Résistance à l'invasion des communautés végétales établies après perturbation. Rôle de la dynamique de colonisation et des effets de priorité

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Présentée par
Manon C. M. Hess

Résistance à l'invasion des communautés végétales établies après perturbation
Rôle de la dynamique de colonisation et des effets de priorité

Early invasion resistance of plant communities established after a disturbance
Role of assembly history and priority effects

Soutenance publique prévue le le 06/11/2020 devant le jury composé de :

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Preface

Cette thèse a été réalisée dans le cadre d'une convention CIFRE (2017/0165) entre la société de construction et de génie civil NGE-GUINTOLI (Saint-Etienne-du-Grès, France), l'Institut de Recheche pour la conservation des zones humides Méditerranéennes Tour du Valat (Arles, France), et l'Institut Méditerranéen de Biodiversité et d'Ecologie marine et continentale (IMBE, Avignon, France) au sein d'Avignon Université (Avignon, France).

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This thesis was carried out under a French CIFRE convention (2017/0165) between the construction and civil engineering company NGE-GUINTOLI (Saint-Etienne-du-Grès, France), the Research Institute for the conservation of Mediterranean wetlands Tour du Valat (Arles, France), and the Mediterranean Institute of marine and terrestrial Biodiversity and Ecology (IMBE; Avignon, France) in Avignon University (Avignon, France).

NGE (*www.nge.fr*) is a French group of construction and civil engineering founded in 2006, realizing thousands of civil works every year mainly in France and in other countries. Activities include land management (soil treatment, mining, urban planning), constructions, riverbank management, and development of underground or surface pipelines and wired networks. The teams are committed to working alongside regional and local authorities to create bridges, roads, railways, optic fiber networks and leisure, and social and educational life spaces. Such actions, especially earthworks, cause deep ecosystem disturbances favoring invasive species establishment. NGE, concerned by environmental protection, fully initiated and funded this thesis project in order to develop revegetation strategies to reduce invasive plant establishment and spread after disturbances. This thesis work therefore aims at better understanding the determinants of early invasion resistance of newly established herbaceous plant communities. Results of this thesis were used to produce a practical guide, property of NGE, which provides revegetation principles to complement the currently known techniques and to improve the control of invasive plants in grassy environments.

Résumé

Les plantes invasives posent d'importants problèmes environnementaux et de santé publique, et leur contrôle est aujourd'hui un défi majeur. Elles rencontrent des conditions particulièrement favorables après des perturbations conduisant à une suppression du couvert végétal et une remobilisation des ressources disponibles. La mise en place d'un couvert végétal séquestrant rapidement ces ressources parait alors une réponse probante pour réduire l'invasion. Néanmoins, les caractéristiques des communautés nécessaires pour exercer une résistance efficace, notamment dans les premières phases d'installation, sont encore peu connues.

Dans cette thèse, je me suis intéressée à deux mécanismes qui pourraient influencer la résistance à l'invasion des communautés végétales herbacées lors des premiers stades d'installation après une perturbation majeure, que sont **(1)** la '*limiting similarity*', impliquant que la coexistence d'espèces partageant la même niche écologique est limitée par l'exclusion compétitive, et **(2)** les effets de priorité, qui surviennent lorsque l'installation d'une espèce affecte la performance ou la survie d'une espèce arrivant par la suite. L'examen de la littérature confirme que l'application de la '*limiting similarity*' pour lutter contre les plantes invasives est complexe et n'a, jusqu'à aujourd'hui, fait preuve d'efficacité. Elle apparait inadaptée aux situations les plus communes. Intégrer les effets de priorité aux méthodes de contrôle des plantes invasives après une perturbation semble d'avantage prometteur. Une des stratégies consiste en la mise en place d'un couvert végétal exerçant de forts effets de priorité négatifs, diminuant le succès d'installation des plantes invasives. Deux expérimentations en serre ont été réalisées à cet effet. Elles visent à jouer sur les effets de priorité de la communauté native receveuse composée d'espèces classiquement utilisées en revégétalisation, afin d'en comprendre l'implication dans la résistance à l'invasion. Dans une première expérimentation, le temps d'avance de la communauté receveuse sur l'arrivée de trois espèces invasives (i.e. *Ambrosia artemisiifolia*, *Bothriochloa barbinodis* et *Cortaderia selloana*), la composition en espèces et la densité des semis ont été manipulés. Une meilleure résistance à l'invasion a été observée lorsque les communautés produisent une forte biomasse aérienne, cette dernière étant associée à la présence d'espèces productives. Retarder l'arrivée des espèces invasives a également réduit le succès d'invasion, mais ceci uniquement lorsque la production de biomasse était suffisamment importante. Une seconde expérimentation a porté sur l'influence de l'identité de la première espèce installée (deux poacées : *Dactylis glomerata* ou *Lolium perenne* et deux fabacées : *Onobrychis viciifolia* ou *Trifolium repens*) dans la communauté receveuse ainsi que l'ordre de semis des espèces (semis simultané de la communauté ou séquentiel) sur la structuration de la communauté et les conséquences sur sa résistance à l'invasion par *A. artemisiifolia*. Des différences minimes dans la dynamique de colonisation de la communauté receveuse a substantiellement affecté sa structure, sa production de biomasse, la concentration du sol en nutriments, ainsi que sa résistance précoce à l'invasion. Le semis séquentiel a généralement diminué la résistance à l'invasion par rapport au semis simultané de l'ensemble de la communauté. Les espèces installées en premier ont généré des effets de priorité d'intensité variable, vraisemblablement par le biais de la compétition racinaire, impactant le succès d'invasion par *A. artemisiifolia*. L'introduction précoce de la fabacée fixatrice d'azote *T. repens* a particulièrement stimulé la performance de *A. artemisiifolia*.

En conclusion, tandis que l'application de la '*limiting similarity*' se révèle être incompatible avec la conception de communautés résistantes à l'invasion précoce, manipuler la dynamique de colonisation et les effets de priorité semble d'avantage prometteur. La dynamique de colonisation a considérablement influencé le succès d'invasion en induisant, chez la communauté receveuse, des différences de production de biomasse et de préemption des ressources. Les effets de priorité des communautés récemment établies et la résistance à l'invasion associée pourraient être améliorés en **(1)** maximisant le temps d'avance à la communauté receveuse par rapport aux espèces invasives, **(2)** introduisant des espèces capables de produire rapidement de la biomasse et de préempter les ressources du sol, et **(3)** évitant le semis séquentiel, en particulier lorsque les premières espèces installées sont des espèces productives fixatrices d'azote.

Mots clés : invasions biologiques ; contingences historiques ; dynamique temporelle ; ordre d'arrivée ; limiting similarity ; revégétalisation ; compétition ; composition ; densité ; biomasse ; communauté herbacée

Abstract

Invasive plant species cause serious environmental and sanitary issues and their control is today a major challenge. Disturbances involving vegetation removal and an increase in resource availability offer particularly favorable conditions for invasive plant colonization. Establishing a plant cover rapidly sequestering resources could be a relevant strategy to limit invasion. However, little is known about the characteristics enabling newly established communities to exert strong invasion resistance, especially in the early growth stages.

In this thesis, I focused on two potential determinants of invasion resistance of herbaceous plant communities in the early growth stages after a major disturbance, which are **(1)** the concept of limiting similarity, stating that the coexistence of species sharing the same ecological niche is limited by competitive exclusion, and **(2)** priority effects, which occur when the establishment of a species affects the performance or survival of later arriving species. The application of limiting similarity to control invasive plants appears complex, ineffective and unsuitable for the most common situations. In contrast, integrating priority effects into invasive plant management strategies seems more promising. One strategy consists in restoring a plant cover exerting strong negative priority effects, decreasing the success of subsequent invasive plant establishment. In two greenhouse experiments, I explored the role of priority effects in early invasion resistance. In a first experiment, I manipulated species composition, sowing density and the elapsed time between community sowing and invasion by *Ambrosia artemisiifolia*, *Bothriochloa barbinodis* and *Cortaderia selloana*. A higher invasion resistance was observed when communities produced a high aboveground biomass, which was associated with the presence of productive species. Delaying invasive species arrival also decreased invasion success, but only if it allowed a sufficient increase in biomass production. A second experiment investigated how the identity of the first native colonizer (one of two grasses: *Dactylis glomerata* and *Lolium perenne*, or one of two legumes: *Onobrychis viciifolia* and *Trifolium repens*) and the timing of species establishment (synchronous *vs.* sequential sowing) influenced the structuration of the recipient community and its resistance to invasion by *A. artemisiifolia*. Small differences in assembly history of the recipient community substantially affected community structure, biomass production, soil nutrient content, as well as early invasion resistance. Sequential sowing generally decreased invasion resistance compared with a synchronous sowing. Early colonizers generated priority effects of variable strength most likely *via* belowground competition, which affected *A. artemisiifolia*'s invasion success. A prior establishment of the N-fixing legume *T. repens* particularly boosted *A. artemisiifolia*'s performance.

In conclusions, this thesis work highlights the inadequacy of revegetation strategies based on limiting similarity and reveals promising perspectives of manipulating assembly history and priority effects for designing invasion resistant communities. Assembly history significantly influenced early invasion success by inducing differences in biomass production and resource preemption by the recipient community. Priority effects of newly established communities and associated invasion resistance could be enhanced by **(1)** giving as much time advance as possible to the recipient community over invasives, **(2)** introducing species displaying an ability to rapidly produce biomass and preempt soil resources, or **(3)** avoiding sequential sowing especially when early colonizers are nitrogen-fixing, productive species.

Key Words : biological invasions ; historical contingencies ; timing ; order of arrival ; limiting similarity ; revegetation ; competition ; composition ; density ; biomass ; herbaceous community

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Nature is not more complicated than you think,
it is more complicated than you CAN think.

Frank Edwin Egler

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General Introduction

I.1 | Biological invasions

I.1.1 | Definition

Invasive alien species (hereafter 'invasive species') can be defined as species introduced outside their normal distribution through human activity, that become established in natural or semi-natural ecosystems or habitat where they cause environmental damage, especially on resident species (Alpert et al. 2000; Shine & Williams 2000). Invasion ecology, the discipline studying the causes and the consequences of biological invasions (Richardson et al. 2011) emerged half a century ago in Charles' Elton seminal book: The Ecology of Invasions by Animals and Plants (1958). After rather hesitant beginnings, research on invasion ecology generated an extended body of literature (Davis 2006; Ricciardi & MacIsaac 2008; Richardson & Pyšek 2008). The field addresses aspects relating the introduction of organisms, their ability to establish, naturalize and invade the target region, their interactions with resident organisms in their new habitat, and the positive or negative impacts of their presence and abundance with reference to human value systems (Richardson & Van Wilgen 2004).

I.1.2 | Impacts of biological invasions

The number of species introduced intentionally or accidentally across their natural dispersal barriers started to increase dramatically 200 years ago with trade globalization (Hulme 2007; Seebens et al. 2017; Simberloff et al. 2013), and this increase is expected to intensify (Sala et al. 2000; Seebens et al. 2015). Organisms surviving to transit and successfully invading new habitats can threaten native biodiversity and ecosystem functions, human well-being, and generate devastating economic costs.

Biodiversity and ecosystem functioning

Invasive species are recognized as one of the leading global threats to biodiversity (Brondizio et al. 2019; Mollot et al. 2017; Sala et al. 2000; Vilà et al. 2011; Wilcove et al. 1998). Invasive species can impair native species distribution and abundance directly through direct consumption (Simberloff et al. 2013), or competitive displacement associated with habitat alterations (e.g. altered disturbance regimes; Gurevitch & Padilla 2004; Hejda et al. 2009), or indirectly by significantly altering disturbance regimes, and/or biogeochemical, hydrological and/or geomorphological ecosystem processes (Levine et al. 2003; Liao et al. 2008). Disruptions to mutualistic plant-animal (i.e. pollination and animal-assisted seed dispersal; Traveset & Richardson 2006) or plant-fungus (i.e. mycorrhizal associations; Roberts & Anderson 2001) interactions caused by invasions also contribute to the alteration of ecosystem functioning and stability.

Invasive species can also threat native species genetic integrity and existence through hybridization (Allendorf et al. 2001; Bleeker et al. 2007; Ellstrand & Schierenbeck 2000; Vilà et al. 2000). Hybrids can either be **(1)** less performant than native species, which can cause from progressive native population declines (Muhlfeld et al. 2009) to species extinction (Rhymer & Simberloff 1996), or **(2)** more vigorous than native species, which can lead to extended spread in new habitats and native species replacement (Majumder et al. 1997).

Human well-being and economy

While some introduced species clearly benefit to humanity (e.g. food crops, species used for biological pest control), others degrade human well-being directly. Invasions can affect constituents of well-being such as human health and quality of life, and also recreational activities and cultural heritage (Charles & Dukes 2008). Invasive species can act as vectors of disease (e.g. the Asian tiger mosquito imported in the U.S. transmit dengue fever and other human viruses; Craven et al. 1988), or provoke themselves health issues (e.g. the common ragweed pollen causing severe allergies; Smith et al. 2013). Invasive species affect nonetheless natural habitats, but also anthropogenic environments such as crops, rangelands and commercial forests, generating major economic losses in lost yields and control efforts (Pimentel et al. 2005; Scalera 2010).

Invasive species management global strategy

The disastrous impacts of invasions make efficient invasive species management a major ecological and conservation challenge worldwide. The emergency to regulate invasive species spread has been internationally acknowledged by the Convention on Biological Diversity international agreement, Article 8(h): 'Each contracting Party shall, as far as possible and as appropriate, prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species'. The European Union Regulation 1143/2014 on Invasive Alien Species provides a list of species of concern for Europe and a set of management measures to be taken for combatting these species. In France, a national strategy on Invasive Alien Species responding to the EU Regulation has been published in 2017 (Stratégie Nationale Relative aux Espèces Exotiques Envahissantes, 2017).

The optimal management strategy changes depending on invasion stage (*Figure I.1*; Simberloff et al. 2013), leading to a hierarchical approach that has been internationally adopted. This approach involves three types of measures: prevention, early detection and eradication, and long-term management. A proactive approach, focused on prevention and early intervention is often the most cost-effective management option (DiTomaso 2000; Sheley et al. 1996). The complete removal of an invasive species would be achievable if detected soon after its introduction and immediately removed (Rejmánek & Pitcairn 2002). When prevention and early eradication fail, management efforts focus on containing the core population to prevent the spread in new areas. Finally, when an invader is widespread and too abundant to contain, eradication becomes unlikely and long-term management is the last option. Long-term management aim at reducing populations to the lowest possible levels and protect specific resources.

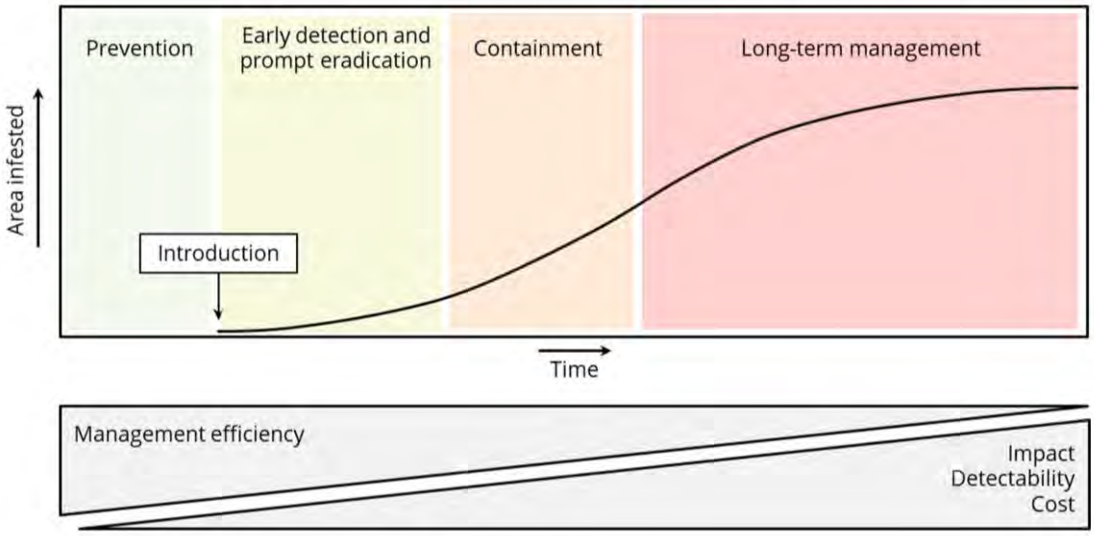

Figure I.1 Hierarchical management strategy against invasive species, *modified from Simberloff et al. (2013) and Harvey and Mazzotti (2014)*. The optimal strategy changes with time since invasive species introduction. Management efficiency decreases over time, while invasive species impact and detectability, as well as management cost increases.

I.2 | Plant invasions

I.2.1 | Distribution

Introductions of alien plants have multiplied through the intensification of global trade (Seebens et al. 2015), agricultural activities, or for cultivation in botanic and private gardens (Hulme 2015). Consequently, 13,000 plant species (corresponding to almost 4% of the global vascular flora) have become naturalized in foreign regions, with the highest numbers recorded in Europe and North America (Van Kleunen et al. 2015). Tropical regions are poorer in naturalized alien plant species than temperate and Mediterranean regions (Van Kleunen et al. 2015), a phenomenon attributed to ecological (i.e. fewer available niches, faster vegetation resilience after disturbance in tropical areas) and historical differences (i.e. lower introduction rate; Van Kleunen et al. 2015). In addition, islands are more invaded than mainland regions (Pyšek et al. 2017; Van Kleunen et al. 2015), presumably because of the presence of unsaturated niches (Denslow 2003) or the higher number of introductions (Van Kleunen et al. 2015).

I.2.2 | Characteristics of plant invaders

There has been a longstanding effort to identify the characteristics enabling a species to invade a habitat, i.e. invasiveness (Figure I.2; Baker 1965; Gallagher et al. 2015; Pandit et al. 2014; Pyšek & Richardson 2008; Razanajatovo et al. 2016; Van Kleunen et al. 2010; van Kleunen et al. 2015). Naturalized alien plant species appear non-randomly distributed over the phylogeny (Pyšek et al. 2017). The Compositae family present the highest absolute number of naturalized alien species (1,343 species), followed by Poaceae (1,267) and Leguminosae (1,189). Some families and genera are over- or under-represented among naturalized alien species, with differences between islands and mainland regions (Pyšek et al. 2017). A markedly high proportion of naturalized plant species are annuals, most likely because of a greater dispersal ability and broader distribution, short generation time and ability to form seed bank, as well as their affinity to anthropogenic habitats (Pyšek et al. 2017).

Whether particular traits are associated to invasiveness has been widely explored (Callaway & Ridenour 2004; Daehler 2003; Davidson et al. 2011; Gallagher et al. 2015; Leffler et al. 2014; Pyšek & Richardson 2008; Roy 1990; Van Kleunen et al. 2010). Invasion success has sometimes been related to higher competitive abilities of invasive species than natives (Golivets & Wallin 2018; Kuebbing & Nuñez 2016; but see Zhang & van Kleunen 2019) or higher phenotypic plasticity (i.e. greater ability to change in phenotypic expression in response to environmental factors; Schweitzer & Larson 1999; Williams et al. 1995; but see Davidson et al. 2011). The meta-analysis of Pyšek and Richardson (2008) provides support for height, vigorous vegetative growth, early and extended flowering, and attractiveness to humans as traits associated with invasiveness in vascular plants. Recent studies suggest that traits allowing non-native species to naturalize in a new environment (i.e. reproduce in the new environment) are dissimilar to those associated with successful invasion (i.e. naturalize and spread over long distances; Catford et al. 2019; Divíšek et al. 2018; Moravcová et al. 2015; Richardson & Pyšek 2012). The lack of constancy between studies, although partly due to methodological issues (e.g. comparator choice; Van Kleunen et al. 2010), as well as complex results including many exceptions, reveal that invasiveness does not drive invasion success by itself.

I.2.3 | The determinants of plant invasion success

Successful invasion depends on multiple factors varying along the invasion course

Invasion success results from interactions between the characteristics of the invader (i.e. invasiveness, see I.2.2) and the susceptibility of the invaded habitat to invasion (i.e. invasibility; Figure I.2). The importance of each of these factors varies during the invasion process.

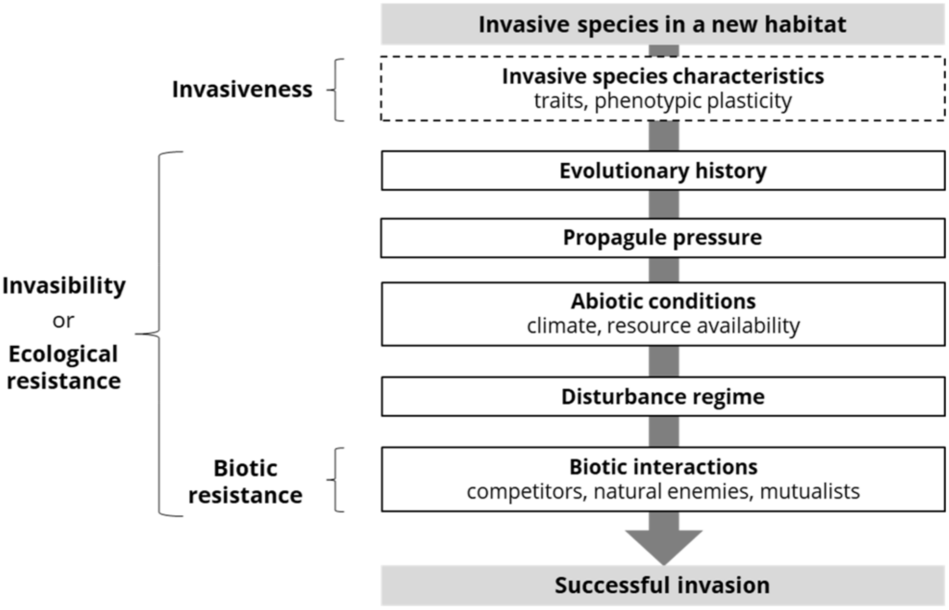

Figure I.2 Main factors influencing plant invasion success.

Invasibility encompasses characteristics of the abiotic environment as well as biotic components. Successful invasion results from multiple interacting processes, including invader characteristics enabling invasion (i.e. invasiveness, see I.2.2) and characteristics determining the susceptibility of the invaded habitat to invasion (i.e. invasibility or ecological resistance; Alpert et al. 2000; Byun et al. 2018). Evolutionary history may affect invasibility as **(1)** habitats in which intense competition occurred over evolutionary time scales may have selected highly competitive native species, which are more likely to outcompete potential invaders, and **(2)** in isolated habitats (islands), a lower selection for competitive abilities may have occurred, resulting in native communities more susceptible to invasion by competitive invaders, and **(3)** habitats with a long history of human disturbance may encounter more native species selected to perform well under disturbed conditions, resulting in a lower vulnerability to invasion (Alpert et al. 2000). Propagule pressure, which is partly determined by the ability of an invader to produce a large amount of propagules, also depends on habitat characteristics: **(1)** the presence of strong dispersal agents (e.g. streams) may increase the frequency of invasion events and the amount of introduced invader propagules (Alpert et al. 2000), and **(2)** the degree of habitat fragmentation influence propagule dispersal (i.e. patchy habitats are more invaded; Harrison 1999). Abiotic conditions are strongly involved in invasibility. Notably, low resource availability (Davis et al. 2000), extreme conditions such as very high temperature and the presence of toxins are expected to lower invasibility (Alpert et al. 2000). Disturbances usually enhance invasibility by increasing resource availability (D'Antonio 2000; Davis et al. 2000; Hobbs & Huenneke 1992). Interactions with biotic components also affect invasion success (Levine et al. 2004). Biotic resistance, describing the ability of resident organisms in a community to resist or limit invasions (Levine et al. 2004) encompasses competition from resident species plants (Levine 2000; Seabloom et al. 2003), interactions with natural enemies (i.e. herbivores, parasites, and pathogens; Keane & Crawley 2002), and mutualists (i.e. soil fungi and bacteria, pollinators, and dispersal agents; Richardson, Allsopp et al. 2000; Traveset & Richardson 2014).

Attempts to apprehend the invasion process have led to developing models that partition the invasion course in several phases (Richardson & Pyšek 2006; Theoharides & Dukes 2007). According to Theoharides and Dukes (2007), transition from 'native' in a given location to 'invasive' in an unoccupied region involves four phases: long-distance transport, colonization, establishment, and landscape spread. Multiple factors determine successful transition from one to another phase. A species is more likely to be transported out of its natural repartition area when possessing a wide native range and horticultural or agricultural qualities, but accidental transportations also occur. Colonization success of an invasive species arriving in a new environment will particularly rely on its ability to cope with environmental conditions such as climate, soil type, pH, resource availability (Davis et al. 2000) and disturbance regime (Lockwood et al. 2013). Moreover, propagule pressure (i.e. combining the number of introduced propagules and invasion events), increasing genetic diversity in the new area, is considered as major determinant of colonization success (Lockwood et al. 2005). Colonizing individuals must then be able to reproduce and form a self-sustaining population to establish. This step is especially constrained by interactions with resident organisms.

Community assembly as a framework for invasion success at the community scale

At the community scale, successful colonization and establishment of an invasive plant species can be considered as governed by similar rules as natives (Pearson et al. 2018). Hence, the establishment success of an invader in a resident community relies on processes driving species assembly and coexistence in an ecological community (i.e. a set of individuals belonging to numerous species that coexist and interact in an area or a habitat; Drake 1990), whatever their status. Community assembly theory focuses on identifying these processes (Weiher & Keddy 1999), and therefore offers a framework for understanding invasion success (Figure I.3; Pearson et al. 2018). Community assembly encompasses the driving forces in the development of ecological communities (Weiher & Keddy 1999) and the mechanisms underlying species coexistence (Mason & Wilson 2006). Community assembly can be represented by a dynamic filter model, which dissociates the different processes influencing the state of a community structure at a site (Temperton et al. 2004).

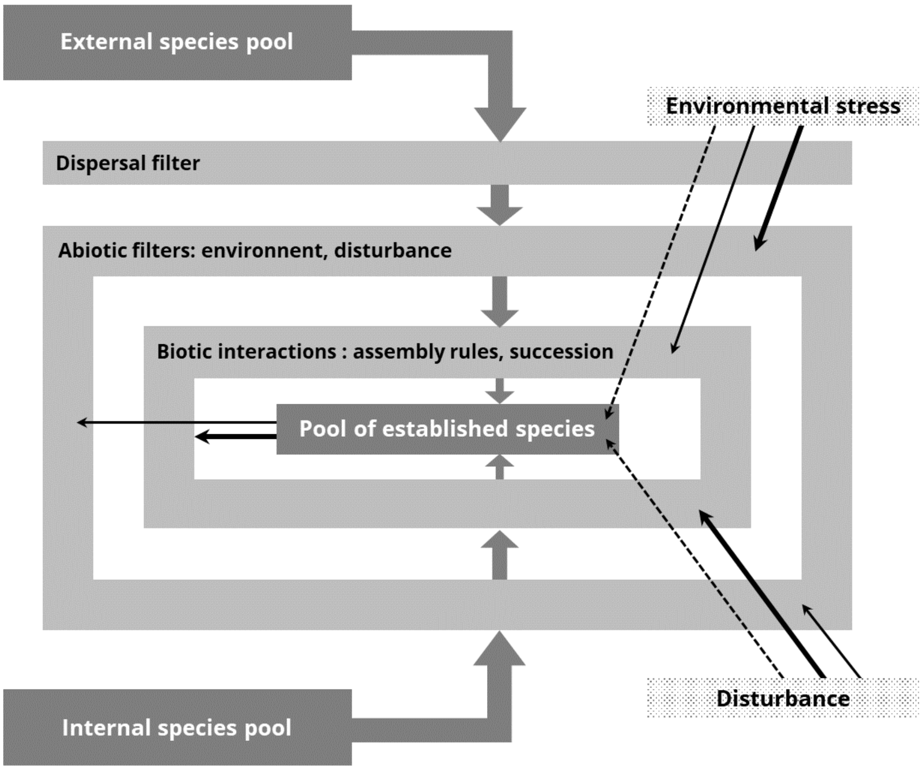

Figure I.3 Schematic representation of the dynamic filter model, *modified from Temperton et al. (2004).*

New species may invade a community from an external species pool, i.e. species in nearby habitat, or from an internal species pool, i.e. species present at the site. Species from the external species pool must be able to pass the dispersal filter, i.e. be transported to from the surroundings by drift, dispersal clonal growth or other mechanisms. Then new species must pass the abiotic filter, i.e. tolerate environmental conditions (chemical and physical characteristics) and endogenous disturbance regime. Finally, to become part of the community, new species must deal with biotic interactions of the environment, including competition with other plants but also interactions with consumers, mutualists and pathogens. Exogenous disturbance and environmental stress (e.g. pollutant release) can influence the filtering process by affecting environmental conditions and generating local species extinctions. Communities and ecosystems are open and dynamic entities (De Leo & Levin 1997; Parker & Pickett 1997; Rykiel 1985), so that filters and their effects change over time. Abiotic conditions and biotic interactions are interdependent and are constantly self-adjusting to each other through feedback loops.

Relationship between invasibility, resource availability and disturbance

Following seed germination and the subsequent consumption of seed reserves, competition for limiting resources, such as space, light, water and nutrients is critical for seedling establishment success (Crawley 1987; Crawley et al. 1999; Davis et al. 2000; Johnstone 1986; Vitousek & Walker 1987). Resource availability naturally differs between ecosystems, and fluctuates with the seasons and at larger time scales. Fluctuation in resource availability is caused by variations in resource supply and uptake by the resident vegetation and other living organisms, themselves caused by meteorological fluctuations or site-specific events such as disturbances, changes in grazing pressure, or pest outbreaks (Davis et al. 2000). An increase in resource availability occurs when **(1)** the use of resources by the resident community declines, or **(2)** resource supply increases at a rate faster that the resident community can sequester it (Davis et al. 2000).

Resource uptake may particularly decline after a disturbance (i.e. a discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability or physical environment; Runkle et al. 1985) that destroyed some or all individuals in a community. The subsequent increase in space, light, water and nutrients availability is expected to provide opportunities for species recruitment – native and invasive ones - into the community (Brown & Peet 2003; Davis et al. 2000; Hobbs & Huenneke 1992; Shea & Chesson 2002). The fluctuation hypothesis theory developed by Davis et al. (2000) also implies that the likelihood of a species to establish successfully may decline as the community grows and efficiently sequester available resources. Inter- and intra-annual variations however occur depending on natural vegetation and ecosystem dynamics and associate resources uptake and supply.

Non-native species benefit more of disturbances than natives (Jauni et al. 2015), most likely because of differences in life history characteristics (i.e. faster growth, higher fecundity, more efficient dispersal of seeds, higher fitness, higher resource-use efficiency; Funk & Vitousek 2007; Pyšek & Richardson 2008; Van Kleunen et al. 2010). Non-native species more rapidly colonize new areas and become established at disturbed sites than natives (Lake & Leishman 2004; Tierney & Cushman 2006), therefore hindering subsequent colonization by natives.

Revegetation as a tool to reduce invasions after a disturbance

According to the resource fluctuation theory (Davis et al. 2000), a reduction of invasive species seedling establishment after a disturbance may be achieved by a quick reduction of available resources (Figure I.4). Decreasing soil fertility through soil amendments or topsoil removal has shown to lower invasions but may cause side effects on soil structure and chemistry (van der Berg et al. 2003), as well on soil fauna (Vergeer et al. 2006), and can be highly expensive (Perry et al. 2010). A way to efficiently decrease soil resources is to actively restore a vegetation cover (Kettenring & Adams 2011).

Establishing a vegetation cover rapidly after a disturbance may quickly sequester available resources, such as soil nutrients, light, space and water (D'Antonio et al. 2001; Perry & Galatowitsch 2006), efficiently reducing invasions or reinvasions (Byun et al. 2018; Byun & Lee 2017; Frankow-Lindberg 2012; Iannone III et al. 2008; Iannone III & Galatowitsch 2008; Kettenring & Adams 2011; Larson et al. 2013; Middleton et al. 2010). The indirect interaction between individuals or species associated with a requirement for shared limiting resources is called exploitative competition (or resource competition), which results in the reduction in one or more fitness components at the individual level or at the population level (Goldberg et al. 1999). Exploitative competition may be a major determinant of biotic resistance of plant communities in the early establishment stages (Frankow-Lindberg 2012; Iannone III & Galatowitsch 2008). For instance, establishing a diverse community that reduced both light and nitrogen decreased the establishment of the invader *Phalaris arundinacea* by 67% (Frankow-Lindberg 2012).

Revegetation may be particularly efficient against early invasions when the restored species preempt the largest amount of limiting resources as quickly as possible (Figure I.4). Establishing a community displaying rapidly a strong invasion resistance should allow **(1)** reducing invasibility when the ecosystem is the most vulnerable (i.e. immediately after a disturbance, when resource availability is high; Figure I.4), and **(2)** targeting the invader at the seedling stage, which is one of the most vulnerable stage in the life cycle of a plant (Kitajima & Fenner 2000).

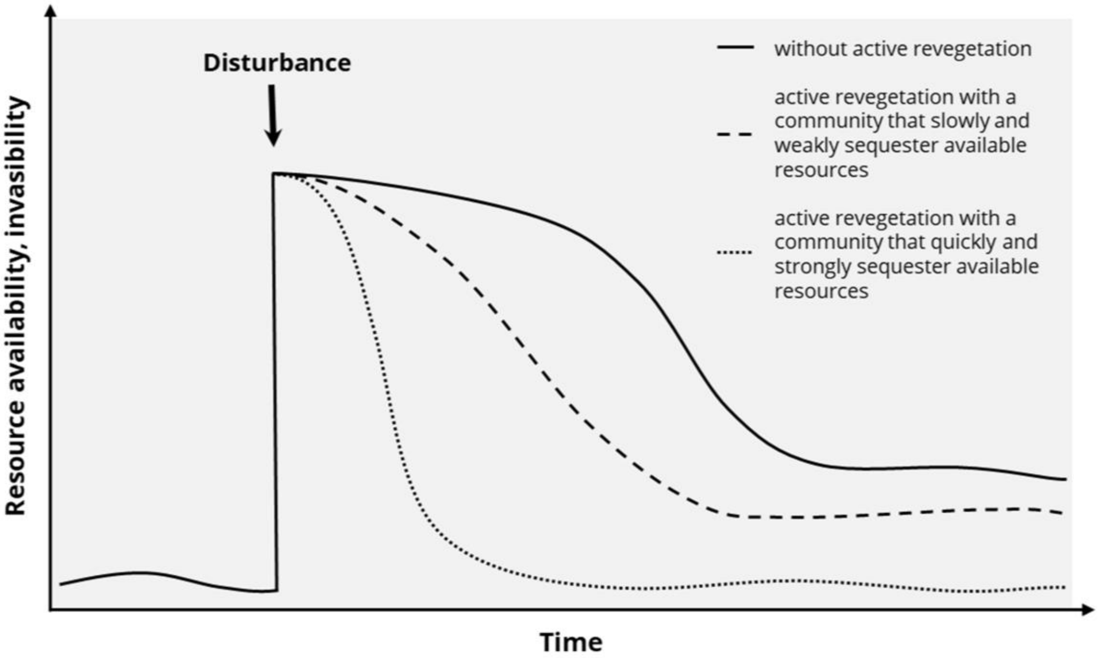

Figure I.4 Schematic representation of resource availability and invasibility over time after a disturbance, depending on different revegetation scenarios. According to the resource fluctuation theory (Davis et al. 2000), invasibility is strongly determined by resource availability (other components that may influence invasibility, e.g. herbivores, pathogens, are not depicted here). Many disturbances increase resource availability or space (Temperton et al. 2004) and so is invasibility. Resource availability and invasibility naturally fluctuate over time. After a disturbance that remobilize resources and increase invasibility, the absence of active revegetation may lead to a slow recovery of vegetation through natural dispersal from surroundings. In this case, resource availability and invasibility may slowly decrease as plant community develops. The efficiency of active revegetation against plant invasions then depends on the ability of the reestablished species to quickly and strongly sequester available resources.

Characteristics of recipient communities affects early invasion success

Not all plant communities are equally resistant to invasions. A significant number of studies explored how certain community characteristics contribute to invasion resistance, with a particular focus on species diversity and identity (Connolly et al. 2017; Dukes 2002; Fargione & Tilman 2005; Hector et al. 2001; Kennedy et al. 2002; Lavorel et al. 1999; Levine & D'Antonio 1999; Naeem et al. 2000; Tilman 1997; Wardle 2001), particular traits (Byun & Lee 2017; Drenovsky & James 2010; Moravcová et al. 2015), or phylogenetical or trait similarity with the invader (Abella et al. 2012; Emery 2007; Larson et al. 2013; Price & Pärtel 2013; Yannelli et al. 2017). Recently, the influence of historical contingencies (i.e. the effect of the order and timing of past events, being either abiotic or biotic; Fukami 2015) in community assembly and invasion has regain attention through the study of priority effects, which arise when early-arriving species affect the establishment, survival, growth or reproductive success of later-arriving species (Helsen et al. 2016). Priority effects may be particularly impactful in the early growth stages (i.e. first growing season; Körner et al. 2008; Plückers et al. 2013; von Gillhaussen et al. 2014), and may influence early invasive species establishment success. For instance, Grman and Suding (2010) found that giving a five-week advance to native species reduced invasive species biomass by 85%, against 8% when planted simultaneously. Taking advantage of priority effects during revegetation procedures and communities restoration may therefore be a powerful tool to reduce invasive species establishment after a disturbance. However, how priority effect strength is affected by community attributes such as species identity, diversity, density or arrival timing has only been subjected to few investigations.

