





ARTICLE

Increasing and fluctuating resource availability enhances invasional meltdown

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Funding information

National Natural Science Foundation of China, Grant/Award Numbers: 31822007, 32071660, 32201438; National Science Foundation EPSCoR Cooperative Agreement, Grant/Award Number: OIA-1757351; Scientific Research Foundation for Returned Scholars, Huazhong Agricultural University, Grant/Award Number: 11042110026

Handling Editor: Helmut Hillebrand

Abstract

Exotic plant invaders can promote others via direct or indirect facilitation, known as “invasional meltdown.” Increased soil nutrients can also promote invaders by increasing their competitive impacts, but how this might affect meltdown is unknown. In a mesocosm experiment, we evaluated how eight exotic plant species and eight Eurasian native species responded individually to increasing densities of the invasive plant *Conyza canadensis*, while varying the supply and fluctuations of nutrients. We found that increasing density of *C. canadensis* intensified competitive suppression of natives but intensified facilitation of other exotics. Higher and fluctuating nutrients exacerbated the competitive effects on natives and facilitative effects on exotics. Overall, these results show a pronounced advantage of exotics over native target species with increased relative density of *C. canadensis* under high nutrient availability and fluctuation. We integrate these results with the observation that exotic species commonly drive increases in soil resources to suggest the Resource-driven Invasional Meltdown and Inhibition of Natives hypothesis in which biotic acceleration of resource availability promotes other exotic species over native species, leading to invasional meltdown.

KEYWORDS

competition, *Conyza canadensis*, facilitation, invasive alien plant species, multispecies invasion, native plant species

INTRODUCTION

The introduction of exotic plant species and anthropogenic disturbances are increasing due to the global rise in the exchange of goods and human populations

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(Early et al., 2016; Kuebbing et al., 2013; Pyšek et al., 2020; Seebens et al., 2021; Stotz et al., 2020). Therefore, understanding what may weaken or exacerbate their spread and impact is crucial. One strikingly counterintuitive, yet potent, biotic process that often intensifies exotic invasions is the positive effect that many invaders have on each other (Braga et al., 2018), dubbed “invasional meltdown” (Simberloff & Von Holle, 1999). The main component of invasional meltdown, that is, facilitation among exotic plants is widely supported in the literature (Braga et al., 2018) but is counterintuitive because competition between exotic invaders and natives is generally quite one-sided in favor of invaders (Callaway et al., 2011; Hierro et al., 2022; Pearse et al., 2019; Richards et al., 2006; Sun et al., 2017; Vilà & Weiner, 2004). In other words, invaders are usually excellent competitors. So why would invaders so often have positive effects on each other? Most reports on invasional meltdown are based on co-occurrence of exotics, which could just indicate a co-preference for particular conditions, such as disturbed habitats, and not facilitation (Braga et al., 2018). There is also experimental support for invasional meltdown, but little in the context of large groups of species or experimental comparisons of exotic and native species (Braga et al., 2018), and importantly the invasional meltdown hypothesis is fundamentally a multispecies, community-based hypothesis.

The mechanisms that drive invasional meltdown are not clear but could include a broad suite of direct and indirect facilitative mechanisms (Callaway, 2007). Nevertheless, it is even less clear what mechanisms might disproportionately benefit other exotic species in a meltdown process relative to native species (but see Flory & Bauer, 2014). One overlooked possible mechanism of invasional meltdown is the general acceleration of productivity and nutrient cycling associated with exotic invasive plants. In a meta-analysis across many taxa of invasive species and invaded habitat types, Liao et al. (2008) found that plant invasions were associated with large increases in aboveground net primary productivity. Also, total nitrogen concentrations in plants increased by 40%, and soil ammonium and nitrate concentrations increased by 30% and 17%, respectively, in association with exotic species. Furthermore, carbon and nitrogen pools in microbial biomass increased by 34% and 26%, respectively (also see Ehrenfeld, 2003). In a more recent meta-analysis, Xu et al. (2022) reported even larger increases in available soil nitrogen and phosphorus. McLeod et al. (2016) reported similar associations between exotic invasive species, productivity, and soil nitrogen, and also that exotics were associated with very large increases in ammonia oxidizing bacteria in soils. Since exotic invaders frequently benefit from

high soil nutrient concentrations (Besaw et al., 2011; Burke & Grime, 1996; Davis et al., 2000; Huenneke et al., 1990; Maron & Connors, 1996; Thompson et al., 2001; Thomsen et al., 2006), and if the positive effects of an exotic species on soil nutrients facilitates other exotic species, this might drive invasional meltdown.

In contrast to the potential facilitative effects of biotically increased soil nutrients, high nutrient availability can intensify competitive interactions, which can also potentially exacerbate invasions (Alba et al., 2019; Besaw et al., 2011; Liu et al., 2017; Olsen et al., 2016; Sardans et al., 2017; Wang & Callaway, 2021; Zhang et al., 2022). This is consistent with analyses of competitive intensity on abiotic gradients (Brooker et al., 2005; Pennings & Callaway, 1992) but might be more pronounced in the disproportionately strong competitive effects exotics have on natives (Golivets & Wallin, 2018; Kuebbing & Nunez, 2016; Pearse et al., 2019; Vilà & Weiner, 2004).

