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REVIEW ARTICLE

Barriers to ecosystem restoration presented by soil legacy effects of invasive alien N_2-fixing woody species: implications for ecological restoration

Mlungele M. Nsikani[1,2], Brian W. van Wilgen[1], Mirijam Gaertner[1,3,4]

Impacts of invasive alien N_2-fixing woody species and how they can persist as soil legacy effects after invasive species control are well appreciated, but how soil legacy effects can present barriers to restoration is poorly understood. Finding better ways to deal with these barriers to restoration is essential to improving restoration outcomes. In this study, we review 440 studies to identify barriers to restoration and potential management actions for the barriers to restoration, and provide practical application examples of the management actions. Our findings suggest that altered soil microbial communities, depleted native soil seed banks, elevated N status, secondary invasion and weedy native species dominance, and reinvasion are potential barriers to restoration. Furthermore, carbon addition, litter removal, soil microbial treatments, establishing species adapted to low N levels, prescribed burning, classical biological control, grazing, mowing, herbicide or graminicide application, manual weeding, soil N management, soil solarization, weed mats, native species reintroduction, and nurse plants are potential management actions for these barriers to restoration. However, there is little evidence suggesting that several of these barriers to restoration hinder improved restoration outcomes and this could be due to little research on them. More research is needed to assess their relative importance in hindering improved restoration outcomes. Management actions are rarely applied in combination, despite that they often address distinct barriers to restoration. Management actions should be combined into an integrated management effort to improve restoration outcomes.

Key words: barriers to restoration, biological invasion, legacy effects, management, N_2-fixing, woody species

Implications for Practice

- To address barriers to restoration from soil legacy effects of invasive alien N_2-fixing woody species during restoration, if available, classical biological control could be established to reduce seed production and seed banks.
- Where appropriate, prescribed burning could be applied after clearing the invasive species. However, where burning is inappropriate, litter could be manually removed. Subsequently, soil solarization or weed mats could be set up to reduce establishment of secondary invaders, weedy native species and a second generation of the invasive species. Mowing, manual weeding, grazing, herbicide or graminicide application could be used to manage any resulting vegetation.
- Subsequently, soil carbon addition and microbial treatments could be applied and native species reintroduced with or without the aid of nurse plants.

Introduction

The widespread introduction of plant species to areas outside of their natural distribution ranges has led to some becoming invasive (Vitousek et al. 1997). Many of these invasive alien species are trees and shrubs (Richardson & Rejmánek 2011) and some are nitrogen-fixing such as Australian acacias (Richardson et al. 2011). Invasive N_2-fixing woody species often transform ecosystems by altering ecosystem processes and displacing native species (Vilà et al. 2011). The negative impacts of invasive N_2-fixing woody species on the soil include altered soil chemistry (Ehrenfeld 2003), establishment of large seed banks (D'Antonio & Meyerson 2002; Richardson & Kluge 2008), deposition of novel allelochemicals (Callaway & Ridenour 2004), and altered soil microbial community composition and function (Inderjit & Van Der Putten 2010). Mechanisms underlying such impacts are well documented (e.g. Levine et al. 2003; Vilà et al. 2011).

Worldwide efforts are underway to clear invasive species and restore historical ecosystems (D'Antonio & Meyerson 2002;

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[1]Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, Stellenbosch, South Africa
[2]Address correspondence to M. M. Nsikani, email mllue06@gmail.com
[3]Invasive Species Unit, Environmental Resource Management Department, City of Cape Town, Westlake Conservation Office, Ou Kaapse Weg, Tokai, 7966, Cape Town, South Africa
[4]Nürtingen-Geislingen University of Applied Sciences (HFWU), Schelmenwasen 4-8, 72622, Nürtingen, Germany

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Suding et al. 2004). It is often assumed that negative impacts of invasive species will diminish after clearing (Wittenberg & Cock 2005), but this is not always the case because the invasive species can leave persistent legacy effects (i.e. measurable changes to biological, chemical, or physical conditions) in the soil (Corbin & D'Antonio 2012). Ecophysiological traits of invasive N_2-fixing woody species (e.g. early and high production of seeds with long dormancy periods, high growth rates, and increasing the N content of N-limited soil) contribute to the persistence of soil legacy effects after their clearing (Pyšek & Richardson 2007). Numerous legacy effects of invasive species have been identified (reviewed by Corbin & D'Antonio 2012). Restoration of historical ecosystems hence often fails after invasive species clearing, probably because soil legacy effects create barriers to restoration (Corbin & D'Antonio 2012).

