Do not come late to the party: initial success of nonnative species is contingent on timing of arrival of co-occurring nonnatives

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Abstract Invasions by multiple nonnative species threaten native communities worldwide. We know that interactions among nonnative species influence nonnative success. However, we know relatively less about the influence of community assembly history on the interactions within nonnative species and thereby invasion success. To investigate this, we transplanted seedlings of two highly invasive shrubs, *Rosa rubiginosa* (hereafter 'rose') and *Cytisus scoparius* (hereafter 'broom')*,* at two different times into mesocosm communities of native and nonnative species. We conducted priority and delay treatments that consisted of the early and late arrival of the invasive shrubs, respectively. We gave full priority/delay to each invasive shrub (rose early/late arrival, broom early/late arrival) and simultaneous priority/delay (simultaneous early/late arrival). We predicted that if assembly history were important, the invasive shrubs will benefit from early-arriving and will be disadvantaged by late-arriving and that arriving before the co-invader shrub will be more beneficial than arriving before the rest of the community. We also predicted that assembly history treatments that gave an advantage to invasive shrubs will more negatively affect native species than nonnative species. We found that the invasive shrubs did not benefit by early-arrival, but they were hindered by the early-arrival of the co-invader. The rose paid a high cost for late-arrival, but the broom was only impaired when its late-arrival implied arriving after the rose. Contrary to our predictions, natives paid a lower cost than nonnatives by arriving late. In general, our mesocosm experiment showed that the success of invasive species depended more on not arriving later than other invaders than on arriving early in the community. We suggest that community assembly history modulates the sign and strength of nonnative species interactions whose consideration might improve management practices.

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Resumen en español *Las invasiones de múltiples especies no-nativas amenazan a las comunidades nativas en todo el mundo. Sabemos que las interacciones entre especies no-nativas influyen en su éxito de invasión. Sin embargo, sabemos relativamente menos sobre la influencia de la historia del ensamble de comunidades en las interacciones entre especies no-nativas y, por lo tanto, en el éxito de invasión. Para investigar esto, trasplantamos plántulas de dos arbustos altamente invasores, Rosa rubiginosa ("rosa") y Cytisus scoparius ("retama"), en dos momentos diferentes en comunidades de mesocosmos de especies nativas y no-nativas. Realizamos tratamientos de prioridad y retraso en la llegada que consistieron en la llegada temprana y tardía de los arbustos invasores, respectivamente. Le dimos prioridad/retraso total a cada especie invasora (llegada temprana/tardía de rosa, llegada temprana/tardía de retama) y prioridad/retraso simultáneo (llegada temprana/tardía simultánea). Predijimos que si la historia de ensamble fuese importante, los arbustos invasores se beneficiarán al llegar temprano y se perjudicarán al llegar tarde, y que llegar antes que el arbusto co-invasor será más beneficioso que llegar antes que el resto de la comunidad. También predijimos que los tratamientos de historia de ensamble que beneficien a los arbustos invasores afectarán más negativamente a las especies nativas que a las no-nativas. Encontramos que los arbustos invasores no se beneficiaron con la llegada temprana, pero se perjudicaron por la llegada temprana del arbusto co-invasor. La rosa pagó un costo alto por llegar tarde, pero la retama solo fue afectada cuando su llegada tardía implicó llegar después de la rosa. Contrariamente a nuestras predicciones, las especies nativas pagaron un costo menor que las especies no-nativas al llegar tarde. En general, nuestro experimento de mesocosmos mostró que el éxito de las especies invasoras dependió en mayor medida de no llegar más tarde que otras especies invasoras que de llegar temprano a la comunidad. Sugerimos que la historia de ensamble modula el signo y la fuerza de las interacciones no-nativas, cuya comprensión puede mejorar las prácticas de manejo.*

Introduction

Multiple nonnative species commonly co-occur in communities worldwide, threatening biodiversity and ecosystem functioning (Kuebbing et al. 2013; Van Kleunen et al. 2015; D'Antonio et al. 2017). Their ability to invade is mainly determined by their ability to establish positive interactions with native and nonnative resident species, and to tolerate or avoid resident's negative interactions (Mitchell et al. 2006; Kuebbing and Nuñez 2016; Pearson et al. 2018). As biotic interactions are commonly shaped by the history of community assembly, particularly the order of species arrival (Drake 1991; Chase 2003; Vannette and Fukami 2014; Fukami 2015), it is possible that the order of nonnative species arrival alters the interaction dynamics among nonnative species, ultimately determining the structure and functioning of multiple-invaded communities.

The order in which species arrive into a community influences community trajectories, having a long-lasting impact on community structure and ecosystem functioning (Chase 2003; Fukami 2015). Early arriving species tend to exhibit an advantage, a priority effect, by controlling size-asymmetric competition (Ejrnæs et al. 2006; Körner et al. 2008; Grman and Suding 2010) and plant-soil feedbacks (Kardol et al. 2007; Grman and Suding 2010). These advantages have been suggested to be greater in invasive species than in native ones (Grman and Suding 2010; Dickson et al. 2012; Young et al. 2015; Yannelli et al. 2020). In addition to arriving early and germinating quickly (Wainwright et al. 2012; Wilsey et al. 2015), invasive species tend to grow faster than native species, reducing resource availability and/or modifying environmental conditions for late-arriving species (Grman and Suding 2010; Van Kleunen et al. 2010; Fukami 2015; Hess et al. 2019). Thus, in invaded communities, priority effects are typically understood in terms of the benefits received by nonnative species over native species. However, in communities invaded by multiple co-occurring nonnative species, priority

effects may be able to shape interactions among nonnatives, ultimately affecting invasion dynamics and the structure of plant communities (D'Antonio et al. 2017).

Resident nonnatives species can strongly influence either positively (facilitation) or negatively (inhibition) the abundance of other nonnative species (Simberloff and Von Holle 1999; D'Antonio et al. 2017). Several studies suggested that early-arriving nonnative species may inhibit late-arriving nonnative species, so that primary invaders increase community resistance to invasion, but their removal would lead to secondary invasions (D'Antonio et al. 2001; Henriksson et al. 2016; Kuebbing and Nuñez 2016). However, early-arriving nonnative species can also facilitate other nonnatives through a wide variety of direct and indirect mechanisms, as proposed by the invasional meltdown hypothesis (Simberloff and Von Holle 1999; Molina-Montenegro et al. 2008; Flory and Bauer 2014; Kuebbing and Nuñez 2016). Therefore, priority effects, both inhibitory and facilitative, can be a fundamental mechanism to understand the accumulation of co-occurring nonnative species in the communities (D'Antonio et al. 2017). Although more and more communities are invaded by multiple nonnative species, there is still no general understanding of how priority effects modulate the accumulation of nonnative species in plant communities.

