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Review

Priority effects: Emerging principles for invasive plant species management

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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 effects-based restoration strategies and define future research questions that need to be addressed to test and improve these strategies.

1. Introduction

The vast literature on biological invasions since Elton’s seminal work (1958) testifies to the complexity of understanding the processes underlying invasion success (Levine et al., 2003; Hayes and Barry, 2008; Simberloff, 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; Richardson et al., 2000; Mooney, 2005) in acquiring resources has long been considered the critical mechanism determining invasion success (Sax and Brown, 2000; Vila and Weiner, 2004; Pyšek and Richardson, 2008). However, invasive species performance also appears to depend on the physical and biological conditions encountered in the introduced range: resource availability and fluctuation (Davis et al., 2000; Shea and Chesson, 2002; Firn et al., 2010; D’Antonio et al., 2017), multi-trophic interactions involving enemies (Mitchell et al., 2006), and resident plant community composition (Levine and D’Antonio, 1999; Fridley et al., 2007). In addition to the deterministic explanations, stochastic dispersal and historical processes also play a crucial role in determining invasion success (Hubbell, 2001; Kolar and

Lodge, 2001; Chase, 2003; Lockwood et al., 2005; Dickson et al., 2012; 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 and 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 (Chase, 2003; Aronson and Galatowitsch, 2008; Körner et al., 2008; Young et al., 2016) and can be implicated in invasion success (Seabloom et al., 2003; Corbin and D’Antonio, 2004; Abraham et al., 2009; Grman and Suding, 2010). One mechanism prevalent in priority effects is resource preemption (Young et al., 2001; Fukami, 2015): 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 (Ross and Harper, 1972; Chase, 2010). 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 (Kourtev et al., 2002; Mangla and Callaway, 2008; Corbin and D’Antonio, 2012). 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 (Hobbs and Huenneke, 1992; Davis et al., 2000). Because of the well-recognized issues raised by invasive species (i.e. human health, crop production, native biodiversity, economic; Vitousek et al., 1997; Kolar and Lodge, 2001; Simberloff, 2013) 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 (Middleton et al., 2010; Hazelton et al., 2014; Byun and Lee, 2017), results are often far from satisfactory (Kellogg and Bridgham, 2002). This has notably been attributed to a failure to account for priority effects, which may play a decisive role in restoration success (Young et al., 2001; Temperton, 2004; Grman and Suding, 2010; Wilsey et al., 2015). Priority effects appear to offer a cost-effective approach to combatting invasive plant species (Chadwell and 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. Dealing with invasive species priority effects

2.1. Priority effects are particularly advantageous to invasive species

Phenological differences between invasive and native species can substantially contribute to invasion success (Wolkovich and 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 and Rice, 1997; Seabloom et al., 2003; Munter, 2008; Wolkovich and Cleland, 2011), but others also profit of being active late in the season (e.g. in California, the invasiveness of *Centaurea silvestris* arises from extending its growing season into the summer when competition from winter annual vegetation for soil water is minimal; Gerlach and Rice, 2003).

Several studies reported that invasive species generate stronger priority effects than natives (Dickson et al., 2012; Wilsey et al., 2015; Stuble and Souza, 2016, but see Cleland et al., 2015). The generally higher growth rate of invasive species (Rejmánek and Richardson, 1996; Reynolds et al., 2001; Grotkopp et al., 2010; Marushia et al., 2010; Dawson et al., 2011) was suggested to underlie this advantage (Stevens and Fehmi, 2009; Dickson et al., 2012). 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 and Rice, 1999; Perry et al., 2003; Ejrnaes et al., 2006). 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 and D'Antonio, 2012). Modifications such as: (1) shifts in nutrient cycling (Ehrenfeld, 2003; Marchante et al., 2008; Flinn et al., 2017) and soil salinity (Novoa et al., 2013), (2) changes in soil microbial communities including pathogens and mycorrhizal fungi (Kourtev et al., 2002; Hawkes et al., 2006; Mangla and Callaway, 2008; Stinson et al., 2006; Kardol et al., 2007; Lorenzo et al., 2010), and (3) the release of allelochemicals (Bais et al., 2003; Stinson et al., 2006; Milchunas et al., 2011; Grove et al., 2012) can all generate priority

137 effects enhancing invasive species performance and inhibiting native plant species (Fig. 1A;
 138 Reinhart and Callaway, 2006; Stinson et al., 2006; van der Putten et al., 2013; Rodriguez-
 139 Echeverria et al., 2013; Meisner et al., 2014). Such invader-mediated soil modifications can
 140 persist after the causal invasive species is removed or dies (Corbin and D’Antonio, 2012;
 141 Hacker and Dethier, 2009; Hamman and Hawkes, 2013), and are commonly termed “soil
 142 legacies” (Fig. 1B).

