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A brooms race: Seed ecology may explain differences in spread of two invasive legumes

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Abstract

1. Biological invasions represent a major threat to biodiversity and ecological integrity worldwide. Shifts in dominance among invasive species provide valuable opportunities to identify the ecological traits that determine invasion success.

2. In the Southern Pampas grasslands of Argentina, two introduced broom species, French broom (FB, *Genista monspessulana*) and Spanish broom (SB, *Spartium junceum*) became prominent invaders and management priorities. Historically, control efforts focused on SB. However, following extensive wildfires (2008 and 2013), FB rapidly expanded and displaced SB.

3. We investigated the demographic and ecological mechanisms that may underlie this shift in species dominance by combining field studies, seed bank assessments, germination experiments under contrasting heat treatments and greenhouse water stress experiments.

4. FB produces ~6 times more seeds/plant and develops seed banks ~5 denser than those of SB. Pre-germination heat treatments resulted in higher germination percentages in both species, but FB maintained faster and greater germination even after severe dry-heat exposure, enhancing post-fire regeneration.

5. FB flowers earlier, providing a temporal advantage in reproduction and seed maturation in relation to seasonal rainfall peaks. It showed only limited changes in growth under reduced irrigation, although overall responses to water availability were similar between species.

6. Implications. Abundant seed production, a high germination rate, a dense seed bank, greater tolerance to fire-related heat, and earlier flowering could explain the rapid spread and predominance of French broom in the grasslands of southwestern Buenos Aires Province. Management strategies should prioritize the early control of plants to prevent seed production, the depletion of the seed bank through prescribed burning and the control of post-fire seedlings to contain further expansion.

[Keywords: invasive species, *Genista monspessulana*, *Spartium junceum*, fire, seed bank, pampas grasslands]

Resumen. Una carrera de escobas: La ecología de las semillas podría explicar diferencias en la propagación de dos leguminosas invasoras

1. Las invasiones biológicas amenazan la biodiversidad e integridad ecológica a nivel mundial. Los cambios en la dominancia entre las especies invasoras permiten identificar cuáles rasgos ecológicos determinan el éxito de la invasión.

2. En los pastizales pampeanos del sur argentino, dos retamas introducidas son invasoras prominentes y prioridades de manejo: retama francesa (*Genista monspessulana*, RF) y retama española (RE, *Spartium junceum*). Históricamente, el control se centró en RE. Tras dos extensos incendios forestales (2008 y 2013), RF desplazó a RE.

3. Investigamos los mecanismos demográficos y ecológicos que explicarían este cambio en la dominancia mediante estudios de campo e invernáculo (banco de semillas, germinación bajo estrés hídrico y temperaturas contrastantes).

4. RF produce ~6 veces más semillas/planta y desarrolla bancos de semillas ~5 veces más densos que RE. Los tratamientos térmicos pregerminativos determinaron mayores porcentajes de germinación en ambas especies. La germinación de RF fue más rápida y abundante, incluso después de una exposición severa al calor seco, lo cual favorecería su regeneración post-incendio.

5. RF florece más temprano. Esto es ventajoso para la reproducción y la maduración de las semillas en relación con los picos de lluvia estacional. La especie solo cambió su crecimiento bajo riego reducido. Las respuestas generales a la disponibilidad de agua fueron similares entre las especies.

6. Implicancias. La producción abundante de semillas, la tasa elevada de germinación, un banco de semillas denso, la floración temprana y una mayor tolerancia al calor relacionado con el fuego explicarían la rápida dispersión y predominio de RF en los pastizales del suroeste de Buenos Aires. Las estrategias de manejo deberían priorizar el control temprano de las plantas para evitar la producción de semillas, el agotamiento del banco de semillas mediante quema prescrita y el control de las plántulas posteriores al incendio para contener una mayor expansión.

[Palabras clave: especies invasoras, *Genista monspessulana*, *Spartium junceum*, fuego, banco de semillas, pastizales pampeanos]

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Introduction

Biological invasions are recognized as one of the major transformative forces of ecosystems and constitute one of the greatest threats to biodiversity worldwide. Invasive alien species alter biodiversity through interspecific interactions (Clout 2002; Donlan and Wilcox 2008), and frequently modify ecosystem structure and functioning by changing vegetation dynamics (Charles and Dukes 2008; Simberloff et al. 2013; Roy et al. 2023). In addition to their ecological impacts, invasive alien species are responsible for significant economic losses (Diagne et al. 2021; Duboscq-Carra et al. 2021) and social impacts (Pimentel et al. 2005; Pratt et al. 2017). Unlike other drivers of biodiversity loss, invasive species often produce persistent ecosystem changes once established, making their management particularly challenging (Doren et al. 2009). Although numerous studies have identified traits associated with invasion success, understanding why some invasive species spread more rapidly than other ecologically similar invaders remains one of the central questions in invasion ecology (Van Kleunen et al. 2010; Gioria et al. 2023). Comparisons between closely related invasive species occupying the same environment provide valuable natural experiments because they minimize environmental variation while allowing differences in life-history strategies to be evaluated directly (Guo et al. 2024). Such comparisons can help identify the ecological mechanisms responsible for contrasting invasion dynamics and improve our ability to predict future invasions.

The differential success of invasive species is determined by multiple interacting processes operating at different stages of the invasion process (Lambrinos 2002; Gioria et al. 2023). Although two species may share biological and ecological traits, their ability to invade and establish in new environments can vary significantly due to differences in life history, biotic interactions and adaptability to local conditions (Lambrinos 2002; Daly et al. 2023). Among these factors, propagule pressure is widely recognized as one of the strongest predictors of invasion success, as the probability of establishment generally increases with the quantity and frequency of propagules reaching suitable habitats (Lockwood et al. 2005; Cassey et al. 2018; Vedder et al. 2021). However, propagule pressure itself results from several underlying life-history traits, including reproductive output, phenology, seed bank persistence, germination ecology and tolerance to environmental stress. Together, these characteristics determine recruitment opportunities, especially following disturbances such as fire, which frequently create windows for invasion (Bonser 2013; Burns et al. 2013).

A group of Mediterranean legume shrubs commonly known as brooms (*Cytisus scoparius*, *C. striatus*, *G. monspessulana* and *S. junceum*) has become highly invasive in many temperate regions worldwide after being widely introduced as ornamental plants (Randall and Hoshovsky 2000; Myers and Bazely 2003; Richardson and Rejmánek 2011; Geerts et al. 2013; Carter et al. 2019). Brooms readily colonize disturbed open habitats, including roadsides and abandoned agricultural fields, but also areas of high conservation value in remnants of natural grasslands, where they frequently develop dense monospecific stands (Sanhueza and Zalba 2014).

Several biological attributes contribute to the invasion success of brooms. They exhibit rapid year-round growth, even in extremely poor, sandy and dry soils, produce abundant hard-coated seeds capable of forming persistent seed banks and fix atmospheric nitrogen, thereby modifying soil fertility and ecological succession (Oneto et al. 2020). Furthermore, as plants mature, their inner stems die and dry out, increasing their flammability. This characteristic, combined with the ability of brooms to resprout from the base of burned stems (Downey 2000) and to germinate massively after fires (Pauchard et al. 2008), contributes to their expansion in fire-prone ecosystems.

