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ABSTRACT

Questions: One strategy to prevent invasive alien plant species from establishing during the restoration process is to early re-introduce native communities. But can seeding a native herbaceous species mixture of local seeds reduce the establishment of an invasive shrub such as *Buddleja davidii*? Specifically, we asked: (1) Does competition by native species reduce *B. davidii* performance? (2) Is this competitive effect on *B. davidii* more important under higher seed densities? (3) Can it be partly attributed to light competition? (4) How do priority effects moderate this competitive effect?

Location: Disturbed embankment, Isère, France.

Methods: We conducted experiments in controlled conditions, in mesocosms and in the field. We compared the performance of *B. davidii* when seeded alone or in competition with local seeds, at different densities, when shaded or not and when sown before or simultaneously with respect to native species.

Results: The seeding of a local seed mixture decreased the height, biomass and early-stage survival of *Buddleja davidii*. Whatever the density, these results were consistent across all three experiments. *Buddleja davidii*'s survival rate was reduced only under the experimental conditions of high shading. When native species were sown after *B. davidii*, their competitive effect was very low.

Conclusions: *Buddleja davidii* appears to be sensitive to competition during the early stages of its invasion, especially when local seedlings benefit from a time advantage, regardless of their density. In restoration contexts, native species can prevent the invasion of *B. davidii* if sowing is carried out as soon as possible.

1 | Introduction

Invasion by alien plant species can be a major cause of revegetation failure. Human-degraded environments may act as new habitats that are often more favourable to invasive alien plants than to native ones (D'Antonio and Meyerson 2002; Valladares et al. 2015). Disturbed conditions, for example, nutrient release due to vegetation clearing or soil aeration, may favour alien species (Daehler 2003) and hinder the establishment of native species (Weidlich et al. 2020). Once established, invasive alien plant species are hard to remove, and can require costly management interventions (Diagne et al. 2021; Novoa et al. 2021). The most cost-efficient strategy is therefore to prevent the establishment from occurring rather than to remove already established populations of invasive species (Simberloff et al. 2013).

One strategy to prevent invasive alien plant species from establishing and later dominating plant communities during the restoration process is to proactively re-introduce competitive native communities (Yannelli 2021). Competition is an important component of biotic resistance (Levine et al. 2004; Gurevitch et al. 2011) and several mechanisms have been proposed to understand the underlying ecological processes. One common mechanism is competition for resources, including competition for light, whereby species competing for the same resource at the same time may exclude each other (Tilman 1990). As a result of this mechanism, the denser a plant community is, the more this community will efficiently pre-empt resources and prevent the establishment of later arriving species (Dommanget et al. 2019; Thomas et al. 2024). Regarding invasive species prevention, seeding native species can be an effective strategy for reducing the success of undesired alien plant species and for attaining restoration goals in a cost-effective manner (Barr et al. 2017; Tarsa et al. 2022). The use of local seeds of native species, that is, collected within the vicinity of the transfer zones, would preserve the original integrity of local flora (Dupré La Tour et al. 2020). Seed density of native plants has been identified as a parameter that can increase the invasion resistance of restored plant communities (Hess et al. 2019; Byun et al. 2020). However, the importance of the effects of seeding density can sometimes be inconsistent (Thomas et al. 2024), and some studies report minor seeding density effects on exotic species cover or biomass (Tarsa et al. 2022).

In recent literature, another mechanism referred to as 'priority effect' has also been proposed, highlighting the particularly important effect of time of arrival of native versus alien species (Hess et al. 2019; Yannelli et al. 2020). Priority effects take place when early-arriving species affect the establishment, survival, growth or reproductive success of later-arriving species (Von Gillhaussen et al. 2014). Invasive alien plants appear to particularly benefit from their relative timing of arrival compared to native species, as they can form near-monocultures when arriving earlier (Dickson et al. 2012; Hess et al. 2019). Conversely, when natives are seeded first, invasive plants may persist but do not manage to dominate (Wilsey et al. 2015; Stuble and Souza 2016). In a restoration context, priority effects can take the form of a race between selected native species and undesirable invasive alien plants, and once understood can be utilised by ecologists to initiate assemblage trajectories towards target reference communities. Manipulating resource pre-emption through seed density and relative timing of arrival (timing of seeding) offers two approaches that can be used to support restoration (Hess et al. 2019); however, their relative roles in invasion resistance still need to be tested in real restoration contexts.

Buddleja davidii is a species native to China that has colonised most temperate zones of the world and is widely present throughout western Europe (Tallent-Halsell and Watt 2009). This shrub species is listed in the IUCN Global Invasive Species Database due to its capacity to develop in monospecific thickets excluding native species (Global Invasive Species Database 2023). Production of numerous light seeds, a short juvenile period and a high growth rate allow *B. davidii* to rapidly colonise new locations and to gain a competitive advantage with respect to native species in open disturbed sites (Campbell 1984). Few recommendations exist on methods to prevent *B. davidii* invasion. Management advice for this species mainly consists of topping the shrubs before the seeds mature to avoid their dispersal. Eradication is very complicated because of the species' regeneration capacity and seed bank. Prevention must thus be preferred whenever possible. Competition with other species is recommended in particular to prevent seedling regrowth (Tallent-Halsell and Watt 2009), but more precise management strategies for *B. davidii* are currently lacking in the literature, leaving land managers clueless when faced with the arrival of this species. Moreover, testing the competitive effect of native species on *B. davidii* invasion represents to our knowledge a novel opportunity to improve our understanding of the role of herbaceous seedlings in managing the invasion of an alien shrub.

Here, we assessed the role of competition for resources in preventing *B. davidii* establishment. More specifically, we investigated the relative effects of seed density and timing of arrival of native herbaceous species on *B. davidii* seedling establishment and growth in the context of a real restoration experiment. Along heavily remodelled riverbanks in a valley experiencing widespread invasion by *B. davidii*, we conducted controlled experiments aimed at better understanding the underlying processes of *B. davidii* establishment and its prevention. In addition to our field experiments, we utilised mesocosms and growth chambers to address our research questions in a more controlled environment. We hypothesised that (i) *B. davidii* survival and growth will be reduced under competition with native species; (ii) the competitive effect of local seeds on *B. davidii* will be higher under greater seed densities; (iii) the competitive effect of local seeds on *B. davidii* is partly attributed to light competition; and (iv) due to priority effect, the competitive effect of local seeds on *B. davidii* will be reduced by later seeding. Finally, we discuss our results in the light of management practices intended to cope with *B. davidii* invasion.

