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Giving recipient communities a greater head start and including productive species boosts early resistance to invasion

Time advance and productivity reduce invasion

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Abstract

Questions: Giving a time advance to restored native plant species has recently been considered a promising way to improve their persistence and reduce invasion success (i.e. through priority effects). However, little is known about the influence of the elapsed time between seeding and invasion and its interaction with other characteristics such as species composition and density, despite the fact that it could substantially help developing effective management strategies.

Methods: In a pot experiment, we simulated invasion by three major invasive species (*Ambrosia artemisiifolia*, *Bothriochloa barbinodis*, and *Cortaderia selloana*) in soil covered with recipient communities differing in species composition (one, three or nine species), density (700 or 2,778 seeds/m²), and time advance (established one or five months previously). We assessed early invasion success by measuring seedling emergence and survival over six months.

Results: Early invasion success was mainly explained by recipient community's time advance and composition (or their interaction), while density had limited influence. Polycultures (three or nine species) showed generally greater invasion resistance, most likely due to high aboveground biomass essentially produced by two species. Species composition interacted with time advance in two ways: **(1)** *Bothriochloa barbinodis* seedling emergence was impacted by composition only in communities having five months of advance, suggesting that the contribution of species composition to invasion resistance varies according to the age of the community, and **(2)** *Ambrosia artemisiifolia* and *Cortaderia selloana* survival was affected by time advance in polycultures only, which produced much more biomass than monocultures, implying that a greater head start provides a competitive advantage only if it allows a sufficient increase in biomass production.

Conclusions: Implementing revegetation as soon as site clearance work is over, as well as establishing productive native species may help reduce invasion success. How much of an advantage recipient community time advance represents depends on biomass production.

Keywords: assembly, biomass, biotic resistance, coexistence, composition, density, historical contingencies, invasive species, multistate models, priority effects, restoration, revegetation

1| Introduction

The alarming rate of biodiversity loss worldwide has been attributed particularly to the constantly increasing spread of invasive species (Mollot et al. 2017; Seebens et al. 2017), highlighting the importance of designing effective and environment-friendly methods of invasive species control. The current expansion of anthropologically disturbed areas promotes plant invasions (Facon et al. 2006; Hobbs & Huenneke 1992), with disturbances like vegetation clearance increasing resource availability and decreasing competition from resident species (Davis et al. 2000). Active reestablishment of native plant cover after a disturbance is increasingly being advocated as a method of reducing invasive plant species colonization and spread locally (Byun & Lee 2017; Larson et al. 2013; Middleton et al. 2010). The idea is that re-established communities exhibit a certain resistance to invasions (biotic resistance; Levine et al. 2004), mainly through resource competition at the neighborhood scale (Goldstein & Suding 2014; Levine et al. 2004). It has also been suggested that it may be more effective to combat invasive species at the seedling stage, since: **(1)** the seedling stage is considered one of the most vulnerable stages in the life cycle of a plant (Kitajima & Fenner 2000); and **(2)** initial seedling establishment largely determines subsequent population success (Albrecht & McCarthy 2009; Kitajima & Fenner 2000).

Consequently, designing native plant communities capable of quickly acquiring robust invasion resistance is a fundamental step in limiting invasive species establishment. Recently, giving a time advance to the native species over invasives has been suggested as a way to improve native species persistence and limit invasive species colonization through priority effects (Delory, Weidlich, Kunz et al. 2019; Firm et al. 2010; Grman & Suding 2010; Hess, Mesléard, Buisson 2019; Vaughn & Young 2015; Wolf & Young 2016). Priority effects, by which early-arriving species affect the establishment, survival, growth or reproduction of later colonizers (Helsen et al. 2016), are considered to be mainly induced by resource preemption (Fukami 2015), but can also arise from alterations of biotic (e.g. soil microorganisms) and abiotic (e.g. allelochemicals, nutrient dynamics) components of the environment (Corbin & D'Antonio 2012; Mangla & Callaway 2008). Prior establishment of native species has been shown to strongly decrease invasion success. For instance, Grman and Suding (2010) found a ten-fold reduction in invasive species biomass when native species were planted five weeks earlier. Delory, Weidlich, Kunz et al. (2019) showed that in the exotic species *Senecio inaequidens* biomass was 96% to 99% lower when arriving with a 21-day delay over native species. However, little attention has been paid to the influence of elapsed time between seeding and invasion in interaction with community characteristics (Helsen et al. 2016; Hess, Mesléard, Buisson 2019; Orloff et al. 2013; von Gillhaussen et al. 2014).

Timing of species arrival can have substantial effects on community assembly (Ejrnæs et al. 2006; Harper 1961; Kardol et al. 2013; Körner et al. 2008; Ross & Harper 1972; Sagar & Harper 1960). Longer time intervals between arrival events are expected to result in greater asymmetry in plant size and stronger priority effects (Kardol et al. 2013; Wilsey et al. 2015), because early-arriving species have time to use available resources more completely. Therefore, extending the time advance of natives over invasives should lead to increased invasion resistance. Since plant species vary in size and biomass production, the benefit of increasing time advance could however depend on species composition. Also, increasing the density of resident individuals in a community (i.e. the number of individuals per surface unit) may also increase priority effects and reduce the recruitment of invasive species (Goldberg et al. 2001; Orloff et al. 2013; Yannelli et al. 2017, 2018), because establishing more individuals is expected to enhance resource acquisition, thereby reducing the resources available for invading species (Gerhardt & Collinge 2007). However, increasing sowing density may only be efficient in the very early stages because biomass production stabilizes over time (i.e. density-dependent effects; (Burton et al. 2006; Carter & Blair 2012; Crawley 2007; Nemeč et al. 2013; von Gillhaussen et al. 2014).

Invasive species management strategies could be substantially improved by a better understanding of how early invasion resistance is influenced by the time advance given to native species and its interaction with species composition and individuals' density, which are three parameters easy to manipulate. In a greenhouse experiment, we investigated how the elapsed time between seeding and invasion (hereafter 'time advance'; one or five months) in interaction with species composition (one, three or nine species) and density of individuals (700 or 2,778 seeds/m²) influenced the early establishment success of three invasive species in Europe: *Ambrosia artemisiifolia*, *Bothriochloa barbinodis* and *Cortaderia selloana*. Early establishment success was monitored by recording seedling emergence and survival over six months.

2| Methods

2.1| Species selection

While many studies assess the response of a single invader (Byun et al. 2013; Byun & Lee 2017; Dukes 2002; Firm et al. 2010), this does not allow for the detection of varying responses from invasive species (Emery 2007). Here, therefore, we monitored early establishment success of three species known to invade disturbed areas in Europe (Domenech & Vila 2008; Fried 2010; Ozaslan et al. 2016) and disperse by seed (Allred 2003; Bassett & Crompton 1975; Fried 2010; Lambrinos 2002): common ragweed (*Ambrosia artemisiifolia* L.), cane bluestem (*Bothriochloa barbinodis* (Lag.) Herter) and pampas grass (*Cortaderia selloana* (Schult. & Schult.f.) Asch & Graebn.).

The common ragweed (*Ambrosia artemisiifolia* L., Asteraceae) is an annual opportunistic weed introduced from North America more than a century ago (Heckel 1906). Thanks to its large ecological amplitude (Leskovsek et al. 2012; Onen et al. 2017) and high seed production (up to 18,650 seeds in France; Fumanal 2007), the common ragweed can successfully invade disturbed areas such as road sides, riverbanks, wastelands as well as cultivated fields (Lavoie et al. 2007; Simard & Benoit 2010).

The cane bluestem (*Bothriochloa barbinodis* (Lag.) Herter, Poaceae) is a perennial warm-season C4-grass growing in upright clumps 60–120 cm tall (De Wet 1968; Koshi et al. 1977) native to the southern USA and Central and South America (Vega 2000). Only recently observed in Europe (1970s in southern France as *Bothriochloa imperatoides* (Hack.) Herter; Auriault 1976), it spreads fast along roadsides, railways and vineyards in large parts of France (Fried 2014; Verloove & Sánchez Gullón 2012) and could become a serious invader (Fried 2010).

The pampas grass (*Cortaderia selloana* (Schult. & Schult.f.) Asch. & Graebn., Poaceae) is a perennial C4-grass introduced from South America into Europe and widely used as an ornamental landscape plant that can be up to 4 m in height and 3.5 m in diameter (Bacchetta et al. 2010; Bossard et al. 2000; Domenech & Vila 2008). The small, wind-dispersed seeds (i.e. 106 seeds per mature plant; Domenech & Vila 2008; Lambrinos 2002) are able to rapidly germinate under a wide range of ecological conditions (Domenech & Vila 2007) and form dense monospecific stands (Bossard et al. 2000; Lambrinos 2002).

