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The tortoise and the hare: reducing resource availability shifts competitive balance between plant species

Dean E. Pearson*[,1,2], **Yvette K. Ortega**[1] and **John L. Maron**[2]

[1]Rocky Mountain Research Station, USDA Forest Service, Missoula, MT 59801, USA; and [2]Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA

Summary

1. Determining how changes in abiotic conditions influence community interactions is a fundamental challenge in ecology. Meeting this challenge is increasingly imperative in the Anthropocene where climate change and exotic species introductions alter abiotic context and biotic composition to reshuffle natural systems.

2. We created plant assemblages consisting of monocultures or equal abundance of the native community dominant bluebunch wheatgrass (*Pseudoroegneria spicata*) and the exotic spotted knapweed (*Centaurea stoebe*), a co-occurring invasive forb that has overtaken grasslands across the western United States. We subjected these composition treatments to drought (20% of average precipitation vs. average) and herbivory on *C. stoebe* by its biocontrol agent *Cyphocleonus achates* to explore how reduced precipitation might influence the effects of competition and biocontrol herbivory on *C. stoebe*'s abundance.

3. At the end of 7 years, *C. stoebe* dominated mixed-species plots under normal precipitation conditions, with biomass 50% greater than that of the native *P. spicata*. However, under drought stress, *P. spicata*'s biomass was >200% greater than *C. stoebe*'s. Interestingly, both species were impervious to drought in monoculture, indicating the importance of the drought by competition interaction. The biocontrol herbivore reduced *C. stoebe* abundance and indirectly increased *P. spicata* biomass in mixed-species drought plots, but these effects were only marginally significant and relatively weak. Overall, *C. stoebe* abundance was primarily driven by the drought by competition interaction, with negatively additive but weak effects of the drought by herbivory interaction.

4. The response of the exotic to the treatments was driven by rapid changes in population density linked to its fast life-history strategy, while the native's response was driven by changes in per capita plant biomass linked to its slower life-history strategy. Individual plant performance metrics did not predict overall population responses for the invader, indicating the importance of longer term population measures.

5. *Synthesis.* These results demonstrate that reduced precipitation inputs linked to climate change can dramatically shift the balance of plant competition, even toggling the advantage from exotic to native dominance. They also illustrate the importance of biotic interactions in predicting species responses to abiotic change.

Key-words: abiotic, anthropogenic change, biological control, climate change, competition, drought, herbivory, invasion, life-history strategy, precipitation

Introduction

Abiotic conditions are known to strongly influence the distribution and abundance of species (Begon, Harper & Townsend 1990; Brown & Lomolino 1998), but understanding how abiotic factors mediate biotic interactions remains a central question in ecology (McGill *et al.* 2006; Agrawal *et al.* 2007). Addressing this question is increasingly important in the Anthropocene where human activities are dramatically altering abiotic and biotic conditions through climate change, nutrient inputs, and introductions of strongly interacting species, all of which serve to restructure native communities

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*Correspondence author. E-mail: dpearson@fs.fed.us

(Tilman & Lehman 2001; Bradley, Oppenheimer & Wilcove 2009; Pyšek & Richardson 2010). Exploring such questions in the context of conservation threats can simultaneously advance ecology and facilitate conservation (Brooker 2006; McGill *et al.* 2006; Agrawal *et al.* 2007).

In plant communities, competition and herbivory are key biotic processes (Tilman 1982; Crawley 1997). Yet, variation in resource availability can alter plant-competition outcomes, plant-herbivore dynamics, and the interplay between these processes in a variety of ways (Tilman 1982; Olff & Richie 1998; Hambäck & Beckerman 2003). Importantly, how different plant species respond to resource availability may be integrally linked to their life-history strategies (Rees *et al.* 2001). For example, species adapted to low resource conditions often exhibit slow life-history strategies associated with low resource uptake, high resource use efficiency and slow population growth rates (Grime 1977). In contrast, species adapted to high resource conditions often express fast life-history strategies characterized by high resource acquisition rates and rapid population growth (Grime 1977). Accordingly, reducing resource availability can shift plant competition in favour of 'slow' species, whereas increasing resource availability can favour 'fast' species (Smith & Huston 1989). Notably, these opposing strategies may be differentially expressed at the community level, with slow species rising to dominance via increases in individual plant size more than recruitment, and fast species attaining dominance more through rapid population growth.

Changing resource conditions can influence plant-herbivore interactions by altering the host plant's ability to tolerate or defend against herbivore attack (Coley, Bryant & Chapin 1985; Huberty & Denno 2004; Wise & Abrahamson 2005) or by influencing how strongly herbivore-driven reductions in fecundity influence recruitment (Maron, Baer & Angert 2014). Studies examining both herbivory and competition demonstrate that their combined effects can be additive, synergistic, or antagonistic, even under constant resource conditions. For example, complex interactions can arise from plant competitors altering herbivore behaviour or abundance by inhibiting or facilitating access to the host or changing resource levels available to or within the host (Hambäck & Beckerman 2003; Haag, Coupe & Cahill 2004; Schädler, Brandl & Haase 2007). Herbivores can also alter competitor dynamics through differential impacts on host abundance or their competitive abilities (Holt 1977; Olff & Richie 1998; Hanley & Sykes 2009). Although incorporating shifting resource conditions into this milieu presents significant challenges, it is a critical next step in elucidating the effects of abiotic conditions on biotic interactions. While many studies address subsets of these interactions (e.g. Hambäck & Beckerman 2003; Haag, Coupe & Cahill 2004; Schädler, Brandl & Haase 2007; Suwa, Louda & Russell 2010) and some examine interactions between competition and herbivory across gradients (Bonser & Reader 1995; Mulder & Ruess 1998; van der Wal *et al.* 2000), few experimentally incorporate all these pieces in field environments (as opposed to greenhouse conditions, but see Ortega *et al.* 2012).

