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REVIEW

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# Using revegetation to suppress invasive plants in grasslands and forests

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## Abstract

1. Following the removal of invasive plant species, most land managers rely on natural succession to re-establish native plant communities. However, insufficient native propagule pressure combined with legacy effects of invasive plant species means that passive approaches to restoration are often inadequate to establish native communities and prevent reinvasion.
2. In this paper, we review literature evaluating the ability of active revegetation to suppress re-establishment of invaders in grasslands and woodlands.
3. We find that existing literature consistently demonstrates reduced performance of invasive plant species in revegetated grasslands, but that the magnitude of impact on invasive plants is highly variable. In contrast, the efficacy of revegetation in woodlands has rarely been reported, but the small number of such studies are consistent with results from grasslands.
4. *Synthesis and applications*. Our review highlights the mechanisms that lead to revegetation suppressing invasive plants in grasslands and identifies knowledge gaps associated with revegetation using woody species or targeting woody invaders. We recommend concerted efforts be made to evaluate the viability of woody plant revegetation and the efficacy of revegetation in woodlands. Furthermore, we suggest that land managers may need to embrace novel species assemblages in order to prevent reinvasion.

KEYWORDS

biotic resistance, forest, grassland, invasion, limiting similarity, restoration, revegetation, seeding

## 1 | INTRODUCTION

Invasive plant species (IPS) often reduce biodiversity and degrade ecosystem function (Ehrenfeld, 2010). Most research to date on the efficacy of various IPS removal methods has been short term and has neglected the long-term resistance of forests and grasslands to reinvasion (Kettenring & Adams, 2011). However, revegetating removal areas may present opportunities to simultaneously restore native plant communities and competitively exclude IPS. While the efficacy of this approach is poorly known, the importance of managing restorations to suppress invasion is receiving greater recognition from researchers and land managers alike.

## 2 | REVEGETATION TO RESTORE NATIVE PLANT COMMUNITIES

Passive approaches to restoring native plant communities (i.e. relying on natural succession) are common and can be effective under a limited set of conditions. Some logged sections of temperate deciduous forests in eastern North America have largely recovered to reflect the composition, structure and diversity of unlogged areas (McLachlan & Bazely, 2001). More generally, passive approaches can do well when the targeted ecosystem has a high degree of natural resilience that allows native plants to regrow quickly, the surrounding landscape provides sufficient native propagule pressure for new colonization, and degradation and disturbance is relatively mild (Holl & Aide, 2011). Passive restoration is also sensitive to the methods of IPS control and site preparation, leading to distinct successional trajectories that may not reach targeted levels of diversity or productivity (Millikin, Jarchow, Olmstead, Krentz, & Dixon, 2016). More commonly, however, natural processes are insufficient to re-establish native plant communities following IPS removal (Bauer & Reynolds, 2016; Holmes, 2001; Swab, Zhang, & Mitsch, 2008), making active restoration via revegetation necessary. Here, we focus on restoring systems following IPS removal unless otherwise noted.

Invaded communities often reach quasi-stable states distinct from their pre-invasion condition (Suding, Gross, & Houseman, 2004; Suding & Hobbs, 2009). The key to a successful restoration is identifying desirable new stable states and determining how to overcome the resilience of the current state in order to transition into the new one (Cortina et al., 2006). This can be particularly difficult since removing IPS often leaves the invaded system primed for reinvasion by the same or different species (Pearson, Ortega, Runyon, & Butler, 2016). Invasion may deplete native seedbanks to the point that native species cannot exert sufficient propagule pressure to occupy the empty niche space left by IPS removal (Greet, 2016; Ogden & Rejmanek, 2005). Native species may be particularly ineffective at recolonizing following IPS removal when confronted with a strong seedbank or abundant re-sprouting of the IPS itself. Invasion also often alters soils such that IPS can receive a greater advantage from priority effects than native species (Dickson, Hopwood, & Wilsey, 2012). Indirect effects of IPS on soil biota and nutrients (Jordan, Larson, & Huerd, 2008; Perkins & Nowak, 2012) and apparent competition (Aronson & Handel, 2011) caused by preferential herbivory of native species (Dangremond, Pardini, & Knight, 2010; Orrock & Witter, 2009) can further inhibit the establishment of native plants following management. Thus, revegetation can aid in establishing native communities by increasing native propagule pressure sufficiently to overcome herbivory and legacy effects of invasion that would otherwise prevent native species establishment (Augustine & Frelich, 1998; Orrock, Witter, & Reichman, 2008). In addition to re-establishing native plant communities, revegetation provides an opportunity to increase biotic resistance against IPS.