For each invasive species, we collected seeds from at least ten individuals from three mature populations in southeastern France (Supplementary material, *Table S3.1*). Seeds from *Ambrosia artemisiifolia* were initially cold-stratified to break dormancy and optimize germination (Bazzaz 1970). Seeds were placed between two cotton layers soaked in distilled water in a hermetically sealed plastic box covered with light-tight aluminum and refrigerated at 4°C for six weeks (Bae et al. 2017). Under favorable conditions, *Cortaderia selloana* and *Bothriochloa barbinodis* are able to rapidly reach high germination rates without cold stratification (Abbott & Roundy 2003; Bacchetta et al. 2010; Costas-Lippmann 1979), and their seeds were therefore not cold-stratified.

Before starting the experiment, we assessed the germination capacity of the three invasive species by placing 120 seeds in Petri dishes on cotton soaked in distilled water. The Petri dishes were placed in a growth chamber (Hotcold-GL: 12K lux; P-Selecta, Barcelona, Spain) and incubated at alternating temperatures (15/25°C) with a photoperiod of 12 hr/12 hr for one month. The highest temperature occurred within the 12-hr light period. Seedling emergence was monitored every three days until no seedling emergence was recorded. Seedlings were removed as they germinated. The results of these preliminary germination tests were used to adjust the number of seeds from each invader sown in the experiment, so as to ensure at least nine viable seeds in each pot (Supplementary material, *Table S3.1*).

To compose our recipient native communities, we selected nine perennial plant species widely used to revegetate roadsides in France: *Achillea millefolium* L., *Dactylis glomerata* L., *Lolium perenne* L., *Lotus corniculatus* L., *Onobrychis viciifolia* Scop., *Plantago lanceolata* L., *Poterium sanguisorba* L., *Schedonorus arundinaceus* (Schreb.) Dumort., and *Trifolium repens* L.. Commercially available seeds were obtained from ZYGENE (Charols, France). Species nomenclature follows TAXREF v13.0 (Gargominy et al. 2019).

2.2| Study site and infrastructure

This experiment was carried over one year (late September 2017 until late September 2018) at the Research Institute of Tour du Valat, France (43°30' N, 4°40' E, 1 m elevation). The climate at the site is Mediterranean, characterized by warm to hot, dry summers and mild, wet winters, with high interannual variability (Lionello et al. 2006). Air temperature and precipitation data were measured continuously at a meteorological station located close to the experimental site (*Figure S3.1* Erreur ! Source du renvoi introuvable.). Plant communities were established in square plastic pots (with a width of 30.5 cm at the top and 25 cm at the bottom, 27 cm deep) containing from bottom to top: (1) a 27-cm diameter polyester textile filter (® Diatex textile (DIATEX, Saint Genis Laval, France) with 50–70 µm mesh size to prevent loss of substrate), (2) a polystyrene bloc (width 20 cm, 10 cm deep) allowing water to flow at the sides, (3) a substrate mixture consisting of 30 vol% vermiculite (® Projar; Projar Group, Valencia, Spain) 2.6 kg/m³, and 70 vol% commercial organic and fertile topsoil (® Geolia; Leroy Merlin, Nîmes, France; *Figure S3.2*). All pots were kept in a greenhouse with ® Diatex mesh walls and roof (600–500 µm mesh size) to ensure that climate conditions were similar to outside conditions and to prevent seed dispersal from the surrounding area. In addition to the ambient precipitation, all pots received equal amounts of demineralized water through sprinklers placed equidistantly. The amount of additional water was adjusted according to weather conditions so as to ensure conditions favorable to germination and plant development.

2.3| Experimental design

The experiment was designed to simulate situations where seeds of invasive plant species (*Ambrosia artemisiifolia*, *Bothriochloa barbinodis* and *Cortaderia selloana*) reach soil covered with native plant species re-established on bare soil after a disturbance or restoration actions involving vegetation clearing.

In each pot, we established recipient communities showing three different species compositions: one, three or nine species (hereafter called respectively '1-sp', '3-sp' and '9-sp' communities; *Table 3.1*). *Lolium perenne* was selected for the 1-sp treatment because it is usually the dominant species in commercial seed mixtures (Arienzo et al. 2004). The 3-sp treatment included *Lolium perenne*, *Plantago lanceolata* and *Trifolium repens*. The 9-sp treatment included all the species cited above (*Table 3.1*). Hereafter, 'monocultures' refers to 1-sp communities, and 'polycultures' refers to 3-sp and 9-sp communities. We tested two levels of species density, sowing either 700 or 2,778 recipient community

Table 3.1 Species composition and density applied per species of recipient communities differing in density (LowD = low density, HighD = high density) and species composition (1-sp = 1 species, 3-sp = 3 species, 9-sp = 9 species).

Functional group	Species	Density (no. seeds/pot)					
		LowD			HighD		
		1-sp	3-sp	9-sp	1-sp	3-sp	9-sp
Grasses	<i>Lolium perenne</i>	63	22	9	250	82	30
	<i>Dactylis glomerata</i>	-	-	4	-	-	20
	<i>Schedonorus arundinaceus</i>	-	-	6	-	-	30
Leguminous forbs	<i>Trifolium repens</i>	-	20	6	-	84	30
	<i>Lotus corniculatus</i>	-	-	6	-	-	25
Non-leguminous forbs	<i>Onobrychis viciifolia</i>	-	-	9	-	-	30
	<i>Plantago lanceolata</i>	-	21	8	-	84	30
	<i>Poterium sanguisorba</i>	-	-	9	-	-	30
	<i>Achillea millefolium</i>	-	-	6	-	-	25

seeds/m² (63 or 235 seeds/pot, hereafter called respectively ‘LowD’ and ‘HighD’ communities; *Table 3.1*, *Figure 3.1*). Recipient community seeds were sown either 175 or 29 days (hereafter called respectively ‘5-month’ and ‘1-month’ communities) before invasive species seeds.

Sowing densities were chosen in line with the densities commonly applied in roadside revegetation. Native species seeds were allocated to positions, (LowD) or (HighD) were fixed either 3.5 cm apart and to ensure invasive individuals surrounded native neighbors (Figures 3.2, 3.3).



Figure 3.1 Recipient communities at the time of invasive species introduction (left: 1-month and right: 5-month communities).

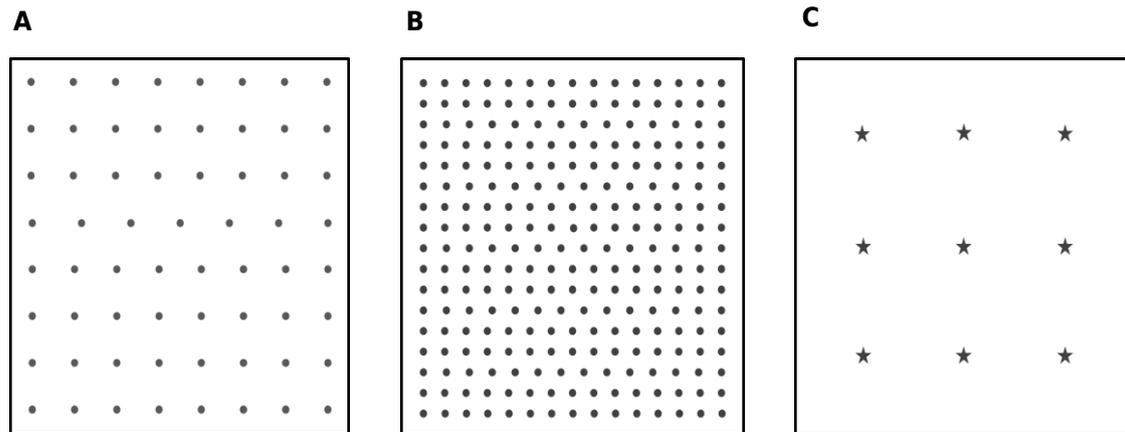


Figure 3.2 Pot spatial arrangement of (A) Low density recipient communities (63 seeds/pot), (B) High density recipient communities (235 seeds/pot) and (C) invasive species seeds.



Figure 3.3 Seed sowing was realized using cardboard with holes (each hole corresponding to a seed) as to ensure a fixed spatial arrangement of the recipient communities.

Before the invasive species were introduced, any ungerminated native species seeds were replaced, to ensure the intended density of seedlings. On March 22, 2018, seeds from one invasive species were sown in each pot at nine fixed positions 8 cm apart. In order to reduce the bias related to the intrinsic germination capacity of the harvested invasive species seeds, we adjusted the number of seeds introduced at each position from two to five (Supplementary material, *Table S3.1*) based on the preliminary germination tests described above (Supplementary material, *Table S3.1*). If several seedlings emerged from the same position, only the seedling at the most advanced development stage was kept. Seedling emergence rate was therefore considered to be 100% when at least one individual emerged at each position.