French broom (*Genista monspessulana*, FB) and Spanish broom (*Spartium junceum*, SB) are among the most important woody invaders of the Pampas grasslands of Argentina (Sanhueza and Zalba 2012), and constitute management priorities in Ernesto Tornquist Provincial Park (ETPP), one of the few protected areas of this biome. Although both species have coexisted in the park for decades and share many ecological characteristics, recent field observations indicate a marked shift in dominance. Until approximately 2010, SB represented the main management concern because of its abundance and rate of spread. Following extensive wildfires in 2008 and 2013, however, FB rapidly expanded across large portions of the reserve and now dominates many areas formerly occupied by

SB. This unexpected replacement provides a unique opportunity to investigate why one invasive species becomes more successful than another under the same environmental conditions, thereby offering insights that may extend beyond the study system. As mentioned above, SB and FB share several traits commonly associated with successful plant invasions. Nevertheless, differences in reproductive investment, propagule production, seed persistence, germination responses and stress tolerance may generate substantial differences in invasion dynamics despite these broad similarities.

We hypothesize that French broom expands more rapidly than Spanish broom because it combines greater propagule production with superior post-disturbance regeneration, resulting in higher recruitment rates and greater long-term population persistence. Specifically, we predict that FB would 1) exhibit earlier or more prolonged reproductive activity; 2) produce substantially more seeds per plant; 3) accumulate larger soil seed banks; 4) show greater germination following fire-related heat treatments; 5) maintain higher germination after persistence in the soil seed bank, and 6) perform better under water limitation. To test these predictions, we compared reproductive phenology, seed production, soil seed banks, germination responses to heat treatments, the effects of seed persistence on germination and seedling performance under contrasting water availability in populations established in Ernesto Tornquist Provincial Park.

Materials and Methods

Study species

SB and FB are perennial shrubs native to the Mediterranean Basin that were introduced into several temperate regions worldwide as ornamental species, and later became invasive in natural and semi-natural ecosystems (Richardson and Rejmánek 2011; Geerts et al. 2013). Both species have invaded grasslands in central Argentina, including the Pampas region, where their spread has increased during recent decades (Sanhueza 2012; Fonseca et al. 2013).

SB can grow up to 4 m and is characterized by cylindrical photosynthetic stems and deciduous leaves, whereas FB is smaller (up to 3 m in height) (Heywood and Ball 1968), presents persistent trifoliate leaves and a denser canopy structure. Previous studies conducted in invaded regions have shown that FB typically initiates flowering during early spring, whereas SB generally flowers later and may maintain reproductive activity well into the summer (Randall and Hoshovsky 2000). These phenological patterns have also been reported for populations established in Argentina (Sanhueza and Zalba 2012). Both species reproduce exclusively by hard-coated seeds capable of forming persistent soil seed banks, a trait frequently associated with invasion success in legumes and other invasive plants (Gioria et al. 2021; Gioria et al. 2023). However, seeds of both species differ noticeably in size. Seeds of SB are flattened and measure approximately 3.2-4.5 × 2.4-3.5 mm (Pandey and Jha 1988), whereas those of FB are nearly spherical and only about 2-2.5 mm in diameter (Weeds of Australia 2026). Persistent seed banks may enhance colonization ability and post-disturbance recruitment by increasing propagule availability through time (Lockwood et al. 2005; Cassey et al. 2018). In Mediterranean Fabaceae, physical dormancy can be broken by exposure to high temperatures associated with fire, promoting post-fire germination and recruitment (Moreira and Pausas 2012; Ooi et al. 2014; He et al. 2019).

Study area

This study was carried out at Ernesto Tornquist Provincial Park (ETPP), a nature reserve aimed at the conservation of native grasslands that covers ~6700 ha in the Ventania mountains, Buenos Aires, Argentina (38°03′ S - 62°02′ W). The area is surrounded by areas intensely transformed by agricultural and intensive livestock production. The region features a wide variety of biotopes, shaped by its diverse terrain, altitudinal gradient (ranging from basal valleys at 350 m to 1200 m above sea level) and a range of substrates, all of which support various forms of life (Frangi and Bottino 1995; Guerrero and Apodaca 2022). Climate is temperate, with an average annual precipitation ranging from 500 to 800 mm, primarily concentrated in spring and late summer, and with occasional snowfall in winter. Average annual temperature is 14 °C (Burgos 1971; Gil and Campo de Ferreras 2006).

Both French and Spanish broom are among the invasive woody species that exert the greatest impact on the reserve. Their rapid growth and expansion have enabled them to colonize extensive areas, posing a significant

threat to the conservation of these relict grasslands (Sanhueza and Zalba 2012).

Fire is a recurrent ecological disturbance throughout the Pampas biome, including the Ventania Mountains (Loydi et al. 2020; de Villalobos and Charles-Dominique 2025; López Mársico et al. 2025). The study area has experienced several large wildfires during recent decades, including extensive fires in 2008 and 2013, which created favorable conditions for broom recruitment and preceded the rapid expansion of French broom.

These conditions make the two species particularly suitable for evaluating which life-history traits best explain differences in invasion success while minimizing phylogenetic and environmental variation. It is important to note, however, that the datasets analyzed in this study were generated as part of different research projects conducted over an extended period. Data for SB were collected between 2004 and 2010, whereas data for FB were obtained during 2017. Although the experiments were not originally designed as components of a single comparative study, they followed comparable sampling and experimental protocols, allowing a standardized comparison of key life-history traits related to invasion success. Because the objective of this study is to compare species-specific demographic and reproductive attributes rather than short-term temporal variation, the datasets were integrated into a common analytical framework.

Assessment of reproductive phenology and seed production

Two sites were selected within the reserve, each consisting of a patch invaded by one or both species. A total of 25 reproductive SB and 35 reproductive FB individuals were monitored, separated by at least 5 meters to reduce spatial autocorrelation. These individuals were randomly chosen. To minimize the influence of plant size on these and the following reproductive comparisons, only adult individuals that had reached the characteristic mature size of each species were selected for analysis. In both species, sampled plants corresponded approximately to the upper quartile of the size distribution observed in the surveyed populations. During the months of October, November and December, we recorded the number of reproductive branches (i.e., those bearing flowers or pods), diameter of the main stem at the base and plant height for each individual. These measurements were used to assess potential relationships between plant size and reproductive output. In addition, four branches were selected per plant, one facing each cardinal direction, and the total number of flowers and pods on each branch was counted (Sanhueza and Zalba 2014). Field observations were conducted from mid-October to mid-December, encompassing the period during which both species initiate flowering and fruit development in the study area. Consequently, the study was designed to compare the timing and progression of reproductive phenology during this critical period rather than to characterize the complete duration of flowering or fruiting.

In November, prior to seed release, 240 mature pods of SB were collected from 25 randomly selected individuals and 277 mature pods of FB were collected from 35 randomly selected individuals. Only mature, reproductively active individuals were included; plants showing signs of damage or disease were excluded. Length and number of seeds were recorded for each pod.

Seed production per plant was estimated as the product of the number of reproductive branches, the mean number of pods per reproductive branch, and the mean number of seeds per pod (Geerts et al. 2013). Estimated seed production per plant was used as an integrative measure of propagule pressure because it combines variation in reproductive branches, pod production and seeds per pod into a single biologically meaningful variable.

General phenological status (reproductive activity) was assessed during field visits conducted between October and December. During each visit, the proportion of flowers and pods was visually estimated for each individual and expressed as percentages of the maximum reproductive display observed for that species. This maximum represented the typical peak abundance of flowers or pods recorded for fully developed individuals during the study period and was determined empirically through repeated observations across sites. Because reproductive output differed between species, reference maxima were established separately for each species. These phenological observations were used for descriptive purposes only and were not subjected to statistical analysis.