Given the dominance of exotic plants in many native communities, understanding how anthropogenic changes in resource conditions will affect community composition requires incorporating this important group of plant competitors (Pyšek & Richardson 2010). It has been widely postulated that many invasive plants will benefit more than natives in the face of anthropogenic change due to broader ecological tolerances, greater plasticity, greater affinity for disturbance, and/or better trait matching to novel conditions (Dukes & Mooney 1999; Hellmann *et al.* 2008; Thuiller, Richardson & Midgley 2008; Walther *et al.* 2009; Davidson, Jennions & Nicotra 2011; Sandel & Dangremond 2012). Some evidence suggests that exotic species may outperform natives under high resource conditions, particularly when they exhibit high resource acquisitive traits, while natives may perform better when resources are scarce (Daehler 2003; Levine *et al.* 2003; van Kleunen, Weber & Fischer 2010; Blumenthal *et al.* 2013; Prevéy & Seastedt 2015; Concilio *et al.* 2015). However, exotic responses to resource influxes can be quite conditional (Eskelinen & Harrison 2014), and exotics can outperform natives under low resource conditions when they bear more 'resource use efficient' strategies than the natives (Funk & Vitousek 2007). Examining the effects of resource changes on native-exotic plant dynamics in the context of life-history strategies may provide insights regarding how conditionality influences invasion outcomes.

As it relates to native-exotic plant dynamics, herbivory can be particularly important. Invasive plants are believed to achieve dominance over natives in part due to the loss of their specialist natural enemies (Elton 1958). Accordingly, classical biological control is often employed to remedy this; host-specific natural enemies are introduced to suppress invasive plant abundance and weaken their competitive advantage over native plants (van Driesche, Hoddle & Center 2008). When effective, such directed asymmetric herbivory can shift the balance of competition to favour natives over their exotic competitors (e.g. Huffaker 1959; Van, Wheeler & Center 1998; Gurr & Wratten 2000). Yet, biocontrol outcomes are often dependent on environmental context (Louda *et al.* 1990; McEvoy & Coombs 1999; Gurr & Wratten 2000; Shea *et al.* 2005). Improving biocontrol and our knowledge of the role of herbivory in competitive outcomes requires studies that experimentally examine the individual and interactive effects of biocontrol and abiotic conditions on competition between invasive and native competitors. Unfortunately, few such studies exist (e.g. Willis, Groves & Ash 1997; Ortega *et al.* 2012).

In this study, we report results of a long-term experiment in which we manipulated plant competition, drought stress, and herbivory to understand how these factors influence the dominance of spotted knapweed (*Centaurea stoebe*), a strong invader in grassland communities of the Intermountain West (DiTomaso 2000; Pearson *et al.* 2016). *C. stoebe* is an exotic perennial forb of Eurasian origins that exhibits a 'fast' life-history strategy, including high resource uptake, substantial recruitment and high population growth rates (Steinger & Müller-Schärer 1992; Blicker, Olson & Wraith 2003; Maron

& Marler 2008). However, *C. stoebe* declines in abundance during drought periods (e.g. Schirman 1981; Boggs & Story 1987) concordant with increases in the native community dominant bluebunch wheatgrass (*Pseudoroegneria spicata*; Pearson & Fletcher 2008). Bluebunch wheatgrass is a long-lived perennial that exhibits a slow life-history strategy including low resource requirements, low fecundity and limited recruitment, and consequently slow population growth rates (Blicker, Olson & Wraith 2003; Mazzola *et al.* 2011; Ortega *et al.* 2012). Using these two species as a case study, we hypothesized that the advantage of *C. stoebe* over *P. spicata* would be reduced or overturned under drought stress, since *P. spicata* exhibits a slower life-history strategy that might enable it to perform relatively better under low resource conditions (Smith & Huston 1989). We further hypothesized that the impacts of herbivory on *C. stoebe* by its biological control insect, *Cyphocleonus achates*, would be exacerbated in drought treatments due to reduced tolerance to herbivory under low resource conditions (Wise & Abrahamson 2005). Finally, we predicted that *C. stoebe* would be suppressed most under the combined effects of drought, competition, and herbivory due to negative additive or synergetic effects of low resources on competition and herbivory.

Our earlier work in this system demonstrated that both short-term spring drought (May–June) and *C. achates* killed individual *C. stoebe* plants, but *C. stoebe* largely compensated for these effects at the population level through increased recruitment (Ortega *et al.* 2012). Here, within the context of this same experiment, we extended the drought treatment through the growing season (May–August) to better match climate projections for increasingly severe drought in western Montana (Gutzler & Robbins 2011). For 4 years of this extended drought treatment, we continued to follow the response of *C. stoebe* and *P. spicata* in monocultures and in plots that had been initiated with an equal mix of the two species. We also maintained our previously imposed biocontrol treatment (*C. stoebe* was either exposed to the biocontrol agent, *C. achates*, or not). We measured changes in the demographics of both species over a total of 7 years, with the last 3 years of data as well as final biomass evaluated here.

Materials and methods

OVERALL DESIGN

To examine the influence of reduced precipitation and herbivory on the dominance of the exotic invader, *C. stoebe*, over the native bunchgrass, *P. spicata*, we conducted an experiment at Diettert Gardens in Missoula, Montana, USA. We created monocultures containing either *C. stoebe* or *P. spicata* and mixed plots containing 50:50 mixes of both species. Each of these composition treatments was factorially crossed with a drought treatment (±drought), and each treatment combination containing *C. stoebe* was also crossed with a biocontrol herbivory treatment (±*C. achates*). Because *C. achates* is a specialist biocontrol agent, the herbivory treatment was not applied to *P. spicata* monocultures. The design yielded 10 treatment combinations, which were randomly assigned to 1 m^2 plots with 1 m spacing, arranged in 15 replicate blocks.