For each invasive species, there were four replicates of each recipient community type (i.e. each combination of recipient species time advance \times composition \times density) and four control pots with bare soil, totaling 156 pots. Pot distribution followed a randomized design and was randomized six times during the experiment to take account of microclimate effects.

2.4| Data collection

The aim of this experiment was to understand the ways by which characteristics of the recipient communities (i.e. time advance, species composition and density) influenced early invasion success. Hence, in addition to monitoring early establishment success of the invasive species, we collected data on the recipient communities' characteristics susceptible to mediate early invasion resistance i.e. biomass production, vegetation cover, and soil nutrient content. We did not seek to evaluate the impact of invasive species on recipient communities.

Early establishment success of invasive species was assessed by monitoring seedling emergence and survival of each invasive plant individual each week for the first six weeks and then every two weeks until the end of the experiment. Seedlings were considered to have emerged when any part was visible. We considered the invasion resistance of the recipient community to have increased when there was a reduction in probability of invasive species establishment (seedling emergence or survival). The aboveground biomass of each native species of the recipient community was measured either: **(1)** once all invasive individuals had died within a pot, even before the end of the experiment; or **(2)** at the end of the experiment, even if individual invasives remained alive. For each pot, aboveground biomass was collected 1 cm above ground level, sorted by species and dried at 80°C for 48 hr until weighed. Total below-ground biomass (native and invasive species roots) was measured at the end of the experiment for six randomly selected pots per recipient community type. For this purpose, one eighth of the pot soil volume was randomly withdrawn. Roots were isolated, washed and sieved with a 250- μ m mesh, dried for 48 hr at 80°C and weighed. We then estimated dry root weight per pot by multiplying the dried sample weight by 8.

To estimate vegetation cover at the time of invasive species seed introduction, digital images of the pots were acquired for computed image analysis via a Nikon D80 (Nikon Corporation, Tokyo, Japan) digital camera with a 10.2 megapixel CDD sensor. The camera was mounted on a 1.4-m high fixed camera stand with the lens facing exactly perpendicular to the ground, where the pots were placed successively.

Soil resource availability influences competition intensity (Craine & Dybzinski 2013), as well as the importance of priority effects (Kardol et al. 2013). We therefore analyzed organic carbon, nitrogen, nitrates, ammonium and available phosphorus on soil samples collected from each pot at the time of invasive species seed introduction. For this purpose, 72 soil cores of 10 mm diameter \times 100 mm deep were collected for each recipient community type (six per pot), pooled and air-dried for 48 hr at 40°C and sieved (<2 mm) to remove roots and rocks. Samples were analyzed for: **(1)** organic carbon by sulfochromic oxidation (NF ISO 14234, 1998); **(2)** total nitrogen by the modified Kjeldhal method (NF ISO 11261, 1995); **(3)** nitrate NO_3^- and ammonium NH_4^+ (NF ISO 14256-2, 2007); and **(4)** available phosphorus P_2O_5 by the Dyer method (NF X31-160, 1999). All soil parameters were determined according to the standard French method AFNOR (Afnor 1994) or standard international method ISO. Analyses were conducted by an accredited soil analysis laboratory following standard protocols (Teysier 2020).

2.5| Data analyses

Modelling invasive species seedling emergence and survival

We used a multistate capture–recapture modeling framework (Lebreton & Cefe 2002) to estimate the seedling emergence and daily plant survival probabilities of introduced invasive individuals. In this study, multistate capture–recapture modeling was preferable to simple logistic regressions, as it allowed the different transition probabilities (seedling emergence, plant survival) to be integrated within a common

framework. Capture (introduction of invasive species seeds) and recapture (subsequent visits) events were defined according to the experimental monitoring protocol. Monitoring intervals were specified in days to take into account unequal time intervals. We considered each individual as being in one of three states: seed (S), plant (P) and dead (D). Seed state means that no part of the emerged seedling was visible. Plant state means that any part of the seedling was visible and alive. Plants were considered dead when no green tissue remained. We examined the additive effects of time advance (time), species composition (comp) and density (den) and their interactions on the probability of seedling emergence (transition from seed to plant) and daily plant survival (transition from plant to dead state) of the three invasive species (*Supplementary material S3.I*). Our controlled conditions eliminated the possibility of individuals being missed during monitoring, so detection probability should be 100%. Therefore, our models can be considered as ‘known-fate’ models, with no goodness-of-fit tests required (Cooch & White 2019).

Model selection and parameter estimation were performed for each invasive species using the program E-SURGE (which stands for multiEvent SURvival Generalized Estimation; Choquet et al. 2009). E-SURGE is a program for fitting multistate/multi-event models to capture–recapture (CR) data. Multistate models are survival models that can integrate state-dependent survival and transition probabilities among states. A state may be described as a categorical individual covariate that can change over time (e.g. seed and plant states).

Transitions may have a different meaning depending on the state definition (in our case probability of seedling emergence and survival). Our initial model was built to cover all the effects we intended to test:

$$\Psi_{time \times comp \times den} \cdot \Phi_{time \times comp \times den}$$

and modeled the probabilities of seedling emergence (ψ) and survival (ϕ). It incorporated the effects of time advance, species composition and density of the recipient community.

We followed a step-down approach proposed by Lebreton et al. (2009) for model selection, focusing first on seedling emergence probabilities and then on survival probabilities. The model selection was based on the Akaike information criterion corrected for overdispersion and small sample size (QAICc). We examined the effect of density, species composition and time advance by comparing QAICc scores, removing one effect at a time. We estimated a 95% confidence interval (CI) for each parameter. Survival probabilities were daily estimates. A generic model description and the steps in the model selection procedure are provided in *Supplementary material S3.I* and *S3.II*.

Total aboveground and belowground biomass of recipient communities

We analyzed differences in final total aboveground and below-ground biomass depending on recipient community type using Kruskal–Wallis rank sum tests. When the type of community had a significant impact on biomass, a *post-hoc* Dunn's test was performed (‘dunn.test’ package; Dinno 2015). Analyses were performed via the R ver. 3.4.3 statistical platform (R Core Team, R Foundation for Statistical Computing, Vienna, Austria). P-values lower than 0.05 were considered as statistically significant.

Recipient vegetation cover

We applied the image analysis method described by Stewart et al. (2007) to estimate percentage of vegetation cover in the pots, using consecutively Adobe 'Photoshop' software ver. 2015.0.1 (Adobe Systems, San Jose, CA, USA) and GIMP ver. 2.10.8 (GNU Image Manipulation Program, Groton, MA, USA) image processing software. Photoshop was used to select color and create the two masks separating vegetation (colored black) from ground (colored white). GIMP was then used to count the number of

black and white pixels. The percentage of vegetation cover was obtained by dividing the number of black (vegetation) pixels by the total number of pixels in the image. We analyzed differences in vegetation cover depending on recipient community type using Kruskal–Wallis rank sum tests. When the type of community had a significant impact on vegetation cover, a *post-hoc* Dunn's test was performed ('dunn.test' package; Dinno 2015). Analyses were performed via the R ver. 3.4.3 statistical platform. P-values lower than 0.05 were considered as statistically significant.

Soil analyses

We analyzed differences both in total organic matter, carbon and nitrogen content, and in nitrate, ammonium and phosphorus content: (1) between soil containing 5-month and 1-month communities; and (2) between soil containing LowD and HighD communities, using a Wilcoxon–Mann–Whitney test. We also analyzed differences between soil with 1-sp, 3-sp and 9-sp communities, using a Kruskal–Wallis rank sum test. Analyses were performed via the R ver. 3.4.3 statistical platform. P-values lower than 0.05 were considered as statistically significant.

3| Results

3.1| Invasive species seedling emergence

The probability of seedling emergence (hereafter 'seedling emergence') was best explained by: (1) time advance for *A. artemisiifolia* and *C. selloana*; and (2) the interaction between species composition and time advance for *B. barbinodis* (Supplementary material S3.II). *Ambrosia artemisiifolia* and *C. selloana* showed lower seedling emergence in 5-month communities than in 1-month communities (Figure 3.4A,C). While *A. artemisiifolia* seedling emergence was higher in the control than in communities (Figure 3.4A), *C. selloana* seedling emergence tended to be similar or lower in the control than in communities (Figure 3.4C). Seedling emergence of *B. barbinodis* was similar in control, 1-month communities and 5-month monocultures, and was lower in 5-month polycultures (Figure 3.4B).