Many studies were conducted on mature communities and aimed at studying long-term trends, without considering early establishment stages. Therefore, determinants of early invasion success (i.e. successful germination and seedling establishment) are still poorly understood.

I.3 | Thesis aim and organization

This thesis aims to identify and test key drivers of community resistance to invasion in the early growth stages and to define the consequences for field application and management of invasive species.

The first step consisted in identifying the mechanisms that may be involved in early invasion resistance and that could be manipulated to design resistant plant communities. I focused on two mechanisms that may be particularly influential: **(1)** limiting similarity, stating that competitive exclusion will limit the coexistence of species sharing the same ecological niche (Abrams 1983), and **(2)** priority effects, which occur when early colonizing species inhibit or facilitate the establishment, growth or reproductive success of later arriving species (Helsen et al. 2016).

In Chapter 1, I explored the use of limiting similarity for controlling early invasion, by asking the following questions:

Research question:

Is limiting similarity a main mechanism involved in early invasion resistance?

In terms of application:

Is limiting similarity applicable and effective in controlling early invasion?

In Chapter 2, I investigated the manipulation of priority effects to reduce early invasion by addressing the following questions:

Research question:

Are priority effects a main mechanism involved in early invasion resistance?

In terms of application:

Can priority effects be used after disturbance, in a restoration context, to design plant communities resisting early invasion?

These two chapters revealed limitations to an efficient application of limiting similarity to hinder plant invasions and encouraging results for manipulating priority effects. Two experiments were then carried out with the aim of experimentally manipulating priority effects and investigating the consequences on invasion resistance.

Chapter 3 reports the results of a first greenhouse experiment, which investigated:

Research question:

How do invasion timing (i.e. elapsed time between recipient community sowing and invasive species introduction), recipient community composition and sowing density interact to influence priority effects and early invasion success?

In terms of application:

Does providing efforts to delay invasion and manipulating the composition and density of seed mixes constitute efficient strategies to reduce early invasion?

Chapters 4 and 5 describe the results of a second greenhouse experiment where assembly history of the recipient community was manipulated.

Chapter 4 focuses on invasive species responses, asking:

Research question:

Does assembly history of the recipient community (timing of species establishment and identity of the first arriving species) influence early invasion resistance?

In terms of application:

Is sequential sowing a possible way to reinforce early invasion resistance?

Chapter 5 focuses on recipient community responses, asking:

Research question:

Does the identity of the first native established species influence early recipient community structuring and priority effects?

In terms of application:

Should we consider the order of native species arrival when implementing a priority effect-based revegetation strategy?

Thesis organization is summarized in the Figure I.5 below:

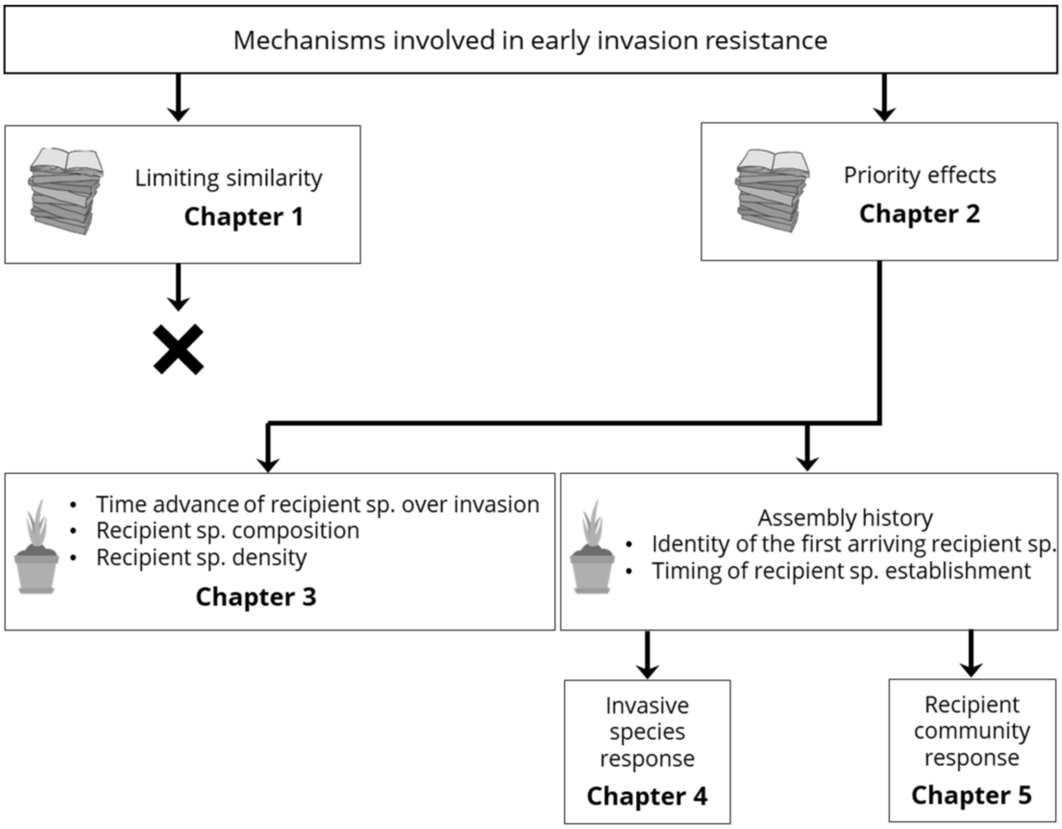

Figure I.5 Thesis organization.

Transition to Chapter 1

In Chapter 1, I focus on the concept of limiting similarity which has been considered for the design of invasion resistant plant communities until recently (e.g. Funk et al. 2008; Price & Pärtel 2013; Yannelli et al. 2017). Through a critical review of the literature, I explore the theoretical and practical issues raised by the application of limiting similarity to design invasion-resistant plant communities.

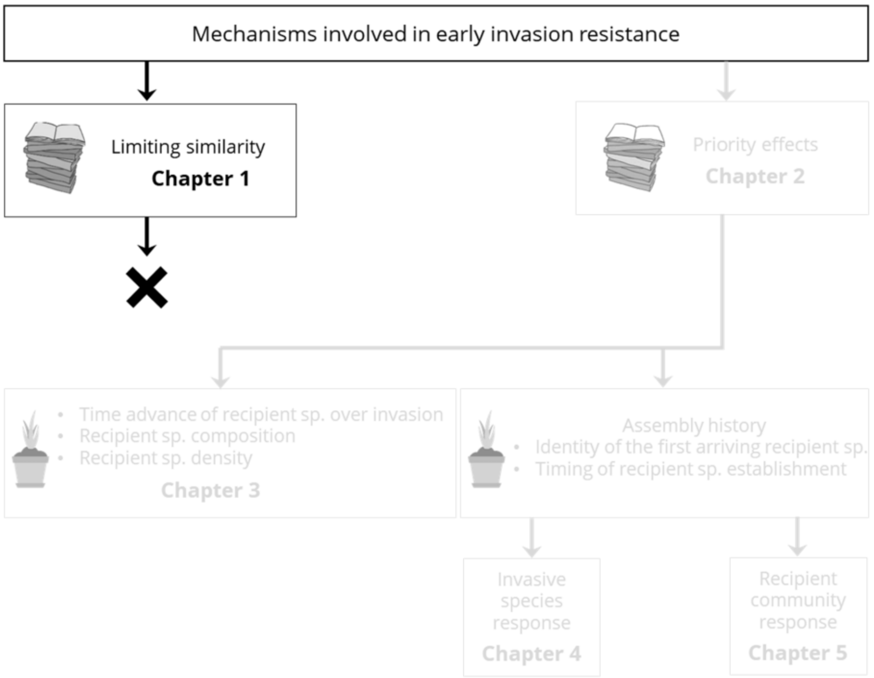

Figure T.1 Chapter 1 in thesis organization.

Chapter 1

Using limiting similarity to enhance invasion resistance: theoretical and practical concerns

Manon CM Hess, Elise Buisson, Renaud Jaunatre, François Mesléard

Reference

Hess MCM, Buisson E, Jaunatre R, Mesléard F (2020) Using limiting similarity to enhance invasion resistance: Theoretical and practical concerns. Journal of Applied Ecology 57:559-565

Chapter 1

Abstract

1. The control of invasive species is a central topic of both applied and theoretical research. Understanding how and which ecological theories can be used to improve invasion resistance of plant communities is essential, to design effective control strategies.

2. The theory of limiting similarity, stating that coexistence between species is more limited by competitive exclusion when species share niche properties, is often considered by applied ecologists as a possible approach to limiting plant invasions at the local scale.

3. The complexity of measuring ecological niche overlap between species as well as the difficulty of disentangling niche from fitness processes currently limit the demonstration and application of this theory. Limiting similarity appears to operate at a time-scale that is too long for efficient impact on invasive species' early establishment. It may also be ineffective against invasions in the long-term, due to environmental changes and community instability. Finally, limiting similarity is not applicable to the most common situations, where there are multiple co-occurring invasive species or no prior identification of potential invasives.

4. *Synthesis and applications*. Whether the theory of limiting similarity, predicting competitive exclusion when species display niche similarities, can be successfully applied to limit plant invasions—or not—is an important issue for practitioners facing invasive species. In practice, using limiting similarity to design invasion-resistant plant communities appears to be complex, ineffective and unsuitable for most common situations.

Keywords: biotic resistance, coexistence, competitive exclusion, ecological niche, fitness, invasive species, restoration

1.1 | Introduction

Invasive species are a key driver of biodiversity loss worldwide (McGeoch et al. 2010). Controlling them (as a conservation objective) is a central topic of both applied and theoretical research (Catford et al. 2009; Davis et al. 2000; Hallett 2006; Shea & Chesson 2002; Tilman 2004). Many studies suggest that more resources are invested in post-invasion control and impact reduction than in prevention or early intervention (Simberloff et al. 2013). In this regard, the establishment of a native resistant plant cover after a disturbance (e.g. after restoration activities implying vegetation clearing) is increasingly recommended to impair invasive plant species colonization and local spread (Byun et al. 2018). One of the ecological theories explored by applied ecologists seeking to improve the invasion resistance of plant communities is limiting similarity. The limiting similarity theory derives from the classical niche theory, which states that a species persists under a specific range of conditions (Hutchinson 1959) and that an overlap in ecological niche with another species can prevent establishment in a community (Case 1983; Diamond 1975; MacArthur & Levins 1967). Limiting similarity theoretically means that competitive exclusion will limit the coexistence of species sharing the same ecological niche (Abrams 1983; Funk et al. 2008; MacArthur & Levins 1964, 1967). This hypothetical competitive exclusion is therefore considered as a possible way to reinforce the biotic resistance of native communities (Funk et al. 2008; Yannelli et al. 2017). In practical terms, attempts to apply limiting similarity involve reassembling plant communities so that the dominant species' ecological niche is similar to that of a target invader. Price and Pärtel (2013) examined experimental evidence of limiting similarity in invasion resistance and found partial support in artificial communities. In this paper, we go further by challenging the theoretical and practical issues raised by the application of limiting similarity to design invasion-resistant plant communities. We aim at answering the following question: Can we predict the competitive impact of a plant community by measuring niche overlap and therefore applying limiting similarity to enhance invasion resistance, and if so, would it be an efficient approach?

1.2 | Applications of limiting similarity involve oversimplification

A species' ecological niche (hereafter termed ‘niche’) is usually defined as an n-dimensional hypervolume (Hutchinson 1957), characterized by axes of resource use and/or environmental conditions within which populations are able to maintain a long-term average net reproductive rate ≥1 (Gause 1934; Silvertown 2004). Originally, this concept was introduced to emphasize the role of habitat and food in defining the niche of an animal (Chase & Leibold 2003). Unlike in many animal communities, plants' coexistence is not explained by the trophic niche: all plants consume the same resources (light, water, CO_2, nitrogen, phosphorus, potassium and other macro- and micronutrients; Silvertown 2004). Two niches are hypothesized to be different if there are differences **(1)** in resource use across time and space, **(2)** in the ratios of limited resources required and **(3)** in the conditions for regeneration, or if there is complementarity of life-forms (Cody 1986; Grubb 1985; Tilman 1982). Thus, the niche appears to be a complex, multidimensional concept that currently escapes comprehensive description. Niche differentiation is therefore usually described on a very limited number of axes, such as environmental (e.g. hydrology, salinity, soil texture or drought) or resource gradients (e.g. light or nitrogen; Silvertown 2004), although some studies also include space and/or time (Fargione & Tilman 2005).

In demonstrations or applications of the limiting similarity theory, niche overlap between species is reduced to similarities quantified by measuring functional traits. The rationale is that these traits relate both to strategies of resource capture and to the effect on the overall pool of resources; they are effect and response traits (Goldberg 1996; Lavorel & Garnier 2002; McGill et al. 2006). Different groups based on similarities in growth form or other morphological or phenological trait similarities have been defined, assuming that species from the same group should have greater niche overlap and compete more intensively than species from different groups (Johansson & Keddy 1991; MacArthur & Levins 1967). However, most studies found no or very limited support for limiting similarity in invasion resistance (Abella et al. 2012; Byun & Lee 2017; Cleland et al. 2013; Daneshgar & Jose 2009; Emery 2007; Eriksson et al. 2006; Fargione et al. 2003; Funk & Wolf 2016; Larson et al. 2013; Longo et al. 2013; Oster & Eriksson 2012; Prieur-Richard et al. 2000; Turnbull et al. 2005; Von Holle 2005; Yannelli et al. 2018). While such failures do not necessarily invalidate the limiting similarity theory, they are probably due to an inability to reach the domain of validity of this theory. For instance, there may be an insufficient degree of niche overlap between selected native and invasive species, or perhaps niche processes are not a determining factor in invasion resistance.

1.2.1 | Getting the degree of niche overlap right is complex

'What degree of niche overlap is required for competitive exclusion?' is one key question that needs to be answered before limiting similarity can be applied successfully. Several categories of similarities between native and invasive species have been explored: in growth form (e.g. C3-grasses, C4-grasses, non-leguminous forbs and legumes; Emery 2007; Fargione et al. 2003; Prieur-Richard et al. 2000; Symstad 2000), in life longevity and phenology (e.g. annuals, perennials, early or late seasonal plants; Abella et al. 2012; Cleland et al. 2013; Larson et al. 2013), in morphology (e.g. woodiness, height, presence of taproot; Byun & Lee 2017; Von Holle 2005) and/or in physiology (e.g. specific leaf area, relative growth rate, leaf dry-matter content; Byun & Lee 2017). The findings from most studies do not support limiting similarity as an efficient, robust way to limit early establishment of invasive species. Among other explanations, this may be because the degree of niche overlap was insufficient to induce competitive exclusion.

1.2.2 | Limiting similarity may have less impact than differences in fitness on early establishment success

A non-negligible role of limiting similarity has indeed been demonstrated in plant community assemblage (i.e. more trait divergence between species of a local assemblage than expected under a random null model; Armbruster 1986; Fukami et al. 2005; Mason &

Wilson 2006; Stubbs & Bastow Wilson 2004; Wilson 2007; Wilson & Whittaker 1995) but see (Mahdi et al. 1989), as well as in invasiveness (i.e. functional similarity to native species facilitates naturalization but hinders invasion; Divíšek et al. 2018; Hamilton et al. 2005). However, its role in early establishment success at the local scale may be limited compared with the effect of differences in fitness (Funk & Wolf 2016; Kunstler et al. 2012). Fitness advantage can arise from greater ability to effectively use resources in a specific range of environmental conditions (Freckleton & Watkinson 2001; Keddy & Shipley 1989; Mesléard et al. 1993), resulting in a competitive hierarchy (Fargione et al. 2007; Herben & Goldberg 2014). Competitive hierarchies have been shown to occur within functional groups (Turnbull et al. 2004, 2005; Wedin & Tilman 1993), contrary to the within-group equivalence predicted by limiting similarity (Hubbell 2001). Accordingly, specific trait values—not necessarily similar to those of the target invader—such as high specific root length (Daneshgar & Jose 2009; Funk & Wolf 2016), large size or height (Byun & Lee 2017), high growth rate (Symstad 2000), or early access to limiting resources (Longo et al. 2013) have been linked to increased invasion resistance (Drenovsky & James 2010). Moreover, competition can be intense between functionally distant species (e.g. between lianas and trees; Schnitzer et al. 2005).

Fitness inequality can also arise from a size-related competitive advantage generated through priority effects (Wilsey et al. 2015), where the species established first sequester resources, thus depriving later colonizers (Byun et al. 2013; Fukami 2015; Vance 1984). Giving reassembled native species a short time advance (i.e. a few weeks) has been shown to create strong priority effects, successfully decreasing invasive species success (e.g. Byun et al. 2013; Grman & Suding 2010; Vaughn & Young 2015; Young et al. 2016). Several studies concluded that difference in fitness is more important than similarity in niche in determining invasion resistance, at least in the short term (Byun et al. 2013; Byun & Lee 2017; Firn et al. 2010; Funk & Wolf 2016; Grman & Suding 2010; Kunstler et al. 2012; Larson et al. 2013; Prieur-Richard et al. 2000; Wang et al. 2013).

Moreover, disentangling niche from fitness processes is not easy, especially when only one invader is tested (e.g. Byun et al. 2013; Dukes 2002; Sheley & James 2010; Symstad 2000; Walder et al. 2018). When a resident species is the most effective in decreasing the success of an invader belonging to the same functional group, it is impossible to conclude on whether the effect is due to differences in niche or in fitness: the experimental design makes it difficult to rule out the possibility that a similar response could have been observed with invaders from other functional groups, which would support differences in fitness as being more important than niche similarity.

1.3 | Limiting similarity may take too long to act

There are several reasons to believe that limiting the establishment of an invasive species demands rapid and robust inhibition of invasive species seedling emergence and survival. The seedling stage offers a critical window of opportunity to control invasive species effectively, for two main reasons. First, the seedling stage is the most vulnerable stage in the life cycle of plants (Baskin & Baskin 1998; Fenner et al. 2005). Second, invasive species often exhibit a high growth rate (Dawson et al. 2011; Marushia et al. 2010; Rejmanek & Richardson 1996) and strong priority effects (Dickson et al. 2012; Stuble & Souza 2016; Wilsey et al. 2015), thus rapidly becoming competitively superior after establishment (Martin & Wilsey 2012). Competitive exclusion via limiting similarity, which may take several generations (Passarge et al. 2006), may therefore act at too long a time-scale to successfully hamper invasive species colonization (Abrams 1983; Price & Pärtel 2013; Stohlgren et al. 2008; Symstad 2000). Seedlings are not necessarily functionally similar to adults (Hooper & Dukes 2010), meaning that it would take too long for the resident species to affect functionally similar invasive species. In support of this, Price and Pärtel (2013) found less effect from limiting similarity on invader colonization (germination, establishment or seedling survival) than on performance (biomass, cover or growth). Limiting similarity thus appears to be an inappropriate approach to hindering the early establishment of invasive species.

But is limiting similarity any more appropriate for limiting invasive species success in the long-term? Its long-term efficiency relies heavily on the stability of the community over time, achieved by maintaining species assumed to prevent the development of similar invasive species. Yet, species dominance in a community can decrease over time through succession, raising the risk that species selected for their similarities with the target invasive species will lose their dominance. In this case, a reasonable hypothesis is that the environmental conditions will also become unfavourable for the invasive species. A more appropriate strategy could be to foster a diverse community where a few species are likely to respond favorably to changes in environmental conditions, especially if the community sown is dominated by perennials (Byun & Lee 2017; Corbin & D'Antonio 2004; Naeem et al. 2000). This might be a surer bet than relying on the capacity of one or a few species resembling the invasive to maintain dominance under changing conditions.

1.4 | Limiting similarity can only be applied to a single target invasive species

The concept of limiting similarity is only applicable to control a single invasive species (or a group of species occupying the same niche). This implies that the target invasive species has previously been identified. The scope is thus narrowed to situations where the target invasive species **(1)** is present at the site prior to management or restoration actions (and its propagules are potentially present in the soil), or **(2)** poses a direct threat to the site through being established nearby. However, previously unnoticed invasive species can emerge from persistent seed banks (Honig et al. 1992; Pyke 1990; Shen et al. 2006) through the soil disturbances generated by restoration activities (Fumanal et al. 2008). Invasive species established several kilometers away can reach the site through long-distance dispersal abilities (Buchanan 1989; Renne et al. 2002; Stansbury 2001). Moreover, there are far more situations where several invasive species co-occur than single-invaded habitats (Kuebbing et al. 2013). The application of limiting similarity may therefore be ineffective in a wide range of common situations, such as when potential invaders are not yet identified and when multiple invaders co-occur.

All these arguments suggest that the application of the theory of limiting similarity to design invasion-resistant plant communities does not seem relevant in most cases. Research efforts should focus on strategies that quickly and significantly reduce invasive species colonization, and that are efficient when there are multiple co-occurring invasive species. Establishing a community displaying a great diversity of functional traits would allow a more effective and stable use of resources over time and space — and the occupation of most of the niches (Sheley et al. 1996). Also, when increasing the number of species in a community, theoretically, the probability of a species being present to be a strong competitor to invasive species increases (Lavorel et al. 1999). Diverse communities may therefore exhibit an increased invasion resistance when fully established. However, diverse communities would include slow growing, low competitive species that would compromise invasion resistance at the first stages of growth. Therefore, in a case where invasive species are already present in the immediate vicinity and thus threatening the site, this strategy may be less effective. Combining this strategy with approaches giving a rapid and strong invasion resistance, for example through priority effects (Hess, Mesléard, Buisson 2019), would seem a more promising way of effectively hinder invasive species' early establishment.

Acknowledgements

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Synthesis of Chapter 1 and transition to Chapter 2

Chapter 1 in a nutshell

Is limiting similarity a main mechanism involved in early invasion resistance?

While there is evidence of a non-negligible role of limiting similarity in the structuring of natural communities, its impact on early invasion resistance may be limited since **(1)** niche overlap may lead to competitive exclusion at a longer timescale, and (2) niche differences may be less impactful than fitness differences in the early stages.

Is limiting similarity applicable and effective in controlling early invasion?

Most studies attempting to apply limiting similarity failed to increase invasion resistance. Limiting similarity does not appear suitable to design plant communities resisting early invasion as **(1)** measuring niche overlap between species and disentangling niche from fitness processes limits an accurate application, and (2) it is not applicable to the most common situations, where there are multiple co-occurring invasive species or no prior identification of potential invasives.

In Chapter 2, I investigate, through a review of the existing literature, the possible ways to manipulate priority effects to reduce plant invasion or reinvasion after a disturbance. I explore strategies to **(1)** reduce priority effects generated by invasive species, and **(2)** create and enhance priority effects of reestablished native species.

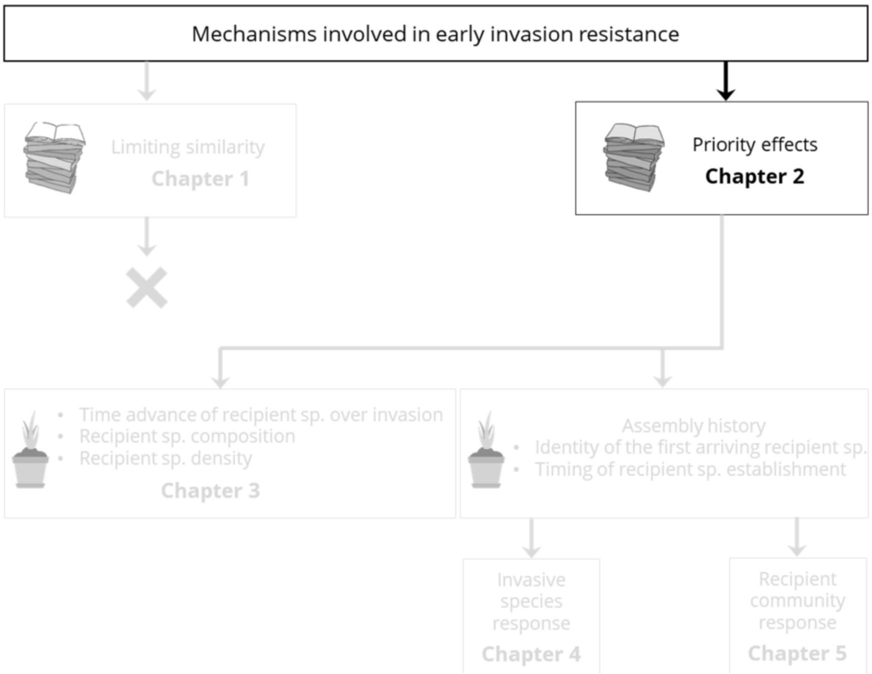

Figure T.2 Chapter 2 in thesis organization.

Chapter 2

Priority effects: Emerging principles for invasive plant species management

Manon CM Hess, François Mesléard, Elise Buisson

Reference

Hess MCM, Mesléard F, Buisson E (2019) Priority effects: Emerging principles for invasive plant species management. Ecological Engineering 127:48-57

Chapter 2

Abstract

Many anthropic activities generate soil disturbances, favoring competitive, fast growing invasive plant species at the expense of natives. Active restoration of invasion-resistant plant communities is increasingly recognized as a relevant strategy to combat invasive plant colonization in disturbed areas, but results are often unsatisfying. Historical effects, referred as 'priority effects' (i.e. the effects generated by the order in which species arrive at a local site), can have a major role in community assembly and invasion success because they involve early colonists altering the performance of later colonists. Taking these priority effects into account in restoration projects is emerging as a relevant way to improve native species restoration success and prevent invasion. The present review discusses two strategies considering priority effects that would help to achieve the classic restoration goal of 'more natives, less invasives'. The first strategy relies on tackling priority effects of invasive plants using different management options adapted to local environmental conditions, including removal, reduction of propagule sources, or mitigation of soil legacies. Indeed, invasive plants often generate strong priority effects providing themselves a substantial competitive advantage through early emergence and quick growth, but also self-induced soil modifications that can persist after their removal or death, commonly termed 'soil legacies'. In fertile and stable conditions, the reduction of invasive species priority effects must be coupled with the restoration of an invasion-resistant native plant cover to avoid reinvasion and secondary invasions. The second strategy is to bring about situations in which the restored native species are more likely to exert strong priority effects, decreasing invasion success. For this purpose, we sketch possible options open to restorationists based on resource or non-resource mechanisms. First, we discuss ways to maximize resource preemption by extending the time advance given to restored native species and manipulating restored species characteristics. Second, we consider the potential effect of increasing niche overlap between native and invasive species. Third, we introduce the potential manipulations of non-resource mechanisms, such as allelopathy, herbivory, disease, or the presence of mycorrhizae, to increase priority effects. This review incorporates recent research on priority effects to draw the outlines of priority effect-based restoration strategies and define future research questions that need to be addressed to test and improve these strategies.

Keywords: invasion resistance, restoration, community assembly history, historical contingency, order of arrival, legacy

2.1 | Introduction

The vast literature on biological invasions since Elton's seminal work (Elton 1958) testifies to the complexity of understanding the processes underlying invasion success (Hayes & Barry 2008; Levine et al. 2003; Simberloff et al. 2013). According to deterministic theories, the outcome of an invasion depends on interactions between the invader and the physical and biological characteristics of the recipient environment (Lonsdale 1999; Williamson 1999). The intrinsic competitive superiority of invasive plant species (i.e. species introduced outside of their distribution areas which are able to grow and proliferate to become an autonomous viable population, and whose expansion can negatively impact local species and ecosystems; (Mooney 2005; Richardson, Pyšek, et al. 2000) in acquiring resources has long been considered the critical mechanism determining invasion success (Pyšek & Richardson 2008; Sax & Brown 2000; Vilà & Weiner 2004). However, invasive species performance also appears to depend on the physical and biological conditions encountered in the introduced range: resource availability and fluctuation (D'Antonio et al. 2017; Davis et al. 2000; Firn et al. 2010; Shea & Chesson 2002), multi-trophic interactions involving enemies (Mitchell et al. 2006), and resident plant community composition (Fridley et al. 2007; Levine & D'Antonio 1999). In addition to the deterministic explanations, stochastic dispersal and historical processes also play a crucial role in determining invasion success (Chase 2003; Dickson et al. 2012; Hubbell 2001; Kolar & Lodge 2001; Lockwood et al. 2005; Wilsey et al. 2015; Young et al. 2015).

Stochastic colonization combined with deterministic interactions between early and later colonizing species lead to priority effects (Case 1990; Chase & Myers 2011), where early-arriving species affect the establishment, survival, growth or reproductive success of later-arriving species (Helsen et al. 2016). There is growing evidence that priority effects play a crucial role in community assembly, especially in productive environments (Aronson & Galatowitsch 2008; Chase 2003; Körner et al. 2008; Young et al. 2016) and can be implicated in invasion success (Abraham et al. 2009; Corbin & D'Antonio 2004; Grman & Suding 2010; Seabloom et al. 2003). One mechanism prevalent in priority effects is resource preemption (Fukami 2015; Young et al. 2001): the reduction of available resources (e.g. space, light, nutrients) by the early colonizers (Vance 1984). This mechanism may allow even weak competitors to persist and maintain long-term dominance (Chase 2010; Ross & Harper 1972). Priority effects also arise from alterations of biotic (e.g. soil microorganisms) and abiotic (e.g. nutrient dynamics, allelochemicals) components of the environment, which can, in some contexts, limit colonization by subsequent colonizers (Corbin & D'Antonio 2012; Kourtev et al. 2002; Mangla & Callaway 2008). Disturbances leading to the removal of most or all plant individuals in a habitat patch initiate a new round of community assembly (Fukami 2015), often favoring competitive, fast growing invasive species at the expense of natives (Davis et al. 2000; Hobbs & Huenneke 1992). Because of the well-recognized issues raised by invasive species (i.e. human health, crop production, native biodiversity, economic; Kolar & Lodge 2001; Simberloff 2013; Vitousek et al. 1997) and because of the evolution of legal framework on invasive species (at least in Europe; Regulation (EU) No 1143/2014), there is clearly an urgent need to develop effective strategies to limit invasions, particularly in newly disturbed areas. However, although active restoration of plant communities is increasingly recognized as a relevant tool to combat invasions (Byun & Lee 2017; Hazelton et al. 2014; Middleton et al. 2010), results are often far from satisfactory (Kellogg & Bridgham 2002). This has notably been attributed to a failure to account for priority effects, which may play a decisive role in restoration success (Grman & Suding 2010; Temperton et al. 2004; Wilsey et al. 2015; Young et al. 2001). Priority effects appear to offer a cost-effective approach to combatting invasive plant species (Chadwell & Engelhardt 2008), but have only been recently considered for invasive species management. Here, we discuss two non-exclusive restoration strategies to achieve the end goal 'more natives, less invasives'. The first strategy consists in tackling priority effects generated by invasive species, while the second is to bring about situations in which the native species are more likely to exert strong priority effects.

2.2 | Dealing with invasive species priority effects

2.2.1 | Priority effects are particularly advantageous to invasive species

Phenological differences between invasive and native species can substantially contribute to invasion success (Wolkovich & Cleland 2011). Distinct phenology allows certain invasive species to fill vacant phenological niches and profit from temporally available space and resources (e.g. light, nutrients, pollinators), sometimes creating seasonal priority effects (i.e. priority effects operating seasonally on a within-year scale; Wolkovich and Cleland, 2011). Numerous invasive species shares the strategy of being active early in the season as to get an early access to resources and acquire a competitive dominance (Dyer & Rice 1997; Munter 2008; Seabloom et al. 2003; Wolkovich & Cleland 2011), but others also profit of being active late in the season (e.g. in California, the invasiveness of *Centaurea solsitialis* arises from extending its growing season into the summer when competition from winter annual vegetation for soil water is minimal; Gerlach & Rice 2003). Several studies reported that invasive species generate stronger priority effects than natives (Dickson et al. 2012; Stuble & Souza 2016; Wilsey et al. 2015 but see Cleland et al. 2015). The generally higher growth rate of invasive species (Dawson et al. 2011; Grotkopp et al. 2010; Marushia et al. 2010; Rejmanek & Richardson 1996; Reynolds et al. 2001) was suggested to underlie this advantage (Dickson et al. 2012; Stevens & Fehmi 2009). A higher growth rate creates a greater asymmetry in plant size (Weiner 1990), resulting in a stronger competitive suppression of the later arriving species (Dyer & Rice 1999; Ejrnaes et al. 2006; Perry et al. 2003). Cleland et al. (2015) found that the stronger priority effects of invasive species were correlated to regeneration trait values, such as higher germination rate and higher light capture during seedling stage, reflecting higher biomass. In addition to these seasonal advantages, invasive species can also profit from priority effects through self-induced soil condition modifications, whether biological, chemical or physical (Corbin & D'Antonio 2012). Modifications such as: **(1)** shifts in nutrient cycling (Ehrenfeld 2003; Flinn et al. 2017; Marchante et al. 2008) and soil salinity (Novoa et al. 2013), **(2)** changes in soil microbial communities including pathogens and mycorrhizal fungi (Hawkes et al. 2006; Kardol et al. 2007; Kourtev et al. 2002; Lorenzo et al. 2010; Mangla & Callaway 2008; Stinson et al. 2006), and **(3)** the release of allelochemicals

(Bais et al. 2003; Grove et al. 2012; Milchunas et al. 2011; Stinson et al. 2006) can all generate priority effects enhancing invasive species performance and inhibiting native plant species (Figure 2.1A; Meisner et al. 2014; Reinhart & Callaway 2006; Rodriguez-Echeverria et al. 2013; Stinson et al. 2006; van der Putten et al. 2013). Such invader-mediated soil modifications can persist after the causal invasive species is removed or dies (Corbin & D'Antonio 2012; Hacker & Dethier 2009; Hamman & Hawkes 2013), and are commonly termed 'soil legacies' (Figure 2.1B).

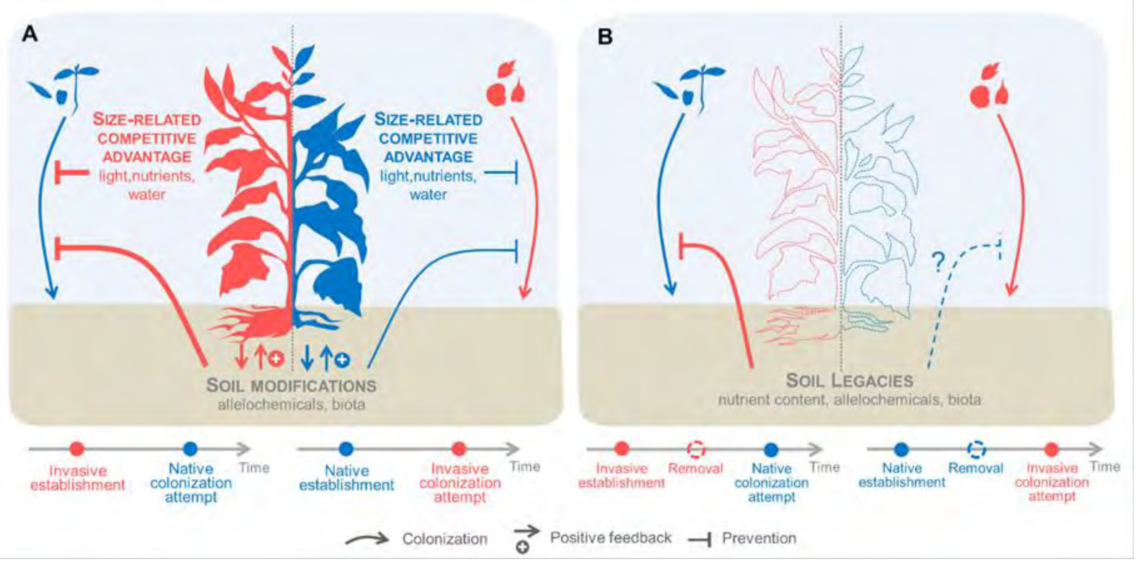

Figure 2.1 Mechanisms driving the consequences of priority effects when the plant individual is present (**A**), or has been removed or died (**B**). (**A**) Early arriving species can limit colonization success of subsequent colonizing species by gaining a size-related competitive advantage, by generating positive plant-soil feedbacks improving its own performance, and by modifying soil conditions. Priority effects are asymmetric between native and invasive species, so that invasive species are less impacted by arriving late compared with natives. (**B**) Plants can also generate priority effects through soil legacies after they were removed or died, that can impact subsequent colonization. While, for many invasive species, persistent soil legacies have been reported to hinder invasive recolonization, little is known about how native species soil legacies could limit invasive species establishment. Note that Grman and Suding (2010) found no impact of native species legacies on invasive species success.

2.2.2 | Countering invasive species priority effects

When it comes to decrease the competitive dominance of an invasive plant species, it is essential to look for abiotic conditions to determine what actions need to be undertaken. In environments with high nutrient resource and water availability, the presence of invasive species could particularly hinder restoration of native communities because of their high competitive abilities (Abraham et al. 2009; Cox & Allen 2008; Grman & Suding 2010). Countering invasive species competitive advantage can be achieved by applying intensive management techniques to reduce invasive species cover (i.e. herbicide applications, mechanical removal; Figure 2.2). Marushia et al. (2010), by applying control methods (herbicide application) early in the season, tackled rapid and early emerging exotic annuals while minimizing impacts on native plants. In favorable conditions, many invasive species are likely to invade in response to the removal of one or more invaders (D'Antonio et al. 2017). Thus, it is particularly relevant to reduce propagule sources in order to limit invasive species recolonization (Figure 2.2; D'Antonio et al. 2017). Common methods to decrease non-desirable species seed bank include topsoil removal (Hölzel & Otte 2004), effective mowing management (i.e. adjusted to phenological development; Milakovic et al. 2014) and artificial flushing of invasive species to induce germination, followed by lethal interventions such as tillage or herbicide application (Wolf & Young 2016). Prescribed burns for fire-prone species or supplying water are two techniques promoting germination (Ooi 2007; Wolf & Young 2016) that could be used to flush invasive plant species and tackle seasonal priority advantage early in the season (Wainwright et al. 2012; Wilsey et al. 2015; Wolkovich & Cleland 2011). Establishing early-emerging and competitive native species (e.g. cover crops) is another option that can help reducing competition from early-germinating invasive species. Indeed, restoring early-emerging species can directly decrease invasive species performance (Blackshaw et al. 2006) and indirectly favor desired native species (Perry et al. 2009). However, so far, these strategies are little explored. To successfully counter seasonal priority effects generated by invasive species, it is crucial to better understand invasive species phenology, requirements and possible interactions with native species, so as to improve existing management techniques (i.e. artificial invasive species flushing, the use of cover crops) and develop new ones.