Beginning in September 2005, we prepared the site by tilling the soil and removing the existing, mostly exotic vegetation (see Ortega *et al.* 2012). We grew *C. stoebe* and *P. spicata* in a greenhouse from locally collected seed for 3 months, and in May 2006, transplanted 36 plants spaced 20 cm apart into a 6 × 6 arrangement within each 1-m^2 plot. This spacing approximates the distribution of the *P. spicata* in natural plant communities. Mixed-species plots were comprised of 18 *C. stoebe* and 18 *P. spicata* plants arranged in an alternating pattern (see Ortega *et al.* 2012 for details). Experimental treatments and sampling were initiated in 2007 and conducted annually through 2013. To avoid edge effects, we sampled only the 0·8 × 0·8 m portion of the plot corresponding to the inner 16 planted individuals, and all stems from edge plants were clipped before seed dispersal. We reported results for 2007–2009 in a previous paper, which focused on population-level compensation of *C. stoebe* for mortality induced by herbivory and spring drought (Ortega *et al.* 2012). Beginning in 2010, we extended the duration of the drought treatment through the growing season to more closely emulate drought conditions associated with natural *C. stoebe* declines (see below) and increasingly severe drought predicted in this region from climate change (Gutzler & Robbins 2011). We applied treatments through 2013, ending the experiment at this point given that population and community-level outcomes appeared stable (Appendix S1, Supporting Information). Here, we report results for the second phase of the experiment, focusing on population and community-level outcomes in the final year.

DROUGHT TREATMENT

We reduced water inputs in drought-treatment plots to 20% of average precipitation (based on levels recorded from 1957 to 2006 in Missoula, Montana) in May–June, 2007–2009, and in May–August, 2010–2013. This decrement in precipitation approximated drought conditions observed in 2000 and 2001, coincident with steep declines in *C. stoebe* in western Montana grasslands (e.g. Pearson & Fletcher 2008), and consistent with predictions for increased severe drought for this region (Gutzler & Robbins 2011). Precipitation was excluded from drought plots using motorized rain covers made from vinyl blinds mounted on PVC frames (see Ortega *et al.* 2012). Drought plots were watered every 2 weeks to attain target inputs. For the non-drought treatment (hereafter 'normal' conditions), and during non-treatment months through September, ambient precipitation was supplemented by watering bimonthly as necessary to attain average precipitation levels. We continuously monitored ambient precipitation levels with a Rain Logger® (Rainwise Inc., Bar Harbor, ME, USA), and measured soil moisture (volumetric water content) at a depth of 12 cm monthly (April–October) using a handheld probe (Field Scout® TDR-100; Spectrum Technologies, Inc., Plainfield, IL, USA).

HERBIVORY TREATMENT

The specialist weevil, *C. achates*, was introduced for *C. stoebe* control in Montana in the early 1990s and has been credited for causing population declines in its host (Corn, Story & White 2006; Story *et al.* 2006). Adult *C. achates* emerge midsummer to breed and lay eggs, and larvae overwinter within and feed on *C. stoebe* roots. By feeding on the central vascular tissue in the roots, these insects can directly affect uptake of water (Steinger & Müller-Schärer 1992), the limiting resource that we manipulate, and so are expected to have greater impacts on the plant at lower levels of this resource according to the Limiting Resource Model (Wise & Abrahamson 2005).

Because *C. achates* is incapable of flight, we controlled access in each plot using a 30·5 cm aluminium barrier buried 10 cm deep and 45 cm from the plot edge (Story, White & Good 1996; see Ortega *et al.* 2012). In August 2007, 16 locally collected adult *C. achates* were added to each herbivore-addition plot. This release density is comparable to that used in other studies reporting impacts of *C. achates* on *C. stoebe* (Corn, Story & White 2006). We conducted two-minute visual searches for adult *C. achates* each year from late August to September (three to five surveys per year), corresponding to the window of adult activity (Clark *et al.* 2001). Other *C. stoebe* biocontrol agents were present at the site at typical field densities reported in western Montana (Ortega *et al.* 2012), including the gall-flies *Urophora affinis* and *Urophora quadrifasciata*, and the weevils *Larinus minutus* and *Larinus obtusus*, all of which attack *C. stoebe* seedheads. Because these biocontrol agents attack seedheads, they could not be excluded without precluding pollinators and impacting plant reproduction. Hence, our experiment tested for effects of *C. achates* in the presence of these other agents. Occurrence of these agents within *C. stoebe* seedheads did not differ significantly among treatments, nor did they appear to substantially suppress *C. stoebe* populations, which increased in all treatments (Ortega *et al.* 2012).

PLANT DEMOGRAPHY AND BIOMASS

We uniquely marked all out-planted individuals with numbered metal tags to track population size and individual performance. In August, we counted flowering stems and marked and counted new adults (defined as flowering plants) that recruited into the population. For each adult *C. stoebe* plant, we counted the number of seedheads on one randomly selected flowering stem. When seeds matured, we collected one randomly selected flowering stem for up to eight *P. spicata* plants per plot and up to 20 randomly selected *C. stoebe* seedheads per plot. From the latter sample, we calculated the mean number of seeds per seedhead and plot. Per capita production of *C. stoebe* seeds for each plot was calculated by multiplying the number of stems per adult plant, the number of seedheads per stem, and the plot-level estimate of seeds per seedhead, and then averaging this measure across plants. To minimize impacts on propagule production, we constrained collection of seedheads and stems to <25% of those present. As a result, samples in later years of the experiment were limited for *P. spicata*, particularly for certain treatments. Given this potential bias, we assessed reproduction for this species using stem counts rather than estimates of seed production. Each fall, we also counted seedlings and juveniles plants (non-reproductive individuals from a prior cohort) of each species at the peak of emergence within a centrally located 0·25 m × 0·25 m subplot.