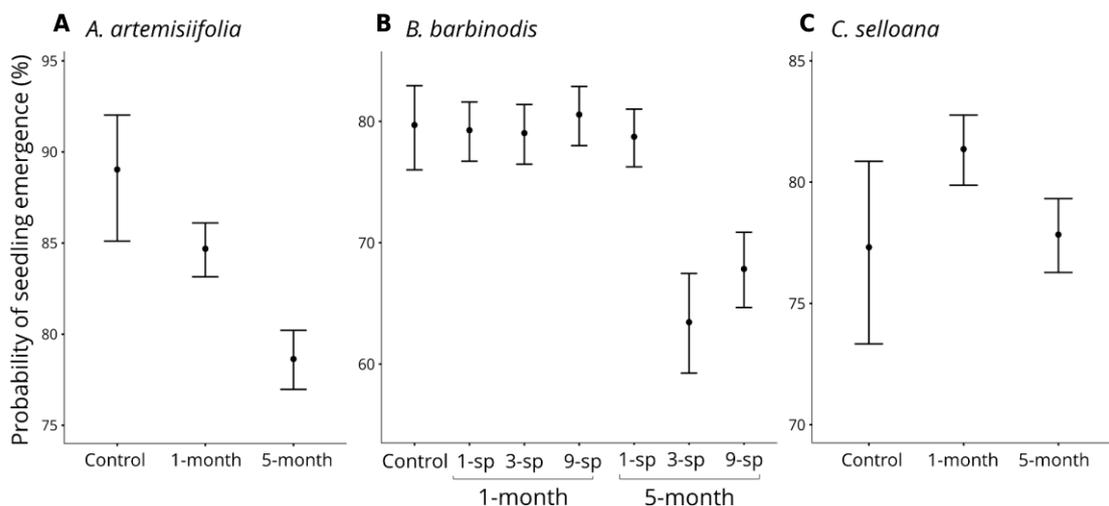


Figure 3.4 Probability of seedling emergence (model estimates; percentage \pm 95% CI) of the invasive species: (A) *Ambrosia artemisiifolia* ($n_{\text{tot}} = 432$); (B) *Bothriochloa barbinodis* ($n_{\text{tot}} = 432$); and (C) *Cortaderia selloana* ($n_{\text{tot}} = 432$), depending on recipient community on recipient community type: time advance over invasive species (one month or five months), species composition (1-sp = one species, 3-sp = three species, 9-sp = nine species), and density (LowD = low density, HighD = high density). Control refers to bare soil.

3.2| Invasive species survival

The daily probability of survival (hereafter ‘survival’) was best explained by: (1) the interaction between density, species composition and time advance for *A. artemisiifolia*; (2) species composition for *B. barbinodis*; and (3) the interaction between species composition and time advance for *C. selloana* (Supplementary material S3.II). Survival was not (*A. artemisiifolia* and *C. selloana*; Figure 3.5A,C) or only slightly (*B. barbinodis*; Figure 3.5B) lower in monocultures than in control. All species survival was lower in polycultures than in control and monocultures (Figure 3.5). Survival of *A. artemisiifolia* and *C. selloana* was lower in 5-month polycultures than in 1-month polycultures and control (Figure 3.5A,C). *A. artemisiifolia* also showed lower survival in HighD than in LowD 1-month polycultures.

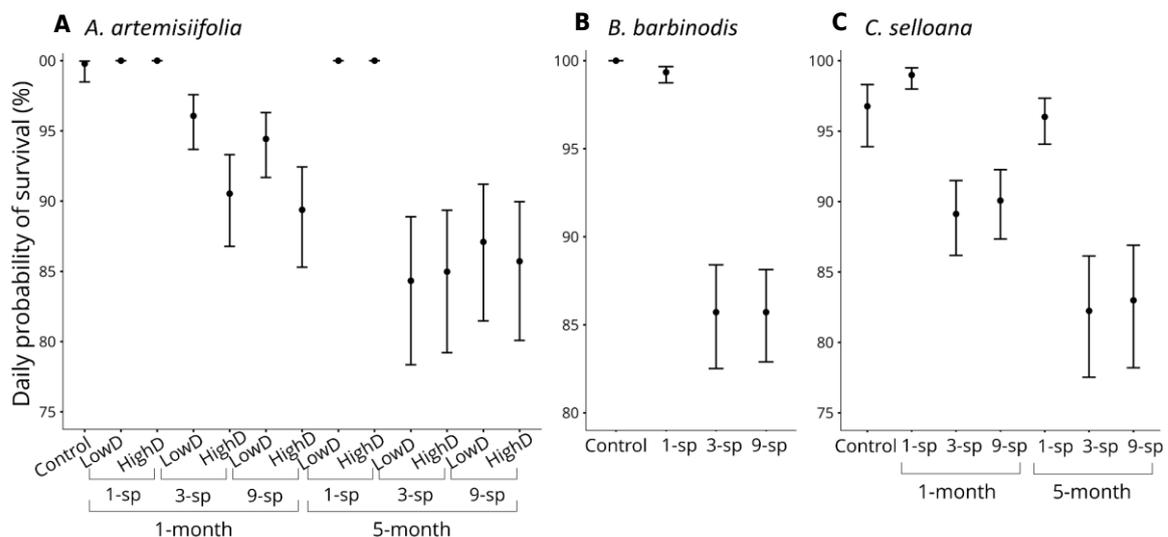


Figure 3.5 Daily probability of survival (model estimates; percentage \pm 95% CI) of the invasive species: (A) *Ambrosia artemisiifolia* ($n_{\text{tot}} = 389$); (B) *Bothriochloa barbinodis* ($n_{\text{tot}} = 336$) and (C) *Cortaderia selloana* ($n_{\text{tot}} = 368$) depending on recipient community type: time advance over invasive species (one month or five months), species composition (1-sp = one species, 3-sp = three species, 9-sp = nine species), and density (LowD = low density, HighD = high density). Control refers to bare soil.

3.3| Total aboveground and belowground biomass of recipient communities

Recipient community type significantly impacted the final total above-ground biomass of the recipient community (Kruskal–Wallis $\chi^2=7.6$, $df=11$, $p<0.001$). Final total aboveground biomass was significantly lower in monocultures than in polycultures (*post-hoc* Dunn's test, $p<0.01$; Figure 3.6), regardless of time advance and density. We found no significant difference between 3-sp and 9-sp communities (*post-hoc* Dunn's test, $p>0.05$; Figure 3.6). *Trifolium repens* largely dominated 3-sp communities, representing on average $76.4\pm 8.2\%$ of the total biomass, while *L. perenne* and *P. lanceolata* only represented 9.1 ± 5.3 and $2.8\pm 1.1\%$ (Figure 3.6). *Lotus corniculatus* dominated 9-sp communities, representing on average $61.3\pm 10.5\%$ of the total biomass, followed by *T. repens* ($16.7\pm 6.6\%$) and *D. glomerata* ($5.9\pm 2.0\%$; Figure 3.6). The cumulative aboveground biomass of other species represented less than 5% of total aboveground biomass. No clear pattern was detected for final total belowground biomass (Supplementary material, Figure S3.3).

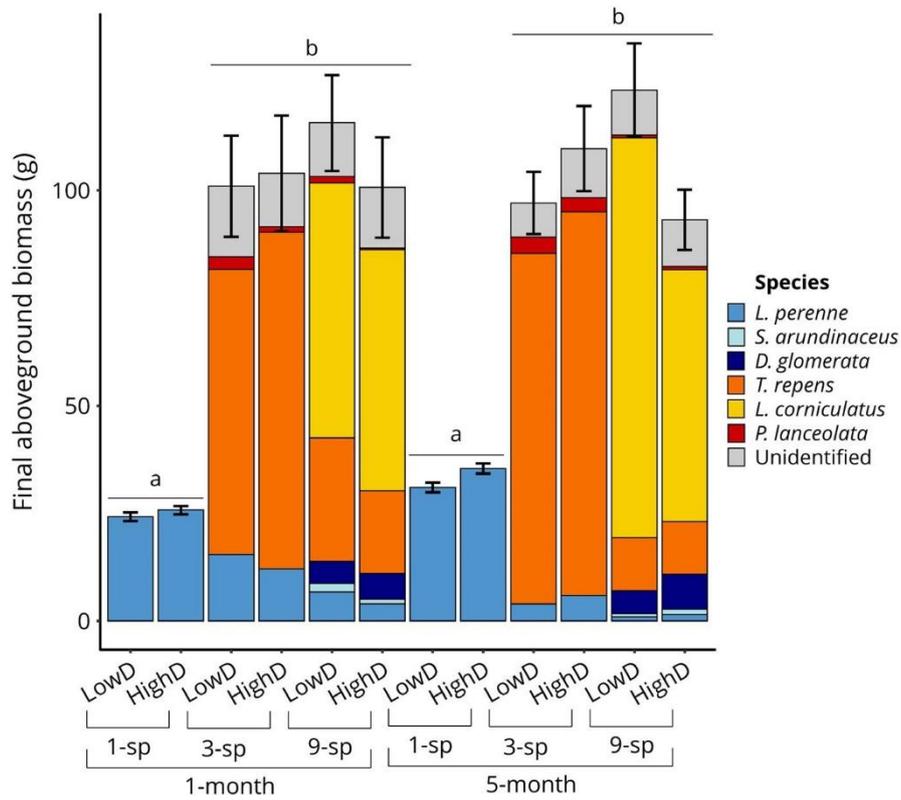


Figure 3.6 Final aboveground biomass of the community (mean \pm SE, n=12) classed by species, depending on recipient community type: time advance over invasive species (1 month or five months), species composition (1-sp = one species, 3-sp = three species, 9-sp = nine species), and density (LowD = low density, HighD = high density). Values below 0.1g are not represented, therefore *Achillea millefolium*, *Onobrychis viciifolia*, and *Poterium sanguisorba* are not shown. Letters (a,b) distinguish total biomass means that are significantly different according to a post-hoc Dunn's test ($\alpha=0.05$).