To limit reinvasion and secondary invasions, invasive species reduction must be coupled with revegetation strategies (Figure 2.2; Pearson et al. 2016) directed towards the limitation of multiple co-occurring invasive plant species. However, because of soil legacies, invasive species removal and propagule pressure reduction are sometimes unlikely to lead to recovery of native communities (Corbin & D'Antonio 2012; Ehrenfeld et al. 2005; Jordan et al. 2012; Suding et al. 2004; van der Putten et al. 2013), and often favor secondary invasions (Dickie et al. 2014; Grove et al. 2015; Yelenik & D'Antonio 2013). When the site was invaded prior to disturbance, it may then be necessary to include measures to deal with soil legacies, rather than simply eliminate invasive species populations (Figure 2.2). Soil legacies can be mitigated by adjusting soil properties, typically *via* topsoil removal or soil amendments (Buisson et al. 2008; Kulmatiski & Beard 2006; Perry et al. 2010). Carbon addition can help lowering nitrogen availability by stimulating nitrogen immobilization (Baer et al. 2003), thereby reducing invasive species performance and concurrently increasing desired species growth (Alpert & Maron 2000; Blumenthal et al. 2003; Eschen et al. 2007; see Perry et al. 2010 for review). However, in the case of restored communities reassembling from seeds, nitrogen management may have no direct positive effect unless a head-start is given to natives (i.e. invasive species are controlled the first growing season; James et al. 2011). Furthermore, success of carbon addition to decrease invasive species dominance also mainly depends on the condition that invasive species is nitrophilic relative to native species (Blumenthal et al. 2003).

To face soil legacies, another restoration approach is to establish species that are tolerant to invasive species legacies (Perry et al. 2005), or that could mitigate legacies before establishing the target community (Eviner & Hawkes 2012; Jordan et al. 2008; Leger & Baughman 2015; Vink et al. 2015). In this sense, restoration of non-susceptible species to

Centaurea maculosa's allelopathic compounds prevented reinvasion and possibly facilitate native species recovery (Callaway et al. 2005; Thorpe et al. 2009). Herron et al. (2001) also showed that establishing native species decreasing nitrogen availability through high nitrogen uptake decreases the prevalence of invasive species favored by soil nitrogen enrichment.

Taking soil legacies into account in restoration projects is however challenging. Soil legacies are difficult to predict and to assess (involving chemical analyses, determination of microbial communities' abundance and composition), and are species-specific (Bardgett & Wardle 2010; Bezemer et al. 2006; Yelenik et al. 2007). Furthermore, their persistence depends on characteristics of the invaded ecosystem (e.g. soil mineralization rates; Stock et al. 1995), on their nature (Corbin & D'Antonio 2012; Levine et al. 2003), and on the duration of invasion (Kulmatiski & Beard 2011; Marchante et al. 2008). For example, while allelopathic compounds are generally short-lived in the soil (i.e. hours to days; Blair et al. 2005; Reigosa et al. 2006), increased nitrogen levels generated by a nitrogen-fixing invasive species can persist for decades (e.g. 35 years; Maron & Jefferies 2001). Long-term studies suggest, however, that invasion impacts on ecosystems, such as increased nitrogen levels, can shift over time (Yelenik & D'Antonio 2013). All this makes it hard to predict the amplitude and persistence of soil legacies for a particular invasive species in a given environment, and calls for high levels of costly technical expertise. Thus, soil legacies are not systematically given the weight they deserve in restoration projects. Yet restoration would clearly benefit from accounting for soil legacies, especially when an invasive species is implicated in strong and persistent legacies and has dominated the target environment for several growing seasons (Figure 2.2; (Kulmatiski & Beard 2011; Marchante et al. 2008). A better understanding of how invasive species induce strong and persistent soil legacies in the habitat they commonly invade would reduce the need for complex and expensive analyses, facilitating development of effective restoration strategies. Cost-effective methods, such as native species germination or survival tests on soil with potential legacies should be developed to rapidly assess their extent.

In harsh environments with extremely limited resources and/or stressful conditions (e.g. extreme temperatures, excessive solar radiation, unstable substrates), invasive species removal often lead to a lower success of a native cover restoration (D'Antonio & Meyerson 2002). In some cases, invasive species are used as nurse plants to facilitate the establishment of native species (Figure 2.2; Becerra & Montenegro 2013; Hanslin & Kollmann 2016). The removal of an invasive species may not result in additional invasions (D'Antonio et al. 2017): the likelihood of other stress-adapted species being present and able to respond quickly is low (Harms & Hiebert 2006), and these systems constrain species to low productivity or capacity to accumulate biomass (D'Antonio et al. 2017). Managers may therefore have ample time to control a secondary invasive species because they commonly have low population growth rates (Funk & Vitousek 2007).

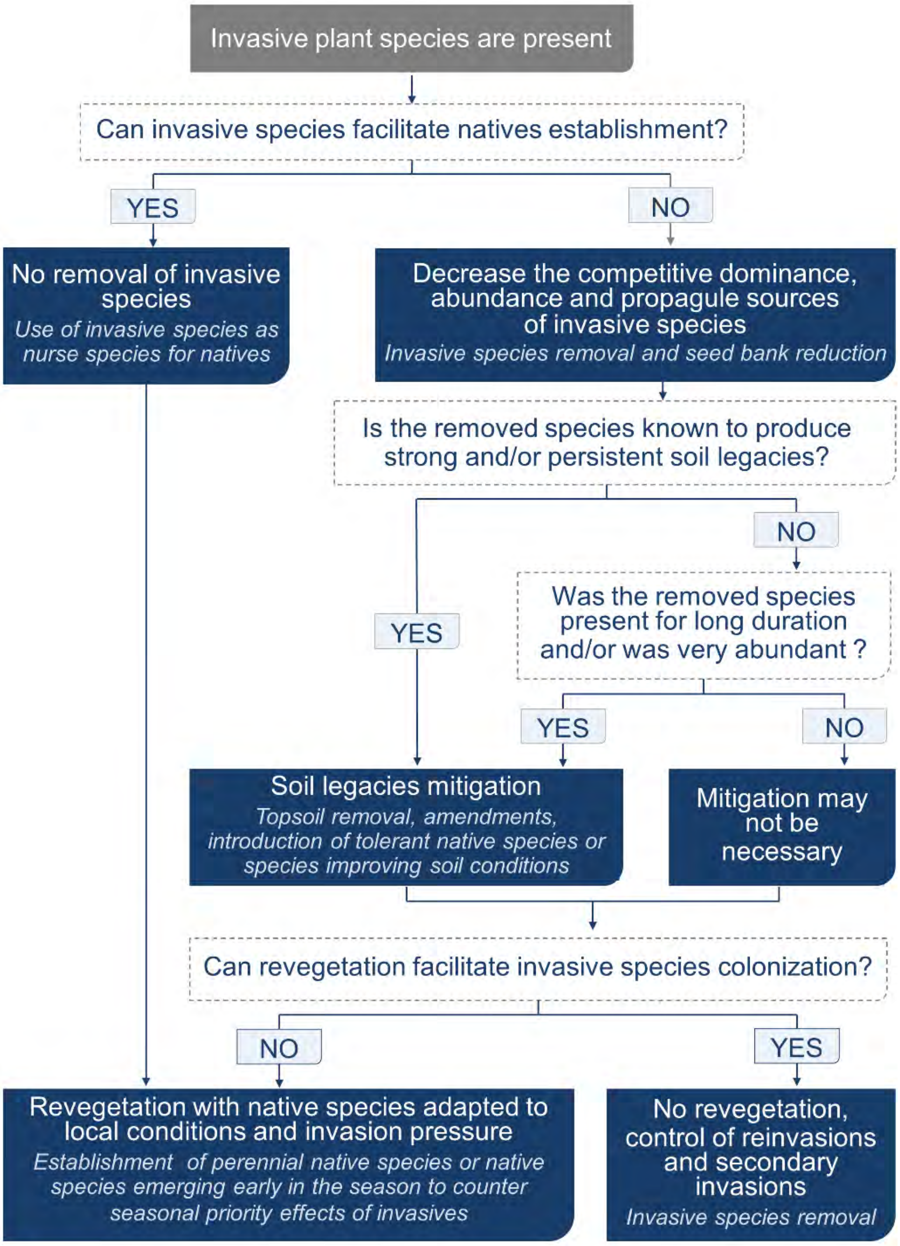

Figure 2.2 Decision support to counter invasive plant species priority effects. When invasive species facilitate the establishment of natives (e.g. in some harsh environments), they should not be removed and can be used as nurse species for restored species. Conversely, when invasive species hinder native species establishment (e.g. in some fertile and stable environments), it is essential to decrease their abundance and prevent secondary invasions, notably via removal and seed bank reduction. After removal, soil legacies generated by invasive species can lower restoration success. These legacies should be particularly considered when the removed invasive species is known to produce strong and/or persistent legacies (e.g. nitrogen levels), and/or or was present in abundance and/or for long duration. Legacies mitigation methods such as topsoil removal, amendments (e.g. carbon addition), or intermediate planting should be adjusted to the nature and intensity of legacies. Finally, the restoration of native species adapted to local conditions and invasion pressure should be undertaken to limit reinvasion and secondary invasions, except when revegetation facilitates invasions (e.g. in some harsh environments).

2.3 | Strengthening native species priority effects

Restoring native communities after a disturbance can have opposite consequences on invasion success depending on abiotic conditions. In harsh environments, native species can create microclimatic conditions that are more favorable to invasive species establishment than the surrounding (Cavieres et al. 2005; Lenz & Facelli 2003; Mason et al. 2013). In such cases, the restoration of a vegetation cover may not be the best option. Removal of invasive species followed by the control of secondary invasions without active revegetation may be a more suitable strategy. Resource availability, especially nitrogen, also strongly influences invasion success through modifications in competition intensity between species (Davis et al. 2000; Davis & Pelsor 2001). Environmental harshness has also been assumed to decrease the importance of stochastic factors because of strong niche selection (Chase 2007; Kardol et al. 2013). In this sense, Kardol et al. (2013) found weaker priority effects under low nutrient supply. In nitrogen-limited systems, restoration of nitrogen-fixing species can also favor the establishment of fast-growing invasive species that overgrow and shade slower-growing native species (Corbin & D'Antonio 2004; Huenneke et al. 1990; Maron & Connors 1996). In such conditions, it may be advisable to restore a native plant cover adapted to low levels of nitrogen and to consider avoiding nitrogen-fixing species and soil nitrogen amendments.

In fertile and relatively stable conditions, restoration of invasion-resistant native plant species is increasingly considered to protect disturbed sites from re-invasion or secondary invasions (Buckley 2008; Byun et al. 2013; Middleton et al. 2010; Pearson et al. 2016; Perry & Galatowitsch 2006). Environmental conditions influence the magnitude of priority effects (Collinge & Ray 2009; Kardol et al. 2013; Symons & Arnott 2014), with stronger impact in productive environments (Kardol et al. 2013; Young et al. 2016). The strength of priority effects also varies with the identity of the earlier- and the later-arriving species (Cleland et al. 2015; Dickson et al. 2012; Stuble & Souza 2016; von Gillhaussen et al. 2014; Wilsey et al. 2015), invasive species being less negatively impacted by arriving late than native species (Figure 2.1A; Stuble & Souza 2016; Wilsey et al. 2015), raising the need to restore native species producing strong priority effects.

Recent work on priority effects also states that the strength of priority effects is notably driven by **(1)** the impact a species has on resource levels (Fargione et al. 2003; Fukami 2015), **(2)** the overlap between competitive species in resource needs (Funk et al. 2008; Vannette & Fukami 2014), and **(3)** the impact a species has on non-resource components of the environment (Bever 2003; Goldstein & Suding 2014; Levine et al. 2004). The following sections will discuss how these emerging properties could be used to reinforce the priority effects of restored native species in invaded habitats (see Supplementary Material, Figure S2.1 for summary).

2.3.1 | Increasing resource preemption

Does the duration of time advance matters?

Numerous studies reported that giving native species a short time advance (one to few weeks) suffices to substantially decrease invasion success in grassland systems (Firn et al. 2010; Grman & Suding 2010; Vaughn & Young 2015; Young et al. 2016). Grman and Suding (2010) found that native species establishment only five weeks before invasive species introduction reduced invasive biomass by 85%, against an 8% decrease when natives and invasives were planted simultaneously. Firn et al. (2010) also found a strong effect of giving a three-week head-start to native grasses on an invasive grass performance. However, few studies investigated the importance of the duration of the time interval between native establishment and invasive species colonization. Asymmetry in plant size has been advocated as one of the most important aspect of priority effects (Wilsey et al. 2015), suggesting that extending duration interval between native species establishment and the later invasion event may give a size advantage strengthening native priority effects. In this sense, von Gillhaussen et al. (2014) found that a six-week head-start resulted in stronger priority effects than a three-week head-start. Young et al. (2016) tested the effect of giving the native perennials a two-week or a one-year seeding advantage over exotic annuals in a four-year experiment. It respectively resulted in a native cover increase of 68% or 128% compared to when natives and exotics were sown at the same time. The positive effect of increasing time advance appeared however inconstant between years and sites, with sometimes an absence of benefit. Better understand how the duration of time advance given to the restored native species influence invasion success would be crucial to develop cost-effective priority effect-based revegetation strategies. To give natives a time advantage over invasives, native species should be actively restored as soon as possible after the disturbance on an invasive species-free soil (Stevens & Fehmi 2009), and a particular attention must be payed to invasive species control in the initial weeks. Providing a short-term priority (several days) could also be achieved by 'pre-germinating' native species seeds. Pre-treatments including seed priming and cold stratification can help ensuring a rapid and complete germination and overcome seed dormancy (Halmer 2004). These treatments therefore appear as opportunities for improving native emergence speed and create priority effects over invasives, but remain yet untested.

Although the eventual success of extending time advance can be judged only against the persistence of priority effects over long periods (i.e. more than one growing season), long-term studies are rare. Vaughn and Young (2015) showed that the effect of a two-week advance in planting can remain visible after three years, favoring native perennials over exotic annuals. Werner et al. (2016) highlighted differences in persistence of a one-year priority between functional groups: the grass priority over forbs was still visible after six to eight years, but the forb priority over grasses did not persist. Designing efficient, cost-effective restoration strategies that allow native species to maintain their dominance over invasive species in the long-term calls for more studies on mechanisms (i.e. duration of time advance, disturbance regime, resource availability, dynamic of sown communities) influencing the persistence of priority effects over long periods.

Manipulate species composition and density

The resource competition model (Goldberg et al. 1990) predicts that the more a species reduces the availability of limited resources, the less these resources are available for later colonizers. Because resource preemption has been identified as one of the main driver of priority effects (Fukami 2015), high resource preemption would lead to strong priority effects (Vannette & Fukami 2014). Fargione et al. (2003) found that C4-grasses inhibited the most the later arriving invasive species, most likely because this guild reduced soil nitrate to the lowest levels compared with other tested functional guilds. This result suggests that restoring native species leading to a strong and rapid reduction of limited resources could help enhancing priority effects. Accordingly, research efforts should be directed towards the identification of species having the ability to **(1)** rapidly occupy of above- and/or below-ground space, thereby limiting light and space availability (often considered as two primary determinants of invasive species germination and establishment; Corbin & D'Antonio 2004; D'Antonio et al. 2001; Iponga et al. 2008), and **(2)** rapidly and effectively preempt soil nutrients, especially in low productivity environments where there is likely to be less above-ground competition for light (Dietz & Edwards 2006; Gioria & Osborne 2014).

At small scale (10 m^2 or less), many studies support the widespread assumption that species diversity confers invasion resistance (Carter & Blair 2012; Levine et al. 2004; Levine & D'Antonio 1999; Tilman 1997), due to fuller use of resources by resident species (complementarity effect; Larson et al. 2013; Lavorel et al. 1999; Levine & D'Antonio 1999; Robinson et al. 1995), or due to the increased probability of a species being present to be a strong competitor for the invasive species when increasing the number of species in a community (sampling effect; Goslee et al. 2013; Kennedy et al. 2002; Lavorel et al. 1999; Wardle 2001). Increasing diversity has been reported to increase primary productivity in grassland systems (Hector et al. 2011), suggesting that diverse communities produce higher rates of biomass and could therefore exert a stronger asymmetric competition with later colonists. Two studies supported the fact that diversity strengthens priority effects in protist and aquatic plant communities (Jiang et al. 2011; Viana et al. 2016), but more studies investigating this relationship in plant communities are needed. The density of individuals also modulates priority effects (Weiner 1990) in the sense that establishing more individuals should lead to increased resource acquisition and competition intensity (Goldberg et al. 1990; Lockwood et al. 2005). The benefit of increasing sowing density may stabilize over time, since the law of constant yields predicts that even-aged populations grown at different densities show the same overall productivity after a certain period of time, with higher number of individuals in high densities but lower standing biomass per individual (Drew & Flewelling 1979). Consistently, von Gillhaussen et al. (2014) found sowing density (1.5, 2.5 and 5 g/m^2) only had a weak influence on aboveground productivity. Increased density is however often associated with improved invasion resistance in short time scales (Carter &

Blair 2012; Gerhardt & Collinge 2007; Vaughn & Young 2015; Yannelli et al. 2017). Accordingly, Yannelli et al. (2017) found that sowing communities at high density (10 g/m^2) is more effective in suppressing invasive species than low density (1 g/m^2). The improved invasion-resistance of high density community may be related to the inability of low density community to fully exploit available resources. Since we are looking for solutions to design restored communities rapidly exerting strong priority effects, increasing sowing densities is an attractive option. However, it remains to determine effective sowing thresholds depending on species used and environmental conditions.

2.3.2 | Increasing niche overlap: applying limiting similarity

Niche overlap, referring to resource use similarity between co-occuring species independent of their rate of resource consumption (Petraitis 1989; Pianka 1974), has been hypothesized to influence invasion-resistance (Abrams 1983; Funk et al. 2008) and more recently priority effects (Vannette & Fukami 2014). Niche overlap is derived from the limiting similarity concept, predicting that species most similar to the invasive species should provide greater invasion resistance because of greater overlap in resource use (Abrams 1983). Accordingly, a high degree of similarity in resource use between first and later colonizers should strengthen priority effects of the recipient species. Attempts to use limiting similarity to limit plant invasions often resulted in failures (Emery 2007; Price & Pärtel 2013; Symstad 2000; Turnbull et al. 2005), highlighting the complexity of selecting plant species having a sufficient degree of niche overlap. With current knowledge, using the limiting similarity concept to limit invasions appears premature. An emerging, more promising strategy consists in focusing on the identification of key functional traits playing a substantial role in invasion resistance and priority effects (Cleland et al. 2013; Drenovsky & James 2010). For example, Cleland et al. (2013) identified phenology as an important determinant of invasion success: high phenological overlap between exotic annual grasses and restored forb species successfully resulted in a decreased abundance of invasive species. These results suggest that restoring early active perennial species may be particularly relevant to decrease the competitive dominance of early active annual invasive species in the long-term. Further investigations are needed to determine how and in which situations such trait-based strategies are efficient.

2.3.3 | Manipulating non-resource components

Few studies have explored ways to enhance invasion-resistance of restored communities by exploiting non-resource priority effects (Bever 2003; Levine et al. 2004) induced by the release of allelopathic compounds, the manipulation of mycorrhizae, or the promotion of pathogens or herbivory (Goldstein & Suding 2014). Non-resource priority effects could act through a direct negative impact on the target invasive species, or by an indirect improvement of native species success.

The use of allelopathy (i.e. the exudation of chemical compounds influencing the growth of other plants or microorganisms) for invasive species control has received special attention, especially in suppressing weeds in agricultural systems (Bhowmik 2003; Jabran 2017; Jabran et al. 2015; Milchunas et al. 2011). The establishment of native allelopathic species can directly reduce the biomass of the target invasive species (Callaway & Ridenour 2004), and indirectly facilitate the desired later-arriving native species (Perry et al. 2009). Indeed, allelopathy is relatively ineffective in interactions between species that frequently co-occur (Fitter 2003) and is more intense in novel interactions, such as between native and exotic species (Callaway & Ridenour 2004; Thorpe et al. 2009). By being established first, native allelopathic species could induce stronger priority effects reducing invasion success, but such assumption needs to be tested. Since the allelopathic effect vary depending on species (Prati & Bossdorf 2004), community density (Weidenhamer et al. 1989), climate conditions (Blair et al. 2006; May & Ash 1990), and substrate characteristics (Parepa & Bossdorf 2016), using allelopathic native species to limit invasion appears complex and may be limited to a set of invasive species. The effectiveness of invasive control strategies based on allelopathic species needs further investigations, in particular the potential use of native allelopathic species to suppress several invasive species.

In addition to plant-plant interactions, biotic resistance can also arise from consumption by herbivores and disease (Levine et al. 2004). Introducing coevolved natural predators or parasites from the native region of the invasive species has been implemented for controlling well-established invasive populations, with mixed results (Clewley et al. 2012). Native herbivores can have various impacts on invasives (Levine et al. 2004; Maron & Vilà 2001), sometimes contributing (i.e. invasive plants are maladapted to deter consumption by native herbivores; Morrison & Hay 2011; Parker & Hay 2005; Petruzzella et al. 2017; Zhang et al. 2018) or not (i.e. native herbivores are maladapted to consume invasive plants; Keane & Crawley 2002; Liu & Stiling 2006; Xiong et al. 2008) to biotic resistance. However, because herbivores have been reported to create disturbances facilitating the establishment of invasive species (Hobbs & Huenneke 1992; Mack 1989), and because young restored native species may be negatively impacted by trampling (Hill & Silvertown 1997), using herbivores in early stages of restoration may not be an advisable option.

Mycorrhizal fungi, forming symbiotic relationships with 80–90% of terrestrial plants (Smith & Read 2010), often strongly influence plant growth and reproduction (Koide & Dickie 2002), plant community structure (Hartnett & Wilson 1999, 2002; Van der Heijden et al. 1998), and invasion success (Callaway et al. 2004; Klironomos 2002). Soil inoculation of arbuscular mycorrhizal fungi can reduce the performance of agricultural non-mycorrhizal weeds (Jordan et al. 2000; Rinaudo et al. 2010; Vatovec et al. 2005; Veiga et al. 2011), raising a potential application in managing non-hosts invasive species (e.g. from Chenopodiaceae and Cruciferae families; Wang & Qiu 2006). In the case of non-hosts invasive species, establishing species having the ability to increase mycorrhizal inoculum potential would facilitate arbuscular mycorrhizal fungi-dependent native species (Eviner & Hawkes 2012), and may enhance their competitive abilities over later arriving invasive species (Smith et al. 1998). In the cases where the presence of mycorrhizae increases invasion success of host invasive species (Marler et al. 1999; Smith & Read 2010), mycorrhizae suppression through fungicide application combined with restoration of non-mycorrhizal species may help limiting invasive species. The feasibility and effectiveness of this approach needs however to be investigated, since mycorrhizae are sometimes essential in some species assemblages (Dostálek et al. 2013).

Overall, whether native herbivores, parasites and symbionts could create priority effects reducing invasive species success remains untested, so that an application in restoration is premature. Because interactions between invasive species and native enemies or symbionts are species or trait-specific (Grutters et al. 2017; Veiga et al. 2011; Zhang et al. 2018), it may be relevant to develop non-resource-based restoration strategies for the most noxious invasive species.

2.4 | Conclusion

Recent research suggests that better considering priority effects of both invasive and native species in restoration strategies could significantly help reducing invasive species colonization on disturbed areas. When invasive plants arrive or emerge earlier than natives, a size-related advantage can hamper native community restoration success, often impelling to reduce or remove invasive propagule sources. Yet, after removal, invasive plants can still threaten restoration success through persisting soil legacies, especially when the invasive species have long been present or when they were very abundant. The processes underlying the magnitude and persistence of soil legacies are however still poorly understood. Research efforts should be directed towards this topic, as well as towards developing cost-effective and rapid methods of assessing invasives-induced soil modifications. In order to avoid reinvasion and secondary invasions, invasive species removal must often be coupled with the restoration of native species. However, before undertaking revegetation, it is advisable to ensure that it will not lead to invasive species facilitation, such as in some harsh environments.

Invasion-resistance of restored native species could be increased by manipulating resource- and non-resource-based priority effects, especially in productive environments. Resource preemption, driving priority effects, may be enhanced by extending native species time advance over invasives and by manipulating the characteristics of the restored native species. Several studies reported a high benefit of giving only few weeks of advance, and the amplitude of the benefit was often correlated to variations in environmental conditions (e.g. climate, rainfall, soil fertility). Extending time advance showed mixed results and has been yet poorly studied, raising the need to multiply studies in order to define durations of time advance which are the most effective and how this effectiveness varies depending on environmental conditions. Resource preemption could also be enhanced by manipulating the characteristics of the restored species (selecting species having traits associated to strong and rapid resource preemption, increasing species diversity or sowing density), but such strategies remain largely untested in the field. Priority effects have also been suggested to be influenced by niche overlap between species, but attempts to use functional similarities to control invasive species often showed unsatisfying results. Focusing on key functional traits playing a substantial role in invasion success (e.g. phenology) appeared more promising, but studies are lacking to evaluate the relevance of this method. The manipulation of non-resource priority effects to limit invasions has been yet poorly studied. Restoring allelopathic native species may decrease invasion success by directly reducing the target invasive species biomass and indirectly facilitating native species. To investigate the potential of this method, research is needed on the interactions between allelopathy and priority effects as well as the use on the ability of native allelopathic species to suppress several invasive species. The manipulation of other non-resource mechanisms to increase priority effects of natives, such as natural enemies of invasive species or mycorrhizae, appears today premature.

Combinations between different priority effect-based strategies have not been explored yet, but may potentially enhance invasive species control. When invasive species are present, it may be relevant to simultaneously tackle their priority effects and increase those of desired native species. Different strategies could also be successively used over time. For example, establishing a community dominated by one competitive species, producing a high rate of biomass, may be an effective way to rapidly increase native cover and counter immediate invasion risk, while subsequently adding seeds from diverse species may help stabilize the community in the long-term.

Acknowledgements

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Supplementary material

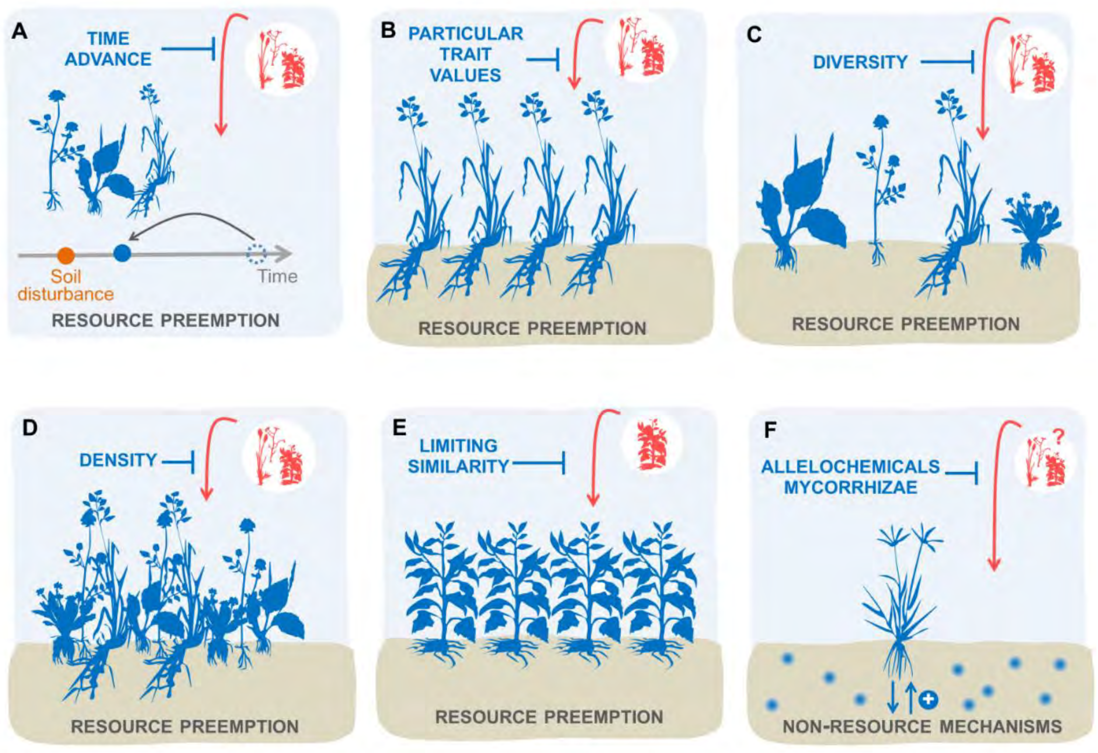

Figure S2.1 Revegetation strategies that could reinforce priority effects of native species and prevent invasive species colonization. Priority effects can be driven by resource preemption or the alteration of non-resource characteristics of the environment (e.g. releasing of allelochemicals, modification of herbivory, pathogens and mycorrhizae). Resource preemption could be enhanced by (**A**) giving natives a large time advance through establishing the community as soon as possible after disturbances, (**B**) establishing a dominant native species with particular trait values enabling to strongly and rapidly preempt limited resources (**C**) increasing species diversity, (**D**) increasing sowing density, and (**E**) establishing a dominant native species with specific trait values similar to one targeted invasive species (limiting similarity). To increase priority effects of native species, non-resource components could be manipulated by (**F**) manipulating non-resource components (e.g. inoculation or suppression of mycorrhizal fungi) or introducing native species inducing soil modifications in releasing allelochemicals or modifying soil biota.

Synthesis of Chapter 2 and transition to Chapter 3

Chapter 2 in a nutshell

Are priority effects a main mechanism involved in early invasion resistance?

There is substantial evidence that priority effects strongly affects invasion resistance. Giving a time advance to native species can increase invasion resistance through an elevation of their fitness compared with later colonizing invasive species.

Can priority effects be used after a disturbance, in a restoration context, to design plant communities resisting early invasion?

While manipulating priority effects to reduce invasion has not been much investigated in the field, we pointed out encouraging results and proposed several promising ways to tackle priority effects of invasive species and enhance priority effects exerted by native species. Further research efforts are however required to test and refine priority effect-based strategies.

In Chapter 2, I underlined several ways to increase priority effects of native species reestablished after a disturbance. In Chapter 3, I report the results of a greenhouse experiment where I tested the influence of several interacting factors potentially influencing priority effects: **(1)** elapsed between recipient community sowing and invasive species introduction, **(2)** recipient community composition and **(3)** sowing density.

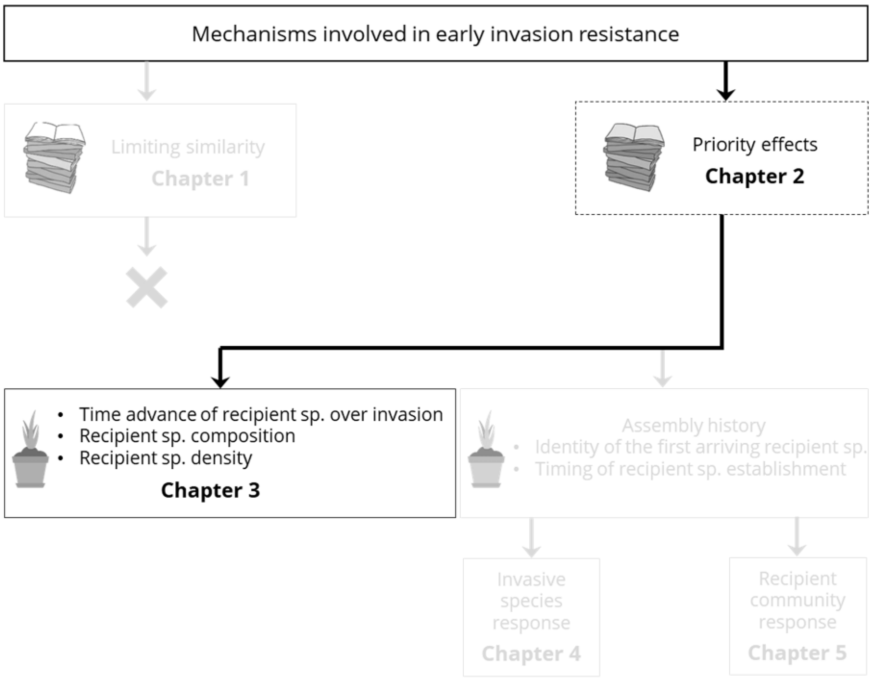

Figure T.3 Chapter 3 in thesis organization.

Chapter 3

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

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Manon CM Hess, Elise Buisson, Hugo Fontes, Léo Bacon,
Florent Sabatier, François Mesléard

Reference

Hess MCM, Buisson E, Fontes H, Bacon L, Sabatier F, Mesléard F (2020) Giving recipient communities a greater head start and including productive species boosts early resistance to invasion. Applied Vegetation Science 23:340-352

Chapter 3

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/m^2), 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

3.1 | 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; Firn 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 (Ejrnaes 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; Nemec 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/m^2) 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.

3.2 | Methods

3.2.1 | Species selection

While many studies assess the response of a single invader (Byun et al. 2013; Byun & Lee 2017; Dukes 2002; Firn 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 & Vilà 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 & Vilà 2008). The small, wind-dispersed seeds (i.e. 106 seeds per mature plant; Domenech & Vilà 2008; Lambrinos 2002) are able to rapidly germinate under a wide range of ecological conditions (Domenech & Vilà 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 temperate 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).

3.2.2 | 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 S3.1Erreur ! 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/m^3), 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.

3.2.3 | 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 seeds/m^2 (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.

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	*Lolium perenne*	63	22	9	250	82	30
	Dactylis glomerata	-	-	4	-	-	20
	Schedonorus arundinaceus	-	-	6	-	-	30
Leguminous forbs	*Trifolium repens*	-	20	6	-	84	30
	Lotus corniculatus	-	-	6	-	-	25
	Onobrychis viciifolia	-	-	9	-	-	30
Non-leguminous forbs	*Plantago lanceolata*	-	21	8	-	84	30
	Poterium sanguisorba	-	-	9	-	-	30
	Achillea millefolium	-	-	6	-	-	25

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

Sowing densities were chosen in line with the densities commonly applied in roadside revegetation. Native species seeds were allocated to fixed positions, either 3.5 cm (LowD) or 1.5 cm (HighD) apart and chosen so as to ensure that all invasive species individuals were surrounded by the same native species neighbors (Figures 3.2, 3.3).

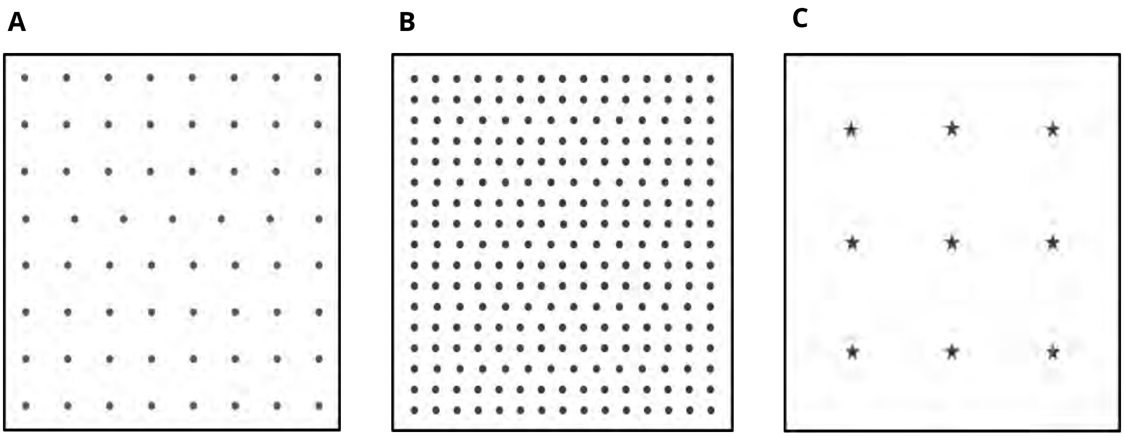

Figure 3.2 Pot spatial arrangement of (**A**) Low density recipient communities (63 seeds/pot), (**B**) High density recipient communities (235 seeds/pot) and (**C**) invasive species seeds.

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 × composition × 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.

3.2.4 | 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-µm 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 × 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 (Teyssier 2020).

3.2.5 | 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:

$$\psi_{time \times comp \times den} , \varphi_{time \times comp \times den}$$

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.

3.3 | Results

3.3.1 | 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).