Analysis of the soil seed bank

To determine whether differences in propagule persistence could contribute to contrasting invasion dynamics, we quantified the density of viable seeds accumulated in the soil beneath adult plants of each species. Seed density was compared before and after the annual seed-dispersal period. Because seed rain was not measured directly, changes in seed-bank density between sampling periods were used as an indirect estimate of the annual input of seeds to the soil.

One site per species was selected (i.e., one site invaded by FB and one site invaded by SB). Within each site, three sampling points were established, and four subsamples were collected at each point, resulting in 12 composite soil samples per species. A site was defined as a continuous invaded patch dominated by the target species with uniform vegetation cover and environmental conditions. Soil samples were collected from sites invaded by each species before seed input from the new reproductive season occurred. In sites invaded by FB, soil samples were obtained using a cylindrical metal corer 3 cm in diameter inserted to a depth of 7 cm. At each sampling point, four subsamples were collected and combined, resulting in 12 composite soil samples, each representing a total sampled volume of 198 cm^3 and a sampled surface area of 28.3 cm^2 per core.

The leaf litter overlying each soil sample was collected separately, yielding 12 soil samples and 12 litter samples. In sites invaded by SB, soil blocks measuring 20×20 cm and 7 cm deep were extracted (volume=2800 cm^3; sampled surface area=400 cm^2), together with the litter layer above each sample (12 soil samples and 12 litter samples). Sampling volume differed between species because to differences in vegetation structure and litter accumulation between invaded stands.

All soil and litter samples were placed in plastic bags and transported to the laboratory, where they were sieved through a 3-mm metal mesh in order to separate seeds from soil particles and organic material. The mesh size was selected based on preliminary observations indicating that seeds of both species were efficiently retained while allowing fine soil particles and debris to pass through (Sanhueza and Zalba 2012).

Effects of fire-related heat treatments on seed germination

Mature pods were randomly collected from 25 SB individuals and 35 FB individuals. Seeds were manually extracted, cleaned and subjected to nine pre-germination treatments involving moist and dry heat at different temperatures. For each species seven Petri dishes containing 20 seeds each were assigned to every treatment, resulting in a total of 1260 seeds per species.

Heat treatments were selected to simulate conditions experienced by seeds in the upper soil layers (0-5 cm depth) during grassland fires. Although soil surface temperatures may briefly exceed 200 °C (Sánchez et al. 1991), such extreme values occur only at the soil-air interface and for very short periods (a few seconds). In contrast, temperatures at depths of 1-2 cm, where most seeds are concentrated, rarely exceed 120-150 °C even during high-intensity fires, because of the low thermal conductivity of soil (Bradstock and Auld 1995). Accordingly, the experimental design followed the methodology proposed by Travlos (2009), using a maximum exposure of 120 °C for 5 min, which approximates the thermal conditions experienced by buried seeds during fire events.

For the moist-heat treatments, seeds were immersed in water at 20 °C for 30 minutes; 45 °C for 5 minutes; 100 °C for 1 minute, and 100 °C for 5 minutes. For the dry-heat treatments, seeds were placed in Petri dishes and exposed in a drying oven for 5 minutes at 45, 80, 100 and 120 °C. The control treatment consisted of untreated seeds, which were used as collected without scarification or soaking.

Following treatment, seeds were lightly dusted with copper sulfate fungicide and placed in Petri dishes containing moist cotton covered with filter paper (Sanhueza and Zalba 2012). Dishes were maintained in a germination chamber under a 12-hour light / 12-hour dark photoperiod, with temperatures of 23 °C during the day and 18 °C at night, and ~80% relative humidity. Seeds were watered every two days, and germination was assessed at each watering event for 38 days. At each inspection, germinated seeds were counted and removed. Germination was defined by radicle emergence. The experiment was terminated when no additional germination was recorded during

ten consecutive observation periods. After radicle emergence, seedlings were removed from the dishes to prevent overcrowding and fungal contamination, which could affect the germination of the remaining seeds (Davies et al. 2015).

Effects of seed persistence in the soil on germination

Germination tests were conducted to compare seeds collected directly from randomly selected reproductive plants (plant seeds, PS) with seeds extracted from soil and litter samples collected for the seed bank assessment (soil seeds, SS).

For each species, 20 Petri dishes were prepared, ten containing PS and ten containing SS. Each contained a layer of cotton covered with filter paper and 20 seeds. Both PS and SS were germinated under the same controlled conditions described above for the heat treatment experiments, including photoperiod (12 h light/12 h dark), temperature (23 °C day / 18 °C night), relative humidity (~80%), watering regime (every two days) and monitoring period (38 days). Germination was assessed using the same criterion: radicle emergence was considered as germination and seedlings were removed upon emergence (Sanhueza and Zalba 2012).

Effects of water availability on seedling performance

For each species, 90 seeds were sown individually in 800 cm^3 plastic cups (one seed per cup). The cups were perforated at the base to allow water drainage and filled with a commercial horticultural substrate commonly used for nursery plant production. Prior to sowing, seeds were scarified with fine sandpaper to promote germination (Sanhueza 2012). All cups received the same irrigation regime (150 mL every other day) until cotyledon emergence, ensuring adequate soil moisture while preventing water accumulation on the surface. A total of 105 seedlings (47 FB and 58 SB) developed cotyledons and were individually transplanted into 800 cm^3 pots. Each seedling was randomly assigned to one of three irrigation treatments (108, 150 or 224 mL), applied three times per week. Each pot containing a single seedling constituted one experimental unit. Seedling growth and survival were monitored throughout the experiment. The irrigation represents low, intermediate and high water availability, respectively, considering the high interannual variability in average precipitation at the study site (annual maxima of 1056 mm and minima of 396 mm) (Gil and Campo de Ferreras 2006). Seedling survival, height (measured from the stem base to the apical meristem) and number of leaves were monitored every 15 days from October to December.

Data analysis

The statistical analyses were structured to evaluate each of the predictions derived from the study hypothesis. Unless otherwise indicated, all analyses were performed in R version 4.1.3 (R Core Team 2025). Assumptions of normality and homogeneity of variances were evaluated prior to each analysis. When these assumptions were not met, non-parametric procedures were applied.

To evaluate differences in reproductive phenology and propagule production between species, normality was assessed using the Shapiro-Wilk test. Most reproductive variables deviated significantly from normality ($P<0.05$), with the exception of the number of reproductive branches ($P=0.7319$) and seeds per pod ($P=0.0619$) in SB. Given the lack of consistent normality across variables and species, all reproductive traits were compared using Wilcoxon rank-sum tests (Mann-Whitney U tests). Variables analyzed included the number of reproductive branches, pods per branch, pod length, seeds per pod and estimated seed production per plant. Median values and interquartile ranges (IQR) are reported. Estimated seed production per plant was calculated as the product of the number of reproductive branches, the mean number of pods per branch and the mean number of seeds per pod. Relationships between pod number and both stem diameter and plant height were evaluated using correlation analyses To estimate the contribution of annual seed rain to soil seed bank replenishment, seed density (seeds/m^2) was compared within each species before and after the annual seed-release period using paired t-tests. To evaluate the effects of fire-related heat treatments on seed germination three response variables were calculated: final germination percentage (%G), mean germination time (T50) (Travlos et al. 2009) and germination rate (GR) (López et al. 1999). Generalized linear models (GLM) were fitted with species, heat treatment and their interactions as fixed factors. Germination percentage was analyzed using a binomial error distribution with a logit link function,

whereas germination rate and T50 were analyzed using gamma error distribution with log link. When significant effects were detected, post-hoc comparisons were performed using Dunnett's test, comparing each treatment with the corresponding control within each species. To assess whether seed persistence affected germination capacity, germination responses of fleshy collected seeds (plant seeds, PS) and seeds recovered from the soil seed bank (soil seeds, SS) were compared using generalized linear models including Species, Seed source and their interaction as fixed factors. Germination percentage was analyzed assuming a binomial distribution, whereas germination rate was analyzed using a gamma distribution. Significant effects were explored using Tukey's post hoc tests. Mean germination time (T50) was calculated only for replicates reaching at least 50% germination and, because this criterion was met by relatively few replicates, particularly among soil seeds, T50 was not included in the statistical analyses. Finally, to evaluate species differences in seedling performance under contrasting water availability, repeated measurements of survival, plant height and leaf number were analyzed using linear mixed-effects models (LMM). Plant identity was included as a random effect to account for repeated observations, whereas Species, Irrigation treatment, Sampling date and their interactions were included as fixed effects. When significant effects were detected, pairwise comparisons among irrigation treatments within each species were performed using Tukey's test.

