Biol Invasions
https://doi.org/10.1007/s10530-022-02833-3

ORIGINAL PAPER

Nitrogen addition, but not pulse frequency, shifts competitive interactions in favor of exotic invasive plant species

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Received: 10 September 2021 / Accepted: 11 May 2022

Abstract Temporally dynamic resource supplies may alter or lead to fluctuations in competitive outcomes. Resource pulses have been theorized to promote incursion by exotic species with environments prone to higher resource fluctuations being more susceptible to invasion than those with more stable resource supplies. This is thought to be due, in part, to the ability of invasive species, especially those that are fast growing, to utilize available resources more rapidly than natives. We compared the effects of high-frequency (more but smaller pulses) versus low-frequency pulses of nitrogen (N) on interactions among two native grasses and two exotic invasive forbs planted alone and in pairs. The total quantity of N added was the same. Nitrogen pulse frequency had no effect on the biomass of exotics or natives when grown without competition. In all treatments combined, the competitive effect of exotics on natives was roughly three times higher than the competitive effect of natives on exotics. The competitive effect of exotics on natives was not affected by N additions, but N additions weakened the competitive effect of natives on exotics. Species-specific patterns in our results suggest that N pulses sometimes impacted competitive intensity, but N pulse frequency did not alter competitive intensity. Our results are inconsistent with the idea that fluctuations in resource supply ubiquitously favor invaders, as native species were as responsive to pulse frequency as exotics. However, increased N, regardless of pulse frequency, favored exotic species, consistent with a large literature showing that high resource supplies favor exotic invaders.

Keywords Competition · Interaction · Invasion · Resource pulse · Relative interaction intensity (RII) · Nitrogen amendment

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Introduction

Nitrogen (N) and water are the primary limiting resources for plants in semiarid ecosystems and their temporal availability is often constrained to brief,

Published online: 05 June 2022

unpredictable periods of time following rainfall events (Noy-Meir 1973; Goldberg and Novoplansky 1997; Austin et al. 2004). Variation in the timing or pulses of such resources can have different effects on plant growth (Farley and Fitter 1999; Chesson et al. 2004; Hodge 2004), but it is difficult to isolate the *timing* of the delivery of these resources from the *quantity* of resources delivered. Species-specific responses to resource pulses, which generally correspond with physiological and morphological traits or trait plasticity (reviewed in Chesson et al. 2004; Hodge 2004), also affect competition (Eskelinen and Harrison 2014; Goldstein and Suding 2014; but see Gebauer et al. 2002). For example, Novoplansky and Goldberg (2001) found that frequent resource pulses favored fast-growing species, but infrequent pulses favored slow growing species in competition. This shift in competitive hierarchy indicates that variability in the timing of resources might affect community composition (Bilbrough and Caldwell 1997; Chesson et al. 2004; Schwinning and Sala 2004; Funk and Vitousek 2007).

Nitrogen pulses might be particularly important to explore in resource limited systems where competitive interactions and exotic plant invasions are often mediated by N availability. In fact, N pulses may have a stronger impact than water pulses on exotic plant growth and exotic invasions (Eskelinen and Harrison 2014). However, few field studies have experimentally addressed how variation in pulsed resources might affect competitive interactions between native and exotic invasive species. Comparisons of exotic invasive and native species' competitive abilities at high or low N levels (not pulsed) suggest that higher N levels may generally favor invasives (Besaw et al. 2011; Mangla et al. 2011; He et al. 2012). There are notable exceptions, for example the exotic invasive grass *Agrostis capillaris* has strong competitive impacts on native species across a N availability gradient (Broadbent et al. 2018).

There are several reasons that resource pulses might favor colonization by exotic invasive species more than natives. One explanation for this is that exotic invasive species may be more plastic, on average, than the natives they displace (Richards et al. 2006), but support for this is mixed (Thompson et al. 1995; Funk 2008; Davidson et al. 2011; Palacio-López and Gianoli 2011). Additionally, there are many successful invasions in low-resource environments where natives should be highly adapted to exploiting temporal resource niches (Daehler 2003; Funk and Vitousek 2007; James et al. 2011) suggesting that exotics might be unusually good at extracting fluctuating resources. Indeed, evidence suggests that exotic invaders may possess more exploitative traits than native species (van Kleunen et al. 2010; Ordonez and Olff 2013; Broadbent et al. 2020; but see Thompson and Davis 2011).