2 | Materials and Methods

2.1 | Overall Experimental Design

We tested the competitive effect of a local seed mixture of native species on *B. davidii* recruitment (measured as the survival rate, i.e., the number of seedlings that have been able to germinate and survive in relation to the number of seeds sown [Eriksson and Ehrlén 2008]) and growth. We conducted three complementary experiments: (i) a controlled-conditions experimental design in a growth chamber to test for competition with the local seed set and focusing specifically on shading effect ('growth chamber experiment'); (ii) a mesocosm experiment testing for the sensitivity of *B. davidii* to competition with a native species seed set through two main mechanisms: density-dependent competition and priority effect ('mesocosm experiment') and (iii) a competition field experiment aimed at getting closer to the conditions of application by relying on a real context of ecological restoration ('field experiment'). We used the same local seed mixture of native plant species for all three experiments. The mixture came from a producer specialised in local seeds (Phytosem, located in Gap, France. The nomenclature used is that of the latest version of the TAXREF repository used in France (Gargominy et al. 2022). The seeds were ready to be sown, with no need for dormancy or stratification. The mixture consisted of 10 local native species, typical of the region's mesophytic grasslands (Appendix S1). We decided to use this mixture given that is readily available to managers, is more diversified than conventional commercial seedlings and uses plants adapted to the study region.

2.2 | Studied Alien Species

Buddleja davidii (Scrophulariaceae) is a perennial and semi-deciduous shrub native to central and western China, growing up to 3000 m above sea level (Zhengyi and Raven 1996). It was introduced as an ornamental plant to Europe, America, Australia and New Zealand by horticulturists. However, *B. davidii* has rapidly spread to open and disturbed natural and anthropised environments, such as transportation corridors and urban wastelands among others (Tallent-Halsell and Watt 2009). It can grow in isolation or in dense thickets. A single plant can cover an area of 2–3 m^2 (Owen and Whiteway 1980; Watt et al. 2007), grow up to 5 m tall (Zhengyi and Raven 1996) and live for up to 40 years (Ebeling et al. 2008). It also has a high growth rate, that is, 0.5–2 m per year (Owen and Whiteway 1980; Watt et al. 2007) and can reproduce both sexually and vegetatively via fragments of roots or stems (Monty et al. 2015), allowing for a strong dispersal capacity. Flowers are grouped on terminal panicles 4–30 cm long (Leeuweberg 1979; Zhengyi and Raven 1996). A single plant can produce millions of small-winged seeds (Campbell 1984) that are dispersed by wind or water after being released from the capsules of mother plants during dry periods (Campbell 1984; Miller 1987). Germination rate has been reported to vary from 32% (Ebeling et al. 2008) to more than 90% (Watt et al. 2010), depending on water availability, temperature (Tallent-Halsell and Watt 2009) and seed burial depth (Miller 1984).

Buddleja davidii seed material was collected next to the field experiment (see 'Field experiment' section for coordinates). In December 2018, we wrapped the panicles of 10 individuals in fine cloth, with a 10 m minimum distance between individuals and returned to collect the seeds in early spring 2019. Seeds collected from the different individuals were all pooled together.

2.3 | Growth Chamber Experiment

We tested the effect of competition on the recruitment and development of *B. davidii* seedlings under controlled conditions. The experiment took place from May to July 2019 in a growth chamber (Percival, Select 41 L) in the following conditions: 16 h at 25°C in light and 8 h at 15°C in dark, with an average humidity of 80%.

Five seeds of *B. davidii* were sown in 9 × 12.8 × 5-cm trays filled with a mixture of two third potting soil and one third perlite. Trays were watered manually every 2 days. In half of the trays, a local seed mixture of native species was sown (see Appendix S1 for seed composition) simultaneously to *B. davidii* at a density of 15 g m^{-2} ('Competition') and in the remaining half, *B. davidii* was seeded alone ('Control'). Seven weeks later, we calculated the survival rate of *B. davidii* per tray as the number of living seedlings divided by the number of planted seeds and measured the height of each living *B. davidii* seedling. *B. davidii* seedlings were then entirely collected (aerial and underground biomass), oven-dried for 24 h at 60°C and weighed. The total plant cover of native species was also visually estimated to the nearest 5%. Each modality (*B. davidii* alone or in competition with local seed mix) was replicated 15 times. The experiment was repeated three times, leading to 45 replicates in total.

In parallel, we tested for potential competition effects due to the specific effect of shading of neighbouring species on the recruitment of *B. davidii*. Here, five seeds of *B. davidii* were sown per tray and allowed to germinate. Two light treatments were tested using one or two layers of a horticultural shading-net (hereafter 'low' and 'high', respectively); shading was 68%–77% with one layer of shading net and 89%–90% with two layers (LI-250A Light Meter Sensor, 2019 LI-COR Inc., Bad Homburg, Germany). The two light treatments were replicated 16 times each. Survival rate was calculated after 7 weeks of growth and compared to the previous no competition treatment ('Control').

2.4 | Mesocosm Experiment

We used the mesocosms experiment to cross-test two of our hypotheses in a completely randomised factorial experimental design: priority effects and local seeding density. Priority effects were tested by sowing seeds at two different times: (i) *B. davidii* was sown 6 weeks before local seeds ('Bfirst') and (ii) *B. davidii* was sown simultaneously to local seeds ('Sync').

The experiment was carried out at the experimental garden located in Gières, France (45°11′59.5″ N 5°46′23.6″ E) within the INRAE Grenoble research center situated at 200 m above sea level. The site receives about 77.9 mm of rain per month, about 172.2 h of sunshine per month and has an average annual temperature of 11.2°C (Grenoble-St Geoirs MeteoFrance Meteorological Station, meteo.data.gouv.fr).

Fifteen-centimetre diameter and 17-cm deep cylindrical pots were filled with a mixture of two-third potting soil and one third perlite. Pots were watered twice a day for 15 min to leave the substrate moist during the entire experiment. This 6-week interval was chosen to ensure a priority effect from the first *B. davidii* leaf stage. To test for the local seeding density effect, we applied two local seed density modalities: a low density of 15 g m^{-2} (chosen in accordance with the density applied on the restoration site for this seed mixture (Weissgerber et al. 2019); 'Low') and a high density of 30 g m^{-2} ('High'). We also carried out a control treatment free of any interspecific competition ('Control'), which consisted of sowing only *B. davidii*. For all experiments, we used a constant density of 10–15 *B. davidii* seeds, sown at 1 cm depth, ensuring that at least one seed would germinate per pot. Ten days after the first germination of *B. davidii*, the three most developed seedlings of *B. davidii* were kept in all treatments in order to eliminate intraspecific competition and to ensure that one seedling per pot was able to develop. The five treatments of biotic environment

('Low_Bfirst', 'High_Bfirst', 'Low_Sync', 'High_Sync' and 'Control') were replicated 15 times each, leading to 75 pots randomly placed in the experimental garden.

We carried out the following measurements 11 weeks after sowing *B. davidii*: total plant cover of the community of native species (visual estimate in percentage) and height of *B. davidii* seedlings (following Pérez-Harguindeguy et al. 2013). We weighed the total dry biomass (aerial and root) of the most developed *B. davidii* seedling in each pot after 24 h at 60°C.

2.5 | Field Experiment

Lastly, we tested the effects of competition with native species on *B. davidii* survival under field conditions, conducting a field experiment within a construction area along the Romanche River near Livet-et-Gavet (France, Isère Department) where bare soil had been exposed. Construction-related excavation in the area had led to exposed slopes, which were quickly colonised by *B. davidii*, raising restoration issues. The site (45°10′10.36″ N; 5°90′63.70″ E) is located 35 km south of Grenoble, 650 m above sea level and is situated between the Belledonne and the Taillefer mountain ranges. It is a deep valley receiving lower sun exposure and is overall colder than the experimental garden in Gières.