143 **Fig. 1.** Mechanisms driving the consequences of priority effects when the plant individual is present (A), or has been
 144 removed or died (B). (A) Early arriving species can limit colonization success of subsequent colonizing species by
 145 gaining a size-related competitive advantage, by generating positive plant-soil feedbacks improving its own
 146 performance, and by modifying soil conditions. Priority effects are asymmetric between native and invasive species, so
 147 that invasive species are less impacted by arriving late compared with natives. (B) Plants can also generate priority
 148 effects through soil legacies after they were removed or died, that can impact subsequent colonization. While, for many
 149 invasive species, persistent soil legacies have been reported to hinder invasive recolonization, little is known about how
 150 native species soil legacies could limit invasive species establishment. Note that Grman and Suding (2010) found no
 151 impact of native species legacies on invasive species success.

152 2.2. Countering invasive species priority effects

153 When it comes to decrease the competitive dominance of an invasive plant species, it
 154 is essential to look for abiotic conditions to determine what actions need to be undertaken. In
 155 environments with high nutrient resource and water availability, the presence of invasive
 156 species could particularly hinder restoration of native communities because of their high
 157 competitive abilities (Cox and Allen, 2008; Abraham et al., 2009; Grman and Suding, 2010).
 158 Countering invasive species competitive advantage can be achieved by applying intensive
 159 management techniques to reduce invasive species cover (i.e. herbicide applications,

mechanical removal; Fig. 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 (Fig. 2; D'Antonio et al., 2017). Common methods to decrease nondesirable species seed bank include topsoil removal (Hölzel and 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 and Young, 2016). Prescribed burns for fire-prone species or supplying water are two techniques promoting germination (Ooi, 2007; Wolf and Young, 2016) that could be used to flush invasive plant species and tackle seasonal priority advantage early in the season (Wolkovich and Cleland, 2011; Wainwright et al., 2012; Wilsey et al., 2015). 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 (Fig. 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 (Suding et al., 2004; Ehrenfeld et al., 2005; Corbin and D'Antonio, 2012; Jordan et al., 2012; van der Putten et al., 2013), and often favor secondary invasions (Dickie et al., 2014; Grove et al., 2015; Yelenik and 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 (Fig. 2). Soil legacies can be mitigated by adjusting soil properties, typically via topsoil removal or soil amendments (Kulmatiski and Beard, 2006; Buisson et al., 2008; 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 and 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 headstart 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 (Jordan et al., 2008; Eviner and Hawkes, 2012; Leger et al., 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 (Bezemer et al., 2006; Yelenik et al., 2007; Bardgett and Wardle, 2010). Furthermore, their persistence depends on characteristics of the invaded ecosystem (e.g. soil mineralization rates; Stock et al., 1995), on their nature (Levine et al., 2003; Corbin and D'Antonio, 2012), and on the duration of invasion (Marchante et al., 2008; Kulmatiski and Beard, 2011). 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 and Jeffries, 2001). Long-term studies suggest, however, that invasion impacts on ecosystems, such as increased nitrogen levels, can shift over time (Yelenik and 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 (Fig. 2; Marchante et al., 2008; Kulmatiski and Beard, 2011). A

228 better understanding of how invasive species induce strong and persistent soil legacies in the
 229 habitat they commonly invade would reduce the need for complex and expensive analyses,
 230 facilitating development of effective restoration strategies. Cost-effective methods, such as
 231 native species germination or survival tests on soil with potential legacies should be
 232 developed to rapidly assess their extent.

233 **Fig. 2.** Decision support to counter invasive plant species priority effects. When invasive species facilitate the
 234 establishment of natives (e.g. in some harsh environments), they should not be removed and can be used as nurse
 235 species for restored species. Conversely, when invasive species hinder native species establishment (e.g. in some fertile
 236 and stable environments), it is essential to decrease their abundance and prevent secondary invasions, notably via
 237 removal and seed bank reduction. After removal, soil legacies generated by invasive species can lower restoration
 238 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).

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 and Meyerson, 2002). In some cases, invasive species are used as nurse plants to facilitate the establishment of native species (Fig. 2; Becerra and Montenegro, 2013; Hanslin and 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 and 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 and Vitousek, 2007).