Most studies on the role of priority effects structuring plant communities are based on above-ground parameters such as biomass, richness or abundance (reviewed by Weidlich et al. 2021). However, a growing body of literature has highlighted the different response of above- and below-ground biomass to priority effects (e.g., Körner et al. 2008; Weidlich et al. 2018). For instance, Weidlich et al. (2018) found that consequences of priority effects remained longer in below- than in above-ground structures. Thus, we may miss important dimensions of priority effects when exploring only above-ground responses. Moreover, if differences in the timing of species arrival occur, one can expect below-ground niche partitioning to occur as a consequence of soil resource preemption and/or niche modification (sensu Fukami 2015) by early-arriving species. Thus, exploring total biomass (root + shoot) and biomass allocation, as we do here, will provide a better understanding of the consequences of different order of arrival of invasive species and provide clues on the relative role of below- vs. above-ground mechanisms determining those consequences.

A central question then is what effect it has on community structure if co-occurring invasive species arrive to the communities at the same time, compared with a more natural situation where there is variability in the timing of arrival of nonnative species. Here, we used a one-year mesocosm experiment to evaluate the influence of the order of arrival of nonnative species on the total biomass and biomass allocation of plant species. We simulated a three-week priority (early-arrival) and delay (late-arrival) in the arrival of two invasive target shrubs in plant communities consisting of six neighbor species (three natives and three nonnatives). We used two widely distributed invasive shrubs in the Patagonian forests, sweetbriar rose (*Rosa rubiginosa,* Rosaceae, hereafter 'rose'*)* and Scotch broom (*Cytisus scoparius*, Fabaceae, hereafter 'broom'), as target species.

We predicted that if the history of community assembly were important, the performance of the target species will vary between early and late arrival treatments; specifically, they will benefit from early arrival and will be disadvantaged by late arrival. Their performance will be strongly influenced by the relative timing of arrival of the co-occurring invasive shrub because invasive species are expected to exert strong priority effects on late-arriving species due to resource preemption. Thus, arriving before the co-invader shrub will be more beneficial than arriving before the rest of the community. Because priority effects of invasive species can strongly hinder native vegetation, we also predicted that assembly history treatments that give an advantage to the target species will reduce the performance of the presumably less competitive native plant neighbors while increasing the performance of nonnative neighbors, as proposed by the invasional meltdown hypothesis. In addition, we explored (1) whether differences in the order of target species affect the biomass allocation of target and nontarget species, and (2) whether these effects were modulated by the biogeographic origin of the species.

Materials and methods

Study system and mesocosm communities

The study was conducted in the northwest of Argentine Patagonia. This region is characterized by a marked East–West precipitation gradient caused by the Andes rain shadow effect, which acts as a barrier to humid air from the Pacific Ocean (Paruelo et al. 1998). Precipitation decreases towards the East from ∼ 3,000 mm to 500 mm per year in 100 km (Jobbágy et al. 1995; Suarez and Kitzberger 2010). Vegetation changes as precipitation decreases; the temperate forests dominated by *Nothofagus spp.,* typical of the more humid places, are replaced by *Austrocedrus chilensis* forests and shrublands (matorral) in the ecotone between the forests and the steppe (Cabrera and Willink 1973). Our mesocosm simulated simplified disturbed communities from the ecotone forest/matorral. In the study region, rainfall is concentrated between April and September and the average annual temperature is 7.9 °C, with maximum temperatures in January and February (Suarez and Kitzberger 2010). The germination and growth pulse of plants occurs during the spring when high availability of water is combined with higher temperatures (Raffaele et al. 2014).

Both target species, the rose and the broom, are frequently associated with disturbed sites such as clearcuts. But they can, although less frequently, invade forest, shrubland, and steppe communities with varying degrees of canopy opening and cover; in some cases driving to monospecific invaded stands, although they co-dominate in some places (Damascos and Gallopin 1992; Bossard and Rejmanek 1994; Torres et al. 2018; Sample et al. 2019). They were introduced from Europe in the nineteenth century for their ornamental value and for their use as living fences and soil stabilizers, while the rose has also been used as food and cosmetics (Koutché 1942; Damascos and Gallopin 1992; Simberloff et al. 2003; Hirsch et al. 2011; Herrera et al. 2016; INBIAR 2021). The rose is a fast growing thorny shrub with deciduous leaves that can reach up to 2 m in height (Damascos and Gallopin 1992). It is a fleshy fruit species that produces abundant fruits and seeds (∼ 20,000 seeds / m^2) and exhibits self-fertilization and apomictic and clonal reproduction, which allows it to rapidly colonize and dominate new sites (Damascos et al. 2004, 2005;

Zimmermann et al. 2010).The rose is an opportunistic shade-intolerant species that frequently colonizes disturbed areas in a wide range of rainfall and in different types of vegetation, with the exception of wetlands or high altitude forests (Damascos and Gallopin 1992). The rose is also characterized by high resistance to hostile conditions (*e.g.,* drought, frost) and high competitive ability (Pierce et al. 2017). On the other hand, the broom is a mesic nitrogen-fixing shrub that grows up to 3 m in height, generally in very dense stands. It has small deciduous leaves and photosynthetic stems (Bossard and Rejmanek 1994). The broom produces abundant seeds and accumulates a large and persistent seed bank (Bossard and Rejmanek 1994). Although most seeds disperse within 1 m of the parent plant, some are expelled as far as 5 m; seeds can also be transported by water and dispersed by animals like ants (Bossard 1991; Fogarty and Facelli 1999). Its seedlings can grow successfully in light regimes ranging from 10% to total incident light (Williams 1981). The broom produces allelophatic compounds that can inhibit the growth of co-occurring species through plant-soil feedbacks (Grove et al. 2012). Observational evidence suggests both species displace native vegetation in our study system (Fogarty and Facelli 1999; Damascos and Svriz 2012), but the rose was also reported acting as a nurse species for native seedlings, probably due to its open architecture that allows light to enter the lower strata while improving micro-environmental conditions and protecting seedlings from herbivory (De Pietri 1992; Svriz et al. 2013). Both target species recruited simultaneously in early-mid spring; we collected rose and broom seedlings in 2017 early November (Online Resource 1 Table S1).

The nontarget neighbor species were a mix of three native species (*Mutisia spinosa, Acaena splendens, Pappostipa speciosa*) and three nonnative species (*Cirsium vulgare, Cynoglossum creticum, Festuca arundinacea)* perennial or biennial species (see Online Resource 1 Table S1) that frequently co-occur with the target species in disturbed sites (Torres et al. 2018; Sample et al. 2019). We collected seeds from natural areas in fall 2017 and seeded them in the greenhouse in May 2017, where they were grown until the beginning of the experiment. When seed collection or germination was not possible, we collected seedlings of similar sizes (with the first pair of true leaves) from the field and then maintained them in seed trays until they were

transplanted to the experimental pots (Online Resource 1 Table S1).

