



Leaf-cutting ants facilitation to non-native plants is passed from one generation to the next

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Abstract In arid environments where soil resources are limiting factors, the presence of soil ecosystem engineers that create new enriched soil habitats can improve the performance of non-native plants growing there. Moreover, these enriched areas may be considered key sources of high-quality seeds, which would favor the spread and invasion success of non-native plant. In Northwestern Patagonian steppe, the non-native grass *Bromus tectorum* is one of the most frequent species that takes advantage of the soil engineering effect of the leaf-cutting ant *Acromyrmex lobicornis*. Here, we evaluated if the facilitative effect of the enriched nest sites of *A. lobicornis* on *B.*

tectorum individuals is also transferred to their offspring. We compared the influence of *B. tectorum*'s seed source (i.e., from plants growing on nest sites vs steppe soil) on seed mass, seed germination, and performance of new individuals growing under the same conditions (i.e., growing in steppe soil, under the same water and temperature conditions). We showed that individuals of *B. tectorum* growing on nest sites produced bigger seeds, with germination rate and germination percentage similar to those of individuals from soil seeds; however, they produced 53% larger seedlings, with 30% less root:shoot ratio and higher probability of having shoots with spikelets. This evidences that the benefits of growing on nest sites pass on to the offspring of *B. tectorum*. Moreover, our results highlight the importance of environmental maternal effects on plant growth and development even after germination and show that soil ecosystem engineers can represent a crucial contribution to the invasion of non-native plants.

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Introduction

Success in the invasion of a new environment by a non-native species depends not only on the intrinsic characteristics of the species and the recipient

community, but also on the establishment of novel interactions with the local biota (Richardson et al. 2000; Nuñez et al. 2009; Prior et al. 2015). Biotic interactions can both hinder or promote the establishment and spread of non-native species. In the first case, it is known that local natural enemies and competitors can limit the success of non-native species (Elton 1958; Maron and Vila 2001; Levine et al. 2004). Resident herbivores, for example, can decrease the growth, fecundity, and population size of non-native plant species (Maron and Vila 2001; Parker et al. 2006). On the other hand, resident species may facilitate the non-natives' success by establishing mutualistic relationships with them (e.g., acting as pollinators or seed dispersers; Richardson et al. 2000; Geerts and Pauw 2009; Heleno et al. 2013). Considering these contrasting pieces of evidence, understanding how biotic interactions regulate biological invasions has become a major goal for basic and applied ecologists.

Ecosystem engineers are species that transform the physical structure and/or chemical composition in the abiotic environment in ways that facilitate other organisms (Jones et al. 1994, 1997). Through this process resident species may promote the successful invasion of non-native ones. This action of resident ecosystem engineers as facilitators of biological invasion has usually been reported through the generation of novel plant-plant interactions. For example, the amelioration of the environmental harshness of high mountains by native cushion plants facilitates the establishment and survival of introduced forbs (Cavieres et al. 2005, 2008; Badano et al. 2007). However, although resident animals such as earthworms and termites create new enriched soil habitats and are considered soil engineers (Le Bayon et al. 2017; Jouquet et al. 2016; Willis and Landis 2018), evidence of their facilitative impact on non-native plant species is scarce. In resource-heterogeneous environments, plants change their resource allocation in response to resource availability; under enriched soil conditions, plants often have higher biomass mostly allocated to shoot growth (i.e., lower root to shoot ratio), and enhanced reproductive performance (Müller et al. 2000; Wang et al. 2019). Moreover, considering that some non-native plant species can take better advantage of the more nutritious substrate than native ones (e.g., Ostertag and Verville 2002; Farji-Brener et al. 2010), it seems essential to increase the knowledge

about how the activities of resident soil engineers can facilitate the invasion of non-native plants.