A growing number of studies describe how soil legacy effects present barriers to restoration after removal of invasive N_2-fixing woody species (Appendix S2) while others present potential management actions to address these barriers to restoration (Appendix S3). Efforts have been made to review potential management actions for these barriers to restoration (e.g. Perry et al. 2010), but these have only focused on management of individual barriers to restoration. We still lack a broad review of barriers to restoration presented by soil legacy effects and management actions that could potentially be used to address them. In this study, we review (1) how soil legacy effects present barriers to restoration after invasive N_2-fixing woody species clearing; (2) potential management actions to address those barriers to restoration; and (3) we give practical examples of their application. To maximize the usefulness of the review to restoration practice, we discuss all soil legacy effects of invasive alien N_2-fixing woody species, not just those directly related to N_2-fixation and elevated soil N.

Table 1. Combinations of search terms designed to locate studies that document barriers to restoration presented by soil legacy effects of invasive alien N_2-fixing woody species and potential management actions to address them.

Barriers to restoration and potential management actions specific to invasive N_2-fixing woody species	*Potential management actions for barriers to restoration that also apply to invasive non-N_2-fixing woody species*	*Potential management actions for each identified barrier to restoration*
exotic* OR invasive* OR invasion* OR alien* OR invader* OR non-native* OR nonnative AND nitrogen-fix* OR nitrogen fix* OR dinitrogen-fix* OR dinitrogen fix* OR N-fix* OR N fix* OR N2-fix OR N2 fix OR actinorhizal* OR legume* OR leguminous* OR root nodule* AND impact* OR effect* OR legacy* OR legacies* OR legacy effect* AND native* OR indigenous* OR restoration* OR recovery* OR reestablishment* OR return* OR manage*	exotic* OR invasive* OR invasion* OR alien* OR invader* OR non-native* AND legac* OR residual* OR long lasting* AND restor* OR recover* OR return* OR manage*	seed bank* OR seedbank* OR microbe* OR reinvasion* OR secondary invad* OR ruderal* OR soil nitrogen* AND native* OR indigenous* OR restor* OR recover* OR return* OR manage* OR reestablishment*

Methods

We searched for relevant articles on the ISI Web of Science database (http://www.webofknowledge.com) with no restriction on publication year, using a range of keywords (Table 1) designed to locate articles that document barriers to restoration presented by soil legacy effects of invasive alien N_2-fixing woody species and their management. Abstracts of retrieved articles were read and those relevant to this study were selected and the full paper content read.

Results

We identified 440 articles (35 on barriers to restoration, 399 on management actions, and 6 discussing both aspects; Appendix S1) that were relevant to this study. Some of those articles were reviews (e.g. Le Maitre et al. 2011) that included studies from the "gray literature"; therefore, we achieved a reasonably good coverage of the literature on barriers to restoration and their management, not restricted to that indexed in the Web of Science. We identified that elevated N status, secondary invasion and weedy native species dominance, reinvasion, depleted native soil seed banks, and altered soil microbial communities have all been noted as barriers to restoration following clearing of invasive, N_2-fixing woody species (Fig. 1). We further identified that carbon addition, litter removal, soil microbial treatments, establishing species adapted to low N levels, prescribed burning, classical biological control, and grazing are methods that have been used to manage these barriers to restoration (Fig. 2). Furthermore, mowing, herbicide or graminicide application, manual weeding, soil N management, soil solarization, weed mats, native species reintroduction, and nurse plants are methods that have been used to manage these barriers to restoration (Fig. 2).

Barriers to Restoration

The subject of barriers to restoration presented by soil legacy effects of invasive N_2-fixing woody species has not been

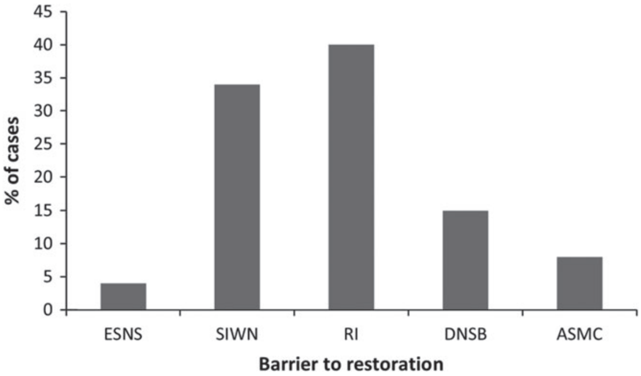

Figure 1. Percentage of cases ($n = 53$) identified from 41 studies describing barriers to restoration presented by soil legacy effects of invasive alien N_2-fixing woody species included in this review. ASMC, altered soil microbial communities; DNSB, depleted native species' soil seed banks; ESNS, elevated soil N status; RI, reinvasion; SIWN, secondary invaders and weedy native species.

extensively reported in the literature as shown by the small number (41) of publications selected for this review. Many important concepts are described by relatively few studies, with a strong bias towards certain regions—e.g. the United States (Appendix S2). While more, and as yet unidentified, barriers to restoration may exist, we believe that the few available studies have allowed us to develop a fairly robust picture of how legacy effects of invasive N_2-fixing woody species could present barriers to restoration. Each of the barriers to restoration is described in the following subsections.