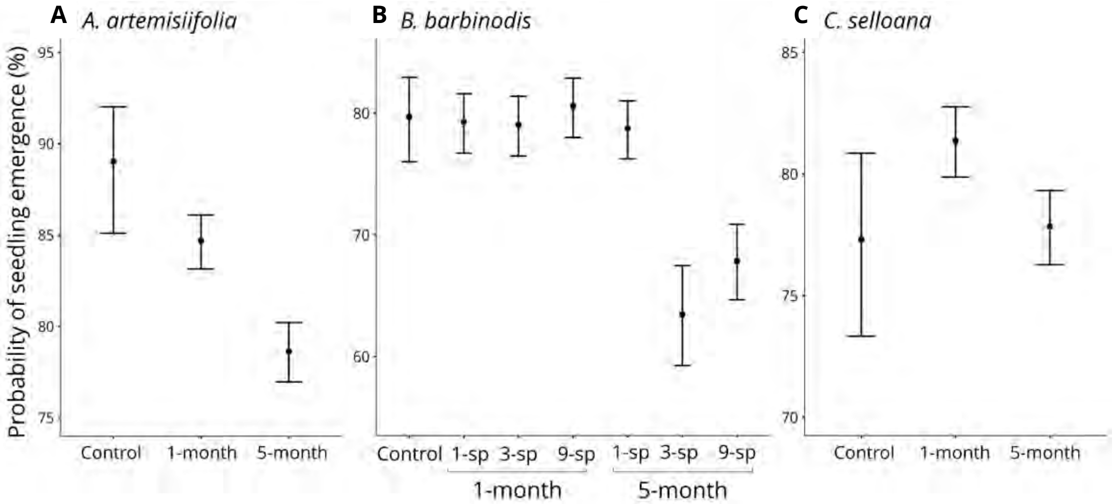

Figure 3.4 Probability of seedling emergence (model estimates; percentage ±95% CI) of the invasive species: (**A**) *Ambrosia artemisiifolia* (n_{tot} = 432); (**B**) *Bothriochloa barbinodis* (n_{tot} = 432); and (**C**) *Cortaderia selloana* (n_{tot} = 432), depending on recipient community on recipient 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.

3.3.2 | 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.

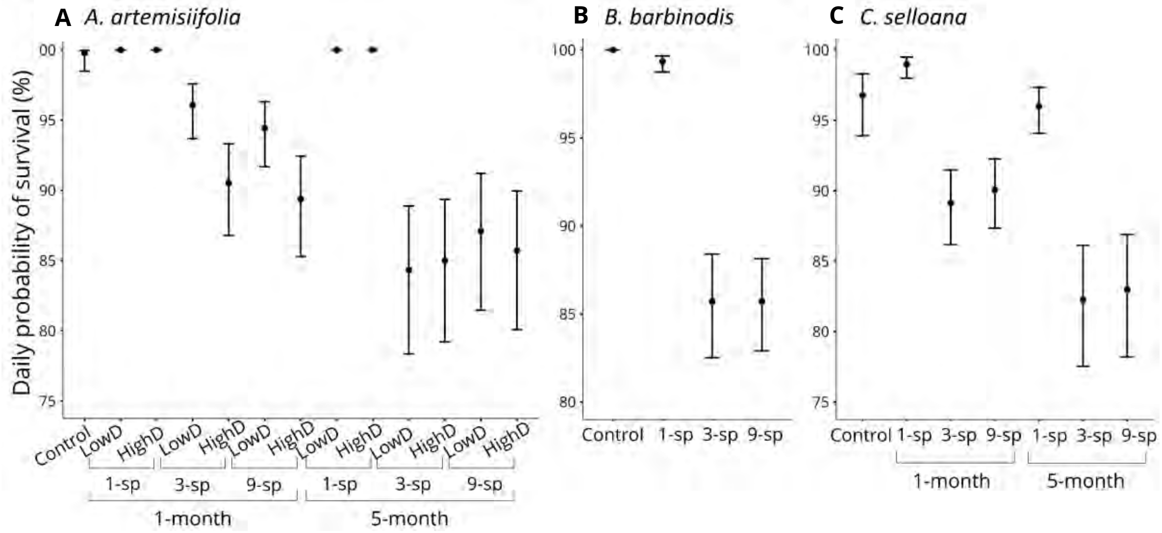

Figure 3.5 Daily probability of survival (model estimates; percentage ±95% CI) of the invasive species: (**A**) *Ambrosia artemisiifolia* (n_{tot} = 389); (**B**) *Bothriochloa barbinodis* (n_{tot} = 336) and (**C**) *Cortaderia selloana* (n_{tot} = 368) depending on recipient community type: time advance 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.

3.3.3 | 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 χ^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±8.2% of the total biomass, while *L. perenne* and *P. lanceolata* only represented 9.1±5.3 and 2.8±1.1% (Figure 3.6). *Lotus corniculatus* dominated 9-sp communities, representing on average 61.3±10.5% of the total biomass, followed by *T. repens* (16.7±6.6%) and *D. glomerata* (5.9±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).

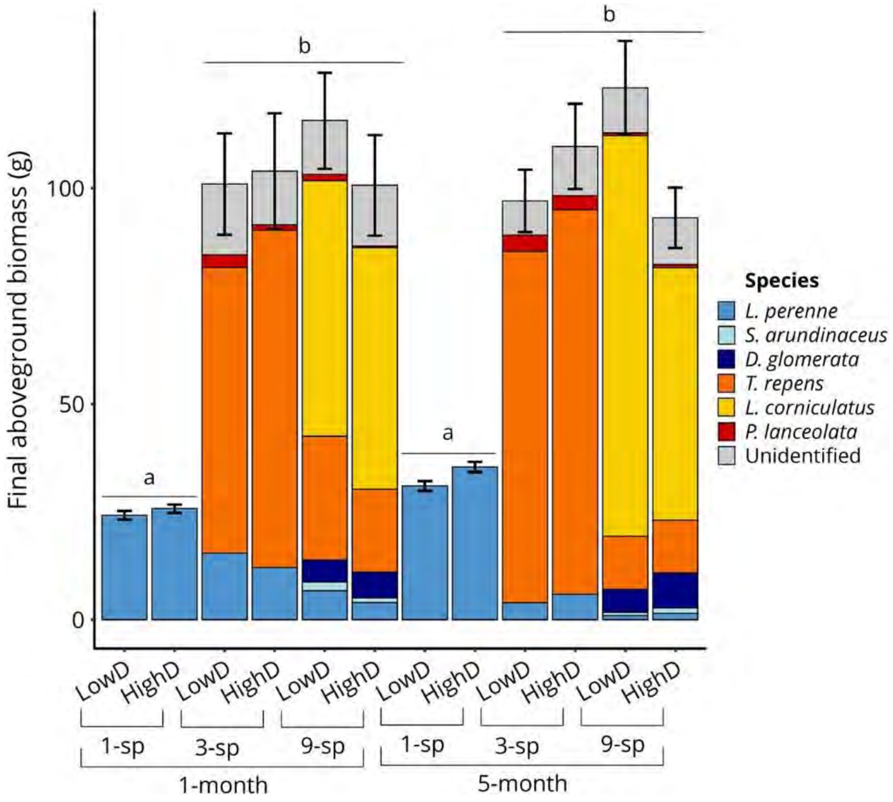

Figure 3.6 Final aboveground biomass of the community (mean±SE, n=12) classed by species, depending on recipient community type: time advance over invasive species (1 month or five months), species composition (1-sp = one species, 3-sp = three species, 9-sp = nine species), and density (LowD = low density, 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 (α=0.05).

3.3.4 | Recipient vegetation cover

Recipient community type significantly impacted vegetation cover percentage at the time of invasive species introduction (Kruskal-Wallis χ^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±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).

3.3.5 | 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).

3.4 | 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.

3.4.1 | 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 & Kozlowski 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.

3.4.2 | 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, were 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
A. artemisiifolia	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
B. barbinodis	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
C. selloana	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

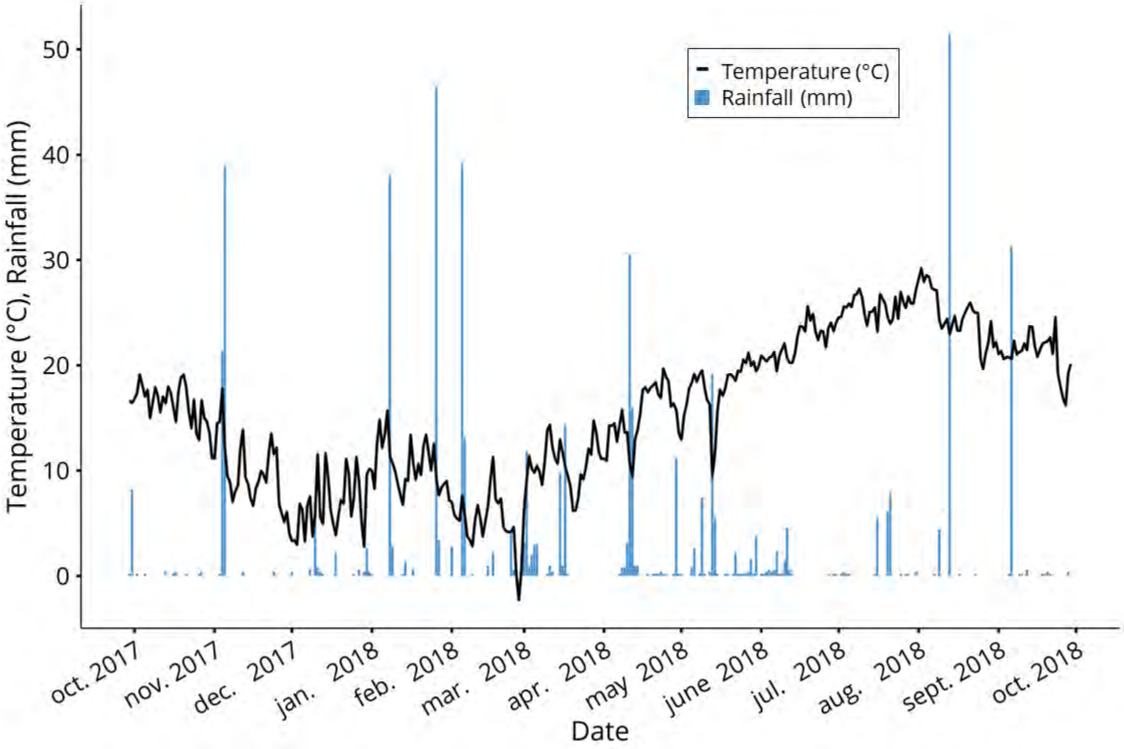


Figure S3.1 Temperature (daily mean in °C) and rainfall (daily sum in mm) recorded during the experiment (Meteo France station number 133004003, Tour du Valat domain, France).

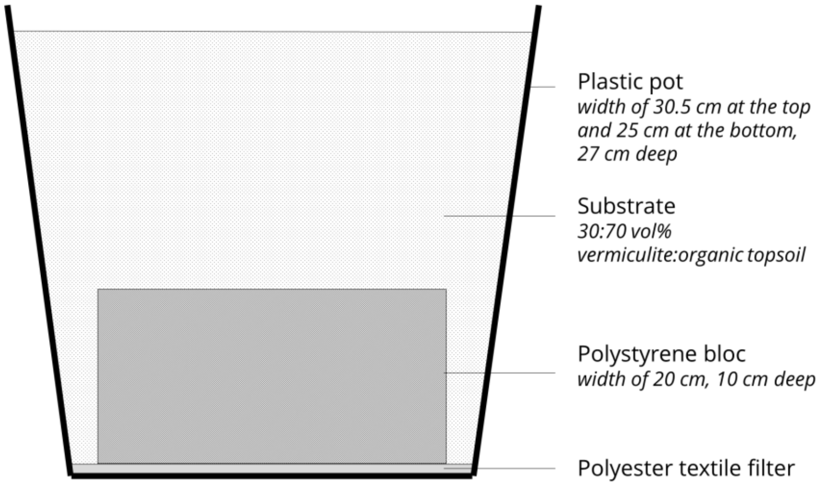
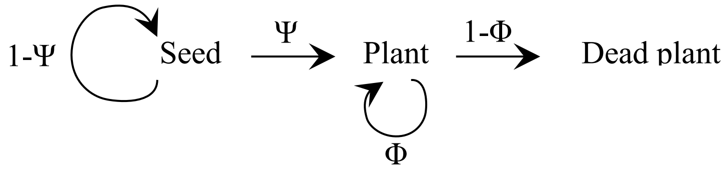


Figure S3.2 Experimental design: pot filling.

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

Matrices

The model considered thtrr 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 State: At the initial state, all individuals are in the seed state

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

With '*' indicating the complementarity parameter (only one '*' by row) and '–' indicating parameters constrained to zero

Transition 1: Estimation of seedling emergence (ψ)

$$\begin{array}{cc} & \begin{array}{ccc} S & P & D \end{array} \\ \begin{array}{c} S \\ P \\ D \end{array} & \begin{pmatrix} * & \psi & - \\ - & * & - \\ - & - & * \end{pmatrix} \end{array}$$

Transition 2: Estimation of daily survival (φ)

$$\begin{array}{cc} & \begin{array}{ccc} S & P & D \end{array} \\ \begin{array}{c} S \\ P \\ D \end{array} & \begin{pmatrix} * & - & - \\ - & \varphi & * \\ - & - & * \end{pmatrix} \end{array}$$

Recapture: Detection probability

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

$$\begin{array}{cc} & \begin{array}{ccc} NO & S & P \end{array} \\ \begin{array}{c} S \\ P \\ D \end{array} & \begin{pmatrix} * & p & - \\ * & - & p \\ * & - & - \end{pmatrix} \end{array}$$

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

Ambrosia artemisiifolia

Model selection for seedling emergence probabilities with survival probabilities [φtime×comp×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	ψden×time	18	2764.46	2800.58
4	ψcomp×time	20	2761.51	2801.66
1	ψden×comp×time	26	2751.82	2804.06
5	ψden	16	2794.73	2826.62
6	ψcomp	19	2790.90	2829.03
2	ψden×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 [ψtime] 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×comp×time**	**16**	**2765.85**	**2797.94**
11	φcomp×time	10	2781.09	2801.12
9	φden×comp	10	2802.37	2822.41
13	φcomp	7	2812.60	2826.62
10	φden×comp	8	3018.89	3034.91
14	φtime	6	3028.34	3040.36
12	φden	6	3038.61	3050.62
15	φ.	4	3086.95	3094.97

Bothriochloa barbinodis

Model selection for seedling emergence probabilities with survival probabilities [φtime×comp×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×time**	**20**	**3052.50**	**3092.64**
1	ψden×comp×time	26	3043.41	3095.64
7	ψtime	16	3106.91	3138.10
3	ψden×time	18	3105.29	3141.40
6	ψcomp	17	3141.23	3175.33
2	ψden×comp	20	3137.28	3177.42
5	ψden	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 [ψtime×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×comp**	**14**	**3064.23**	**3092.30**
4	φden×comp×time	20	3052.50	3092.64
13	φcomp	11	3070.70	3092.75
11	φcomp×time	14	3065.32	3093.39
14	φtime	10	3282.99	3303.02
10	φden×time	12	3281.66	3305.71
12	φden	10	3287.51	3307.54
15	φ.	14	3337.65	3353.68

Cortaderia selloana

Model selection for seedling emergence probabilities with survival probabilities [φtime×comp×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	ψden×time	18	3503.29	3539.42
4	ψcomp×time	20	3499.37	3539.52
8	ψ.	14	3516.59	3544.67
6	ψcomp	17	3512.23	3546.34
5	ψden	16	3514.37	3546.47
1	ψden×comp×time	26	3495.14	3547.40
2	ψden×comp	20	3510.29	3550.45

Model selection for daily plant survival probabilities with best model for emergence probabilities [ψtime] 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×time**	**10**	**3510.30**	**3530.34**
7	φden×comp×time	16	3504.46	3536.56
13	φcomp	7	3539.91	3553.93
9	φden×comp	10	3534.68	3554.72
14	φtime	6	3652.54	3664.55
10	φden×time	8	3650.52	3666.55
12	φden	6	3668.1691	3680.19
15	φ.	4	3680.52	3688.52

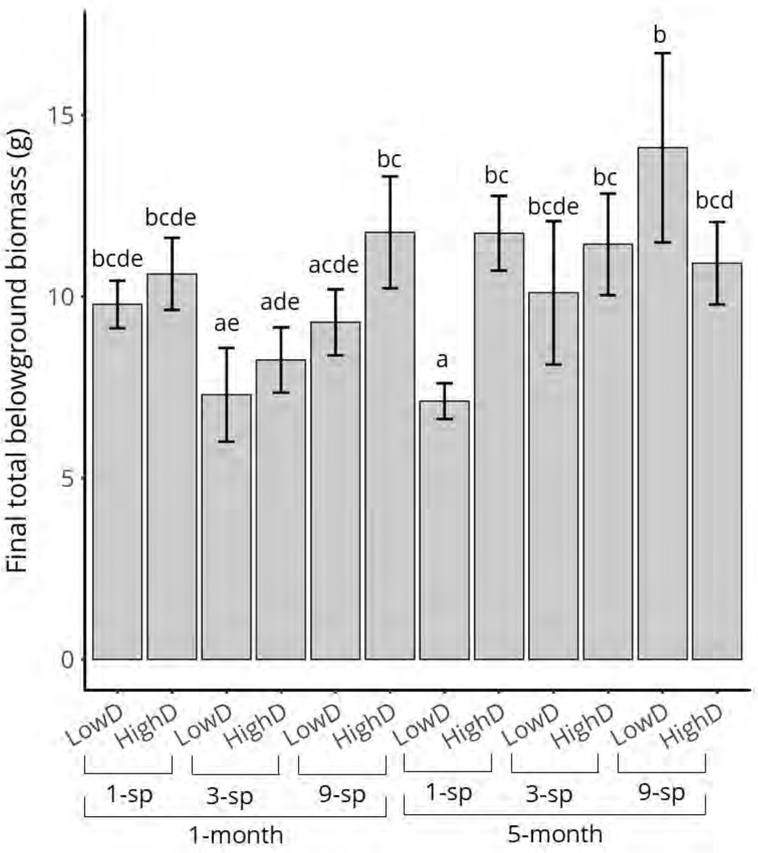


Figure S3.3 Final total belowground biomass (mean±SE, n=6) depending on recipient community type: time advance over invasive species (1- or 5-month), species composition (1-sp = 1 species, 3-sp = 3 species, 9-sp = 9 species) and density (LowD = low density or HighD = high density). Community type significantly impacted final total belowground biomass (Kruskal-Wallis χ^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 (α=0.05).

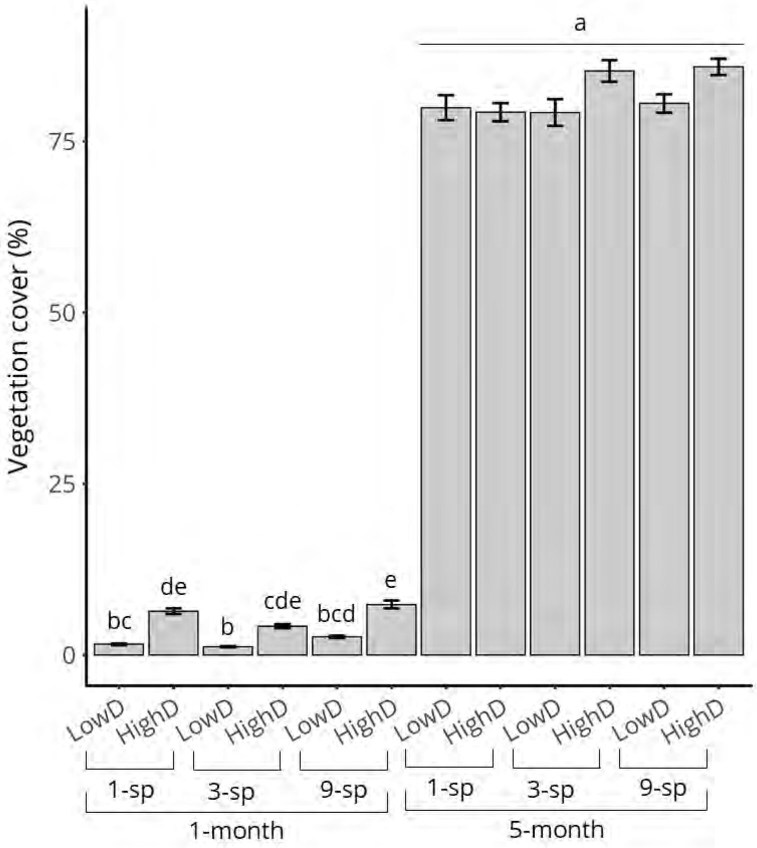


Figure S3.4 Vegetation cover of the recipient communities at the time of invasive species introduction (%mean±SE, n=12) depending on recipient community type: time advance over invasive species (1- or 5-month), species composition (1-sp = 1 species, 3-sp = 3 species, 9-sp = 9 species), and density (LowD = low density or HighD = high density). Letters (a,b,c,d,e) distinguish vegetation cover percentage means that are significantly different according to a post-hoc Dunn's test (α=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_2O_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

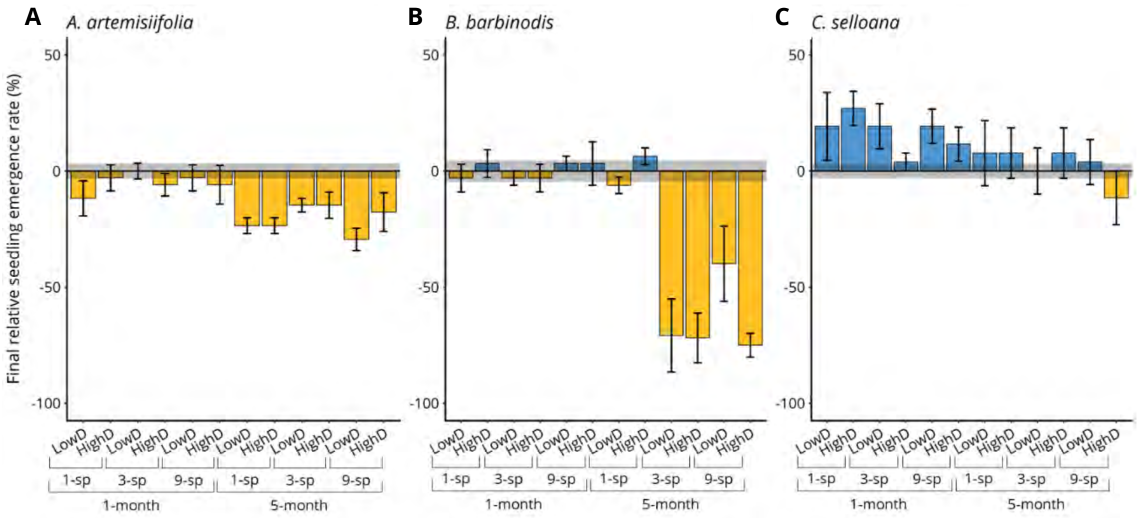


Figure S3.5 Final seedling emergence rate (mean±SE, n=4) relative to the control (0) of the invasive species (**A**) *A. artemisiifolia*, (**B**) *B. barbinodis* and (**C**) *C. selloana*, depending on recipient community type: time advance over invasive species (1- or 5-month), species composition (1-sp = 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.

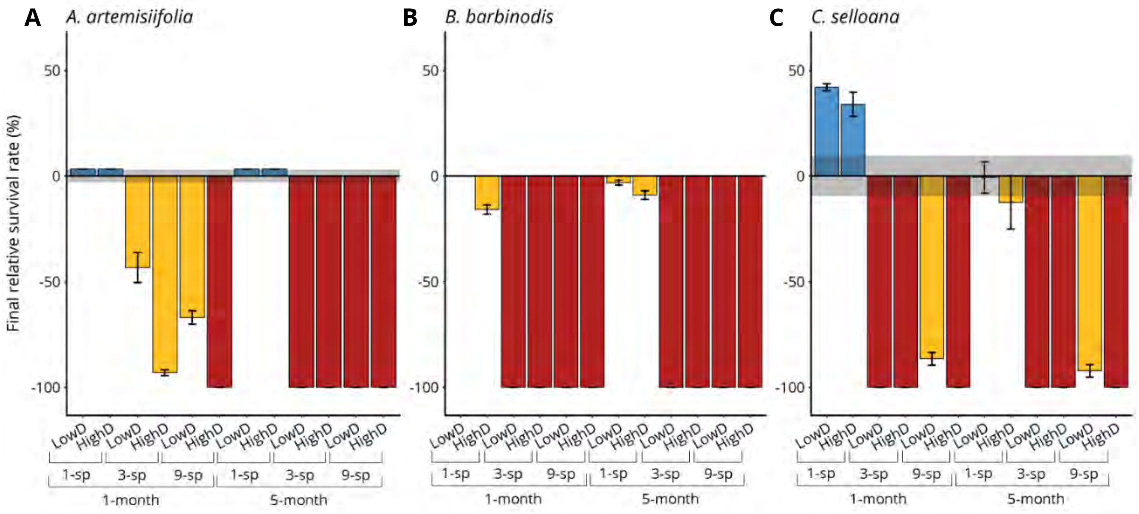


Figure S3.6 Final survival rate (mean±SE, n=4) relative to the control (0) of the invasive species (**A**) *A. artemisiifolia*, (**B**) *B. barbinodis* and (**C**) *C. selloana*, depending on recipient community type: time advance over invasive species (1- or 5-month), species composition (1-sp = 1 species, 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.

Synthesis of Chapter 3 and transition to Chapter 4

Chapter 3 in a nutshell

How do invasion timing (i.e. elapsed time between recipient community sowing and invasive species introduction), recipient community composition and sowing density interact to influence priority effects and early invasion success?

Giving a greater time advance to the recipient community enhanced early invasion resistance when the community produced a sufficient amount of aboveground biomass. The amount of biomass produced was related to species composition. Sowing density had a limited influence.

Does providing efforts to delay invasion and manipulating the composition and density of seed mixes constitute efficient strategies to reduce early invasion?

Manipulating species composition by including productive species could particularly improve early invasion resistance, while increasing sowing density appeared less impactful. Managing the timing of recipient community and invasive species establishment could also help decreasing invasion success.

In Chapter 4 and 5, I focus on the results of a greenhouse experiment where assembly history of the recipient community was manipulated prior to invasion. I tested whether establishment timing of the recipient species (synchronous *vs.* sequential sowing) and the identity of the first established species influence recipient community structuring and subsequent invasion success. In Chapter 4, I focus on invasive species response.

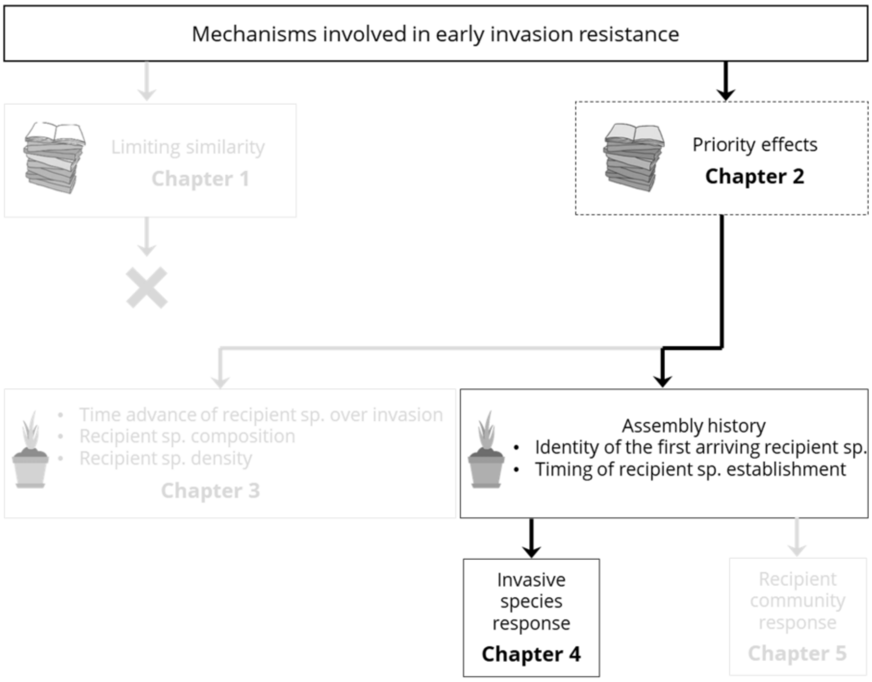


Figure T.4 Chapter 4 in thesis organization.

Chapter 4

Altering assembly history influences performance of an annual invader

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Nathan Haveneers, Elise Buisson

Sumbitted to Biological Invasions on June 5, 2020

Chapter 4

Abstract

Understanding the determinants of early invasion resistance is a major challenge for designing plant communities that efficiently repel invaders. Recent evidence highlighted the significant role of priority effects in early community assembly by affecting species composition, structure and functional properties, but few studies have investigated consequences of assembly history on invasion success. In a greenhouse experiment, we investigated how **(1)** the identity of the first native colonizing species (one of two grasses: *Dactylis glomerata* and *Lolium perenne*, or two legumes: *Onobrychis viciifolia* and *Trifolium repens*), each introduced four weeks before the rest of the native community, and **(2)** timing of species establishment (synchronous *vs.* sequential sowing), influenced early establishment success of *Ambrosia artemisiifolia*, an annual noxious weed in Europe. First colonizer identity and establishment timing both affected early biomass production and composition of the community as well as soil nutrient content, and had implications for A. *artemisiifolia* performance. Invasion resistance increased when all native individuals were sown simultaneously, quickly generating a high biomass production, and when the grass species L. *perenne* was sown first, most likely because of a high belowground biomass production. Giving a priority to the productive N-fixing legume T. *repens* conversely boosted A. *artemisiifolia* performance, presumably because of a lower belowground competition arising from a low initial biomass production, elevated soil N levels and low grass content. These findings support that assembly history matters to invasion resistance in the early growth stages, thus opening the way to more effective revegetation strategies.

Key Words: priority effects, historical contingencies, revegetation, restoration, competition, *Ambrosia artemisiifolia*

4.1 | Introduction

An increasing number of invasive species is causing disastrous consequences on the environment (Brondizio et al. 2019; Mollot et al. 2017), human well-being and economy (Charles & Dukes 2008; Pimentel 2009), and this increase is expected to intensify (Sala et al. 2000; Seebens et al. 2015). Invasions are also often a serious impediment to the successful restoration of damaged environments (Norton 2009; Rowe 2010; Stromberg et al. 2007). Restorative activities, including soil disturbance and vegetation clearing, increase resource availability and decrease competition from neighbors, and can promote plant invasion (Cherwin et al. 2009; Davis et al. 2000; Jauni et al. 2015; Mack et al. 2000; McIntyre & Lavorel 1994; Smith & Knapp 1999). Susceptibility to invasion decreases over time as the restored community establishes and displays a more complete use of available space and resources. Reducing invasive species establishment success in the early, vulnerable stages of community growth is therefore critical. Restoring a rapidly competitive native plant cover has been advocated as a method to reduce invasions (Blumenthal et al. 2003, 2005; Byun & Lee 2017; Larson et al. 2013; Middleton et al. 2010). However, the mechanisms generating rapid invasion resistance are still poorly known.

Recent advances in community ecology have highlighted the defining role of historical contingencies (i.e. the effect of the order and timing of past events, being either abiotic or biotic) in community assembly and invasibility (Chase 2003; Fukami 2004, 2015; Körner et al. 2008; Suding et al. 2004; Švamberková et al. 2019; Werner et al. 2016; Young et al. 2016). Priority effects, the ability of an early-arriving species to either inhibit or facilitate the establishment, growth or reproductive success of species arriving later (Drake 1991; Helsen et al. 2016), have recently received particular attention. Although priority effects often do not systematically generate changes persisting in the long-term (Collinge & Ray 2009; Young et al. 2016), numerous studies showed that even small differences in species arrival can induce dramatic changes in composition, structure and functional properties (e.g. productivity) at least for one growing season (Delory, Weidlich, von Gillhaussen et al. 2019; DeMalach & Fukami 2018; Ejrnaes et al. 2006; Grman & Suding 2010; Körner et al. 2008; Martin & Wilsey 2012; Plückers et al. 2013; Sarneel et al. 2016; Stevens & Fehmi 2011; Stuble & Young 2020; Vaughn & Young 2015; von Gillhaussen et al. 2014; Weidlich et al. 2018; Werner et al. 2016; Young et al. 2016). Priority effects could therefore affect early invasion resistance (Lang et al. 2017; Stevens & Fehmi 2011; Vaughn & Young 2015) and could be manipulated to design invasion resistant restored communities (Hess, Mesléard, Buisson 2019). In the early stages of community development, priority effects could be particularly impactful by influencing biomass production and species composition.

Several studies have advocated for a substantial role of biomass production in invasion resistance, i.e. high biomass associated to lower invasibility (Byun & Lee 2017; Gaudet & Keddy 1988; Hess et al. 2020; Jiang et al. 2006; Lulow 2006; MacLaren et al. 2019; Mason et al. 2017; Rinella et al. 2007; Symstad 2000; Weigelt et al. 2002). Biomass production is an indicator of competitive ability (Gaudet & Keddy 1988), and high biomass may reflect a high consumption of available resources so that, especially in the early stages, a highly productive community may preempt more resources than a less productive community may. Specifically, a high aboveground productivity is expected to increase competition for light, therefore being determinant for invasion success following disturbances and vegetation clearance (Baruch et al. 2000; Corbin & D'Antonio 2004; D'Antonio et al. 2001; Forrest Meekins & McCarthy 2001; Vitousek & Walker 1987).

Other studies demonstrated that invasion resistance is strongly linked with community composition, i.e. the identity of the dominant species or functional group (e.g. Byun et al. 2013; Crawley et al. 1999; Dukes 2002; Fargione & Tilman 2005; Hector et al. 2001; Mason et al. 2017; Symstad 2000). Notably, increased invasion resistance has been attributed to the presence of grasses (Crawley et al. 1999; Dukes 2002; Fargione & Tilman 2005; Mason et al. 2017; Mwangi et al. 2007; Prieur-Richard et al. 2002; Scherber et al. 2006, 2010; Stuble & Young 2020), likely because of their ability to strongly compete for limiting belowground resources such as nitrates thanks to a dense root system (Fargione et al. 2003; Scherber et al. 2010; Scherer-Lorenzen et al. 2003) or the reduction of light and space availability (Mason et al. 2017). In contrast, prior colonization by legumes has been shown to facilitate subsequent species establishment and performance (Frankow-Lindberg 2012; Temperton et al. 2007; von Felten et al. 2009; von Gillhaussen et al. 2014; Weidlich et al. 2016, 2018), and the presence of legumes has been positively correlated to a greater invasion success (Scherber et al. 2006; Mwangi et al. 2007). This facilitative effect has been attributed to their ability to fix atmospheric nitrogen and directly transferring it to neighbors via root exudation and mycorrhizal links (Govindarajulu et al. 2005; Paynel et al. 2001), or releasing it into the soil by decomposition (Tomm et al. 1995). In addition, due to nitrogen fixation, nitrogen-fixing legumes display a small root system and preempt low amounts of soil nitrogen, leaving more opportunities for root and nutrient foraging of subsequent arriving species (Temperton et al. 2007; von Felten et al. 2009). In general, invasive plants are favored by higher soils nutrient levels (Zefferman et al. 2015) . Conversely, the presence of legumes also has been associated with a high aboveground productivity (Hess et al. 2020; von Gillhaussen et al. 2014; Weidlich et al. 2016), so that a prior establishment of legumes may lead to a higher biomass (Delory, Weidlich, von Gillauhssen et al. 2019; Frankow-Lindberg 2012; Mwangi et al. 2007; Roscher et al. 2011), and could therefore reduce invasion success.

In the context of invasions, priority effects have usually been examined in terms of the consequences for invasive species to arrive before or after natives (Delory, Weidlich, Kunz et al. 2019; Grman & Suding 2010; Lang et al. 2017; Stevens & Fehmi 2011; Stuble & Souza 2016; Vaughn & Young 2015). Studies investigating how differences in native assembly history affect subsequent invasion events are scarcer. In a greenhouse experiment, we established native perennial communities differing by **(1)** the identity of the first colonizer (either of two grasses: *Dactylis glomerata* and *Lolium perenne*, or two legumes: *Onobrychis viciifolia* and *Trifolium. repens*), and **(2)** timing of species establishment (synchronous *vs.* sequential sowing), in which we subsequently simulated invasion by introducing seeds of *Ambrosia artemisiifolia*, a noxious weed in Europe (Ozaslan et al. 2016). We sought to examine whether these differences community assembly influence the success of subsequent invasion, and if so, assessing whether invasion success is related to variations in biomass production, soil chemistry, and/or community composition (i.e. the identity of the dominant species or functional group).

4.2 | Material and Methods

4.2.1 | Native species selection

Six perennial plant species widely used for revegetation in France were selected to compose the recipient native communities: *Dactylis glomerata* (Poaceae), *Lolium perenne* (Poaceae), *Onobrychis viciifolia* (Fabaceae), *Trifolium repens* (Fabaceae), *Plantago lanceolata* (Plantaginaceae), and *Poterium sanguisorba* (Rosaceae). Commercial seeds were purchased from seed suppliers ZYGENE and SCHEIER *France*.

4.2.2 | Invasive species seed collection and stratification

The common ragweed (*Ambrosia artemisiifolia* L., Asteraceae) is an annual plant native from North America (Heckel 1906) successfully invading disturbed areas such as roadsides, riverbanks, abandoned and cultivated fields in numerous European countries (Smith et al. 2013). The species can produce up to 14,000 achenes per plant, which are mainly dispersed by human activities (Bassett & Crompton 1975). Achenes from A. *artemisiifolia* were collected from at least ten individuals from each of three mature populations in South-eastern France in autumn 2018 and pooled (population 1: 43°33'4.5" N, 4°7'40.8" E; population 2: 43°31'2.2" N, 5°19'56.2" E; population 3: 43°34'17.8" N, 4°17'8.8" E). Before starting the experiment, achenes were put between two layers of cotton soaked with distilled water and cold-stratified for 20 weeks (wet, dark stratification at 4°C) in order to break primary dormancy. After stratification, we assessed the germination capacity of 50 seeds placed in Petri dishes on cotton soaked in distilled water. Petri dishes were placed in optimum germination conditions (25 °C/12 h day and 15 °C/12 h night; Fumanal et al. 2007), and germination was recorded every two days until no additional germination was recorded. After ten days, the final germination rate was of 98.0%±2.0 (mean±SE).