Plants growing on nutrient-enriched substrates usually have larger sizes, higher seed production, and enhanced seed quality than those growing on nutrient-poor substrates (Weiner 1988; Farji-Brener and Ghermandi 2008; Farji-Brener et al. 2010). As the quality of the seed affects the emergence, growth, and performance of the new plant (Adebisi et al. 2013), the substrate on which the mother plant grows may be considered an important determinant of their offspring quality. In fact, a plant with more resources can produce larger seeds (i.e., with more reserves), resulting in seedlings better able to establish than those from smaller seeds produced by plants growing in poorer resource conditions (Bonal et al. 2007; Perea et al. 2011). For example, nitrogen addition increases the seed mass of the desert shrub *Sarcobatus vermiculatus* (Drenovsky and Richards 2005) and the Eurasian steppe grass *Leymus chinensis* (Gao et al. 2020), which positively influence seedling recruitment and survival. Considering this, if the soil enrichment by ecosystem engineers favors the offspring quality of non-native plants (measured as seed size, germination percentage, and offspring size), it may promote their successful establishment and spread.

Particularly, in the northwestern Patagonian steppe, where soil resources are limiting factors (Matteucci 2012), the leaf-cutting ant *Acromyrmex lobicornis* acts as an ecosystem engineer because the colony activities alter the pattern of soil nutrients and water availability (Farji-Brener and Ghermandi 2008). As a consequence, the areas around their nests become enriched-resource patches (hereafter nest sites) that have greater diversity, and give rise to more vigorous individuals than adjacent areas, especially of non-native plants (Farji-Brener and Ghermandi 2000, 2008; Farji-Brener et al. 2010; Pirk and Farji-Brener 2013). However, there is little information regarding the impact of the engineering effect of *A. lobicornis* on the reproductive performance of most of these non-native plants, and even less on the performance of seeds from nest sites once they reach the nutrient-poor steppe soils. This information is crucial to understand the role of ant nests in the success of non-native plants spreading.

Here, we evaluated if the facilitative effect of nest sites is also transferred to the offspring of one of the most frequent species that take advantage of

the soil engineering effect of *A. lobicornis*: the non-native *Bromus tectorum* (cheatgrass; winter annual grass). This species, which has a great capacity to alter the ecosystems it colonizes (CABI-Invasive Species Compendium), is a recent invader in Patagonia (Speziale et al. 2014). It has high adaptability and capacity to invade multiple habitats within the Patagonian steppe (Speziale et al. 2018). Moreover, in ecologically equivalent invaded ecosystems from USA, *B. tectorum* produces severe impacts (Seabloom et al. 2003; Sperry et al. 2006; Bradley 2009). For example, areas invaded by *B. tectorum* are detrimental to economic activities such as cattle grazing because, although livestock may consume it, the grazing period is short and when seeds mature their stiff awns cause mouth and throat irritation (Whitson and Koch 1998; Velazco and Siffredi 2013). Also, *B. tectorum* is highly competitive in displacing native plants (Johnson and Aguirre 1991; Franzese et al. 2021), and favors a higher incidence of fires since it increases the abundance of fine fuels (D'Antonio and Vitousek, 1992). Previous studies show that individuals of *B. tectorum* are more abundant, and gain considerably more biomass when growing on nest sites of *A. lobicornis* than in the poor-nutrient steppe soils (Farji-Brener et al. 2010). Taking into account that there is a positive association between plant size and fecundity (Horvitz and Schemske 2002 and references therein), and resource availability and offspring quality (Drenovsky and Richards 2005), nest sites may be considered key sources of high-quality seeds, which can represent a crucial contribution to the success of non-native plant invasion, such as that of *B. tectorum*.

We compared the influence of the seed source (i.e., from plants growing on nest sites vs natural steppe soil, hereafter “nest seeds” and “soil seeds”, respectively) on the seed mass and seed germination. Also, we examined the performance of individuals from different seed sources growing under the same conditions (i.e., growing in steppe soil, and under the same water and temperature conditions). We hypothesized that the soil engineering effect of *A. lobicornis*, through its positive effect on seed quality of *B. tectorum*, enhances the emergence, growth, and performance of the new individuals, so we expected higher seed mass and germination from nest seeds compared to soil seeds. Moreover, we expected higher plant

biomass and reproductive performance, and a lower root:shoot ratio of plants developed from nest seeds compared to those from soil seeds.

