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4 **Review**

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6 **Priority effects: Emerging principles for invasive plant species management**

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19 **Keywords:** Invasion resistance; Restoration; Community assembly history; Historical contingency;
20 Order of arrival; Legacy

21
22 **Abstract**

23 Many anthropic activities generate soil disturbances, favoring competitive, fast
24 growing invasive plant species at the expense of natives. Active restoration of invasion-
25 resistant plant communities is increasingly recognized as a relevant strategy to combat
26 invasive plant colonization in disturbed areas, but results are often unsatisfying. Historical
27 effects, referred as “priority effects” (i.e. the effects generated by the order in which species
28 arrive at a local site), can have a major role in community assembly and invasion success
29 because they involve early colonists altering the performance of later colonists. Taking these
30 priority effects into account in restoration projects is emerging as a relevant way to improve
31 native species restoration success and prevent invasion. The present review discusses two
32 strategies considering priority effects that would help to achieve the classic restoration goal of
33 “more natives, less invasives”. The first strategy relies on tackling priority effects of invasive
34 plants using different management options adapted to local environmental conditions,
35 including removal, reduction of propagule sources, or mitigation of soil legacies. Indeed,
36 invasive plants often generate strong priority effects providing themselves a substantial

37 competitive advantage through early emergence and quick growth, but also self-induced soil
38 modifications that can persist after their removal or death, commonly termed “soil legacies”.
39 In fertile and stable conditions, the reduction of invasive species priority effects must be
40 coupled with the restoration of an invasion-resistant native plant cover to avoid reinvasion and
41 secondary invasions. The second strategy is to bring about situations in which the restored
42 native species are more likely to exert strong priority effects, decreasing invasion success. For
43 this purpose, we sketch possible options open to restorationists based on resource or non-
44 resource mechanisms. First, we discuss ways to maximize resource preemption by extending
45 the time advance given to restored native species and manipulating restored species
46 characteristics. Second, we consider the potential effect of increasing niche overlap between
47 native and invasive species. Third, we introduce the potential manipulations of non-resource
48 mechanisms, such as allelopathy, herbivory, disease, or the presence of mycorrhizae, to
49 increase priority effects. This review incorporates recent research on priority effects to draw
50 the outlines of priority effects-based restoration strategies and define future research questions
51 that need to be addressed to test and improve these strategies.

52 **1. Introduction**

53 The vast literature on biological invasions since Elton’s seminal work (1958) testifies
54 to the complexity of understanding the processes underlying invasion success (Levine et al.,
55 2003; Hayes and Barry, 2008; Simberloff, 2013). According to deterministic theories, the
56 outcome of an invasion depends on interactions between the invader and the physical and
57 biological characteristics of the recipient environment (Lonsdale, 1999; Williamson, 1999).
58 The intrinsic competitive superiority of invasive plant species (i.e. species introduced outside
59 of their distribution areas which are able to grow and proliferate to become an autonomous
60 viable population, and whose expansion can negatively impact local species and ecosystems;
61 Richardson et al., 2000; Mooney, 2005) in acquiring resources has long been considered the
62 critical mechanism determining invasion success (Sax and Brown, 2000; Vila and Weiner,
63 2004; Pyšek and Richardson, 2008). However, invasive species performance also appears to
64 depend on the physical and biological conditions encountered in the introduced range:
65 resource availability and fluctuation (Davis et al., 2000; Shea and Chesson, 2002; Firn et al.,
66 2010; D’Antonio et al., 2017), multi-trophic interactions involving enemies (Mitchell et al.,
67 2006), and resident plant community composition (Levine and D’Antonio, 1999; Fridley et
68 al., 2007). In addition to the deterministic explanations, stochastic dispersal and historical
69 processes also play a crucial role in determining invasion success (Hubbell, 2001; Kolar and