All statistical analyses and graphical outputs were performed using the R packages: car (Fox and Weisberg 2019), dplyr (Wickham et al. 2025a), ggplot2 (Wickham 2016), tidyr (Wickham et al. 2025b), emmeans (Lenth 2025), lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017).

Results

Assessment of reproductive phenology and seed production

Reproductive phenology showed different temporal patterns between SB and FB. In FB, flowering decreased progressively from 50% on 15 October to 0% by 17 December. Meanwhile, pod development increased steadily over the same period, from 50% on 15 October to 100% by 17 December. In SB, flowering increased rapidly to 100% by 12 November and remained high (80-90%) thereafter, whereas pod production remained low throughout the study period, reaching a maximum of only 20% by 17 December.

No significant difference was detected in the number of reproductive branches between the species (Wilcoxon rank-sum test, P=0.14). However, significant differences were detected for pods, pod length and seeds per pod (P<0.001 for all). FB produced more pods (median: 622.5 vs. 101.0), whereas SB had longer pods (median: 6.4 cm vs. 2.2 cm) and more seeds per pod (median: 10.0 vs. 5.0) (Table 1).

Seed production per plant was significantly higher in FB (median=71370, IQR=27300-189924) than in SB (median=18018, IQR=7440-25916; Wilcoxon rank-sum test, W=359, P<0.001). No significant correlations were found between pod production and either plant height or stem diameter in either species. For FB: height (r=0.2834, gl=33, P=0.102), stem diameter (r=0.3290, gl=33, P=0.055). For SB: height (r=0.1236, gl=23, P=0.558), stem diameter (r=0.2241, gl=23, P=0.284). Estimated seed production per plant was subsequently used to interpret differences in the annual contribution of propagules (seed rain) to the soil seed bank.

Table 1. Reproductive traits of French broom (*G. monspessulana*, n=35) and Spanish broom (*S. junceum*, n=25) at Ernesto Tornquist Provincial Park, Buenos Aires Province, Argentina. Values represent medians and P-values derived from Wilcoxon rank-sum test (Mann-Whitney U test).

Tabla 1. Características reproductivas de la retama francesa (*G. monspessulana*, n=35) y la retama española (*S. junceum*, n=25) en el Parque Provincial Ernesto Tornquist, provincia de Buenos Aires, Argentina. Los valores representan las medianas. Los valores P se derivaron de la prueba de Wilcoxon (Mann-Whitney).

Variable	French broom median	Spanish broom median	P-value
Seed production per plant	71370	18018	0.001
Reproductive branches per plant	20	15	0.1401
Pods per plant	622.5	101	0
Pod length	2.2	6.4	0
Seeds per pod	5	10	0

Analysis of the soil seed bank

To estimate the contribution of annual seed rain, seed bank density was compared before and after the annual seed-release period.

Comparisons between species showed that before seed dispersal, seed density was significantly higher beneath FB stands (10545.63±441.94 vs. 247.92±51.56 seeds/m², P=0.0006). Within each species, seed density increased significantly after seed dispersal relative to pre-dispersal values (FB: 21646.83±4194.94 seeds/m² representing a ~2-fold increase, P=0.0009; SB: 968.75±75.13 seeds/m² representing a ~4-fold increase, P=0.00005). Following seed dispersal, seed density remained significantly higher in FB-invaded sites than in SB-invaded sites (P=0.00001).

Effects of fire-related heat treatments on seed germination

The GLM analysis revealed significant effects of Species, Treatment and their interaction on all germination variables. For germination percentage, germination rate and T50, the Species × Treatment interaction was highly significant (P<0.001 for all), indicating that the response to pre-germination treatments differed between FB and SB across all variables (Table 2).

In SB, the highest germination percentages (100%) were observed following exposure to dry heat at 100 °C and 120 °C, as well as moist heat at 100 °C for 1 and 5 minutes, all significantly higher than the control (48.57±2.37%, P<0.05). The germination rate was significantly higher than the control (0.73±0.06 seeds/day) for most heat treatments, with the highest rate recorded under moist heat at 100 °C for 5 minutes (3.15±0.14 seeds/day, P<0.05). Similarly, T50 was significantly reduced by dry heat at 80 °C and 100 °C, and by moist heat at 100 °C (1 and 5 minutes), with the shortest mean germination time observed under moist heat at 100 °C for 5 minutes (6.83±1.04 days vs. 33.0±2.04 days in the control, P<0.05) (Table 3, Figure 1).

In FB, the highest germination percentage (100%) was achieved after dry heat at 120 °C, which was significantly higher than the control (25.0±3.45%, P<0.05). Most dry and moist heat treatments also significantly increased germination percentage compared to the control, with the exception of moist heat at 20 °C (22.86±3.91%, not significant, P>0.05). Germination rate was significantly enhanced by dry heat at 80 °C, 100 °C, and 120 °C, and by moist heat at 100 °C for 1 and 5 minutes, compared to the control (0.33±0.05 seeds/day, P<0.05). The highest rate was recorded under moist heat at 100 °C for 5 minutes (1.42±0.14 seeds/day, P<0.05). In contrast, neither moist heat at 20 °C (0.23±0.04 seeds/day) nor moist heat at 45 °C (0.50±0.09 seeds/day) differed significantly from the control. Regarding T50, unlike SB, significant reductions were only observed for dry heat at 80 °C, 100 °C, and 120 °C, and for moist heat, at 100 °C for 1 and 5 minutes, compared to the control (37.84±0.16 days), with the shortest T50 recorded under moist heat at 100 °C for 5 minutes (15.44±2.0 days, P<0.05) (Table 3, Figure 1).

Table 2. Statistical parameters from generalized linear models (GLM) for germination percentage, germination rate and T50. Chi-square (χ^2) values are reported for germination percentage (binomial error distribution), F-values for germination rate and T50 (gamma error distribution). All effects were significant at P<0.05. df=degrees of freedom.

Tabla 2. Parámetros estadísticos de los modelos lineales generalizados (GLM) para el porcentaje de germinación, la tasa de germinación y el T50. Se reportan valores de chi-cuadrado (χ^2) para el porcentaje de germinación (distribución binomial), valores de F para la tasa de germinación y T50 (distribución gamma). Todos los efectos fueron significativos (P<0.05). df=grados de libertad.

