

REVIEW ARTICLE

Priority effects and ecological restoration

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Priority effects refer to the order or timing of species arrival, including how species that arrive early at a site either positively or negatively affect establishment, growth, or reproduction of species that arrive later. Despite the clear implications of priority effects for ecological restoration, there have been no reviews of how and where priority effects have been studied and the extent to which findings can be applied to restoration. Here, we systematically review the literature on priority effects by (1) synthesizing information from papers that compared simultaneous and nonsimultaneous planting or sowing; (2) discussing the mechanisms through which priority effects operate, (3) considering how these mechanisms might be manipulated to achieve restoration goals; and (4) highlighting future research needed to improve the use of priority effects in restoration. In a term-targeted search, we found 43 studies that experimentally manipulated the order of arrival of different species. Overall, these concluded that even small delays in arrival time, as opposed to simultaneous arrival of species, can promote differences in subsequent community composition as well as ecosystem functions. There were very few studies on the long-term stability of these priority effects, and the majority were conducted in temperate grasslands. Our findings suggest that creating alternative vegetation states via priority treatments is a promising avenue for restoration. However, for the concept to be best operationalized for restoration, we need research in more ecosystems that are priorities for restoration, and treatments that are followed over extended time periods.

Key words: community assembly, competition, facilitation, historical contingency, plant order of arrival

Implications for Practice

- Judicious use of priority effects can promote the establishment of preferred native species and resist exotic invaders.
- For priority effects to become a useful restoration tool, we need more large-scale long-term experimental studies in a wider variety of systems that also consider how long the effects persist.
- The use of priority effects in restoration can be system-specific, thus local knowledge of natural history is important for success.

structure and function, and especially in the context of restoration.

Priority effects are important components of historical contingency, and refer to the order or timing of species arrival, or “who arrives when” (Alford & Wilbur 1985; Fukami 2015). For example, priority effects include how species arriving early during assembly either positively or negatively affect subsequent plant establishment, growth, or reproduction (Vaughn & Young 2015; Temperton et al. 2016; Delory et al. 2019a). Plant communities with the same species pool, but differing in species arrival order during assembly, may shift to alternative stable

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Introduction

Ecological restoration involves the reassembly of ecological communities after degradation. As such, theory related to community assembly and succession is relevant to improve restoration of degraded plant communities (Temperton et al. 2004; Walker et al. 2007; Young et al. 2017; Wilsey 2020). Historical contingency, that is the chance arrival of species after degradation, is key to community assembly and succession, but a detailed and predictive understanding of contingency is still emerging (Grman et al. 2013; Fukami 2015). We lack a generalized understanding of how contingency can influence ecosystem

states, alternative transients states, or compositional cycles (Fukami & Nakajima 2011; Fukami 2015). These priority effects can have long-lasting effects on the structure and functioning of plant communities and thus have important implications for restoration efforts (Martin & Wilsey 2012; Wilsey et al. 2015; Weidlich et al. 2018).

One of the first experiments addressing priority effects was performed by Harper in the early 1960s (see Morin 2011). He planted two grass species either simultaneously or at different times and found that this difference in planting time affected the relative abundance of these species. Later, Connell and Slatyer (1977) postulated that the first colonists at a disturbed site may have positive (facilitative), negative (inhibition), or neutral (tolerant) effects on later species. Quinn and Robinson (1987) coined this term as the “priority effect,” focusing primarily on how early-arriving species suppressed later arrivals. Since then, studies reporting the importance of priority effects for the structure and functioning of ecological communities have proliferated (Ejrnæs et al. 2006; Körner et al. 2008; Grman & Suding 2010; Sarneel et al. 2016; Weidlich et al. 2018).

In restoration, manipulating the order of arrival of plants, or groups of plants, can lead to communities that differ in structure and function, which together with other biotic and abiotic filters can help achieve desired plant communities (Hobbs & Norton 2004; Temperton et al. 2019). For example, in some systems it might be necessary to manipulate the identity of early-arriving species to promote positive interactions between early- and late-arriving species (e.g. Zwiener et al. 2014). Padilla and Pugnaire (2006) reviewed how such facilitation by early-arriving nurse species has been used in restoration of degraded

lands. Understanding these patterns of variation and their drivers is critical for improving restoration outcomes. For instance, priority effects may not be evident in systems with strong equilibrium dynamics, but they might be important drivers of assembly in systems that easily shift into multiple alternative states (Chase 2003; Vannette & Fukami 2014; D’Antonio et al. 2017). Thus, strategies for using priority effects in restoration efforts are likely to be system-specific.

Restoration often involves manipulating which plant species are introduced, sown, planted, or transferred to a disturbed or degraded site at a given time (Weidlich et al. 2020). If the order of arrival of these species can affect ecosystem functioning or community composition over time, then priority effects can determine successful or unsuccessful restoration. This can be important for sustaining preferred species and resisting undesired species such as exotic invaders. Steering restored communities along particular temporal trajectories or toward particular ecosystem functions by using priority effects can be a powerful tool (Fig. 1). Examples in the literature include reducing invasive species (Abraham et al. 2009; Stuble et al. 2016; Lang et al. 2017), sustaining species that promote pollinator communities (Pocock et al. 2012), improving nutrient cycling, or increasing ecosystem productivity (Popp et al. 2017).