We carried out the experiment on a slope surface inside the construction area, where we set up twelve 1-m^2 contiguous randomly distributed plots along a rectangular grid. After plant removal from excavation, the slope was covered in autumn 2018 by sediments extracted from an upstream dam (20 μm median diameter).

Half of the 12 replicates were seeded with the local seed mix (see Appendix S1 for local seed composition) at a density of 30 g^{-2} (hereafter 'Competition', the other half named 'Control') and all 12 plots were sown with *B. davidii* seeds at a density of 0.03 g^{-2}. Seeds were planted on 23 March 2019.

Sixteen weeks after sowing, the following variables were measured in the central quadrats of 50 × 50 cm within each plot: number of *B. davidii* seedlings and height of the three most developed ones, per cent cover of seeded native plants and spontaneously recruited species by visual estimation to the nearest 5%.

2.6 | Statistical Analyses

We quantified the effects of competition in growth chambers on *B. davidii* individual height and biomass using generalised linear mixed models with competition as a fixed factor, trays as a random factor and *B. davidii* individual height and biomass as response variables. We used a Gamma distribution with an inverse link function as this method is adapted to continuous positive variables. Analyses here were performed using the LME4 package and glmer function (Bates et al. 2015). We tested the effect of both shading and competition on *B. davidii* seedling survival in the growth chamber using generalised linear models with a quasibinomial distribution and a logit link function adapted to proportional data using the CAR package and glm function (Fox and Weisberg 2019). We used seedling survival as the response variable and shading as the explanatory variable for a first test and biotic environment as the explanatory variable for a second test.

The effect of biotic environment on *B. davidii* height and biomass in mesocosms was tested using generalised linear models with a Gamma distribution and an inverse link function as this approach is adapted to continuous positive variables with the same approach as described for the growth chamber experiment. *B. davidii* height and biomass were response variables and biotic environment was the explanatory variable. We assessed the relationship between native species biomass (in growth chamber) or cover (in mesocosms) and *B. davidii* biomass using the same modelling approach. *B. davidii* biomass was the response variable and native species biomass or cover were the explanatory variables.

For the field experiment, we tested for competition effects from seeding of native species on *B. davidii* seedling number using a generalised linear model. Given that variables were discrete and non-negative, we applied a quasipoisson distribution with a log link function using the CAR package and glm function (Fox and Weisberg 2019) with *B. davidii* seedling number as the response variable and biotic environment as the explanatory variable. As no *B. davidii* seedlings were found under the competition treatment in the field experiment, we were unable to carry out a statistical test on *B. davidii* height or linking the latter to total native plant species cover.

For all the models, the independence of residuals was visually checked with the plotresid function from the RVAIDEMEMOIRE package (Hervé 2022). For distributions other than Gamma, we assessed the dispersion of residuals by dividing the model residual deviance by the model residual degrees of freedom. If below 1.5, the dispersion was considered to be acceptable (Hervé 2022). The significance of explanatory factors in all models was tested with a Wald Chi-square test using the CAR package and ANOVA function (type = 'II', (Fox and Weisberg 2019)). Post hoc tests were performed using estimated marginal means with the EMMEANS package and emmeans function (Lenth 2023). Table 1 provides a summary of model structure and statistical methods used for each of the three experiments.

All the analyses were conducted using R 4.2.2 (R Core Team 2022).

3 | Results

3.1 | Growth Chamber Experiment

Competition significantly influenced both *B. davidii* height (Table 1; Figure 1a) and biomass (Table 1; Figure 1b). Height in the growth chamber was higher (2.5 ± 0.2 cm) when *B. davidii* was sown alone than under competition (1.2 ± 0.1 cm). *Buddleja davidii* also had higher biomass when sown alone (3.9 ± 0.3 g), compared to under competition (0.5 ± 0.1 g). The relatively high *B. davidii* survival rate (71% ± 5%) was consistent and not influenced by competition (Table 1; Figure 1c). Biomass of *B. davidii* individuals varied between 0.2 and 1.5 g, while total *B. davidii*

TABLE 1 | Characteristics and results summary of generalised linear models (except for *Buddleja davidii* height and biomass in the growth chamber experiment for which generalised linear mixed models were applied) for the three experiments. 'X^2' stands for Chi-square; 'Df' stands for degrees of freedom.

Experiment	Response variables	Explanatory variables (factor levels)	Random factor	Family	Link function	X^2	Df	*p*
Growth chamber	Height	Biotic environment (Control, With competition)	Tray	Gamma	Inverse	21.70	1	<0.001
	Biomass		—	Gamma	Inverse	62.07	1	<0.001
	Survival rate		—	Quasibinomial	Logit	0.19	1	0.665
	Survival rate	Light interception (Control, Low, High)	—	Quasibinomial	Logit	77.06	2	<0.001
	Individual *B. davidii* biomass	Native species total biomass	—	Gamma	Identity	1.20	1	0.274
	Total *B. davidii* biomass		—	Gamma	Identity	0.022	1	0.882
Mesocosm	Height	Biotic environment (Control, High-density *B. davidii* first, Low-density *B. davidii* first, High-density simultaneous, Low-density simultaneous)	—	Gamma	Inverse	108.50	4	<0.001
	Biomass		—	Gamma	Inverse	411.00	4	<0.001
	Total *B. davidii* biomass when *B. davidii* sown first	Total native species biomass	—	Gamma	Inverse	1.55	1	0.214
	Total *B. davidii* biomass when *B. davidii* and native species sown simultaneously		—	Gamma	Inverse	0.54	1	0.461
Field	Seedling number	Biotic environment (Control, With competition)	—	Quasipoisson	Log	8.81	1	0.003