## 3 | REVEGETATION TO SUPPRESS REINVASION: PRINCIPLES AND MECHANISMS

The role of revegetation in suppressing IPS is commonly linked to the concept of limiting similarity, wherein multiple native plant species occupy the niche space of would-be invaders (Shea & Chesson, 2002). Limiting similarity in restoration has previously been reviewed by Funk, Cleland, Suding, and Zavaleta (2008), who concluded that more functionally diverse plant communities can be effective at increasing biotic resistance when invasion is largely the result of limited native propagules, low biotic resistance via competition, or high resource availability. Restoration ecologists must also consider the traits of species at the time of their introduction to the system (Martin & Wilsey, 2014; Mwangi et al., 2007) since species' traits vary over their life cycle (Cabin, Weller, Lorence, Cordell, & Hadway, 2002). It is insufficient to only consider the traits of mature individuals since they must first possess traits that enable them to compete with IPS as juveniles and survive to maturity. However, these factors are rarely considered in depth by land managers, who commonly revegetate with the goal of increasing native diversity, reducing erosion or providing forage (Gornish, Brusati, & Johnson, 2016). Revegetation is less commonly focused on preventing future reinvasions.

In the short term, revegetation is often challenged by large stores of IPS seed in soil seedbanks left behind following years of prolific IPS seed production. These seedbanks are often stimulated into germination by disturbance associated with IPS removal, and the suppression of resulting germinants is critical to successful revegetation (reviewed by D'Antonio & Meyerson, 2002). At a minimum, land managers must design revegetation practices to compete against IPS for the length of time required to deplete the seedbank (Regan, McCarthy, Baxter, Dane Panetta, & Possingham, 2006).

The ability (or more often, inability) of many native plants to compete with IPS for diverse resources is well-documented. Competition for light can exclude some shade-intolerant species from grasslands (Blumenthal, Jordan, & Svenson, 2005; Hautier, Niklaus, & Hector, 2009) and strongly regulates community assembly, canopy regeneration and invasion in forests (Kunstler et al., 2012; Ramos, Gastauer, de Cordeiro, & Meira-Neto, 2015). In Hawaiian forests, shading by native canopy suppresses invasive grasses *Pennisetum clandestinum* (Kikuyu grass) and *Ehrharta stipoides* (Meadow ricegrass) more than it suppresses native shrubs and trees (Funk & McDaniel, 2010). These differences are associated with leaf chlorophyll content, leaf mass per area and quantum yield, suggesting that managers seeking to suppress forest invasions might be able to exploit differences in leaf traits to their benefit. Increased shading from dense native cover could aid in restoration and improve biotic resistance in forests. In temperate deciduous forests, spring ephemeral species that may offer greater resistance at the start of the growing season may not naturally re-establish following IPS control (McLachlan & Bazely, 2001). Thus, actively revegetating with these species may be an important component of competing against invasive shrubs with early spring phenology. Similarly, revegetating with deciduous species that retain their leaves later may be necessary to suppress invasive species with extended autumn phenology (Fridley, 2012). In addition to light, greater functional overlap between native species and IPS can increase biotic resistance via competition for water (Davis, Wrage, & Reich, 1998; Mason, French, & Russell, 2012) and nutrients (Hooper & Dukes, 2010), especially in grasslands.

Although direct resource competition is often presumed to be the largest contributor to biotic resistance, competition varies over time and other factors (e.g. disturbance and propagule pressure) may play larger roles in explaining the invasibility of some communities. For instance, indirect effects of productive native plant communities can also reduce invasion. Revegetation can increase litter depth, reducing germination rates for invasive species. The presence of temperate tree leaf litter reduces germination rates of the invasive *Rhamnus cathartica* (Common buckthorn) by more than 50% (Fisichelli et al., 2014). Revegetating with relatively flammable plants, such as graminoids in woodlands, can fuel fires that suppress reinvasion by woody plants (Boyce, 2010). Thus, understanding the specific mechanisms of invasion for a system undergoing restoration is essential (D'Antonio & Meyerson, 2002).