3.4| Recipient vegetation cover

Recipient community type significantly impacted vegetation cover percentage at the time of invasive species introduction (Kruskal-Wallis $\chi^2=127.07$, $df=11$, $p<0.001$). We found no statistical difference between 5-month communities, whatever the density or species composition (*post-hoc* Dunn's test, $p>0.05$; Supplementary material, *Figure S3.4*). 5-month communities had significantly higher vegetation cover than 1-month communities ($81.7\pm 5.9\%$ and 3.9 ± 2.6 respectively, *post-hoc* Dunn's test, $p<0.05$; Supplementary material, *Figure S3.4*). In 1-month communities, increasing density significantly increased vegetation cover for each species composition (*post-hoc* Dunn's test, $p<0.05$). Species composition did not impacted vegetation cover in 1-month communities so that no statistical difference was found between 1-month LowD communities ($p>0.05$), nor between 1-month HighD communities ($p>0.05$; Supplementary material, *Figure S3.4*).

3.5| Soil analyses

Control soil was fertile (total nitrogen =3.54 g/kg, nitrate NO_3^- =0.092 g/kg, ammonium NH_4^+ =0.0446 g/kg, available phosphorus P_2O_5 =0.273 g/kg) and had a high total organic matter content (5.1%; Supplementary material, *Table S3.2*). Total nitrogen, NO_3^- , NH_4^+ and P_2O_5 contents were higher in control soil than in soil supporting recipient communities (Supplementary material, *Table S3.2*). We found no statistical difference in any measured soil parameter between soil supporting (1) LowD and HighD communities, nor (2) 1-sp, 3-sp and 9-sp communities ($p>0.05$; Supplementary material, *Table S3.2*). Soil supporting 5-month communities showed no difference in similar contents of total organic matter, carbon and nitrogen contents ($p>0.05$), and lower NO_3^- ($p=0.005$), NH_4^+ ($p=0.005$) and P_2O_5 ($p=0.002$) contents than soil supporting 1-month communities (Supplementary material, *Table S3.2*).

4| Discussion

Overall in this experiment, establishing a recipient community negatively impacted invasive species early establishment success (*Figures 3.3, 3.4*; Supplementary material, *Figures S3.5, S3.6*), supporting revegetation as a relevant tool to limit invasions (Byun & Lee 2017; Larson et al. 2013; Middleton et al. 2010). Responses varied depending on the characteristics of the recipient communities and on the invasive species.

4.1| Time advance mainly determined invasive species seedling emergence

On its own, the time advance given to the recipient community mainly explained variations in seedling emergence of *A. artemisiifolia* and *C. selloana*, which tended to decrease with increasing time advance (*Figure 3.4A,C*). Germination is regulated by environmental components, mainly temperature, light, water (Koller & Kozłowski 1972), and soil nitrate concentration (Pons 1989). Seeds can detect the presence of neighboring plants early on, in particular by perceiving (1) spectral changes in the light environment resulting from the presence of a canopy (Batlla et al. 2000), or (2) low nitrate availability resulting from nitrate preemption by plants (Pons 1989). Thus, the decrease in seedling emergence observed with increasing recipient community time advance (*Figure 3.4A,C*) may be related to both phenomena, since (1) vegetation percentage cover was much higher in 5-month than in 1-month communities (Supplementary material, *Figure S3.4*), and (2) significantly lower soil nitrate content was found for 5-month than for 1-month communities at the time invasive species were introduced (Supplementary material, *Table S3.2*).

Responses differed between invasive species. While seedling emergence of *A. artemisiifolia* tended to be the lowest in both 5-month and 1-month recipient communities, *C. selloana* showed the highest seedling

emergence in 1-month communities (*Figure 3.4A,C*). This suggests that the communities established for 1 month facilitated *C. selloana* seedling emergence through the creation of better conditions than bare soil, probably by retaining humidity and generating adequate shade conditions (Domenech 2005; Holmgren et al. 1997).

The interaction between time advance and species composition of the recipient community best explained variations in seedling emergence of *B. barbinodis* (*Figure 3.4B*). Species composition impacted seedling emergence in 5-month communities, where seedling emergence was lower in polycultures; however, it had no impact in 1-month communities. It seems unlikely that the effect of species composition in 5-month polycultures is driven by variations in vegetation cover or soil parameters, which were similar to monocultures at the time of invasive species introduction (Supplementary material, *Figure S3.4, Table S3.2*). We therefore hypothesize that a higher overlap between resident species foliage occurred in 5-month polycultures (likely more productive than monocultures; *Figure 3.6*), generating variations in the light environment that impacted *B. barbinodis* germination (Benech-Arnold et al. 2000). Also, we suggest that the absence of impact of species composition in 1-month communities may be due to the similarities in cover, nutrient contents, and biomass production between the different communities at this very early growth stage. These results imply that the species composition contribution to invasion resistance may vary depending on the stage of community growth, and on the invasive species.

4.2| Time advance interacted with species composition to determine invasive species survival, density had a limited impact

Invasive species survival was strongly affected by the species composition of the recipient community. Species composition alone determined *B. barbinodis* survival, but also strongly influenced, in interaction with other community characteristics, *A. artemisiifolia* and *C. selloana* survival. An identical response pattern was observed for the three invasive species: 3-sp and 9-sp communities reduced the invasives' survival to the same extent: the survival rate was lower than in monocultures, where it remained comparable to bare soil (*Figure 3.5*). This pattern appeared strongly correlated to total aboveground biomass production of the recipient communities: biomass production was 3 to 4 times lower in monocultures than in polycultures. Another factor, however, is that 3-sp and 9-sp communities were dominated by two different species (*T. repens* and *L. corniculatus* respectively; *Figure 3.6*). Therefore, we found that the total biomass produced explained the enhanced invasion resistance in polycultures rather than the number of species (i.e. high species richness is often associated with increased resistance to invasion at small scales; (Byun et al. 2013; Dukes 2002; Fargione & Tilman 2005; Kennedy et al. 2002; Levine & D'Antonio 1999), or the identity of the dominant species.

The prevalent role of biomass was also highlighted by *A. artemisiifolia* and *C. selloana* survival patterns. *A. artemisiifolia* and *C. selloana* survival was influenced by the interaction between time advance and species composition (*Figure 3.5A,C*). In polycultures, survival was lower in 5-month than 1-month communities, supporting the assumption that a greater time advance increases competitive abilities compared to later-arriving invasive species (Wilsey et al. 2015) and enhances invasion resistance (Orloff et al. 2013; von Gillhaussen et al. 2014; Young et al. 2016). However, time advance did not impact as much monocultures' invasion resistance, most likely due to too low biomass production (*Figure 3.6*). These results suggest that it is not the time advance per se, but rather the amount of biomass produced (and thus the amount of limiting resource preempted) that determines the size of the competitive advantage given to the previously-established species, and in this case, invasion resistance. Overall, these findings (i.e. biomass prevailing over species composition or time advance) are consistent with previous

studies showing that stand biomass is a major determinant of invasibility (Lulow 2006; Mason et al. 2017; Rinella et al. 2007).

In most cases, density did not impact early establishment success of the invasive species (*Figures 3.4, 3.5*). Density only appeared to strongly impact *A. artemisiifolia* survival in 1-month communities, where higher density tended to decrease the survival rate in polycultures (*Figure 3.5A*). The higher number of individuals may have led, in very early stages of community growth, to greater resource preemption, thereby hindering *A. artemisiifolia* survival. The absence of impact from density (**1**) in 5-month communities may have been caused by biomass stabilization over time (*Figure 3.6*; von Gillhaussen et al. 2014), and (**2**) in 1-month monocultures may be due to insufficient aboveground biomass production (*Figure 3.6*). It is possible that biomass stabilized over time, with both LowD and HighD communities reaching the biomass threshold value (i.e. the carrying capacity) of the habitat. In this case, a further increase in biomass can only be achieved if mortality causes reductions in density and frees up space for survivors (i.e. self-thinning; Crawley 2007; Stoll et al. 2002). Since only one invasive species was impacted by community density, our results provide little support for the hypothesis that increasing density lowers early establishment success of invasive species at the early stage of community growth. However, this should be tested in field conditions, where carrying capacity may be less restrictive.