Variable	Effect	Statistic	df	P
Germination (%)	Species	65.36	1	<0.001
Germination (%)	Treatment	853.7	8	<0.001
Germination (%)	Species:Treatment	68.26	8	<0.001
Germination rate	Species	175.26	1	<0.001
Germination rate	Treatment	57.72	8	<0.001
Germination rate	Species:Treatment	6.73	8	<0.001
T50	Species	35.92	1	<0.001
T50	Treatment	51.58	8	<0.001
T50	Species:Treatment	8.2	8	<0.001

Table 3. Germination parameters (mean±SE) and significance of each treatment compared to the control (Dunnett's test) for French broom *(G. monspessulana*) and Spanish broom (*S. junceum*). Asterisks indicate significant differences from the control within each species (P<0.05). ns=not significant.

Tabla 3. Parámetros de germinación (media±EE) y significancia de cada tratamiento comparado con el control (prueba de Dunnett) para retama francesa (*G. monspessulan*a) y retama española (*S. junceum*). Los asteriscos indican diferencias significativas con respecto al control dentro de cada especie (P<0.05). ns=no significativo.

Species	Treatment	n	Germination	Rate	T50
French broom	Control	7	25±3.45	0.33±0.05	37.84±0.16
French broom	Dry 45	7	50±4.76 *	0.52±0.05 *	31.37±2.21 ns
French broom	Dry 80	7	88.57±2.83 *	0.91±0.03 *	20.47±0.58 *
French broom	Dry 100	7	81.43±4.72 *	0.86±0.06 *	22.91±1.61 *
French broom	Dry 120	7	100±0 *	1.09±0.04 *	19.27±1.22 *
French broom	Moist 20	7	22.86±3.91 ns	0.23±0.04 ns	36.86±1.14 ns
French broom	Moist 45	7	51.43±8 *	0.5±0.09 ns	33.29±2.77 ns
French broom	Moist 100 (1)	7	75.71±5.17 *	1.08±0.14 *	20.03±1.74 *
French broom	Moist 100 (5)	7	95±3.45 *	1.42±0.14 *	15.44±2 *
Spanish broom	Control	7	48.57±2.37	0.73±0.06	33±2.04
Spanish broom	Dry 45	7	51.43±4.59 ns	0.74±0.06 ns	33.42±1.94 ns
Spanish broom	Dry 80	7	91.43±3.03 *	1.44±0.11 *	15.23±1.01 *
Spanish broom	Dry 100	7	100±0 *	1.56±0.1 *	13.53±1.55 *
Spanish broom	Dry 120	7	100±0 *	1.05±0.06 ns	20.85±1.6 *
Spanish broom	Moist 20	7	54.29±4 ns	0.83±0.07 ns	32.11±1.99 ns
Spanish broom	Moist 45	7	72.86±5.86 *	0.96±0.11 ns	24±2.92 ns
Spanish broom	Moist 100 (1)	7	100±0 *	2.44±0.15 *	8.82±0.58 *
Spanish broom	Moist 100 (5)	7	100±0 *	3.15±0.14 *	6.83±1.04 *

In interspecific comparisons, SB consistently exhibited higher germination performance than FB across most variables. Under control conditions, SB showed significantly higher germination percentage, germination rate and a significantly shorter T50. Following heat treatments that promoted germination (e.g., moist heat at 100 °C for 5 minutes), SB reached higher germination rates than FB (3.15±0.14 vs. 1.42±0.14 seeds/day) and achieved a shorter T50 (6.83±1.04 vs. 15.44±2.0 days). Notably, while both species reached 100% germination under certain treatments (dry heat at 120 °C for FB; dry heat at 100 °C and 120 °C and moist heat at 100 °C for SB), SB achieved this with a broader range of treatments and faster germination rates, suggesting a broader and faster germination response to fire-related heat cues.

Effects of seed persistence in the soil on germination

Both germination percentage and germination rate were significantly affected by Species and Seed Source (P<0.001 for all), while the interaction between these factors was not significant for either variable (P>0.05) (Table 4), indicating a consistent reduction in germination associated with soil persistence in both species.

Germination percentage was significantly higher for plant seeds than for soil seeds in both species: SB (46.5±3.42% vs. 17.5±3.10%)

Table 4. Statistical parameters from generalized linear models for germination percentage (χ^2, binomial error distribution) and germination rate (F, gamma distribution) of plant seeds and soil seeds for *G. monspessulana* and *S. junceum*. Significant effects (P<0.05) are indicated in bold. df=degrees of freedom.

Tabla 4. Parámetros estadísticos de los modelos lineales generalizados para el porcentaje de germinación (χ^2, distribución binomial) y la tasa de germinación (F, distribución gamma) de semillas de las plantas vs. semillas del banco del suelo para *G. monspessulana* y *S. junceum*. Los efectos significativos (P<0.05) se indican en negrita. df=grados de libertad.

Variable	Effect	Statistic	df	P
Germination (%)	Species	3618	1	<0.001
Germination (%)	SeedSource	6612	1	<0.001
Germination (%)	Species:SeedSource	29	1	**0.592**
Germination rate	Species	4779	1	<0.001
Germination rate	SeedSource	2795	1	<0.001
Germination rate	Species:SeedSource	31	1	**0.579**

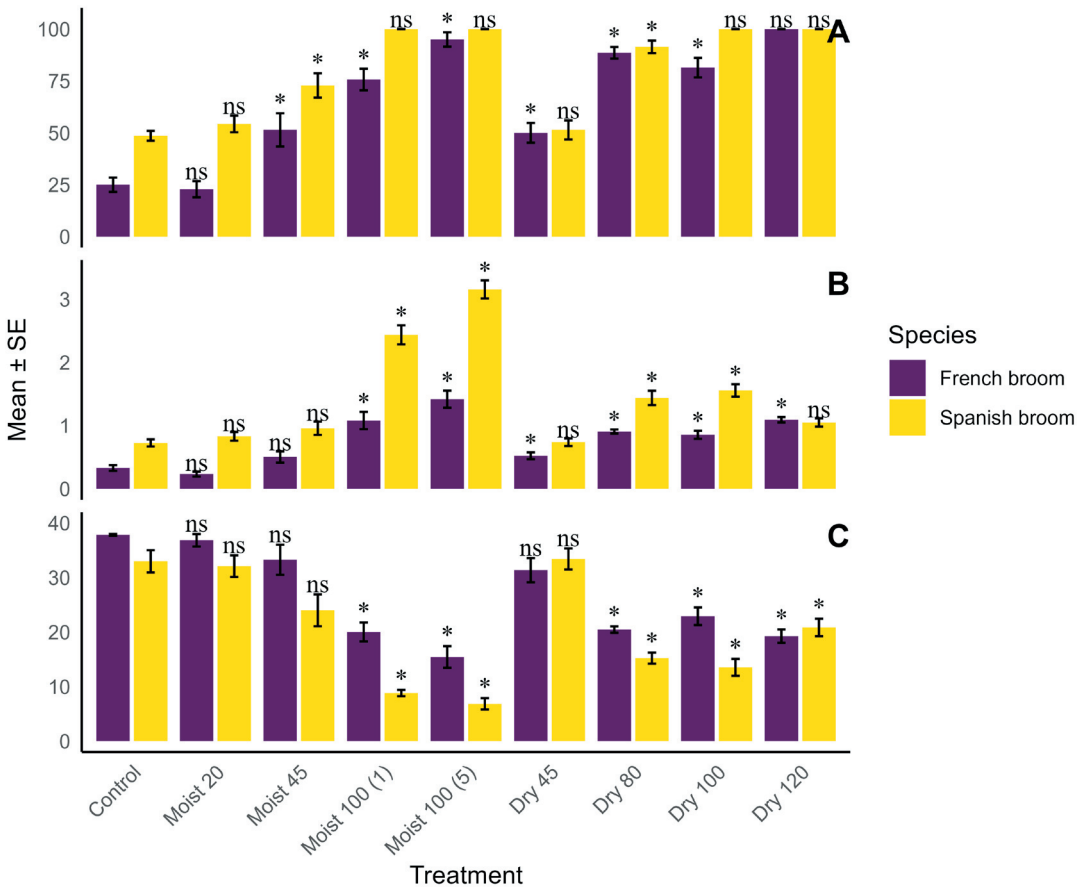

Figure 1. Germination parameters (mean±SE) of French broom (*G. monspessulana*) and Spanish broom (*S. junceum*) invading Ernesto Tornquist Provincial Park (Buenos Aires province, Argentina) exposed to moist and dry pre-germination heat treatments simulating soil temperatures during fires. A) Germination percentage. B) Germination rate. C) Mean germination time (T50). Asterisks indicate significant differences from the control within each species (Dunnett's test, P<0.05). ns=not significant.