4.2.3 | Study site and infrastructure

The experiment was conducted over six months (early March until early September 2019) in a greenhouse at the Research Institute of Tour du Valat, France (43°30'N, 4°40'E, 1m elevation). Walls and roof of the greenhouse are made of Diatex mesh (500-600 µm) so that similar ambient climate conditions occurred inside but seed dispersal was prevented. The site was subjected to a Mediterranean climate, characterized by warm and dry summers and mild, wet winters, with high variability between years (Lionello et al. 2006). Precipitation and air temperature data were recorded using a meteorological station located close to the experimental site (Supplementary material, Figure S4.1). We established the artificial plant communities in square plastic pots with an upper width of 30.5 cm and a bottom width 25 cm, 27 cm deep, which were filled with, from bottom to top **(1)** a 27 cm diameter polyester tissue (© Diatex, 50-70 µm mesh size) to prevent loss of substrate, **(2)** a 20 cm width × 10 cm deep polystyrene bloc allowing water to flow at the sides, and **(3)** a substrate mixture of vermiculite (30 vol%; © Projar, 2.6 kg/m^3) and commercial organic fertile topsoil (70 vol%; © Géolia) (Figure S3.2) . Pots were watered with equal amounts of water through sprinklers. The amount of supplied water was regularly adjusted to ensure moisture conditions suitable to germination and plant development. We ended the experiment in early September to avoid confounding effect of A. *artemisiifolia* natural senescence (Li et al. 2015).

4.2.4 |Experimental design

We designed six types of recipient plant communities differing by the identity of the first species established, but all getting all six species eventually (Figure 4.1). We ensured an identical final spatial arrangement of the communities by using cardboard patterns with holes, each hole corresponding to a seeding location. On March 6, we created four priority treatments by introducing 18 seeds of either **(1)** D. *glomerata* (treatment name Dactylis$_{f}$, with 'f' standing for 'first'), **(2)** L. *perenne* (Lolium$_{f}$), **(3)** O. *viciifolia* (Onobrychis$_{f}$), or **(4)** T. *repens* (Trifolium$_{f}$) per pot. We also introduced **(5)** three seeds of each of the six species per pot, for the same number of initial seeds as the priority treatments (Synchronous$_{seq}$) or **(6)** 18 seeds of each of the six species per pot, which corresponds the simultaneous sowing of all individuals at full density (Synchronous). Ungerminated seeds were regularly replaced by individuals sown in separate pots on March 6 to ensure similar age and density of individuals. After four weeks (i.e. on April 3), we carried out a second sowing (except for Synchronous) by adding the rest of the species so that each pot contained 18 individuals of each of the six species, achieving a total of 108 seeds (corresponding to 1200 seeds/m^2). *Plantago lanceolata* and P. *sanguisorba* were added to the four priority-tested species in order to create communities that were more diverse and to reach the desired individuals density while keeping an identical and adequate spatial pattern. Therefore, Synchronous$_{seq}$ had the same density and sowing timing as Dactylis$_{f}$, Lolium$_{f}$, Onobrychis$_{f}$ and Trifolium$_{f}$, but did not give priority to any particular species. This assembly type tested the role of sowing density in itself to invasion resistance. Ungerminated seeds were regularly replaced by individuals sown in separate pots on April 3.

On April 18, six weeks after the first sowing event and two weeks after the second sowing event, we introduced in each pot nine seeds of A. *artemisiifolia* at fixed positions, 8 cm apart from each other (Figure 4.1). There were 12 replicates of each assembly type (Dactylis$_{f}$, Lolium$_{f}$, Onobrychis$_{f}$, Trifolium$_{f}$, Synchronous$_{seq}$ and Synchronous), totaling 72 pots (Figure 4.2). Pot distribution in the greenhouse followed a randomized design and pots was randomized every two weeks.

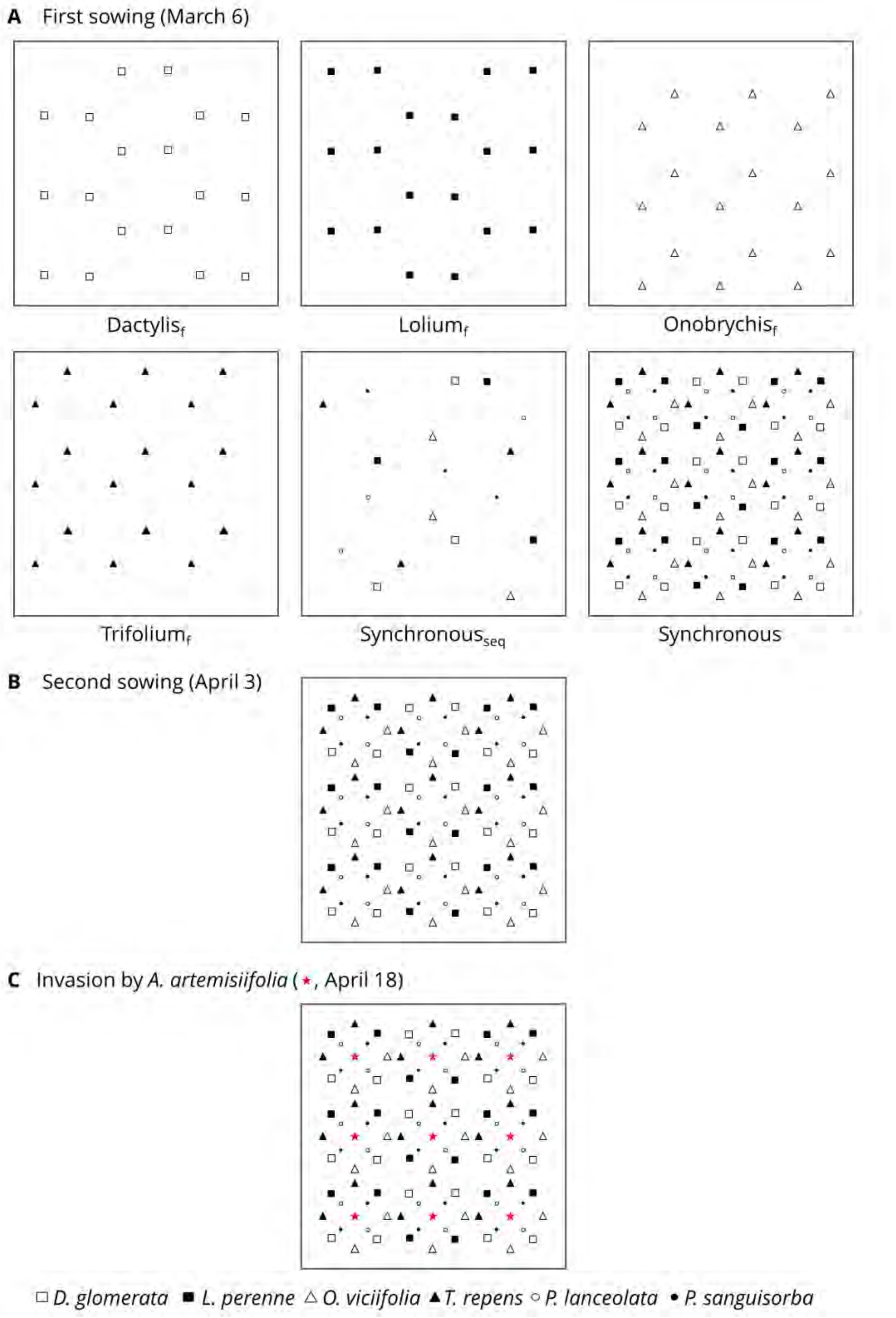

Figure 4.1 Experimental design. Spatial arrangement of individuals in pots (represented by squares) is depicted depending on assembly type. In the second sowing, all communities were completed to achieve same species abundance and spatial pattern (no seed was added for Synchronous).

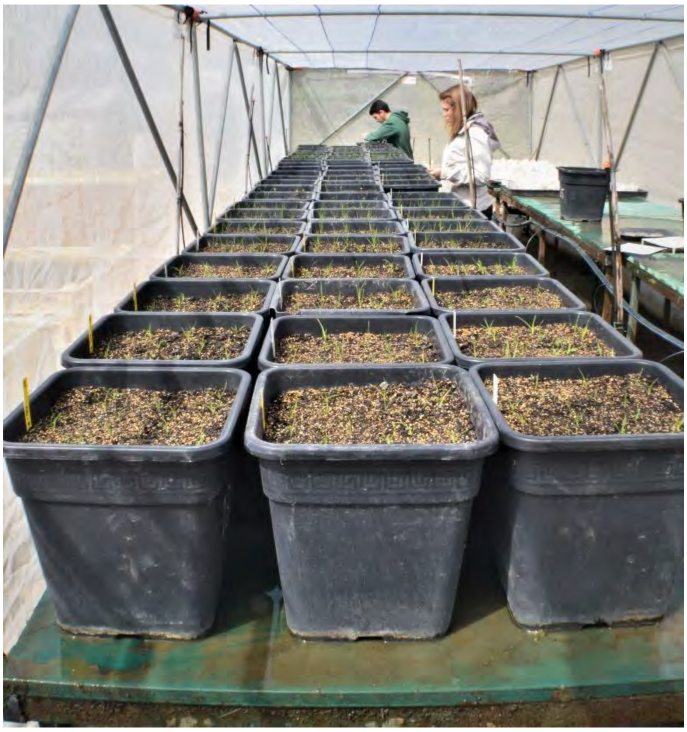

Figure 4.2 Recipient communities on April 3, 2019.

4.2.5 | Data collection

Invasive species early establishment success

We assessed early establishment success of A. *artemisiifolia* by monitoring seedling emergence and survival each week from April 30 to September 2, the number of leaves every two weeks (from June 18 to August 27), and final aboveground biomass (September 2). Aboveground biomass of each individual was collected 0.5 cm above ground level, dried at 60°C for 72h and weighed. Growth-related parameters (i.e. number of leaves and aboveground biomass) are hereafter referred as 'performance'.

Recipient communities

We measured aboveground and belowground biomass of the communities three times during the experiment. For this purpose we harvested **(1)** three pots per assembly type when A. *artemisiifolia*'s seeds were introduced (hereafter 'initial' – on April 18), **(2)** three pots per assembly type midway through the experiment, on June 13 (hereafter 'intermediate'), and **(3)** six pots per assembly type at the end of the experiment (hereafter 'final' – September 2). For each pot, aboveground biomass was harvested, sorted by species and dried at 60°C for 72h until weighed. Belowground biomass was measured by collecting one soil core (12 cm diameter × 16 cm deep) at the center of each pot. Since we were not able to identify and sort the roots of the different species, we measured total belowground dry biomass including native species and A. *artemisiifolia* roots. Roots were isolated from soil, washed and sieved with a 250µm mesh, dried at 60°C for 72 h, and weighed.

Soil analyses

One of the ways that established community composition and biomass production can influence subsequent colonizing species success is through modification of soil resource availability (MacLaren et al. 2019; Temperton et al. 2007; von Felten et al. 2009). We therefore analyzed organic carbon, nitrogen, nitrates, ammonium and available phosphorus on soil samples collected from each pot at the end of the experiment. For each assembly type, we collected 24 soil cores of 10 mm diameter × 100 mm deep (four per pot), which were pooled and dried for 48h at 40°C and sieved (<2 mm) to remove roots and rocks. Control soil (i.e. soil before recipient community establishment) was also added to the analyses. 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). Standard French method AFNOR or standard international method ISO were used to determine soil parameters. Analyses were performed by the accredited soil analysis laboratory Teyssier (Bourdeaux, France), following standard protocols.

4.2.6 | Data analyses

Invasive species early establishment success

We used generalized linear mixed models (GLMMs) with Laplace approximation ('glmer' function in the 'lme4' package; Bates 2010) for maximum likelihood estimation of the parameters (Bolker et al. 2009) to analyze variations in **(1)** cumulative final seedling emergence (until June 4; no new emergence was recorded after this date) and survival (September 2) of A. *artemisiifolia* seedlings, with a binomial error distribution and a logit-link function (Table 4.1) **(2)** final number of leaves (i.e. August 27) of A. *artemisiifolia* individuals with negative binomial error distribution to account for overdispersion and a log-link function, and **(3)** number of leaves of A. *artemisiifolia* individuals over time with Poisson error distribution and a log-link function. We analyzed variations in final aboveground biomass (i.e. September 2) of A. *artemisiifolia* using a linear mixed model with Gaussian error distribution (data was log transformed to fit into a Gaussian distribution; 'lmer' function of the 'lme4' package; Bates 2010).

Analyses of seedling emergence, survival, final number of leaves and final aboveground biomass included assembly type ($Dactylis_f$, $Lolium_f$, $Onobrychis_f$, $Trifolium_f$, $Synchronous_{seq}$, Synchronous) as fixed predictor variable and pot as random factor. Upon finding a significant effect of the fixed effect assembly type (significance tested using type II sums of squares using the 'Anova' function in 'car' package; Fox & Weisberg 2019), we conducted *post-hoc* pairwise contrasts comparisons with a Tukey adjustment ('emmeans' package; Lenth et al. 2019).

Analyze of number of leaves over time included assembly type in interaction with date (monitoring date, each two weeks) as fixed predictor variables and pot and individuals nested within pots as random factors. Two models were built to analyze the first slow growing phase (June 18 to July 30) and a second faster growing phase (July 30 to August 27) separately. Upon finding a significant effect of the interaction between assembly type and date, we conducted *post-hoc* comparisons of interaction terms (i.e. slope estimates) between each pair of assembly types using the function 'emtrends' ('emmeans' package; Lenth et al. 2019), with a Tukey adjustment.

Analyze of seedling emergence included the 81 seeds sown per assembly type and survival included emerged individuals in six pots per assembly type (from 50 to 54 individuals; Supplementary material, Table S4.1). Analyze of performance (i.e. number of leaves and biomass) included all individuals surviving until the end of the experiment in six pots per assembly type (from 40 to 53 individuals; Supplementary material, Table S4.1).

Recipient communities

We analyzed the effect of assembly type on **(1)** total recipient species aboveground biomass and **(2)** total belowground samples (native and invasive) biomass for the three harvests using a one-way ANOVA. When a significant effect was found, we performed pairwise comparisons on the least-squares means (LSM) with a Tukey adjustment ('emmeans' package; (Lenth et al. 2019). When residuals did not satisfied normality and/or homoscedasticity assumptions, we performed Welch's heteroscedastic F tests with trimmed means and Winsorized variances ('welch.test' function in 'onewaytests' package; Dag et al. 2018; Welch 1951), which are relatively insensitive to the combined effects of non-normality and heteroscedasticity (Keselman et al. 2008). When a significant effect was found, *post-hoc* multiple pairwise comparison tests were performed with a BH adjustment ('paircomp' function in 'onewaytests' package; Dag et al. 2018). All analyses of biomass were conducted on three pots per assembly types, except final aboveground biomass conducted on six pots per assembly type. We also calculated the contribution of legumes and grasses by summing aboveground biomass of O. *viciifolia* and *T. repens*, and *D. glomerata* and *L. perenne*, respectively.

All analyses were performed using R software (ver. 3.6.2). The p-values lower than 0.05 were considered as statistically significant.

4.3 | Results

4.3.1 | Invasive species early establishment success

Seedling emergence and survival of A. *artemisiifolia* were high across all assembly types (i.e. 97.3%±1.0 and 93.3%±3.1, mean±SE, respectively; Supplementary material, Table S4.1). Assembly type did not significantly affect A. *artemisiifolia* seedling emergence (Wald χ^2=3.70, df=5, p=0.59) or survival (Wald χ^2=4.48, df=5, p=0.48).

Assembly type significantly affected A. *artemisiifolia* final number of leaves (Anova Type II: Wald χ^2=53.37, df=5, p<0.001) and final aboveground biomass (Anova Type II: Wald χ^2=59.056, df=5, p<0.001). Both final number of leaves and aboveground biomass were **(1)** significantly lower for Synchronous than for all other assembly types except Lolium_f (Figure 4.3), and **(2)** significantly higher for Trifolium$_f$ than for all other assembly types (Figure 4.3), except in Onobrychis$_f$ and Dactylis$_f$ for final aboveground biomass (Figure 4.3B).

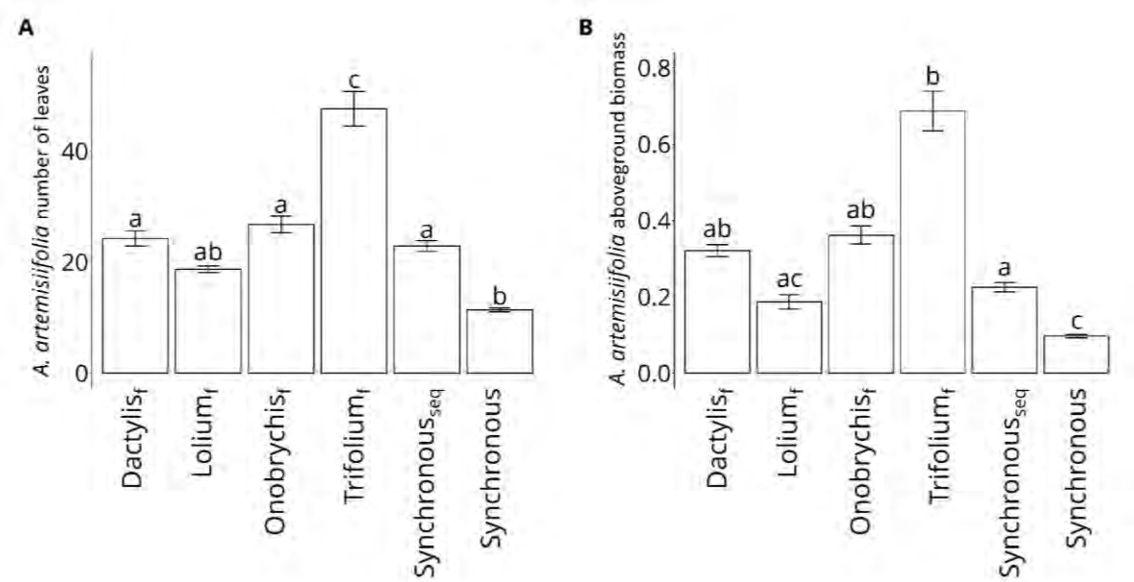

Figure 4.3 *Ambrosia artemisiifolia* (**A**) final number of leaves, and (**B**) final aboveground biomass depending on assembly type (mean per individual ±SE, n_{tot}=324). Assembly types with no letter in common are significantly different (pairwise contrasts comparisons with Tukey adjustment; p<0.05).

For the two considered growing phases, A. *artemisiifolia* number of leaves over time depended upon assembly type (June 18 to July 30: Anova Type II: Wald χ^2=21.84, df=5, p<0.001; July 30 to August 27: Anova Type II: Wald χ^2=174.947, df=5, p<0.001; Figure 4.4). From June 18 to July 30, the slope (i.e. increase in leaf number) was significantly lower for Synchronous than for all other assembly types except for Synchronous$_{seq}$ (Figure 4.4B). From July 30 to August 27, the slope was **(1)** significantly lower for Synchronous than for all other assembly types except for Lolium$_f$ and Onobrychis$_f$, and **(2)** significantly higher for Trifolium$_f$ than for all other assembly types (Figure 4.4D).

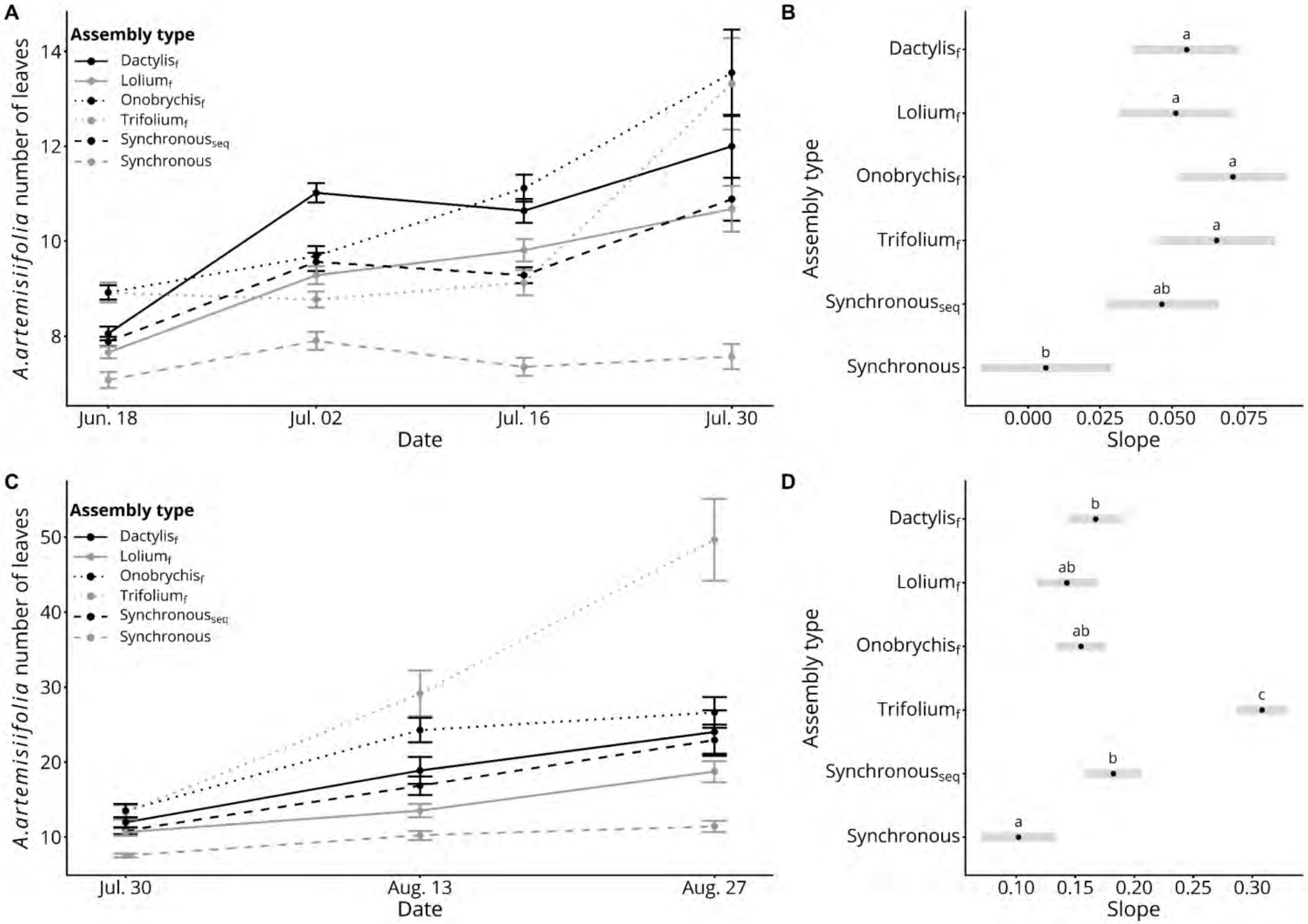

Figure 4.4 Number of leaves (mean per individual ±SE, n_{tot}=324) of *A. artemisiifolia* over time, depending on assembly type (**A**) from June 18 to July 30, and (**C**) from July 30 to August 27 (note the changing y-axis scales) and slope estimates (interaction between date × assembly type) of the GLMM modeling the variation of number of leaves of *A. artemisiifolia* depending on time and assembly type (**B**) from June 18 to July 30 and (**D**) from July 30 to August 27. Assembly types with no letter in common are significantly different (pairwise contrasts comparisons with Tukey adjustment; p<0.05).

4.3.2 | Recipient community biomass

Assembly type significantly affected recipient communities above- and belowground biomass, at all harvest times (Figure 4.5; Supplementary material, Table S4.2). For the initial harvest, **(1)** aboveground biomass was significantly higher in Synchronous than in all other assembly types and significantly lower in Trifolium$_f$ than in all other assembly types except Synchronous$_{seq}$ (Figure 4.5A), and **(2)** belowground biomass was significantly higher in Synchronous than in all other assembly types (Figure 4.5D). Also, legumes contributed to aboveground biomass **(1)** more than grasses in Onobrychis$_f$, Trifolium$_f$ and Synchronous$_{seq}$, and **(2)** less than grasses in Dactylis$_f$, Lolium$_f$ and Synchronous (Table 4.1). For the intermediate harvest, **(1)** aboveground biomass was significantly higher in Trifolium$_f$ than in all other assembly types (Figure 4.5B), and **(2)** belowground biomass was not significantly different between assembly types (Figure 4.5E). Also, legumes contributed to aboveground biomass **(1)** more than grasses in Trifolium$_f$, and **(2)** less than grasses in all other assembly types (Table 4.1). For the final harvest, **(1)** aboveground biomass was significantly lower in Dactylis$_f$ and Lolium$_f$ than in Synchronous (Figure 4.5C), and **(2)** belowground biomass was significantly higher in Lolium$_f$ than in Onobrychis$_f$ and Trifolium$_f$ (Figure 4.5F). Legumes contributed to aboveground biomass **(1)** less than grasses in Lolium$_f$, and **(2)** more than grasses in all other assembly types (Table 4.1).

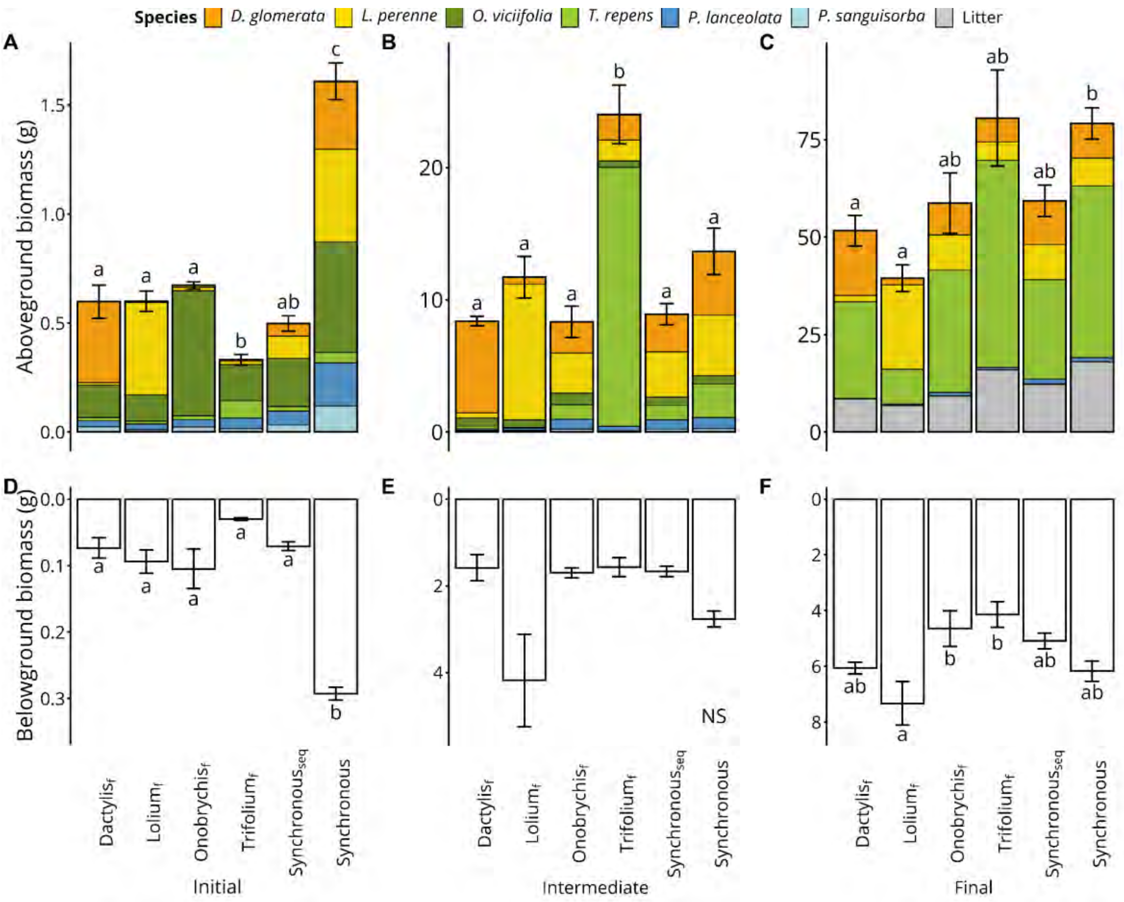

Figure 4.5 Above and belowground biomass of the recipient communities depending on assembly type for (**A**,**B**) initial (April 18), (**B**,**E**) intermediate (June 13), and (**C**,**F**) final (September 2) harvests. Aboveground biomass (**A**,**B**,**C**) represents total biomass per pot (mean±SE, $n_{a,b}$=3, n_c=6) and includes native species only, while belowground biomass (**D**,**E**,**F**) represents sample biomass per pot (mean±SE, n=3) and includes both native and invasive species. Treatments with no letter in common are significantly different (pairwise comparisons with Tukey adjustment; p<0.05). 'NS' indicates to non-significant *post-hoc* differences between assembly types.

Table 4.1 Aboveground biomass of legumes (sum of *O. viciifolia* and *T. repens*, mean±SE) and grasses (sum of *D. glomerata* and *L. perenne*, mean±SE) for each assembly type for initial (April 18, n=3), intermediate (June 13, n=3), and final (September 2, n=6) harvests. Contribution to total biomass (mean%±SE), and ratio between mean biomass of legumes and grasses ('Ratio L:G'; mean±SE) are also indicated, with ratios > 1 in bold (i.e. mean biomass of legumes exceeds mean biomass of grasses).

	Legumes		Grasses		
	Biomass (g)	Contribution to biomass (%)	Biomass (g)	Contribution to biomass (%)	Ratio L:G
Initial					
Dactylis$_{f}$	0.16±0.00	28.2±3.9	0.38±0.09	62.1±8.4	0.42
Lolium$_{f}$	0.13±0.01	22.3±1.1	0.43±0.04	71.6±1.7	0.30
Onobrychis$_{f}$	**0.59±0.02**	**87.9±0.2**	**0.02±0.00**	**3.6±0.1**	**29.5**
Trifolium$_{f}$	**0.25±0.03**	**73.1±5.6**	**0.02±0.00**	**7.1±0.6**	**12.5**
Synchronous$_{seq}$	**0.24±0.02**	**48.8±2.7**	**0.16±0.03**	**32.0±3.3**	**1.5**
Synchronous	0.55±0.03	34.5±1.4	0.74±0.03	46.0±1.5	0.74
Intermediate					
Dactylis$_{f}$	0.81±0.15	9.6±1.6	7.34±0.3	87.5±1.5	0.11
Lolium$_{f}$	0.64±0.04	5.6±0.5	10.79±1.56	91.5±1.1	0.06
Onobrychis$_{f}$	1.98±0.64	22.6±4.0	5.36±0.52	65.2±2.6	0.37
Trifolium$_{f}$	**20.05±2.29**	**83.2±2.1**	**3.5±0.19**	**14.9±1.9**	**5.72**
Synchronous$_{seq}$	1.72±0.24	19.3±2.3	6.28±0.62	70.5±2.1	0.27
Synchronous	3.16±0.77	22.7±3.0	9.40±0.95	69.4±3.0	0.37
Final					
Dactylis$_{f}$	**24.75±3.18**	**47.5±3.2**	**18.23±1.44**	**35.7±2.6**	**1.35**
Lolium$_{f}$	8.90±3.09	20.3±6.0	23.35±1.65	61.5±6.5	0.38
Onobrychis$_{f}$	**31.38±7.59**	**49.1±7.0**	**17.15±1.11**	**32.8±5.5**	**1.79**
Trifolium$_{f}$	**53.15±11.73**	**64.1±4.3**	**10.91±1.81**	**14.2±2.5**	**4.87**
Synchronous$_{seq}$	**25.40±4.17**	**41.8±4.5**	**20.27±1.40**	**35.1±3.4**	**1.25**
Synchronous	**44.08±3.58**	**55.3±2.2**	**15.98±0.98**	**20.5±1.9**	**2.75**

4.3.3 | Soil analyses

Compared to control soil (i.e. soil before recipient community establishment), all planted treatments depleted the soil of available phosphorus and nitrates (Table 4.2). Trifolium$_f$ communities produced soils with greater concentrations of nitrates and ammonium than any other treatments, including the other legume species. Lolium$_f$ showed the lowest content of nitrates.

Table 4.2 Results of soil analyses performed at the end of the experiment. Control soil refer to soil before recipient community establishment.

	Total organic matter (%)	C (g/kg)	N (g/kg)	NO_3^- (g/kg)	NH_4^+ (g/kg)	P_2O_5 (g/kg)
Dactylis$_f$	11.0	63.6	4.1	0.007	0.012	0.078
Lolium$_f$	11.1	64.6	4.4	0.003	0.010	0.074
Onobrychis$_f$	11.3	65.7	5.0	0.005	0.012	0.076
Trifolium$_f$	11.1	64.3	5.2	0.010	0.015	0.070
Synchronous$_{seq}$	11.3	65.7	4.6	0.007	0.012	0.070
Synchronous	11.4	66.1	4.4	0.008	0.010	0.083
Control soil	11.2	65.0	4.5	0.011	0.005	0.136

4.4 | Discussion

This study provides evidence for a significant role of assembly history in invasion resistance during the early stages of community development and thus corroborates numerous recent studies (Delory, Weidlich, Kunz et al. 2019; Firn et al. 2010; Grman & Suding 2010; Lang et al. 2017; Stevens & Fehmi 2011; Stuble & Young 2020; Vaughn & Young 2015; Young et al. 2016). Altering **(1)** the identity of the first colonizer, whose establishment preceded other species arrival by four weeks, and **(2)** species establishment timing (i.e. synchronous *vs.* sequential sowing) both significantly affected the performance (i.e. leaf and biomass production) of the invasive plant A. *artemisiifolia* (Figures 4.3, 4.4). Seedling emergence and survival did not significantly differ and were high across all communities (97.3%±1.0 and 93.3%±3.1, mean±SE, respectively; Supplementary material, Table S4.1). This finding is in accordance with the results of the meta-analysis of Levine et al. (2004) showing that competitive interactions with native species are more likely to reduce invaders performance than totally repel invasions.

Differences in assembly history influenced early community composition, although it tended to converge after six months (Figure 4.4). *Ambrosia artemisiifolia* exhibited the lowest overall performance in Synchronous, where all recipient individuals were sown at the same time (Figures 4.3, 4.4). Receiving more seeds in the first two weeks allowed Synchronous to reach high biomass more quickly (Figure 4.4A,D), which is likely to be responsible for lower A. *artemisiifolia* success at the end of the experiment. This is particularly underlined by the lower resistance of $\text{Synchronous}_{\text{seq}}$ (sequential sowing), since both assembly types differed in initial biomass production while sharing close intermediate and final biomass (Figure 4.5B,C,E,F), species composition (Figure 4.5B,C; Table 4.1) and soil nutrient contents (Table 4.2). These results emphasize the importance of an initial quick and high biomass production to counter invasion (Lulow 2006; Mason et al. 2013, 2017; Rinella et al. 2007; Symstad 2000). These results also indicate that sequential sowing may increase community vulnerability to invasion (Martin & Wilsey 2012; Stuble & Young 2020), challenging the implementation of this sowing technique in invaded restoration sites.

Competition for light is considered to be particularly limiting in early community assembly, especially in high soil resource conditions (Kardol et al. 2013). Our results however suggest that belowground competition had a substantial implication in early invasion resistance. *Ambrosia artemisiifolia* final leaf and biomass production appeared to be similarly affected in Lolium_{f} and Synchronous (Figure 4.2), while Lolium_{f} displayed a lower aboveground biomass (Figure 4.5A,C). Invasion resistance of Lolium_{f} was presumably associated to its high intermediate and final belowground biomass (Figure 4.5E,F) and low nitrate soil content (Table 4.2), both most likely arising from a low legumes:grasses ratio (Table 4.1) and *L. perenne* dominance, which is a strong competitor for belowground resources (Frankow-Lindberg 2012; Snaydon & Howe 1986). The importance of competition for soil resources was also supported by the enhanced performance of *A. artemisiifolia* in $\text{Trifolium}_{\text{f}}$. Despite producing high intermediate and final community aboveground biomass, (Figure 4.5B,C), prior establishment of the N-fixing legume *T. repens* boosted *A. artemisiifolia* performance (Figures 4.3, 4.4C,D). The reduced invasion resistance of $\text{Trifolium}_{\text{f}}$ may result from a lower competition for root space and belowground resources (Scherber et al. 2010; Scherer-Lorenzen et al. 2003) arising from a **(1)** low total initial biomass production of the community (Figure 4.5A,D), **(2)** greater response of *A. artemisiifolia* to elevated soil N level (Table 4.2; Govindarajulu et al. 2005; Paynel et al. 2001; Temperton et al. 2007; von Felten et al. 2009), or **(3)** a low grass content (Table 4.1). Such results contrast with the findings of Rinella et al. (2007), where productivity of certain plant groups did not matter for invasion success while overall productivity did. In their study, invasion however occurred in diverse, well-established communities after the removal of particular plant groups, which led to a high remaining species diversity and signs of diversity saturation.

In opposition to our findings, Mason et al. (2013) found that different arrival orders of native functional groups did not affect the abundance and cover of the exotic shrub *Chrysanthemoides monilifera* spp. *rotundata*, nor biomass production of the recipient community or soil resources availability. The main impactful difference between our two studies seems to be that Mason et al. (2013) avoided planting nitrogen fixers, which generated contrasting compositions in our study (Figure 4.4). Including legumes in our recipient communities was relevant in an applied perspective, since seed mixes used for restoration and revegetation often contain nitrogen-fixing species (Beyhaut et al. 2014). In addition, since Mason et al. (2013) simulated invasion seven months after the first sowing event (against six weeks in our study): initial differences between communities may have decrease over time (Körner et al. 2008), less affecting subsequent invaders. Finally, they used a competitive shrub successfully colonizing mature plant communities (French et al. 2008; Mason et al. 2012), which may be less sensitive to competition than A. *artemisiifolia*, reported as a weak competitor in resource-rich environments (Leskovsek et al. 2012). Therefore, the identity of the invasive species may have also contributed to these contrasting findings.