70 Lodge, 2001; Chase, 2003; Lockwood et al., 2005; Dickson et al., 2012; Wilsey et al., 2015;
71 Young et al., 2015).

72 Stochastic colonization combined with deterministic interactions between early and
73 later colonizing species lead to priority effects (Case, 1990; Chase and Myers, 2011), where
74 early-arriving species affect the establishment, survival, growth or reproductive success of
75 later-arriving species (Helsen et al., 2016). There is growing evidence that priority effects
76 play a crucial role in community assembly, especially in productive environments (Chase,
77 2003; Aronson and Galatowitsch, 2008; Körner et al., 2008; Young et al., 2016) and can be
78 implicated in invasion success (Seabloom et al., 2003; Corbin and D'Antonio, 2004; Abraham
79 et al., 2009; Grman and Suding, 2010). One mechanism prevalent in priority effects is
80 resource preemption (Young et al., 2001; Fukami, 2015): the reduction of available resources
81 (e.g. space, light, nutrients) by the early colonizers (Vance, 1984). This mechanism may allow
82 even weak competitors to persist and maintain long-term dominance (Ross and Harper, 1972;
83 Chase, 2010). Priority effects also arise from alterations of biotic (e.g. soil microorganisms)
84 and abiotic (e.g. nutrient dynamics, allelochemicals) components of the environment, which
85 can, in some contexts, limit colonization by subsequent colonizers (Kourtev et al., 2002;
86 Mangla and Callaway, 2008; Corbin and D'Antonio, 2012). Disturbances leading to the
87 removal of most or all plant individuals in a habitat patch initiate a new round of community
88 assembly (Fukami, 2015), often favoring competitive, fast growing invasive species at the
89 expense of natives (Hobbs and Huenneke, 1992; Davis et al., 2000). Because of the well-
90 recognized issues raised by invasive species (i.e. human health, crop production, native
91 biodiversity, economic; Vitousek et al., 1997; Kolar and Lodge, 2001; Simberloff, 2013) and
92 because of the evolution of legal framework on invasive species (at least in Europe;
93 Regulation (EU) No 1143/2014), there is clearly an urgent need to develop effective strategies
94 to limit invasions, particularly in newly disturbed areas. However, although active restoration
95 of plant communities is increasingly recognized as a relevant tool to combat invasions
96 (Middleton et al., 2010; Hazelton et al., 2014; Byun and Lee, 2017), results are often far from
97 satisfactory (Kellogg and Bridgham, 2002). This has notably been attributed to a failure to
98 account for priority effects, which may play a decisive role in restoration success (Young et
99 al., 2001; Temperton, 2004; Grman and Suding, 2010; Wilsey et al., 2015). Priority effects
100 appear to offer a cost-effective approach to combatting invasive plant species (Chadwell and
101 Engelhardt, 2008), but have only been recently considered for invasive species management.
102 Here, we discuss two non-exclusive restoration strategies to achieve the end goal “more
103 natives, less invasives”. The first strategy consists in tackling priority effects generated by

104 invasive species, while the second is to bring about situations in which the native species are
105 more likely to exert strong priority effects.

106 **2. Dealing with invasive species priority effects**

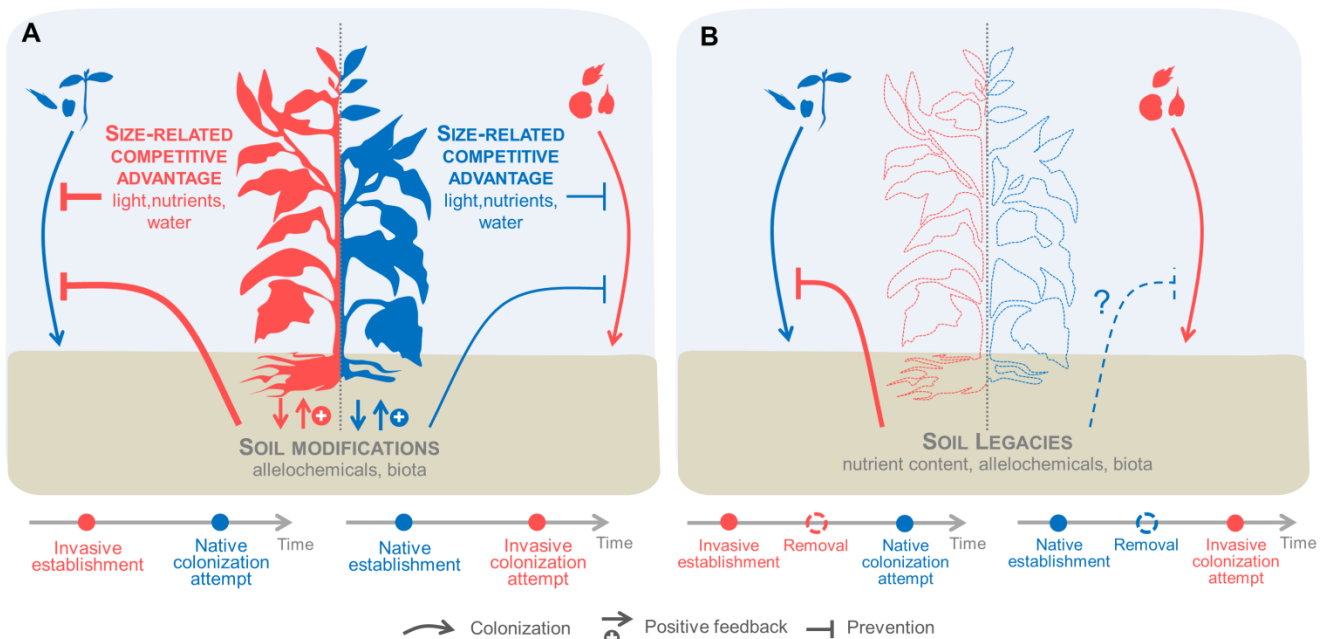
107 *2.1. Priority effects are particularly advantageous to invasive species*