We conducted a field experiment in which we added N pulses of different frequencies but in the same total quantity and compared the growth and competitive intensities of two slow growing native grasses (*Pseudoroegneria spicata* and *Poa secunda*) and two fast growing exotic invasive forbs (*Centaurea stoebe* and *Linaria dalmatica*). Faster growing species, with their higher resource uptake capacity, should benefit more from frequent resource pulses, whereas the lower resource needs of slower growing species should favor less frequent resource pulses (Campbell and Grime 1989; Novoplansky and Goldberg 2001). Thus, we hypothesized that (1) when plants were grown alone, N pulses would increase the biomass of the faster growing exotic invasive forbs more than the slower growing native grasses, (2) N additions should alter the competitive intensity in favor of exotic invasive species more than natives, and (3) frequent N pulses should have a stronger effect on exotic invader competitive intensity than less frequent N pulses.

Materials and methods

Study system

Intermountain grasslands are dominated by perennial bunchgrasses and increasingly threatened by exotic plant invasions. We evaluated two dominant native and two exotic invasive species that co-occur and thus interact frequently in this region. Our experimental bunchgrass species included *Pseudoroegnaria spicata* and *Poa secunda* (hereafter *Pseudoroegneria* or *Poa*), two of the most common species in this region (Mueggler and Stewart 1980). We also included *Centaurea stoebe* and *Linaria dalmatica* (hereafter *Centaurea* and *Linaria*), two of the most common perennial exotic invasive forbs that rapidly replace native species in the region, including *Pseudoroegneria* and

Poa (Callaway et al. 2005; Besaw et al. 2011; Pearson et al. 2015). *Pseudoroegnaria* and *Poa* are drought tolerant perennial bunchgrasses. *Pseudoroegneria* has deep fibrous root systems (Zlatnik 1999) while *Poa* is more shallow-rooted (Howard 1997). *Poa* is one of the first native grasses in the region to green up in the spring and completes spring growth earlier than most other perennial grasses (Blaisdell 1958; Scianna and Winslow 2016). *Centaurea* and *Linaria* are both prolific producers of high viability seed that germinates early in the season. Plants grow rapidly, producing deep taproots capable of accessing late season water sources as plants mature (Jacobs and Sheley 1998; Whaley and Piper 2017). Disturbance has marked effects on the densities of our experimental species in this region. Prior to disturbance, native bunchgrasses occur as spatially distinct clumps separated by significant portions of bare ground (Kaiser 1961). However, disturbance, natural and anthropogenic, is a key precursor of successful plant invasions in these grasslands and can promote high densities of *Centaurea* and *Linaria* (Ferguson et al. 2007; Gundale et al. 2008).

Experimental design

Seeds of the four species were collected in the Missoula Valley in summer 2016. Because germination times and early rates of growth vary for these species (M.L. Slate and R.M. Callaway, *personal observations*), we sowed seeds of *Pseudoroegneria*, *Poa*, and *Linaria* on February 10th and seeds of *Centaurea* on March 17, 2017, in the University of Montana's research greenhouse. Once a few weeks old, seedlings were planted into 500 mL pots filled with a mixture of 75% native soil: 25% silica sand and maintained until transplanted in early May.

We tilled a 15 m × 15 m area in early spring at the Fort Missoula common gardens, Missoula, Montana, an area likely to have been historically occupied by intermountain prairie (Fig. 1). Soils consisted of gravelly loamy Mollisols (www.websoilsurvey.sc.egov.usda.gov) and are generally infertile (Mueggler and Stewart 1980). Precipitation in Missoula, MT averages 325 mm a year and falls primarily in May and June. Late summers receive little precipitation (www.ncdc.noaa.gov).