## 4 | REVEGETATION TO SUPPRESS INVASION: EVIDENCE

The efficacy of revegetation in suppressing reinvasion is rarely reported in the literature. One meta-analysis found revegetation was conducted in only a third of studies published on control of IPS between 1960 and 2009 despite consistently insufficient native propagule pressure in invaded systems (Kettenring & Adams, 2011). However, increasing interest in revegetation as a method to control IPS has produced a growing body of literature that can inform our understanding of revegetation efficacy and future research needs. To this end, we conducted a literature search using the core collection of ISI Web of Science on April 19, 2017 with keywords seed*, restoration, native, invas*, exotic and revegetation. Of the results, we considered only field experiments where IPS had been mechanically removed, or chemically treated prior to seed addition or planting of native species. Furthermore, studies had to report a metric of IPS abundance (e.g. cover) in both revegetated and not-revegetated areas following invasive control. Through this process, we identified 40 studies that tested the ability of revegetation to reduce invasion following IPS mechanical removal or chemical control (Table S1). For each selected study, we categorized the study system, the duration of the experiment, the growth form of the revegetated species, the number of species used in revegetation, the maximum number of species in any one revegetation treatment, and the growth form and identity of the managed IPS. We also evaluated the degree to which the study supported the hypothesis that revegetation reduces the performance of IPS. Studies that showed consistent reduction in IPS productivity or abundance when native species were revegetated following IPS control were categorized as supporting the hypothesis. Studies that showed context-dependent reductions in IPS performance or reductions in only some metrics of IPS performance were categorized as offering some support for the hypothesis, and those that did not find a significant reduction in IPS performance were categorized as not supporting the hypothesis (Table 1).

Overall, the majority of published studies (30 of 40) found at least partial support for revegetation reducing performance of IPS. Most studies occurred over three or fewer years (25 of 40 studies) and tested mixtures of 10 or fewer species (26 of 40 studies, Table 1). Consistent with expectations that more diverse systems are less prone to invasion (Lavorel, Prieur-Richard, & Grigulis, 1999; Tilman, 1997), 32% of studies that used species-poor mixtures (≤10 species) found no support for suppressive effects of revegetation on IPS compared to only 13% of studies that included more diverse mixtures. Similarly, short-term experiments (≤3 years) had a greater incidence of negative results than longer-term experiments (again, 32% compared to 13%).

Evidence supporting the efficacy of revegetation in suppressing reinvasion is stronger and more abundant in grasslands compared to woodlands (Figure 1a). Of the considered studies, 26 were conducted in grasslands and a large majority (85%) of those found revegetation to reduce IPS performance in at least some circumstances. For instance, seeding native grasses led to a 20% reduction in cover of the invasive forb *Potentilla recta* (Sulphur cinquefoil) 6 years after treatments in Oregon, USA (Endress, Parks, Naylor, Radosevich, & Porter, 2012). Seeding a mixture of six commercial species (*Festuca rubra*, *Lolium perenne*, *Lolium multiflorum*, *Lotus corniculatus*, *Poa pratensis*, and *Trifolium hybridum*) also resulted in a 96% reduction in cover of *Ambrosia artemisiifolia* (Annual ragweed) in European grasslands. Similarly, revegetating native prairie plants reduced light availability and impeded the overall performance of 12 herbaceous IPS in Minnesota, USA, but only in the absence of anthropogenic nitrogen enrichment (D. M. Blumenthal et al., 2005). In contrast to grasslands, few revegetation studies have been performed in woodlands. We were able to identify 11 tests of revegetation in woodlands or forests, six of which showed at least some evidence that revegetation reduces IPS success. In temperate deciduous forest, transplanting the browse-resistant grass *Elymus virginicus* (Virginia wildrye) and seeding six native forb species at 6,000 seeds/m$^2$ reduced abundance of the invasive forb *Alliaria petiolata* (Garlic mustard) regardless of browsing pressure from deer (Martinez & Dornbush, 2013). In contrast, Cuneo and Leishman (2015) found seeding herbaceous species into a woodland where invasive *Olea europaea* (European olive) had been removed initially reduced IPS abundance, but that both revegetated and non-revegetated areas had equally low IPS abundance after 3 years.

Revegetation following IPS removal rarely uses woody species or aims to suppress woody IPS. Instead, revegetation has been evaluated almost wholly within the context of herbaceous natives suppressing herbaceous IPS. Indeed, 80% of studies of herbaceous revegetation (28 of 35) found herbaceous revegetation to suppress IPS under at least some conditions and 75% of studies targeting herbaceous IPS (27 of 36) reported herbaceous IPS to be suppressed under at least some circumstance. Only five of the considered studies tested revegetation of woody native species (Figure 1b). Of those five, two found at least mixed support for woody revegetation suppressing IPS. Cabin, Weller, Lorence, Cordell, and Hadway (2002) found planting and seeding native Hawai'ian woody species increased understorey cover and reduced invasion of the grass *Pennisetum setaceum* (Fountain grass), whereas