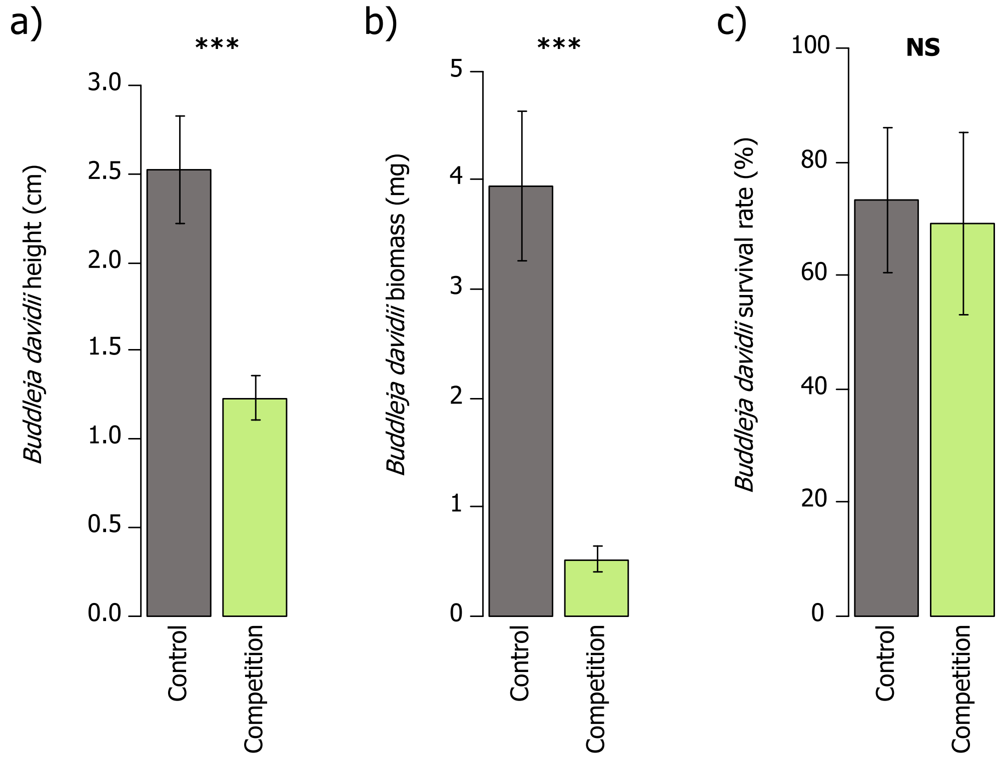

FIGURE 1 | Effects of competition by local seed mixture on seedlings of the invasive *Buddleja davidii*, as measured in height (a), biomass (b) and survival rate (c) in the growth chamber experiment. 'Competition' indicates that *B. davidii* was sown in competition with native species and 'Control' that it was sown alone. Bars represent means and whiskers represent confidence interval (95%) based on standard deviation (generalised linear model; ***$p<0.001$; **$p<0.01$; *$p<0.05$; NS, $p>0.05$.).

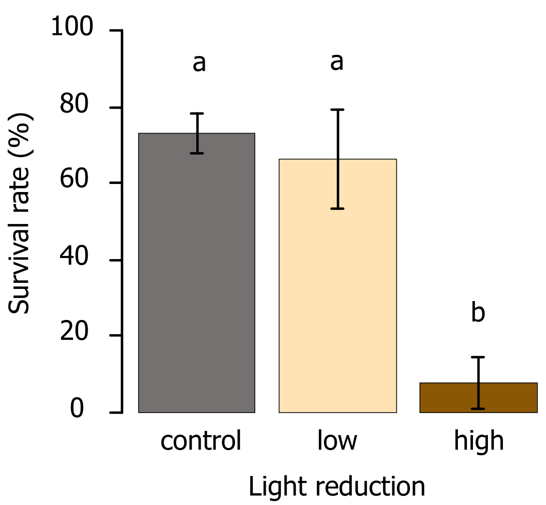

FIGURE 2 | Effect of light interception on *Buddleja davidii* survival rate in the growth chamber experiment; 'low' and 'high' respectively indicate that one (68%–77% of light intercepted) or two (89%–90% of light intercepted) layers of shading net were used. Bars represent means and whiskers represent confidence interval (95%) based on standard deviation. Different letters above bars indicate a statistically significant difference among treatments according to post hoc tests based on estimated marginal means ($p<0.05$).

biomass per pot varied between 0.5 and 4.5 g. Biomass of native species varied between 180 and 600 g per pot. We did not observe a significant effect of total native species biomass on individual *B. davidii* biomass (Table 1). High shading of 89%–90% significantly reduced *B. davidii* survival rate by almost 10-fold, whereas low shading did not significantly affect *B. davidii* survival rate (Table 1; Figure 2).

3.2 | Mesocosm Experiment

Biotic environment had a significant effect on *B. davidii* height (Table 1; Figure 3a) and biomass (Table 1; Figure 3b). *Buddleja davidii* individuals grew smaller when they were sown synchronously with native species (1.71 ± 0.11 cm) compared to when sown before (4.84 ± 0.40), or when sown alone (4.73 ± 0.49). *Buddleja davidii* height did not show any difference between high and low densities whether sown before or with native species (Figure 3a). However, *B. davidii* exhibited the highest biomass when sown alone in the control treatment (318.4 ± 39.8 mg) and attained the second highest biomass when sown before native species (127.1 ± 19.1 mg) and reached its lowest biomass when sown simultaneously with native species (1.36 ± 0.18 mg). *Buddleja davidii* biomass did not show any difference between high and low densities whether sown before or with native species (Figure 3b). The relationship between native species cover and *B. davidii* total biomass was not significant (Table 1).

3.3 | Field Experiment

Competition significantly reduced *B. davidii* seedling number from 7.2 ± 4.0 to zero (Table 1; Figure 4a). Surviving seedlings measured 1.2 ± 0.2 cm (Figure 4b).

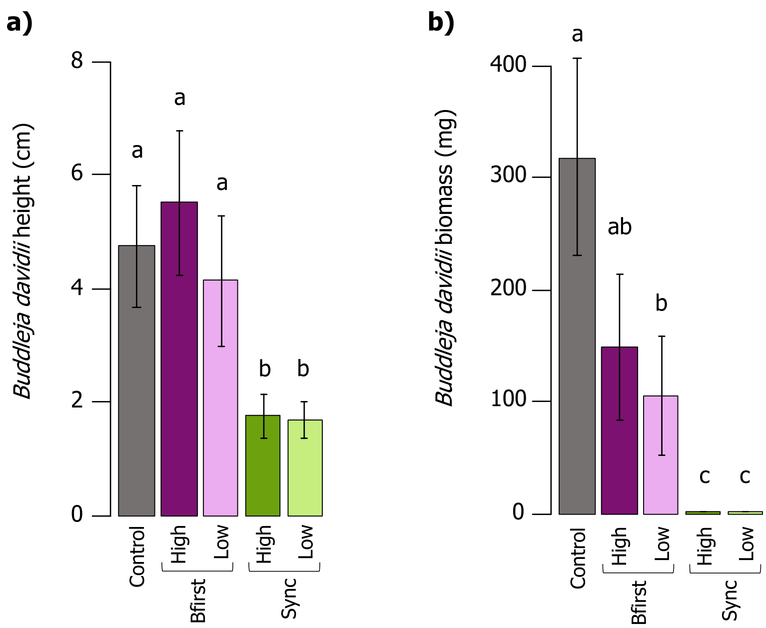

FIGURE 3 | Effect of biotic environment on *Buddleja davidii* height (a) and biomass (b) in the mesocosm experiment. 'High' and 'Low' indicate native species sowing densities of 15 and 30 g m^{-2}, respectively. 'Bfirst' and 'Sync' indicate that the sowing of native species occurred after and at the same time as the *B. davidii* sowing, respectively. Bars represent means and whiskers represent confidence interval (95%) based on standard deviation. Different letters above bars indicate a statistically significant difference among treatments according to post hoc tests based on estimated marginal means ($p<0.05$).