Before planting, we covered the soil surface with landscape fabric to reduce weeds and fenced the site. Seedlings were transplanted on May 10, 2017, when plants were less than 4 cm tall (Figure 1b) and roots had not reached the base of their 500 mL pots. Seedlings were planted into 15 cm × 15 cm plots (240 total) cut into the landscape fabric; with each plot 30 cm from the next closest to prevent shoot and root overlap among plots. In each plot, we planted one plant of either an exotic or native species alone (control; n = 30 each species; 120 plots) or in combined pairs with each native planted with each exotic (two plants per plot; n = 30 each native—exotic pair; 120 plots).

Young plants were watered and established for 50 days to allow time for plant roots in pairs to make contact before pulse treatments. On June 30, when plant shoots had begun to overlap within plots and plants were in their most vigorous stage of growth (M.L. Slate and R.M. Callaway, personal observations), each planting combination received one of three N treatments: control (no N pulse; to evaluate how N additions impacted plant growth and competitive interactions relative to background levels of N), one single large N pulse (1.24 g N), or a series of three frequent small N pulses (0.41 g N) that delivered the same total amount of N as the single large pulse over the duration of the experiment (for each species grown alone by N pulse treatment or plant

Fig. 1 Common garden location in Missoula, MT before planting in late April (**a**). Greenhouse grown seedlings at size transplanted into common garden on May 10 (**b**)

combination pair by N pulse treatment n = 10). We applied N to each plot using a 20-0-0 liquid fertilizer (Vigoro®) containing 17.5% N in the form of urea (quickly available N) and 2.5% triazone (slowly available N), diluted in 60 mL of water. The same amount of water was also added to the no N pulse treatment. These amounts were within the range of N additions used by other researchers (James and Richards 2006; Lamb et al. 2007; Drenovsky et al. 2008) and within the range of soil N mineralization rates for the region (Chen and Stark 2000; Booth et al. 2003). The two other small pulses were applied on July 10 and July 19 (10 day intervals), while plants were still in their vegetative growth stage. Our N pulse intervals were similar to those used in other studies (James et al. 2006 (6 or 7 day intervals); Parepa et al. 2013 (10 day intervals); Liu and van Kleunen 2017 (7 day intervals); Tao et al. 2021 (7 day intervals)). There was no shoot (and most likely no root) overlap among plots when N treatments were added. All plots were watered immediately after N pulses were added to eliminate water pulse effects within the N addition treatments. Plots were watered daily, in the absence of precipitation, with an oscillating sprinkler to maintain high soil moisture levels and separate the effects of N pulses. The duration of each watering varied, becoming longer as summers progressed (from 10 min per day in late June (each watering simulated a 4 mm rain event) to 15 min intervals that were repeated 4 times each day in August (each watering simulated a 6 mm rain event)). The soil was well-drained and at no point did we see water pooling on the soil surface. All plots were hand weeded regularly. Aboveground biomass was harvested on August 28, dried at 60º C until dry, and weighed.

Analyses

All analyses were conducted in R version 3.5.1 (R Core Team 2018). Distributions of means were checked for normality using the Shapiro–Wilk test and homogeneity of variance was assessed with Levene's test. Post-hoc contrasts were conducted with the emmeans package (Lenth 2018) where appropriate. To understand how N pulses impacted growth when plants were grown individually, we tested the individual and interacting effects of N pulse treatments and species as fixed factors with plant biomass as a dependent variable in a generalized linear model to account for data skewness (hypothesis 1). We accounted for overdispersion by applying the gamma family and log-link function. X^2- and p-values were estimated using the Anova function in the car package (Fox and Weisberg 2011).