In addition to total resource supply, the timing of resource delivery can affect the outcome of competition and has been hypothesized to favor exotic invasion: the “fluctuating resources” hypothesis (Davis et al., 2000). It is thought that ruderal species are better at rapidly exploiting dynamic resources than species in other functional groups. However, not all invaders are ruderal (see Huang et al., 2009; Reinhart et al., 2005), and a single species can show highly competitive traits in exotic ranges versus weak competitive traits in native ranges (Callaway et al., 2011; Sun et al., 2015). Furthermore, disturbance can have far more positive effects on invasion in exotic ranges than in native ranges (Hierro et al., 2006). Regardless, some studies support the fluctuating resource hypothesis (Eskelinen & Harrison, 2014; Goldstein & Suding, 2014) and others do not (Gebauer et al., 2002; James et al., 2006; Slate et al., 2022). Biotically increased and potentially fluctuating nutrient supply may contribute to invasional meltdown and to the suppression of native species by exotics, and all may be accelerating as global problems.

Global nitrogen deposition is substantial (Ackerman et al., 2019), and fluctuating resources are believed to have a significant impact on invasibility (Davis & Pelsor, 2001), which may become more prevalent due to the expansion of agro-ecosystems (Dematté et al., 2020). However, to our knowledge, no studies have explored these processes simultaneously or their potential interactions at the level of multispecies communities. Insight into competition in the context of different facets of resource supply can be gained from the responses of target individuals to varying relative densities of competitors (Sun et al., 2013). For example, as the relative density of

neighbors increases, competition would be demonstrated by a decreasing biomass of the target, a negative slope, whereas facilitation would be demonstrated by a positive slope. For example, evidence for invasional meltdown would be a positive correlation between increasing relative densities of an exotic invader and the individual biomass of exotic neighbors (Kuebbing et al., 2013). The effect of total resource ability or the dynamics of resource supply can be evaluated by comparing these slopes.

We experimentally explored the interactions among total nutrient supply, fluctuating resources, and possible invasional meltdown caused by the invasive plant *Conyza canadensis* L. (synonym *Erigeron canadensis*). We conducted experiments with *C. canadensis* interacting with eight exotic versus eight native plant species, all individually, that naturally coexist with *C. canadensis* in China (<http://www.iplant.cn>). For all pairwise interaction combinations, we also varied the total nitrogen supply and its timing. We asked the following questions: (1) How does the growth of exotic versus native species respond to increasing competition with *C. canadensis*? (2) Does total nutrient supply change the interactions? And (3) does a fluctuating supply of nitrogen change the interactions between *C. canadensis* and exotic species versus the interactions between *C. canadensis* and native species?

MATERIALS AND METHODS

Study system

Conyza canadensis is an annual plant that is native throughout most of North America and Central America and is now widely naturalized throughout most of the world (Bajwa et al., 2016). In its native range, *C. canadensis* is the prototype of a ruderal species (Weaver, 2001), and thus good for tests of fluctuating resources. In its native range, increasing abundance of *C. canadensis* has no relationship with the richness of other species in ruderal communities (Shah et al., 2014). But it is highly competitive with crops (Bajwa et al., 2016), and, in its exotic range, increases in its abundance are strongly correlated with decreases in community richness (Shah et al., 2014). In China, it was first recorded in Yantai, Shandong Province in the 19th century, and has since become one of the region's most problematic and widespread noxious invasive species (Wu et al., 2019; Yan et al., 2020).

In disturbed habitats in parts of its exotic ranges, *C. canadensis* can spread rapidly and become dominant by displacing other species. In such habitats, other exotic species are commonly found (van Kleunen et al., 2015),

thus, during its spread, *C. canadensis* is interacting with both exotic and native species. We selected eight exotic and eight native plant species that naturally coexist with *C. canadensis* (pers. observation; Appendix S1: Table S1; Figure 1). The seeds of all 17 species were collected in the field in Wuhan, in at least three populations for each species and subsequently pooled for each species.

Experimental setup

We conducted the experiment in a greenhouse at the Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan, China (30.51° N, 114.54° E). We sowed the seeds of each species separately in germination trays (16 cm × 8 cm × 4.5 cm) filled with potting soil. To ensure that all the species were at a similar developmental stage at the beginning of the experiment, we sowed them on various dates. After one or two weeks of growth, we used similar-sized seedlings (two-leaves) from each *C. canadensis* individual, eight exotic and eight native species and then transplanted them into 2.5-L circular plastic pots filled with a 1:1 mixture of sand and fine vermiculite to exclude most microbiota and create a low background nutrient level before the experimental nutrient application. We chose pots large enough to keep most plant species from becoming pot bound by the end of the experiment but small enough to allow for intensive species interactions.

To examine different intensities of the effect of *C. canadensis* on the individual performance of exotic versus native species, we used a replacement design with a constant total density while systematically altering the ratios of *C. canadensis* to target species ($n = 4$; Harper, 1977). Specifically, for each of the 16 pairwise combinations, we grew one individual of *C. canadensis* with three target individuals, two *C. canadensis* individuals with two target individuals, and three *C. canadensis* individuals with one target individual (Figure 2a). This setup was repeated across four nutrient treatments to investigate how nutrient supply and fluctuations affects species interactions (Figure 2b). Although replacement designs are frequently used in competition experiments (e.g., Wagg et al., 2011), it should be noted that this design inherently confounds inter- and intraspecific interactions (Jolliffe, 2000). This is because when the number of plants of the interspecific competitor increases, the number of intraspecific plants automatically decreases. However, as it applies equally across both exotic and native target species and among the nutrient treatments in our experiment, the replacement design still allowed us to test the impact of the relative density of *C. canadensis* on the comparative performance of