**TABLE 1** Categorization of considered studies. Studies that showed consistent reduction in Invasive plant species (IPS) productivity or abundance when native species were revegetated following IPS control were categorized as supporting revegetation suppressing reinvasion. Studies that showed context-dependent reductions in IPS performance or reductions in only some metrics of IPS performance were categorized as offering partial support for revegetation suppressing reinvasion, and those that did not find a significant reduction in IPS performance were categorized as having no support for revegetation suppressing reinvasion

| Reference | Duration (years) | System | Revegetation growth form | Number of species[a] | Invader growth form | Invader ID[b] | Support for revegetation suppressing reinvasion |
|---|---|---|---|---|---|---|---|
| Alday et al. (2013) | 10 | Heathland | Herbaceous | 2 | Herbaceous | *Pteridium aquilinum* | None |
| Bakker et al. (2003) | 3 | Grassland | Herbaceous | 5 | Herbaceous | *Agropyron cristatum* | Partial |
| Blumenthal et al. (2003) | 7 | Grassland | Herbaceous | 18 | Herbaceous | Many | Support |
| Blumenthal et al. (2005) | 7 | Grassland | Herbaceous | 18 | Herbaceous | Many | Support |
| Cabin, Weller, Lorence, Cordell, and Hadway (2002) | 2 | Woodland | Woody | 6 | Herbaceous | *Pennisetum setaceum* | None |
| Cabin, Weller, Lorence, Cordell, Hadway, et al. (2002) | 2 | Woodland | Woody | 12 | Herbaceous | *Pennisetum setaceum* | Support |
| César, Brancalion, Rodrigues, dos Oliveira, and Alves (2013) | 1 | Woodland | Herbaceous | 1 (2) | Herbaceous | *Urochloa decumbens* | None |
| Cuneo and Leishman (2015) | 3 | Woodland | Herbaceous | 7 | Woody | *Olea europaea* | Partial |
| Cutting and Hough-Goldstein (2013) | 3 | Grassland | Herbaceous | 5 | Herbaceous | *Persicaria perfoliata* | Support |
| Davies and Bates (2014) | 4 | Woodland | Herbaceous | 3 | Herbaceous | *Bromus tectorum, Alyssum desertorum* | None |
| DeSandoli et al. (2016) | 2 | Woodland | Herbaceous | 9 (14) | Herbaceous | *Bromus tectorum, Bromus japonicus, Bromus squarrosus* | Support |
| Endress, Parks, Naylor, and Radosevich (2008) | 3 | Grassland | Herbaceous | 5 | Herbaceous | *Potentilla recta* | Support |
| Endress et al. (2012) | 6 | Grassland | Herbaceous | 5 | Herbaceous | *Potentilla recta* | Support |
| Enloe, Loewenstein, Held, Eckhardt, and Lauer (2013) | 2 | Grassland | Herbaceous | 15 | Herbaceous | *Imperata cylindrica* | Support |
| Falk et al. (2013) | 2 | Grassland | Herbaceous | 29 | Herbaceous | Many | Support |
| Gentili et al. (2015) | 1 | Grassland | Herbaceous | 6 (11) | Herbaceous | *Ambrosia artemisiifolia* | Support |
| Herron et al. (2013) | 4 | Grassland | Herbaceous | 17 | Herbaceous | *Bromus tectorum* | Support |
| Jones, Dreyer, and Barrett (2013) | 5 | Grassland | Herbaceous | 23 | Herbaceous | Many | Support |
| Knutson et al. (2014) | 21 | Woodland | Herbaceous | 28 | Herbaceous | Many | Partial |
| Larson et al. (2013) | 5 | Grassland | Herbaceous | 34 | Herbaceous | *Cirsium arvense* | Support |