To understand how N pulses influenced competitive intensity of native vs exotic invasive species, we tested the effect of N pulse treatments as a fixed factor with Relative interaction intensity (RII; Armas et al. 2004) as the dependent variable for native or exotic species in one-way ANOVAs (hypotheses 2 and 3; two one-way ANOVAs). T-test comparisons were used to evaluate whether RII values differed significantly from zero for each N pulse treatment to understand the direction of response to N pulses for natives or exotics. Values of zero denote no interaction while negative values that differ significantly from zero indicate negative or competitive interactions. RII provides a measure of the strength of the interaction intensity between species with negative values between 0 and − 1 indicating competitive effects (lower negative values denote stronger competitive effects) and positive values between 0 and +1 indicating facilitation. RII was calculated for each competing pair as: $(N_{competition} - N_{alone})/(N_{competition} + N_{alone})$ where N represents the biomass of the focal native or exotic species (Armas et al. 2004). The biomass of each target species grown alone (control) was averaged for each N pulse treatment prior to these calculations and used for the pairwise RII calculations and 95% confidence intervals values were determined for each replicate pair. We also tested the effect of N pulse treatments (fixed factor) on the RII (dependent variable) of each focal species x plant-interaction treatment in one-way ANOVAs to understand species-specific differences (4 one-way ANOVAs).

Results

When grown alone, *Centaurea* was roughly 30 to 100 times larger than the two native species (EMM: *Poa:* z-ratio = 203.0, $p < 0.001$; *Pseudoroegneria:* z-ratio = − 205.5, $p < 0.001$), and *Linaria* was roughly 15 to 50 times larger than the two natives (EMM: *Poa*: z-ratio = 85.10, $p < 0.001$; *Pseudoroegneria*: z-ratio = −87.58, $p < 0.001$; Fig. 2; hypothesis 1).

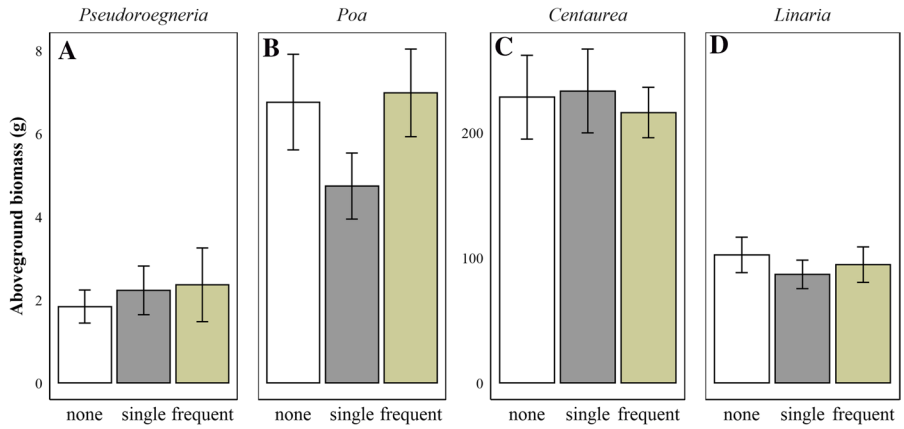

Fig. 2 Aboveground biomass of two native (*Pseudoroegneria* (**a**) and *Poa* (**b**)) and two exotic invasive (*Centaurea* (**c**) and *Linaria* (**d**)) species when grown alone and treated with one of the following N pulse treatments: no N pulse (none), single large N pulse, or frequent small N pulses (equal in total N to the single large N pulse). Please note that the scale varies by plant origin. Means ± SE

Table 1 Results from a GLM used to evaluate how N pulse treatments impacted aboveground biomass of our study species

	X^2	*P*-value
N pulse treatments	5.280	0.071
Species	1825	< 0.001
N pulse x Species	3.890	0.691

None of the four species grew larger with either N pulse frequency when grown alone (Table 1; Fig. 2).

Competition between natives and exotics was highly skewed in favor of the exotic species. Natives had a moderate competitive effect on exotics when no resource pulses were added (RII = − 0.22, *T*-test: $t = -1.140$, $p < 0.001$), but N additions shifted the interactions so that there were no longer detectable competitive effects of natives on exotics (single pulse RII = − 0.04, *T*-test: $t = -1.140$, $p = 0.267$; frequent pulse RII = − 0.05, *T*-test: $t = -1.255$, $p = 0.221$; Fig. 3a; hypothesis 2). In contrast, the competitive effect of exotics on natives, across all species and treatments, was consistently high (average RII = − 0.30; *T*-tests: none: $t = -9.519$, $p < 0.001$; single pulse: $t = -5.101$, $p < 0.001$; frequent pulse: $t = 5.353$, $p < 0.001$; Fig. 3b; hypothesis 2). Frequent N pulses had the same effect as less frequent N pulses on the competitive effect of natives on exotics (EMM: *t*-ratio = 0.039, $p = 0.999$; Fig. 3a; hypothesis 3) and the competitive effect of exotics on natives (EMM: *t*-ratio = -0.489, $p = 0.877$; Fig. 3b; hypotheses 3).