There have been thorough reviews of the mechanisms of historical contingency (Fukami 2015), community assembly and restoration (Young et al. 2001, 2005), and exotic invasions (Thomsen et al. 2011; D’Antonio et al. 2017; Hess et al. 2019). However, to date there are no summary reviews showing how and where priority effects have been studied (either native vs. native, or native vs. exotics). This information is needed to advance our basic understanding of priority effects in

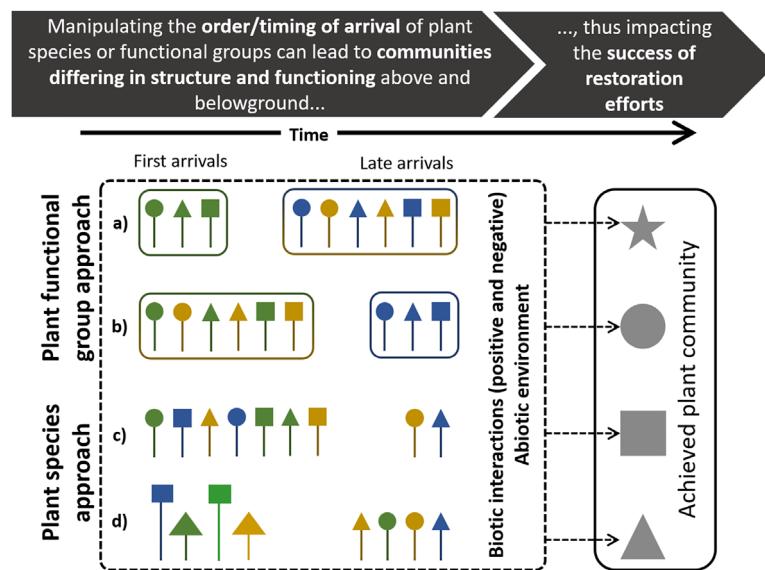


Figure 1. Examples illustrating how priority effects might foster restoration within a plant functional group or species approach. (A) The potentially strong facilitative role of legumes when they arrive before nonlegumes. (B) A situation where one plant functional group was sown later than two others, for instance sowing a mixture of forbs and legumes first, and grasses arriving later, which might promote facilitation and allow deep rooting forbs species to establish before more shallow rooting grasses. (C) Priority effects caused by natives that resist invasion by later arriving exotic. (D) Species that grow fast and provide shade may suppress invasive species, to the benefit of native species arriving later. Symbols with same color represent the same plant functional group.

community assembly and to the practice of ecological restoration. Here, we systematically review the literature on priority effects, and synthesize information from papers that compared simultaneous and nonsimultaneous planting or sowing. We then discuss mechanisms by which priority effects operate, with an eye toward how these mechanisms can be manipulated to achieve particular restoration goals. Finally, we highlight key gaps in the literature and suggest where future research is needed to better our understanding of how best to manipulate priority effects to advance restoration.

Literature Review

We conducted a literature search in Web of Science using the following terms: “PRIORITY EFFECT” or “PRIORITY EFFECTS” and “PLANT*,” refined into seven categories (Ecology, Plant Sciences, Evolutionary Biology, Forestry, Biodiversity Conservation, Environmental Science, Biology) and two document types (articles and reviews). Our survey addressed only English-language papers published until December 2019. We chose this set of keywords to focus on studies that explicitly compared simultaneous and nonsimultaneous sowing or planting. In order to focus solely on studies that experimentally manipulated plant order of arrival, other priority effect-related terms such as facilitation, regeneration, seed bank, or soil legacy were not included in our literature search.

We found 138 articles (Table S1) in our literature search, with the annual rate of studies increasing dramatically since roughly 2000 (Fig. 2A). Of this total, 62 papers used the term priority effect only to interpret their findings, 43 articles experimentally tested priority effects (comparing simultaneous and nonsimultaneous sowing/planting; Table S3), and 18 papers investigated the role of early-arriving species in the context of natural regeneration. Eight articles examined how evolutionary dynamics

affect priority effects of early-arriving lineages (e.g. Wittmann & Fukami 2018), while seven papers evaluated sowing communities with different species richness rather than manipulating order of arrival (Carter & Blair 2012; Plückers et al. 2013). Most of the studies tested or discussed priority effects with the motivation to apply results to management practices in restoration (Fig. 2B), indicating the applied relevance of priority effects.