Experimental design

We assembled 70 mesocosms contained in 15-L pots (30 cm height × 28 cm diameter) filled with matorral soil in the greenhouse of the Universidad Nacional del Comahue (41°08' S, 71°18' W). Each mesocosm was randomly assigned to one of the seven treatments (10 replicates) where we manipulated the timing of arrival of the target species so that they arrived earlier, later or simultaneously than the co-invader and the nontarget neighbor species (Fig. 1). In early arrival treatments (hereafter 'priority experiment') we planted rose seedlings (rose priority), broom (broom priority) and

both (simultaneous priority) in December 2017, while the neighbor community and the non-priority co-invader (if present) were planted three weeks later (Fig. 1a). In late arrival treatments (hereafter 'delay experiment') we planted the neighbor community and the non-delayed co-invader (if present) in December 2017 and the rose seedlings (rose delay), the broom (broom delay) and both (simultaneous delay) were planted three weeks later (Fig. 1b). In control treatments, we planted target and neighbor species simultaneously in December 2017 (Fig. 1c). The three-week interval between the early and late arrival events is a commonly used time period in priority effects experiments in greenhouse which facilitate comparison among studies (*e.g.,* Körner et al. 2008; Wilsey et al. 2015; Delory et al. 2019). More importantly, we
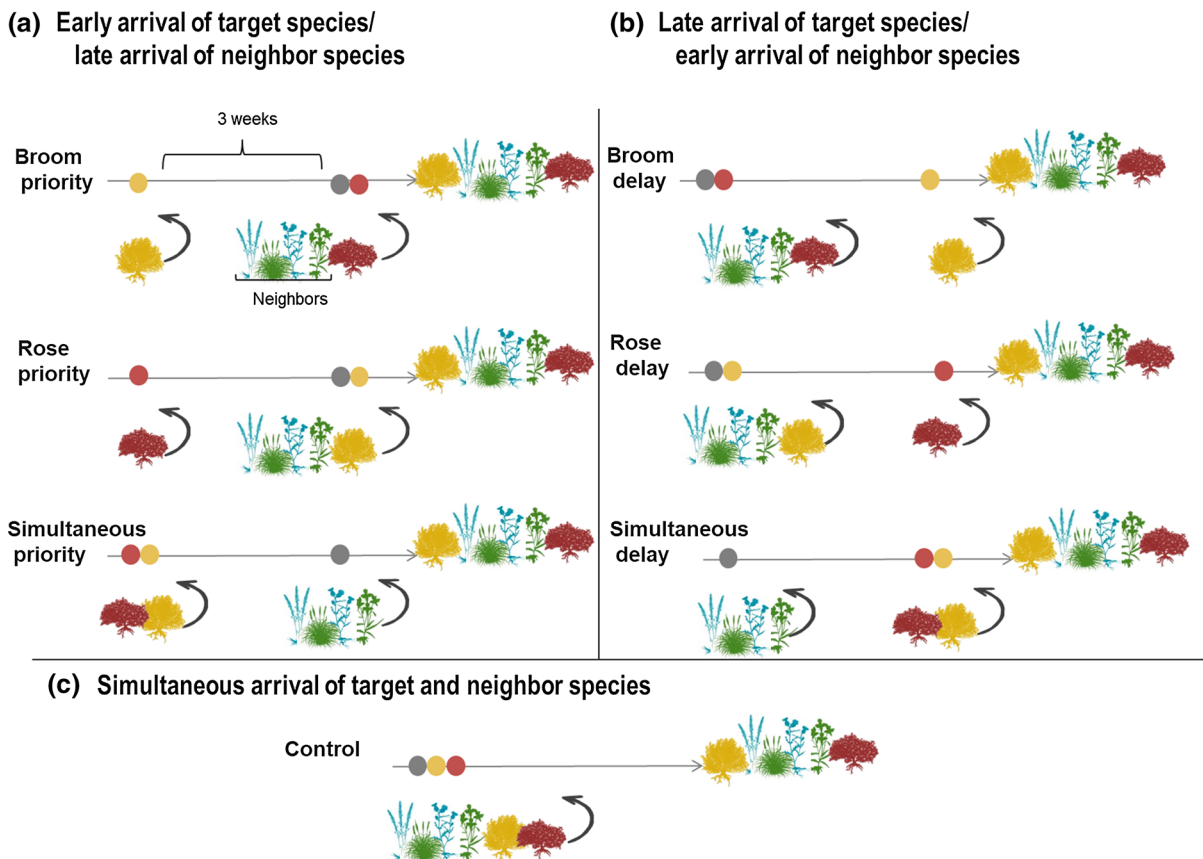

Fig. 1 Schematic treatments implemented to evaluate the effect of the early arrival (panel **a**) and late arrival (panel **b**) of the broom, the rose and both simultaneously, in relation to a control treatment (panel **c**) in which the target and neighbor species arrive to the community at the same time. In the diagram, the yellow and red shrubs represent the broom and the rose, respectively. Native neighbor species are represented in green and nonnative neighbor species in blue. The arrow indicates the time and the colored points, arrival events (yellow point: arrival of the broom, red point: arrival of the rose, gray point: arrival of the neighbor species)

simulated a three-week priority or delay because the target species used in our experiment overlapped their recruitment period; therefore, a three-week difference in the timing of arrival is a realistic difference in the arrival of species with a potential long-lasting impact on community assembly.

We created mesocosms from seedlings to specifically control with great accuracy the order of arrival of the species as opposed to the order of germination where timing cannot be equally controlled; this is a common approach in experiments testing priority effect (e.g.,Maron and Marler 2008; Kardol et al. 2013; Stuble and Souza 2016). Ultimately, our mesocosms contained all eight species (two individuals of each). For planting, we established 16 fixed planting spots for each of the individuals within the pot so that they were 5 cm from the edge of the pot and equidistant from each other, and we then randomized the species and the individuals that occupied each of these spots. We kept these mesocosms under greenhouse conditions (watered to the point of saturation every day in summer and every week in winter with temperatures below 25 °C in the summer). Thus, the mesocosms were subjected to more benign conditions than natural communities, without variability in water availability throughout the growing season and with less hostile temperatures for plant growth both in the cold months (protection against frost) and in hot months (refrigeration).

At the end of the experiment (13 months), we harvested the above and below ground biomass of each species. To determine the roots of the species, we first removed the excess dry soil by opening the pots on a 1 cm mesh and keeping the dirty biomass in bags. In the laboratory, we removed small leaves and branches from aerial shoots to avoid their loss during root cleaning, but preserved the base of the stems (tagged) to facilitate root determination. We carefully separated the roots of the species with a tweezers on a 1 mm sieve. As grasses formed a highly intricate matrix of fine roots, we patiently (1) removed the non-grasses from the matrix following stem instruction (i.e., indication of root identity following previously tagged stems). Color contrasts among species allowed rapid identification of non-grasses species into grasses matrix (grass roots were clearer and more yellowed than those of non-grasses, except for broom roots which were thicker and less branched than that of grasses) and among non-grasses species

(Cynoglossum and Mutisia showed darker roots than the rose and Acaena), and (2) separated Pappostipa from Festuca roots following stem instruction and branching differences. Although we were very careful with the handling of the plant material, it is likely that some of the fine roots were lost during processing. However, we assumed that the amount of roots lost was similar among treatments. We pooled the biomass of all individuals of each species in a pot, and weighed above and below ground biomass per species per pot, after drying at 65° C for 48 h in an oven. We estimated the total biomass per species per pot (hereafter, total biomass) by adding the above and belowground biomass of the individuals of the same species in each pot, and the shoot-to-root ratio per species per pot (hereafter, shoot-to-root ratio) by dividing aboveground over belowground biomass of the individuals of the same species in each pot.