Materials and methods

Study area and system

The northwestern Patagonian steppe is a temperate cold region with a mean annual temperature of 8 °C and mean annual precipitation of 600 mm, concentrated mainly in the autumn–winter months. The dominant native vegetation includes perennial tussock grasses such as *Pappostipa speciosa* and *Festuca pallescens*, and shrubs such as *Azorella prolifera*, *Senecio bracteolatus*, and *Acaena splendens* (Correa 1988). Disturbances like anthropogenic fires and grazing by domestic and other non-native animals are important in this region (Veblen et al. 1992), favoring the spread of non-native plants as *Bromus tectorum*, *Carduus thoermeri*, *Verbascum thapsus* within native communities (Pirk and López de Casenave, 2017).

Soil nutrients and water availability in this region are considered the main limiting factors for plant recruitment (Soriano et al. 1994; Satti et al. 2003), but the presence of the leaf-cutting ant *Acromyrmex lobicornis* increases the availability of these resources (Farji-Brener and Ghermandi 2000, 2008). Ants' activities increase these limiting resources around their nest in two ways. On the one hand, the construction and maintenance of the nests alter the physical properties of the soil (e.g., increasing the porosity and infiltration, Eldridge and Pickard 1994). On the other hand, their feeding habits generate and concentrate large amounts of organic waste creating nutrient hot spots (Farji-Brener and Ghermandi 2000, 2008). These enriched nest sites affect the abundance and performance of plants and plant-associated organisms; therefore, these ants are considered ecological engineer species (Farji-Brener and Werenkraut 2015). Regarding the vegetation patterns, non-native species are particularly favored at nest sites; species such as *B. tectorum*, *Hordeum comosum*, and *C. thoermeri* are more abundant on nests of *A. lobicornis* than in nutrient-poor steppe soils (see ESM A, Fig. A1), and their individuals usually have higher growth rate and biomass when growing on nest compared with those growing on non-nest soil (Farji-Brener et al.

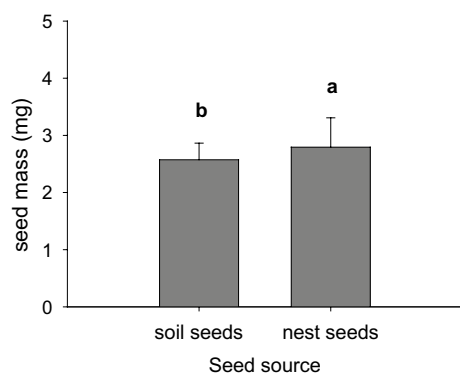


Fig. 1 Seed mass (mean \pm SE) from each seed source: nests of *Acromyrmex lobicornis* (nest seeds) and nutrient-poor steppe soils (soil seeds). Different lower case letters indicate statistically significant differences between substrates ($p < 0.05$)

2010). Among these non-native species, *B. tectorum* deserves our particular attention because of its potential threat to the integrity of the northwestern Patagonian ecosystem (Speziale et al. 2018; Franzese et al. 2021). Thus, it is necessary to know the determining factors of its propagation into the northwestern Patagonian steppes, especially those that can facilitate its establishment and spread.

Experimental design and analyses

To assess the potential effect of *A. lobicornis* nests on the performance of *B. tectorum*'s offspring, we randomly collected seeds from plants growing on *A. lobicornis* nests and on steppe soil sites in a continuous area of approximately 100×8000 m of roadside steppes. Seeds from nest plants were collected from 18 nests at least 20 m apart. Soil seeds were collected from plants growing on natural steppe soils, in 18 sites not influenced by the nests, but in the vicinity of them. Seeds from each source (nest or soil) were pooled and randomized before sorting them into 50 sets of 10 seeds per source.