108 Phenological differences between invasive and native species can substantially
109 contribute to invasion success (Wolkovich and Cleland, 2011). Distinct phenology allows
110 certain invasive species to fill vacant phenological niches and profit from temporally available
111 space and resources (e.g. light, nutrients, pollinators), sometimes creating seasonal priority
112 effects (i.e. priority effects operating seasonally on a within-year scale; Wolkovich and
113 Cleland, 2011). Numerous invasive species shares the strategy of being active early in the
114 season as to get an early access to resources and acquire a competitive dominance (Dyer and
115 Rice, 1997; Seabloom et al., 2003; Munter, 2008; Wolkovich and Cleland, 2011), but others
116 also profit of being active late in the season (e.g. in California, the invasiveness of *Centaurea*
117 *silsitialis* arises from extending its growing season into the summer when competition from
118 winter annual vegetation for soil water is minimal; Gerlach and Rice, 2003).

119 Several studies reported that invasive species generate stronger priority effects than
120 natives (Dickson et al., 2012; Wilsey et al., 2015; Stuble and Souza, 2016, but see Cleland et
121 al., 2015). The generally higher growth rate of invasive species (Rejmánek and Richardson,
122 1996; Reynolds et al., 2001; Grotkopp et al., 2010; Marushia et al., 2010; Dawson et al.,
123 2011) was suggested to underlie this advantage (Stevens and Fehmi, 2009; Dickson et al.,
124 2012). A higher growth rate creates a greater asymmetry in plant size (Weiner, 1990),
125 resulting in a stronger competitive suppression of the later arriving species (Dyer and Rice,
126 1999; Perry et al., 2003; Ejrnaes et al., 2006). Cleland et al. (2015) found that the stronger
127 priority effects of invasive species were correlated to regeneration trait values, such as higher
128 germination rate and higher light capture during seedling stage, reflecting higher biomass.

129 In addition to these seasonal advantages, invasive species can also profit from priority
130 effects through self-induced soil condition modifications, whether biological, chemical or
131 physical (Corbin and D'Antonio, 2012). Modifications such as: (1) shifts in nutrient cycling
132 (Ehrenfeld, 2003; Marchante et al., 2008; Flinn et al., 2017) and soil salinity (Novoa et al.,
133 2013), (2) changes in soil microbial communities including pathogens and mycorrhizal fungi
134 (Kourtev et al., 2002; Hawkes et al., 2006; Mangla and Callaway, 2008; Stinson et al., 2006;
135 Kardol et al., 2007; Lorenzo et al., 2010), and (3) the release of allelochemicals (Bais et al.,
136 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,

160 mechanical removal; Fig. 2). Marushia et al. (2010), by applying control methods (herbicide
161 application) early in the season, tackled rapid and early emerging exotic annuals while
162 minimizing impacts on native plants. In favorable conditions, many invasive species are likely
163 to invade in response to the removal of one or more invaders (D'Antonio et al., 2017). Thus, it
164 is particularly relevant to reduce propagule sources in order to limit invasive species
165 recolonization (Fig. 2; D'Antonio et al., 2017). Common methods to decrease undesirable
166 species seed bank include topsoil removal (Hölzel and Otte, 2004), effective mowing
167 management (i.e. adjusted to phenological development; Milakovic et al., 2014) and artificial
168 flushing of invasive species to induce germination, followed by lethal interventions such as
169 tillage or herbicide application (Wolf and Young, 2016). Prescribed burns for fire-prone
170 species or supplying water are two techniques promoting germination (Ooi, 2007; Wolf and
171 Young, 2016) that could be used to flush invasive plant species and tackle seasonal priority
172 advantage early in the season (Wolkovich and Cleland, 2011; Wainwright et al., 2012; Wilsey
173 et al., 2015). Establishing early-emerging and competitive native species (e.g. cover crops) is
174 another option that can help reducing competition from early-germinating invasive species.
175 Indeed, restoring early-emerging species can directly decrease invasive species performance
176 (Blackshaw et al., 2006) and indirectly favor desired native species (Perry et al., 2009).
177 However, so far, these strategies are little explored. To successfully counter seasonal priority
178 effects generated by invasive species, it is crucial to better understand invasive species
179 phenology, requirements and possible interactions with native species, so as to improve
180 existing management techniques (i.e. artificial invasive species flushing, the use of cover
181 crops) and develop new ones.