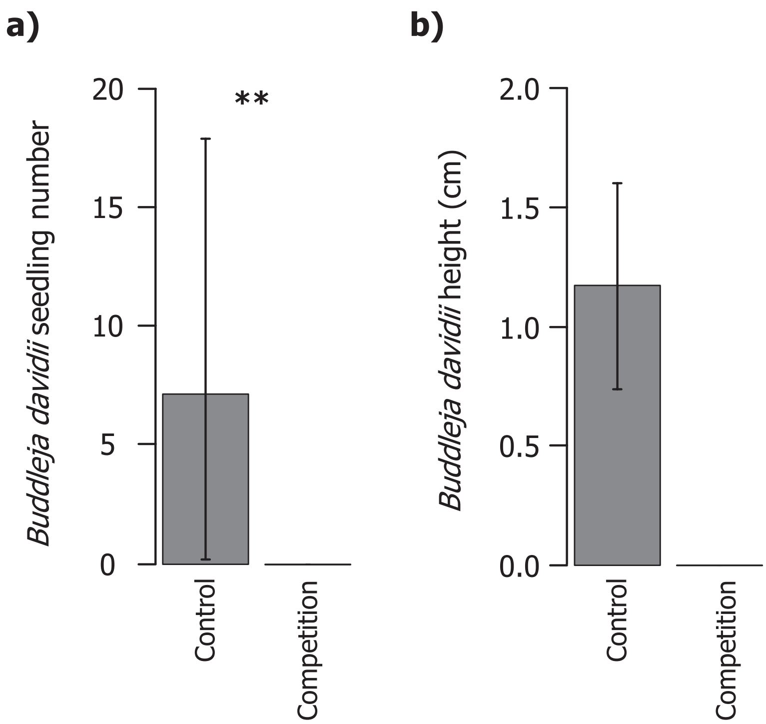

FIGURE 4 | Effect of competition from local seed mixture on *Buddleja davidii* seedling number (a) and individual height (b) in the field experiment. 'Competition' indicates that *B. davidii* was sown in competition with native species and 'Control' that it was sown alone. Bars represent means and whiskers represent confidence interval (95%) based on standard deviation (generalised linear model; ***$p<0.001$; **$p<0.01$; *$p<0.05$; NS, $p>0.05$.). No statistical test has been performed for height as there was no *B. davidii* in the competition plots.

4 | Discussion

4.1 | Effects of Native Seedlings on *B. davidii*

The seeding of a native species mixture of local seeds decreased the height, biomass and early-stage survival rate of *B. davidii*. These results were consistent, whether the experiment was performed in a growth chamber, in mesocosms or under field conditions. The effect of seeding a native species mixture was strong: *B. davidii* height was reduced by at least 50% in mesocosms and the growth chamber; *B. davidii* biomass was reduced by at least 75% in mesocosms and the growth chamber; and *B.*

davidii survival was reduced to zero in the field experiment. Our first hypothesis is therefore confirmed, which is consistent with previous studies reporting that sowing native species can reduce seedling survival (Corbin and D'Antonio 2004; Bell et al. 2019) or growth (Simmons 2005; Bell et al. 2019) of alien species.

4.2 | No Effect of the Density of Local Seeds

In contrast, our second hypothesis was not confirmed. Sowing density did not significantly influence the competitive capacity of native species as measured by *B. davidii* biomass or height. Even when we tested the influence of percent cover of native species on the biomass of *B. davidii*, there was no significant effect, neither in the growth chamber nor in the mesocosm experiment. Theoretically, the ability of a habitat to resist invasion is thought to depend on the ratio of invasive and non-invasive propagules (Holle and Simberloff 2005). In practice, some experiments show that high native cover can negatively affect the seedling establishment of alien species (Bakker and Wilson 2004; Lulow 2006; Bell et al. 2019; Brisson et al. 2020; Csákvári et al. 2023). For two of these experiments (Bakker and Wilson 2004; Bell et al. 2019), the negative effect of native cover on the alien species performance was asymptotic. In our case, it is possible that the low-density seeding already induced 'enough' native biomass to effectively reduce *B. davidii* growth, which could explain the absence of a seed density effect in our experiments.

4.3 | Effects of Light Competition on the Survival Rate of *B. davidii* Seedlings

Shading is one of the major processes inducing competition effects (Hautier et al. 2009). Here, we explored this process in the growth chamber experiment. The results confirmed our third hypothesis: *B. davidii* survival rate was not affected when 75% of light was intercepted, but when 90% of light was intercepted, *B. davidii* germination rate decreased by 10-fold. Our results indicate that *B. davidii* survival is only affected when the amount of light is greatly reduced. During the germination stage, *B. davidii* can be considered shade-tolerant up to a limit ranging from 80% to 100% of light filtration. Miller (1984) indeed found that *B. davidii* germination did not depend on light but rather on temperature. This pattern has also been reported for other woody alien plant species (Pepe et al. 2020). Here, we defined survival rate after 7 weeks as the result of germination success and seedling emergence and survival. Our result might thus be explained by a light-reduction effect on seedling survival rather than germination, in line with the findings of Zimmermann et al. (2017). The results of the field experiment support this assumption, as *B. davidii* was able to germinate in all plots, but in the end, individuals survived only in 'control' treatments.

In our experiments, *B. davidii* biomass was more affected by competition than *B. davidii* height, which may be another indicator of the importance of competition for light (Sher and Marshall 2003; Dommanget 2014). Indeed, most plant species can compensate for shading by growing longer stems in order to gain height, a mechanism which in this case may have reduced the magnitude of the height response to shading. *B. davidii* responses to both competition and shading in our experiments point to the importance of light competition as a key process mediating interactions with native plants. Our results underscore the importance of rapidly establishing a dense cover of native species to induce severe light depletion and very low *B. davidii* seedling survival.

4.4 | Competition Between *B. davidii* and Native Species Seeds Is Moderated by a Priority Effect

Competition was reduced when native species were sown after *B. davidii*, which confirms our fourth hypothesis. This result indicates that priority effects were moderating the competition between *B. davidii* and native species. In other words, seeding native species to reduce *B. davidii* invasion would be effective only if native plants are sown just after the disturbance and before *B. davidii* emerges. Our results are consistent with an experiment carried out on grassland species that showed that seeding density was less important than the timing of sowing in reducing the biomass of studied species (Von Gillhaussen et al. 2014). Species that emerge first likely use resources before their neighbours (Schantz et al. 2015), thus increasing the occupation of the environment (Satterthwaite 2007) and its resistance to invasions (Shea and Chesson 2002). Moreover, the impact of the timing of native species seeding on alien species also suggests that the speed at which the seeding cover is established is likely a key parameter affecting competition with shrubs such as *B. davidii* (Hess et al. 2019; Yannelli et al. 2020). Indeed, the seedling stage appears to be the most vulnerable time in the life cycle of *B. davidii*, as is the case for most plants (Gioria et al. 2018). Once its leaves are above the herbaceous cover, *B. davidii* can grow and continue its reproduction and colonisation cycle and becomes difficult to eradicate. Thus, the timing of sowing is one of the parameters that can provide a priority to native species, as well as species-specific functional traits such as speed of germination. If rapid seeding of native plants is used to reduce *B. davidii*, particular attention should be paid to the germination and establishment traits of the sown species, which of course should also be selected for their compatibility with the environmental conditions of the disturbed site.