It appears from our results that extending the time advance of native species on invasive species seed arrival can reinforce priority effects, therefore reducing invasion success on soil cleared of vegetation. How much of an advantage this time advance represents will, however, depend on biomass production. The positive effect could be maximized by clearing soil of invasive species propagules and vegetative parts before rapidly sowing native plant communities, and by carefully controlling invaders during the first few weeks. Eliminating rhizomes fragments may be particularly critical since rhizome emergence is less sensitive to the presence of neighbors than seedling emergence (Kettenring et al. 2015), and rhizomes are likely to have greater overall establishment success than seeds because they are better provisioned (Silvertown 2008; Winkler & Fischer 2002).

The benefits from giving a time advance to certain species can remain visible for years (Young et al. 2016), so this strategy may also pay off in the long term. In our short-term experiment, the contribution of only a few species to invasion resistance in polycultures implies that establishing a few productive species may be an efficient strategy to repel invasive species colonization at the early stages of community growth. On the other hand, long-term studies suggest that implementing diverse communities may ensure ecosystems against declines in productivity (Lawton & Brown 1994; Yachi & Loreau 1999) and reduce biomass and resource-use fluctuations over time (Cottingham et al. 2001; Hooper et al. 2005), potentially leading to greater resistance in the long term (Dunstan & Johnson 2007). Further research will be needed to determine whether combinations of different seeding strategies (i.e. early sowing of a few productive species, followed by late sowing of species mixtures) can help to reinforce invasion resistance in both short and longer terms.

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Supplementary material

Table S3.1 Results of preliminary invasive species germination tests realized before the experiment and used to define the number of introduced seeds for the three harvested populations (GPS coordinates indicated) of each of the three tested invasive species. Based on the results of preliminary germination rates ('Germination rate'), we determined the theoretical number of seeds required to achieve one emerged individual ('Theoretical No. of seeds'). The final number of seeds introduced ('Applied No. of seeds') was then calculated by rounding the theoretical number of introduced seeds up to the next whole number (i.e. in order to theoretically achieve at least one emerged individual). This adjustment aimed at reducing the bias linked with the intrinsic germination capacity of the harvested invasive species seeds in the experiment.

Species	Population location (GPS coordinates)	Germination rate (%)	Theoretical No. of seeds	Applied No. of seeds
<i>A. artemisiifolia</i>	Pop. 1 : 44°0'44.3" N, 4°52'13.8" E	67.5	1.48	2
	Pop. 2 : 43°54'27.2" N, 4°52'13.8" E	23.9	4.18	5
	Pop. 3 : 43°51'57.1" N, 4°35'46.8" E	67.5	1.48	2
<i>B. barbinodis</i>	Pop. 1 : 43°33'23.1" N, 4°19'16.1" E	89.7	1.11	2
	Pop. 2 : 43°40'7.9" N, 3°58'31.9" E	25.8	3.88	4
	Pop. 3 : 43°39'39.9" N, 4°38'28.6" E	69.4	1.44	2
<i>C. selloana</i>	Pop. 1 : 43°41'47.1" N, 4°38'41.1" E	38.6	2.59	3
	Pop. 2 : 43°23'22.9" N, 4°34'28.1" E	46.0	2.17	3
	Pop. 3 : 43°23'50.3" N, 5°7'54.6" E	64.2	1.56	2

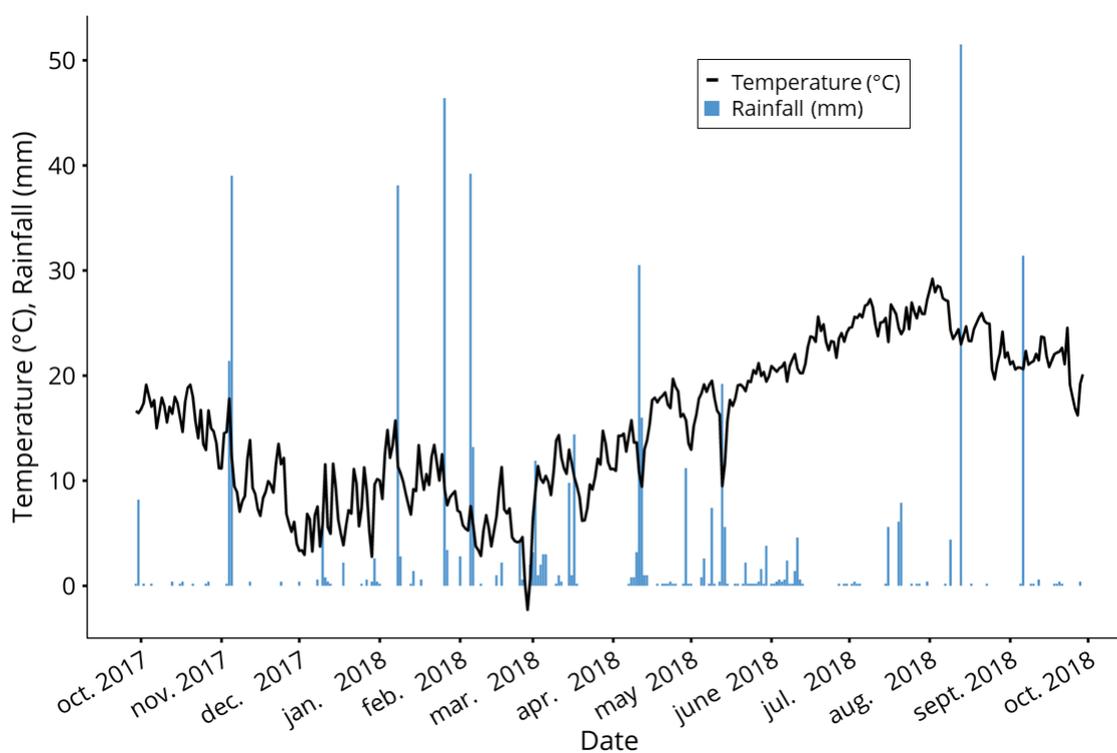


Figure S3.1 Temperature (daily mean in °C) and rainfall (daily sum in mm) recorded during the experiment (Meteo France station number 133004003, Tour du Valat domain, France).

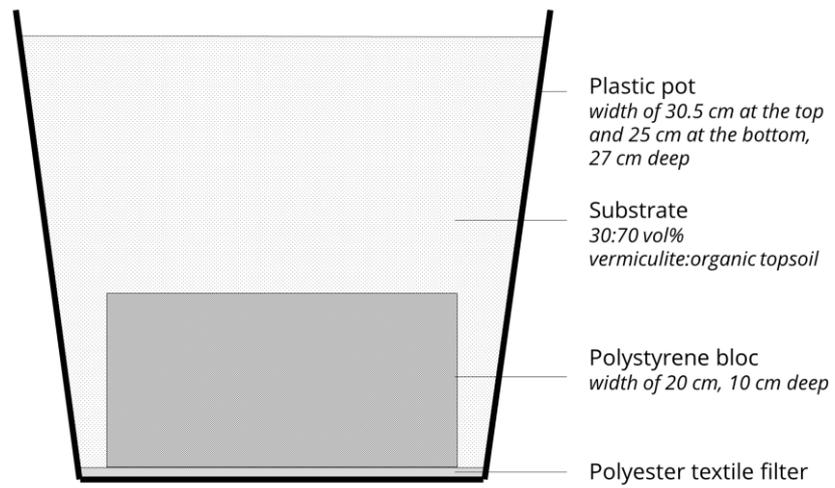
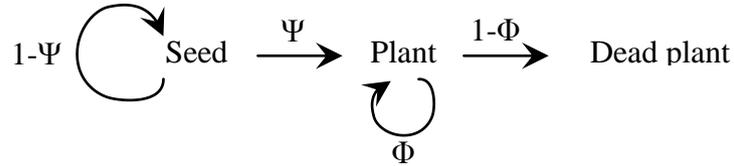


Figure S3.2 Experimental design: pot filling.