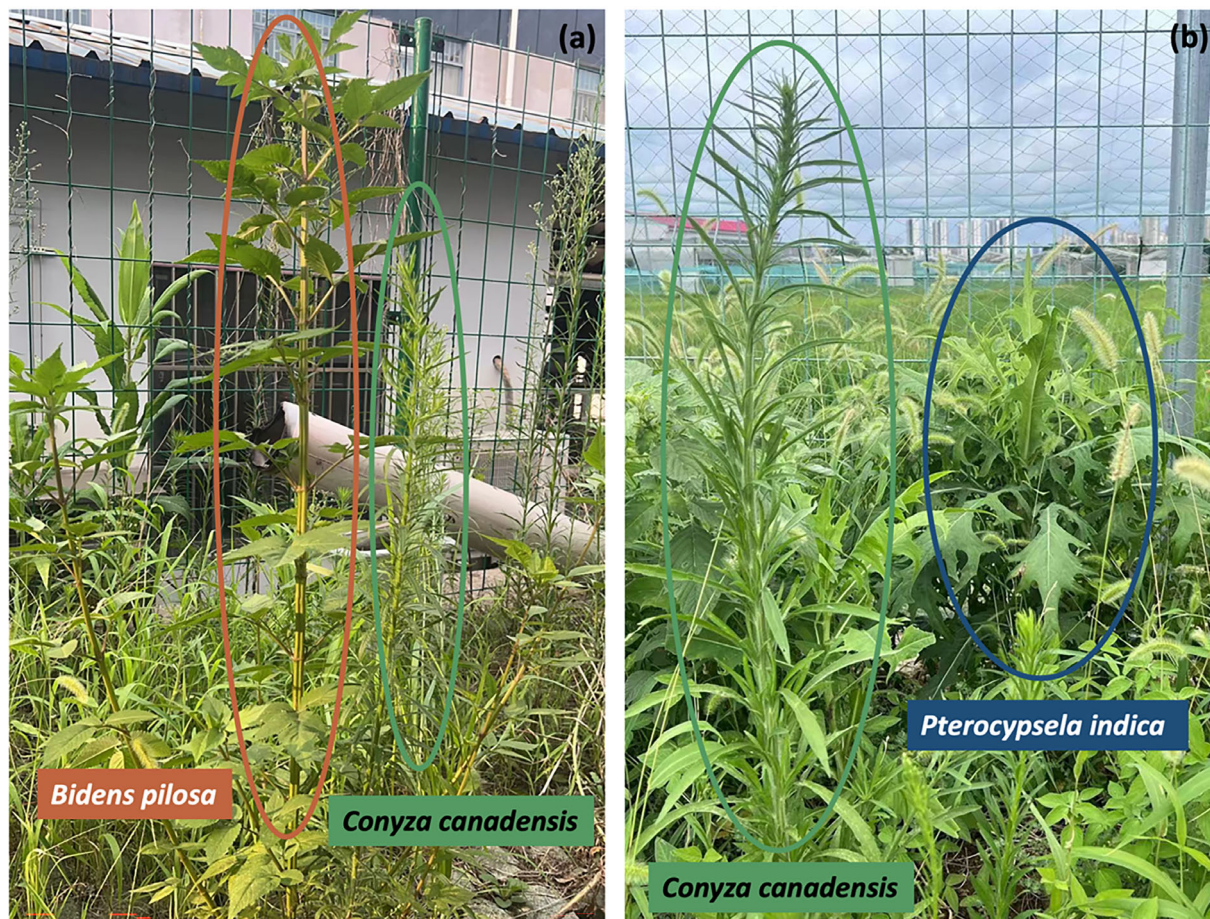


FIGURE 1 Pictures illustrating the coexistence of *Conyza canadensis* in the wild with our target exotic plant species, *Bidens pilosa* (a), and our target native plant species, *Pterocypsela indica* (b). Photo credits: Zhi-Kun Ren.

exotic and native target plant species under varying nutritional conditions.

Nutrient treatments began 1 week after transplanting using a Hoagland solution fertilizer at weekly intervals for a total of 10 weeks. We conducted four nutrient supply patterns: (1) constant low, (2) constant high, (3) high single pulse, and (4) high multiple pulses (Figure 2b). The low-nutrient treatment (1) received a total of 100 mL of a 400%-strength Hoagland solution. Treatments (2) to (4) were all high-nutrient treatments that received 400 mL of a 400%-strength Hoagland solution throughout the experiment but differed in the temporal pattern of nutrient supply (Figure 2b). To avoid water-supply bias among treatments, we added extra water to each pot so that the total solution volume was always 250 mL. We watered the plants with the same amount every 3 days. There were six replicates per target species for each of the relative abundance and nutrient treatment combinations, resulting in 1152 pots. After transplanting, plants were exposed to natural light conditions supplemented by metal halide bulbs, following a 14/10 h day/night cycle at a 22/28°C temperature cycle in the greenhouse. During

the experiment, we randomly arranged pots on tables and switched tables weekly. One week after completing the last nutrient application, we harvested the above-ground biomass of the target plants. Importantly, because there were different numbers of target individuals in the competition treatments (1, 2, or 3), we used the mean individual biomass of the targets for analyses. Because the roots in the pots were intertwined, we could not harvest the roots of the target species separately from *C. canadensis*. The aboveground biomass was then dried at 80°C for 72 h before being weighed.