*(Continues)*

**TABLE 1** (Continued)

| Reference | Duration (years) | System | Revegetation growth form | Number of species[a] | Invader growth form | Invader ID[b] | Support for revegetation suppressing reinvasion |
|---|---|---|---|---|---|---|---|
| Lawson, Ford, and Mitchley (2004) | 2 | Grassland | Herbaceous | 18 | Herbaceous | Many | Support |
| Li et al. (2015) | 1 | Grassland | Herbaceous | 1 (2) | Herbaceous | *Ipomoea cairica* | Support |
| Mahaney, Gross, Blackwood, and Smemo (2015) | 3 | Grassland | Herbaceous | 1 (6) | Herbaceous | Many | Support |
| Martin and Wilsey (2014) | 8 | Grassland | Herbaceous | 28 | Herbaceous | *Bromus inermis, Poa pratensis* | Support |
| Martinez and Dornbush (2013) | 3 | Woodland | Herbaceous | 8 | Herbaceous | *Alliaria petiolata* | Support |
| McAlpine, Howell, and Wotton (2016) | 2 | Woodland | Woody | 3 | Woody | *Pinus contorta* | None |
| Medeiros and Ferreira (2011) | 2 | Grassland | Herbaceous | 3 (5) | Herbaceous | *Eragrostis plana* | Support |
| Middleton, Bever, and Schultz (2010) | 8 | Grassland | Herbaceous | 11 | Herbaceous | Many | Support |
| Nyamai, Prather, and Wallace (2011) | 1 | Grassland | Herbaceous | 5 | Herbaceous | Many | Partial |
| Owen et al. (2011) | 2 | Woodland | Woody | 2 | Herbaceous | *Bromus tectorum* | None |
| Phillips-Mao, Larson, and Jordan (2014) | 4 | Woodland | Herbaceous | 10 | Herbaceous | *Alliaria petiolata* | Partial |
| Porensky et al. (2014) | 5 | Grassland | Herbaceous | 1 (5) | Herbaceous | Many | Partial |
| Pretorius, Esler, Holmes, and Prins (2008) | 8 | Riparian | Herbaceous | 18 | Woody | *Acacia mearnsii* | Support |
| Smith, Reinhardt Adams, Wiese, and Wilson (2016) | 1 | Grassland | Herbaceous | 4 | Herbaceous | *Ruellia simplex* | None |
| Suding and Gross (2006) | 2 | Grassland | Herbaceous | 22 | Herbaceous | Many | None |
| Török et al. (2010) | 2 | Grassland | Herbaceous | 3 | Herbaceous | Many | Support |
| Vranjic, Morin, Reid, and Groves (2012) | 3 | Sand Dune | Woody | 3 | Woody | *Chrysanthemoides monilifera* | Partial |
| Wilcox, Healy, and Zedler (2007) | 2 | Grassland | Herbaceous | 33 | Herbaceous | *Phalaris arundinacea* | None |
| Woods, Fehmi, and Backer (2012) | 2 | Grassland | Herbaceous | 6 | Herbaceous | *Pennisetum ciliare* | None |
| Young, Barney, Kyser, Jones, and DiTomaso (2009) | 5 | Grassland | Herbaceous | 6 (18) | Herbaceous | *Centaurea solstitialis* | Partial |

[a]The total number of species considered is provided in parentheses for studies that did not test a complete mixture and only tested subsets of species.
[b]Invader ID for studies that consider four or more invasive species or that do not identify invasive plants to the species level is listed as “many”.

Owen, Sieg, and Gehring (2011) found seeding native shrubs to be ineffective at suppressing the grass *Bromus tectorum* (Cheatgrass). Notably, Knutson et al. (2014) was not included in our evaluation of woody revegetation despite including shrubs in their seed mixture because seeding failed to affect shrub cover. We identified four studies that targeted woody IPS with revegetation (Figure 1c): three of these four studies reported woody IPS to be suppressed by revegetation under at least some circumstance. The strongest support for suppression of woody IPS was provided by experiments that revegetated with herbaceous species (Table 1). Based on these few case studies, woody invaders may be good candidates for suppression via revegetation, but woody invaders may be better suppressed by herbaceous than woody species due to many herbaceous species' ability to establish and spread more quickly and land managers' ability to feasibly provide sufficient propagule pressure (Kimball et al., 2015). In comparison to herbaceous species, many woody species have slow growth rates and limited commercial seed availability. Therefore, in order to establish sufficient cover of many woody species to compete with IPS over short time periods, planting juveniles at high density would be necessary. Few studies reported transplanting seedlings of woody species as a method of revegetation (Cabin, Weller, Lorence, Cordell, Hadway, et al., 2002; Gabler & Siemann, 2013).

The outcome of revegetation efforts can be highly variable. The small number of studies we identified and the diverse methods and metrics used within those studies prevent us from conducting a robust meta-analysis. However, studies that supported the efficacy of revegetation reported IPS cover or biomass to be reduced 11%–94% by revegetation (Blumenthal, Jordan, & Svenson, 2003; Herron, Jonas, Meiman, & Paschke, 2013). Although it is important to consider these responses within the context of potential positive-outcome publication bias (Fanelli, 2012), this wide range emphasizes that the results of restoration efforts may be context dependent and that there is a need to identify which conditions maximize the ability of revegetation to suppress IPS.