In August of 2013, the final year of the experiment, we visually estimated percent cover of each species in each plot within a 0·8 m × 0·8 m frame demarcated in units of 1%. We could not harvest the experiment after completion of all sampling in 2013 because survival assessments/adult population censuses were necessarily conducted at the end of the growing season well after peak biomass (July/August). Therefore, at peak biomass in 2014, we collected cover data (same observer as 2013) and harvested biomass for a randomly selected subset of 10 of 15 blocks. We then used these 2014 data to translate 2013 cover measures to final biomass estimates for *C. stoebe* and *P. spicata*. To do so, we first used a generalized linear mixed model (PROC GLIMMIX, SAS version 9.4; SAS Institute 2013) to construct an equation for each species that related cover to biomass measurements using 2014 data. The response variable for each species was biomass, evaluated with a lognormal distribution. Cover, species composition, and their interaction were included as fixed factors, and block as a random factor. We then used the resultant parameter estimates to convert cover measured in 2013 to estimated biomass for that year.

STATISTICAL ANALYSES

We used generalized linear mixed models (PROC GLIMMIX, SAS version 9.4) to test for effects of drought, species composition, and herbivory on all response variables for *C. stoebe* and *P. spicata*, respectively. Block was treated as a random factor in models. Models for *C. stoebe* included all three experimental factors and their interactions as fixed factors. For *P. spicata*, we could not construct a full factorial model because the herbivory treatment was not applied to monocultures. Instead, we combined species composition and herbivory treatments into one factor, i.e. *P. spicata* only; *P. spicata* with *C. stoebe*, herbivore added; and *P. spicata* with *C. stoebe*, herbivore excluded. We then used this combined factor and its interaction with drought to construct contrasts for the following effects: species composition, drought × species composition; and for mixed-species plots only, herbivory and herbivory × drought. For response variables describing final population-level outcomes (estimated biomass and numbers of adult plants per plot), we used data from 2013, the last year treatments were applied. To explicitly evaluate the effect of species composition on final population size for each species, we ran a separate model treating the change in numbers of adults from inception to 2013 as the response variable to account for the fact that populations started at differing numbers in mixed-species plots vs. monocultures (i.e. $n = 8$ vs. 16 plants). We note that for other population-level response variables (e.g. biomass, recruitment etc.), we did not attempt to account for the initial difference in population size given that there was no way to approximate its long-term effect on outcomes. However, this difference should have had little influence on our conclusions given that our focus was not on the difference between mixed-species plots and monocultures *per se*, but rather on how these different plot types responded to drought and herbivory (i.e. interactions between species composition and these other factors). For response variables potentially contributing to final population-level outcomes (i.e. recruitment of adults and younger age classes, per capita performance), we included data from 2011 to 2013, the last three treatment years. For these multi-year analyses, we included year and its interaction with experimental factors in initial models. We then successively dropped non-significant interactions ($P > 0{\cdot}05$) involving year to arrive at a reduced model. Multi-year models included plot within block as an additional random factor to account for repeated sampling across years. To further evaluate interactions involving year, we tested for *post hoc* differences between treatment means within each sampling year using multiple comparisons adjusted for the number of comparisons via the Bonferroni method. We also used multi-year models to test for differences in monthly soil moisture and in the number of *C. achates* adults detected per plot (averaged across all surveys per year). For soil moisture, we compared months when the drought treatment was applied (May–August) vs. not (April, September, October), including interactions with treatment factors, with month and plot × month included as random factors.

Each response variable was modelled with the distribution that provided the best fit (SAS Institute 2013). For most response variables, this was the lognormal distribution, with the addition of a small constant when necessary to assure that the smallest value was >0. Response variables evaluated using other distributions were as follows: *C. stoebe* seedling and juvenile counts (negative binomial), *P. spicata* seedling and juvenile counts (Poisson distribution, modified for overdispersion) and annual per capita survival of adult plants (binomial distribution, i.e. alive or dead as of fall). To summarize results, we present least squares means and SEs back-transformed from the scale used in analysis. For brevity, we combine statistics from multiple non-significant tests by presenting minimum *P*-values. Individual test statistics are presented in referenced tables and appendices.

Results

The drought treatment reduced soil moisture during the treatment months of May through August, 2011–2013 (volumetric water content: drought $\bar{x} = 4{\cdot}1 \pm 0{\cdot}7\%$, normal $\bar{x} = 7{\cdot}5 \pm 1{\cdot}3\%$), but not during non-treatment months (drought $\bar{x} = 12{\cdot}3 \pm 2{\cdot}4\%$, normal $\bar{x} = 12{\cdot}0 \pm 2{\cdot}4\%$; drought × treatment period: $P < 0{\cdot}001$; Table S1). Although the magnitude of the drought effect during treatment months relative to non-treatment months varied among years (drought × treatment period × year: $P = 0{\cdot}012$), within each year, the pattern held where the treatment significantly reduced soil moisture during treatment months (*post hoc* test: $t_{2448} > 15{\cdot}8$, $P < 0{\cdot}001$) and not during remaining months (*post hoc* test: $t_{2448} < 1{\cdot}0$, $P > 0{\cdot}9$). In no case did the drought treatment interact with the species composition or herbivory treatments to affect soil moisture ($P > 0{\cdot}5$).

The no-herbivory treatment reduced abundance of the biocontrol agent *C. achates* in plots containing its host *C. stoebe*, 2011–2013 ($P < 0{\cdot}001$; herbivory $\bar{x} = 4{\cdot}0 \pm 0{\cdot}2$ adults, no-herbivory $\bar{x} = 0{\cdot}6 \pm 0{\cdot}1$ adults; Table S2). The number of *C. achates* counted was higher in drought compared to normal precipitation plots ($P < 0{\cdot}001$), and in mixed-species plots compared to *C. stoebe* monocultures ($P = 0{\cdot}032$). These differences may be attributable to the herbivore's affinity for hotter conditions associated with drought plots and a bias towards increased observations of this cryptic insect on non-host plants in mixed-species plots (Story, White & Good 1996). The difference between herbivory and no-herbivory treatments varied significantly in magnitude by drought and year (herbivory × year, drought × herbivory × year, $P < 0{\cdot}04$), but the number of *C. achates* was significantly higher in herbivory vs. no-herbivory treatments in all cases (*post hoc* test: $t_{228} > 5{\cdot}8$, $P < 0{\cdot}001$). Remaining interactions among treatments were not significant ($P > 0{\cdot}13$).