Statistical analysis

To investigate the effects of the relative abundance of *C. canadensis*, target species origins (exotic vs. native), and their interactions, on the aboveground biomass of target species under four different nutrient treatments, we performed a linear mixed model (LMM) with relative abundance of *C. canadensis*, origin of target plants, nutrient treatments, and their interactions as fixed factors,

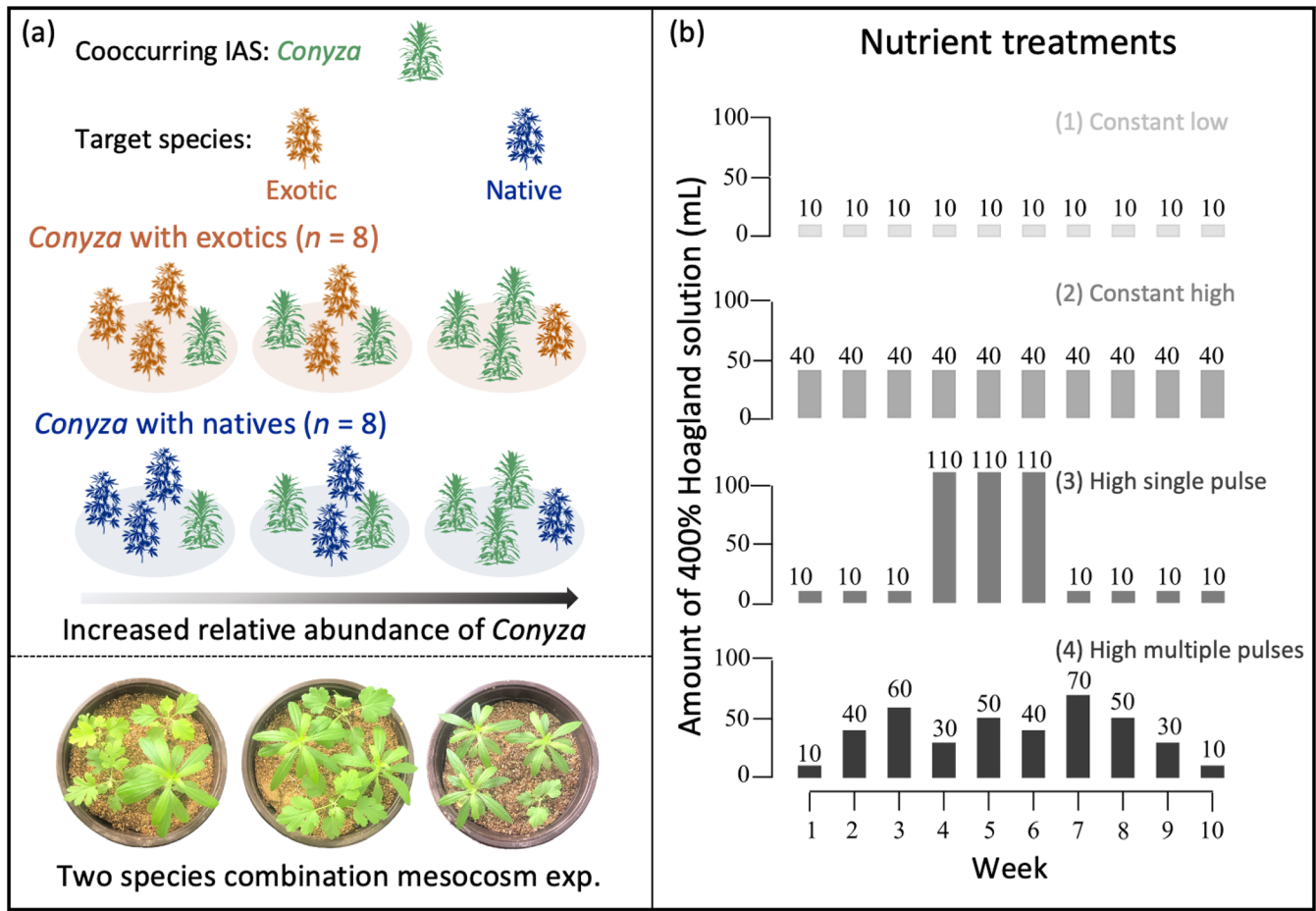


FIGURE 2 Graphical illustration of the experimental design for the potential effect of resource availability on the interactions between the relative abundance of a focal plant invader and exotic as compared with native target species. We designed a two-species interaction study that compared eight exotic versus eight native plant species grown with three relative abundances of the focal invasive alien species (IAS) *Conyza canadensis* (a) and under four different nutrient regimes (b). Each bar represents the amount of nutrient solution supplied each week during the 10 weeks of the experiment. The total amount of nutrients added in the constant low-nutrient treatment was 100 mL and in all high-nutrient treatments 400 mL; the latter was further divided into constant, single pulse, and multiple pulse nutrient additions. Photo credits: Zhi-Kun Ren. exp., experiment.

and with target species as random factor. When there was a significant interactive effect, multiple comparisons were carried out using least square mean post hoc tests (LSM), and *p*-values were adjusted by false discovery rate (FDR; Benjamini & Hochberg, 1995). All statistical analyses were performed with R (version 4.0.5) using the “car” (Fox & Weisberg, 2018), “lme4” (Bates et al., 2014), “lsmeans” (Lenth, 2016), and “multcomp” (Hothorn et al., 2008) packages.