Supplementary material S3.I Description of Capture-Marking-Recapture modeling

Matrices

The model considered three states, the seed state (S), the plant state (P), and the dead state (D) to estimate two transition probabilities: seedling emergence (ψ) and daily survival (ϕ):



Individual life history in the context of the study protocol

Initial

Initial State: At the initial state, all individuals are in the seed state

$$\begin{matrix} S & P \\ (* & -) \end{matrix}$$

With ‘*’ indicating the complementarity parameter (only one ‘*’ by row) and ‘-’ indicating parameters constrained to zero

Transition 1: Estimation of seedling emergence (ψ)

$$\begin{matrix} S & P & D \\ S \begin{pmatrix} * & \psi & - \\ P \begin{pmatrix} - & * & - \\ D \begin{pmatrix} - & - & * \end{pmatrix} \end{pmatrix} \end{pmatrix} \end{matrix}$$

Transition 2: Estimation of daily survival (ϕ)

$$\begin{matrix} S & P & D \\ S \begin{pmatrix} * & - & - \\ P \begin{pmatrix} - & \phi & * \\ D \begin{pmatrix} - & - & * \end{pmatrix} \end{pmatrix} \end{pmatrix} \end{matrix}$$

Recapture: Detection probability

Detection probability (p) was equal to 1 so the non-observed rate (NO) was equal to 0.

$$\begin{matrix} NO & S & P \\ S \begin{pmatrix} * & p & - \\ P \begin{pmatrix} * & - & p \\ D \begin{pmatrix} * & - & - \end{pmatrix} \end{pmatrix} \end{pmatrix} \end{matrix}$$

Supplementary material S3.II Model selection for invasive species seedling emergence and survival

Ambrosia artemisiifolia

Model selection for seedling emergence probabilities with survival probabilities [φ time \times comp \times den] for *A. artemisiifolia*. Models are ranked by decreasing value of QAICc, with the best model in bold. Number of estimable parameters (NP) and model deviance are also given.

Model	Seedling emergence	NP	Deviance	QAICc
7	ψtime	16	2765.85	2797.94
3	ψ den \times time	18	2764.46	2800.58
4	ψ comp \times time	20	2761.51	2801.66
1	ψ den \times comp \times time	26	2751.82	2804.06
5	ψ den	16	2794.73	2826.62
6	ψ comp	19	2790.90	2829.03
2	ψ den \times comp	20	2789.63	2829.77
8	ψ .	14	2807.59	2835.66

Model selection for daily plant survival probabilities with best model for emergence probabilities [ψ time] for *A. artemisiifolia*. Models are ranked by decreasing value of QAICc, with the best model in bold. Number of estimable parameters (NP) and model deviance are also given.

Model	Survival	NP	Deviance	QAICc
7	φden\timescomp\timestime	16	2765.85	2797.94
11	φ comp \times time	10	2781.09	2801.12
9	φ den \times comp	10	2802.37	2822.41
13	φ comp	7	2812.60	2826.62
10	φ den \times comp	8	3018.89	3034.91
14	φ time	6	3028.34	3040.36
12	φ den	6	3038.61	3050.62
15	φ .	4	3086.95	3094.97

Bothriochloa barbinodis

Model selection for seedling emergence probabilities with survival probabilities [φ time \times comp \times den] for *B. barbinodis*. Models are ranked by decreasing value of QAICc, with the best model in bold. Number of estimable parameters (NP) and model deviance are also given.

Model	Seedling emergence	NP	Deviance	QAICc
4	Ψcomp\timestime	20	3052.50	3092.64
1	ψ den \times comp \times time	26	3043.41	3095.64
7	ψ time	16	3106.91	3138.10
3	ψ den \times time	18	3105.29	3141.40
6	ψ comp	17	3141.23	3175.33
2	ψ den \times comp	20	3137.28	3177.42
5	ψ den	16	3166.56	3198.65
8	ψ .	14	3172.94	3201.01

Model selection for daily plant survival probabilities with best model for emergence probabilities [ψ time \times comp] for *B. barbinodis*. Models are ranked by decreasing value of QAICc, with the best model in bold. Number of estimable parameters (NP) and model deviance are also given.

Model	Survival	NP	Deviance	QAICc
9	φden\timescomp	14	3064.23	3092.30
4	φ den \times comp \times time	20	3052.50	3092.64
13	φ comp	11	3070.70	3092.75
11	φ comp \times time	14	3065.32	3093.39
14	φ time	10	3282.99	3303.02
10	φ den \times time	12	3281.66	3305.71
12	φ den	10	3287.51	3307.54
15	φ .	14	3337.65	3353.68

Cortaderia selloana

Model selection for seedling emergence probabilities with survival probabilities [φ time \times comp \times den] for *C. selloana*. Models are ranked by decreasing value of QAICc, with the best model in bold. Number of estimable parameters (NP) and model deviance are also given.

Model	Seedling emergence	NP	Deviance	QAICc
7	ψtime	16	3504.46	3536.56
3	ψ den \times time	18	3503.29	3539.42
4	ψ comp \times time	20	3499.37	3539.52
8	ψ .	14	3516.59	3544.67
6	ψ comp	17	3512.23	3546.34
5	ψ den	16	3514.37	3546.47
1	ψ den \times comp \times time	26	3495.14	3547.40
2	ψ den \times comp	20	3510.29	3550.45

Model selection for daily plant survival probabilities with best model for emergence probabilities [ψ time] for *C. selloana*. Models are ranked by decreasing value of QAICc, with the best model in bold. Number of estimable parameters (NP) and model deviance are also given.

Model	Survival	NP	Deviance	QAICc
11	φcomp\timestime	10	3510.30	3530.34
7	φ den \times comp \times time	16	3504.46	3536.56
13	φ comp	7	3539.91	3553.93
9	φ den \times comp	10	3534.68	3554.72
14	φ time	6	3652.54	3664.55
10	φ den \times time	8	3650.52	3666.55
12	φ den	6	3668.1691	3680.19
15	φ .	4	3680.52	3688.52

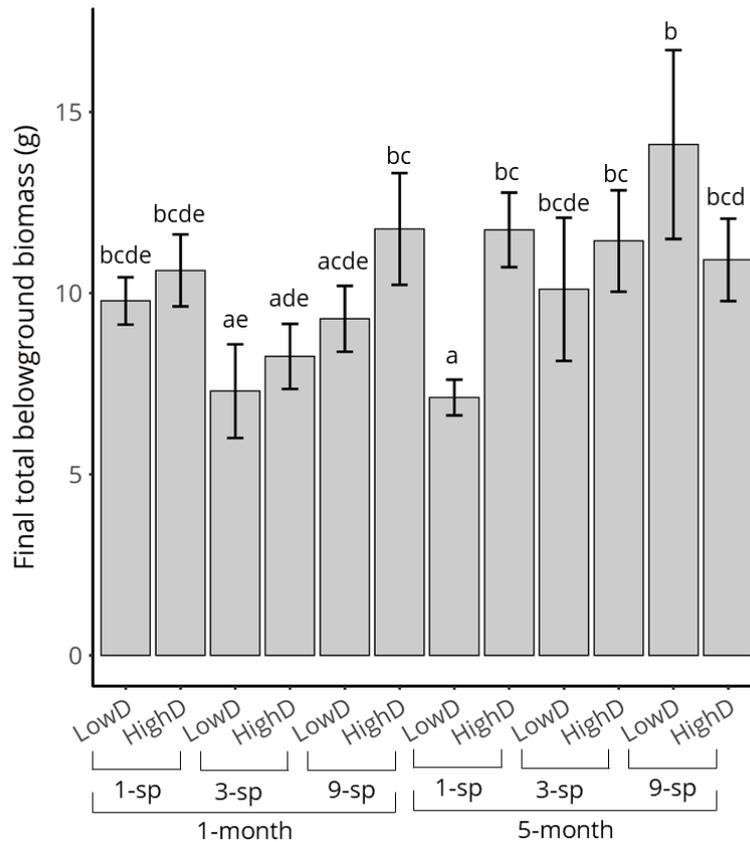
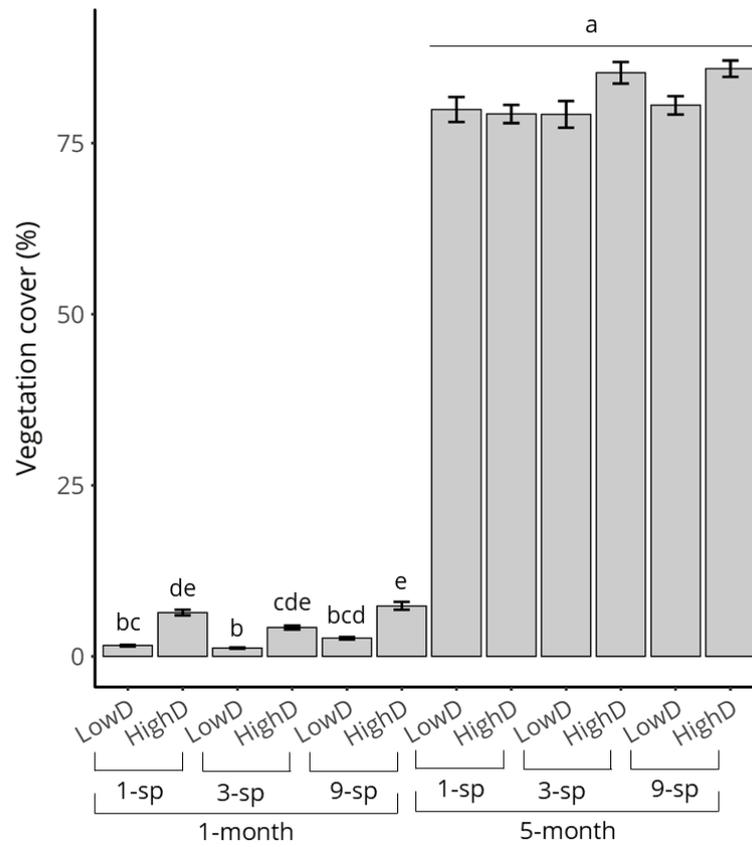