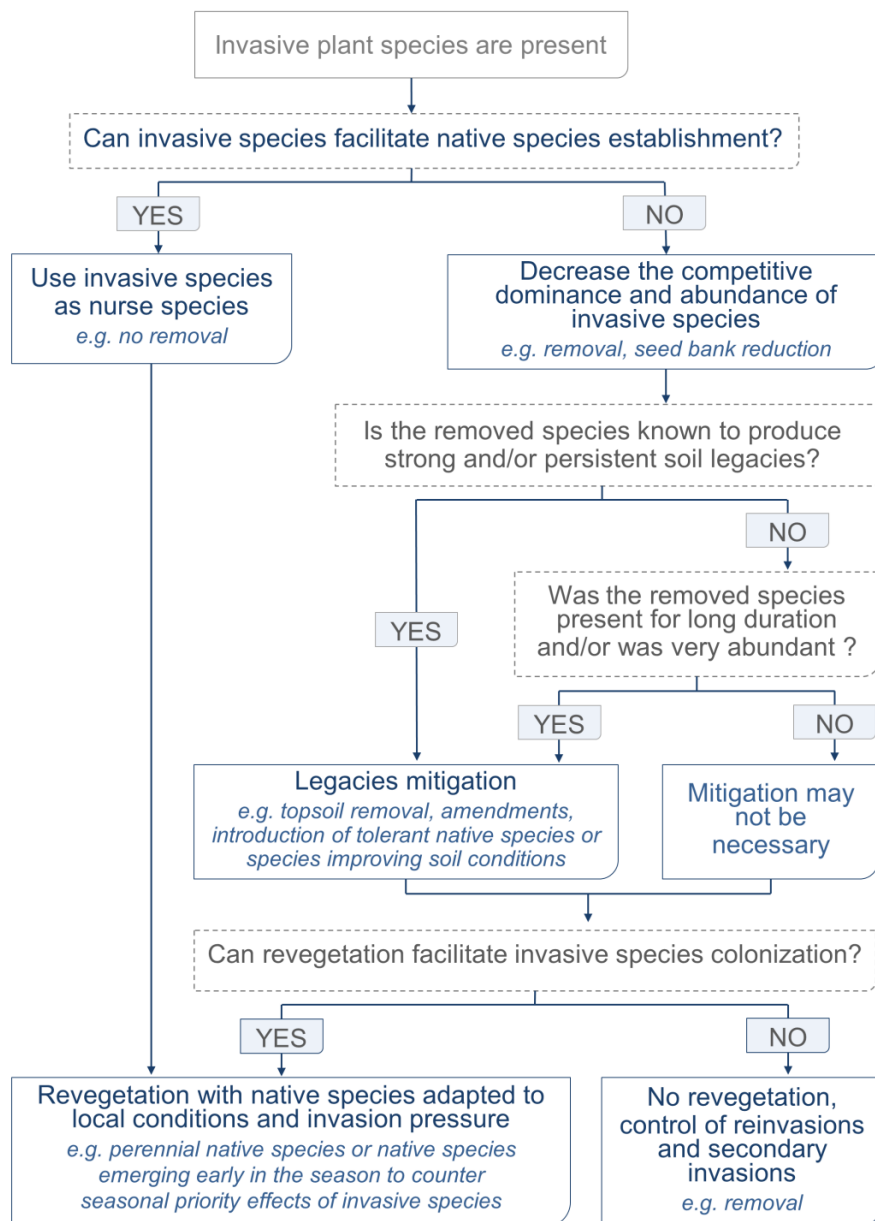
182 To limit reinvasion and secondary invasions, invasive species reduction must be
183 coupled with revegetation strategies (Fig. 2; Pearson et al., 2016) directed towards the
184 limitation of multiple co-occurring invasive plant species. However, because of soil legacies,
185 invasive species removal and propagule pressure reduction are sometimes unlikely to lead to
186 recovery of native communities (Suding et al., 2004; Ehrenfeld et al., 2005; Corbin and
187 D'Antonio, 2012; Jordan et al., 2012; van der Putten et al., 2013), and often favor secondary
188 invasions (Dickie et al., 2014; Grove et al., 2015; Yelenik and d'Antonio, 2013). When the
189 site was invaded prior to disturbance, it may then be necessary to include measures to deal
190 with soil legacies, rather than simply eliminate invasive species populations (Fig. 2). Soil
191 legacies can be mitigated by adjusting soil properties, typically via topsoil removal or soil
192 amendments (Kulmatiski and Beard, 2006; Buisson et al., 2008; Perry et al., 2010). Carbon
193 addition can help lowering nitrogen availability by stimulating nitrogen immobilization (Baer

194 et al., 2003), thereby reducing invasive species performance and concurrently increasing
195 desired species growth (Alpert and Maron, 2000; Blumenthal et al., 2003; Eschen et al., 2007;
196 see Perry et al., 2010 for review). However, in the case of restored communities reassembling
197 from seeds, nitrogen management may have no direct positive effect unless a headstart is
198 given to natives (i.e. invasive species are controlled the first growing season; James et al.,
199 2011). Furthermore, success of carbon addition to decrease invasive species dominance also
200 mainly depends on the condition that invasive species is nitrophilic relative to native species
201 (Blumenthal et al., 2003).