Figura 1. Parámetros de germinación (media±EE) de retama francesa (*G. monspessulana*) y retama española (*S. junceum*) en el Parque Provincial Ernesto Tornquist, provincia de Buenos Aires, Argentina, expuestas a tratamientos de calor húmedo y seco previos a la germinación, simulando temperaturas del suelo durante incendios. A) Porcentaje de germinación. B) Tasa de germinación. C) Tiempo medio de germinación (T50). Los asteriscos indican diferencias significativas con respecto al control dentro de cada especie (prueba de Dunnett, P<0.05). ns=no significativo.

and FB (23.0±4.29% vs. 5.5±1.17%) (Figure 2A). Germination rate followed a similar pattern, with plant seeds germinating faster than soil seeds in both species: SB (1.01±0.09 vs. 0.44±0.08 seeds/day) and FB (0.30±0.07 vs. 0.10±0.02 seeds/day) (Figure 2B). In both plant- and soil-derived seeds, SB consistently showed higher germination percentage than FB (plant seeds: 46.5±3.42% vs. 23.0±4.29%; soil seeds: 17.5±3.10% vs. 5.5±1.17%, P<0.05 in both cases) (Table 5, Figure 2).

Although T50 was not statistically analyzed due to insufficient replicates reaching 50% germination, descriptively FB tended to take longer to germinate than SB from plant-derived seeds (32.51±8.98 vs. 19.63±6.92 days). Interestingly, soil-derived seeds showed the opposite trend, with FB reaching T50 faster than SB (10.2±4.69 vs. 15.96±12.27 days).

Effects of water availability on seedling performance

Both species exhibited strong growth responses to water availability, and the overall pattern of these responses was consistent across species. Plant height and leaf production increased significantly over time in both species (Day effect height: $F_{6,681}$=441.03,

Table 5. Germination parameters (mean±SE) of plant seeds (PS) and soil seeds (SS) for French broom (*G. monspessulana*) and Spanish broom (*S. junceum*). Different letters within each variable indicate significant differences among groups (Tukey's test, P<0.05). n=number of replicates per treatment.

Tabla 5. Parámetros de germinación (media±EE) de semillas de planta (PS) y semillas del banco de suelo (SS) para retama francesa (*G. monspessulana*) y retama española (*S. junceum*). Letras distintas dentro de cada variable indican diferencias significativas entre grupos (prueba de Tukey, P<0.05). n=número de réplicas por tratamiento.

Species	SeedSource	n	Germination (%)	Germination rate
French broom	PS	10	23±4.29 b	0.303±0.07 b
French broom	SS	10	5.5±1.17 a	0.0969±0.02 a
Spanish broom	PS	10	46.5±3.4 c	1.0123±0.09 c
Spanish broom	SS	10	17.5±3.09 b	0.4366±0.08 b

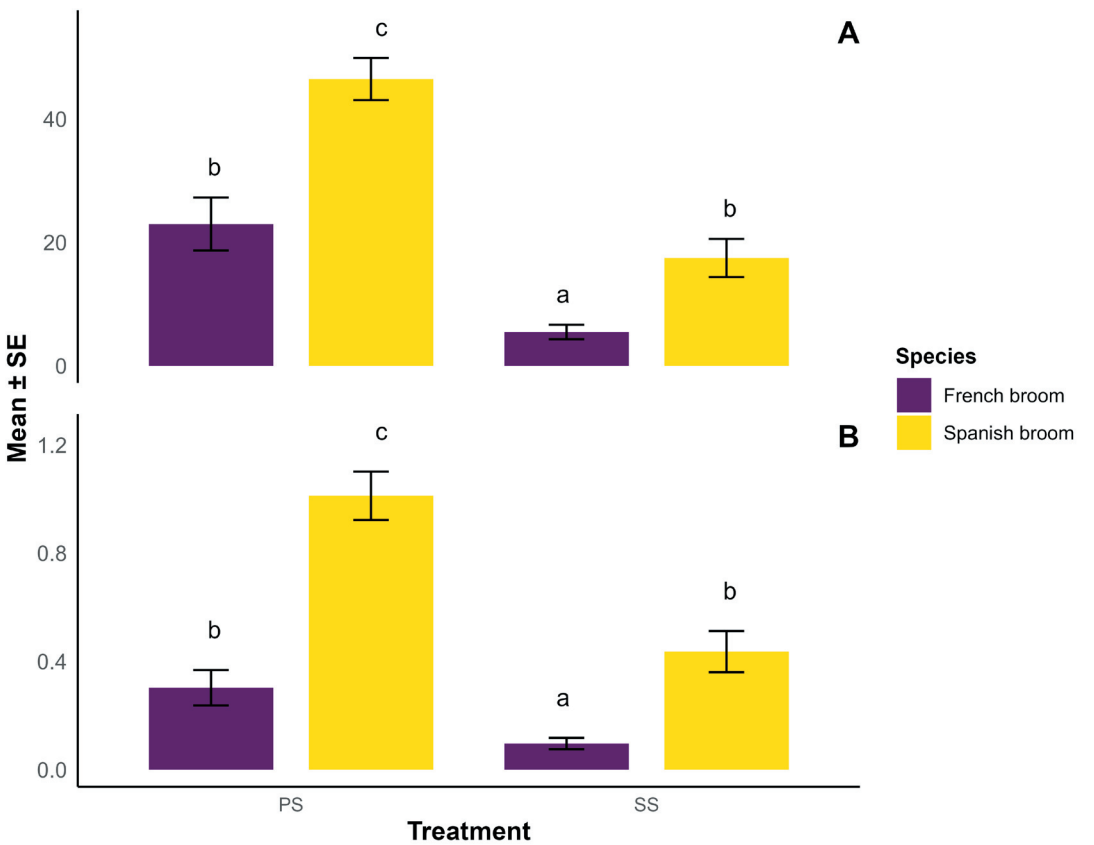

Figure 2. Germination percentage (A) and germination rate (B) (mean±SE) of French broom (*G. monspessulana*) and Spanish broom (*S. junceum*) seeds collected directly from plants (PS) and from the soil seed bank (SS). Bars show mean values±SE. Different letters indicate significant differences among groups within each variable (Tukey's test, P<0.05).

Figura 2. Porcentaje (A) y tasa (B) de germinación (media±EE) de semillas de retama francesa (*G. monspessulana*) y retama española (*S. junceum*) recolectadas directamente de plantas (PS) y del banco de semillas del suelo (SS). Las barras representan la media±EE. Letras distintas indican diferencias significativas entre grupos dentro de cada variable (prueba de Tukey, P<0.05).