For species-specific competitive outcomes, neither the competitive effect of *Pseudoroegneria* on *Centaurea* (*Pseudoroegneria* (ANOVA): $F = 1.988$, $p = 0.199$) nor the competitive effect of *Centaurea* on *Pseudoroegneria* (*Centaurea* (ANOVA): $F = 2.629$, $p = 0.133$) were affected by N addition or N pulse frequency (Fig. 4a, c). However, the competitive effect of *Poa* on *Centaurea* weakened significantly with frequent N pulses, relative to the control (EMM: *t*-ratio = −2.616, $p = 0.041$), but the effect of frequent pulses did not differ from the single N pulse treatment (EMM: *t*-ratio = -1.292, $p = 0.415$; Fig. 4a). The competitive effect of *Poa* on *Linaria* weakened with a single N pulse relative to the control (EMM: *t*-ratio = 3.078, $p = 0.014$), but the effect of a single N pulse did not differ from frequent N pulses (EMM: *t*-ratio = 1.011, $p = 0.577$; Fig. 4b). The competitive effect of *Linaria* on *Pseudoroegneria* decreased with frequent N pulses (EMM: *t*-ratio = -3.215, $p = 0.023$), but the effect of frequent N pulses was not different than the single N pulse (EMM: *t*-ratio = − 1.034, $p = 0.574$; Fig. 4c). Finally, neither N additions nor pulse frequency altered the effects of either *Centaurea* or *Linaria* on *Poa* (*Centaurea* (ANOVA): $F = 0.437$, $p = 0.652$; *Linaria* (ANOVA): $F = 1.122$, $p = 0.342$; Fig. 4d).

Discussion

We found no clear effect of pulse frequency on competitive interactions between exotic invasive and native species. But, N addition, regardless of pulse frequency, tipped competitive outcomes in favor of exotics—natives had much weaker competitive effects on exotics when N was added. There are other aspects of exotic invasions that might be affected by pulse

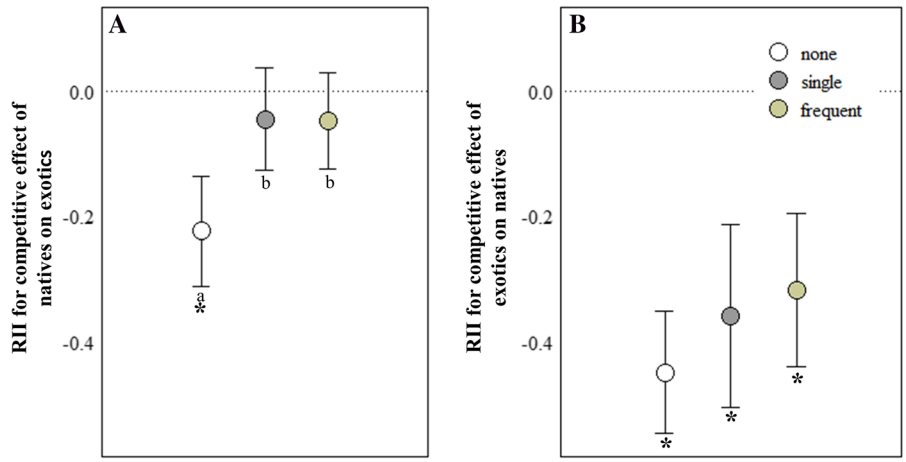

Fig. 3 RII (relative interaction intensity) for the competitive effect of native on exotic species and one of three N pulse treatments (**a**). RII for the competitive effect of exotic on native species (**b**). RIIs that share a letter within each plant-interaction treatment are not significantly different (Estimated marginal means; $P < 0.05$). Asterisks indicate significant competitive effects (*t*-test; $P < 0.05$). Means ± 95% CI