Figure S3.3 Final total belowground biomass (mean±SE, n=6) depending on recipient community type: time advance over invasive species (1- or 5-month), species composition (1-sp = 1 species, 3-sp = 3 species, 9-sp = 9 species) and density (LowD = low density or HighD = high density). Community type significantly impacted final total belowground biomass (Kruskal-Wallis $\chi^2=20.61$, $df=11$, $p=0.038$). Increasing density significantly increased belowground biomass only for the 5-month monocultures (post-hoc Dunn's test, $p=0.035$). Increasing time advance significantly (1) increased belowground biomass for the 3-sp HighD and 9-sp LowD communities (post-hoc Dunn's test, $p=0.031$ and $p=0.042$, respectively) and (2) decreased belowground biomass for the LowD monocultures (post-hoc Dunn's test, $p=0.048$). Finally, species composition significantly impacted belowground biomass as following: (1) in LowD 5-month communities, monocultures showed significantly lower belowground biomass than polycultures (post-hoc Dunn's test, $p=0.048$ and $p=0.001$ for 3-sp and 9-sp, respectively), and (2) in HighD 1-month communities, 3-sp communities showed significantly lower belowground biomass than 9-sp communities ($p=0.036$). Letters (a,b,c,d,e) distinguish values that are significantly different according to a post-hoc Dunn's test ($\alpha=0.05$).



community type: time advance over invasive species (1- or 5-month), species composition (1-sp = 1 species, 3-sp = 3 species, 9-sp = 9 species), and density (LowD = low density or HighD = high density). Letters (a,b,c,d,e) distinguish vegetation cover percentage means that are significantly different according to a post-hoc Dunn's test ($\alpha=0.05$).

Table S3.2 Results of soil analyses. Soil parameters depending on community type: time advance over invasive species (1- or 5-month), species composition (1-sp = 1 species, 3-sp = 3 species, 9-sp = 9 species) and density (LowD = low density or HighD = high density). Here, time advance corresponds to the age of the recipient community at the time of soil analyses.

			Total organic matter (%)	C (g/kg)	N (g/kg)	NO ₃ ⁻ (g/kg)	NH ₄ ⁺ (g/kg)	P ₂ O ₅ (g/kg)
Control (bare soil)			5.1	29.5	3.54	0.092	0.0446	0.273
1-month	1-sp	LowD	5.1	29.6	2.39	0.042	0.0044	0.209
		HighD	5.0	29.1	2.72	0.032	0.0037	0.219
	3-sp	LowD	5.1	29.5	2.54	0.031	0.0042	0.211
		HighD	5.1	29.6	2.56	0.048	0.0049	0.222
	9-sp	LowD	5.0	28.9	2.39	0.028	0.0036	0.207
		HighD	5.0	28.7	2.33	0.063	0.0039	0.214
5-month	1-sp	LowD	5.0	29.0	2.64	0.010	0.0013	0.141
		HighD	5.2	29.9	2.49	0.005	0.0007	0.165
	3-sp	LowD	5.2	29.6	2.35	0.008	0.0011	0.176
		HighD	5.2	30.0	2.41	0.014	0.0013	0.161
	9-sp	LowD	5.2	30.0	2.47	0.010	0.0014	0.159
		HighD	5.1	29.6	2.56	0.010	0.0012	0.150

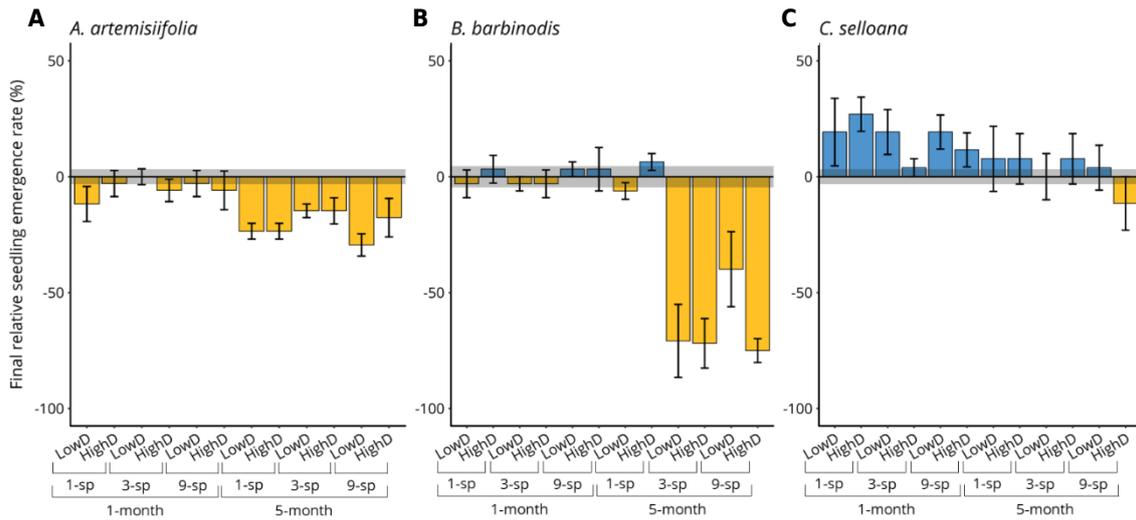


Figure S3.5 Final seedling emergence rate (mean±SE, n=4) relative to the control (0) of the invasive species **(A)** *A. artemisiifolia*, **(B)** *B. barbinodis* and **(C)** *C. selloana*, depending on recipient community type: time advance over invasive species (1- or 5-month), species composition (1-sp = 1 species, 3-sp = 3 species, 9-sp = 9 species), and density (LowD = low density or HighD = high density). Values below or above zero refer respectively to decreased or increased final seedling emergence rate compared to the control. SE of the control (bare soil) is represented by a grey area.

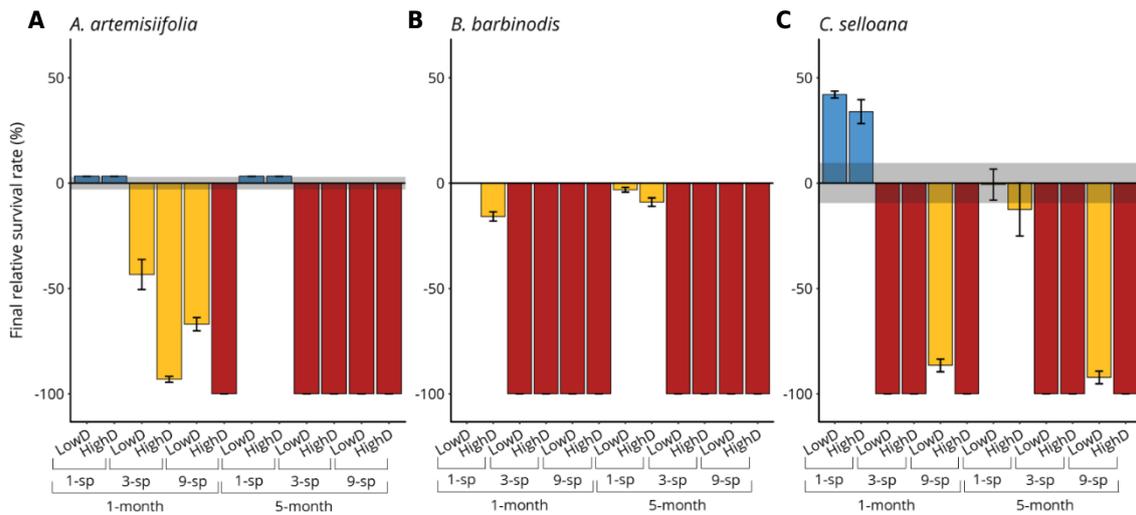


Figure S3.6 Final survival rate (mean±SE, n=4) relative to the control (0) of the invasive species **(A)** *A. artemisiifolia*, **(B)** *B. barbinodis* and **(C)** *C. selloana*, depending on recipient community type: time advance over invasive species (1- or 5-month), species composition (1-sp = 1 species, 3-sp = 3 species, 9-sp = 9 species) and density (LowD = low density or HighD = high density). Values below or above zero refer respectively to decreased or increased final germination rate compared to the control. Red bars indicate no survivors. SE of the control (bare soil) is represented by a grey area.