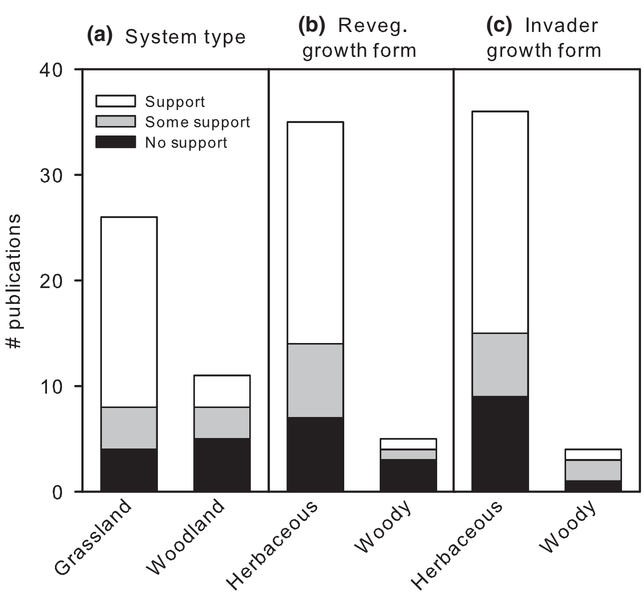


**FIGURE 1** The number of publications assessed to support (white), partially support (grey), and not support (black) the hypothesis that revegetating sites where invasive plants were removed or controlled suppresses invasive plant regeneration. Studies are partitioned by (a) system type, (b) the growth form of plants used in revegetation efforts and (c) the growth form of the targeted invasive species

## 5 | RESEARCH NEEDS: WOODLANDS AND WOODY INVADERS

The current literature largely supports herbaceous revegetation (mostly via seeding) reducing reinvasion following IPS removal in grasslands, but data are insufficient to evaluate the efficacy of revegetation for suppressing reinvasion outside of this context, particularly over a longer term and in settings with continued ecological management (e.g. follow-up herbicide applications, managed grazing, prescribed burns, etc.). Further research is needed to evaluate the ability of revegetation to suppress IPS in diverse settings and through a variety of methods.

Woodlands are drastically under-represented in the revegetation literature. This can be partially explained by mature forests being less easily invaded than successionally younger forests and grasslands, potentially due to many IPS' low shade tolerance (Flory & Clay, 2006). There may be less demand for revegetation in woodlands, yet some of the most damaging IPS are still able to establish under almost full light interception (Funk, 2013). Common buckthorn (*Rhamnus cathartica*), a woody IPS in North America, can tolerate extremely low light availability (Grubb, Lee, Kollmann, & Wilson, 1996), allowing it to exclude native species even in some of the darkest forests (Knight, Kurylo, Endress, Stewart, & Reich, 2007; Kurylo, Knight, Stewart, & Endress, 2007). Revegetation may be able to increase the resistance of these systems by elevating native propagule pressure, cover and light interception beyond what would occur without human intervention, although establishing sufficient cover to affect IPS may be challenging. Revegetation could potentially also suppress functionally similar *Frangula alnus* (formerly *Rhamnus frangula*, Glossy buckthorn), which also invades darker woodlands. Since *F. alnus* is less shade tolerant than *R. cathartica* (Cunard & Lee, 2009), it may be less challenging to identify plant communities capable of suppressing it. However, most restoration experiments focus on short-term, small-scale grassland community dynamics (Kettenring & Adams, 2011) and do not consider the longer and larger scale dynamics associated with woody plants. Even outside the context of revegetation following IPS removal, the use of woody plants in restoration is uncommon (Padilla & Pugnaire, 2006). Concerted efforts are needed to evaluate the practical and economic feasibility of woody species revegetation as well as the impacts of revegetation on woody IPS.

## 6 | SPECIES SELECTION FOR USE IN REVEGETATION

If IPS are able to re-establish from seedbanks or resprouts more rapidly than native species can establish (Pearson et al., 2016), how can revegetation efforts relying on competition be successful? Successful revegetation relies on exploiting priority effects and niche pre-emption to establish dense cover quickly. In light-limited environments, this means revegetated species must be established before IPS can grow taller than them and escape light competition. One way this can be achieved is by seeding fast-growing native species, including ruderals, at high densities where light and other environmental factors permit (Foster et al., 2007; Iannone, Galatowitsch, & Rosen, 2008). This contrasts with a common focus on planting climax species that are intended to eventually dominate the revegetated community. Additionally, planting juveniles of competitive native species can partially alleviate priority effects that benefit IPS over native species in areas that were heavily invaded and have a well-established seedbank (Kim, Ewing, & Giblin, 2006; Knight, 2006; Stuble & Souza, 2016).