Overall, our study supports that colonization history matters to invasion success when invasion occurs in the early stages of community assembly. Altering the timing of species establishment (all together or sequential sowing) and the identity of the first native colonizer affected early biomass production and composition of the community as well as soil nutrient content, and had implications for invader's performance. Notably, communities reached a higher invasion resistance when displaying quickly a high native below or aboveground biomass, a reduced early contribution of productive legumes, or both. Thus, when immediate invasion risk is high in a restored site, establishing productive, densely sown native communities and avoiding an early planting of highly productive N-fixing legumes may help decrease invasion success.

Acknowledgements

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Supplementary material

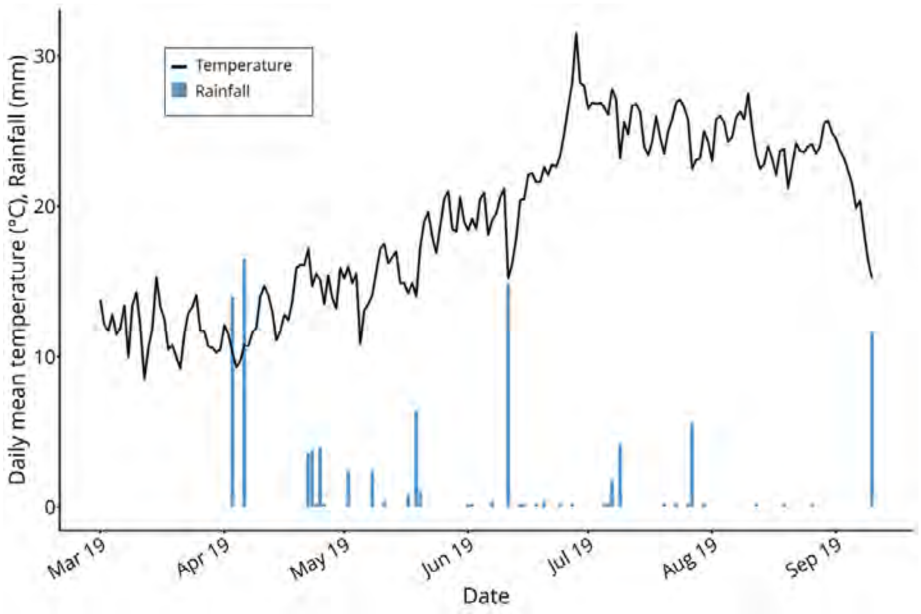

Figure S4.1 Temperature (daily mean in °C) and rainfall (daily sum in mm) recorded during the experiment (Meteo France station number 133004003, Tour du Valat domain, France).

Table S4.1 Final cumulative percentage of seedling emergence (4 June, mean of nine pots ±SE) and survival (2 September, mean of six pots ±SE) depending on assembly type. For each assembly type, total number of individuals included in the analyses (ntot), total number of emerged individuals (nemerged) and total number of surviving individuals (nsurvival) are also indicated.

Seedling emergence	n_{tot}	$n_{emerged}$	% (mean±SE)
$Dactylis_f$	81	81	100.0±0.0
$Lolium_f$	81	79	97.5±1.6
$Onobrychis_f$	81	80	98.8±1.2
$Trifolium_f$	81	76	93.8±2.7
$Synchronous_{seq}$	81	80	98.8±1.2
Synchronous	81	77	95.1±2.7
Survival	n_{tot}	$n_{survival}$	% (mean±SE)
$Dactylis_f$	53	53	100.0±0.0
$Lolium_f$	54	53	98.1±1.9
$Onobrychis_f$	53	49	90.7±3.4
$Trifolium_f$	50	40	80.5±10.2
$Synchronous_{seq}$	53	53	100.0±0.0
Synchronous	51	46	90.2±4.5

Table S4.2. Results of one-way ANOVA and Welch's heteroscedastic *F* tests testing the effect of assembly type on above- and belowground biomass of the communities for initial (April 18, n=3), intermediate (June 13, n=3), and final (September 2, n=6 for aboveground, n=3 for belowground) harvests. Statistical analysis, test statistic (F), degrees of freedom (df) and p-values (p) are indicated.

	Statistical analysis	F	df	p
Initial				
Aboveground	ANOVA	71.21	5	<0.001
Belowground	ANOVA	27.57	5	<0.001
Intermediate				
Aboveground	ANOVA	17.33	5	<0.001
Belowground	Welch's heteroscedastic F	4.78	5	0.049
Final				
Aboveground	Welch's heteroscedastic F	10.46	5	<0.001
Belowground	ANOVA	5.49	5	0.007

Synthesis of Chapter 4 and transition to Chapter 5

Chapter 4 in a nutshell

Does assembly history of the recipient community (timing of species establishment and identity of the first arriving species) influence early invasion resistance?

Both **(1)** timing of recipient species establishment (synchronous or sequential arrival) and **(2)** identity of the first arriving species influenced early invasion resistance. Sequential sowing overall weakened invasion resistance compared to a synchronous sowing. The identity of the first arriving species influenced invasive species performance most likely through the preemption of aboveground resources (i.e. a quick a high preemption leading to greater resistance).

Is sequential sowing a possible way to reinforce early invasion resistance?

Sequential sowing generally decreased invasion resistance, and therefore does not appear as a potential method to reinforce invasion resistance of newly established communities.

In Chapter 4, I focused on invasive species response to differences in assembly history of the invaded community. In Chapter 5, I analyze more specifically how priority effects generated by differences in assembly history affect the structuring of the native community.

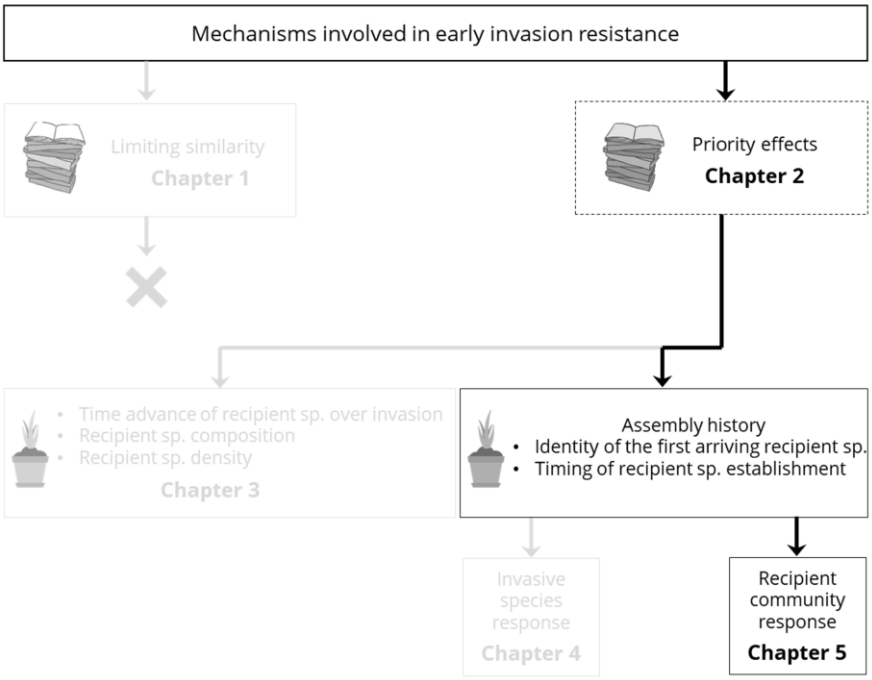

Figure T.5 Chapter 5 in thesis organization.

Chapter 5

Species-specific priority effects influence early community structuring

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Manon CM Hess, Elise Buisson, Truman P Young, François Mesléard

Chapter 5

Abstract

How historical contingencies affect plant community assembly is poorly known. The influence of priority effects, arising from the order by which species establish in a community, has been mainly investigated at the functional group level (e.g. grasses, non-leguminous forbs and legumes). However how within-group species identity matters has only been rarely explored. In a greenhouse experiment, we investigated how species identity (*Dactylis glomerata* or *Lolium perenne*, two grass species, and *Onobrychis viciifolia* or *Trifolium repens*, two legume species) established four weeks before the rest of the community influenced community structuring (i.e. aboveground biomass composition) over one growing season. Early sown species benefited differently from time advance. Time priority benefited less to **(1)** *T. repens*, which displayed competitive abilities allowing it to dominate the community when sown in advance or simultaneously to the rest of the community, and **(2)** *O. viciifolia*, for which a four-week time advance was not sufficient to enable it to persist. *L. perenne* benefited the most of a time advantage, most likely because of its high ability to preempt soil resources and space. Our results overall show that assembly history (i.e. timing of species arrival) interacts with deterministic processes (i.e. species-specific competitive abilities) to drive early community assembly.

Keywords: historical contingencies, community assembly, assembly history, order of arrival, perennial, competition, grass, legume

5.1 | Introduction

Community assembly has received considerable attention for more than a century, with an early focus on succession theory (Clements 1916; Cowles 1899). Community succession theory posits that community assembly under identical environmental conditions will follow deterministic rules and converge toward a single, deterministic set of species, where the most competitive species dominates regardless of history. Alternatively, assembly theory assumes a crucial role for historical contingencies so that communities diverge toward multiple, stochastic endpoints based on events occurring during the assembly process (Chase 2003; Diamond 1975; Drake 1990). In this scenario, assembly outcome is strongly dependent on stochastic historical events being either abiotic (i.e. disturbances such as fire, flood or landslide) or biotic (i.e. the frequency of colonization events for a given species, or the order of species arrival (Fukami 2015). Specifically, the order of species arrival can influence species effects on one others through priority effects (Drake 1991). Priority effects arise from multiple non-exclusive processes, such as resource preemption (i.e. reduction of available space, light, and/or nutrients by early colonizers; Cleland et al. 2015; Kardol et al. 2013; Marushia et al. 2010; Vance 1984; Wainwright et al. 2012), or alteration of biotic (e.g. predators, soil microorganisms) and abiotic (e.g. nutrient dynamics, allelochemicals) components of the environment (Corbin & D'Antonio 2012; Helsen et al. 2016; Mangla & Callaway 2008). Early colonizers can therefore dominate or persist in a community even if they are poor competitors, because priority effects allow equalizing or elevating their fitness relative to later colonizers (Chase 2010; De Meester et al. 2016; Ejrnaes et al. 2006; Ross & Harper 1972; Weiner 1990).

Priority effects have mainly been investigated at the functional group level such as grasses and forbs (Stuble & Young 2020; Werner et al. 2016) or grasses, non-leguminous forbs and legumes (Delory, Weidlich, von Gillhaussen et al. 2019; Körner et al. 2008; von Gillhaussen et al. 2014; Weidlich et al. 2018, 2016). Grasses have been shown to cause strong negative priority effects because of a higher investment in root biomass than forbs (Körner et al. 2008; Poorter et al. 2015), and a strong competition for belowground resources (Scherber et al. 2010; Scherer-Lorenzen et al. 2003). Legumes in contrast may facilitate subsequent species establishment because of their ability to fix atmospheric nitrogen and transferring it to neighbors through mycorrhizal links and root exudation (Govindarajulu et al. 2005; Paynel et al. 2001), or through decomposition (Tomm et al. 1995). However, within-group competitive hierarchies have been highlighted (Turnbull et al. 2004, 2005), so that species-specific variations could occur. In a greenhouse study, we tested whether the identity of the first established species, introduced four weeks before the rest of the community, influenced community structuring (i.e. aboveground biomass composition) over one growing season. Time priority was given to one of two grass species, *Dactylis glomerata* or *Lolium perenne* or one of two nitrogen-fixing legumes, *Onobrychis viciifolia* or *Trifolium repens*.

5.2 | Materials and Methods

The study site and experimental design are described in details in Chapter 4. Here, we only reiterate aspects of relevance to the current study.

5.2.1 | Study site and infrastructure

The experiment took place in 2019 in a greenhouse at the Research Institute of Tour du Valat, France (43°30'N, 4°40'E, 1m elevation). Plant communities were established in square plastic pots (upper width of 30.5 cm and 25 cm width at the bottom, 27 cm deep) filled with, from bottom to top **(1)** a 27 cm diameter polyester tissue (© Diatex, 50-70 µm mesh size) to prevent loss of substrate, **(2)** a polystyrene bloc (20 cm width × 10 cm deep) allowing water to flow at the sides, and **(3)** a substrate mixture of vermiculite (30 vol%; © Projar, 2.6 kg/m^3) and commercial organic fertile topsoil (70 vol%; © Géolia), which was fertile (N=4.520 g/kg, NO_3^- =0.011 g/kg, NH_4^+ =0.005 g/kg, P_2O_5 =0.136 g/kg; Figure S3.2). Water was supplied through sprinklers placed equidistantly.

5.2.2 | Experimental design

Communities were composed of six native perennial plant species in France: *Dactylis glomerata* L. (Poaceae), *Lolium perenne* L. (Poaceae), *Onobrychis viciifolia* Scop. (Fabaceae), *Plantago lanceolata* L. (Plantaginaceae), *Poterium sanguisorba* L. (Rosaceae), and *Trifolium repens* L. (Fabaceae). Commercial seeds were purchased from seed suppliers ZYGENE and SCHEIER *France*.

We established five communities differing by the identity of the first colonizer (i.e. five assembly types), but all getting all six species eventually. The final spatial arrangement of the communities was fixed by cardboards with holes used to proceed to community sowing, each hole corresponding to a seeding location. On March 6, we sowed 18 seeds per pot of either **(1)** *D. glomerata* (assembly type 'Dactylis$_f$, with 'f' standing for 'first'), **(2)** *L. perenne* (Lolium$_f$), **(3)** O. *viciifolia* (Onobrychis$_f$), or **(4)** T. *repens* (Trifolium$_f$). A fifth assembly type was added, which consisted in the simultaneous sowing of all individuals at full density (i.e. no priority; Synchronous; see Figure 4.1). Ungerminated seeds were replaced by individuals sown in separate pots on March 6 to ensure similar age and density of individuals. Four weeks after the first sowing (on April 3), we performed the second sowing for all communities except Synchronous by adding the rest of the species. Each pot contained 18 individuals of each of the six species to achieve a final density of 108 seeds/pot (1200 seeds/m^2). Again, ungerminated seeds were replaced by individuals sown in separate pots on April 3. Twelve replicates per assembly type (Dactylis$_f$, Lolium$_f$, Onobrychis$_f$, Trifolium$_f$, Synchronous) were established, totaling 60 pots. Pots were distributed in a randomized design and pots were randomized every two weeks.

5.2.3 | Data collection

We harvested aboveground biomass three times during the experiment; three pots on April 18 (i.e. week 6 after the first sowing) and June 13 (i.e. week 14), and six pots on September 2 (i.e. week 26). For each pot, aboveground alive biomass (litter was not taken into account) was collected as close as possible to soil surface, sorted by species, dried at 60°C for 72h, and weighed (0.01g accuracy). We measured belowground biomass by collecting one soil core of 12 cm diameter × 16 cm deep at the center of each pot, isolating and washing the roots using a 250 µm mesh, and drying the sample at 60°C for 72h before the weigh. Because A. *artemisiifolia* **(1)** was sown at the same density 6 weeks after the establishment of the first native species, **(2)** had similar survival rates in all community types (Chapter 4), and **(3)** represented only 0.42%±0.05 (mean±SE) of final aboveground biomass of the communities (data not shown), we did not considered A. *artemisiifolia* in biomass analyses.

Soil nitrogen (modified Kjeldhal method; NF ISO 11261, 1995), nitrates and ammonium (NF ISO 14256-2, 2007), and available phosphorus (Dyer method; NF X31-160, 1999) were measured on soil samples collected at the end of the experiment (week 26). For this purpose, four soil cores (10 mm diameter × 100 mm deep) were collected per pot, totaling 24 samples per assembly type. Each sample was dried for 48h at 40°C and sieved (<2 mm) to remove roots and rocks. Control soil, i.e. soil before community establishment was also analyzed. Soil analyses were conducted following the standard French method AFNOR (Afnor 1994) and standard international method ISO and performed at the soil analysis laboratory Teyssier (Teyssier 2020).

5.2.4 | Data analyses

Priority advantage was calculated, for each species subjected to a priority treatment (i.e. D. *glomerata*, L. *perenne*, O. *viciifolia* and T. *repens*) and each harvest, as natural log response ratio (adapted from Dickson et al. 2012; Goldberg et al. 1999; Sarneel et al. 2016):

$$\text{Priority advantage} = \ln(\frac{\text{Biomass}(\text{i}_\text{f})}{\text{Biomass}(\text{i}_\text{synch})})$$

where $\text{Biomass}(\text{i}_\text{f})$ is the biomass of the species i when it was sown first and $\text{Biomass}(\text{i}_\text{synch})$ is the biomass of the same species when it was sown simultaneously with other species (Synchronous). Positive values indicate that the species considered benefited from being sown first (i.e. Biomass_f exceeding $\text{Biomass}_\text{synch}$). Negative values indicate that the species considered did not benefit from being sown first (i.e. was not disadvantaged from being sown simultaneously to others) and that $\text{Biomass}_\text{synch}$ exceeded Biomass_f. Null values indicate that Biomass_f was equal to $\text{Biomass}_\text{synch}$.

To visualize community trajectories over time, we ordinated the compositions of communities using non-metric multidimensional scaling (NMDS) based on aboveground biomass per species. We used data from three pots for weeks 6 and 14, and six pots for week 26. To recompose community trajectories, we calculated mean scores values for each assembly type. The analysis was performed using the function 'metaMDS' in the 'vegan' package (Oksanen et al. 2007).

We analyzed the effect of assembly type on total final aboveground biomass (six replicates per assembly type) using a Welch's heteroscedastic F test with trimmed means and Winsorized variances ('welch.test' function in 'onewaytests' package; Dag et al. 2018; Welch 1951), which is relatively insensitive to the combined effects of non-normality and heteroscedasticity (Keselman et al. 2008). When a significant effect was found, a *post-hoc* multiple pairwise comparison test was performed with a BH adjustment ('paircomp' function in 'onewaytests' package; Dag et al. 2018). The effect of assembly type on total final belowground biomass (three replicates per assembly type) was analyzed using a one-way ANOVA. When a significant effect was found, we performed pairwise comparisons on the least-squares means (LSM) with a Tukey adjustment ('emmeans' package; Lenth et al. 2019). We also calculated the contribution (in percent) of each species to total aboveground biomass for each of the three harvests.

Analyses were performed using R software (ver. 3.6.2). P-values lower than 0.05 were considered as statistically significant.

5.3 | Results

All species benefited from priority sowing all over the experiment (i.e. positive priority advantage; Figure 5.1), except *L. perenne* in the first harvest. *Trifolium repens*, which benefited more in the first and the second harvest than other species, showed a very low benefit after 26 weeks. Priority advantage increased over time for *D. glomerata* and *L. perenne*, and was the highest for *L. perenne* at week 26. *Onobrychis viciifolia*, which increasingly benefited of priority after 6 and 14 weeks, was absent from the final harvest in both assembly types, so that priority advantage was null.

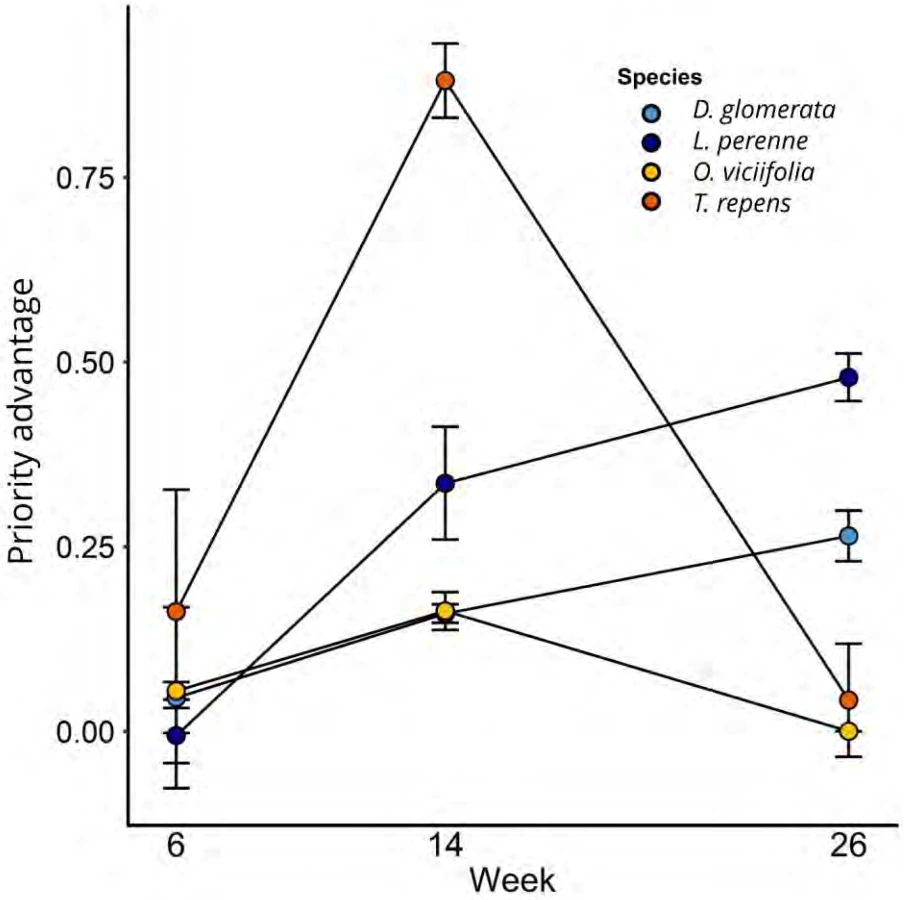

Figure 5.1 Priority advantage (natural log response ratio of the aboveground biomass of a considered species in priority treatment divided by its biomass in simultaneous sowing; mean±SE) for the four species considered for the three harvests (week 6, 14 and 26 after the first sowing). There were three replicates for week 6 and week 14, and six for week 26.

The NMDS ordination analysis (stress = 0.070) revealed an overall divergence of community trajectories (i.e. biomass composition) over time (Figure 5.2). Onobrychis$_f$ and Synchronous displayed close trajectories; the contribution of O. *viciifolia* to aboveground biomass at week 6 was higher in Onobrychis$_f$ than in Synchronous, and decreased until no alive individuals subsisted at week 26 (Figure 5.3). Trifolium$_f$ showed a closer trajectory to Onobrychis$_f$ and Synchronous than to the grass-priority communities. The trajectories of Lolium$_f$ and Dactylis$_f$ diverged over time, with Lolium$_f$ being the most divergent community after 26 weeks.

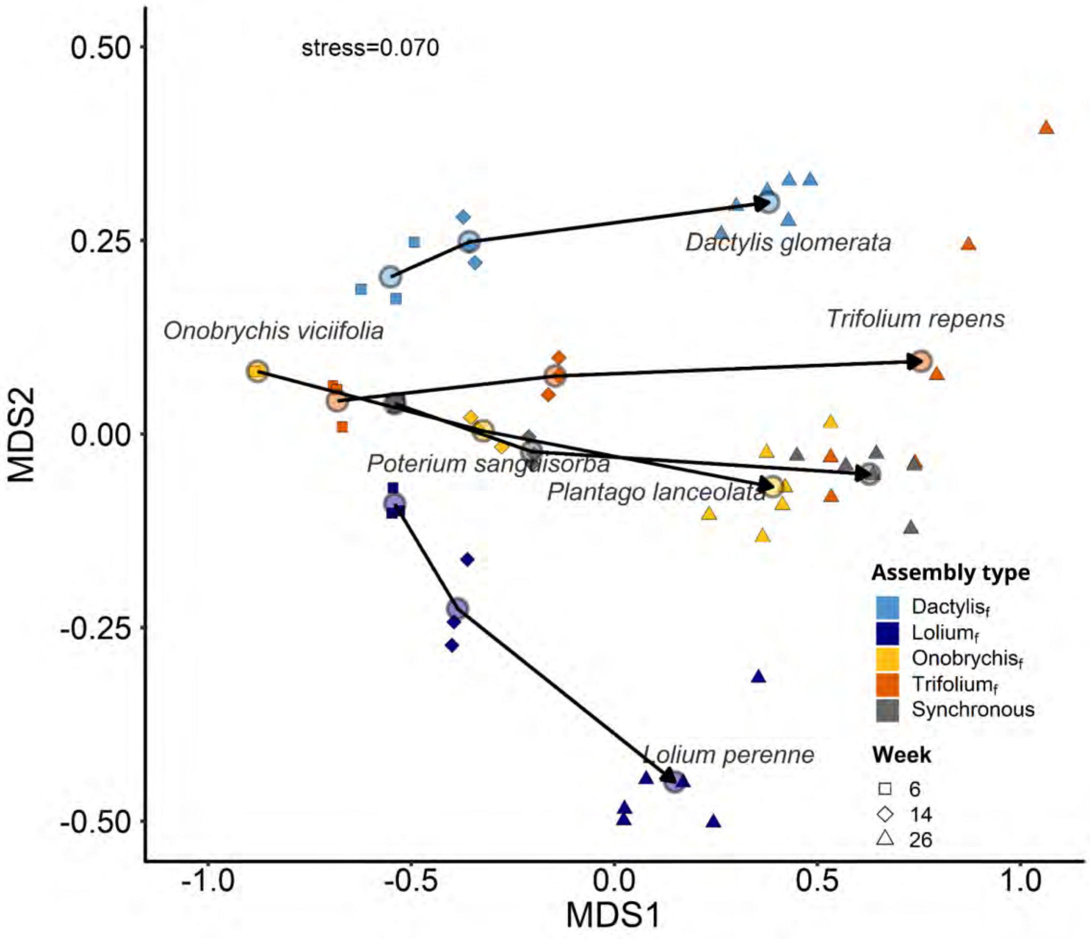

Figure 5.2 Trajectories of communities based on non-metric multi-dimensional scaling (NMDS) ordination of aboveground biomass sorted by species. The figure shows the two-dimensional solution exhibiting the least stress (0.070). Each community type is associated to a specific color. The trajectory of each community type is represented by circles linked by arrows. Circles refer to means of the NDMS axes for each harvest (6, 14 and 26 weeks after the first sowing). Replicates are depicted using squares (week 6), diamonds (week 14) and triangles (week 26).

Assembly type significantly affected total final aboveground biomass (Welch's heteroscedastic F test; F=10.1, df=4, p<0.001) and total final belowground biomass (ANOVA; F=5.8, df=4, p=0.011). Synchronous showed a significantly higher total final aboveground biomass than Dactylis$_f$ (p=0.017) and Lolium$_f$ (p=0.001; Table 5.1). Lolium$_f$ had a significantly lower total final belowground biomass than Onobrychis$_f$ (p=0.032) and Trifolium$_f$ (p=0.012; Table 5.1).

Table 5.1 Results of soil analyses and final above and belowground biomass (mean%±SE, n=6) recorded at the end of the experiment (week 26). Letters refer to post-hoc tests: assembly types with no letter in common are significantly different (p<0.05).

	NO$_3^-$ (g/kg)	NH$_4^+$ (g/kg)	P$_2$O$_5$ (g/kg)	Total aboveground biomass (g)	Total belowground biomass (g)
Dactylis$_f$	0.007	0.012	0.078	51.7±3.9^{a}	6.1±0.2^{ab}
Lolium$_f$	0.003	0.010	0.074	39.4±3.4^{a}	7.3±0.8^{a}
Onobrychis$_f$	0.005	0.012	0.076	58.7±7.7^{ab}	4.6±0.6^{b}
Trifolium$_f$	0.010	0.015	0.070	80.5±12.3^{ab}	4.1±0.5^{b}
Synchronous	0.008	0.010	0.083	79.1 ±4.1^{b}	6.2± 0.4^{ab}

A four-week time advance allowed *D. glomerata*, *L. perenne* and *O. viciifolia* to contribute respectively to 60.1%, 70.5% and 85.2% to total aboveground biomass at week 6, while *T. repens*'s contribution was only of 23.1% (Figure 5.3). In Trifolium$_f$ and Synchronous, *O. viciifolia* was the most represented species at week 6 with a contribution of 50.0% and 31.4%, respectively. *Dactylis glomerata*, *L. perenne* and *T. repens* contributions reached respectively 82.7%, 86.9% and 81.2% at week 14 when benefiting from early sowing. *O. viciifolia*'s contribution drastically decreased in Onobrychis$_f$ to reach 11.4% at week 14, and was absent at week 26. *Dactylis glomerata* and *L. perenne* were the most contributing species in Synchronous at week 14, with 35.5% and 33.9%, respectively. After 26 weeks, *T. repens* contributed to more than 55% in all community assembly types except in Lolium$_f$, where *L. perenne* contributed to 68.4%.

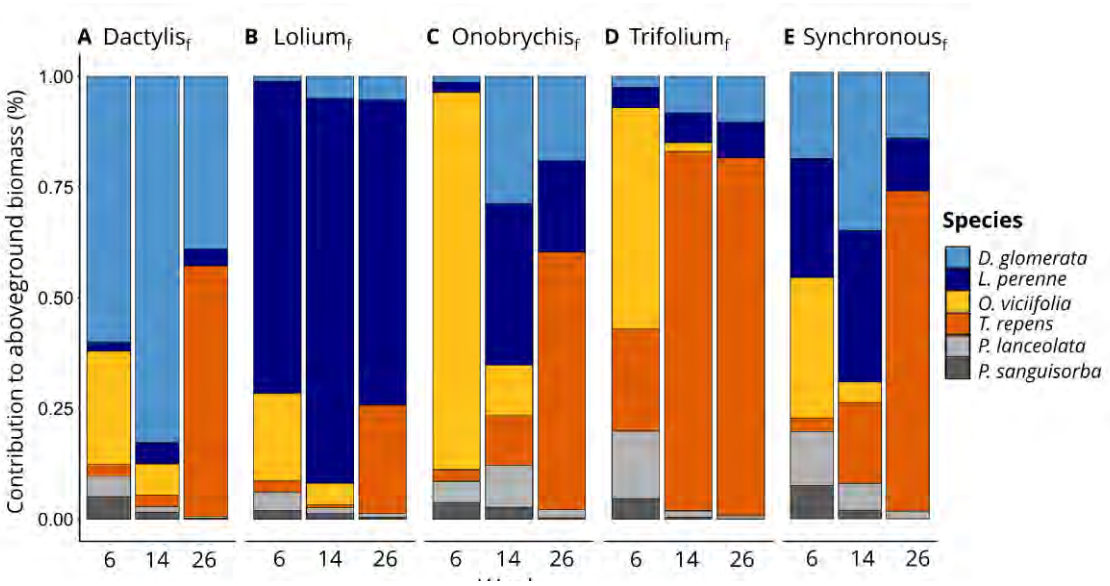

Figure 5.3 Species contribution to aboveground biomass (mean in percent) for each harvest (6, 14 and 26 weeks after the first sowing). There were three replicates for week 6 and week 14, and six for week 26.

All communities showed lower nitrates and phosphorus soil contents than control soil, but higher ammonium content (Table 5.1). Among communities, Lolium$_f$ had the lowest nitrate content and mean total final aboveground biomass and Trifolium$_f$ had the highest ones. Total final belowground biomass was higher in grass-priority communities than in legume-priority communities, with Lolium$_f$ showing the highest value and Trifolium$_f$ the lowest.

5.4 | Discussion

Giving a four-week time advance to various species generated priority effects of varying strength (Figure 5.1) and affected community structuring and productivity (Figures 5.2, 5.3; Table 5.1). Time advance globally benefited to the species sown first by allowing them to produce more biomass than when sown simultaneously to the rest of the community (Figure 5.1), with *D. glomerata* and *L. perenne* showing an increasing priority advantage over time. An early sowing of the two grass species led to diverging trajectories (Figure 5.2) most likely because strong priority effects impaired subsequent arriving species establishment and growth. This result is consistent with previous studies showing strong and persistent priority effects of grasses (Stuble & Young 2020; Werner et al. 2016) but we highlighted here differences between them. *L. perenne* benefited the most of an early sowing after 26 weeks (Figure 5.1). Lolium$_f$, whose aboveground biomass was dominated by *L. perenne* by 68.8% (Figure 5.3), showed the highest belowground productivity and the lowest nitrate soil content (Table 5.1), and the lowest aboveground productivity (Table 5.1). Because *L. perenne* dominated aboveground biomass (Figure 5.3) and is known to form dense root systems (Frankow-Lindberg 2012), we can reasonably argue that the high belowground biomass and nitrate depletion was generated by *L. perenne*, although we were not able to separate roots by species. Therefore, these results suggest that an early sowing of *L. perenne* allowed this species to rapidly preempt belowground space and deplete soil nitrate, hindering subsequent species establishment and growth. *Dactylis glomerata* did not benefit as much of a time advance most likely because of a lower nitrate depletion and belowground productivity (Table 5.1). Overall, while we could expect that light preemption would mainly underlie priority effects in such plant communities newly established on fertile soil conditions (Wilson & Tilman 1993), we highlight here that strong priority effects can arise from the preemption of soil resources and space.

Several studies have shown that priority effects of legumes are weak and poorly persistent (Körner et al. 2008; von Gillhaussen et al. 2014; Weidlich et al. 2018), which has been attributed to a facilitative effect of early sown legumes to subsequent arriving species (von Gillhaussen et al. 2014) through direct nitrogen transfer or nitrogen sparing (i.e. legumes actively fixing atmospheric nitrogen display a smaller root system and leave more opportunities for neighbor species for root space and nutrient foraging; Chalk 1998). Here, the two legume species O. *viciifolia* and T. *repens* showed contrasting behaviors. T. *repens* did not benefited much of priority sowing after 26 weeks because this species was able to dominate the community without having a time advance (Figure 5.3), most likely because of its high aboveground biomass production. *Onobrychis viciifolia*, in contrast, was not able to persist whether it was sown in advance or simultaneously to other species, although it dominated aboveground biomass in the very early stages (Figure 5.3), reflecting weak competitive abilities. The greater ability of T. *repens* to produce and maintain a high aboveground biomass led to the convergence of Onobrychis$_f$, Trifolium$_f$ and Synchronous trajectories (Figure 5.2), with T. *repens* dominating the three communities after 26 weeks (Figure 5.3).

5.5 | Conclusions

Our results overall show that assembly history (i.e. timing of species arrival) interacts with deterministic processes (i.e. species-specific competitive abilities) to drive early community assembly. Species-specific differences occurred within functional groups. The strong competitive abilities of T. *repens* allowed this species to dominate the community without benefiting of a time advantage, while O. *viciifolia* presented too weak competitive ability to persist even when being sown four weeks before the rest of the species. In our experiment, priority effects were most likely driven by belowground competition, with L. *perenne* benefiting the most of an initial advantage thanks to its ability to preempt soil resources and space. This highlights the need to consider belowground competition as a potential driver of priority effects and early community structuring, although aboveground competition is most commonly monitored (Weidlich et al. 2018). This ability to preempt resources by developing a dense root system could be decisive in the longer term in community structuring, by preventing other species from establishing, in a positive (invasive species) or negative (local species) way. Depending on the objective, such species should or may not be included in seed mixes used in restoration work.

Acknowledgements

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Synthesis of Chapter 5

Chapter 5 in a nutshell

Does the identity of the first native established species influence early recipient community structuring and priority effects?

The identity of the first established species affected early community biomass and structure (i.e. species contribution to aboveground biomass), as well as soil nutrient content. Species-specific priority effects occurred, most likely driven by differences in belowground competition.

Should we consider the order of native species arrival when implementing a priority effect-based revegetation strategy?

When implementing a priority effect-based revegetation strategy, the order of native species arrival should be carefully considered since species-specific priority effects substantially influence community structuring, and could, by this way, affect early invasion resistance.

General Discussion

Many research efforts are currently directed towards the understanding of the processes underlying invasion resistance (e.g. Beaury et al. 2019; Byun et al. 2018; Davies & Johnson 2017; Walder et al. 2018; Zhang et al. 2018) and the design of invasion resistant plant communities (e.g. Byun et al. 2018; Drenovsky & James 2010; Yannelli et al. 2017). In this thesis, I investigated two main mechanisms that could contribute to early invasion resistance: **(1)** limiting similarity, predicting that two species sharing the same ecological niche are not able to coexist (Abrams 1983), and **(2)** priority effects, occurring when early-arriving species affect the establishment, growth or reproductive success of later-arriving species (Drake 1991; Helsen et al. 2016). In the first part of the discussion, I briefly discuss the suitability of both approaches based on literature review to improve revegetation strategies. In two greenhouse experiments, I manipulated priority effects of the recipient community and monitored the consequences on invasion resistance. The second part of the discussion relates the main findings in terms of research advances and application for the four investigated mechanisms: elapsed time between recipient community sowing and invasive species introduction (II.2.1), sowing density (II.2.2), species composition (II.2.3), and assembly history (i.e. the identity of the first native colonizing species and timing of recipient species establishment (synchronous or sequential sowing; II.2.4). The role of biomass production as an indicator of invasion resistance is discussed in a third part (II.3.1), with a focus on the particular case of nitrogen-fixing legumes (II.3.2). Then, perspectives on species selection for revegetation (II.4.1), consequences of priority effects on invasibility and community assembly in the long-term (II.4.2) and limits and perspectives of application (II.4.3) are reported in a fourth part.