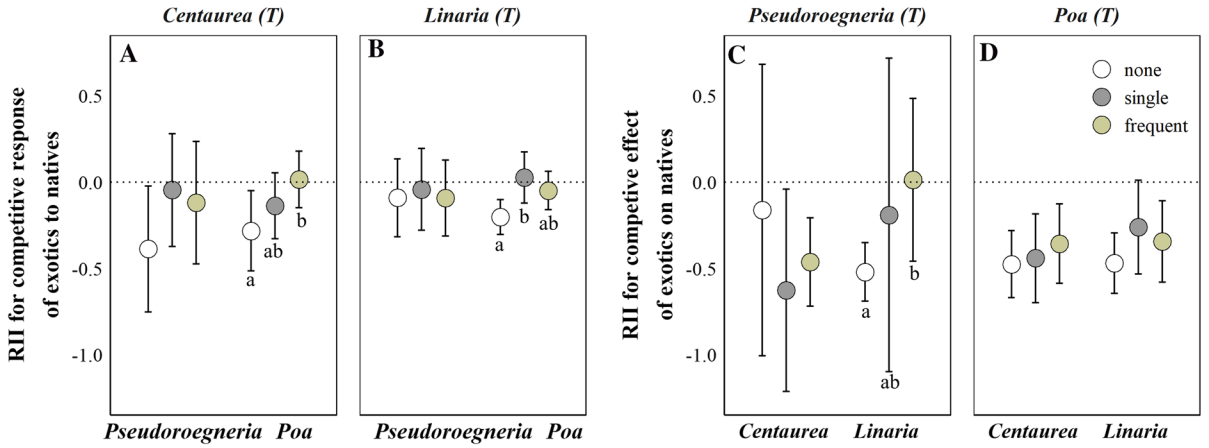

Fig. 4 RII (relative interaction intensity) for the competitive effect of the two native species on the two target (T) exotic invasive species (*Centaurea* (**a**) and *Linaria* (**b**)). RII for the competitive effect of the two exotic invasive species on the two target (T) native species (*Pseudoroegneria* (**c**) and *Poa* (**d**)). RII were determined for the following N pulse treatments: no N pulse (none), single large N pulse, or frequent small N pulses (equal in total N to the large N pulse). Values below zero represent competitive interactions with lower negative values denoting stronger competitive effects. RIIs that share a letter within each plant-interaction treatment are not significantly different (Estimated marginal means; $P < 0.05$). Means ± 95% CI

frequencies (e.g., recruitment, response to physical disturbances, temporally asymmetric interactions) that were not considered here but should be addressed in future research.

Why might the frequency of pulsed resources, in general, not give the fast growing exotic species considered here competitive advantages when resource additions often do regardless of pulse frequency (Kolb et al. 2002; Kolb and Alpert 2003; Besaw et al. 2011; James et al. 2011)? First, experimental applications, such as those applied in the current study, may not apply the appropriate limiting resource. However, nitrogen is limiting in grasslands globally (You et al. 2017), at the latitude of our site (Fay et al. 2015), and in our experimental garden (Maron and Marler 2007), so we think this explanation is unlikely. Further, the fact that our competitive effects differed with N additions suggests that N was limiting in our experiment even if the frequency of N addition did not impact competitive outcomes. Second, the quantity of the resource pulse may not have been great enough to produce an effect. However, we

