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RE-NEW (OPINION) ARTICLE

Exploring the potential of using priority effects during ecological restoration to resist biological invasions in the neotropics

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Manipulating plant order of arrival, a process that creates priority effects, may be an unexplored powerful tool to hinder the establishment of invasive non-native plants in sites under restoration. Knowledge and experimental studies on priority effects in the neotropics are scarce. Here, we propose a research agenda that investigates whether manipulating plant order of arrival can create priority effects in the neotropics, and if this strategy can be used to avoid the spread of undesired species in restoration projects. We also describe our view on expanding existing knowledge on priority effects to the neotropics and identifying key questions for future research.

Key words: community assembly, competition, facilitation, invasive non-native species, plant order of arrival

Implications for Practice

- Manipulating plant order of arrival can create priority effects that may promote the early establishment of native species, creating a more resistant community to plant invasion.
- Priority effects have great potential as a novel strategy to control invasive species in restoration sites in the tropics and subtropics.
- A network of scientists that replicate similar experiments in different biomes can offset the lack of studies on priority effects in the neotropics.

As communities can develop into several alternative states after disturbance, the resulting assembly depends on specific biotic and abiotic events covered by the umbrella term historical contingency (Sutherland 1974; Bagchi et al. 2013; Fukami 2015). Priority effects, a biotic component of historical contingency, are defined as effects of differences in the order or timing of arrival of plant species or functional groups of plants, so that the organisms that arrive first on a site affect the establishment, growth, and/or reproduction of the species that arrive afterwards (Temperton et al. 2016; Weidlich et al. 2018). Priority effects can occur by niche pre-emption, when species that arrive first reduce the amount of resources available to the following ones (inhibitory effects), or by niche modification, when the species that arrive first change the niches available, hence modifying the identity of the species able to arrive afterwards (inhibitory or facilitative effects) (Fukami 2015). Both mechanisms are related to direct or indirect competition and facilitation.

A recent review on priority effects showed that 95% of the papers that experimentally manipulated plant order of arrival were performed in Europe and North America (Weidlich et al. 2020a). Additionally, there is a growing interest in understanding the role of plant order of arrival to create communities that are more resistant to plant invasions (Hess et al. 2019). In contrast, there is no specific knowledge on the role of priority effects in neotropical ecosystems, which have been increasingly invaded by non-native plants (Fine 2002; Foxcroft et al. 2010; Essl et al. 2020). Considering that the control of invasive non-native plants is often part of restoration projects/programs (Machado et al. 2020; Weidlich et al. 2020b), manipulating plant order of arrival can be an alternative strategy to thwart the establishment of invasive non-native plants by steering the community along a desired trajectory (Young et al. 2017).

Invasive non-native species are transported and introduced by human action to new regions and must overcome several barriers to establish populations beyond the point of introduction (Richardson et al. 2000; Blackburn et al. 2011). The interaction of three key factors mainly determines biological invasions: introduced species invasiveness; ecosystem invasibility; propagule pressure (e.g. number of introduction events + number of propagules released in each event) (Lonsdale 1999; Pyšek & Richardson 2007; Simberloff 2009).

Tropical forests have historically been considered resistant to biological invasions for reasons varying from fast native

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vegetation recovery after disturbance to few available ecological niches (Lonsdale 1999; Fridley et al. 2007). These reasons have been associated with the hypothesis of biotic resistance, which states that more biodiverse systems are more resistant to non-native species than ecosystems with lower biodiversity (Elton 1958; Levine & D'Antonio 1999). Thus, ecosystems with high biodiversity tend to have a low number of vacant niches (as native species fill most niches). As a consequence, non-native species have few opportunities to establish and resistance to invasion is high. However, the biotic resistance hypothesis has been supported by only a small number of studies, possibly because it is too focused on the recipient ecosystem, and not on the combination of introduced species traits and the recipient ecosystem, which may include positive interactions among native and introduced species (Jeschke et al. 2012). In the context of ecological restoration, a question that may arise is: can we induce ecosystems to become more resistant to plant invasion by manipulating the identity and order of arrival of plant species or functional groups?