202 To face soil legacies, another restoration approach is to establish species that are
203 tolerant to invasive species legacies (Perry et al., 2005), or that could mitigate legacies before
204 establishing the target community (Jordan et al., 2008; Eviner and Hawkes, 2012; Leger et al.,
205 2015; Vink et al., 2015). In this sense, restoration of non-susceptible species to *Centaurea*
206 *maculosa*'s allelopathic compounds prevented reinvasion and possibly facilitate native species
207 recovery (Callaway et al., 2005; Thorpe et al., 2009). Herron et al. (2001) also showed that
208 establishing native species decreasing nitrogen availability through high nitrogen uptake
209 decreases the prevalence of invasive species favored by soil nitrogen enrichment.

210 Taking soil legacies into account in restoration projects is however challenging. Soil
211 legacies are difficult to predict and to assess (involving chemical analyses, determination of
212 microbial communities' abundance and composition), and are species-specific (Bezemer et
213 al., 2006; Yelenik et al., 2007; Bardgett and Wardle, 2010). Furthermore, their persistence
214 depends on characteristics of the invaded ecosystem (e.g. soil mineralization rates; Stock et
215 al., 1995), on their nature (Levine et al., 2003; Corbin and D'Antonio, 2012), and on the
216 duration of invasion (Marchante et al., 2008; Kulmatiski and Beard, 2011). For example,
217 while allelopathic compounds are generally short-lived in the soil (i.e. hours to days; Blair et
218 al., 2005; Reigosa et al., 2006), increased nitrogen levels generated by a nitrogen-fixing
219 invasive species can persist for decades (e.g. 35 years; Maron and Jeffries, 2001). Long-term
220 studies suggest, however, that invasion impacts on ecosystems, such as increased nitrogen
221 levels, can shift over time (Yelenik and D'Antonio, 2013). All this makes it hard to predict the
222 amplitude and persistence of soil legacies for a particular invasive species in a given
223 environment, and calls for high levels of costly technical expertise. Thus, soil legacies are not
224 systematically given the weight they deserve in restoration projects. Yet restoration would
225 clearly benefit from accounting for soil legacies, especially when an invasive species is
226 implicated in strong and persistent legacies and has dominated the target environment for
227 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

239 strong and/or persistent legacies (e.g. nitrogen levels), and/or or was present in abundance and/or for long duration.
240 Legacies mitigation methods such as topsoil removal, amendments (e.g. carbon addition), or intermediate planting
241 should be adjusted to the nature and intensity of legacies. Finally, the restoration of native species adapted to local
242 conditions and invasion pressure should be undertaken to limit reinvasion and secondary invasions, except when
243 revegetation facilitates invasions (e.g. in some harsh environments).

244 In harsh environments with extremely limited resources and/or stressful conditions
245 (e.g. extreme temperatures, excessive solar radiation, unstable substrates), invasive species
246 removal often lead to a lower success of a native cover restoration (D'Antonio and Meyerson,
247 2002). In some cases, invasive species are used as nurse plants to facilitate the establishment
248 of native species (Fig. 2; Becerra and Montenegro, 2013; Hanslin and Kollmann, 2016). The
249 removal of an invasive species may not result in additional invasions (D'Antonio et al., 2017):
250 the likelihood of other stress-adapted species being present and able to respond quickly is low
251 (Harms and Hiebert, 2006), and these systems constrain species to low productivity or
252 capacity to accumulate biomass (D'Antonio et al., 2017). Managers may therefore have ample
253 time to control a secondary invasive species because they commonly have low population
254 growth rates (Funk and Vitousek, 2007).

255 **3. Strengthening native species priority effects**

256 Restoring native communities after a disturbance can have opposite consequences on
257 invasion success depending on abiotic conditions. In harsh environments, native species can
258 create microclimatic conditions that are more favorable to invasive species establishment than
259 the surrounding (Lenz and Facelli, 2003; Cavieres et al., 2005; Mason et al., 2013). In such
260 cases, the restoration of a vegetation cover may not be the best option. Removal of invasive
261 species followed by the control of secondary invasions without active revegetation may be a
262 more suitable strategy. Resource availability, especially nitrogen, also strongly influences
263 invasion success through modifications in competition intensity between species (Davis et al.,
264 2000; Davis and Pelsor, 2001). Environmental harshness has also been assumed to decrease
265 the importance of stochastic factors because of strong niche selection (Chase, 2007; Kardol et
266 al., 2013). In this sense, Kardol et al. (2013) found weaker priority effects under low nutrient
267 supply. In nitrogen-limited systems, restoration of nitrogen-fixing species can also favor the
268 establishment of fast-growing invasive species that overgrow and shade slower-growing
269 native species (Huenneke et al., 1990; Maron and Connors, 1996; Corbin and D'Antonio,
270 2004b). In such conditions, it may be advisable to restore a native plant cover adapted to low
271 levels of nitrogen and to consider avoiding nitrogen-fixing species and soil nitrogen
272 amendments.