used N pulse concentrations at realistic levels for our system (Chen and Stark 2000; Booth et al. 2003) to account for this. Third, the duration and frequency of resource pulses might differentially affect growth and competition. For example, when pulses are very brief, plants may not have enough time to respond (Cui and Caldwell 1997; Ivans et al. 2003; James et al. 2009). To address this concern in the current study, we selected pulse frequencies that were similar to those used in recent studies with related research questions (Perepa et al. 2013; Liu and van Kleunen 2017; Tao et al. 2021). However, our semiarid climate varied considerably from the wetter climates of these previous studies so we cannot discount the possibility that resources applied at different pulse frequencies may have yielded different results. Fourth, plants may uptake resources differently according to their life-stage (e.g., Miao and Bazzaz 1990; Bilbrough and Caldwell 1997; Tao et al. 2021). Our plants were all the same age and in their most vigorous vegetative growth stage when we added N pulses (June through mid-July; 4 months old). This timing is several weeks late in the general growth phenology of the two native grasses in natural grasslands and *Linaria*, but not *Centaurea* (M.L. Slate and R.M. Callaway, *personal observations*). However, in unusually wet years the dominant species in these grasslands continue growing well into July, and our watering treatments mimicked these years and reduced water limitations for all species. Lastly, we compared the competitive abilities of exotic invasive forbs with native bunchgrasses. Although our comparisons mimicked interactions that regularly follow disturbances in this nutrient limited study system, a recent meta-analysis found that grasses respond more favorably to N addition than forbs (You et al. 2017). Thus, we may have seen an even stronger competitive effect had our target species been native forbs.

Early studies suggest that resource pulses might have important effects on community composition by favoring some species over others (Noy-Meir 1973; Goldberg and Novoplansky 1997). Consistent with these ideas, research in controlled settings has found that exotic invasive species can be favored over natives in competitive interactions when resource pulses are less predictable (Parepa et al. 2013) or when low magnitude resource pulses are added at middle or later stages of growth (Tao et al. 2021). In contrast, the few field studies to experimentally address this have generally found that pulsed resources do not impact competitive interactions. Gebauer et al. (2002) conducted a neighbor removal experiment in a cold desert while simulating precipitation and N pulse additions. They found that shrub species used resource pulses differently, but found no evidence that the timing of pulsed resources changed competitive interactions. Similarly, James et al. (2006) experimentally applied water and N to plots containing native shrubs and that were being invaded by the North African/Asian grass *Schismus arabicus*. They found that when resource pulses were added during times when shrubs were most physiologically active, the density and biomass of *S. arabicus* was reduced. They concluded that *S. arabicus* was a more successful invader under continuous rather than pulsed resource supply. Neither field study considered how variation in pulse frequency impacted competitive interactions.

Our results indicate that rather than differences in pulse frequency, a general increase in soil N shifts competitive effects in favor of exotic invasive species. Therefore, at least some exotic invasions appear to be promoted less by resource pulses than the ability to respond to higher resource levels in general. This suggests that plant communities experiencing increases in total available resources, regardless of frequency, may be more susceptible to biological invasion. In these systems, managing the quantity of overall resource input, rather than the frequency of resource pulses, may be a more effective strategy for reducing the success and spread of invasive species.

Acknowledgements We thank B. Davis, S. Debnam, B. Flanagan, D. Hooper, N. Hupp, J. Liming, J. Lucero, J. Mouton, M. Marler and staff of the Missoula Native Plant Garden for help with field work and J. Maron for generous use of his lab facilities. We are grateful for comments from reviewers and editors, which improved this manuscript considerably.

Authors' contributions MLS and RMC designed the study; MLS, NM, and AA carried out the field experiment and collected all data; MLS analyzed the data; all authors contributed to writing and gave final approval for publication.

Funding MLS was supported by a NSF Graduate Research Fellowship, NSF Postdoctoral Fellowship [DBI-1907214], and the UM Research and Creative Scholarship Fund. AA thanks MPG Ranch for support. NM thanks the UM Davidson Honors College Undergraduate Research Award for support. RMC and

MLS thank the NSF EPSCoR Track-1 [EPS-1101342, INSTEP 3] and the NSF EPSCoR Cooperative Agreement [OIA-1757351] for support.

Data availability material Data deposited in figshare, https://doi.org/10.6084/m9.figshare.c.5977759.v1 (Slate et al. 2022).

Code availability Not applicable.

Declarations

Conflicts of interest The authors have no competing interests to declare.

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