RESULTS

Across all treatments, the mean individual aboveground biomass of native target plants was reduced by the density of *C. canadensis*, that is, its increasing relative abundance (χ^2 91.3, *p* < 0.001), indicating overall

competitive effects of the invader (Figure 3). In contrast, other exotic species experienced facilitation with the increasing abundance of *C. canadensis*. The effect of target species origin was substantial (χ^2 9.9, *p* < 0.001) with exotic target plants having higher mean individual aboveground biomass than natives (χ^2 8.49, *p* 0.004). Thus, the interaction of target species origin \times *C. canadensis* relative abundance was highly significant (χ^2 752.1, *p* < 0.001), with differences between exotic and native target plants becoming larger with increasing *C. canadensis* density. Initially, at low density of *C. canadensis*, the individual aboveground biomass of exotic and native target plants was comparable, however, as *C. canadensis* density increased, the exotic target species obtained a clear biomass advantage over the natives (Table 1). In the constant low nutrient treatment (Figure 3a), the relative abundance of *C. canadensis* was

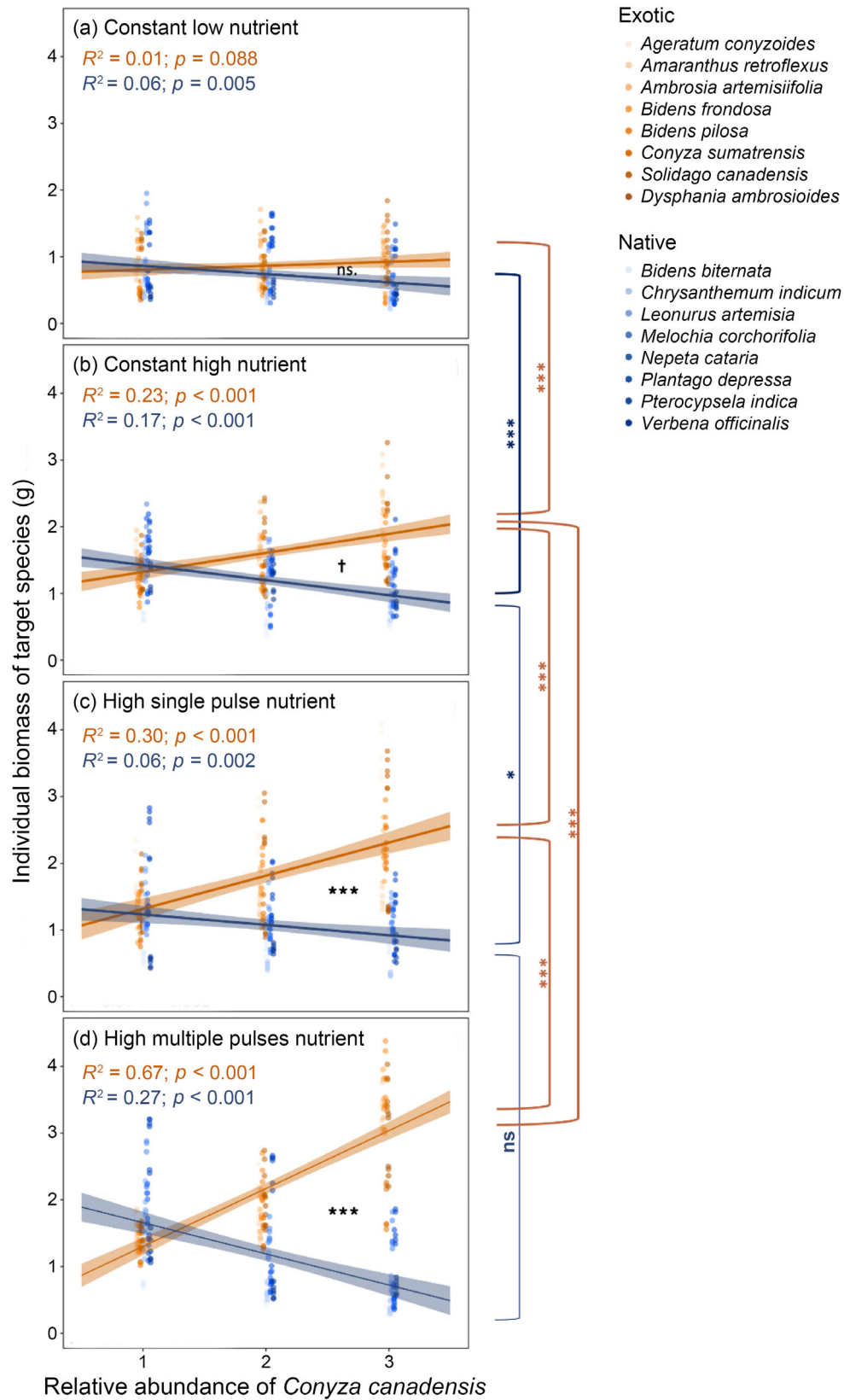


FIGURE 3 Key results of the effect of resource availability on the interactions between the relative abundance of a focal plant invader and exotic as compared with native target species, shown for the four nutrient treatments (a–d). Orange and blue points represent individual biomass of target exotic and native plant species in each pot, respectively. The varied shade orange and blue colors indicate the eight target exotic and native plant species, respectively. Differences between treatments are indicated by ns (not significant); † $p \leq 0.1$; * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

TABLE 1 Results of linear mixed-effect models that examined the effects of the density of the focal invader *Conyza canadensis* (1:3, 2:2, and 3:1), the origin of the target species (exotic vs. native), the different nutrient treatments (constant low, constant high, high single pulse, and high multiple pulses) and their interactions on the growth of the different target species.