Invasive species with traits that are uncommon amongst the native community can sometimes establish with little resistance (Gilbert & Lechowicz, 2005). This phenomenon suggests that current invasions are at least partially attributable to insufficient biotic resistance from the historic community (Levine, Adler, & Yelenik, 2004) and that novel communities may provide greater resistance (D'Antonio & Meyerson, 2002; Hobbs, Higgs, & Harris, 2009). Consequently, the assemblages of native species that best suppress reinvasion by IPS may often be distinct from the perceived historic, un-invaded state. For example, stands of the tree *Acer saccharum* (Sugar maple) can create exceptionally heavy shade and be resistant to invasion of *R. cathartica* in northeastern North American (McCay & McCay, 2009). In the same region, stands of oak trees (*Quercus* spp.) and other less shaded forests can be easily invaded (Kurylo et al., 2007). Managers and stake-holders may prefer attempting to maintain oak-dominated systems over incorporating additional species. However, intense planting of *A. saccharum* could potentially increase biotic resistance of some oak systems to invasion and be more desirable than a IPS-dominated community. If land managers must choose between a native community that is different than the historic one and a highly invaded community, the former may often be the better option given the economic and ecological costs of invasion (Ehrenfeld, 2010; Pimentel, Zuniga, & Morrison, 2005).

It may be necessary to select species for revegetation with phenology that closely resembles that of the targeted IPS even if those revegetation species were not historically present at the site, since many woody IPS in deciduous forests escape competition from native species by displaying leaves for longer periods than native species (Fridley, 2012). As phenology of native and invasive species respond differently to climate, species that once had poorly matched phenology may become more similar (Buitenwerf, Rose, & Higgins, 2015; Fisichelli et al., 2014; Gill et al., 2015). Some IPS that keep their leaves well into the autumn are unable to extend their photosynthetic period even further with warming because photoperiod presents a constraint that is independent of climate (Gallinat, Primack, & Wagner, 2015), so natives that keep their leaves longer due to warming may be able to "catch up" to IPS and offer greater competitive resistance in the future. Continued changes in climate will likely alter competitive interactions between native and invasive species (Bradley, Blumenthal, Wilcove, & Ziska, 2010), so there is a need to evaluate the ability of species used in revegetation to suppress reinvasion within the context of projected changes in $CO_2$, temperature and rainfall.

Non-invasive, non-native species may present a viable option for out-competing IPS when native species are not well-suited, either due to growth requirements or vulnerability to exclusion by IPS (D'Antonio & Meyerson, 2002). For example, the non-native mangrove trees *Sonneratia apetala* (Sonneratia mangrove) and *Sonneratia caseolaris* (Firefly mangrove), while not themselves invasive, have been shown to control the invasive grass *Spartina alterniflora* (Smooth cordgrass) (Zhou et al., 2015). However, using non-native species for revegetation is unattractive for many conservationists due to a desire to recreate perceived historical conditions and risks associated with species introductions (Gornish et al., 2016). In a survey of 192 Californian land managers, fewer than half reported that they had used non-native species for revegetation (Gornish et al., 2016). Despite apprehension by some land managers, revegetation using non-native species may create more functional communities than an alternative IPS-dominated system (D'Antonio & Meyerson, 2002). The use of non-native species may also be more acceptable when used to provide transient cover that suppresses IPS until slower growing native species displace the planted non-native species. For instance, non-native *Sonneratia apetala* (Sonneratia mangrove) grows faster than native *Aegiceras corniculatum* (Black mangrove) in the open, but slower than *A. corniculatum* under self-shading, suggesting that this non-native species could rapidly re-establish mangroves and then give way to native mangroves over time in some systems (Chen, Peng, Li, Lin, & Zeng, 2013). The time required to transition from non-native to native cover is likely to vary by species: short-lived herbaceous species may more readily give way to more shade-tolerant native species compared to longer lived woody species. Non-native annual agronomic plants (e.g. Italian ryegrass, *Lolium multiflorum*) establish quickly and affordably at high density, allowing them to serve as transient cover until native species establish sufficiently well to suppress invasion (DeSandoli, Turkington, & Fraser, 2016; Gentili, Gilardelli, Ciappetta, Ghiani, & Citterio, 2015; Macdonald, Snively, Fair, & Landhaeusser, 2015). Woody species should be allowed to persist as long as needed to deplete targeted IPS in the seedbank (see Regan et al., 2006), but could potentially be removed afterwards to facilitate the transition into a community dominated by native species. Tests are needed of the efficacy of different native and non-native species for IPS suppression in various ecological contexts. Furthermore, the methods used to establish these species following IPS removal must be evaluated relative to the social and economic constraints faced by land managers. These practices, if found to be effective, need to be deliberately presented to land managers, since restoration is often based on managers' personal experience and anecdotal trials with little input from peer-reviewed literature or controlled experiments (Matzek, Covino, Funk, & Saunders, 2014).