Some well-known studies that use nurse plants to evaluate the effects of the initial species on assembly were not included in our review because they did not experimentally manipulate plant order of arrival. For example, studying successional dynamics in central Amazonian, Norden et al. (2011) found that differences in recruitment (caused by the species that first colonized) were the major drivers of alternative states. Other examples of studies have found that tropical forest restoration can use exotic trees as nurse plants to establish late successional tree species and speed up the recovery of forest functions (Ashton et al. 2014; Brancalion et al. 2020). In Costa Rica, planting tree seedlings in small patches has been proposed as a good alternative restoration method that facilitates forest recovery (Holl et al. 2011; Zahawi et al. 2013). This “applied nucleation” is less expensive than fully planting large areas, and a cost-efficient alternative to large-scale plantings (Corbin & Holl 2012). Even though these studies can be considered a type of priority effect, we did not include them in our review, because they did not have simultaneous planting or sowing as an experimental control treatment.

General Patterns From Studies That Tested Priority Effects

Priority effects can be asymmetric, contingent on environment and species composition, and persistent or not (Young et al. 2017)

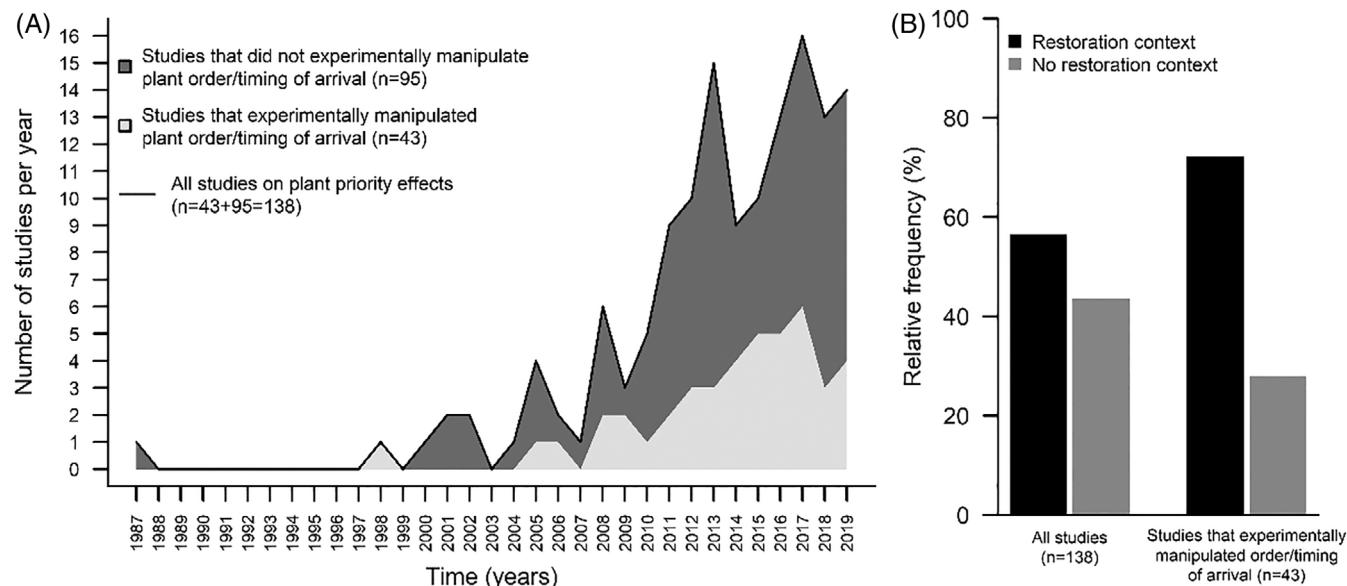


Figure 2. (A) Number of studies published per year on priority effects in plant communities. (B) Frequency of studies performed within a restoration context for each pool of papers. Among the 138 articles that mentioned plant priority effects, only 43 studies experimentally manipulated order/timing of arrival. The literature search was conducted until December 2019.

and in this context, 42 of the 43 studies that experimentally manipulated the order of arrival of different species found evidence for some sort of priority effect. For example, Sarneel et al. (2016) found that small differences in arrival time affected plant community assembly and diversity, both in the greenhouse and in the field. A number of experiments found that sowing legumes before other functional groups resulted in greater above-ground biomass production over time (Körner et al. 2008; von Gillhaussen et al. 2014; Weidlich et al. 2017) and lower total root length density and biomass in the upper layers of soil (Weidlich et al. 2018). The only study that found no evidence of priority effects when comparing simultaneous and nonsimultaneous plantings was Mason et al. (2013). Using a mesocosm experiment, they tested whether manipulating the order of arrival of

three plant functional groups typical of Australian coastal dune communities (grasses, herbs, and shrubs) would increase resistance of native communities to an exotic species. They found that manipulating the arrival order of native functional groups did not improve the resistance of plant communities to invasion by the exotic, which established successfully regardless of native priority. The authors argued that the resource use by the native species used in the experiment was insufficient to affect germination of the exotic due to its lower resource requirements.