Variables	Biomass of target species		
	df	χ^2	<i>p</i>
Fixed effect			
Origin	1	9.793	0.002
Density	2	89.899	<0.001
Nutrient	3	1068.761	<0.001
Origin × Density	2	770.331	<0.001
Origin × Nutrient	3	266.672	<0.001
Density × Nutrient	6	98.870	<0.001
Density × Origin × Nutrient	6	305.985	<0.001
Random effects			
Species			<0.001

Note: Significant fixed effects ($p < 0.05$) are highlighted in bold font.

weakly positively related to the mean individual biomass of exotic target species ($R^2 = 0.01$, $p = 0.088$), whereas this relationship for native target species was significantly negative ($R^2 = 0.06$, $p = 0.005$). The slopes of these regressions, however, were not different ($p = 0.529$; Figure 3a) indicating that the origin of target species did not change the effect of increasing *C. canadensis* density at low, constant nutrient application. For all high nutrient treatments (constant high, high single pulse, and high multiple pulses), relationships between the relative abundance of *C. Canadensis* and the biomass of the target native species were negative ($R^2 \geq 0.06$, $p \leq 0.002$), but positive for target exotic species ($R^2 \geq 0.23$, $p < 0.001$; Figure 3b–d). The relative slopes marginally differed between exotic versus native target species ($p = 0.054$) in the constant high nutrient treatment (Figure 3b). However, under fluctuating nutrient conditions, this difference became highly significant ($p < 0.001$; Figure 3c,d), with nutrient-fluctuating treatments enhanced most positive correlations between the relative abundance of *C. canadensis* and the mean individual biomass of exotic target species ($p = 0.001$), and this effect was more pronounced with nutrient pulses ($p < 0.001$). In contrast, nutrient fluctuation generally increased the negative correlations between *C. canadensis* density and the mean individual biomass of native species ($p = 0.045$ for all, but not between high single versus high multiple pulses; Figure 3c,d). Overall, our results illustrated a pronounced advantage of exotics over native target species under high nutrient availability and fluctuation.

DISCUSSION

Our most striking result was that pulsed nutrient supply increased the competitive effect of invasive *C. canadensis* on native species but increased the facilitative effect of the invasive *C. canadensis* on other exotic species, marking a clear shift in the competitive and facilitative effects, favoring exotics over natives with increasing relative abundance of *C. canadensis*. These competitive effects are consistent with a large body of literature showing that exotic plant invaders commonly have disproportionately strong negative effects on natives (Callaway et al., 2011; Hierro et al., 2022; Vilà & Weiner, 2004), and these facilitative effects are a good example of the main component of invasional meltdown (Simberloff & Von Holle, 1999). The other component, a synergistic effect of multiple invasives was not part of our study.

Interactions of *C. canadensis* with exotic and native target plant species

Ideally, we would have also assessed the growth of the exotic and native target species in isolation and used multiple co-occurring focal invaders. Even so, our results clearly show that with increasing *C. canadensis* abundance, the relative biomass advantage of the exotics over the natives increased. The striking difference between competitive inhibition of natives and facilitation of other exotics is unusual in the literature, and presently we can only speculate about the mechanisms for this.

The negative relationship between the relative abundance of *C. canadensis* and aboveground biomass of the native target plants follows the predicted relationship outlined in *Introduction*. This indicates that resource competition may be an important driver of the interaction between *C. canadensis* and natives, and if so *C. canadensis* may have a higher capability of exploiting resources than the native species (Sun et al., 2013). Zhang and van Kleunen (2019), found that common exotics had higher growth rates (grew larger) and experienced stronger intraspecific competition than natives. Thus, reducing intraspecific competition by replacing conspecific neighbors with *C. canadensis*, the remaining exotic individual might benefit from reduced intraspecific competition. For small natives, on the other hand, replacement of conspecifics with a taller exotic could increase competitive suppression. We found that the exotics were larger, overall, than the natives, thus Zhang and van Kleunen (2019) might provide an explanation. Our results correspond, in part, with correlational studies

in the field and experimentally controlled interactions between *C. canadensis* and other species (Shah et al., 2014). Furthermore, if our experimentally increased nutrient status mimics the increase in soil nutrients associated with exotic invasions (Ehrenfeld, 2003; Liao et al., 2008; Xu et al., 2022), this could be consistent with nutrient-facilitated meltdown involving groups of exotic species, and nutrient-facilitated competitive suppression of natives (Besaw et al., 2011; Maron & Connors, 1996; Thompson et al., 2001; Thomsen et al., 2006).

There is also good evidence that *C. canadensis* is allelopathic (Djurđević et al., 2011) and exotic invaders often have stronger allelopathic effects on species native to the invader's new range than species from the invader's native range (Becerra et al., 2018; Callaway & Aschehoug, 2000; Qin et al., 2013; Zhang et al., 2021). Such a biogeographical pattern of allelopathy is not known for *C. canadensis*, but in controlled experiments Shah et al. (2014) found that other North American species suppressed *C. canadensis* (competitive response) much more than species from Europe, China, or Kashmir. However, counterintuitively, *C. canadensis* had stronger competitive effects on North American species than species from other ranges in two of three experiments (Shah et al., 2014).