In the final year of the experiment, 2013, biomass in mixed-species plots was 50% greater for the exotic invader *C. stoebe* relative to the native grass *P. spicata* under normal precipitation conditions, while under drought stress, *P. spicata* biomass was >200% greater than *C. stoebe*'s (Fig. 1). Drought depressed *C. stoebe* biomass ($P < 0{\cdot}001$), but only in mixed-species plots and not monocultures, indicating an interactive effect of abiotic stress and competition (drought × species composition: $P < 0{\cdot}001$; Fig. 2a; Table 1). At the same time, drought promoted the biomass of *P. spicata* ($P < 0{\cdot}001$) in mixed-species plots and not monocultures (drought × species composition: $P < 0{\cdot}02$; Fig. 2b; Table 1). For both species, biomass was reduced in mixed-species plots relative to monocultures ($P < 0{\cdot}001$), particularly under drought vs. normal conditions (i.e. drought × species composition). Herbivory by *C. achates* did not significantly affect *C. stoebe* biomass (all effects: $P > 0{\cdot}2$; Fig. 2a). However, there was a marginally significant trend towards a positive effect of herbivory on *P. spicata* biomass in mixed-species plots ($P = 0{\cdot}068$), evident particularly under drought conditions (drought × herbivory: $P = 0{\cdot}094$); i.e. drought-induced increases in *P. spicata* biomass in mixed-species plots tended to be stronger in herbivory vs. no-herbivory treatments (Fig. 2b).

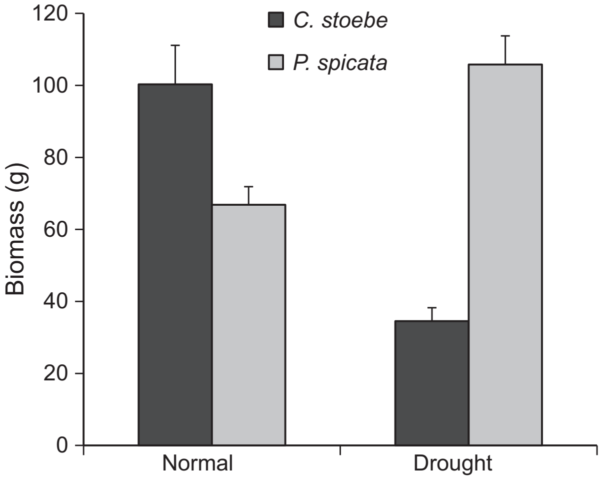

Fig. 1. Comparison of final estimated total biomass per plot ($\bar{x}$ + SE) for the exotic forb, *Centaurea stoebe*, and the native grass, *Pseudoroegneria spicata*, following 7 years of drought treatment (reduced vs. normal precipitation inputs) in mixed-species assemblages initiated with equal densities of each species. Drought effects were significant for both species in mixed-species plots but not monocultures (drought × composition: $P < 0{\cdot}02$). Data are pooled across herbivory treatments, which did not show significant differences ($P > 0{\cdot}05$).

Evaluation of demographic results relative to biomass results helped to elucidate the differences in species responses to treatments as a function of their differing life-history strategies. Overall, *C. stoebe*'s demographic changes closely paralleled its biomass response, indicating that the latter was driven by changes in population abundance. Across all treatments, *C. stoebe* adult population size more than doubled between the beginning and end of the experiment (Fig. 3a). Drought reduced the final number of *C. stoebe* adults ($P = 0{\cdot}005$), but only in mixed-species plots (drought × species composition: $P < 0{\cdot}001$; Fig. 3a; Table 1). The absolute increase in *C. stoebe* population size was lower in mixed-species plots relative to monocultures ($P = 0{\cdot}002$) under drought but not normal precipitation conditions (drought × species composition: $P = 0{\cdot}001$). Herbivory had no overall effect on final *C. stoebe* population size ($P > 0{\cdot}2$), but there were marginally significant interactive effects involving herbivory that were not evident at the biomass level (Fig. 3a). Specifically, herbivory tended to reduce final numbers of adult *C. stoebe* under drought but not normal precipitation conditions (drought × herbivory: $P = 0{\cdot}057$) and in mixed-species plots

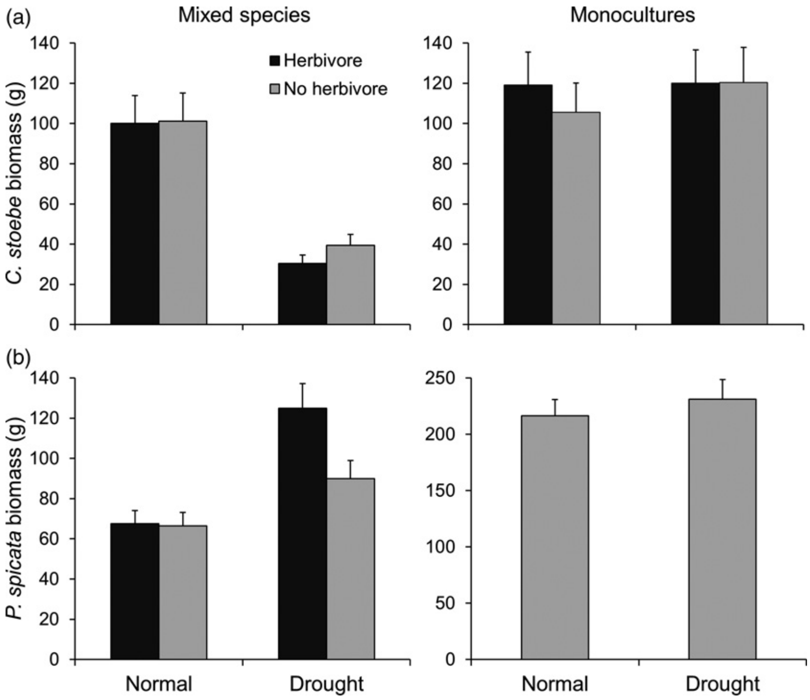

Fig. 2. Final estimated total biomass per plot ($\bar{x}$ + SE) for (a) the exotic forb, *Centaurea stoebe* and (b) the native grass, *Pseudoroegneria spicata*, following 7 years of drought treatment (reduced vs. normal precipitation inputs) in either mixed-species assemblages (initiated with 8 plants per species) or monocultures (initiated with 16 plants) that allowed or impeded access of the herbivore *Cyphocleonus achates* to its host plant *C. stoebe*. Both plant species responded differently to drought in mixed-species assemblages vs. monocultures (drought × composition: $P < 0{\cdot}02$), while herbivory effects were relatively weak ($P > 0{\cdot}05$).