Data analyses

To understand whether invaders benefit from early arrival and if they show a cost associated with arriving late, we fitted separated Hurdle Models for each target species total biomass in priority and delay experiments. The Hurdle models, which accounts for zero-inflated data, were fitted by first modelling the presence-absences (hereafter, 'survivals'), and then the abundances conditional on presences (hereafter, 'biomass COP') (Ovaskainen and Abrego 2020). First, to assess whether there were changes in target survivals due to history of arrival, we fitted quasi-binomial (link = 'logit') models, given that the binomial distribution showed over-dispersion. We regressed target survivals (total biomasses truncated to presence–absence where zeros were kept as zeros and all non-zero values were set to one) as a function of the priority (four levels: control, rose priority, broom priority, simultaneous priority) or delay treatments (four levels: control, rose delay, broom delay, simultaneous delay). Second, to evaluate whether there were changes in target total biomasses due to arrival history, we fitted a Gamma (link = 'log') model where we regressed the biomass COP (all biomasses that were zeros were declared as missing data points) as a function of the priority (four levels: control, rose priority, broom priority, simultaneous priority) or delay treatments (four levels: control, rose delay, broom delay, simultaneous delay). On the other

hand, to evaluate whether neighbor's total biomass depended on the history of arrival and species origin, we fitted a Generalized Linear Model (GLM) for priority and delay experiments in which we set total biomass of all natives (*i.e.,* all three native species together) and total biomass of all nonnatives (*i.e.,* all three nonnative species together) as response variable and priority or delay treatments, four levels each, as fixed predictor. We also included the biogeographic origin of the species as an interactive fixed predictor. We used a Gamma distribution (link = 'log') because the biomass can only take positive values and the histogram of frequency of the total native and nonnative biomasses were zero-skewed. Neither the Hurdle models nor the Gamma GLMs had random effects. For easier visualization, we report in Fig. 2 the

effect sizes calculated as a log response ratio (Hedges et al. 1999; Stuble and Souza 2016). We calculated the response to early arrival as *ln (total biomass when early arriving/total biomass in control)* and to late arrival as *ln (total biomass when late arriving/total biomass in control).* Effect sizes were used only for visualization, but the statistical support of the differences between each arrival treatment in priority (rose priority, broom priority, simultaneous priority) and delay (rose delay, broom delay, simultaneous delay) experiments compared to the control were determined by the models.

Additionally, we analyzed the species-specific responses of the neighbors with Hierarchical Models of Species Communities (HMSC), a joint species modelling implemented with Bayesian statistics
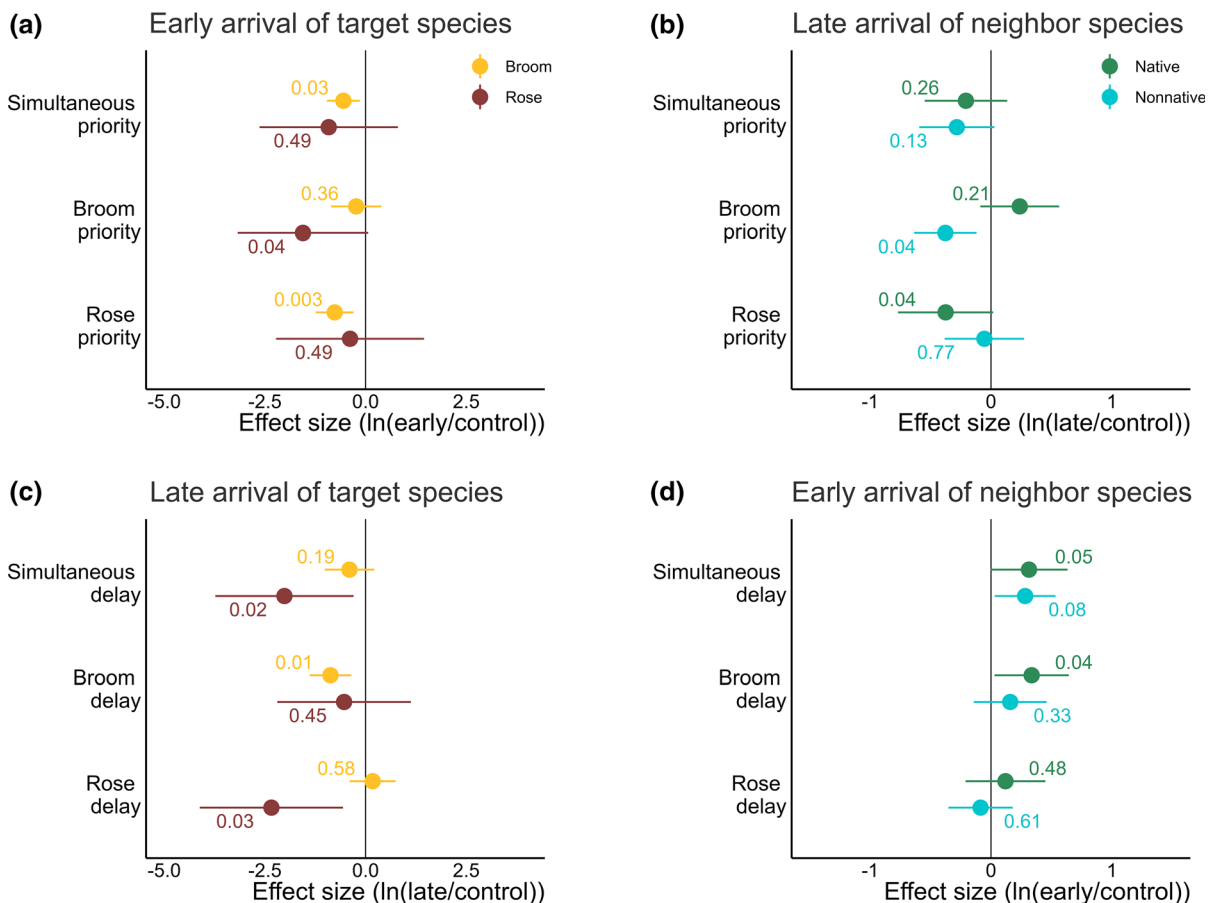

Fig. 2 Effect size (log response ratio) representing the response of the total (shoot + root) biomass (compared to the control) of target species when arrived (**a**) early and (**c**) late, and the response of native and nonnative neighbor species associated with (**b**) early arrival and (**d**) late arrival of target species. Note

that effect sizes were estimated for visualization purposes but the statistical support of biomass comparisons come from the Hurdle Models for the biomass conditional on presence. Labels indicate the p-value from Hurdle Models comparing the average treatment estimation with control estimation