A possible explanation for the increase in mean biomass of exotic species (note they were grown and analyzed as single species and as random factor in the experiments), is increased intraspecific, or density-dependent, competition among *C. canadensis* individuals, which could weaken interspecific competitive effects of *C. canadensis* on targets. Moreover, the concomitant lower density of the exotic species resulted in less self-limitation through intraspecific competition. The idea that intraspecific competition exceeds interspecific competition is a major component of coexistence theory (Chesson, 2000) and a common outcome of field observational studies and experiments (Adler et al., 2018). However, to substantially confound our results, this idea would need to apply exclusively to the exotic target species and not to the native target species. This might be because exotic species are phenotypically more plastic, which might allow them to take up more resources as nutrient supply increases (Davidson et al., 2011; Hiatt & Flory, 2020; Matesanz & Sultan, 2013). Indeed, phenotypic plasticity has frequently been proposed to explain invasion success (Gioria et al., 2023; Richards et al., 2006; Wang & Althoff, 2019).

Other studies indicate that invasional meltdown might be mediated, in part, by soil microbes (Chen & van Kleunen, 2022; Zhang et al., 2020). However, we used sand and vermiculite, which are initially nearly sterile, as the growth substrate, and therefore the

effect of soil microbiota in our study should be limited. The root exudates of other species can have positive effects (Bi et al., 2022; Hierro & Callaway, 2021), but it is not clear if these effects are direct or mediated through soil biota. The bottom line is that the facilitative effects of increasing relative abundance of *C. canadensis* on exotics is unusual and without clear mechanisms.

High nutrient supply and dynamics

In our experimental setup, fluctuating resources had very strong effects on both the intensity of competition and of facilitation, and have been proposed to promote invasion, or the recruitment of new species in a community in general (Davis et al., 2000). For example, greenhouse and mesocosm studies have found that exotic invasive species can outcompete natives when resource pulses are applied (Parepa et al., 2013; Tao et al., 2021). In contrast, a number of field experiments have not found pulses to affect interactions (Gebauer et al., 2002; James et al., 2006; Slate et al., 2022; but see Pearson et al., 2018; Slate et al., 2021).

In contrast to the mixed literature on the importance of pulsed resources to exotic invasion, the evidence for high resource supply more consistently favoring invaders is strong (Besaw et al., 2011; Liu et al., 2018; Mangla et al., 2011; Maron & Connors, 1996; Slate et al., 2022; Yu & He, 2021). Resource addition decreases the number of limiting resources and thereby promotes dominance of one of the species (Harpole & Tilman, 2007; Zhang et al., 2022). Furthermore, high resource supply can increase overall competitive intensity (but not necessarily importance; Brooker et al., 2005), and since invaders are often strong competitors, they perhaps benefit disproportionately from conditions that promote the general intensity of interactions. Invaders may gain advantages in both high resource and pulsed resource environments due to high plasticity (Richards et al., 2006), but evidence for this varies substantially (Davidson et al., 2011; Palacio-López & Gianoli, 2011; Thompson et al., 1995; Wang & Callaway, 2022). Invasive species may benefit, relative to natives, by generally being more on the “fast side” of the plant economics spectrum, and interestingly common garden experiments indicate that invasive plants may be evolving even faster capabilities in their exotic ranges (Montesinos, 2022).

It is important to note that replacement series designs inherently confound variation in intraspecific competition with competition between the two target species (Jolliffe, 2000). However, to increase the overall impact of *C. canadensis*, increasing the number of individuals was necessary, while the only way to hold total density

constant was to reduce the number of the target species. Despite the inherent constraints of replacement series, the confounding effect of increasing numbers of *C. canadensis* was the same in both native and non-native treatments, and in the different nutrient treatments, and thus is highly unlikely to explain the differences between exotic and native target species. Furthermore, while variation in intraspecific interactions might ameliorate competitive effects among other species, this alone is highly unlikely to actually facilitate other species. Additionally, our most fundamental finding can be seen in just the high-density *C. canadensis* treatment, thus bypassing the most significant issues with replacement design experiments. Finally, we tested eight exotic and eight native species, and the patterns were consistent, thus unlikely that changing intraspecific competition among *C. canadensis* would affect all exotics versus all natives differently, which indicate a clear advantage for exotic over native target species as *C. canadensis* relative density increases, reinforcing the concept of invasional meltdown rather than simple competitive dynamics. One should still further explore these interactions, particularly focusing on distinguishing between direct facilitative effects and the reduction of intraspecific competition, to more accurately characterize the mechanisms underlying the competitive advantage of exotics over natives.

We found that the effects of increased resource availability and resource fluctuations appeared to interact in ways that created larger differences in exotic versus native responses to *C. canadensis* (Figure 3). Different competitive effects of exotics on native and exotic plants have important consequences for the spread of exotic invasive species, perhaps in agro-ecosystems in particular. Owing to fertilizer applications, agricultural land is nutrient rich, making it susceptible to invasions by exotic invaders. At the edges of agriculture, resources might fluctuate due to fertilizer spillover of nutrients. Our findings suggest that these circumstances would favor the accumulation of exotics species and thus might explain the fact that exotic plant species often aggregate with other exotic species, especially in species-poor, high-biomass communities in their exotic range, relative to patterns in native ranges (Stotz et al., 2020).