273 In fertile and relatively stable conditions, restoration of invasion-resistant native plant
274 species is increasingly considered to protect disturbed sites from re-invasion or secondary
275 invasions (Perry and Galatowitsch, 2006; Buckley, 2008; Middleton et al., 2010; Byun et al.,
276 2013; Pearson et al., 2016). Environmental conditions influence the magnitude of priority
277 effects (Collinge and Ray, 2009; Kardol et al., 2013; Symons and Arnott, 2014), with stronger
278 impact in productive environments (Kardol et al., 2013; Young et al., 2016). The strength of
279 priority effects also varies with the identity of the earlier- and the later-arriving species
280 (Dickson et al., 2012; von Gillhaussen et al., 2014; Cleland et al., 2015; Wilsey et al., 2015;
281 Stuble and Souza, 2016), invasive species being less negatively impacted by arriving late than
282 native species (Fig. 1A; Wilsey et al., 2015; Stuble and Souza, 2016), raising the need to
283 restore native species producing strong priority effects.

284 Recent work on priority effects also states that the strength of priority effects is
285 notably driven by (1) the impact a species has on resource levels (Fargione et al., 2003;
286 Fukami, 2015), (2) the overlap between competitive species in resource needs (Funk et al.,
287 2008; Vannette and Fukami, 2014), and (3) the impact a species has on nonresource
288 components of the environment (Bever, 2003; Levine et al., 2004; Goldstein and Suding,
289 2014). The following sections will discuss how these emerging properties could be used to
290 reinforce the priority effects of restored native species in invaded habitats (see Figure A1 in
291 Appendix for summary).

292 *3.1. Increasing resource preemption*

293 *3.1.1. Does the duration of time advance matters?*

294 Numerous studies reported that giving native species a short time advance (one to few
295 weeks) suffices to substantially decrease invasion success in grassland systems (Firn et al.,
296 2010; Grman and Suding, 2010; Vaughn and Young, 2015; Young et al., 2016). Grman and
297 Suding (2010) found that native species establishment only five weeks before invasive species
298 introduction reduced invasive biomass by 85%, against an 8% decrease when natives and
299 invasives were planted simultaneously. Firn et al. (2010) also found a strong effect of giving a
300 threeweek head-start to native grasses on an invasive grass performance. However, few
301 studies investigated the importance of the duration of the time interval between native
302 establishment and invasive species colonization. Asymmetry in plant size has been advocated
303 as one of the most important aspect of priority effect (Wilsey et al., 2015), suggesting that
304 extending duration interval between native species establishment and the later invasion event
305 may give a size advantage strengthening native priority effects. In this sense, von Gillhaussen

306 et al. (2014) found that a six-week head-start resulted in stronger priority effects than a three-
307 week head-start. Young et al. (2016) tested the effect of giving the native perennials a two-
308 week or a one-year seeding advantage over exotic annuals in a four-year experiment. It
309 respectively resulted in a native cover increase of 68% or 128% compared to when natives
310 and exotics were sown at the same time. The positive effect of increasing time advance
311 appeared however inconstant between years and sites, with sometimes an absence of benefit.
312 Better understand how the duration of time advance given to the restored native species
313 influence invasion success would be crucial to develop cost-effective priority effects- based
314 revegetation strategies. To give natives a time advantage over invasives, native species should
315 be actively restored as soon as possible after the disturbance on an invasive species-free soil
316 (Stevens and Fehmi, 2009), and a particular attention must be payed to invasive species
317 control in the initial weeks. Providing a short-term priority (several days) could also be
318 achieved by “pre-germinating” native species seeds. Pre-treatments including seed priming
319 and cold stratification can help ensuring a rapid and complete germination and overcome seed
320 dormancy (Halmer, 2004). These treatments therefore appear as opportunities for improving
321 native emergence speed and create priority effects over invasives, but remain yet untested.

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

333 *3.1.2. Manipulate species composition and density*

334 The resource competition model (Tilman, 1990) predicts that the more a species
335 reduces the availability of limited resources, the less these resources are available for later
336 colonizers. Because resource preemption has been identified as one of the main driver of
337 priority effects (Fukami, 2015), high resource preemption would lead to strong priority effects
338 (Vannette and Fukami, 2014). Fargione et al. (2003) found that C4-grasses inhibited the most
339 the later arriving invasive species, most likely because this guild reduced soil nitrate to the

340 lowest levels compared with other tested functional guilds. This result suggests that restoring
341 native species leading to a strong and rapid reduction of limited resources could help
342 enhancing priority effects. Accordingly, research efforts should be directed towards the
343 identification of species having the ability to (1) rapidly occupy of above- and/or below-
344 ground space, thereby limiting light and space availability (often considered as two primary
345 determinants of invasive species germination and establishment; D'Antonio et al., 2001;
346 Corbin and D'Antonio, 2004a; Iponga et al., 2008), and (2) rapidly and effectively preempt
347 soil nutrients, especially in low productivity environments where there is likely to be less
348 above-ground competition for light (Dietz and Edwards, 2006; Gioria and Osborne, 2014).