which considers the non-independency of co-occurring species through a multivariate distribution (Ovaskainen and Abrego 2020). We fitted a Hurdle model for priority and delay experiments (priority and delay models) consisting in two submodels: (i) a presence-absence model that evaluated changes in species survival as a function of the arrival treatments, fitted with a probit distribution (0, 1) and (ii) a biomass COP model that evaluated changes in species biomass conditional on the presence as a function of the arrival treatments. The biomass COP model was fitted with a log-normal distribution (Gaussian distribution with log-transformed biomass). For both the priority and delay models, we used the log-transformed biomass of each species as response variable (the Y HMSC matrix of $n_s x n_y$, see Ovaskainen et al. 2017) and the priority or the delay treatments, four levels each, as fixed effects (X HMSC matrix of $n_s x n_c$, see Ovaskainen et al. 2017); where n_y is the number of species, n_s is the number of sample units, and n_c is the number of priority/delay treatment' levels. We included a pot-level random effect to control for unexplained variation at the mesocosm level in order to estimate species interactions not explained by our model through the residuals of the covariance between species (Ovaskainen et al. 2017; Ovaskainen and Abrego 2020); results not shown as no residual association was found. We fitted both models with the R-package Hmsc (Tikhonov et al. 2020) in R 3.6.3 (R Core Team 2021) assuming the default prior distributions (Ovaskainen and Abrego 2020). We sampled the posterior distribution of two Markov Chain Monte Carlo (MCMC), a simulation technique to obtain the distribution of each parameter in a model (Online Resource 2, Fig. S1, Fig. S2). MCMC convergence was examined with the effective sample size and potential scale reduction factor (Gelman and Rubin 1992) for the model parameters of both survival and biomass COP (Online Resource 2 Fig. S1, Fig. S1). To help comparison among target and nontarget species, the percentage change of the target species from previous GLMs is provided in Fig. 3.

To evaluate whether the target species biomass allocation (above vs. below) depended on arrival treatments, we evaluated shoot-to-root ratio responses to arrival treatments in priority and delay experiments. For target species, we fitted Gamma-distributed GLMs to separately model the shoot-to-root ratio of each

target species (response variable) as a function of the priority and delay predictors (four levels each). Instead, to understand whether neighbor shoot-to-root ratio was affected by arrival treatments, we fitted Gamma-distributed GLMs for priority and delay experiments in which total neighbor ratio (response variable) was regressed as a function of the priority/ delay predictors in interaction with the origin of the species. None of the GLMs mentioned above had random effects. All the GLMs of this study were fitted with the R-base *glm* function and conducted in R 3.6.3 (R Core Team 2021). We interpreted our results mainly based on effect sizes while reporting the statistical support of punctual estimations. We reported p- and f-values for GLMs and JSMs, respectively, as statistical support. We concluded there were no differences in species responses when models reported low statistical support, *i.e.,* when there were compatible results (within the 95 CI) showing the opposite trend to that of the punctual estimation (Amrhein et al. 2019).

Results

None of the target species had higher survival than in the control when given a three-week priority (Online Resource 3 Fig S3). Indeed, survival of target species was mainly unaffected by history of arrival, especially broom survival (Online Resource 3 Fig S3). None of the target species had higher biomass than in the control when given a three-week priority, but both of them were negatively affected when the co-invader was given a three-week priority (Fig. 2a, Online Resource 4 Fig. S4). Specifically, the rose biomass was not different in its full and simultaneous priority treatments than the control ($p_{rose-priority}$ = 0.49, $p_{simultaneous-priority}$ = 0.17; Fig. 2a, Online Resource 4 Table S2). Instead, the biomass of the rose was on average 81% lower than the control when the broom arrived earlier in the community ($p_{broom-priority}$ = 0.04; Fig. 2a, Online Resource 4 Table S2). Similarly, the broom biomass was not different in its priority treatment than in the control ($p_{broom-priority}$ = 0.36), but accumulated 54% less biomass when the rose arrived earlier alone and 42% less biomass when both targets arrived simultaneously early ($p_{rose-priority}$ = 0.003, $p_{simultaneous-priority}$ = 0.03; Fig. 2a, Online Resource 4 Fig. S4, Table S2). As expected, the

(a)

Late arrival of neighbor species
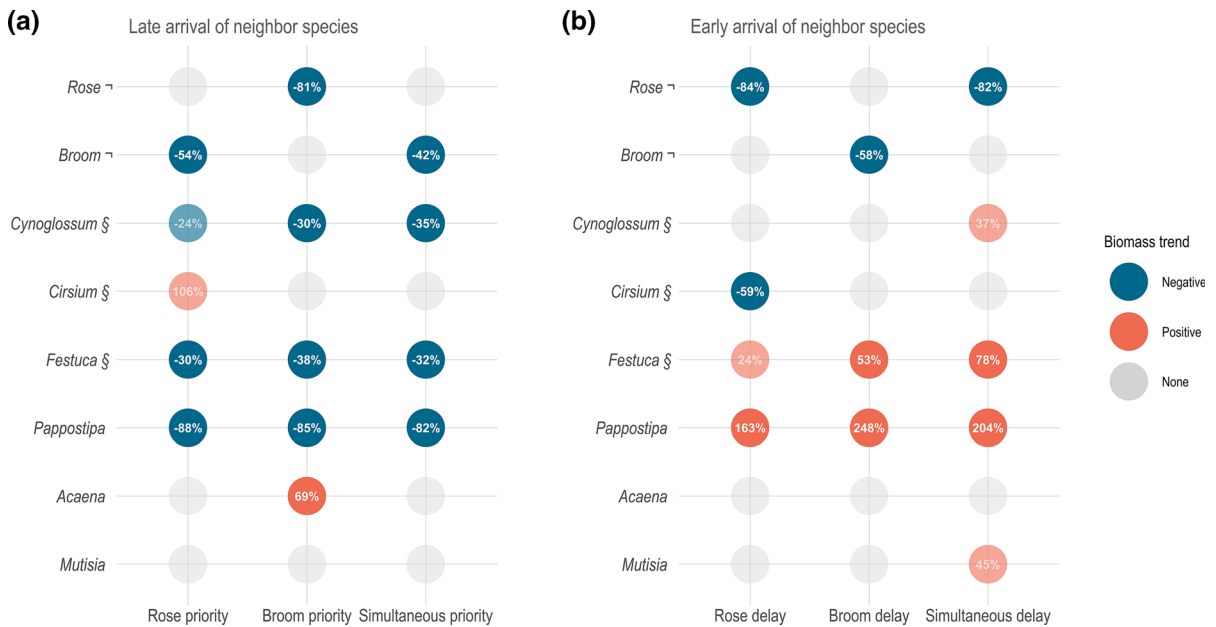

(b)

Early arrival of neighbor species

Fig. 3 HMSC estimated effect sizes representing the response of the biomass of neighbor and target species associated with (**a**) late arrival of neighbor species (*i.e.,* early arrival of target species) and (**b**) early arrival of neighbor species (*i.e.,* late arrival of target species). Values represent percent changes in biomass compared to the control (effect sizes). For neighbor species, full-colored and transparency indicate $f \geq 0.95$ and $f \geq 0.85$, respectively, where f are measures of the statistical support of the estimations that represent the proportion of the credible intervals with the same sign as the means (more details on statistical support in Online Resource 6 Fig. S8). For target species, full-colored indicate $p \leq 0.05$. Note that effect size estimations and statistical support for target species come from the Hurdle Models for the biomass Conditional on Presence whereas effect size estimations and statistical support of neighbor species come from Hierarchical Modelling of Species Communities. § indicates nonnative neighbor species, ¬ indicates nonnative target species

biomass of the target species was lower when given a three-week delay in arrival (*i.e.,* when arriving after the neighbor species) (Fig. 2c). The rose had $\sim 80\%$ less biomass than in the control when arriving late to the community, regardless of the timing of arrival of the broom ($p_{\text{rose-delay}} = 0.03$, $p_{\text{simultaneous-delay}} = 0.02$; Fig. 2c, Online Resource 4 Table S3). Instead, the broom had 58% less biomass than the control when arriving after the rose ($p_{\text{broom-delay}} = 0.01$), but its biomass was not affected when they arrived simultaneously late ($p_{\text{simultaneous-delay}} = 0.19$; Fig. 2c, Online Resource 4 Table S3).

