species that loses nearly all photosynthetically active
496biomass during the prolonged summer drought in this MTE. In contrast, *E.*
497*fasciculatum* is a drought tolerant evergreen species which retains a large
498proportion of photosynthetically active biomass throughout the year.
499Deciduous species tend to have higher nutrient demand than evergreen

500species (Lambers & Poorter 1992), and studies from this region support the
501idea that deciduous species are restricted to areas with higher nutrient
502supply (Mooney & Dunn 1970). Increasing soil moisture in this experiment
503was associated with declining soil nitrate levels, potentially due to a
504combination of increased plant uptake and increased loss rates through
505leaching. When in competition with the exotic grass, the biomass of *E.*
506*californica* seedlings declined steeply from low to medium water supply
507rates, and then leveled off with similar biomass from medium to high water
508supply rate. This pattern was similar to soil nitrate levels (compare Figs. 1b
509and 2b), consistent with nutrient limitation as a mechanism for the
510saturating growth response of this species with increasing water supply. *E.*
511*californica* also allocated a greater portion of biomass to roots (RMF)
512compared to *E. fasciculatum*, suggesting *E. californica* was allocating more
513biomass to roots in order to obtain limiting soil resources (Gleeson & Tilman
5141992). However, there are important caveats for these analyses of allocation.
515Plants can respond to nutrient limitation through changes in uptake rates,
516such as via greater specific root length, instead of through changes in
517proportional root or shoot allocation (Poorter et al. 2012). Further, we only
518estimated root allocation in the absence of competition, and allocation can
519change in competitive contexts (McNickle & Dybzinski 2013, but see Cahill
5202003).

521 A key finding of this study was the frequency of curvilinear
522relationships between water supply and growth, both with and without

523competition. For instance, in the absence of competition we saw a positive,
524saturating relationship between biomass and water supply for all three focal
525species. While many modeling studies of species interactions along gradients
526assume one limiting resource, this is likely an unrealistic assumption
527(discussed in Rees 2013). The curvilinear relationship we observed could be
528caused by co-limited by nitrogen and water, such that nitrogen limitation is
529more severe more under wet than dry conditions (Hooper & Johnson 1999;
530Harpole, Potts & Suding 2007; Eskelinen & Harrison 2015b). Patterns of
531allocation were also consistent with this interpretation, as well as the
532predictions of optimal allocation theory; both *A. fatua* and *E. fasciculatum*
533reduced root allocation with increasing levels of water addition until reaching
534a saturation point.

535 Austin & Smith (1989) reviewed theories of species growth and
536abundance responses along resource gradients and conclude that complex
537functional relationships are likely due to variation in competitive interactions,
538but also predictable on the basis of species' responses to the resource
539gradients when grown in monoculture. Everard et al. (2010) developed
540model for nitrogen competition predicting dominance of exotic annual
541species in dry sites and native perennial species in wet sites, parameterized
542with data from Southern California species. This was the result of both
543biomass and water uptake rates of native versus exotic species - their
544parameters assumed exotic species water uptake rate declined as soil
545moisture increased, while native species uptake rate increased. In our

546experiment, we saw the opposite pattern where biomass of the exotic annual
547grass increased faster than biomass of the native shrubs with increasing soil
548water supply, and there was greater competitive suppression of the native
549shrubs by exotic grasses at high soil water supply. However, the modeling
550study (Everard et al. 2010) and our experiment concur with Austin and Smith
551(1989) in that the dynamics of species growth in monoculture predict the
552nature of competitive dynamics along a resource gradient. Our findings join
553the few experiments that provide empirical evidence for these theoretical
554expectations (Pickett & Bazzaz 1978; Kadmon 1995), and demonstrate the
555insights that can be gained from conducting experiments along controlled
556environmental gradients.

557 This study focused on the first growing season following shrub seedling
558germination; drought-deciduous shrubs in coastal sage scrub will lose their
559leaves during the summer drought, hence the time of sensitivity to soil
560moisture is likely to be greatest during this first growing season (DeSimone &
561Zedler 1999). Competition from exotic annual species often suppresses
562shrub seedling growth in coastal sage scrub communities (Eliaison & Allen
5631997; Cione, Padgett & Allen 2002). However, in subsequent years following
564establishment native shrubs can tolerate and even competitively suppress
565co-occurring exotic annual grasses (Goldstein & Suding 2014), and grass
566litter can promote adult shrub growth by maintaining soil moisture
567(Wolkovich et al. 2010). In this system, there is strong phenological overlap
568in the growing seasons of both native and herbaceous species, but

569 differences in seasonal phenology between native and exotic species could
570 also influence competitive interactions (Wolkovich & Cleland 2011). For
571 instance, DeFalco et al. (2007) found that the exotic annual grass *Bromus*
572 *rubens* competitively suppressed growth of perennials with overlapping
573 growing season phenology, but not with the shrub *Larea tridentata*, which
574 continued to grow after *B. rubens* had senesced. Hence the relationship
575 between resource supply and competition intensity is likely to vary with
576 ontogenetic stage as well as species' phenology, and the present study can
577 only conclude that high water supply increases competitive suppression of
578 shrubs by exotic grasses at the seedling stage. However, because shrub
579 survival was strongly impacted by grasses, the effect of competition on
580 mortality in the first year would be likely to continue to impact the
581 community in subsequent years.