4.5 | Herbaceous Species Can Compete With a Shrub at Seedling Stage

Selecting the most appropriate seeded species is important for successful prevention of alien species establishment (Abella et al. 2012). Some authors suggest that similar traits between native and alien species would be more efficient to compete with the invasive alien species (Funk et al. 2008; Yu et al. 2020), but others suggest this rule is not applicable for in situ conservation measures (Hess et al. 2020). Our results show that even herbaceous plant cover can be sufficient to prevent invasive shrub colonisation and growth. While there are indeed examples of the failure of native herbaceous plants to compete with woody alien species (Franco et al. 2022; Schuster et al. 2022), to the best of our knowledge, our work provides one of the first examples of native herbaceous species effectively outcompeting an invasive woody alien shrub. In our case, however, the small herbaceous native species did not compete with a large established shrub but with small germinations and young seedlings of *B. davidii*. The timing of sowing appears, therefore, to be critical to maintain this hierarchy of biomass and height between the competitors and to reduce the window of opportunity for the invasive (Johnstone 1986). Accordingly, capitalising on the priority effect appears to be a key strategy for outcompeting potential invaders (Gioria et al. 2018).

A next step for future research would be to investigate how native species seeding may reduce not only *B. davidii* but also other invasive alien species in a context of multiple invasions. Moreover, native community development depends on interannual climatic variability (Bell et al. 2019). This may therefore limit the effect of alien species reduction if, for instance, the sowing occurs in a very dry or cold year that would delay native community growth without affecting the alien invader. Besides species-specific and conditions-specific effects, further studies are needed to better understand how native species seeding affects the spontaneous recruitment of other native species. It would be, indeed, counterproductive for restoration to lead to an impoverished diversity of native species when the very aim of efforts to limit exotic species is to combat biotic homogenisation and the loss of biodiversity. In support of using local seeding mixtures of native species, a previous study found that native species recruitment was less affected by native species seeding than that of alien species (Simmons 2005).

5 | Conclusion for Managers

Early sowing of native species mixture of local seeds can prevent woody alien species invasion. The tested seed densities (15 and 30 $g\,m^{-2}$) did not influence resistance to invasion by *B. davidii*; however, the timing of sowing was critical. In order to be efficient, the seed mixture should be chosen to germinate fast and induce high shading by rapidly establishing plant cover. Ideally, the seed mixture should be sown immediately following disturbance.

Author Contributions

P.D., F.D. and R.J. conceived and designed the research; P.D. performed the experiments; R.J. and F.D. analysed the data and wrote the manuscript, and all the authors improved the text and gave final approval for publication.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Code and data are also publicly available at https://forgemia.inra.fr/renaud.jaunatre/buddleja_ep. The source code and the original dataset are publicly available at https://forgemia.inra.fr/renaud.jaunatre/buddleja_ep.

References

Abella, S. R., D. J. Craig, S. D. Smith, and A. C. Newton. 2012. "Identifying Native Vegetation for Reducing Exotic Species During the Restoration of Desert Ecosystems." *Restoration Ecology* 20, no. 6: 781–787. https://doi.org/10.1111/j.1526-100X.2011.00848.x.

Bakker, J. D., and S. D. Wilson. 2004. "Using Ecological Restoration to Constrain Biological Invasion." *Journal of Applied Ecology* 41, no. 6: 1058–1064. https://doi.org/10.1111/j.0021-8901.2004.00962.x.

Barr, S., J. L. Jonas, and M. W. Paschke. 2017. "Optimizing Seed Mixture Diversity and Seeding Rates for Grassland Restoration." *Restoration Ecology* 25, no. 3: 396–404. https://doi.org/10.1111/rec.12445.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67, no. 1: i01. https://doi.org/10.18637/jss.v067.i01.

Bell, M. D., M. E. Lulow, K. R. Balazs, et al. 2019. "Restoring a Mediterranean-Climate Shrub Community With Perennial Species Reduces Future Invasion." *Restoration Ecology* 27, no. 2: 298–307. https://doi.org/10.1111/rec.12851.

Brisson, J., V. Teasdale, P. Boivin, and C. Lavoie. 2020. "Plant Cover Restoration to Inhibit Seedling Emergence, Growth or Survival of an Exotic Invasive Plant Species." *Écoscience* 27, no. 3: 185–194. https://doi.org/10.1080/11956860.2020.1753313.

Byun, C., M. Oh, E. J. Lee, and H. Kang. 2020. "Seed Density Is as Important as Limiting Similarity, Diversity Effect, and Propagule Pressure in Plant Restoration to Control Invasion." *Ecological Engineering* 144: 105712. https://doi.org/10.1016/j.ecoleng.2019.105712.

Campbell, D. J. 1984. "The Vascular Flora of the DSIR Study Area Lower Orongorongo Valley, Wellington, New Zealand." *New Zealand Journal of Botany* 22, no. 2: 223–270. https://doi.org/10.1080/0028825X.1984.10425254.

Corbin, J. D., and C. M. D'Antonio. 2004. "Competition Between Native Perennial and Exotic Annual Grasses: Implications for an Historical Invasion." *Ecology* 85, no. 5: 1273–1283. https://doi.org/10.1890/02-0744.

Csákvári, E., N. Sáradi, B. Berki, et al. 2023. "Native Species Can Reduce the Establishment of Invasive Alien Species if Sown in High Density and Using Competitive Species." *Restoration Ecology* 31, no. 5: e13901. https://doi.org/10.1111/rec.13901.

Daehler, C. C. 2003. "Performance Comparisons of Co-Occurring Native and Alien Invasive Plants: Implications for Conservation and Restoration." *Annual Review of Ecology, Evolution, and Systematics* 34, no. 1: 183–211. https://doi.org/10.1146/annurev.ecolsys.34.011802.132403.

D'Antonio, C., and L. A. Meyerson. 2002. "Exotic Plant Species as Problems and Solutions in Ecological Restoration: A Synthesis." *Restoration Ecology* 10, no. 4: 703–713. https://doi.org/10.1046/j.1526-100X.2002.01051.x.

Diagne, C., B. Leroy, A. C. Vaissière, et al. 2021. "High and Rising Economic Costs of Biological Invasions Worldwide." *Nature* 592, no. 7855: 571–576. https://doi.org/10.1038/s41586-021-03405-6.

Dickson, T. L., J. L. Hopwood, and B. J. Wilsey. 2012. "Do Priority Effects Benefit Invasive Plants More Than Native Plants? An Experiment With Six Grassland Species." *Biological Invasions* 14, no. 12: 2617–2624. https://doi.org/10.1007/s10530-012-0257-2.

Dommanget, F. 2014. Interactions entre espèces invasives et communautés végétales des berges de cours d'eau: vers l'utilisation du génie écologique dans la lutte contre les Renouées asiatiques. These de doctorat. Montpellier, SupAgro. https://www.theses.fr/2014NSAM0004.

Dommanget, F., A. Evette, V. Breton, et al. 2019. "Fast-Growing Willows Significantly Reduce Invasive Knotweed Spread." *Journal of Environmental Management* 231: 1–9. https://doi.org/10.1016/j.jenvman.2018.10.004.