The 43 studies that experimentally manipulated the order of arrival of species were performed in four different biomes (Fig. 3A), but 30 of them (70%) were in temperate grasslands. The over-representation of temperate ecosystems, particularly grasslands, derived from 63% of the studies being in North

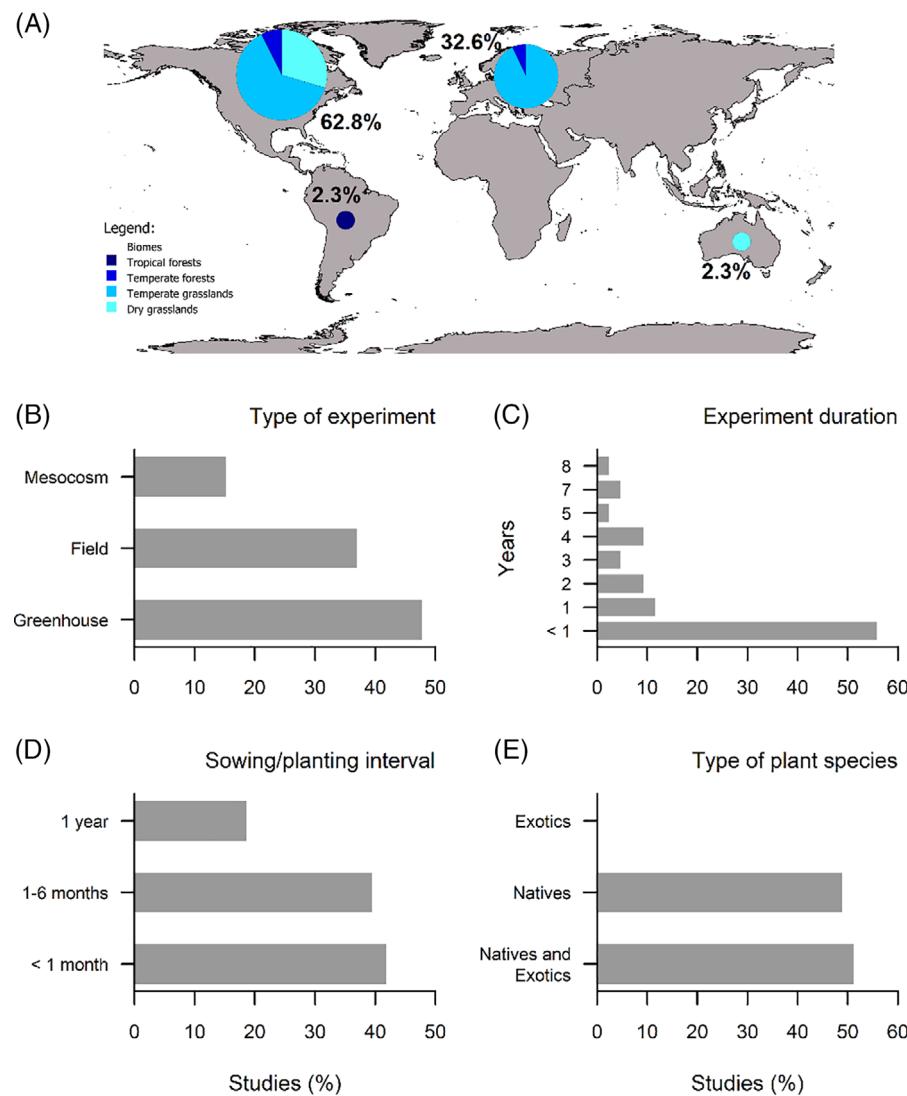


Figure 3. The majority of experiments that manipulated plant order/timing of arrival were performed in North America and Europe (A), in the greenhouse or in the field (B), and lasted less than a year (C). In the majority of studies, priority effects were created using a sowing interval shorter than a month (D) and involved either natives only or natives and exotics (E).

America (27 papers) and 33% in Europe (14 papers), where around one-third of the landscape is grassland and grass-dominated landscapes. Also, the high proportion of studies in grasslands may reflect the fact that they are easier to manipulate than shrub- and tree-dominated systems. There were far fewer studies in tropical and subtropical wooded and grassland systems. However, because of our search terms, as noted above, our analysis does not take into account a substantial number of tropical studies of “nurse trees” as restoration tools, and such facilitation is inherently a priority effect (e.g. Aerts et al. 2007; Anthelme et al. 2014; Bertoncello et al. 2016; Section Synthesis of General Mechanisms Driving Priority Effects and Their Relevance to Restoration below).

Only 17 studies (37%) were performed in natural field communities, while 22 experiments were in greenhouses (48%), and 7 in outdoor common gardens with constructed communities (15%; Fig. 3B). Most experiments (24 papers, 56%) lasted less than 1 year (Fig. 3C), which is mainly due to the large number of greenhouse experiments conducted under controlled conditions. Such experiments typically last less than a year, but are particularly useful to better understand the mechanisms leading to priority effects in plant communities.