The priority treatments of the target species influenced the performance of native and nonnative neighbor species (Fig. 2b, Online Resource 5 Fig. S5). Nonnative biomass was 31% lower when the broom was given priority ($p_{\text{broom-priority}} = 0.04$), but not different to the control when the rose arrived early alone or with the broom ($p_{\text{rose-priority}} = 0.77$, $p_{\text{simultaneous-priority}} = 0.13$; Fig. 2b, Online Resource 5 Fig. S6a). On the contrary, native biomass was 31%

lower when the rose was given priority ($p_{\text{rose-priority}}$ = 0.04), but not different to the control when the broom arrived early alone or with the rose ($p_{\text{broom-priority}}$ = 0.21, $p_{\text{simultaneous-priority}}$ = 0.26; Fig. 2b, Online Resource 5 Fig. S6a). Yet, nonnative biomass was higher than native biomass across the priority treatments of the target species (*i.e.,* late neighbor arrival) (Online Resource 5 Fig. S6a). However, neighbor species showed species-specific responses to contingencies in the arrival of the target species (Fig. 3a). Within nonnatives, two of the three nontarget nonnative species (*Festuca* and *Cynoglossum*) had lower performance when target species were given priority, but nonnative *Cirsium vulgare* benefited when the rose arrived earlier in the community, but not at the same time as the broom (Fig. 3a). Compared to the control, *Cirsium* survival was 269% and its biomass was 106% higher when the rose arrived earlier in the community (Fig. 3a, Online Resource 6 Fig. S7). The response of the native species was also variable among species. *Pappostipa* and *Mutisia* showed 65 and 41% lower

survival when arriving after both target species. *Pappostipa* accumulated $\sim 80\%$ less biomass with early arrival of either of the target species, but *Mutisia* biomass was not affected by priority treatments of the invasive species. Finally, and in contrast to our expectations, *Acaena* showed 69% higher biomass when the broom arrived earlier in the community (Fig. 3a).

Neighbor species were in general benefited or not affected by the late arrival of the target species, but nonnative biomass was higher than native biomass regardless of delay treatments (Online Resource 5 Fig. S6b). There was a $\sim 40\%$ increase in native biomass when the broom arrived later in the community, alone or with the rose, compared to the control ($p_{broom-delay} = 0.04$, $p_{simultaneous-delay} = 0.05$),   but showed no difference when the rose arrived late alone ($p_{rose-delay} = 0.48$;   Fig. 2d,   Online   Resource   5 Fig. S6b). Nonnative biomass presented a similar pattern, but its biomass tended to be 33% higher only when both target species arrived in simultaneously late ($p_{simultaneous-delay} = 0.08$; Fig. 2d, Online Resource 4 Fig. 6b). Within each group, there was also variability among neighbors in their responses to the late arrival of the target species (Fig. 3b). With the exception of *Cirsium,* all neighbors showed greater survival when arriving earlier than the rose or than the broom (Online Resource 6 Fig. S7). The two grasses, which were disadvantaged by the early arrival of the target species, achieved the greatest benefit due to late arrival treatments (Fig. 3b). *Mutisia* and *Cynoglossum* accumulated greater biomass when arriving before the two target species (Fig. 3b). Only one species, *Cirsium,* accumulated 59% lower biomass when arriving earlier than the rose (Fig. 3b). *Acaena*, which was supposed to be facilitated by the early arrival of the broom, showed similar biomass when arriving early in the community than in the control (Fig. 3b).
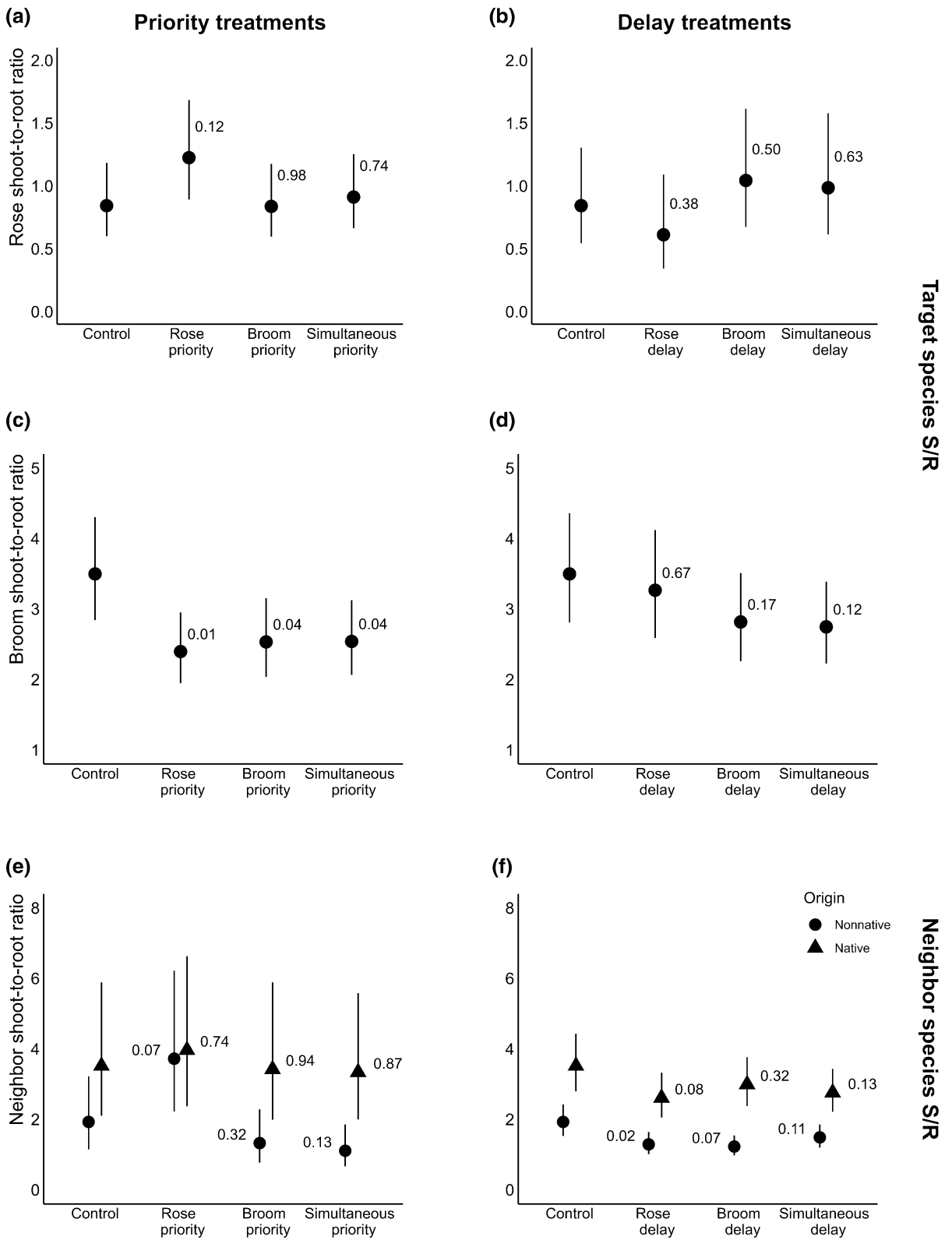
The effect of the history of arrival on the biomass allocation of the target species was dependent on the species. The rose allocated, on average, 46% more biomass to shoots (higher shoot-to-root ratio) when given full priority than in the control, although this effect had low statistical support ($p_{rose-priority} = 0.12$; Fig. 4a, Online Resource 7 Table S3). On the contrary, the broom allocated higher biomass to the roots (on average, 29% lower shoot-to-root ratio) when target species arrived early in the community, either alone or simultaneously,   than   in   the   control   (p_{rose-}