Dupré La Tour, A., J. Labatut, and T. Spiegelberger. 2020. "Unraveling the Concept of Local Seeds in Restoration Ecology." *Restoration Ecology* 28, no. 6: 1327–1334. https://doi.org/10.1111/rec.13262.

Ebeling, S. K., I. Hensen, and H. Auge. 2008. "The Invasive Shrub *Buddleja davidii* Performs Better in Its Introduced Range." *Diversity and Distributions* 14, no. 2: 225–233. https://doi.org/10.1111/j.1472-4642.2007.00422.x.

Eriksson, O., and J. Ehrlén. 2008. "Seedling Recruitment and Population Ecology." In *Seedling Ecology and Evolution*, edited by M. A. Leck, V. T. Parker, and R. L. Simpson, 239–254. Cambridge University Press. https://doi.org/10.1017/CBO9780511815133.013.

Fox, J., and S. Weisberg. 2019. *An R Companion to Applied Regression*. 3rd ed. SAGE.

Franco, J. R. A., G. B. Paterno, and G. Ganade. 2022. "The Influence of Herbaceous Vegetation on the Colonization of Native and Invasive Trees: Consequences for Semiarid Forest Restoration." *Restoration Ecology* 30, no. 5: e13595. https://doi.org/10.1111/rec.13595.

Funk, J. L., E. E. Cleland, K. N. Suding, and E. S. Zavaleta. 2008. "Restoration Through Reassembly: Plant Traits and Invasion Resistance." *Trends in Ecology & Evolution* 23, no. 12: 695–703. https://doi.org/10.1016/j.tree.2008.07.013.

Gargominy, O., S. Tercerie, C. Régnier, et al. 2022. *TAXREF, référentiel taxonomique pour la France: méthodologie, mise en œuvre et diffusion*, 47. Muséum national d'Histoire naturelle.

Gioria, M., P. Pyšek, and B. A. Osborne. 2018. "Timing Is Everything: Does Early and Late Germination Favor Invasions by Herbaceous Alien Plants?" *Journal of Plant Ecology* 11, no. 1: 4–16. https://doi.org/10.1093/jpe/rtw105.

Global Invasive Species Database. 2023. Species profile: *Buddleja davidii*. http://www.iucngisd.org/gisd/species.php?sc=650.

Gurevitch, J., G. A. Fox, G. M. Wardle, Inderjit, and D. Taub. 2011. "Emergent Insights From the Synthesis of Conceptual Frameworks for Biological Invasions." *Ecology Letters* 14, no. 4: 407–418. https://doi.org/10.1111/j.1461-0248.2011.01594.x.

Hautier, Y., P. A. Niklaus, and A. Hector. 2009. "Competition for Light Causes Plant Biodiversity Loss After Eutrophication." *Science* 324, no. 5927: 636–638. https://doi.org/10.1126/science.1169640.

Hervé, M. 2022. "RVAideMemoire: Testing and Plotting Procedures for Biostatistics." R package version 0.9-81-2. https://CRAN.R-project.org/package=RVAideMemoire.

Hess, M. C. M., E. Buisson, R. Jaunatre, and F. Mesléard. 2020. "Using Limiting Similarity to Enhance Invasion Resistance: Theoretical and Practical Concerns." *Journal of Applied Ecology* 57, no. 3: 559–565. https://doi.org/10.1111/1365-2664.13552.

Hess, M. C. M., F. Mesléard, and E. Buisson. 2019. "Priority Effects: Emerging Principles for Invasive Plant Species Management." *Ecological Engineering* 127: 48–57. https://doi.org/10.1016/j.ecoleng.2018.11.011.

Holle, B. V., and D. Simberloff. 2005. "Ecological Resistance to Biological Invasion Overwhelmed by Propagule Pressure." *Ecology* 86, no. 12: 3212–3218. https://doi.org/10.1890/05-0427.

Johnstone, I. M. 1986. "Plant Invasion Windows: A Time-Based Classification of Invasion Potential." *Biological Reviews* 61, no. 4: 369–394. https://doi.org/10.1111/j.1469-185X.1986.tb00659.x.

Leeuweberg, A. J. M. 1979. "The Loganiaceae of Africa XVIII. *Buddleja* L. II. Revision of the African and Asiatic Species." *Mededelingen Landbouwhogeschool Wageningen* 79, no. 6: 1–163.

Lenth, R. 2023. "emmeans: Estimated Marginal Means, aka Least-Squares Means." R package. https://CRAN.R-project.org/package=emmeans.

Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. "A Meta-Analysis of Biotic Resistance to Exotic Plant Invasions: Biotic Resistance to Plant Invasion." *Ecology Letters* 7, no. 10: 975–989. https://doi.org/10.1111/j.1461-0248.2004.00657.x.

Lulow, M. E. 2006. "Invasion by Non-native Annual Grasses: The Importance of Species Biomass, Composition, and Time Among California Native Grasses of the Central Valley." *Restoration Ecology* 14, no. 4: 616–626. https://doi.org/10.1111/j.1526-100X.2006.00173.x.

Miller, A. 1984. "The Distribution and Ecology of *Buddleia davidii* Franch. in Britain, with Particular Reference to Conditions Supporting Germination and the Establishment of Seedlings." Thesis (Ph.D). Oxford. https://radar.brookes.ac.uk/radar/items/e5341f12-d088-4aa3-b578-adfb723d505f/1/.

Miller, T. E. 1987. "Effects of Emergence Time on Survival and Growth in an Early Old-Field Plant Community." *Oecologia* 72, no. 2: 272–278. https://doi.org/10.1007/BF00379278.

Monty, A., M. Eugène, and G. Mahy. 2015. "Vegetative Regeneration Capacities of Five Ornamental Plant Invaders After Shredding." *Environmental Management* 55, no. 2: 423–430. https://doi.org/10.1007/s00267-014-0398-4.

Novoa, A., D. Moodley, J. A. Catford, et al. 2021. "Global Costs of Plant Invasions Must Not Be Underestimated." *NeoBiota* 69: 75–78. https://doi.org/10.3897/neobiota.69.74121.

Owen, D. F., and W. R. Whiteway. 1980. "Buddleia Davidii in Britain: History and Development of an Associated Fauna." *Biological Conservation* 17, no. 2: 149–155. https://doi.org/10.1016/0006-3207(80)90045-2.

Pepe, M., L. Gratani, G. Fabrini, and L. Varone. 2020. "Seed Germination Traits of *Ailanthus altissima*, *Phytolacca americana* and *Robinia pseudoacacia* in Response to Different Thermal and Light Requirements." *Plant Species Biology* 35, no. 4: 300–314. https://doi.org/10.1111/1442-1984.12286.

Pérez-Harguindeguy, N., S. Díaz, E. Garnier, et al. 2013. "New Handbook for Standardised Measurement of Plant Functional Traits Worldwide." *Australian Journal of Botany* 61, no. 3: 167. https://doi.org/10.1071/BT12225.

R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/.