Seed mass

In order to assess the differences in seed mass from each seed source, we weighed each set of 10 seeds and estimated seed mass as the total weight divided by 10 ($n=50$ per source). To examine the effect of seed source on seed mass we fitted a linear model using the seed mass (in mg) as the response variable,

and the seed source as a categorical explanatory variable, using R software (R Core Team 2020). We assumed a Normal distribution of residuals and checked all model assumptions.

Seed germination

To determine whether seed source differentially affects the probability of *B. tectorum* seeds germination through time, we randomly selected 20 seed sets (10 seeds each) from each source for a germination trial. We placed the seeds of each set over filter paper in a Petri dish. Each Petri dish ($n=10$ per seed source) was moistened with distilled water and a fungicide solution, and incubated in a germination chamber under controlled temperature and photoperiod (12 h light at 18 °C and 12 h dark at 10 °C). We checked the Petri dishes every 2 days for a period of 5 weeks recording the number of germinated seeds and removing them from the dish. This allowed us to estimate a germination curve through time for nest and soil seeds.

To assess the effect of seed source on germination dynamics, we fitted a Bayesian hierarchical non-linear model using the accumulated number of germinated seeds in each Petri dish as the response variable, and time (in days) as the explanatory variable for both seed sources. We assumed a Binomial distribution (with parameter $N=10$ seeds) for the number of germinated seeds. The model fitted was hierarchical because it allowed us to model the potential lack of independence between the seeds that were germinating in the same Petri dish. The non-linear function fitted was a saturating exponential function that represents the typical behavior of germination curves: a rapid increase of the number of germinated seeds at the beginning of the trail, and a decreasing germination rate when the curve is close to the asymptote (the total number of germinated seeds). The saturating exponential function has two parameters: the asymptote (α) and the rate (β). To assess the potential differences in the germination curve for nest and soil seeds, we compared the posterior distribution of these two parameters for both seed sources, and estimated the proportion of overlap between them to provide a quantitative measure of their differences. This model was fitted using R software and JAGS (Plummer 2003).

Plant growth and reproductive performance

We conducted a greenhouse experiment to evaluate whether the source of seeds differentially affected the growth and reproductive performance of new individuals of *B. tectorum* growing under the same conditions (i.e., nutrient-poor steppe soils). We randomly selected 10 seed sets (10 seeds each) from each source, and put them into a germination chamber during early autumn 2017. After the seeds developed a visible radicle (≥ 0.5 cm), we randomly selected 25 seedlings per source, and transplanted them into individual pots (one plant per pot; $n=25$ pots per seed source). All pots ($15 \times 8 \times 8$ cm) were filled with steppe soil, and randomly placed in a greenhouse. They grew under natural daylight and temperature conditions being watered as needed until the end of the experiment (late spring 2017). Before transplantation, we measured the initial length (maximum shoot+root length) of all seedlings, and after 38 weeks, we registered the presence or absence of shoot with spikelets as a proxy for reproductive potential (since it is an annual plant whose reproduction depends on seeds and due to viable seeds were not produced during the experiment). Finally, we harvested, washed, and oven-dried all plants at 60°C for 2 days. Then, we weighed and registered the total biomass (roots+shoots dry weight) and calculated the root:shoot biomass ratio.

To assess the effect of seed source on total biomass, we fitted a linear model using the `lm` R function with total biomass as the response variable and seed source as a categorical explanatory variable. We log-transformed the response variable to accomplish the Normal distribution assumption of this model. The same linear modeling approach was used to assess the effect of seed source on root:shoot ratio. For the presence of shoots with spikelets, we fitted a generalized linear model using the `glm` R function, assuming a Bernoulli distribution (i.e., Binomial distribution with parameter $N=1$) and a logit link function. In this case, the response variable was binary, with a value of 1 when we detected shoots with spikelets, and 0 when they were absent, and the explanatory variable was the source of seeds. For the three models, we included the initial length (in cm) as a covariate that could capture the potential influence of any other factors that affected plant growth and reproduction before the greenhouse experiment in the models.