Fig. 4 Shoot-to-root ratio of target and neighbor species in ▶ response to priority and delay treatments. In panels a-d: fitted values from Gamma Generalized Linear Models (GLMs) testing whether shoot-to-root ratio of the rose and the broom in priority or delay treatments differed from the control. In panels e–f: fitted values from Gamma GLMs testing whether shoot-to-root ratio of native and nonnative neighbors in priority or delay treatments differed from the control. Estimated mean shoot-to-root ratio $\pm$ 95% confidence interval across arrival treatments are shown. Labels indicate the p-value from GLMs comparing the average treatment estimation with control estimation within natives and nonnatives

$_{priority} = 0.01$, $p_{broom-priority} = 0.04$, $p_{simultaneous-priority}$ $= 0.04$; Fig. 4c, Online Resource 7 Table S3). On the other hand, the shoot-to-root ratio was not affected by late arrival treatments in any of the target species (Fig. 4b-d, Online Resource 7 Table S4). Regarding neighbor species, biomass allocation showed no difference between native and nonnative species across all treatment of early arrival of target species, but there was a trend of higher allocation to nonnative shoots (on average, 93% higher ratio) in rose priority treatment compared to the control ($p_{rose-priority} = 0.07$; Fig. 4e, Online Resource 8 Table S5). In contrast, when the target species arrived late in the community, native species allocated more biomass to shoots than nonnative species, regardless of delay treatment (Fig. 4f, Online Resource 8 Table S6). Furthermore, nonnative species showed a trend to $\sim 50\%$ lower shoot-to-root ratio than control when rose and broom arrived   late   alone   ($p_{rose-delay} = 0.02$, $p_{broom-delay}$ $= 0.07$, Fig. 4f, Online Resource 8 Table S6), but not at the same time ($p_{simultaneous-delay} = 0.11$). The biomass allocation of native species did not change due to late arrival treatments, except for a trend to lower native shoot allocation (on average, 25% lower ratio) in rose delay treatment ($p_{rose-delay} = 0.08$) (Fig. 4f, Online Resource 8 Table S6).

Discussion

Invasive shrubs accumulated less biomass than control both when arriving after the co-invader and when arriving after neighbor species. Neither the broom nor the rose showed an advantage either by arriving earlier or by arriving later than neighbor species. Specifically, the rose showed a consistent disadvantage by late

(a) Priority treatments

(b) Delay treatments

(c)

(d)

(e)

(f)

Target species S/R

Neighbor species S/R

Origin
● Nonnative
▲ Native

arrival that seems to be independent of the timing of arrival of the broom, whereas the broom was negatively affected by the early arrival of the co-invader. Despite the lack of a strong response from the target species, neighbor species were generally advantaged by the late arrival of the target and disadvantaged by their early arrival, although responses varied between native and nonnative species. Our results were consistent with a growing body of literature that posits that contingencies in the timing of arrival of nonnative species modulate invasion dynamics in several ecosystems (*e.g.,* Grman and Suding 2010; Young et al. 2015; Yannelli et al. 2020). But our findings do not support the idea that invasive species tend to benefit by early arrival to the communities (Dickson et al. 2012; Wilsey et al. 2015; Delory et al. 2019) or that they are less affected by late arrival than co-occurring natives (Stuble and Souza 2016). Although the success of the invasive shrubs is likely not fully determined by their history of assembly, our results suggest that for the target species arriving early is not as important as not being late. An understanding of the effect of historical contingencies on interactions among nonnative species is needed to understand the final structure of multiple-invaded plant communities.

Although there is evidence that nonnative species may benefit from early arrival to a greater extent than natives, some studies have found no difference in the strength of priority benefits incurred by native and nonnative plant species (Cleland et al. 2015; Stuble and Souza 2016). Similarly, in our study, both invasive shrubs showed no difference in biomass between priority and control treatments, while native neighbors benefited to some extent from a three-week priority over the broom. Long-lived shrubs have been suggested to fail outcompete grasses and herbs when arriving early in the community due to lower resource acquisition (DeMalach and Fukami 2018). Indeed, most of the evidence on priority effects is based on the benefits obtained by grasses and herbs by early arrival (Weidlich et al. 2021). Yet, in our study, target invasives were more affected by the co-invader than by neighboring grasses and herbs. Furthermore, native plants that benefited from early arrival were also perennial woody. Thus, we suggest that the interaction between invaders modulates the absence of priority effects more than woody-herb competition.

It is important to note that our findings that target invasive species do not benefit by early arrival are likely affected by the fact that we used seedlings instead of seeds to propagate our mesocosms, thereby eliminating the priority advantage conferred by a potential quick germination (Wainwright et al. 2012; Wilsey et al. 2015). Instead, we focused on the presumably potential of the target invasive species to capitalize on early arrival in a community through quick growth and strong competition (Maron and Marler 2008; Van Kleunen et al. 2010; Kuebbing and Nuñez 2016; Stuble and Souza 2016; Golivets and Wallin 2018), as has been hypothesized. By using seedlings instead of seeds, we were able to strongly control the differences in arrival time that, if seeds were used, would have combined with the effect of differences in germination time, thereby confusing our results (*e.g.,* Wilsey et al. 2015). It can then be hypothesized that early germination, but not quick growth and strong competition, could be the driving force explaining the high abundance of the broom and the rose in disturbed sites in our study system. Although the target species recruited simultaneously the year the experiment started, it is likely that the timing of recruitment of species varies between years due to changes in environmental conditions (*e.g.,* winter-spring precipitation, early spring temperature) and particularly in the face of climate change, reinforcing the importance of understanding the temporal dynamic of invasions and how it affects nonnative interactions.