582 Although this study focused on shrub seedling survival growth during
583 only the first growing season, it has important implications for restoration of
584 semi-arid shrublands. High soil moisture is well known to promote shrub
585 establishment in drylands (Holmgren et al. 2006). However, our results
586 suggest that when there is an abundant seedbank of exotic species, high soil
587 moisture could prevent native shrub establishment due to strong competitive
588 suppression by exotic species. Our study was in a greenhouse, but similar
589 findings have been found in field experiments. Consistent with our findings, a
590 restoration study in coastal sage scrub found that while supplemental
591 watering increased shrub seedling growth, it did not increase shrub seedling

592 survival for most species (including *E. californica*), and even decreased
593 seedling survivorship of some species (notably *E. fasciculatum*; (Padgett, Kee
594 & Allen 2000)). In a restoration experiment involving seeding over 20 years
595 in a sagebrush system in the U.S. Great Plains, high rainfall years resulted in
596 increased grass cover and decreased shrub cover (Rinella et al. 2015). And in
597 the Mediterranean, studies along natural rainfall gradients have found that in
598 drier sites shrubs can have higher performance than in wet sites (Seifan,
599 Tielborger & Kadmon 2010), because grasses have less of a competitive
600 impact on shrub seedling survival (Rysavy et al. 2014). Together these
601 studies suggest that when dryland restorations use supplemental watering,
602 additional techniques may need to be employed to avoid competitive effects
603 of exotic species. Options include herbicide (Cione, Padgett & Allen 2002),
604 carbon additions to lower nitrogen (Blumenthal 2009; but see James et al.
605 2011), or planting under nurse shrubs to facilitate woody plant establishment
606 (Gómez-Aparicio 2009).

607 The results from this experiment add to a growing literature
608 highlighting the importance of indirect effects for predicting species
609 responses to climate change (Suttle, Thomsen & Power 2007; Tylianakis et
610 al. 2008; Kleinhesselink & Adler 2015; Alexander et al. 2016). These results
611 also have relevance for understanding the potential for native shrub-
612 dominated ecosystems to reestablish during the critical first few months
613 following disturbances such as fire. Invasion by exotic annual grasses has
614 increased fire frequency in the Western United States (Balch et al. 2013).

615 This acceleration of the disturbance regime in concert with climate change
616 (Bradley 2009) could facilitate a type-conversion from native shrublands to
617 persistent exotic-annual grasslands (Cione, Padgett & Allen 2002). With
618 climate change, the conditions for successful regeneration for woody species
619 in drylands are predicted to become less frequent (Petrie et al. 2017). This
620 study shows that while native shrub seedlings have higher potential for
621 growth and survival under conditions of high soil moisture, and traditionally
622 high rainfall years have been opportunities for shrub establishment,
623 invasions by exotic annuals in this other MTEs (Sandel & Dangremond 2012;
624 Funk et al. 2016) could be "changing the rules," by restricting native shrub
625 establishment in high rainfall years.

626

627 **Author's Contributions**

628 EC conceived the ideas and designed methodology; AA and CK
629 collected the data; EE and EC analysed the data; EE and EC led the writing of
630 the manuscript. All authors contributed critically to the drafts and gave final
631 approval for publication.

632

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645

646**Data Accessibility**

647-R scripts: uploaded to the The Knowledge Network for Biocomplexity under
648the same name as this manuscript

649-Biomass and Survival data: uploaded to the The Knowledge Network for
650Biocomplexity under the same name as this manuscript

651

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1043**Tables**

1044

1045**Table 1.** Summary of effects of competition (C), watering amount (W), and a
1046quadratic term for watering amount (W^2) on measured responses using type
1047II tests, separated by focal shrub species. Dashes “-” indicate that the term
1048was not used in the best model. ‘NA’ indicates that the factor was not
1049included in the experimental design for that test. Bold p -values indicate
1050significance at $p < 0.05$.