Then, we assessed if models' goodness of fit was affected by this variable using information criterion (AIC and BIC, Burnham and Anderson 2002). In all cases, the inclusion of this variable decreased models' fit, and for this reason, we interpreted the models that had seed origin as the only explanatory variable.

Results

The results from models fit showed that the seed source (i.e., nest seeds vs soil seeds) affected seed mass; nest seeds had 12% higher seed mass than soil seeds (t value: -3.93 ; df: 98; $p < 0.001$; Fig. 1). The observed seed mass for nest seeds was, on average 2.79 mg (\pm std. error: 0.4 mg), while for soil seeds the average mass was 2.57 mg (\pm std. error: 0.2 mg). However, no matter the seed source, the general germination peak was observed within 4–6 days, and seeds had a similar germination percentage (99% germination for soil seeds with a 95% Credible Interval (CI), and 95% germination for nest seeds, with a 95% CI; df: 506; Fig. 2; and ESM, B; Fig. B1 and Table B1). Also, germination rate resulted similar between seed sources, with a rate of 0.56 (95% CI: 0.44, 0.68 for soil seeds) and 0.52 (95% CI: 0.44, 0.57 for nest seeds) (ESM, B; Fig. B1 and Table B1).

After germination, the performance of the new individuals depended on seed source. Individuals from nest seeds had 53% more total biomass than those from soil seeds (t-value: -3.79 ; df: 45;

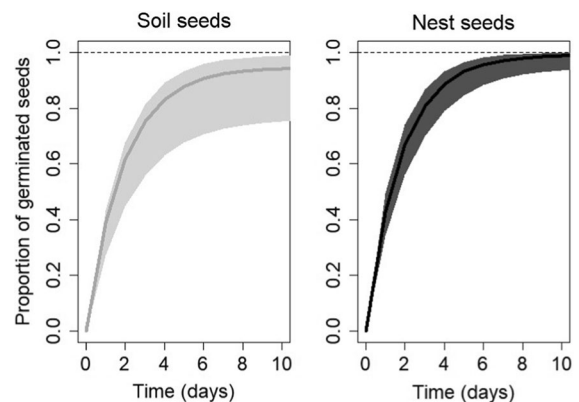


Fig. 2 Germination dynamics of seeds from each source: nests of *Acromyrmex lobicornis* (nest seeds) and nutrient-poor steppe soils (soil seeds). The gray area around the estimated line represents the 95% credible interval

$p < 0.001$; Fig. 3A). Moreover, the mean total biomass of individuals from nest seeds was 4.75 g (\pm std error: 0.18) while for individuals from soil seeds it was 3.10 g (\pm std error: 0.19). The root:shoot ratio also depended on the seed source (t-value: 2.03 ; df: 45 ; $p < 0.05$; Fig. 3B). Individuals from nest seeds showed a 30% lower root:shoot ratio than those from soil seeds (1.89 ± 0.13 and 2.36 ± 0.11 , respectively, mean \pm std error). Moreover, the probability of having shoots with spikelets was higher for individuals from nest seeds than those from soil seeds (0.44 and 0.17 respectively, t-value: -4.12 ; df: 45 ; $p < 0.01$).

Discussion

Given that facilitative interactions are expected to be important in harsh environments (Bertness and Callaway 1994; Bruno et al. 2003), soil engineering effects might be a significant mechanism in promoting invasions of non-native plants in regions where