Evidence suggests that belowground responses to priority effects may differ significantly to those aboveground (Körner et al. 2008; Weidlich et al. 2018). Despite both target species accumulated less biomass when the co-invader was given priority, differences in biomass allocation were found between target species. Given that neighbor species, particularly grasses, were disadvantaged when arriving later than the targets, it is possible that the simultaneous arrival of the targets and neighbors produced a highly competitive aboveground environment compared to those in priority treatments, which could explain the higher shoot allocation in the broom when both target species had priority. Indeed, previous studies found a negative effect of grasses on the broom, but unlike those studies, our results do not suggest that this negative effect was mediated by belowground competition (Lang et al. 2017). On the other hand, the rose allocated 46% more biomass to the shoots when given priority alone, but the effect had low statistical

support. Changes in biomass allocation can influence resource acquisition and ultimately affect future plant growth and competitive ability (Tilman 1988). Although the rose did not have higher biomass when given full priority, its early arrival may determine long-term consequences in community structure that we were unable to detect during the early assemblages of plant communities studied here.

The ability of nonnative species to establish and dominate communities from low abundances at later stages of community assembly may contribute to their success (Stuble and Souza 2016). In fact, species introduced into already established communities tend to establish at relatively low abundances, but some strong invaders can surpass this filter and achieve high abundances either way (MacDougall et al. 2009). However, we found that one of our invasive shrubs, the rose, was more disadvantaged for arriving late in the community than several co-occurring native and nonnative neighbor species. Because the rose showed in our mesocosms a lower performance than expected due to its invasive characteristic, this result may need to be taken with caution. On the contrary, the broom showed similar biomass when arriving late to the community than in the control scenario, although the broom paid a cost for arriving late when it implies arriving after the co-invader. This suggests that the ability of the broom to establish from low abundance could be an important factor in determining its invasiveness, but that it may be strongly modulated by its interaction with the co-invader.

We predicted that native species may be more vulnerable than nonnative species to invaders' priority effects, as has been previously reported (Stuble and Souza 2016). However, our results did not fully support this idea. Although native and nonnative neighbors generally suffered from arriving later than the invasive shrubs used in our experiment, nonnatives were only negatively affected when they were planted later than the broom, while native neighbors were negatively affected when arriving later than the rose. Indeed, the native shrub *Acaena splendens* seemed to benefit from arriving after the broom. *Acaena* could be expected to benefit from an increase in soil nitrogen content provided by the early arrival of the broom, the only nitrogen fixer. This may be surprising, as previous evidence suggests that nonnative legumes in general and broom in particular frequently facilitate the establishment of other nonnative species,

particularly those of rapid resource acquisition, instead of native species (Grove et al. 2015; Carter et al. 2019). For instance, in our mesocosm communities, *Acaena* co-occurred with highly opportunistic species, *Cirsium* and *Cynoglossum*, which were not able to benefit from broom early arrival. This allows considering the existence of other indirect mechanisms; given that early arrival of the broom produced the strongest reduction in nonnative biomass, it can be hypothesized that the broom benefited *Acaena* through a reduction of the nonnative neighbor competition when the broom was given three weeks priority. Our results suggest an alternative possibility by which the invasive broom may initially hinder other nonnatives while favoring some native species.

Interactions between nonnative species in general and priority effects in particular may explain the accumulation of invasive species in communities (Simberloff and Von Holle 1999; Kuebbing and Nuñez 2016; D'Antonio et al. 2017). Of particular importance is the idea that established nonnative species can facilitate the establishment of secondary invaders through a wide variety of mechanisms because it implies a positive feedback among nonnatives that would lead communities to highly invaded stages (Simberloff and Von Holle 1999; Simberloff 2006). Generally, our results did not support this hypothesis as target species tended to pay a cost when arriving at the community after the co-invader. Furthermore, we found that early arrival of invasive target species generally inhibited the performance of nonnative neighbors. Therefore, we provide partial support to the idea that the accumulation of nonnative species in Patagonian forests may be a secondary effect of disturbances and/or human management by which the removal of a nonnative species releases other nonnatives from competition and favors their establishment and/or increase in abundance (Henriksson et al. 2016; Pearson et al. 2016; D'Antonio et al. 2017). However, one species-specific interaction suggests that there would still be room for facilitation among nonnatives. For example, *Cirsium vulgare* showed a large increase in its biomass when it arrived after the rose. Although the nurse effect of the rose in our study system has been mainly attributed to protection against ungulate herbivores (De Pietri 1992; Svriz et al. 2013), given the absence of herbivores in our experiment, our results suggest other possible mechanisms: (1) positive plant-soil

feedbacks related to increasing contents of labile carbon and nitrogen hypothetically attributable to the associated micro- and meso-fauna (de Paz et al. 2017, 2018). (2) Positive indirect interactions mediated by the reduction of co-occurring species, particularly a combined reduction of broom and native biomass. Although the existence of priority effects mediated by indirect interactions has been less reported than other mechanisms, evidence suggests that it could be more frequent than imagined (Metlen et al. 2013; Flory and Bauer 2014; Kuebbing and Nuñez 2016).

Mesocosm studies such as the one presented here have both benefits and limitations. Controlling abiotic and biotic factors in the greenhouse, as well as propagule size, germination rates, and initial species composition, allowed isolating the role of species order of arrival on invasion dynamics. However, we acknowledge that the response of mesocosm communities to assembly contingencies represented a simplified version of reality since differences in germination rate and time as well as the presence of other biotic (*e.g.,* herbivores) and/or environmental factors (*e.g.,* dry periods) could differentially affect the performance of the species and lead to more complex and, in some cases, unpredictable outcomes. For instance, the absence of environmental variability between arrival events can blur the overall benefit of target species by early arrival if arriving three weeks earlier in natural communities meant a significant improvement in soil water content. Moreover, because the late arrival events were compared to a control situation in which all species arrived in the first arrival event, we were not able to distinguish between the effects of arriving later than neighbor species from being transplanted three weeks later; future studies discerning the effect of order *vs.* the effect of the moment *per se* are necessary. Furthermore, a trait-based approach to study the effect of the order of arrival among invaders will increase our ability to make broader management recommendations that are not contingent on the identity of the species involved, although considering species-specific interactions can also provide insightful understanding of nonnative accumulation dynamics. Despite all this, our design made it possible to specifically evaluate how priority effects modulate the accumulation of nonnatives, which was our main objective. Of course, the implications of these historical contingent interactions on the accumulation of nonnatives at landscape scale remains an open question, since other factors (*e.g.,* disturbance level and propagule pressure) could override the consequences of local interactions.

Priority effects are gaining momentum as a means to manage invasive species and restore degraded habitat (Temperton et al. 2016; Young et al. 2017; Weidlich et al. 2021). An alternative is to manipulate the assembly of plant communities to promote native species that will ultimately exert strong priority effects on nonnative species (Hess et al. 2019). Despite the limitations of this study, our results suggest that the response of species to historical contingencies in community assembly depends on the timing of arrival of the co-occurring invaders. Therefore, our results are in line with recent studies suggesting that interactions between nonnative species play a key role in determining the invasion of multiple species in communities (Kuebbing et al. 2013; Kuebbing and Nuñez 2016; D'Antonio et al. 2017) but, to our knowledge, this is the first study that experimentally evaluated how the order of arrival of invasive species affected the trajectory of the community and the accumulation of nonnative species (Weidlich et al. 2021). Overall, we argue that understanding how historical contingencies modulate the sign and strength of interactions between nonnative species could contribute to planning more effective management practices.

Data availability All data generated or analyzed during this study is included in the Online Resource 10.

Code availability The code of the models is available in the Online Resource 9.

Declarations

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