The role of order of arrival of native and invasive species has been experimentally explored mainly in temperate grasslands. Overall, natives seem to be able to outcompete invasive non-native plants if they arrive first in the system. For example, studies in North America have shown that invasive non-native species can generate stronger priority effects than natives, decreasing community diversity and establishment (Goodale & Wilsey 2018), and that while native and invasive non-natives benefit from arriving earlier, only non-native species were less affected by arriving later (Stuble et al. 2016). Examples from Europe show similar patterns. Lang et al. (2017) found that an invasive shrub was suppressed by increasing the biomass of a native European grass when it was planted before the shrub arrived, while Delory et al. (2019) showed that an invasive non-native forb benefited more from arriving early than did the native European grassland community.

Even though lessons learned from studies on priority effects in temperate ecosystems can be useful, we need to apply this knowledge to the restoration of neotropical ecosystems from a different perspective. As young scientists working on biological invasions and priority effects, we recommend that the expansion of existing knowledge on priority effects in the neotropics should follow four main directions. First, we need to test whether manipulating order of arrival (native vs. native) in neotropical biomes will generate priority effects that affect community assembly. Second, we need to investigate how to steer communities toward the desired trajectory by promoting the establishment of preferred native species and resistance against invaders (native vs. invaders) at the same time. Third, cost-effectiveness needs to be assessed 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) in restoration sites. Fourth, whether priority effects are driven by climate should also be investigated, considering climate change events and the fact that they may be contingent over time (Grman et al. 2013; Werner et al. 2016). While shedding light on these main issues, it will be important to further explore the mechanisms behind priority effects, gaining a complete understanding of these processes and better planning the restoration of neotropical ecosystems.

As different ecosystems may respond in different ways to species order of arrival, these four main issues need to be explored in different neotropical biomes. For instance, the use of priority effects to control common invasive non-native grasses typically sown as forage grasses in pasture systems in Brazil (e.g. *Urochloa humidicola* or *U. decumbens*) may be system-specific. The only study that explicitly manipulated the order of arrival in a tropical ecosystem found that when a native macrophyte was planted 4 weeks before an invasive grass, the grass's establishment was thwarted (Evangelista et al. 2017). Two other studies discussed the role of early arrival species in natural regeneration in the neotropics but did not manipulate arrival (Santilli & Durigan 2014; Suganuma et al. 2014). Considering that nurse plants can be determinant for the trajectory of plant communities in different biomes in the neotropics (Dalotto et al. 2018; Sühs et al. 2018) and may benefit ecological restoration (Gómez-Aparicio et al. 2004), we propose that promoting positive priority effects to hinder the establishment of invasive plants constitutes a promising research topic to be explored in the neotropics. These studies would gain from focusing not only on forbs, grasses, and shrubs invading open ecosystems such as grasslands and savannas but also on non-native trees invading neotropical forests. Thus, to perform experiments involving the manipulation of order of arrival of different functional groups seem to be an interesting approach considering, for instance, that successful tree invaders were found to be functionally different from resident native plants in temperate and subtropical deciduous forests (Dechoum et al. 2015; Jo et al. 2015).

To efficiently test priority effects in the neotropics and combine efforts and resources, we suggest creating a network of scientists and practitioners. People engaged in this network would plan and test similar experimental designs to find patterns of priority effects (including different effect sizes) and verify their potential application in restoration activities in the neotropics in order to answer the following questions: Can plant order of arrival create priority effects in neotropical biomes that influence assembly both in terms of diversity and ecosystem function outcomes? Will patterns and mechanisms be similar to the ones already observed in temperate ecosystems, and how do they vary within and among ecosystems? Can priority effects play a role in reducing plant invasions in neotropical biomes? Is it feasible to apply existing knowledge on priority effects to restoration efforts in the neotropics? Equipped with answers to these questions, a window of opportunity to apply priority effects to improve biodiversity restoration success in the neotropics would open.

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