soil resources are limiting factors. Particularly, in arid and semi-arid regions, where plant growth is limited by moisture and soil nutrient (Noy-Meir 1973), soil engineering by animals generates fertility islands that can favor the diversity and biomass of non-native plants (e.g., Farji-Brener and Ghermandi 2000, 2004). An earlier study also examined the maternal effects of ant nests on non-native plants; there, Farji-Brener and Ghermandi (2008) germinated seeds of exotic thistles from individuals growing on nest sites vs natural steppe soil, but they found that seedling traits were not influenced by the maternal growing substrate. Thus, our work is the first to demonstrate that the facilitative effect of soil ecosystem engineers is transferred to the offspring of a non-native plant with high invasive potential. Moreover, it goes a step further by analyzing this facilitative effect up to the reproductive stage of the new plant offspring. Our results showed that individuals of *Bromus tectorum* growing on enriched-resource patches generated by the leaf-cutting ant *Acromyrmex lobicornis* produce bigger seeds, which do not determine their germination rate or germination percentage, but give rise to larger seedlings, with less root:shoot ratio and higher probability of having shoots with spikelets than individuals from soil seeds.

The environment in which the mother plant grows may influence the performance of its offspring (i.e., environmental maternal effects, reviewed by Roach and Wulff 1987; Uller 2008; Wolf and Wade 2009). Among the maternal abiotic environment, the availability of soil nutrients is often considered an important factor that contributes to inducing morphological and physiological changes in seeds (Wulff and Bazzaz 1992; Galloway 2001). For example, a plant growing in a more nutritious substrate can produce larger and/or heavier seeds than plants from nutrient-poor soil (e.g., Aarssen and Burton 1990; Schmitt et al. 1992; Wulff and Bazzaz 1992; Galloway 2001). Also, the germination success and germination rate of these seeds will be increased compared with small and light seeds (e.g., Bonal et al. 2007; Perea et al. 2011). Here we found that seeds of *B. tectorum* from an enriched substrate (i.e., nest sites) were 12% heavier than those from steppe soil, but the germination timing was independent of the seed size (and thus seed source). The germination process is highly important for annual plant fitness (Donohue 2002; Lu et al. 2014, 2016) since faster germination can enhance

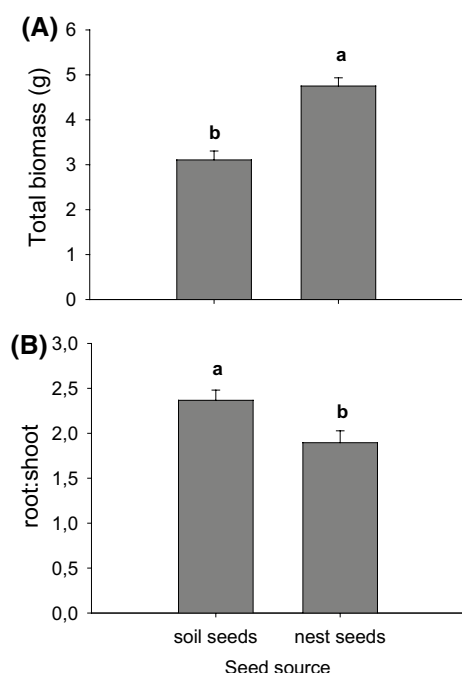


Fig. 3 Performance of the new individuals from each seed source: nests of *Acromyrmex lobicornis* (nest seeds) and nutrient-poor steppe soils (soil seeds). **A** Total biomass (mean \pm SE) and **B** Root:shoot ratio. Different lower case letters indicate statistically significant differences between substrates ($p < 0.05$)

their competitive ability (Rice and Dyer 2001). Thus, we expected that through the impact on the germination process, the seeds from *B. tectorum* plants growing on nest sites could facilitate their invasion into the Patagonian steppe. However, in our study, the seed source does not appear to influence the percentage of germination and the germination speed of *B. tectorum*. The facilitative effect of growing on nest sites for *B. tectorum* seems to be reflected in the stage subsequent to germination, at the seedling stage.