Satterthwaite, W. H. 2007. "The Importance of Dispersal in Determining Seed Versus Safe Site Limitation of Plant Populations." *Plant Ecology* 193, no. 1: 113–130. https://doi.org/10.1007/s11258-006-9252-y.

Schantz, M. C., R. L. Sheley, and J. J. James. 2015. "Role of Propagule Pressure and Priority Effects on Seedlings During Invasion and Restoration of Shrub-Steppe." *Biological Invasions* 17, no. 1: 73–85. https://doi.org/10.1007/s10530-014-0705-2.

Schuster, M. J., P. D. Wragg, A. M. Roth, P. Bockenstedt, L. E. Frelich, and P. B. Reich. 2022. "Using Plants to Control Buckthorn (*Rhamnus cathartica*): Improved Biotic Resistance of Forests Through Revegetation." *Ecological Engineering* 182: 106730. https://doi.org/10.1016/j.ecoleng.2022.106730.

Shea, K., and P. Chesson. 2002. "Community Ecology Theory as a Framework for Biological Invasions." *Trends in Ecology & Evolution* 17, no. 4: 170–176. https://doi.org/10.1016/S0169-5347(02)02495-3.

Sher, A. A., and D. L. Marshall. 2003. "Seedling Competition Between Native *Populus deltoides* (Salicaceae) and Exotic *Tamarix ramosissima* (Tamaricaceae) Across Water Regimes and Substrate Types." *American Journal of Botany* 90, no. 3: 413–422. https://doi.org/10.3732/ajb.90.3.413.

Simberloff, D., J. L. Martin, P. Genovesi, et al. 2013. "Impacts of Biological Invasions: What's What and the Way Forward." *Trends in Ecology & Evolution* 28, no. 1: 58–66. https://doi.org/10.1016/j.tree.2012.07.013.

Simmons, M. T. 2005. "Bullying the Bullies: The Selective Control of an Exotic, Invasive Annual (*Rapistrum rugosum*) by Oversowing With a Competitive Native Species (*Gaillardia pulchella*)." *Restoration Ecology* 13, no. 4: 609–615. https://doi.org/10.1111/j.1526-100X.2005.00078.x.

Stuble, K. L., and L. Souza. 2016. "Priority Effects: Natives, but Not Exotics, Pay to Arrive Late." *Journal of Ecology* 104, no. 4: 987–993. https://doi.org/10.1111/1365-2745.12583.

Tallent-Halsell, N. G., and M. S. Watt. 2009. "The Invasive *Buddleja davidii* (Butterfly Bush)." *Botanical Review* 75, no. 3: 292–325. https://doi.org/10.1007/s12229-009-9033-0.

Tarsa, E. E., B. M. Holdaway, and K. M. Kettenring. 2022. "Tipping the Balance: The Role of Seed Density, Abiotic Filters, and Priority Effects in Seed-Based Wetland Restoration." *Ecological Applications* 32, no. 8: e2706. https://doi.org/10.1002/eap.2706.

Thomas, P. A., E. Buisson, G. E. Overbeck, and S. C. Müller. 2024. "Exploring Seed Density and Limiting Similarity to Reduce Invasive Grass Performance for Grassland Restoration Purposes." *Applied Vegetation Science* 27, no. 3: e12804. https://doi.org/10.1111/avsc.12804.

Tilman, D. 1990. "Constraints and Tradeoffs: Toward a Predictive Theory of Competition and Succession." *Oikos* 58, no. 1: 3. https://doi.org/10.2307/3565355.

Valladares, F., C. C. Bastias, O. Godoy, E. Granda, and A. Escudero. 2015. "Species Coexistence in a Changing World." *Frontiers in Plant Science* 6: 866. https://doi.org/10.3389/fpls.2015.00866.

Von Gillhaussen, P., U. Rascher, N. D. Jablonowski, C. Plückers, C. Beierkuhnlein, and V. M. Temperton. 2014. "Priority Effects of Time of Arrival of Plant Functional Groups Override Sowing Interval or Density Effects: A Grassland Experiment." *PLoS ONE* 9: e86906. https://doi.org/10.1371/journal.pone.0086906.

Watt, M. S., D. Whitehead, D. J. Kriticos, S. F. Gous, and B. Richardson. 2007. "Using a Process-Based Model to Analyse Compensatory Growth in Response to Defoliation: Simulating Herbivory by a Biological Control Agent." *Biological Control* 43, no. 1: 119–129. https://doi.org/10.1016/j.biocontrol.2007.06.011.

Watt, M. S., V. Xu, and M. Bloomberg. 2010. "Development of a Hydrothermal Time Seed Germination Model Which Uses the Weibull Distribution to Describe Base Water Potential." *Ecological Modelling* 221, no. 9: 1267–1272. https://doi.org/10.1016/j.ecolmodel.2010.01.017.

Weidlich, E. W. A., F. G. Flórido, T. B. Sorrini, and P. H. S. Brancalion. 2020. "Controlling Invasive Plant Species in Ecological Restoration: A Global Review." *Journal of Applied Ecology* 57, no. 9: 1806–1817. https://doi.org/10.1111/1365-2664.13656.

Weissgerber, M., R. Jaunatre, F. Dommanget, F. Jacob, G. Huyghe, and A. Evette. 2019. "Seeding Dynamics From a Local Seed Mixture on a Bioengineered Riverbank Protection Structure." *Environmental Management* 64, no. 2: 178–189. https://doi.org/10.1007/s00267-019-01180-9.

Wilsey, B. J., K. Barber, and L. M. Martin. 2015. "Exotic Grassland Species Have Stronger Priority Effects Than Natives Regardless of Whether They Are Cultivated or Wild Genotypes." *New Phytologist* 205, no. 2: 928–937. https://doi.org/10.1111/nph.13028.

Yannelli, F. 2021. "Applying Competition Theory to Ensure Ecological Restoration and Prevent Plant Invasions." *Biodiversity* 22, no. 1–2: 82–86. https://doi.org/10.1080/14888386.2021.1905548.

Yannelli, F. A., C. MacLaren, and J. Kollmann. 2020. "Moving Away From Limiting Similarity During Restoration: Timing of Arrival and Native Biomass Are Better Proxies of Invasion Suppression in Grassland Communities." *Frontiers in Ecology and Evolution* 8: 238. https://doi.org/10.3389/fevo.2020.00238.

Yu, H., M. Yue, C. Wang, J. J. le Roux, C. Peng, and W. Li. 2020. "Priority Effects and Competition by a Native Species Inhibit an Invasive Species and May Assist Restoration." *Ecology and Evolution* 10, no. 23: 13355–13369. https://doi.org/10.1002/ece3.6938.

Zhengyi, W., and P. H. Raven. 1996. *Flora of China. 15: Myrsinaceae Through Loganiaceae*. Missouri Botanical Garden Press.

Zimmermann, T. G., A. C. S. Andrade, and D. M. Richardson. 2017. "Abiotic Barriers Limit Tree Invasion but Do Not Hamper Native Shrub Recruitment in Invaded Stands." *Biological Invasions* 19, no. 1: 109–129. https://doi.org/10.1007/s10530-016-1267-2.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.