P<0.0001; leaves: $F_{6,674}$=444.49, P<0.0001), and water stress had a pronounced negative effect on growth (Treatment effect height: $F_{2,684}$=34.07, P<0.0001; leaves: $F_{2,677}$=80.07, P<0.0001).

No significant Species × Treatment interactions were detected for either trait (height: $F_{2,684}$=0.5, P=0.61; leaves: $F_{2,677}$=1.57, P=0.21), indicating that both species responded similarly to water limitation. Nevertheless, SB exhibited consistently higher values than FB throughout the experiment, both in terms of height ($F_{1,699}$=53.43, P<0.0001) and leaf production ($F_{1,691}$=204.24, P<0.0001). The

negative effect of water stress was evident in both species: for FB, plants under low irrigation showed significantly reduced height compared to those under high irrigation (estimate=2.37, t=4.90, P<0.0001). Height was also significantly lower under medium irrigation compared with high irrigation (estimate=1.97, t=4.15, P=0.0001), whereas low and medium irrigation did not differ significantly from each other (estimate=0.40, t=0.83, P=0.68). Similarly, leaf production in FB was significantly reduced under low irrigation relative to high irrigation (estimate=2.86, t=7.42, P<0.0001). Leaf production was also significantly lower under medium irrigation compared with high irrigation (estimate=2.99, t=7.90, P<0.0001), whereas low and medium irrigation did not differ significantly from each other (estimate=0.14, t=0.36, P=0.93). At the end of the experiment, FB plants under high irrigation reached a mean height of 21.4±0.93 cm and had produced 18.7±1.08 leaves on average.

SB showed a similar pattern, with low irrigation significantly reducing height compared to high irrigation (estimate=2.81, t=6.39, P<0.0001) and medium irrigation (estimate=1.04, t=2.37, P=0.047); additionally, medium irrigation also resulted in significantly reduced height relative to high irrigation (estimate=1.77, t=4.16, P=0.0001). For leaf production, low irrigation similarly yielded significantly fewer leaves than both high irrigation (estimate=2.09, t=5.95, P<0.0001) and medium irrigation (estimate=0.98, t=2.79, P=0.015). Additionally, medium irrigation also produced significantly fewer leaves than high irrigation (estimate=3.07, t=9.07, P<0.0001). Under high irrigation, SB reached

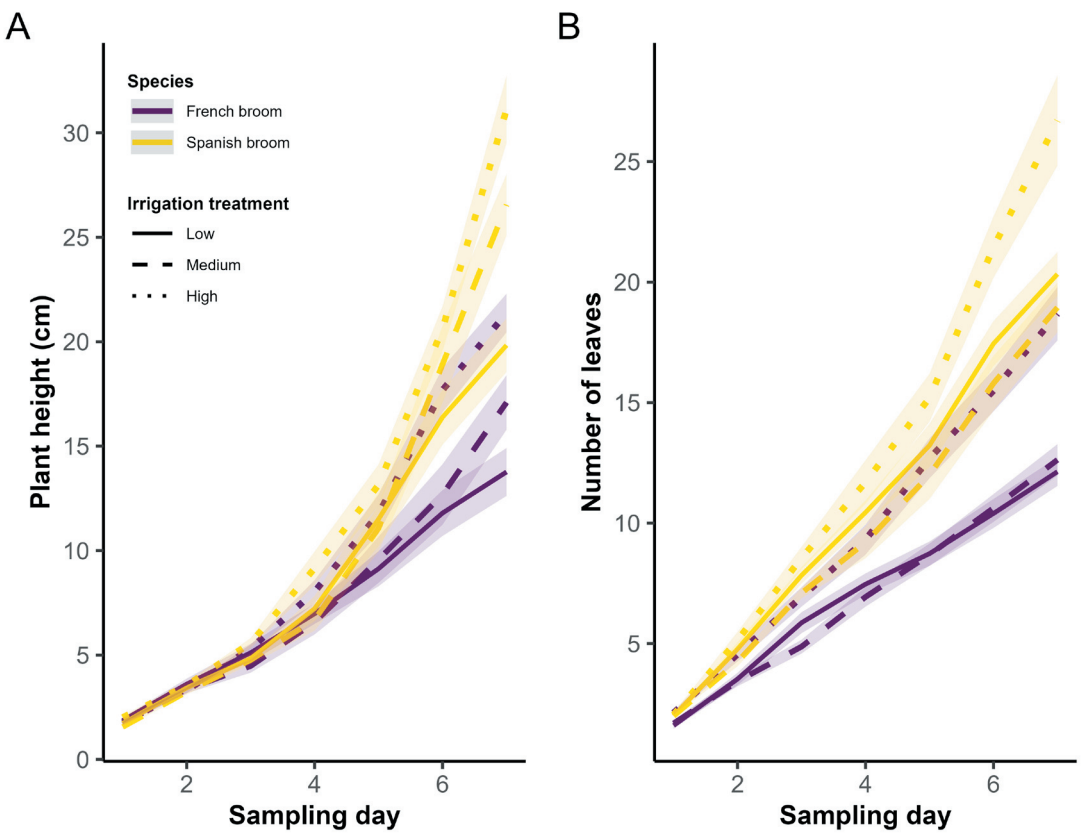

Figure 3. Plant growth parameters (mean±SE) of French broom (*G. monspessulana*) and Spanish broom (*S. junceum*) under three irrigation treatments (Low, Medium, High). A) plant height (cm). B) Number of leaves across sampling days. Line color indicates species and line type indicates irrigation treatment.

Figura 3. Parámetros de crecimiento (media±EE) de retama francesa (*G. monspessulana*) y retama española (*S. junceum*) bajo tres tratamientos de riego (Bajo, Medio, Alto). A) Altura de la planta (cm). B) Número de hojas a lo largo de los días de muestreo. El color de la línea indica la especie y el tipo de línea indica el tratamiento de riego.

a mean height of 31.1±1.62 cm and produced 26.7±1.82 leaves by the end of the experiment (Figure 3).

Discussion

Understanding the characteristics that modulate the expansion capacity of an invasive species is a key tool for preventing new invasions and establishing control priorities. Our study revealed several features that help explain the more rapid expansion of *G. monspessulana* compared to *S. junceum* in grasslands of the Southern Pampas of Argentina, where FB has progressively displaced SB as the dominant woody invader during the last decades. Consistent with our hypothesis, FB combined a suite of reproductive traits that together increased propagule pressure and enhanced opportunities for post-disturbance recruitment. FB produced almost six times more seeds per plant and accumulated a soil seed bank approximately five times denser than SB. Although both species retained the ability to germinate after being stored in the soil, FB's much larger seed bank size made this trait more impactful for population buildup over time. Both species also responded well to heat treatments mimicking fire; however, FB maintained high germination percentages (up to 93%) and faster germination even after intense dry heat (120 °C), which may be crucial for post-fire regeneration. In addition, FB initiated reproduction approximately one month earlier than SB, potentially increasing the likelihood of successful seed maturation before the onset of the summer fire season. These findings provide a mechanistic explanation for the marked increase in FB dominance observed after the large wildfires that affected the study area in 2008 and 2013, which originally motivated this study.