Resource-driven Invasional Meltdown and Inhibition of Natives

We propose a general hypothesis in which the effects of many exotic species on resources may feedback to stimulate the growth of the first exotic species and

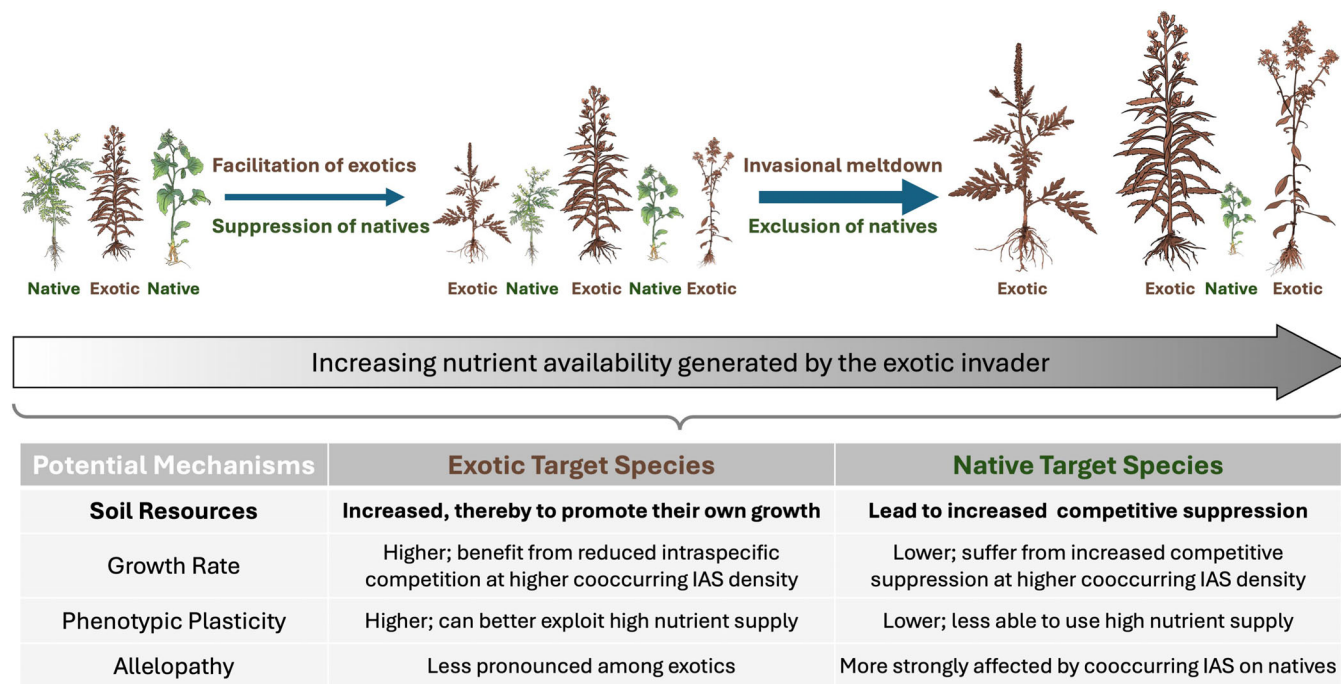


FIGURE 4 The Resource-driven Invasional Meltdown and Inhibition of Natives (RIMIN) hypothesis: Invader-driven increase in soil resources will feedback to promote the growth of the exotic invasive alien species (IAS) and enhance the facilitation effect on other exotic invader species, while it intensifies the competitive effect on native species. This will eventually drive invasional meltdown and lead to the exclusion of natives (from thinner blue line to thicker blue line). The table highlights the RIMIN hypothesis (in bold) together with alternative mechanisms discussed in the text. Illustrations were made by Y. Sun.

promote other exotics, driving invasional meltdown. Concomitantly, invader-driven increases in soil resources should exacerbate the inhibition of natives by exotics. Based on such feedbacks between exotic invaders, soil resources, and native species, we propose the Resource-driven Invasional Meltdown and Inhibition of Native (RIMIN) hypothesis (Figure 4). This is the idea that when exotic invaders increase soil resources, they promote the growth of themselves and other exotics, and, conversely, this intensifies their competitive effects on native species. In conclusion, the biogeographic origin, or provenance, of species appears to have powerful effects on interactions regardless of nutrient supply or dynamics (e.g., Pearse et al., 2019), but these interactions between exotic and native plants can be highly altered by resource availability. We acknowledge that the underlying mechanisms of RIMIN remain speculative, and we look forward to studies shedding light on this.

AUTHOR CONTRIBUTIONS

Wei Huang, Yan Sun, and Zhi-Kun Ren conceived the idea. Zhi-Kun Ren conducted the experiments. Yan Sun and Zhi-Kun Ren performed the statistical analysis. Yan Sun, Ragan M. Callaway, Mark van Kleunen, Heinz Müller-Schärer, and Wei Huang developed the conceptual structure and interpretation. Yan Sun and Zhi-Kun Ren wrote the first draft of the manuscript. All authors contributed substantially to the final version.

ACKNOWLEDGMENTS

Wei Huang acknowledges the National Natural Science Foundation of China (#32071660, #31822007). Yan Sun acknowledges funding through the National Natural Science Foundation of China (#32201438) and the Scientific Research Foundation for Returned Scholars, Huazhong Agricultural University (#11042110026) for funding. Ragan M. Callaway thanks the National Science Foundation EPSCoR Cooperative Agreement (OIA-1757351). We also thank Evan Siemann for commenting on an earlier version of the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Sun et al., 2024) are available in Figshare at <https://doi.org/10.6084/m9.figshare.26201549>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Sun, Yan, Zhi-Kun Ren, Heinz Müller-Schärer, Ragan M. Callaway, Mark van Kleunen, and Wei Huang. 2024. "Increasing and Fluctuating Resource Availability Enhances Invasional Meltdown." *Ecology* 105(9): e4387. <https://doi.org/10.1002/ecy.4387>