Focal Species	Factor	<i>A. fatua</i> above-ground biomass		Shrub above-ground biomass		Shrub seedling survival		Soil Moisture		Soil nitrate availability	
		χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>
<i>E. californica</i>	C	NA	NA	635.0	<0.001	105.2	<0.001	1099.1	<0.001	356.7	<0.001
	W	121.7	<0.001	2.58	0.11	41.7	<0.001	132.4	<0.001	5.78	0.016
	W ²	64.2	<0.001	1.51	0.22	34.4	<0.001	92.3	<0.001	12.7	<0.001
	C:W	NA	NA	14.4	<0.001	4.5	0.034	43.7	<0.001	25.2	<0.001
	C:W ²	NA	NA	9.17	0.002	4.7	0.030	28.3	<0.001	28.7	<0.001
<i>E. fasciculatum</i>	C	NA	NA	303.4	<0.001	94.6	<0.001	25.2	<0.001	NA	NA
	W	39.3	<0.001	9.22	0.002	0.066	0.79	99.9	<0.001	NA	NA
	W ²	9.75	0.002	4.17	0.041	--	--	15.5	<0.001	NA	NA
	C:W	NA	NA	9.31	0.002	11.6	<0.001	1.98	0.16	NA	NA
	C:W ²	NA	NA	4.23	0.040	--	--	4.53	0.033	NA	NA

1051

1053

1054 **Table 2.** Summary of effects of watering amount (W) and the inclusion of a
 1055 quadratic term for watering amount (W^2) term on belowground responses,
 1056 separated by each species. Dashes “-” indicate that the term was not used in
 1057 the best model. Bold p - values indicate significance at $p < 0.05$.

Focal Species	Factor	Root Biomass		Root Mass Fraction	
		X^2	p	X^2	p
<i>A. fatua</i>	W	11.1	<0.001	19.9	<0.001
	W^2	-	-	14.0	<0.001
<i>E. californica</i>	W	14.2	<0.001	5.6	0.018
	W^2	-	-	5.3	0.021
<i>E. fasciculatum</i>	W	22.9	<0.001	15.4	<0.001
	W^2	-	-	11.8	<0.001

1058

1059

1060 **Figure legends**

1061 Figure 1. Relationship between percent soil moisture (a) and available nitrate
1062 captured by ion exchange membranes (b). Lines represent the best fit with
1063 quadratic functions. Error bars represent $\pm 1SE$.

1064

1065 Figure 2. Aboveground biomass responses (points) and survival (grey bars)
1066 of focal shrubs to water and competition treatments (grown alone a, c; grown
1067 in competition b, d). Lines represent the best fit linear or quadratic model for
1068 the aboveground biomass responses.

1069

1070 Figure 3. Belowground biomass responses to water treatments for root
1071 production (a) and root mass fraction (b) when each species was grown
1072 alone. Lines represent the significant, best fit linear models.

1073 **Supporting Information, Esch et al. 2018 " Competition reverses the**
 1074 **response of shrub seedling mortality and growth along a soil**
 1075 **moisture gradient"**

1076

1077 **Table S1.** *Monthly average soil moistures*

1078 Monthly average soil moisture (m³/m³) at a 5 cm soil depth measured at the
 1079 U.S. Climate Reference Network southern California station Fallbrook 5 NE
 1080 located in Fallbrook, CA.

Mont h	Year						
	2010	2011	2012	2013	2014	2015	2016
Jan.		22.8 6	18.4 5	22.2 5	12.7 1	20.9 2	21.0 5
Feb.		22.9 1	19.0 3	22.0 0	15.1 3	17.2 2	17.7 3
Marc h		24.4 5	21.6 7	18.5 5	19.9 7	17.6 5	17.7 0
April	24.2 5	19.0 8	20.0 8	12.9 9	15.6 0	11.6 6	12.9 8
May	15.8 7	16.0 3	14.4 4	13.8 7	11.6 6	16.1 0	12.2 6
June	12.4 1	13.1 4	11.6 4	11.1 0	10.6 4	12.0 8	11.0 1
July	11.4 8	11.7 6	10.8 0	10.4 8	10.3 5	15.1 9	10.4 5
Aug.	10.8 2	11.2 5	10.9 1	10.0 9	14.0 1	11.9 5	10.0 5
Sept.	10.2 1	10.6 5	10.0 3		10.5 5	13.7 5	10.4 3
Oct.	18.6 2	15.8 4	11.3 1	10.1 3		14.6 5	10.7 1
Nov.	21.3 3	21.3 9	11.3 7	14.6 9	11.5 6	11.8 6	
Dec.	24.9 0	19.2 7	21.8 4	20.0 7	22.9 0	16.3 8	

1081

1082

1083 **Figure S2.** *Distribution of focal species*

1084 The following maps show the distributions of our three focal species within
1085 California; data were drawn from Calflora (www.calflora.org) for *A. fatua* (a),
1086 *E. californica* (b), and *E. fasciculatum* (c).