We found a small number of field experimental studies, and only a few of them lasted more than 3 years. They were performed in North American (Collinge & Ray 2009; Martin & Wilsey 2012, 2014; Werner et al. 2016; Young et al. 2017; Wohlwend et al. 2019) or European grasslands (Weidlich et al. 2017, 2018). Most of these experiments showed strong and persistent effects of plant order of arrival on the structure and functioning of plant communities, and highlighted the potential of using priority effects as a restoration tool. Martin and Wilsey (2012) established a grassland field experiment in which the identity and timing of arrival (spring or summer) of four early-emerging native species was manipulated. A seed mixture containing common prairie species was added at the same time as early-emerging species (no priority effect) or a year later (with priority effect). After 5 years, they found higher diversity, lower invasion by exotics, and higher aboveground biomass production in plots sown in spring and without priority effects. These results persisted up to 8 years after the start of the experiment and were not affected by the addition of seeds to increase native species propagule pressure (Martin & Wilsey 2014). Collinge and Ray (2009) manipulated the order of arrival of two groups of species including grasses and nonleguminous forbs at a field site in California, giving species from one group a 12-month advantage over later ones. They found strong evidence for priority effects, with most species being more abundant in pools where they were sown first. However, these priority effects faded over time and were not evident for the majority of species 7 years after the start of the experiment. In another study performed in California grasslands, Werner et al. (2016) reported results from an 8-year priority effect in which native grasses and forbs were planted either simultaneously or with a 1-year priority over the other functional group. Plots in which grasses and forbs were grown on their own were also included. Overall, they found that temporal priority persisted for the 8 years for some species and resulted in different

community compositions. Similarly, Young et al. (2017) tested four priority effect scenarios at three restoration sites in California grasslands. They investigated the extent to which giving a 2-week or a 1-year seeding advantage to native perennial grasses over exotic annual grasses, as well as giving native grasses and forbs a 1-year seeding advantage over the other functional group, would affect the structure of plant communities. They found that manipulating plant order of arrival can strongly affect interspecific relationships and benefit subordinate plant species, but that these priority effects were sometimes asymmetric and contingent on environmental factors and species composition. In a 7-year restoration experiment in U.S. prairies, Wohlwend et al. (2019) tested how the timing of arrival of an invasive legume (*Lespedeza cuneata*) and native grasses and forbs would affect the structure of plant communities and whether or not results met specific restoration goals. Early arrival of native species (over the exotic legume) led to a desired restoration outcome with plant communities having a greater abundance of native species and a lower abundance of non-native species. In Europe, a 4-year grassland experiment located in Germany showed that sowing legumes before grasses and forbs resulted in greater aboveground biomass production in some years (Weidlich et al. 2017) and a lower root length density and biomass in the topsoil layer (Weidlich et al. 2018). In addition, results from this experiment also highlighted the strong interlinkage existing between priority and biodiversity effects in grasslands (Delory et al. 2019a).

The time interval between the first and second sowing used in the nonsimultaneous treatments in experiments testing priority effects varied from 5 days to 3 years (Fig. 3D), but in 18 studies (42%) it lasted less than a month. Thus, our survey showed that even small delays in arrival time can promote differences in the community (as opposed to simultaneous sowings), but also that a large number of studies did not determine the stability of these effects. Two of the 43 experimental studies tested different sowing intervals (von Gillhaussen et al. 2014; Young et al. 2017), and both concluded that a longer interval between sowings can create stronger priority effects. Young et al. (2017) compared two experiments that delayed the arrival of exotic annual grasses for 2 weeks versus 1 year and found that final native perennial cover was greater when the initial priority effect was allowed to establish for a longer time. Testing priority effects, sowing density, and interval in European grasslands, von Gillhaussen et al. (2014) found that longer intervals between the first and second sowings of different functional groups led to experimental communities that were more productive. Interestingly, the priority effect on aboveground community biomass found by von Gillhaussen et al. (2014) was stronger than sowing density or sowing interval effects.

Twenty-two studies (51%) compared priority effects between native and exotic species, while 21 papers (49%) tested interactions between native species (Fig. 3E). Studies testing the effects of an exotic arriving before or after a native species were mostly in North America (17 papers; 77%), whereas tests of natives versus natives were more common in Europe (11 papers; 52%). In North America, South America, and Australasia, invasive exotic species strongly limited restoration success. Recent reviews

have shown that there are more studies of controlling invasive species in restoration in North America compared to other countries (Kettenring & Adams 2011; Weidlich et al. 2020). Thus, the main goal of using priority effects derived from native species was to make communities more resistant to invasion (Funk et al. 2008). In contrast, researchers in Europe tended to alter the order of arrival of different plant functional groups in order to study ecosystem functions (Weidlich et al. 2018), or to increase diversity and yield (Bullock et al. 2001, 2007), and less to investigate exotic invasion (Delory et al. 2019b).