Table 1. Results from generalized linear mixed model analysis of biomass and numbers of adult plants for the exotic forb, *Centaurea stoebe*, and the native grass, *Pseudoroegneria spicata*, in the final year of a 7-year common-garden experiment. Experimental factors were drought (±), species composition (*C. stoebe* only, *P. spicata* only, or a mix of both), and herbivory (±*Cyphocleonus achates*, applied only in plots containing its host, *C. stoebe*). Models for each species included data from corresponding monocultures and mixed-species plots (d.f. = 1 and 96 for *C. stoebe*, and d.f. = 1 and 70 for *P. spicata*)

	Biomass				No. Adults			
	C. stoebe		*P. spicata*		*C. stoebe*		*P. spicata*	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Drought	33·9	<0·001	18·9	<0·001	8·5	0·005	1·1	0·293
Composition*	62·2	<0·001	148·9	<0·001	62·6	<0·001	285·9	<0·001
Herbivory	0·2	0·661	3·4	0·068	1·6	0·213	0·2	0·649
Drought × composition	43·9	<0·001	6·1	0·016	13·2	<0·001	0·7	0·403
Drought × herbivory	1·2	0·285	2·9	0·094	3·7	0·057	8·2	0·006
Composition × herbivory	1·3	0·257	–	–	2·8	0·095	–	–
Drought × composition × herbivory	0·1	0·713	–	–	0·9	0·359	–	–

*Note that for each species, twice as many plants were initially established in monocultures vs. mixed-species plots. Hence, we also ran models comparing the change in numbers of adults in monocultures vs. mixed-species plots, which altered results somewhat for *P. spicata* ($F = 2{\cdot}0$, $P = 0{\cdot}158$) but not for *C. stoebe* ($F = 10{\cdot}0$, $P = 0{\cdot}002$). Interactive effects of composition were comparable regardless.

but not monocultures (composition × herbivory: $P = 0{\cdot}095$). Hence, there was a trend towards stronger effects of drought with herbivory, specifically in mixed-species plots, although the three-way interaction among experimental factors was not significant ($P = 0{\cdot}36$). These population-level responses of *C. stoebe* were driven by differences in recruitment of new adults seen 2011–2013, with recruitment of *C. stoebe* seedlings and juvenile plants generally paralleling patterns seen for adult recruitment over this period (Appendix S2; Fig. S1; Table S3), and effects on individual performance (per capita biomass, reproduction and survival) varying little across treatments (Appendix S3; Fig. S2; Tables S4 and S5).

In contrast to *C. stoebe*'s demographic response, *P. spicata*'s response was driven largely by per capita changes in plant biomass, with relatively little change in population size. Drought had no effect on the final number of *P. spicata* adults (Fig. 3b), either independently or in combination with the presence of *C. stoebe* (drought, drought × composition: $P > 0{\cdot}2$; Table 1). The presence of *C. stoebe* did not significantly affect the change in *P. spicata* population size regardless of drought (composition, drought × composition: $P > 0{\cdot}1$). In mixed-species plots, herbivory on *C. stoebe* had no overall effect on the final number of *P. spicata* adults ($P = 0{\cdot}65$), but herbivory interacted significantly with drought

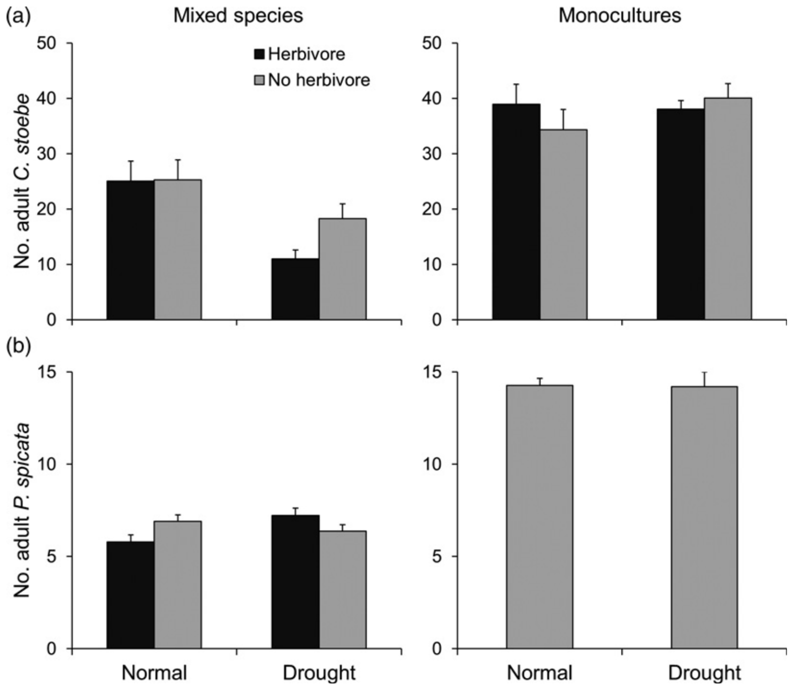

Fig. 3. Final population size per plot ($\bar{x}$ + SE) for (a) the exotic forb, *Centaurea stoebe* and (b) the native grass, *Pseudoroegneria spicata*, following 7 years of drought treatment (reduced vs. normal precipitation inputs) in eight mixed-species assemblages (initiated with eight plants per species) or monocultures (initiated with 16 plants) that allowed or impeded access of the herbivore *Cyphocleonus achates* to its host plant *C. stoebe*. Drought interacted significantly with competition to suppress *C. stoebe* population size in mixed-species assemblages ($P < 0{\cdot}001$), while effects of herbivory were relatively weak ($P > 0{\cdot}05$). For *P. spicata* in mixed-species assemblages, drought effects varied between herbivory treatments (drought × herbivory: $P < 0{\cdot}01$).