349 At small scale (10m² or less), many studies support the widespread assumption that
350 species diversity confers invasion resistance (Tilman, 1997; Levine and D'Antonio, 1999;
351 Levine et al., 2004; Carter and Blair, 2012), due to fuller use of resources by resident species
352 ("complementarity effect"; Robinson et al., 1995; Lavorel et al., 1999; Levine and D'Antonio,
353 1999; Larson et al., 2013), or due to the increased probability of a species being present to be
354 a strong competitor for the invasive species when increasing the number of species in a
355 community ("sampling effect": Kennedy et al., 2002; Wardle, 2001; Lavorel et al., 1999;
356 Goslee et al., 2013). Increasing diversity has been reported to increase primary productivity in
357 grassland systems (Hector et al., 2011), suggesting that diverse communities produce higher
358 rates of biomass and could therefore exert a stronger asymmetric competition with later
359 colonists. Two studies supported the fact that diversity strengthens priority effects in protist
360 and aquatic plant communities (Jiang et al., 2011; Viana et al., 2016), but more studies
361 investigating this relationship in plant communities are needed.

362 The density of individuals also modulates priority effects (Weiner, 1990) in the sense
363 that establishing more individuals should lead to increased resource acquisition and
364 competition intensity (Goldberg, 1990; Lockwood et al., 2005). The benefit of increasing
365 sowing density may stabilize over time, since the law of constant yields predicts that even-
366 aged populations grown at different densities show the same overall productivity after a
367 certain period of time, with higher number of individuals in high densities but lower standing
368 biomass per individual (Drew and Flewelling, 1979). Consistently, von Gillhaussen et al.
369 (2014) found sowing density (1.5, 2.5 and 5 g/m²) only had a weak influence on aboveground
370 productivity. Increased density is however often associated with improved invasion resistance
371 in short time scales (Gerhardt and Collinge, 2007; Carter and Blair, 2012; Vaughn and Young,
372 2015; Yannelli et al., 2017). Accordingly, Yannelli et al. (2017) found that sowing
373 communities at high density (10 g.m²) is more effective in suppressing invasive species than

374 low density (1 g.m²). The improved invasion-resistance of high density community may be
375 related to the inability of low density community to fully exploit available resources. Since we
376 are looking for solutions to design restored communities rapidly exerting strong priority
377 effects, increasing sowing densities is an attractive option. However, it remains to determine
378 effective sowing thresholds depending on species used and environmental conditions.

379 *3.2. Increasing niche overlap: Applying limiting similarity*

380 Niche overlap, referring to resource use similarity between co-occurring species
381 independent of their rate of resource consumption (Pianka, 1974; Petraitis, 1989), has been
382 hypothesized to influence invasion-resistance (Abrams, 1983; Funk et al., 2008) and more
383 recently priority effects (Vannette and Fukami, 2014). Niche overlap is derived from the
384 limiting similarity concept, predicting that species most similar to the invasive species should
385 provide greater invasion resistance because of greater overlap in resource use (Abrams, 1983).
386 Accordingly, a high degree of similarity in resource use between first and later colonizers
387 should strengthen priority effects of the recipient species. Attempts to use limiting similarity
388 to limit plant invasions often resulted in failures (Symstad, 2000; Emery, 2007; Turnbull et
389 al., 2005; Price and Pärtel, 2013), highlighting the complexity of selecting plant species
390 having a sufficient degree of niche overlap. With current knowledge, using the limiting
391 similarity concept to limit invasions appears premature. An emerging, more promising
392 strategy consists in focusing on the identification of key functional traits playing a substantial
393 role in invasion resistance and priority effects (Drenovsky and James, 2010; Cleland et al.,
394 2013). For example, Cleland et al. (2013) identified phenology as an important determinant of
395 invasion success: high phenological overlap between exotic annual grasses and restored forb
396 species successfully resulted in a decreased abundance of invasive species. These results
397 suggest that restoring early active perennial species may be particularly relevant to decrease
398 the competitive dominance of early active annual invasive species in the long term. Further
399 investigations are needed to determine how and in which situations such trait-based strategies
400 are efficient.

401 *3.3. Manipulating non-resource components*

402 Few studies have explored ways to enhance invasion-resistance of restored
403 communities by exploiting non-resource priority effects (Bever, 2003; Levine et al., 2004)
404 induced by the release of allelopathic compounds, the manipulation of mycorrhizae, or the
405 promotion of pathogens or herbivory (Goldstein and Suding, 2014). Non-resource priority

406 effects could act through a direct negative impact on the target invasive species, or by an
407 indirect improvement of native species success.