II.1 | Manipulating priority effects to design plant communities resisting early invasion appears more suitable than using limiting similarity

A successful application of limiting similarity to design invasion-resistant communities faces several theoretical and practical issues, while, in contrast, the use of priority effects appears promising (Chapters 1 and 2). Limiting similarity derives from the niche concept, and assumes that species sharing the same ecological niche (i.e. having the same requirements to enable them to exist) will compete until one is be competitively excluded (Abrams 1983). The practical application of limiting similarity involves reassembling plant communities dominated by a species having a similar ecological niche to that of a target invasive species. This would require being able to accurately apprehend and measure plant species niche overlap, which is deeply complex. In contrast, priority effects rely on fitness differences, so that a time advantage will give a size-related competitive advantage to an early colonizer, equalizing or elevating its fitness relative to later colonizers (Chase 2010). We showed, through theoretical and practical considerations, that the use of priority effects is more suitable than limiting similarity to the design of invasion-resistant plant communities (Table II.1). Our results are in line with the recent experimental study of (Yannelli Lucero et al. 2020); they found that giving to the recipient community a two-week time advance over invasives (i.e. priority effects) effectively decreased invasive species performance compared with a simultaneous sowing, while maximizing ecological similarity between invasive species and the recipient community (i.e. limiting similarity) did not increased invasion resistance.

Table II.1 Manipulating priority effects appears more suitable than limiting similarity to design plant communities resisting early invasion.

	Limiting similarity	Priority effects
Theoretical approach	Measuring niche overlap and determining which degree of niche overlap between the invader and recipient species is necessary to competitively exclude the invader is too complex	Easy to apprehend, i.e. time advance gives a size-related competitive advantage to the first established species through fitness differences
Timing	May only act in the long-term, making this strategy inefficient for combatting early invasion	High impact in early community structuring, potentially highly efficient for combatting early invasion
Suitability to the most common situations i.e. several co-occurring invaders or no prior identification of potential invaders	• Only applicable to target one invasive sp. or a group of sp. sharing the same niche • The target invasive sp. needs to be identified before revegetation planning	• Can be effective against functionally different invaders at a time • Can be planned without a prior identification of the invader(s)
Evidence in the literature	Biased or no support (Abella et al. 2012; Cleland et al. 2013; Emery 2007; Eriksson et al. 2006; Fargione et al. 2003; Funk & Wolf 2016; Larson et al. 2013; Longo et al. 2013; Oster & Eriksson 2012; Prieur-Richard et al. 2000; Turnbull et al. 2005; Von Holle 2005; Yannelli et al. 2018; Yannelli Lucero et al. 2020)	Support for efficiency (Delory, Weidlich, Kunz et al. 2019; Firn et al. 2010; Grman & Suding 2010; Ulrich & Perkins 2014 ; Vaughn & Young 2015; Yannelli Lucero et al. 2020; Young et al. 2016)

II.2 | Manipulating priority effects to enhance early invasion resistance

In two greenhouse experiments (Chapters 3, 4 and 5), I investigated the role of several aspects that are hypothesized to influence priority effects and associated invasion resistance *via* resource preemption: **(1)** elapsed time between recipient community sowing and invasive species introduction, **(2)** sowing density, **(3)** species composition, **(4)** the assembly history of the species composing the recipient community, i.e. timing of recipient species establishment (synchronous or sequential sowing) and identity of the first arriving species.

II.2.1 | Increasing elapsed time between native community sowing and invasive species introduction enhances invasion resistance

The size-related competitive advantage gained by the early colonizer is one of the main drivers of priority effects, equalizing or elevating its fitness relative to later colonizers (Wilsey et al. 2015). A time advance as short as few weeks can be efficient in reducing invasive species colonization success (Firn et al. 2010; Grman & Suding 2010; Ulrich & Perkins 2014; Vaughn & Young 2015; Yannelli Lucero et al. 2020; Young et al. 2016). Giving a greater head start to the recipient community over invasive species is expected to generate a greater size advantage and therefore, stronger priority effects leading to a lower invasive species establishment success. As expected, increasing time advance globally increased invasion resistance (one *vs*. 5 months of advance; Chapter 3), which is consistent with previous studies (De Meester et al. 2016; von Gillhaussen et al. 2014; Young et al. 2016). However, time advance interacted with biomass production. Low-productive communities composed by *Lolium perenne* did not benefited much of a greater time advance. This suggests that it is not the time advance *per se*, but rather the amount of biomass produced and the related amount of limiting resources pre-empted that determined the size of the competitive advantage given to the first established species and invasion resistance.

In terms of application

Measures should be undertaken to give as much time as possible to the target community to establish and produce biomass before invasion. Several non-exclusive actions for improving native emergence speed and create priority over invasives can be considered: **(1)** limiting or ideally suppressing all sources of invasive species propagules and adult plants before revegetation, **(2)** actively reestablishing target native species as soon as possible after the disturbance, **(3)** carefully controlling invasive species in the initial weeks after revegetation, and **(4)** using ‘pre-germinating’ native species seeds. Adding fertilizers would however not be advisable to boost native species biomass production since it may favor fast-growing invasive species.

II.2.2 | Increasing sowing density leads to mixed results

The density of individuals in the recipient community (i.e. the number of individuals per surface unit) may influence priority effects because increasing the number of individuals is expected to enhance resource acquisition, leaving less resource available for subsequent colonizers (Gerhardt & Collinge 2007). Increasing density could be particularly efficient in reducing invasion in the early stages of community growth, since biomass and resource preemption tend to stabilize over time (i.e., density-dependent effects; Burton et al. 2006; Carter & Blair 2012; Crawley 2007; Nemec et al. 2013; von Gillhaussen et al. 2014; Yannelli et al. 2017). Increasing sowing density from 700 to nearly 3000 seeds/m^2 (four-time fold) had a limited effect on invasion resistance (Chapter 3). An effect of sowing density was only detected when *Ambrosia artemisiifolia* was introduced in one-month old communities composed of three or nine species (i.e. survival was lower with increased density). This weak impact could result from a rapid biomass stabilization of both high and low density communities, which may have been catalyzed by **(1)** the fertile and moist soil conditions in the experiment which may have favor a rapid community development **(2)** restrictive carrying capacity that may have occur due to pot conditions - but see Yannelli et al. (2017) where a ten-time increase in sowing density (1 to 10 g/m^2) enhanced invasion resistance in a pot experiment.

We could hypothesize that sowing density may be more determinant in field conditions, where less favorable conditions induce a slower development of communities, and where reaching carrying capacity takes longer (Carter & Blair 2012; Olsen et al. 2006). In this sense, Carter and Blair (2007) found in a field experiment that a lower cover of exotic species in high-density treatments (328-344 live seeds/m^2) compared with low-density treatments (164-172 live seeds/m^2). However, other field studies reported a weak density effect on invasibility (Nemec et al. 2013; Quinn & Holt 2009).

Overall, these mixed results do not support that sowing density substantially influence priority effects and invasion resistance in newly established communities.

In terms of application

The minimum seeding rate required to ensure a sufficient development of the target community depends on the ability of selected species to preempt space and other resources, intrinsic germination capacity and environmental conditions encountered for germination and seedling development (notably resource availability and carrying capacity). Maximizing sowing density does not necessarily lead to a greater plant cover (due to density-dependent mortality), and would increase revegetation cost. For these reasons, predicting which sowing density needs to be applied in a particular revegetation context appears complex. Performing small-scale tests *in situ* before applying large-scale revegetation would help to determine an adequate sowing density.

II.2.3 | Species composition influences invasion resistance through biomass production

The influence of species composition on invasion success has been explored since the premises of invasion ecology (Elton 1958). Species-rich communities have long been associated with increased invasion resistance at the local scale (e.g. Byun et al. 2013; Connolly et al. 2017; Dukes 2002; Fargione & Tilman 2005; Hector et al. 2001; Kennedy et al. 2002; Levine & D’Antonio 1999; Maron & Marler 2007; Naeem et al. 2000; Tilman 1997), because of their ability to use more resources and generate more biomass (Carpinelli 2000; Hector et al. 1999; Nyfeler et al. 2009; Tilman 1999; Tilman et al. 2001). Diversity-resistance has been attributed to **(1)** a greater likelihood of including particularly competitive resident species or functional groups (i.e. identity or sampling effect; Crawley et al. 1999; Huston 1997; Wardle 2001), **(2)** increased complementary resource use among species (i.e. complementarity effect; Lavorel et al. 1999; Maron & Marler 2007; Robinson et al. 1995), or both these factors (Cardinale et al. 2007; Fargione & Tilman 2005). However, because it takes several growing seasons for complementary effects to cause overyielding (Cardinale et al. 2007), species composition, i.e. the presence of competitive species (identity effect) might be determinant in early invasion resistance of diverse communities, i.e. through greater resource preemption and increased biomass production.

Species composition strongly affected invasive species survival, with three-species and nine-species recipient communities both showing a higher invasion resistance than one-species communities (Chapter 3). The increased resistance of polycultures was most likely related to the three to four time higher final aboveground biomass production than monocultures, and seemed unaffected by species richness or species identity of the dominant species (*T. repens* dominated three-species communities, while *L. corniculatus* dominated nine-species communities). These results support that the introduction of productive species in the recipient community may boost invasion resistance through an overall increase in aboveground biomass production (see II.3 for biomass discussion).

In terms of application

Attention must be paid on carefully selecting productive species that are able to develop well on site conditions and preempt soil resources. Although a high diversity may not reinforce early invasion resistance, selecting several species increases the probability to include species that are able to develop well in a particular context. In addition, in the longer term, diverse communities may be more resistant than poorly diverse ones due to complementarity effects and reduced resource fluctuations and biomass over time. Hence, applying seed mixes with a certain number of species may be safer and more efficient in the long-term than relying in the ability of a few species to develop a dense and efficient cover in a particular context. In addition, the use of native local species (which are expected to be adapted to local conditions and develop better than non-local species) may contribute to a greater establishment success of the target community and therefore be more resistant to invasion.

II.2.4 | Altering assembly history and the identity of the first colonizer affected invasion resistance

Studies investigating the influence of native species' order and timing of arrival on subsequent invasion success are scarce (Mason et al. 2013). Hence, in addition to the theoretical knowledge that such experiment may bring to community ecology, it is of direct interest to practitioners since sequential sowing is currently considered to increase the establishment success of target species in restoration (Young et al. 2016).

In our greenhouse experiment (Chapters 4 and 5), small differences in assembly history altered community structure (i.e. the identity of the dominant species; Körner et al. 2008; Weidlich et al. 2018), biomass production (Körner et al. 2008; von Gillhaussen et al. 2014; Weidlich et al. 2016, 2018), soil chemistry, and invasion resistance (Lang et al. 2017; Young et al. 2016). Giving a four-week time advance generally allowed the generation of priority effects (early sown species produced more biomass than when sown simultaneously to the rest of the species), but species-specific differences occurred (Chapter 5). These results indicate that deterministic processes (species-specific competitive abilities) interact with temporal colonization dynamics to drive early community assembly and invasion resistance.

Consequences of sequential sowing on biomass production and nitrate preemption impacted invasion resistance (Chapter 4). A synchronous sowing of the whole community led to the highest invasion resistance most likely because of a quick biomass production and associated high resource preemption, which is consistent with studies associating high biomass production to a greater invasion resistance (Lulow 2006; Mason et al. 2013, 2017; Rinella et al. 2007; Symstad 2000). Communities where the grass species *L. perenne* was sown first were more resistant than communities where priority was given to the legume *T. repens*. Difference in invasion resistance was most likely related to the preemption of belowground resources and space; an early sowing of *L. perenne* allowed this species to rapidly dominate the community and quickly preempt soil resources and space which were therefore no longer available for subsequent colonizing invaders, while introducing *T. repens* first led to a lower belowground biomass production and high soil nitrate content, boosting invasion.

In terms of application

Giving a time priority to certain species did not increase invasion resistance compared with the synchronous sowing of all species, although some early sown species induced a higher belowground (*L. perenne*) or aboveground biomass production (*T. repens*) after a few weeks. Accordingly, our results do not support that sequential sowing is a potential way to increase invasion resistance of communities established after a disturbance, and could even increase vulnerability to invasion. Applying sequential sowing may therefore not be recommended on invaded site.

II.3 | Biomass production as an indicator of invasion resistance

II.3.1 | Aboveground and belowground biomass production affects early invasion resistance

High biomass production has been repeatedly associated with increased invasion resistance (Lulow 2006; Mason et al. 2013, 2017; Rinella et al. 2007; Symstad 2000; Yannelli Lucero et al. 2020). Biomass production is an indicator of competitive ability (Gaudet & Keddy 1988), and high biomass can reflect a high consumption of available resources such as light, water or nutrients. Our findings provide support for a major role of biomass production in early invasion resistance at least in the initial stages (Chapters 3 and 4).

In the early stages of community growth, a high aboveground biomass production is expected to increase competition for light and therefore may be determinant for invasion resistance following disturbances and vegetation clearance (Baruch et al. 2000; Corbin & D'Antonio 2004; D'Antonio et al. 2001; Forrest Meekins & McCarthy 2001; Vitousek & Walker 1987). The most resistant communities were those that produced high aboveground (Chapter 3) or total (Chapter 4) biomass, despite a final dominance of legumes (whose presence was often associated with greater invasion success; Mwangi et al. 2007; Scherber et al. 2006). These results agree with Rinella et al. (2007), where overall productivity mattered whereas species identity did not.

Belowground biomass production can also play a determinant role in early invasion resistance. The findings of the second experiment support that a high belowground biomass production and preemption of soil resources (here, mostly nitrate) in the very early stages can substantially affect early invasion resistance (Chapter 4). The highly resistant community where *L. perenne* was sown first, showed a high belowground biomass production and a high nitrate preemption while displaying the lowest final aboveground biomass production (and total biomass). Moreover, communities where *T. repens* was sown first were the least resistant to invasion, although rapidly reaching a high aboveground biomass. The low resistance was most likely due to of an initial lower competition for root space and higher belowground resources arising from the dominance of *T. repens*.

Overall, our results underline that a quick, high biomass production and preemption of soil resources play a significant role in early invasion resistance. They also provide evidence that strong priority effects can arise from belowground competition in the early stages of community establishment (Weidlich et al. 2018).

II.3.2 | The case of nitrogen-fixing species

Legumes can help developing a greater vegetation cover and decrease invasive species survival (most likely through competition for light; Chapter 3), but can also boost invasive species performance especially when benefiting from a head start (Chapter 4). Legumes may also particularly favor invasion when established in environments with limited resources and/or stressful conditions, because legumes may enrich soil with nitrogen and turn conditions and favor weedy, fast-growing invasive species (Dornbusch et al. 2018; Maron & Connors 1996). Therefore, when **(1)** invasion risk is high and immediate, and **(2)** soil resources are limited and/or in stressful conditions, including early emerging and/or productive legumes in seed mixes should be avoided.

II.4 | Perspectives

II.4.1 | Species selection for revegetation

A functional trait approach to select adequate species

Broad functional groups (i.e. grasses, legumes and non-legume forbs) do not appear to be good indicators of priority effects strength and invasion resistance (Chapters 3, 4 and 5). Species presenting an ability to rapidly produce high biomass and capture soil resources contributed to invasion resistance. In this sense, results of Zuo et al. (2016) indicate that a high root:shoot ratio and high competitive abilities allow greater priority effects. Searching for particular functional traits associated to high growth rate and high resource capture may be more relevant than focusing on functional groups (Drenovsky & James 2010), especially since Violle et al. (2009) demonstrated that instantaneous measures of plant traits are good indicators of resource depletion over time. Drenovsky and James (2010) showed that SLA (Specific Leaf Area; leaf area produced per unit biomass invested in leaf) is a very good predictor of plant growth and resource capture rates (i.e. high SLA associated to higher growth rate and resource use), and could therefore be a key trait to look at for species selection.

It should however be noticed that traits that matter to invasion resistance may vary depending on site conditions. For instance, in nutrient-limited systems, selecting species presenting a high nutrient use efficiency (i.e. a great ability to detect areas where nutrients are located and to use these nutrients efficiently in photosynthesis) may be more relevant than focusing on SLA (Drenovsky & James 2010). Further research efforts on identifying traits associated to strong priority effects and invasion resistance depending on the biotic (e.g. presence of herbivores) or abiotic (e.g. resource availability) context would help design more resistant communities.

Perennial vs. *annual species*

In our experiments, we used perennial species to compose the recipient native communities. Perennial species are expected to grow larger in each successive year after sowing, maintaining or increasing the preempted resources, therefore exerting an increasing priority advantage and invasion resistance over time (Corbin & D'Antonio 2004; Dyer & Rice 1999; Lulow 2006; Morghan & Rice 2006). Using perennial species appears therefore relevant to allow a long-term persistence of an initial sowing advantage. Annual species however often present a higher competitive ability at the establishment stage than perennials (Bartolome & Gemmill 1981; Dyer & Rice 1997; Hamilton et al. 1999; Young et al. 2015), and could therefore rapidly preempt a large amount of resources and exert strong priority effects against invaders. In this sense, Herron (2010) found that including annuals in revegetation mixes may present some advantage when target sites are invaded by fast-growing, competitive invasive species. However, whether annual native species could perpetuate their initial advantage over several generations (i.e. increasing population density through a greater reproductive success) has not been experimentally studied yet.

II.4.2 | Consequences of priority effects on community assembly and invasibility in the long-term

This thesis work focused on invasion resistance and priority effects in the very early stages of community growth to target the post-disturbance stage particularly vulnerable to invasion, considering competitive interactions and processes occurring over one growing season.

While long-term studies are rare, there is a few experimental evidence that priority effects can have long-lasting consequences on invasibility and community structure. Vaughn and Young (2015) showed that giving a two-week time advance to native species favored those species over invasives for four years. Werner et al. (2016) found that benefits of temporal priority persisted for eight years in a grassland experiment. Moreover, Švamberková et al. (2019) detected an effect of initial species composition on community structure 20 years after sowing. These studies support that order and timing of species immigration during community assembly may influence long-term community structure and may lead to alternative stables states – implying that several final states of species composition can occur depending on immigration history even under similar environmental conditions and species pool (Fukami & Nakajima 2011). A significant impact of species colonization history to long-term community structure would have deep implications for understanding, conserving and restoring species diversity. For instance, restoring specific sequences of species arrival may be required to favor certain target species over undesirable ones (Young et al. 2016). Quantifying to which extent priority effects are influencing community structure is challenging since immigration history is impossible to reconstruct in sufficient detail for most natural communities. Restoration contexts appear therefore particularly suitable to the study of such historical factors since species order of arrival can be monitored and experimental manipulations of immigration history can be implemented.

II.4.3 | Limits and perspectives of application

Priority effect direction and strength are context-dependent

Predicting the efficiency of priority effects in revegetation strategies in a particular context is challenging, because the direction (positive or negative) and strength of priority effects are strongly dependent on the interacting species as well as on environmental conditions.

- Influence of the characteristics of first arriving species and later colonizers

Several studies underline that the identity of the first arriving species influence the direction, strength and persistence of priority effects (Cleland et al. 2015; Delory, Weidlich, Kunz et al. 2019; Dickson et al. 2012; Stuble & Souza 2016; Werner et al. 2016; Young et al. 2016; Zuo et al. 2016). Werner et al. (2016) highlighted differences at the functional group level, with grasses exerting strong and persistent priority effects over forbs, while forbs over grasses did not. Stuble and Souza (2016) found that species origin influenced priority effect strength, with late arrival being less detrimental to exotic than native species. Zuo et al. (2016) showed that species displaying a high root:shoot ratio and greater competitive ability are more likely to generate strong priority effects. We also highlighted species-specific differences in priority effect strength, with species quickly preempting nitrate and producing a high belowground biomass generating stronger priority effects (Chapter 5).

However, priority effects may also depend on the characteristics of later colonizers. The three invasive species tested, *Ambrosia artemisiifolia*, *Bothriochloa barbinodis* and *Cortaderia selloana* shared some response patterns to manipulation of priority effects but displayed some species-specific differences (Chapter 3). For instance, the presence of a one-month community tended to facilitate *C. selloana* seedling emergence while it was deleterious to *A. artemisiifolia*'s ones. The apparent facilitation of *C. selloana* seedling emergence could be related to its ecological requirements for germination and early seedling development (i.e. a one-month vegetation cover may have generated better conditions than bare soil by retaining humidity and providing adequate shade conditions; Domenech 2005; Holmgren et al. 1997). Importantly, weaker priority effects can be observed when later colonizers are able to tolerate low concentrations of resources (occurring when colonizers established earlier already preempt resources) and high levels of competition (Stuble & Souza 2016), so that they are less impacted by arriving late. Accordingly, invasive species tolerating higher competition levels and lower resource availability may be less sensitive to priority effect-based strategies than ruderal, invasive species establishing in disturbed environments.

- Influence of environmental conditions

Priority effect strength depends in part upon whether site conditions allow for early colonizing species survival, rapid growth and resource preemption (Fukami 2015). Site conditions include resource availability but also biotic components such as the presence of herbivores and pathogens. Priority effects are expected to be stronger under high resource availability and favorable conditions which tend to accentuate competitive interactions (Chase 2003; Collinge & Ray 2009; Fukami 2015; Kardol et al. 2013; Young et al. 2016). In this sense, Young et al. (2016) found priority effects to be weaker in the least productive site and when initial sowing occurred during years with relatively less rainfall and lower cover production. Moreover, the study of Kardol et al. (2013) indicated greater priority effects under a high nutrient supply that allowed early arriving species to preempt light more quickly, therefore decreasing the successful establishment of subsequent arriving species. Biotic components of the environment can also influence the strength of priority effects.

Notably, when herbivory pressure is high, priority effects of early-established species can be limited because early emergence increases their vulnerability to herbivores (Wainwright et al. 2012).

Although the level of efficiency of priority effect-based strategies appears context-dependent, there is growing evidence that it could substantially help decreasing plant invasion across many systems and species (Firn et al. 2010; Grman & Suding 2010; Vaughn & Young 2015; Yannelli Lucero et al. 2020; Young et al. 2016). Hence, developing priority effect-based strategies appears promising and should be further explored. To improve the predictability of such revegetation strategies, research is needed to better characterize the influence of abiotic (e.g. resource availability, temperature, rainfall) and biotic (e.g. characteristics or traits of interacting species, and influence of other organisms such as herbivores, soil biota, symbionts and pathogens) attributes of the environment.

Situations where priority effect-based revegetation strategies appear unsuitable

There are several contexts where priority effect-based revegetation strategies appear inappropriate to control plant invasions.

- In harsh environments

The use of revegetation and priority effects as a way to reduce plant invasions relies on the assumption that competitive interactions are the dominant forces structuring the community. According to the 'stress-gradient hypothesis' (Bertness & Callaway 1994), this occurs when the physical environment is relatively benign (fertile and relatively stable conditions) and consumer pressure is low. However, in harsh environments with limited resources and/or stressful conditions, facilitative interactions are expected to prevail so that revegetation may facilitate invasive species establishment rather than preventing it (Cavieres et al. 2005; Lenz & Facelli 2003; Mason et al. 2013). In these cases, actively restoring a native cover has to be considered carefully.

- In environments subjected to frequent disturbances

A priority effect-based revegetation strategy is unsuccessful in environments subjected to frequent disturbances involving a severe destruction of the vegetation cover. Disturbances disrupt the priority effects of well-established resident species, reducing resource uptake and creating opportunities for invaders to establish (D'Antonio et al. 1999; Davis et al. 2000). For instance, applying a priority effect-based revegetation strategy appears inappropriate in riverbanks prone to frequent flooding or in sites exposed to severe trampling.

- In environments with a large invasive species propagule bank

In order to benefit from priority effects, native species must gain a sufficient time advantage over invasive species. Therefore, it is mandatory to remove invaders (present as adult plants or propagules) before revegetation. Restoring a native cover by seeding may be poorly efficient against resprouting of rhizome propagules, since the latter establish generally more successfully than seeds regardless of the presence of a disturbance or competition from resident plants, because rhizomes possess better reserves than seeds (Silvertown 2008; Winkler & Fischer 2002). Several methods are available for eliminating invasive species propagules, such as topsoil removal (Hölzel & Otte 2004), effective mowing management (i.e. adjusted to phenological development; Milakovic et al. 2014) and artificial flushing of invasive species to induce germination, followed by lethal interventions such as tillage or herbicide application (Wolf & Young 2016). Alternative approaches, such as microwave soil heating are also currently considered to eliminate invasive species seed banks (Hess et al. 2018; Hess, Buisson, Mesléard 2019). However, in cases where invasive species propagules bank cannot be removed before applying revegetation because of practical (e.g. deep soil disturbances unwanted, presence of protected native species) or financial reasons, implementation of a priority-based strategy appears unlikely to be successful.

- In highly variable environments

Using priority effect-based revegetation strategies is challenging in highly variable environments (such as ecosystem under Mediterranean climate presenting a high inter-annual variability in temperature and rainfall; see Appendix 1), since the outcome is strongly dependent on specific years and environmental conditions (Stuble et al. 2017). Environments where environmental conditions are more predictable could me more suited to the implementation of priority effect-based revegetation strategies.

Conclusions

The global increase in invasions and associated disastrous consequences require rapid solutions to reduce invasive species spread. This thesis combines literature synthesis with greenhouse experiments in order to move towards a better understanding of invasion resistance of newly established communities and develop improved revegetation strategies against plant invasions. Two main concepts were explored, which were limiting similarity and priority effects. We provide evidence that limiting similarity is likely to play a limited role in early invasion and that its application appears unsuitable to the design of invasion resistant communities. Managing priority effects (i.e. reducing invasive species ones and enhancing those of natives) appears much more promising. The two greenhouse experiments highlighted how temporal assembly dynamics (i.e. elapsed time between recipient community sowing and invasive species introduction; timing of recipient species arrival) interacts with community characteristics (i.e. composition, density, species identity) to generate priority effects of variable strength and substantially affect early invasion resistance. Strong priority effects and early invasion resistance were associated to a quick, high production of biomass and a high preemption of soil nitrogen. According to the results, **(1)** giving as much time advance as possible to the recipient community over invasives, **(2)** including species displaying an ability to rapidly produce biomass and preempt soil resources and **(3)** avoiding sequential sowing especially when early colonizers are nitrogen-fixing, productive species.

Overall, this thesis brings new knowledge on early invasion resistance of newly established herbaceous plant communities. The results, highlighting the inadequacy of revegetation strategies based on limiting similarity and the promising perspectives of manipulating priority effects, will help designing more efficient revegetation strategies against plant invasions.

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Appendix 1

In-situ experiment: Influence of invasion timing, recipient community composition, sowing density and study site on early invasion success under field conditions

Results for native vegetation dynamics

Appendix 1

A | Study aims

An *in-situ* experiment was set up early 2019 addressing a similar research question to the greenhouse experiment reported in Chapter 3, to find out: How do invasion timing (i.e. elapsed time between recipient community sowing and invasive species introduction), recipient community composition and sowing density interact to influence priority effects and early invasion success of communities sown after a disturbance?

Experiments in controlled conditions make it possible to neutralize the effect of some uncontrollable factors influencing vegetation responses in the field (e.g. variability in precipitations, heterogeneity in soil nutrient content, herbivory), allowing the study of specific mechanisms. Controlled experiments are particularly adapted to study the influence of assembly history since precisely monitoring species immigration in a field context is challenging. Nevertheless, implementing a field experiment appeared particularly relevant within the framework of this thesis, which aims to apply the demonstrated principles to the development of more efficient revegetation practices against plant invasions. Environmental conditions encountered in the field **(1)** are expected to be less favorable to the establishment and growth of sown communities than the greenhouse conditions in Chapter 3 (i.e. frequent watering, fertile topsoil, no competition with unsown species, no herbivory or seed predation), **(2)** and imply potential interactions with unsown plant species and other trophic levels, both being likely to affect vegetation dynamics and invasibility. Pot and field conditions also differ in carrying capacity (i.e. limited pot capacity can be restricting for root growth), which would also contribute to response differences.

This experiment also aimed at testing whether site conditions and the identity of the species used for revegetation influenced invasibility of sown communities, with the assumption that resident species better adapted to site conditions would generate stronger priority effects and better resist invasion. For this purpose, the same experimental design was implemented on two sites in Southeastern France ('TDV' and 'PSJ' sites) differing by soil conditions (respectively clay loam *vs.* sandy texture), and two sets of species were tested, each one being composed of species adapted to clayish (**A**) or sandy soils (**B**). We expected a greater establishment success and lower invasibility of **(1)** the species set (**A**) in the TDV experiment, and **(2)** the species set (**B**) in the PSJ experiment.

The dramatic development of the weedy species *Chenopodium album* from the natural seed bank in the PSJ site led to the abandonment of the experimental site. On the TDV site, the introduced invasive species did not emerged in the first two growing seasons, so that we were not able to test our research question. This Appendix aims at presenting the experimental protocol and synthesizing the results obtained on native communities.

B | Methods

B.1 | Experimental sites

Location

The experiment was carried out on two sites distant by 34 km, located on the domain of Tour du Valat (clay loam soil texture; hereafter 'TDV'; 43°30'06.2"N 4°41'30.7"E, Arles, France), and the domain of Petit-Saint-Jean (sandy soil texture; hereafter 'PSJ'; 43°34'24.9"N 4°16'52.6"E, Saint-Laurent-d'Aigouze, France) in South-Eastern France. The sites were subjected to a Mediterranean climate, having warm and hot, dry summers and mild wet winters with a high interannual variability (Lionello et al. 2006). Before implementing the experiments, both sites were hay meadow that have not been ploughed for several years.

Sites preparation and maintenance

The PSJ site was first ploughed in November 2018, sown with mustard to prevent wind erosion during winter and plowed again at the end of January 2019, a few days before sowing. The TDV site was ploughed once in late January 2019 (Figure A.1A). To provide a uniform and favorable seedbed, each sown plot (see B.3) was cleared of large clods and residual (generally sparse) vegetation, and flattened by hand (Figure A.1B).

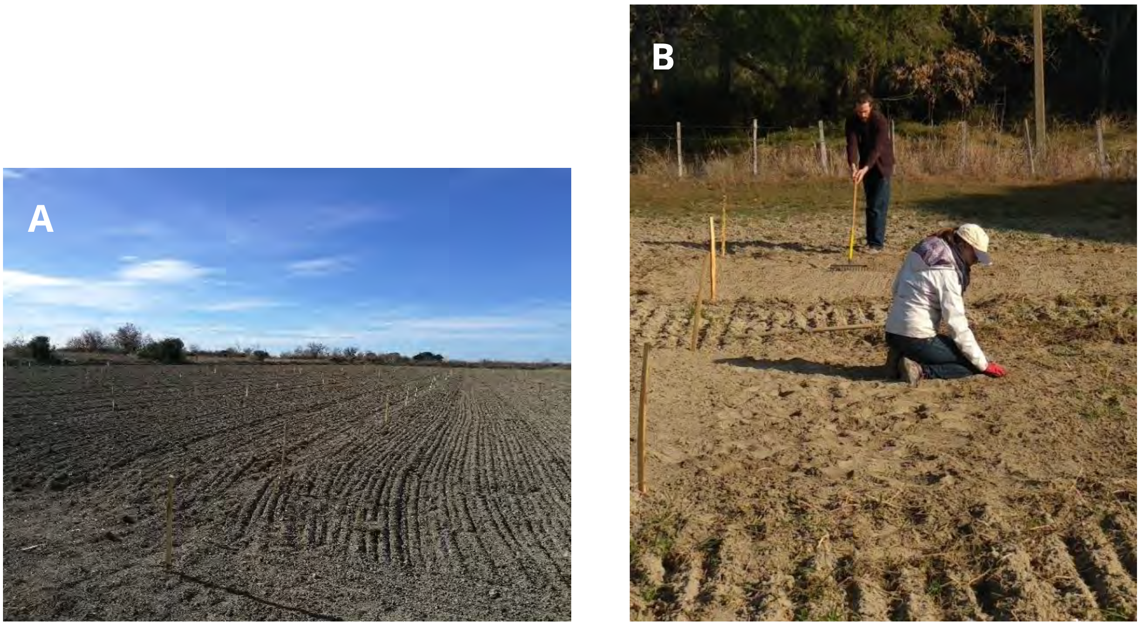

Figure A.1 Site preparation. (**A**) TDV site after plowing, and (**B**) preparation of sown plots at the PSJ site.

On the TDV site, three unsown taxa invaded the plots after plowing, which were *Helminthotheca echioides* L., *Polygonum aviculare* L. and thistles (mostly *Cirsium* sp.) In order to reduce competition from these species with the sown communities, the largest individuals were removed by hand in mid-April and early July, 2019.

B.2 | Species selection

Native species selected for sowing

Species composing the sown communities were selected on the basis that **(1)** their ecological requirements matched climate and soil conditions of one site (clay loam or sandy soils) **(2)** their seeds were commercially available and used in revegetation in France (NGE internal investigation, data not shown). Seeds were purchased at the commercial seed supplier SCHEIER France. Before starting the experiment, we assessed germination capacity by placing 50 seeds (five replicates of ten seeds) in Petri dishes on cotton soaked with distilled water. Petri dishes were placed in a growth chamber (Hotcold-GL: 12K lux; P-Selecta, Barcelona, Spain) with a photoperiod of 12 hr / 12hr and alternating temperature (15/25°C), and germination was recorded every three days for one month. The results were used to adjust the number of seeds sown in the experiment, to ensure germination rates equivalent to the expected final densities.

Invasive species

Introducing invasive species to a free site poses obvious ethical problems. For this reason, we selected invasive species present on site or nearby. Accordingly, we selected two invasive species (i.e. *Bothriochloa barbinodis* (Lag.) Herter and *Cortaderia selloana* (Schult. & Shult.f.) Asch. & Graebn.) to introduce in the TDV site and three (*Ambrosia psilostachya* DC., *Bothriochloa barbinodis*, and *Cortaderia selloana*) in the PSJ site. As to prevent the spread of introduced invasive species, we aimed at removing emerging individuals before flowering throughout the experiment.

The western ragweed (*Ambrosia psilostachya* DC., Asteraceae) is a perennial species native to North America (Fried et al. 2015). Introduced in France in the 19th century, this clonal species colonizes ruderal and cultivated environments particularly abundant in the start of succession. Dense populations have been observed in certain sensitive or degraded Mediterranean areas, potentially threating native biodiversity. Descriptions of *B. barbinodis* and *C. selloana* are available in Chapter 3.

For each invasive species, seeds were harvested at maturity in 2018 from at least ten individuals from three populations located in South-Eastern France. Before starting the experiment, seeds of *A. psilostachya* were cold-stratified to break dormancy (Montagnani et al. 2017). For this purpose, we placed seeds between two cotton layers soaked in distilled water in a hermetically sealed plastic box covered with light-tight aluminum and refrigerated it at 4°C for seven weeks (Bae et al. 2017).

Prior to the experiment, germination capacity of each species was evaluated according to the protocol described above. Test results were used to adjust the number of seeds sown as to ensure germination rates equivalent to expected densities.

B.3 | Experimental design

The aim of the experiment was to evaluate whether **(1)** elapsed time between recipient community sowing and invasive species introduction (0, 2, 4 months), **(2)** seeding density (1800 or 6000 live seeds/m²), and **(3)** species composition (Table A1) influenced invasion resistance of sown communities in field conditions. Species were sown in equal proportions.

Table A.1 Description of native sown communities.

	Richness	Species	Total seeding density (live seeds/m²)	Community type
Set of sp. (**A**) 'Clay-adapted'	1 sp.	*Lolium perenne* L.	1800	A-1SP-D1
			6000	A-1SP-D2
	3 sp.	*Lolium perenne* L. *Plantago lanceolata* L. *Trifolium repens* L.	1800	A-3SP-D1
			6000	A-3SP-D2
	9 sp.	*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. *Trifolium repens* L.	1800	A-9SP-D1
			6000	A-9SP-D2
Set of sp. (**B**) 'Sand-adapted'	1 sp.	*Elytrigia repens* L.	1800	B-1SP-D1
			6000	B-1SP-D2
	3 sp.	*Elytrigia repens* L. *Plantago coronopus* L. *Trifolium pratense* L.	1800	B-3SP-D1
			6000	B-3SP-D2
	9 sp.	*Anthyllis vulneraria* L. *Cynodon dactylon* L. *Elymus repens* L. *Festuca rubra* L. *Helichrysum stoechas* L. *Medicago sativa* L. *Plantago coronopus* L. *Silene latifolia* subsp. *alba* (Mill.) Greuter & Burdet *Trifolium pratense* L.	1800	B-9SP-D1
			6000	B-9SP-D2
Control		No seeding		CONTROL

On January 18, 2019 (TDV) and January 25, 2020 (PSJ), each community type (composition × density; Table A1) was sown by hand on plots of 24 m^2 (6 × 4 m^2), with five replicates per community type (Figure A.2A). As to disentangle the effect of sown and unsown species, five control plots where added to the experiment where no recipient community was sown, totaling 65 plots per site. Treatments were implemented according to a systematic arrangement plan (Figure A.3). Plots were separated by at least 3 m.

Figure A.2 Native community sowing and invasive species introduction. (**A**) Native community sowing by hand, Installation of colored sticks signaling invasive species seed introduction in the (**B**) TDV and (**C**) PSJ sites. (**D**) Invasive species seed introduction.

Figure A.3 Spatial arrangement of the experiment. In each plot is indicated, from left to wright: **(1)** the absolute number of the plot preceded by 'P', (**2**) the set of recipient species (**A**) or (**B**), species richness (1SP = one species, 3SP = three species and 9SP = nine species), seeding density (D1 = 1800 seeds/m² and D2 = 6000 seeds/m²), and (**3**) the spatial arrangement of the three double-lines of invasive species seed introduction (1=simultaneously to the recipient communities, 2= two months later, 3 = four months later). Control plots refer to absence of native species seeding.