Synthesis of General Mechanisms Driving Priority Effects and Their Relevance to Restoration

Understanding the mechanisms that drive priority effects is essential. Using a niche-based framework, Fukami (2015) proposed grouping priority effects mechanisms into two broad processes: niche preemption and niche modification. In niche preemption, the species that arrives first reduces the resources available to late-arriving species, resulting in inhibition. In niche modification, early-arriving species affect the identity of the species able to further establish by modifying the types of niches available for late-arriving species, resulting in either inhibition or facilitation. These two processes can be divided into direct and indirect competition, and direct and indirect facilitation. Direct competitive effects might include disproportionate resource uptake or allelopathy (Aschelou et al. 2016), whereas indirect competition may occur through complex multispecies interactions (Levine et al. 2017), associational vulnerability to consumers (Barbosa et al. 2009), or changes in soil biota that suppress other species (Lekberg et al. 2018). Direct facilitative effects include providing shade, enhancing soil moisture through hydraulic lift, or increasing soil fertility, whereas indirect effects may be manifest through associational defenses or changes in soil biota that favor other species (Callaway 2007).

Combining both direct and indirect inhibitory mechanisms, Grman and Suding (2010) suggested that priority effects arise from asymmetric competition and soil legacies. Asymmetric competition occurs when interacting plants that differ in size create unbalanced competitive interactions, with the large plant having a much higher chance of outcompeting the smaller one. Soil legacies occur when the presence of a specific plant species affects the microbial community in ways that affect the plant itself or other individuals of the same or different species. On the other hand, Gómez-Aparicio et al. (2004) found that tree seedlings planted under different nurse shrub species experienced both direct and indirect facilitation.

These inhibitory and facilitative processes that drive priority effects are difficult to use in restoration because general predictions of which processes are occurring or most important are difficult to make because of context specificity. This is because system-specific or species-specific information and in-depth natural history expertise are often necessary, although trait-based assessments allow some generalization. For example, if preferred species are succulent, they are highly likely to need nurse species (Valiente-Banuet et al. 2006; Romo-Campos et al. 2013), and the same is likely to be true for late-successional perennial species in

general, such as in oak woodland restoration (Callaway & D'Antonio 1991; Perea & Gil 2014). At more geographic or landscape scales, theory indicates that a need for facilitators might be more common in abiotically harsh conditions such as arid or alpine ecosystems (see Castro et al. 2004). For example, Dalotto et al. (2018) found evidence that nurse species play a key role in regenerating coastal sandy dunes in Southern Brazil, where their presence is critical for maintaining ecosystem diversity and functioning. Padilla and Pugnaire (2006) noted that facilitation "has a practical side when applied to the restoration of degraded environments, particularly drylands, alpine, or other limiting habitats." Gómez-Aparicio et al. (2004) conducted a meta-analysis of experimental plantings of tree seedlings under different potential nurse shrub species and found much stronger facilitation in a dry year than wet years, at drier and hotter low altitudes, and on sunny slopes than on shaded slopes. But, facilitation can also promote restoration in many other systems. Evidence of facilitation in more moderate environments does suggest that its role may have been overlooked because of assumptions derived from the stress gradient hypothesis (Temperton et al. 2007; Holmgren & Scheffer 2010).

The judicious use of facilitative mechanisms may be advantageous early on in restoration, but priority effects caused by facilitation can also have a "dark side" (Lucero et al. 2019). Depending on the mechanism, exotic invasive species may be more strongly facilitated than natives (Maron & Connors 1996; Bulleri et al. 2008). Lucero et al. (2019) found that the highly invasive Eurasian annual grass *Bromus rubens* occurred at far greater abundance under shrubs than away from shrubs in many sites across the Mojave and San Joaquin deserts (U.S.A.). The very high density of *B. rubens* under shrubs correlated with very low abundances of native species. Desert shrubs commonly form "islands of fertility," and exotic invaders often benefit disproportionately from nutrient enrichment. Aschelou and Callaway (2014) found that enriched soil fertility beneath *Quercus douglasii* trees shifted competitive advantages toward exotic annual species, to the virtual exclusion of native *Nassella pulchra*. Thus, nutrient enrichment as a facilitative priority effect may be problematic in restoration projects with a high potential for exotic invasions.

Nurse species can also have species-specific effects and mechanisms (Callaway 1998) that can be important in restoration. Gómez-Aparicio et al. (2004) compared the nurse effects of many different shrub species and found that legumes, small shrubs, and spiny shrubs showed consistent positive effects on tree seedlings, but that rockroses had negative effects on seedlings. These results, in general, suggest that knowledge about the ecological traits, behavior, and natural history of species involved in facilitation in the restoration process is important.

The apparent suppression of natives by facilitated exotics (e.g. Lucero et al. 2019) illustrates how competitive priority effects may impede restoration (Dormann et al. 2000; Rinella et al. 2015). For example, in striking contrast to facilitative processes in shrub restoration in the semiarid Mediterranean (Gómez-Aparicio et al. 2004; Rinella et al. 2015), Putz and Canham (1992) found that intense competition from several shrub species for soil resources and light created strong negative

priority effects in disturbed northeastern United States forests by retarding colonization by late successional tree species. However, competitive mechanisms varied with conditions; below-ground competition was strongest in resource-poor soil and competition for light more important at fertile sites.