The higher seed production of FB compared to SB is a key factor underlying its greater expansion capacity. Elevated fecundity translates directly into increased propagule pressure, a well-established predictor of invasion success (Lockwood et al. 2005). A larger seed rain increases the likelihood that some propagules will find safe sites for establishment despite stochastic losses due to predation, competition, or unfavorable microsite conditions (Cassey et al. 2018). This may allow FB to colonize newly opened patches and recover more rapidly following disturbances, thereby reinforcing its dominance over SB. Unfortunately, direct comparisons with native woody species are difficult because the Pampas grasslands are dominated by perennial grasses and herbaceous species, with very few native shrubs. The few woody native species occurring in the region, such as *Discaria americana* (Rhamnaceae) and *Schinus longifolius* (Anacardiaceae), are phylogenetically and functionally distinct from the invasive brooms, differing markedly in growth form, reproductive biology and regeneration strategies. Consequently, meaningful comparisons of reproductive output and seed-bank dynamics are currently not feasible. Rather than competing with ecologically equivalent native shrubs, FB invades an ecosystem largely lacking native woody species with comparable life-history strategies, a circumstance that may further facilitate its establishment and expansion.

Differences in seed persistence and viability further reinforce FB's competitive advantage. Persistent seed banks allow species to distribute recruitment over time, thus mitigating the risks of unfavorable years and providing a long-term reservoir of viable propagules (Gioria et al. 2021). Buried propagules act as long-term reservoirs for regeneration, enabling repeated recruitment events over time and allowing populations to recover even after aboveground individuals are removed through disturbance or control measures (Holmes and Newton 2004; Moravcová et al. 2022). In the Pampas grasslands, the large seed bank of FB likely plays a decisive role in ensuring population resilience and expansion.

The germination responses of both species to heat treatments indicate adaptation to fire-related cues, although their responses differed in magnitude and consistency. Both species possess physically dormant seeds whose dormancy can be broken by heat shock (Moreira and Pausas 2012), a characteristic widely associated with persistence in fire-prone Mediterranean ecosystems. FB maintained high germination percentages under the most intense dry-heat treatment (120 °C), whereas SB reached maximum germination across a broader range of dry- and moist-heat treatments. The contrasting responses to dry and moist heat are noteworthy because these treatments simulate different thermal environments that seeds may experience during or after fire. Dry heat generally produced stronger germination responses in FB, whereas SB responded positively to both heat types, suggesting differences in the mechanisms by which dormancy is

released. Because seed viability was not independently assessed after the treatments, we cannot determine whether the lower germination observed following some moist-heat treatments reflects incomplete dormancy release, heat-induced embryo mortality, the induction of secondary dormancy, or other physiological responses. Consequently, our results should be interpreted as evidence of contrasting germination responses rather than definitive evidence of differences in post-fire seed survival. Nevertheless, the ability of FB to maintain high germination after exposure to extreme dry heat suggests that this species may be particularly well adapted to exploit severe post-fire conditions, where soil temperatures can be high and competition from established vegetation is greatly reduced (He et al. 2019). The rapid expansion of FB following the 2008 and 2013 wildfires in Ernesto Tornquist Provincial Park is therefore consistent with fire acting as a selective ecological filter favoring FB over SB.

Phenological differences may also contribute to SB's displacement. FB began flowering roughly one month earlier than SB, granting it a temporal advantage in resource acquisition and reproduction. Early flowering enhances the competitive impact of invasive species, enabling them to secure resources and establish seedlings before later-flowering competitors (Alexander and Levine 2019). FB reached maximum pod production sooner than SB, allowing seed maturation and dispersal to occur under favorable climatic conditions. Rainfall in the Ventania Mountains is highly seasonal. The region has a temperate to subhumid climate with most of the rain concentrated in spring and late summer/early fall, and monthly rainfall usually peaking in October-November, although with significant year-to-year variations (Gil and Campo de Ferreras 2006). The peak of pod-set in FB coincides with the typical period of most intense rainfall, potentially freeing its seeds from the environmental limitation that low soil moisture can represent and facilitating germination and seedling establishment. In fire-prone systems, on the other hand, such early phenology could be especially advantageous: FB may complete seed production before summer fires, augmenting its reproductive output. Our observations were limited to the early reproductive phase and therefore do not allow us to compare the overall duration of flowering or fruiting between species. Nevertheless, they clearly demonstrate that FB initiated flowering and pod development earlier than SB under the environmental conditions of the study area. Thus, although SB may maintain reproductive activity for a longer period, the earlier onset of reproduction in FB may still confer an ecological advantage by allowing seed maturation before the onset of summer drought and prior to late-season fires.

Finally, the two species exhibited broadly similar responses to reduced water availability. In both species, growth declined under reduced irrigation, although the pattern of decline differed slightly. FB exhibited similar growth under low and medium irrigation, whereas SB showed a more gradual reduction across decreasing water availability. These contrasting response patterns may reflect subtle differences in growth plasticity, but they provide little evidence for meaningful differences in drought tolerance between species. Consequently, water availability alone is unlikely to explain the greater invasion success of FB, which is more consistently associated with its substantially higher reproductive output, larger persistent seed bank, earlier reproductive phenology and strong post-fire regeneration.

Taken together, these attributes: high reproductive output, a dense and persistent seed bank, greater tolerance to fire-related heat, earlier flowering and massive flower and pod production, could be acting synergistically to promote the rapid spread and dominance of FB over SB in the grasslands of the Southern Pampas. They also underscore the multifaceted nature of the invasion's success, which is not driven by a single trait but by a set of interacting characteristics that together create a strong demographic advantage.

One limitation of this study is that the datasets for the two species were generated during different research projects conducted over different years rather than as a single coordinated experiment. Consequently, temporal variation in environmental conditions cannot be completely excluded as a potential confounding factor. However, the variables compared here represent fundamental life-history traits, including reproductive investment, seed-bank formation, germination responses and seedling performance, that are generally considered species-specific characteristics and are therefore expected to be less sensitive

to interannual environmental variation than demographic parameters such as population size or recruitment. Accordingly, we interpret the consistent differences observed across multiple independent traits as evidence of contrasting invasion strategies rather than as artifacts of sampling year. The integration of datasets from different years also reflects the natural history of the invasion process in the study area, where the replacement of SB by FB occurred progressively over time; this ongoing process motivated the present comparative analysis. Nevertheless, future studies evaluating both species simultaneously under identical environmental conditions would provide an important opportunity to further validate these conclusions.

Our results demonstrated that the recent replacement of SB by FB in the Pampas grasslands is best explained by the interaction of multiple demographic processes acting throughout the life cycle rather than by a single dominant trait. FB combined exceptionally high reproductive output, rapid accumulation of persistent soil seed banks, earlier reproductive onset and strong post-fire recruitment potential, creating a cumulative demographic advantage that is likely to accelerate population growth and landscape-scale spread. More generally, this study highlights the value of comparing closely related invasive species occupying the same environment as a powerful natural experiment for identifying the ecological mechanisms underlying differential invasion success while minimizing environmental variation. Such comparative approaches may improve our ability to anticipate which invasive species are most likely to become dominant following disturbance and therefore deserve the highest management priority.

FB clearly represents a particularly challenging invader once established. Based on our results, effective control of FB should focus primarily on preventing seed production and progressively depleting the persistent soil seed bank. Repeated removal of reproductive individuals before pod maturation is likely to provide the greatest long-term reduction in propagule pressure. Because FB maintains a large and persistent seed bank and exhibits strong recruitment following fire-related heat exposure, fire management should be accompanied by systematic post-fire monitoring and rapid removal of newly emerged seedlings to prevent massive recruitment events. Likewise, early detection and eradication of newly established populations outside currently invaded areas should remain a regional priority, since interventions conducted before substantial seed-bank accumulation are expected to be considerably more effective and cost-efficient than attempting to control well-established infestations. Together, these actions provide an integrated management strategy directly supported by the demographic mechanisms identified in this study and may contribute to limiting the continued expansion of FB throughout the Southern Pampas and other Mediterranean-type ecosystems invaded by this species.

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