The benefits of higher seed size are expected to become less relevant with the advancement of plant development (Breen and Richards 2008). However, experimental studies have shown that maternal effects may determine not only seed size and germination time, but also early growth (Roach and Wulff 1987; Helenurm and Schaal 1996) and later development, such as the timing of flowering and reproductive success of plants (Schmid and Dolz 1994; Helenurm and Schaal 1996; but see Bischoff and Muller-Scharer 2010). The seed source could influence the early growth of seedlings through increased metabolic resources present in larger seeds and retained in the cotyledons after germination, which can then be mobilized for the growth, maintenance, and repairing of the seedling (Green and Juniper 2004). This may provide young seedlings with advantages in dealing with environmental stressors (Martínez-González et al., 2021), which results in a positive correlation between seed size and seedling growth (Moles and Westoby 2004; Hanley et al. 2007). According to these ideas, we found that the performance of the offspring depended on the seed source. Individuals developed from nest seeds had 53% higher plant biomass and higher reproductive performance compared to those from soil seeds. Our results on *B. tectorum* plants that grew under the same nutrient-poor soil condition (and also light, temperature, and irrigation conditions) highlight that environmental maternal effects influence the growth and development of plants even after germination.

Many factors have the potential to influence root:shoot ratios, including site moisture, nutrient availability, and competition (Mokany et al. 2006). Moreover, in nutrient-poor soils, carbon allocation in favor of belowground organs can be key to ensuring the nutrient uptake (Chapin et al. 1987; Chapin 1991). This could be the case for *B. tectorum* individuals growing in the Patagonian steppe, where water

and soil nutrients have been considered more limiting than light (Fowler 1986; Matteucci 2012). However, seedlings from nest seeds, whose mother plant grew in enriched-resource patches, may allocate the extra resource to the initial growth of above-ground biomass. This may stimulate a shift in their root:shoot ratio compared with plants from soil seeds and may explain how the nest sites of *A. lobicornis* favor the above-ground performance of *B. tectorum*. Although in open steppe areas the seedlings of perennial species usually have a high root:shoot to deal with summer water stress (Franzese et al. 2009), this strategy might not be necessary for *B. tectorum* since it is an annual winter plant that due to its early maturation avoids the most critical summer periods. Therefore, a lower root:shoot ratio, by stimulating faster above-ground growth, could be a successful strategy for a winter annual species when their seeds are dispersed to nutrient-poor steppe soils as the characteristics of this high-quality offspring could favor their success.

The enriched-resource patches created by *A. lobicornis* not only stimulate the growth and reproductive performance of plants (as shown in previous studies, e.g., Farji-Brener et al. 2010; Lescano et al. 2012; Pirk and Farji-Brener 2013), but also environmental maternal effect may be considered as a key source of high-quality *B. tectorum* propagules. Moreover, the enhanced probability of having shoots with spikelets of individuals from nest sources may promote higher production of *B. tectorum* propagules, which represents an increased probability of colonizing a greater proportion of available sites and establishing in new areas. Taking into account that *B. tectorum* invasion is increasing in NW Patagonian given the increased land disturbance and its highly competitive ability (Speziale et al. 2018; Franzese et al. 2021), the presence of *A. lobicornis* as a hot spot of *B. tectorum* propagules, which have higher invasion potential, could enhance its strong negative impact on the community. So, the management and conservation strategies to eradicate this threatening species could be enhanced by removing plants growing on the nest sites of *A. lobicornis* and reducing disturbance by restoring the areas around nests with native species. Finally, our results highlight the importance of understanding the relevant role that native animal ecosystem engineers play as high-quality offspring promoters, and thus, facilitators of the invasion process of non-native plant species.

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Author contributions All authors contributed to the study conception, design, and data collection. Data analysis was performed by AdV. The first draft of the manuscript was written by MNL and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript. All authors whose names appear on the submission made substantial contributions to the conception or design of the work, drafted the work or revised it critically for important intellectual content; approved the version to be published; and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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Data availability Data data will be permanently archived in the Institutional Digital Repository of Universidad Nacional del Comahue (<http://rdi.uncoma.edu.ar>).

Declarations

Conflict of interest The authors declare that there is no conflict of interest. The authors have no relevant financial or non-financial interests to disclose.

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