Although competitive priority effects can impede succession and restoration outcomes in some cases, in others competitive priority effects could enhance restoration objectives by providing resistance to exotic invaders (D'Antonio & Meyerson 2002). A number of studies suggest that giving natives a head start may help to resist invasion (Dickson et al. 2012; Ulrich & Perkins 2014; Cleland et al. 2015). For example, Delory et al. (2019a, 2019b) manipulated the timing of arrival of an exotic invasive species in Europe and the composition of the native community and found that inhibitory priority effects created by natives can decrease the risk of invasion by the exotic *Senecio inaequidens*. Stuble et al. (2016) varied the order of arrival of native and exotic species in a mesocosm experiment and found that both benefited from arriving early, but late arrival of exotic species affected their establishment less than that of late natives.

Competition among plants may be for resources, or through the release of harmful chemicals that negatively influence other species (Aschehoug et al. 2016). Allelopathy, or negative interactions mediated by chemistry, has been cited frequently as a mechanism promoting exotic invasion (Callaway & Ridenour 2004; Murrell et al. 2011), but whether allelopathic priority may frequently impede restoration is not clear. Lankau (2012) transplanted the late successional *Quercus rubra* at eight different sites where the exotic *Alliaria petiolata* occurred. These sites varied in their invasion history and soil allelochemical concentrations. He found that native seedlings grew faster at sites with a longer history of invasion and lower allelochemical concentrations. He also found that the benefits of inoculating soil with native soil biota had stronger positive effects on the growth of the native species in newly invaded sites with more highly allelopathic invader populations. Lankau's results provide circumstantial evidence for allelopathy as a direct mechanism that can influence restoration, but the chemical effects of the exotic may be indirect, functioning through the suppression of mycorrhizae (Callaway et al. 2008), as suggested by the effects of soil biota inoculation in Lankau's research.

As for indirect facilitation, indirect competition is more difficult to detect or to use in predictable ways in a restoration context than direct competition. Priority effects involving indirect competition may occur when early-arriving species attract consumers that attack desired late-arriving species in restoration, or when they create strong plant–soil feedbacks that inhibit later species. Priority effects involving indirect competition may also occur when some species modify competition among other species (Metlen et al. 2013).

Restoration success often depends on indirect relationships with beneficial soil microbes that form symbiotic relationships with plant roots (Harris 2009; Neuenkamp et al. 2019). These relationships can change over time with reciprocal feedback effects of symbionts on plants and plants on symbionts. Such

plant–soil feedbacks, which can involve the effects of soil biota as a whole, correspond with successional sequences of species (Kardol et al. 2006; van de Voorde et al. 2011), and thus are likely to affect restoration outcomes (Eviner & Hawkes 2008). We know of no experiments that have fully tested the *reciprocal* feedback process in the context of restoration (as opposed to succession), but tests of particular components suggest that the role of feedbacks in priority effects may be exceptionally strong. For example, Middleton and Bever (2012) experimented with early, mid, and late successional plant species planted near to or far from nurse plants that had received inoculation with native soil biota or not. They found negative effects of inoculation on early successional plants but positive effects of inoculation on mid to late successional plants, suggesting that feedback relationships in the context of restoration can contribute to priority effects that may be crucial to restoring late successional communities. Brinkman et al. (2017) found that conditioning degraded fen soil with plant species common in intact fen meadows produced more biomass of desired *Carex* species than when soils were conditioned with species from degraded fens. They proposed that growing typical fen meadow plant species in soil favored priority effects that improved the growth of other fen meadow species (also see Larios & Suding 2014). In contrast, Yelenik and Levine (2011) found that plant–soil feedbacks did not match patterns of reestablishment of native plant species. They reported that climate and direct competition had stronger effects on native seedlings.

Knowledge Gaps and Future Perspectives

The Need for Large-Scale and Long-Term Experimental Studies in the Field

Most of the experiments in our review lasted less than a year (24 of 43) and most of these short-term studies were performed under controlled conditions in a greenhouse (20 of 24). Although experiments performed under controlled conditions are well suited to investigate the mechanisms creating priority effects in plant assemblages, we see three main arguments calling for more long-term field experiments conducted in a variety of biomes and ecosystems. First, long-term field experiments would allow ecologists to investigate how persistent priority effects are in a variety of environments (Vaughn & Young 2015; Werner et al. 2016; Weidlich et al. 2017). Second, the setup of multiple experiments with the same design at different locations and/or different time points would allow tests of the importance of site and year effects for priority effects (Stuble et al. 2017; Werner et al. 2020). Third, we argue that some coexistence mechanisms would be more accurately tested in the field than in experiments where root growth is constrained by the size of pots or mesocosms. For instance, if the extent to which below-ground spatial resource partitioning is affected by plant order of arrival, a field experiment using resource tracers (Jesch et al. 2018) or investigating how roots are distributed in the soil (Oram et al. 2018) would be ideal.