(drought × herbivory: $P = 0{\cdot}006$). Specifically, herbivory tended to promote *P. spicata* population size under drought conditions while depressing it under normal conditions, and conversely, drought positively affected *P. spicata* population size only in the presence of herbivory. However, these differences were small (Fig. 3b). In contrast to *C. stoebe* and consistent with a slow life-history strategy, *P. spicata* recruited very few adults or juvenile plants over the course of the experiment (Appendix S2, Table S6). Rather its overall response was driven by large per capita changes in biomass (Appendix S3, Fig. S2, Table S4), translating to increased total biomass in mixed-species plots faced with drought.

Discussion

Anthropogenic activities are simultaneously shifting abiotic conditions and introducing strongly interacting organisms with profound effects on the structure and function of native ecosystems. Yet, how these processes interact to restructure communities is poorly understood. Here, we demonstrate that the dominance of *C. stoebe*, one of most widespread, high-impact invaders in western North America (DiTomaso 2000; Pearson *et al.* 2016), is conditionally dependent on precipitation inputs. Under normal precipitation conditions, *C. stoebe* achieved dominance over the native *P. spicata*. However, reducing precipitation inputs dramatically shifted the outcome of competition and facilitated dominance by the native bunchgrass. These results are consistent with field observations in western Montana showing that normal precipitation conditions are associated with *C. stoebe*'s dominance, but during drought, *C. stoebe*'s abundance is reduced concordant with increases in *P. spicata* cover (Pearson & Fletcher 2008). While the biocontrol agent *C. achates* reduced *C. stoebe* abundance and its impacts on *P. spicata* biomass under drought and competition, these effects were only marginally significant and relatively weak. The cumulative effect of the drought by competition and drought by herbivory interactions on total *C. stoebe* abundance was additive, but these interactions may vary in complex ways across systems. Interestingly, individual plant performance did not correspond with overall population responses for the invader, emphasizing the importance of directly quantifying population-level responses and elucidating the linkages and discrepancies between plant performance and population outcomes.

In our experiment, the balance of competitive interactions toggled from favouring the invader's fast life-history strategy under high resource conditions to favouring the native's slow life-history strategy under low resource conditions, consistent with expectations. Mechanistically, the invader's response was driven by rapidly recruiting new adults and increasing plant densities under normal precipitation conditions. Interestingly, this population response appeared to be driven by higher seed to seedling and seedling to adult recruitment rates and not by changes in individual plant fecundity (Fig. 3a, Appendix S2). In contrast, the ability of the native to exhibit higher individual growth rates (i.e. increase biomass) under low resource conditions allowed it to dominate community biomass under low precipitation inputs with little change in population density (Fig. 3b, Appendix S3). Hence, individual plant performance was sufficient to explain overall responses for *P. spicata* but not for *C. stoebe*, emphasizing the importance of quantifying population-level responses (Maron & Crone 2006).

Our results also demonstrate an important interplay between abiotic context and biotic interactions. In monoculture, each of our species was impervious to drought, but only *C. stoebe* was negatively affected by drought in competition. This result was attributable to the fact that in monoculture, *C. stoebe* compensated for drought-induced adult mortality (Appendix S2) via recruitment into the adult cohort, but competition with *P. spicata* suppressed this population-level compensatory response (Fig. 3a, Appendix S3). Our earlier experiments in this system demonstrated that under less extended spring drought, *C. stoebe* was able to compensate for the effects of both drought and competition through this mechanism (Ortega *et al.* 2012). Hence, the extended drought of the current study appeared to shut down this compensatory response. Other studies confirm that *C. stoebe* is fairly sensitive to drought while *P. spicata* is quite tolerant (Blicker, Olson & Wraith 2003; Maines, Knochel & Seastedt 2013). The finding that neither species responded significantly to drought treatments in monoculture emphasizes the potential importance of biotic interactions in determining the effects of climate change on plants. This result has important ramifications for climate envelope modelling and climate-based conservation strategies like assisted migration, which emphasize abiotic conditions over biotic interactions when projecting climate effects on species distributions or proposing to translocate species threatened by climate change (e.g. Bradley, Oppenheimer & Wilcove 2009; McLane & Aitken 2012; Boiffin, Badeau & Bréda in press).

In contrast to the strong effects of competition, top-down control from the biological control agent did not substantially suppress *C. stoebe* abundance or biomass. Based on the limiting resource model (Wise & Abrahamson 2005), we expected that the biocontrol agent would have its greatest impacts on *C. stoebe* when the plant experienced water stress (due to reduced tolerance of individual plants) and this would translate to indirect benefits to *P. spicata* in competition. In monoculture, there was no clear indication of any impact of the biocontrol agent on *C. stoebe* populations under normal precipitation conditions or drought stress. In competition with *P. spicata* and under drought stress, there was evidence (albeit statistically weak) that *C. achates* reduced *C. stoebe* populations and that this indirectly increased *P. spicata* biomass. However, average adult plant performance did not correspond with the population-level response of *C. stoebe* to herbivory (Appendix S3). Thus, rather than limiting opportunities for compensation at the individual level, our results suggest that lowered resources combined with competition limited opportunities for compensatory responses at the population level.