408 The use of allelopathy (i.e. the exudation of chemical compounds influencing the
409 growth of other plants or microorganisms) for invasive species control has received special
410 attention, especially in suppressing weeds in agricultural systems (Bhowmik, 2003;
411 Milchunas et al., 2011; Jabran et al., 2015; Jabran, 2017). The establishment of native
412 allelopathic species can directly reduce the biomass of the target invasive species (Callaway
413 and Ridenour, 2004), and indirectly facilitate the desired later-arriving native species (Perry et
414 al., 2009). Indeed, allelopathy is relatively ineffective in interactions between species that
415 frequently co-occur (Fitter, 2003) and is more intense in novel interactions, such as between
416 native and exotic species (Callaway and Ridenour, 2004; Thorpe et al., 2009). By being
417 established first, native allelopathic species could induce stronger priority effects reducing
418 invasion success, but such assumption needs to be tested. Since the allelopathic effect vary
419 depending on species (Prati and Bossdorf, 2004), community density (Weidenhamer et al.,
420 1989), climate conditions (May and Ash, 1990; Blair et al., 2006), and substrate
421 characteristics (Parepa and Bossdorf, 2016), using allelopathic native species to limit invasion
422 appears complex and may be limited to a set of invasive species. The effectiveness of invasive
423 control strategies based on allelopathic species needs further investigations, in particular the
424 potential use of native allelopathic species to suppress several invasive species.

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

439 Mycorrhizal fungi, forming symbiotic relationships with 80–90% of terrestrial plants
440 (Smith and Read, 2008), often strongly influence plant growth and reproduction (Koide and
441 Dickie, 2002), plant community structure (van der Heijden et al., 1998; Hartnett and Wilson,
442 1999, 2002), and invasion success (Klironomos, 2002; Callaway et al., 2004). Soil inoculation
443 of arbuscular mycorrhizal fungi can reduce the performance of agricultural non-mycorrhizal
444 weeds (Jordan et al., 2000; Vátovec et al., 2005; Rinaudo et al., 2010; Veiga et al., 2011),
445 raising a potential application in managing non-hosts invasive species (e.g. from
446 Chenopodiaceae and Cruciferae families; Wang and Qiu, 2006). In the case of non-hosts
447 invasive species, establishing species having the ability to increase mycorrhizal inoculum
448 potential would facilitate arbuscular mycorrhizal fungi-dependent native species (Eviner and
449 Hawkes 2012), and may enhance their competitive abilities over later arriving invasive
450 species (Smith et al., 1998). In the cases where the presence of mycorrhizae increases
451 invasion success of host invasive species (Marler et al., 1999; Smith and Read, 2008),
452 mycorrhizae suppression through fungicide application combined with restoration of non-
453 mycorrhizal species may help limiting invasive species. The feasibility and effectiveness of
454 this approach needs however to be investigated, since mycorrhizae are sometimes essential in
455 some species assemblages (Dostálek et al., 2013).

456 Overall, whether native herbivores, parasites and symbionts could create priority
457 effects reducing invasive species success remains untested, so that an application in
458 restoration is premature. Because interactions between invasive species and native enemies or
459 symbionts are species or trait-specific (Veiga et al., 2011; Grutters et al., 2017; Zhang et al.,
460 2018), it may be relevant to develop non-resource-based restoration strategies for the most
461 noxious invasive species.

462 **4. Conclusion**

463 Recent research suggests that better considering priority effects of both invasive and
464 native species in restoration strategies could significantly help reducing invasive species
465 colonization on disturbed areas. When invasive plants arrive or emerge earlier than natives, a
466 size-related advantage can hamper native community restoration success, often impelling to
467 reduce or remove invasive propagule sources. Yet, after removal, invasive plants can still
468 threaten restoration success through persisting soil legacies, especially when the invasive
469 species have long been present or when they were very abundant. The processes underlying
470 the magnitude and persistence of soil legacies are however still poorly understood. Research
471 efforts should be directed towards this topic, as well as towards developing cost-effective and

472 rapid methods of assessing invasives-induced soil modifications. In order to avoid reinvasion
473 and secondary invasions, invasive species removal must often be coupled with the restoration
474 of native species. However, before undertaking revegetation, it is advisable to ensure that it
475 will not lead to invasive species facilitation, such as in some harsh environments.

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

500 Combinations between different priority effect-based strategies have not been explored
501 yet, but may potentially enhance invasive species control. When invasive species are present,
502 it may be relevant to simultaneously tackle their priority effects and increase those of desired
503 native species. Different strategies could also be successively used over time. For example,
504 establishing a community dominated by one competitive species, producing a high rate of
505 biomass, may be an effective way to rapidly increase native cover and counter immediate

506 invasion risk, while subsequently adding seeds from diverse species may help stabilize the
507 community in the long term.

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511 **Appendix A. Supplementary data**

512 Supplementary data to this article can be found online at

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