The Need to Evaluate Other Metrics of Priority Effects in Addition to Aboveground Biomass

In experiments evaluating priority effects, aboveground biomass was the most common variable measured (27 of the 84 response variables measured, 32%; Table S2). This may not be sufficient to evaluate all aspects of priority effects, as other parameters might lead to different results. For instance, Körner et al. (2008) assessed aboveground and belowground productivity in the context of priority effects, as did Weidlich et al. (2017, 2018). Both Körner et al. (2008) and Weidlich et al. (2017, 2018) found that when legumes were sown first, plants invested less in roots and more in shoots, thus producing different directional priority effects aboveground and belowground. Results from these studies highlight that, depending on the variable measured during an experiment, we may miss important dimensions of priority effects. Additionally, the use of metrics allowing the standardized quantification of priority effects might facilitate the comparison of results between studies (e.g. Sarneel et al. 2016; Delory et al. 2019a, 2019b).

The Need to Study Priority Effects in More Biomes or Vegetation Types, and to Test Weather Effects

The large majority of studies on priority effects in our analysis were in temperate grasslands, possibly because grasslands are much more degraded by humans than other biomes. Thus, more studies are needed in other commonly restored habitats such as wetlands, forests, heathlands, and savannas. Tropical and subtropical ecosystems, which harbor many of the global biodiversity hotspots, and have received global commitments to landscape restoration (Brancalion et al. 2019a), represented only one study (2%). This paper tested the role of order of arrival in resistance to common invasive grass species (Evangelista et al. 2017). Since the mechanisms creating priority effects likely depend on environmental conditions, their importance may not be the same in biomes with different climates, species richness, consumer pressures, or susceptibilities to invasion by exotic species. In order to understand better the general importance of priority effects and their applicability for restoration activities, we argue that there is a need to set up replicated experiments testing similar priority effect scenarios in different biomes and vegetation types.

Interannual variation in weather can create “year effects” in the composition of plant communities. Thus, very similar restoration approaches may produce very different outcomes depending on the year restoration was initiated (see Vaughn & Young 2010; Werner et al. 2020). However, few studies have experimentally tested how the year of initiation of a priority effect experiment affects the structure and functioning of plant communities, and what would be the main environmental drivers. For example, the structure of experimental plant communities in California grasslands differed between years and sites (Stuble et al. 2017), illustrating the importance of weather-driven year effects in driving restoration outcomes. Using a large dataset of data collected at several grassland restoration sites, Groves et al. (2020) found that temperature and

precipitation in the planting year affected the relative dominance of different native and non-native species. If the strength and direction of priority effects are sensitive to climate conditions during early establishment, understanding local and global generalities in climate, or year effects is important.

The Need to Study How Priority Effects Determine Multiple Functions in Landscapes and Its Feasibility for Implementation in Restoration

Producing multifunctional landscapes in ecological restoration, to mitigate both biodiversity and climate issues, requires framing land management in a multifunctional landscape context (Manning et al. 2018). At times, restoring biodiversity and carbon storage can occur simultaneously, whereas in other cases achieving a key outcome may preclude achieving other important outcomes (Temperton et al. 2019). Thus, studies that measure multifunctionality are important and needed. It might be possible to create priority effects that project landscape patches toward particular trajectories, for instance, inducing communities to become more resistant to plant invasion (Hess et al. 2019), or increase biomass production and hence also methane yields for bioenergy use by sowing plant functional groups first (Popp et al. 2017). However, implications in relation to restoration goals should be pondered, striving to maximize ecosystem service bundles where possible, but also clearly weighting different desired outcomes (sensu Manning et al. 2018), since a process designed to achieve high biodiversity might be different than one aiming for increasing productivity.

Additionally, the feasibility to implement priority effects in restoration need to be tested. The cost-effectiveness of using priority effects in restoration needs to be assessed in order to verify whether, in practice, the gains of manipulating species order of arrival would compensate for the cost of a second intervention (a second sowing/planting). Recent studies have shown that ecological restoration success is higher for passive than for active restoration in tropical forests (Crouzeilles et al. 2017), and that natural and assisted regeneration is less expensive than active restoration in tropical forests (Brancalion et al. 2019b). Considering these two important findings, priority effects could be used to assist such kind of passive restoration in areas with low potential for natural regeneration, reducing further interventions and costs in the neotropics.

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Supporting Information

The following information may be found in the online version of this article:

Table S1 List of 138 articles surveyed that addressed priority effects in plants.

Table S2 Response variables (relative number) used to evaluate priority effects in the 43 studies that manipulated order of arrival.

Table S3 Main information extracted from the 43 papers that experimentally tested priority effects (compared simultaneous and nonsimultaneous sowings), as well as the references for each article.

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