Recent declines in *C. stoebe* populations in our system have been attributed to *C. achates* herbivory based on observational studies (Story *et al.* 2006). However, other corollary studies have shown that *C. stoebe* declines occurred over large areas affected by drought even in locales where *C. achates* was absent or poorly established (Sturdevant *et al.* 2006; Pearson & Fletcher 2008). While experimental studies indicate that *C. achates* can kill adult *C. stoebe* plants (Corn, Story & White 2006; Ortega *et al.* 2012), *C. stoebe* can readily compensate for mortality caused by both *C. achates* and short-term drought through increased population-level recruitment (Ortega *et al.* 2012). In contrast, under the extended drought scenario of the current study, while *C. stoebe* was still largely able to compensate for *C. achates* herbivory, its ability to tolerate drought in competition was greatly reduced. These results support the hypothesis that widespread declines in *C. stoebe* populations in this system are likely driven by drought, with possible additive effects of *C. achates* (Sturdevant *et al.* 2006; Pearson & Fletcher 2008). Interestingly, greenhouse studies in the native range intended to evaluate the viability of *C. achates* as a biological control agent for *C. stoebe* generated similar findings to ours – competition with the native bunchgrass caused strong reductions in *C. stoebe* biomass, while *C. achates* herbivory had much weaker effects that were minimally additive (Steinger & Müller-Schärer 1992).

The overall effect of resource changes on plant interactions will depend in part on the independent and interactive effects of resource changes on competition and on herbivory. In our system, the overall outcome was attributable to additive negative effects of resource reductions on competition and on herbivory, with competitive effects predominating. Other studies have shown that herbivory and competition can interact in additive, synergistic, or antagonistic ways even under constant resource conditions (Hambäck & Beckerman 2003; Agrawal 2004; Haag, Coupe & Cahill 2004; Schädler, Brandl & Haase 2007) and resource gradients can strengthen or weaken these interactions (e.g. Bonser & Reader 1995; Mulder & Ruess 1998; van der Wal *et al.* 2000). Of these interactions, antagonistic effects are most confounding for predicting overall effects. While not commonly documented, antagonistic interactions have been linked to simple, potentially common, feedbacks wherein competitors affect herbivore abundance and/or attack rates. Whether competition or herbivory generally dominate under certain resource conditions and whether their independent effects predictably forecast complex interactions remains unclear (e.g. Gurevitch, Morrison & Hedges 2000). Also uncertain is whether plants that exhibit fast life-history strategies are more sensitive to both resource reductions (Smith & Huston 1989) and herbivory (Coley, Bryant & Chapin 1985) relative to plants exhibiting slow strategies. Clearly, more experiments are needed that explicitly manipulate abiotic conditions and these biotic interactions.

In our experiment, reduced water inputs predictably toggled competitive dominance in favour of the slow, native 'tortoise' over the fast, invasive 'hare'. We focused on these two species because they are representative of a drama being played out repeatedly around the globe: a native community dominant pitted against a usurping invader. This two-species focus allowed us to examine the interaction of multiple factors over an extended time period while collecting intensive data to evaluate individual and population-level responses. However, it limited us to a case study with no replication across species differing in life-history strategies, and species provenance was confounded with life-history strategy. We therefore cannot generalize our results beyond the two species we studied. However, we propose that the more general framework presented here, which places our results in the context of plant life-history theory, provides an interesting rationale for future study.

If life-history trade-offs related to resource acquisition/use broadly determine plant success across varying abiotic conditions (Grime 1977; Smith & Huston 1989), then life-history trade-offs could provide a basis for predicting plant responses to abiotic changes, including anthropogenic change. Recent empirical work demonstrates that these opposing life-history strategies can explain competitive outcomes and successional dynamics of tree species under varying conditions around the globe (Kunstler *et al.* 2016). With regard to biological invasions, it is widely speculated that anthropogenic change should favour invaders over natives due to their greater plasticity, competitive ability, affinity for disturbance, and/or broader ecological tolerances (Dukes & Mooney 1999; Thuiller, Richardson & Midgley 2008; Davidson, Jennions & Nicotra 2011; Sandel & Dangremond 2012). However, anthropogenic change can drive either increases or decreases in critical limiting resources depending on location (Intergovernmental Panel on Climate Change 2007, 2014; Bobbink *et al.* 2010), and invaders may not always represent fast life-history strategies (Funk & Vitousek 2007). Thus, we propose that life-history strategy rather than species origin will likely best predict native vs. invader responses to anthropogenic change, with provenance being important to the extent that it aligns with life-history strategies. Testing these ideas will require examining plant responses to abiotic change across many species representing differing life-history strategies. Our work further suggests that understanding the mechanisms underlying these responses may require longer term experiments that examine not just plant performance, but also population-level responses to changes in specific resource conditions.

Author's contributions

The study idea was conceived by D.E.P.; study design was developed by Y.K.O., D.E.P., and J.L.M.; field experiment was executed by Y.K.O. and D.E.P.; data analysis was done by Y.K.O.; manuscript was written by D.E.P., Y.K.O., and J.L.M. funding was acquired by D.E.P. and Y.K.O.

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Data accessibility

Data from this paper are archived at the Dryad Digital Repository https://doi.org/10.5061/dryad.jd423 (Pearson, Ortega & Maron 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Recruitment of adult *Centaurea stoebe* plants.

Fig. S2. Per capita biomass of *Centaurea stoebe* and *Pseudoroegnaria spicata.*

Table S1. Summary statistics from analysis of soil moisture.

Table S2. Summary statistics from analysis of herbivore counts.

Table S3. Summary statistics from analysis of *Centaurea stoebe* recruitment.

Table S4. Summary statistics from analysis of per capita biomass.

Table S5. Summary statistics from analysis of individual reproduction and survival.

Table S6. Summary statistics from analysis of *Pseudoroegnaria spicata* recruitment.

Appendix S1. Testing for stability of experimental outcomes.

Appendix S2. Results for recruitment of adults, juvenile plants and seedlings.

Appendix S3. Results for individual performance measures.