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 (Lenz and Facelli, 2003; Cavieres et al., 2005; 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 and 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 (Huenneke et al., 1990; Maron and Connors, 1996; Corbin and D'Antonio, 2004b). 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 (Perry and Galatowitsch, 2006; Buckley, 2008; Middleton et al., 2010; Byun et al., 2013; Pearson et al., 2016). Environmental conditions influence the magnitude of priority effects (Collinge and Ray, 2009; Kardol et al., 2013; Symons and 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 (Dickson et al., 2012; von Gillhaussen et al., 2014; Cleland et al., 2015; Wilsey et al., 2015; Stuble and Souza, 2016), invasive species being less negatively impacted by arriving late than native species (Fig. 1A; Wilsey et al., 2015; Stuble and Souza, 2016), 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 and Fukami, 2014), and (3) the impact a species has on nonresource components of the environment (Bever, 2003; Levine et al., 2004; Goldstein and Suding, 2014). 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 Figure A1 in Appendix for summary).

3.1. Increasing resource preemption

3.1.1. 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 and Suding, 2010; Vaughn and 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 effect (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 effects-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 and Fehmi, 2009), and a particular attention must be paid 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.

3.1.2. *Manipulate species composition and density*

The resource competition model (Tilman, 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 and 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; D'Antonio et al., 2001; Corbin and D'Antonio, 2004a; 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 and Edwards, 2006; Gioria and Osborne, 2014).

At small scale (10m^2 or less), many studies support the widespread assumption that species diversity confers invasion resistance (Tilman, 1997; Levine and D'Antonio, 1999; Levine et al., 2004; Carter and Blair, 2012), due to fuller use of resources by resident species ("complementarity effect"; Robinson et al., 1995; Lavorel et al., 1999; Levine and D'Antonio, 1999; Larson et al., 2013), 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": Kennedy et al., 2002; Wardle, 2001; Lavorel et al., 1999; Goslee et al., 2013). 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, 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 and 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 (Gerhardt and Collinge, 2007; Carter and Blair, 2012; Vaughn and 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.m²). 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.

3.2. Increasing niche overlap: Applying limiting similarity

Niche overlap, referring to resource use similarity between co-occurring species independent of their rate of resource consumption (Pianka, 1974; Petraitis, 1989), has been hypothesized to influence invasion-resistance (Abrams, 1983; Funk et al., 2008) and more recently priority effects (Vannette and 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 (Symstad, 2000; Emery, 2007; Turnbull et al., 2005; Price and Pärtel, 2013), 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 (Drenovsky and James, 2010; Cleland et al., 2013). 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.

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 and 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; Milchunas et al., 2011; Jabran et al., 2015; Jabran, 2017). The establishment of native allelopathic species can directly reduce the biomass of the target invasive species (Callaway and 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 and 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 and Bossdorf, 2004), community density (Weidenhamer et al., 1989), climate conditions (May and Ash, 1990; Blair et al., 2006), and substrate characteristics (Parepa and 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 (Maron and Vilà, 2001; Levine et al., 2004), sometimes contributing (i.e. invasive plants are maladapted to deter consumption by native herbivores; Parker and Hay, 2005; Morrison and Hay, 2011; Petruzzella et al., 2017; Zhang et al., 2018) or not (i.e. native herbivores are maladapted to consume invasive plants; Keane and Crawley, 2002; Liu and Stiling, 2006; Xiong et al., 2008) to biotic resistance. However, because herbivores have been reported to create disturbances facilitating the establishment of invasive species (Mack, 1989; Hobbs and Huenneke, 1992), and because young restored native species may be negatively impacted by trampling (Clear-Hill and 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 and Read, 2008), often strongly influence plant growth and reproduction (Koide and Dickie, 2002), plant community structure (van der Heijden et al., 1998; Hartnett and Wilson, 1999, 2002), and invasion success (Klironomos, 2002; Callaway et al., 2004). Soil inoculation of arbuscular mycorrhizal fungi can reduce the performance of agricultural non-mycorrhizal weeds (Jordan et al., 2000; Vátovec et al., 2005; Rinaudo et al., 2010; Veiga et al., 2011), raising a potential application in managing non-hosts invasive species (e.g. from Chenopodiaceae and Cruciferae families; Wang and 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 and 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 and Read, 2008), 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 (Veiga et al., 2011; Grutters et al., 2017; Zhang et al., 2018), it may be relevant to develop non-resource-based restoration strategies for the most noxious invasive species.

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.

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Appendix A. Supplementary data

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