## 7 | MANAGEMENT CONSIDERATIONS AND RISKS

Of the studies we examined, those that include more species-rich revegetation mixtures had a lower incidence of finding negative results (Table 1), potentially due to more diverse mixtures incorporating more diverse ways of suppressing IPS. Land managers that design more diverse revegetation mixtures to utilize multiple mechanisms may have greater success in suppressing IPS (Larson et al., 2013). Competition for water and nutrients can be an important component to the success of revegetation, particularly in resource-poor environments (Funk et al., 2008; Owen et al., 2011). Additionally, the ability of revegetation to withstand allelopathic impacts of IPS (Hierro & Callaway, 2003; Orr, Rudgers, & Clay, 2005) or to combat IPS with their own allelopathy (Fabbro, Güsewell, & Prati, 2014) can facilitate successful revegetation despite differences in plants' competitive abilities. Therefore, there are potentially multiple mechanisms through which revegetation can affect IPS at any particular site in addition to competition for light.

In addition to boosting species richness, species used in revegetation may have long-lasting impacts on the structure and function of ecosystems. The suppressive effects of revegetation on IPS can also reduce recruitment of native species and therefore limit the composition of future successional stages (Belsky, 1994; Bond, 2008; Holl, 1998; Hooper, Legendre, & Condit, 2005; McCormick & Bowersox, 1997). However, some species, particularly shrubs, can facilitate the establishment of late-successional woody species by improving microsite conditions when used in revegetation in resource-poor environments (Gomez-Aparicio et al., 2004; Padilla & Pugnaire, 2006; Yelenik, DiManno, & D'Antonio, 2015). While preventing reinvasion must be a priority if restorations are to be successful, land managers should also consider the consequences of revegetation for successional trajectories.

The use of non-native species in revegetation presents distinct risks. A major challenge is that it is impossible to know if a currently non-invasive species will become invasive in the future. Indeed, traits that would allow non-native species to suppress invaders are traits that many invasive species themselves possess (Leishman, Haslehurst, Ares, & Baruch, 2007), and non-native species can still inhibit native regeneration even if they do not become invasive (Flory & Clay, 2010; Knutson et al., 2014; Rydgren et al., 2016). Some agronomic species (e.g. *Lolium* spp.) can become invasive in frequently disturbed systems, especially grasslands, due to a lack of competition from native species (Stromberg, Corbin, & Antonio, 2007). Therefore, these species may be best-suited for use in forests, where disturbance is low and native canopy and understorey plants can offer sufficient competition to prevent long-term dominance of agronomic cover plants (Carter & Ungar, 2002; Papanastasis, 1976). Invasiveness metrics like the Z function (Rejmanek & Richardson, 1996), which considers reproductive physiology to rate a species' potential invasiveness, can be potentially useful in identifying species for revegetation. The Z function is based exclusively on *Pinus* spp., but similar functions could be developed for other taxa to help select non-native species that are competitive but lack the high reproductive output associated with many invasive species.

## 8 | CONCLUSIONS

The ability of revegetated native plants to suppress invasion is likely a critical component of successful grassland restorations, but it remains unclear how well the same mechanisms apply to woodlands and woody invaders. By investigating the efficacy of revegetation in woodlands, ecologists may be able to identify practical, long-term approaches to woodland restoration that simultaneously increase native biodiversity, improve ecosystem function and reduce invasibility. Restoration objectives may need to be altered to result in a community with high biotic resistance to invasion. This includes considering transitioning systems from their historical composition into something novel, potentially including the use of non-invasive exotic species.

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### AUTHORS' CONTRIBUTIONS

M.J.S. and P. D.W. gathered literature, M.J.S. analysed literature and wrote the manuscript with P.D.W. and P.B.R. contributing to interpretation and presentation of findings. All authors provided final approval for publication.

### DATA ACCESSIBILITY

Data available via the Data Repository for the University of Minnesota https://doi.org/10.13020/d6jx0p (Schuster, Wragg, & Reich, 2018).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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