In each plot, invasive species seeds were introduced by hand at fixed positions marked with colored sticks (Figure A.2B,D). Three double-lines were set up to test the three introduction times (i.e. simultaneous to community sowing, two months, and four months later; Figure A.4). To avoid bias related to the position in the plot, the spatial position of introduction times were randomized according to a systematic arrangement plan (Figure A.3). For each introduction time, we aimed at monitoring invasive species response on min. 50 individuals (ten per replicate). According to the results of germination tests realized before the experiment (data not shown), we introduced either 15 (*A. psilostachya*), 14 (*B. barbinodis*) or 13 (*C. selloana*) seeds for each introduction time in each replicate (Figure A.4).
Seed positions were distant by 20 m.

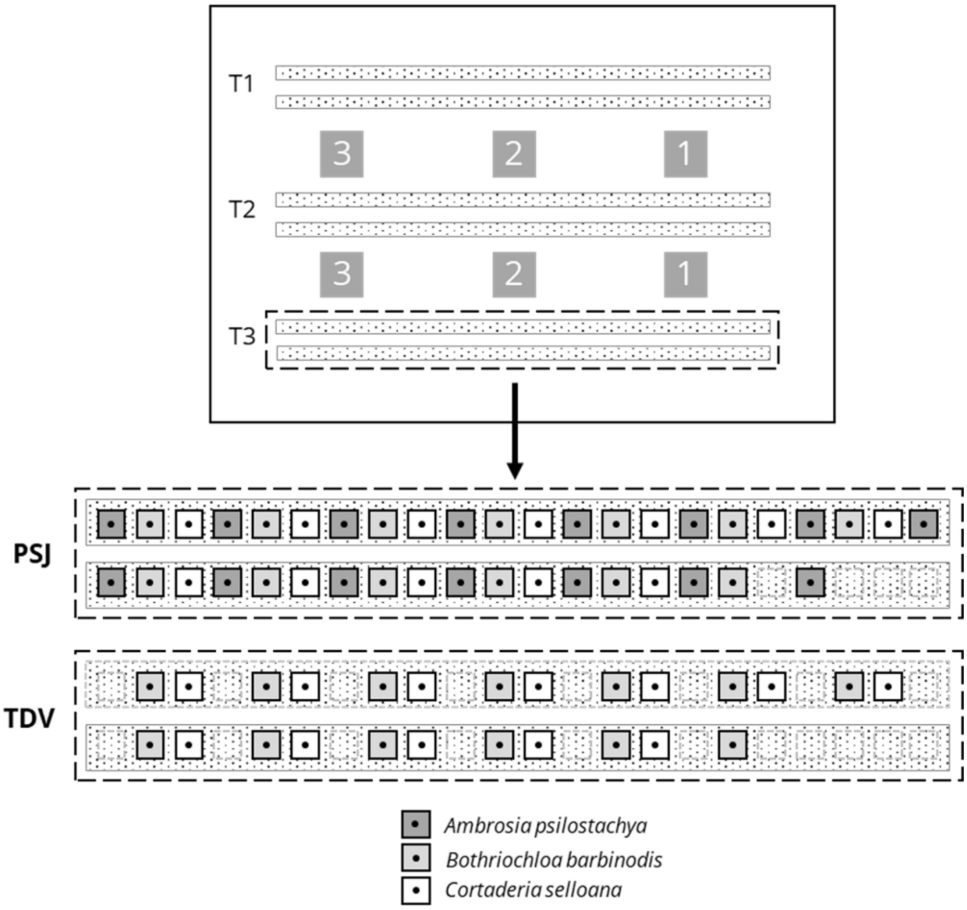

Figure A.4 Spatial arrangement of invasive species seed introduction. In each plot, seed introduction was planned on three double lines (T1, T2 and T3) corresponding to the three introduction times (0, 2 or 4 months after native community sowing). Position of the three 25 × 25 cm quadrats used for aboveground biomass harvest is indicated by grey squares with numbers (1: July 2019, 2: November 2019, 3: June 2020). Invasive species seeds arrangement per double-line is indicated for the PSJ and TDV sites using a different grey shade for each species. Positions where seeds were introduced are represented by black dots.

What was done

The first invasive species seed introduction was performed simultaneously to community sowing (late January). The second introduction, initially planned for late March, was delayed until April 29-30 due to a very poor vegetation development attributed to particularly dry conditions in the region in early spring 2019 (Météo France 2020). The third introduction was not carried out due to the delay.

In each site, four additional plots of 72 m² (12 m × 6 m) were sown using a hydroseeder prototype (SCHEIER ECO 500) as to investigate the influence of sowing practice on community development and invasibility (Figure A.5). Hydroseeding is a common practice for revegetating large and steep areas (Albaladejo Montoro et al. 2000; Tormo et al. 2007), which consists in projecting seeds mixed with water, fertilizers and sometimes other substances aiming at improving soil properties and increase vegetation establishment success. Here, the hydroseeding mix only consisted in seeds and water. Four treatments were tested, which were: A–1SP–D1, A–1SP–D2, A–9SP–D1, A–9SP–D2. In each plot, we aimed at establishing three × three double-lines of invasive species, as to investigate the response of at least 30 individuals of each invasive species per treatment.

Figure A.5. Hydroseeding of the native communities in the TDV site.

B.4 | Soil analyses

In order to assess potential in-site variability in soil characteristics, sites were divided in four equal zones of 0.182 ha in which ten soil cores (7 mm diameter × 150 mm deep) were collected. Samples extracted from each zone were pooled and analyzed for granulometry and chemistry (pH, total organic matter, total C, N and Ca, nitrates (NO_3^-), ammonium (NH_4^+), phosphorus pentoxide (P_20_5), potassium oxide (K_2O), magnesium oxide (MgO), and calcium oxide (CaO). Soil analyses were performed by the professional soil laboratory Teyssier (Teyssier 2020).

B.5 | Invasive species success

In order to measure early invasion success, we planned to monitor the number of emerged individuals of invasive species four times in the first year, and three times in the second year. To measure invasive species performance, we intended to measure final biomass at the end of the second growing season.

What was done

We monitored invasive species seedling emergence in the TDV experiment on June 26, 2019. Invasive species monitoring was not performed in the PSJ experiment because of the uncontrollable development of an undesirable species from the natural seed bank (i.e. *Chenopodium album* L., 1753, see B.6).

B.6 | Vegetation monitoring

Before plowing the site and destructing the existing vegetation, we performed a species inventory at both sites (Supplementary material; Table SA.1). In order to assess community structuring and productivity, we intended to record species composition by evaluating vegetation cover by species and measure aboveground biomass several times during the experiment.

What was done

In the PSJ site, the unsown, weedy species C. *album* rapidly dominated all plots in early spring 2019 until reaching several meters high and forming a dense and impenetrable canopy (Figure A.6). C. *album* is one of the most abundant weeds in many crops in Europe (Schroeder et al., 1993) which successfully grows on disturbed soils with high nitrogen levels. We were therefore unfortunately constrained of giving up on the PSJ experiment.

Figure A.6 Colonization of the PSJ site by *Chenopodium album*, forming a dense canopy (July 03, 2019).

Because plots located at the edge of the site (the line of plots on the right on Figure A.3), were highly invaded by thistle in autumn 2019 despite our removal efforts, we decided not to consider these plots in our vegetation survey. We therefore monitored four replicates for all community types except for B–1SP–D2, B–3SP–D2, B–9 SP–D2 and Control for which we monitored three replicates. Vegetation surveys were carried out in July 2019, November 2019, and June 2020 using two 25 × 25 cm quadrats per replicate. Quadrat position was fixed and differed between harvest dates (distant from 75 cm; Figure A.4) as to avoid an effect of a vegetation removal from the precedent harvest. Measures realized on vegetation are indicated in Table A2 below. Total aboveground biomass per quadrat was harvested as close as possible to soil surface, dried for 48h at 50°C and weighed.

Table A.2 Measures on vegetation realized in the TDV site.

Date	Measures
July 2019	Species inventory Total aboveground biomass (g)
November 2019	Species inventory Species contribution (%) to total biomass ($\sum_{\text{all species}} = 100$) Total aboveground biomass (g)
June 2020	Species inventory Species contribution to vegetation cover (%) ($\sum_{\text{all species}} > 100$) Coefficient attribution: 1: <1% 2: 1-5% 3: 5-15% 4: 15-25% 5: 25-50% 6: 50-75% 7: 75-100% Total vegetation cover (%) Litter cover (%) Bare soil cover (%) Total aboveground biomass (g)

B.7 | Data analyses (TDV experiment)

Community trajectories

To visualize the influence of sown community type on species composition dynamics over time, we ordinated species compositions using non-metric multidimensional scaling (NMDS) based on species presence/absence recorded during the three harvests (July 2019, November 2019 and June 2020), depending on sown community type. We used data from plots with communities seeded by hand, with eight replicates from four plots for all community types except for B–1SP–D2, B–3SP–D2, B–9 SP–D2 and Control for which we had six replicates from three plots. To recompose community trajectories, we calculated mean scores values for each sown community type and each harvest date. The analysis was performed using the function 'metaMDS' in the 'vegan' package (Oksanen et al. 2007)

Community structure

To visualize the influence of sown community type on community structure, we ordinated species abundances using non-metric multidimensional scaling (NMDS) using data of June 2020 based on cover coefficients (Table A2), depending on sown community type. We used data from plots with communities seeded by hand, with eight replicates from four plots for all community types except for B–1SP–D2, B–3SP–D2, B–9 SP–D2 and Control for which we had six replicates from three plots. The analysis was performed using the function 'metaMDS' in the 'vegan' package (Oksanen et al. 2007).

Seeding method

To visualize the influence of the seeding method (by hand *vs.* hydroseeding) on community structure, we ordinated species abundance of the sown community types A-1SP-D1, A-1SP-D2, A-9SP-D1 and A-9SP-D2 using non-metric multidimensional scaling (NMDS) using data of June 2020 based on cover coefficients (Table A2), depending on the seeding method. We had eight replicates from four plots for each sown community type and seeding method. The analysis was performed using the function 'metaMDS' in the 'vegan' package (Oksanen et al. 2007).

C | Results and discussion

C.1 | Soil analyses

Soil of the TDV site was characterized by a clay loam texture composed of 65% of silt while soil of the PSJ site was characterized by a sandy soil texture composed of 65% of coarse sand (Supplementary material; Table SA.2). Both soils were alkaline (pH_{TDV}=8.2 pH_{PSJ}=8.3) and contained high total Ca (Ca_{TDV}=31% and Ca_{PSJ} =22.5%) and and CaO contents (CaO_{TDV}=10.3 g/kg and CaO_{PSJ}=7.8 g/kg), intermediate N (N_{TDV}=1.7 g/kg and N_{PSJ} =0.7 g/kg) and low P_2O_5 (P_2O_{5TDV}=42.8 mg/kg and P_2O_{5PSJ}=54.3) and K_2O levels (K_2O_{TDV}=198.5 mg/kg and K_2O_{PSJ}=66.0 mg/kg). Soil of the TDV site was richer in total organic matter (TOM_{TDV}=3.1%) than the PSJ site (TOM_{PSJ}=1.1%). Soil of the TDV site also contained particularly elevated levels of MgO (382.5 mg/kg) and Na_2O (159 mg/kg). In summary, the two sites differ by their soil texture, soil organic matter, magnesium oxide and sodium contents. Unfortunately, because *C. album* strongly colonized the PSJ site in early spring 2019 and the subsequent abandonment of this experimental site (Figure A.6; see B.6), we were not able to test whether these differences in soil conditions influenced sowing success and invasibility. The rest of the results will discuss the results of the TDV experiment only.

C.2 | Invasion resistance (TDV experiment)

We did not recorded any sown invasive species emergence during the two first growing seasons although a high germination rate was observed in controlled conditions. Therefore, we were not able to evaluate early invasion resistance.

The absence of invasive species emergence may be due to **(1)** unfavorable abiotic conditions for seedling emergence, notably the particularly dry spring conditions, **(2)** competition with established native species, and/or **(3)** seed predation or disease. An influence of sowing on invasive species seedling emergence is unlikely since no emergence was recorded in unsown control plots.

C.3 | Vegetation survey (TDV experiment)

Species inventory

The three vegetation surveys carried out in June 2019, November 2019 and June 2020 allowed us to record 61 taxa with 43 identified at the species level, among which 30 were not sown (Supplementary Material; Table SA.3). This result indicates a strong emergence of species from the remaining seed bank.

Influence of initial seeding on vegetation

Initial seeding affected species richness (Figure A.7), the evolution of species composition over time (Figure A.8), and final community structure in the second year (Figure A.9), but did not clearly influenced aboveground biomass production of the communities compared to the unsown control plots (Figure A.10).

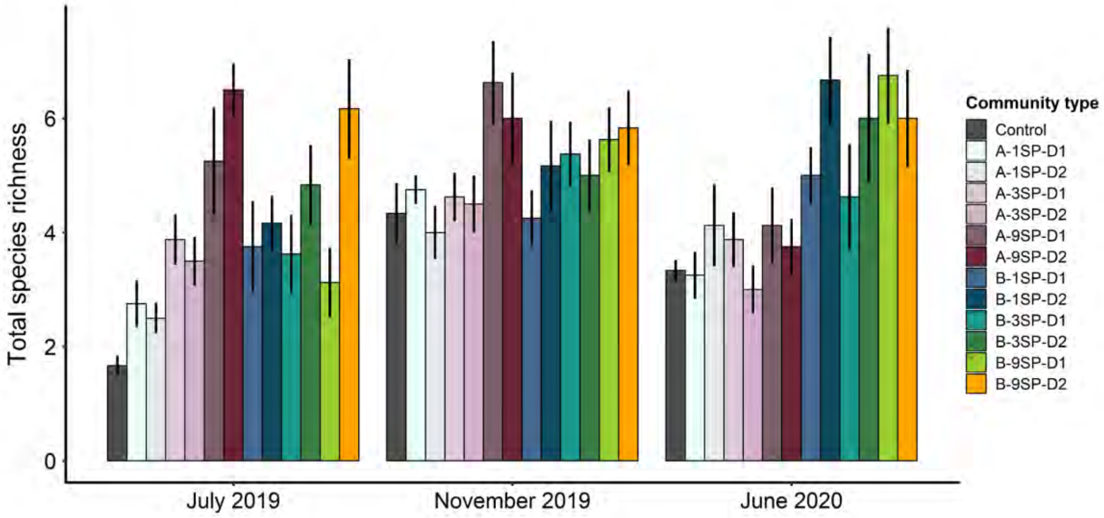

Figure A.7 Species richness (mean per 25 × 25 cm quadrat ±SE) of the communities monitored in the TDV experiment for the three harvests (July 2019, November 2019 and June 2020) depending on community type (see *Table A1* for code names).

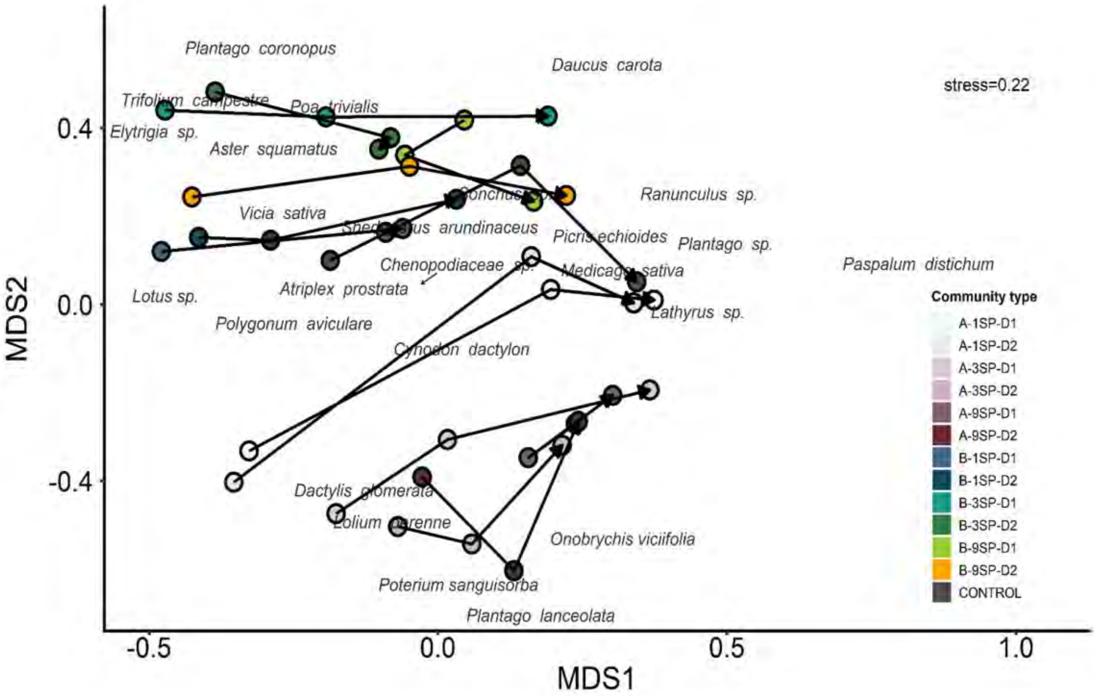

Figure A.8 Trajectories of communities based on non-metric multi-dimensional scaling (NMDS) ordination of species presence/absence (TDV site). The figure shows the two-dimensional solution exhibiting the least stress (0.22). Each community type (see *Table A1* for code names) is associated to a specific color. The trajectory of each community type is represented by the circles (means of the NMDS axes for each harvest – July 2019, November 2019 and June 2020) linked by arrows. Species occurring at least ten times during the surveys are depicted.

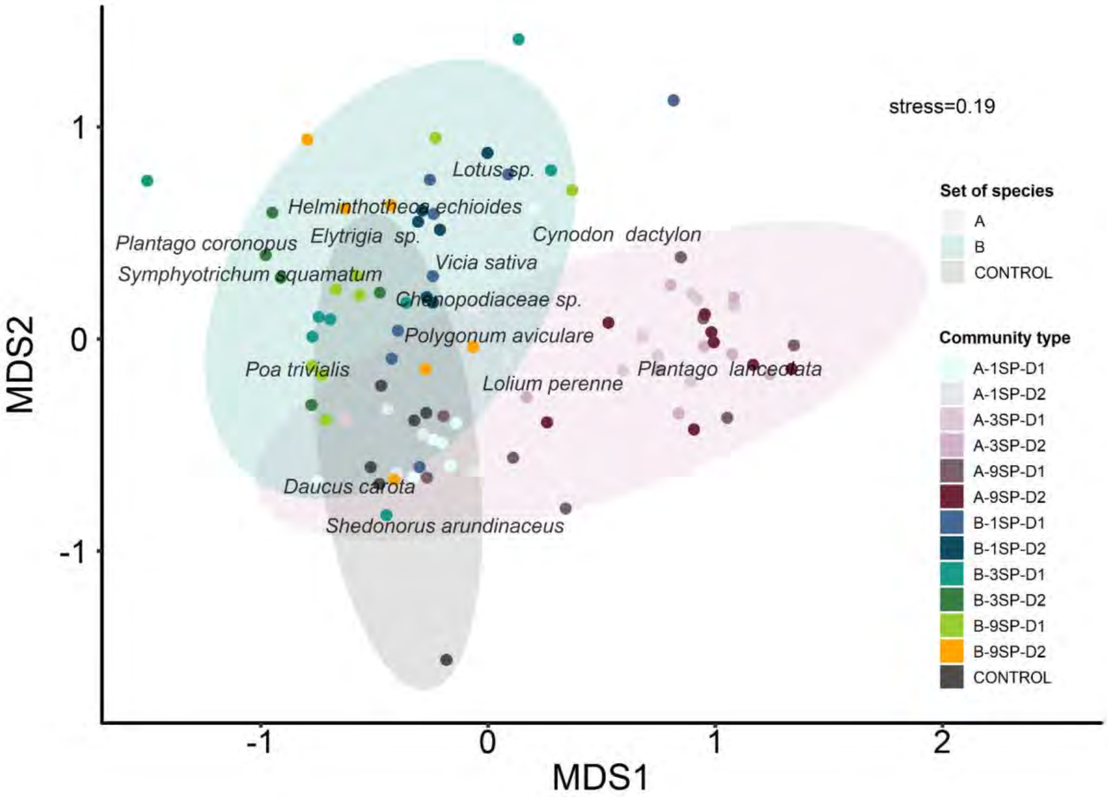

Figure A.9 Results of the non-metric multi-dimensional scaling (NMDS) ordination of species abundance in June 2020 (TDV site). The figure shows the two-dimensional solution exhibiting the least stress (0.19). Each community type (see *Table A1* for code names) is associated to a specific color, with each point representing a replicate. Ellipses represent the two set of sown species (see *Table A1* for code names). Species occurring at least ten times during the survey are depicted.

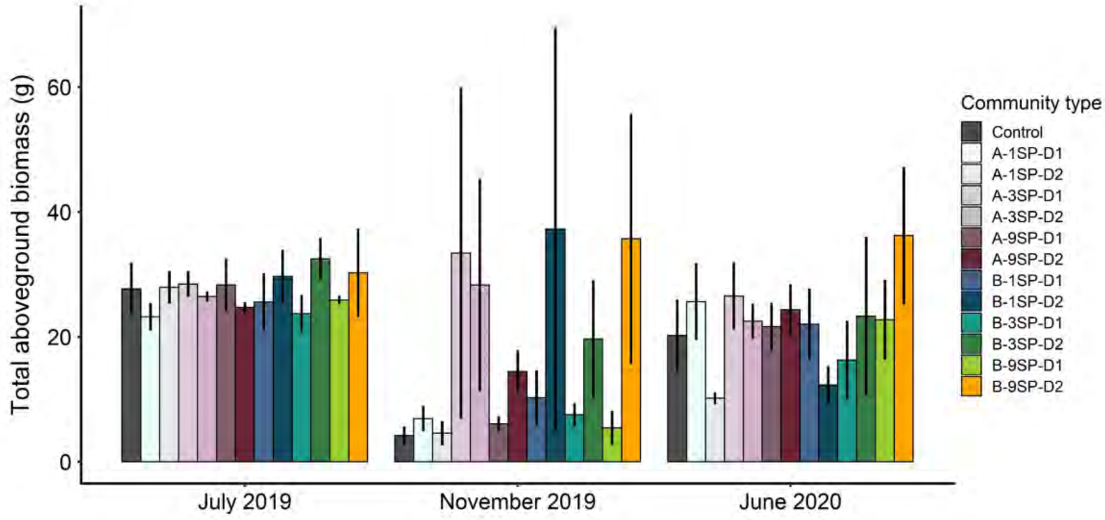

Figure A.10 Total aboveground biomass (mean per 25 × 25 cm quadrat ±SE) of the communities in the TDV experiment for the three harvests (July 2019, November 2019 and June 2020) depending on community type (see *Table A1* for code names).

Sown species identity influenced community structuring, while density had a limited influence

The set of species sown ((**A**) or (**B**); Table A1), and at a lesser extent, species richness (one, three or nine species; Table A1) had a noticeable effect on community composition and structure while the influence of seeding density seemed limited (Figures A.8, A.9), which is in accordance with the results of Chapter 3. Numerous unsown species established during the two growing seasons (Supplementary material; Table SA.3). Some ruderal, fast-growing species, such as *Helminthotheca echioides*, *Polygonum aviculare* and thistles (mostly *Cirsium* sp.), emerged abundantly from the seedbank (a dispersal from the surroundings is less likely in view of the rapid and profuse emergence) and became rapidly dominant. We consequently removed the largest individuals to favor the establishment of sown species. This result points out how the presence of a large seed bank could potentially hamper the successful establishment of desired species.

The results indicate a variable establishment success of the sown species. Communities that received three or nine species of the species set (**A**) (i.e. A-3SP-D1, A-3SP-D2, A-3SP-D1, A-9SP-D1, A-9SP-D2) showed close, converging trajectories (Figure A.8) and structure in the second year after sowing (Figure A.9), most likely due to the high occurrence of the sown species *D. glomerata*, *L. perenne*, *O. viciifolia*, *P. lanceolata* and *P. sanguisorba*. This result supports that these species may have successfully established from seed (i.e. only *P. lanceolata* was recorded on the site before sowing), which influenced community structuring. The convergence of communities sown with *L. perenne* (A-1SP-D1 and A-1SP-D2) and unsown control communities suggests however that the initial influence of *L. perenne* seeding did not persisted much over time. The composition of all communities globally tended to converge over time (Figure A.8), which would suggest that initial sowing advantage faded with time (Young et al. 2016).

Results also suggest a greater establishment success of species from the species set (**A**) compared with species of the set (**B**), since **(1)** (**B**) community types showed an overall closer trajectory (Figure A.8) and structure (Figure A.9) to unsown control communities than (**A**) community types, and **(2)** we found a low occurrence of numerous (**B**) species (Figure A.9). This is in agreement with our hypothesis that species better adapted to clayish soil will better establish. However, the lack of comparison with the PSJ site does not allow us to draw robust conclusions: these species may have also better established in other soil conditions, in which case their success would not be due to a better adaptation to soil conditions.

The seeding method (by hand or hydroseeding) did not affected community structure

Our results demonstrate that seeding method (by hand or hydroseeding) did not affected community structure (Figure A.11). The use of hydroseeding may particularly influence vegetation growth when containing fertilizers and mulch composed of cellulose fiber, which hold moisture to allow the proper and rapid germination of sprayed seeds (Parsakhoo et al.

2018). Here, the revegetation mix was composed of water and seeds only, which may explain the weak difference with a hand sowing.

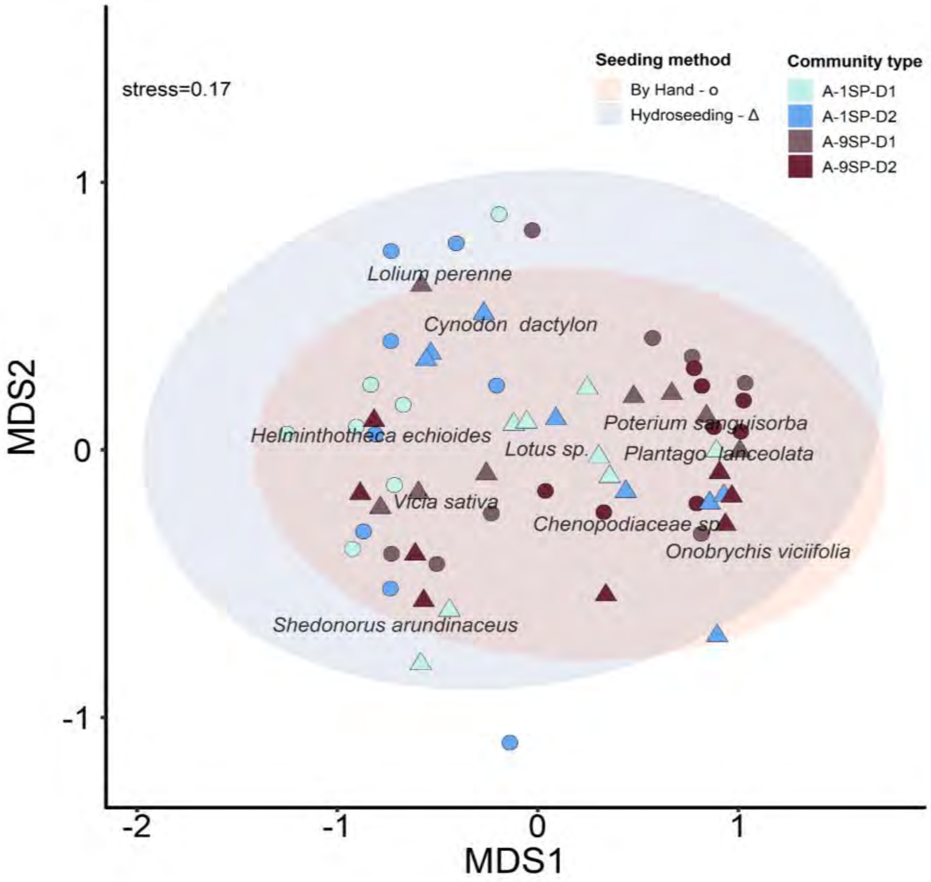

Figure A.11 Results of the non-metric multi-dimensional scaling (NMDS) ordination of species abundance in June 2020 (TDV site) depending on community type and seeding method. The figure shows the two-dimensional solution exhibiting the least stress (0.17). Each community type (see *Table A1* for code names) is associated to a specific color, with each dot representing a replicate. The two seeding methods are indicated by different symbols. Ellipses represent the two seeding methods. Species occurring at least ten times during the survey are depicted.

D | Conclusions and perspectives

We can reasonably suggest that the absence of seedling emergence of the sown invasive species (as well as the variable establishment success of sown species) was at least partly due to the very dry conditions encountered at the time of sowing and that lasted several months. Guaranteeing the success of a revegetation-based strategy in environments subjected to strong inter-annual variabilities in temperature and rainfall (such as in Mediterranean areas), may thus prove to be challenging.

The high species emergence from the seedbank completely cancelled the effect of sowing in the PSJ site (Figure A.6; see B.6) and may have buffered differences between community types in the TDV site (see below). Civil works such as roadside construction generally involve deep soil disturbances (e.g. removal of thick soil layers, substrate addition), which can potentially dilute the natural seed bank. On construction sites, a lower emergence from the seed bank is therefore expected, implying that **(1)** active revegetation is all the more necessary to limit invasion, and **(2)** a greater establishment of the sown species is more likely.

The results of the TDV experiment overall support that initial seed addition, and especially the identity of the species sown, influenced community structuring over two growing seasons. A variable establishment success and persistence of initial sowing advantage occurred between species, generating differences in community structuring. Species richness and aboveground productivity were however less impacted by sowing, reflecting the successful establishment of numerous unsown species. The high occurrence of unsown species producing large individuals (field observation), in particular *H. echioides* (recorded in 63% of all quadrats all surveys combined) may have buffered the differences between community types on aboveground biomass production.

Finally, long-term studies assessing the effect of colonization history on community structuring are rare. Maintaining vegetation surveys for several years would improve our knowledge about long-term effects of initial sowing.

Hypotheses on invasion resistance

The results of summer harvests in the first and the second years indicate a low difference in aboveground biomass production between sown and unsown control communities (Figure A.10). On the assumption that increasing total biomass enhances early invasion resistance (e.g. Lulow 2006; Rinella et al. 2007; Yannelli Lucero et al. 2020), we could expect here a weak effect of sowing on early invasion success. However, unsown control communities were dominated by the annual weedy species *H. echioides* (recorded in 77% of the quadrats, and displaying a median cover of 75 – 100% in June 2020), which dominance may decrease over time. Therefore, sown communities displaying a much lower cover of *H. echioides* (median cover 5 – 15 %) may, in the longer term, offer a greater biomass stability and invasion resistance.

Species richness tended to be lower in unsown control communities than in most sown communities (Figure A.7), suggesting that some sown species successfully established and/or that seeding facilitated the recruitment of unsown species. Several studies associate a higher species richness to a greater invasion resistance (e.g. Byun et al. 2013; Connolly et al. 2017; Levine & D'Antonio 1999; Tilman 1997). Following this hypothesis, sown communities may present a stronger resistance to invasion.

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Supplementary material

Table SA.1 Species inventory in TDV and PSJ site before plowing (May 05, 2018).

TDV	PSJ
Bromus hordeaceus L.	*Ambrosia psilostachya* DC.
Capsella bursa-pastoris subsp. *bursa-pastoris* (L.) Medik.	*Anisantha diandra* (Roth) Tutin ex Tzvelev
*Carex otrub*ae Podp.	*Anisantha sterilis* (L.) Nevski
Cerastium glomeratum Thuill.	*Arenaria leptoclados* (Rchb.) Guss.
Crepis vesicaria subsp. *taraxacifolia* (Thuill.) Thell. ex Schinz & R.Keller	*Avena barbata* Pott ex Link
Cynodon dactylon (L.) Pers.	*Bromus hordeaceus* L.
Daucus carota L.	*Catapodium rigidum* (L.) C.E.Hubb.
Dittrichia viscosa (L.) Greuter	*Cerastium pumilum* Curtis
Ervum gracile (Loisel.) DC.	*Cerastium semidecandrum* L.
Geranium dissectum L.	*Convolvulus arvensis* L.
Helminthotheca echioides (L.) Holub	*Cynodon dactylon* (L.) Pers.
Hirschfeldia incana (L.) Lagr.-Foss.	*Fallopia convolvulus* (L.) Á.Löve
*Holcus lan*atus L.	*Hordeum murinum* subsp. *murinum* L.
Hordeum murinum subsp. *leporinum* (Link) Arcang.	*Lagurus ovatus* L.
Lactuca L.	*Lathyrus cicera* L.
Lotus corniculatus L.	*Lolium rigidum* Gaudin
Malva nicaeensis All.	*Lysimachia arvensis* (L.) U.Manns & Anderb.
Medicago polymorpha L.	*Medicago sati*va subsp. *sativa* L.
Medicago sativa L.	*Papaver rhoeas* L.
Melilotus indicus (L.) All.	*Plantago coronopus* L.
Papaver rhoeas L.	*Plantago lanceolata* L.
*Picris hieracioide*s subsp. *hieracioides* L.	*Poa annua* L.
Plantago coronopus L.	*Polygonum aviculare* L.
Plantago lanceolata L.	*Rumex crispus* L.
Poa annua L.	*Silene conica* L.
Poa trivialis L.	*Silene latifolia* Poir.
Podospermum laciniatum (L.) DC.	*Silene vulgaris* (Moench) Garcke
Polygonum aviculare L.	*Stellaria pallida* (Dumort.) Piré
Ranunculus bulbosus L.	*Trifolium cam*pestre Schreb.
*Ranunculus sardou*s Crantz	*Trifolium nigrescens* Viv.
Rumex crispus L.	*Verbascum sinuatum* L.
Schedonorus arundinaceus (Schreb.) Dumort.	*Veronica arvensis* L.
Senecio vulgaris subsp. *vulgaris* L.	*Vulpia ciliata* Dumort.
Silybum marianum (L.) Gaertn.	
Sonchus asper (L.) Hill	
Symphyotrichum squamatum (Spreng.) G.L.Nesom	
Trifolium campestre Schreb.	
Trifolium pratense L.	
Trifolium repens L.	
Trifolium squamosum L.	
Trigonella officinalis (L.) Coulot & Rabaute	
Verbena officinalis L.	
*Vicia angu*stifolia L.	

Table SA.2 Results of soil analyses for the TDV and PSJ sites. Values refer to means of the four samples ±SD.

	Soil texture				
	Clay (%)	Fine silt (%)	Coarse silt (%)	Fine sand (%)	Coarse sand (%)
TDV	24.33±0.87	40.95±0.58	24.83±1.64	8.78±2.24	1.13±0.1
PSJ	3.25±0.88	8±0.73	8.8±3.08	15.1±1.16	64.88±5.57

	Soil chemistry											
	pH	Ca tot. (%)	Organic matter tot. (%)	P_2O_5 (mg/kg)	K_2O (mg/kg)	MgO (mg/kg)	CaO (g/Kg)	Na_2O (mg/kg)	N tot. (g/Kg)	C tot (g/kg)	NO_3^- (mg/kg)	NH_4^+ (mg/kg)
TDV	8.2±0.1	31.0±0.8	3.1±0.3	42.8±4.7	198.25±26.9	382.5±21.8	10.3±0.4	159±22.05	1.7±0.2	17.89±1.64	12.0±0.5	4.6±0.4
PSJ	8.3±0.1	22.5±0.6	1.1±0.3	54.3±2.9	66.0±10.7	88.5±14.3	7.8±0.3	12±1.15	0.7±0.1	6.5±1.55	10.6±2.9	2.5±0.2

Table SA.3 Species inventory carried out in TDV (pooled inventories of July 2019, November 2019 and June 2020) and PSJ (April 22, 2019) sites.

TAXA
Aeluropus littoralis (Gouan) Parl., 1850
Anthyllis vulneraria L., 1753
Aster sp.
Symphyotrichum squamatum (Spreng.) G.L. Nesom, 1995
Atriplex prostrata Boucher ex DC., 1805
Beta vulgaris subsp. *maritima* (L.) Arcang., 1882
Bromus hordeaceus L., 1753
Bupleurum sp.
Chenopodiaceae sp.
Cirsium arvense (L.) Scop., 1772
Cirsium sp.
Cirsium vulgare (Savi) Ten., 1838
Convolvulus arvensis L., 1753
Cynodon dactylon (L.) Pers., 1805
Dactylis glomerata L., 1753
Daucus carota L., 1753
Elytrigia sp.
Geranium molle., 1753
Helminthotheca echioides (L.) Holub, 1973
Hordeum marinum Huds., 1778
Lactuca saligna L., 1753
Lactuca serriola L., 1756
Lactuca sp.
Lathyrus sp.
Lepidium draba L., 1753
Lolium perenne L., 1753
Lotus sp.
Malva nicaaensis All., 1785
Malva sylvestris L., 1753
Medicago polymorpha L., 1753
Medicago sativa L., 1753
Medicago sp.
Melilotus sp.
Onobrychis viciifolia Scop., 1772
Paspalum distichum L., 1759
Picris hieracioides L., 1753
Plantago coronopus L., 1753
Plantago lanceolata L., 1753
Plantago sp.
Poa trivialis L., 1753
Polygonum aviculare L., 1753
Poterium sanguisorba L., 1753
Ranunculus sp.
Rumex crispus L., 1753
Rumex sp.
Schedonorus arundinaceus (Schreb.) Dumort., 1824
Senecio sp.
Sinapis arvensis L., 1753
Sonchus asper (L.) Hill, 1769
Sonchus oleacerus L., 1753
Sonchus sp.
Trifolium campestre schreb., 1804
Trifolium fragiferum L., 1753
Trifolium squamosum L., 1759
Trifolium pratense L., 1753
Trifolium repens L., 1753
Trifolium sp.
Trigonella esculenta Willd., 1809
Vicia sativa L., 1753
Vicia sp.

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