Elevated Soil N Status. Invasive N_2-fixing woody species generally increase soil N through N_2-fixation and production of N-rich litter (Vitousek & Walker 1989; Malcolm et al. 2008). After clearing, elevated N content and availability, and altered N mineralization, can persist and increase further with decomposition of invader litter and roots that remain. Alterations to soil N status are often measured through soil sample analysis by comparing non-invaded, invaded, and/or previously invaded sites (Yelenik et al. 2004; Von Holle et al. 2013). Native species in some habitats are adapted to low soil N—e.g. pine-oak systems in the United States; hence, persistent elevated soil N status can directly hinder restoration by negatively affecting their germination, growth, diversity, and/or indirectly hinder restoration by giving a competitive advantage to weedy species adapted to high N availability (Rice et al. 2004).

Secondary Invasion and/or Weedy Native Species Dominance. Seeds of alien or native nitrophilous species can be present in the soil seed bank of restoration sites or disperse to such sites from surrounding areas (Yelenik et al. 2004; Pearson et al. 2016). These nitrophilous species are often more competitive than native restoration species under high N conditions (Pearson et al. 2016). Such species often take advantage of the conditions created by removing invasive N_2-fixing woody species to establish (Pearson et al. 2016). Moreover, the elevated soil N status created by the invasive N_2-fixing woody species facilitates such species' growth and dominance (Vitousek & Walker 1989; Le Maitre et al. 2011). Secondary invaders and weedy native species have been observed to hinder restoration by limiting the growth of native restoration species (Maron & Connors 1996; Yelenik et al. 2004; Marchante et al. 2009; Von Holle et al. 2013).

Reinvasion. Invasive N_2-fixing woody species often produce copious amounts of seed that can persist in the seed bank for extended periods (Oneto et al. 2010). This often leads to germination and reinvasion after clearing. Furthermore, clearing the invasive species often leaves roots or stumps of the plants, which can resprout in some cases (Shortt & Vamosi 2012; Souza-Alonso et al. 2013). Reinvasion of restoration sites (through persistent seed and/or vegetative propagules) allows the invasive species to once again dominate the ecosystem, leading to failed restoration (Holmes & Cowling 1997).

Depleted Native Soil Seed Banks. Invasive N_2-fixing woody species often compete with and exclude native species (Vilà et al. 2011). The exclusion of native species can lead to depleted native soil seed banks—due to native species becoming greatly reduced in numbers, and with survivors producing less seed as they either do not reach maturity or do not flower under the canopy of the invader. After clearing the invasive species, the depleted native soil seed banks often become a barrier to reestablishment of native communities (Malcolm et al. 2008; Le Maitre et al. 2011).

Altered Soil Microbial Communities. Invasive N_2-fixing woody species can alter the soil microbial community composition, diversity, and function through several mechanisms such as deposition of allelochemicals and introduction of novel microbes (Inderjit & Van Der Putten 2010). The soil mycorrhizal community and symbioses of native species are often disrupted and such changes can persist after clearing the invasive species and limit the germination and/or growth of native species (Corbin & D'Antonio 2012; Boudiaf et al. 2013).

Management of Barriers to Restoration

These barriers to restoration can be addressed using a range of appropriate management actions (Table 2). Potential management actions for different barriers to restoration are described and illustrated using selected examples below.

Elevated Soil N Status. Prescribed burning can be used to remove the invasive species' litter to prevent it from contributing to the soil N pool in the long term (Mitchell et al. 2000). The slash can be spread over the restoration site and burnt, instead of being stacked before burning (DiTomaso et al. 2006). Prescribed burning will initially cause a strong pulse of released N previously immobilized in the litter (Fenn et al. 1998). A significant portion of the released N will be volatilized (Riggan et al. 1994; Marchante et al. 2009), whereas released NH_4^+ will probably be nitrified after burning and result in leached NO_3^- (Dunn et al. 1979). Repeated burning can deplete soil N through

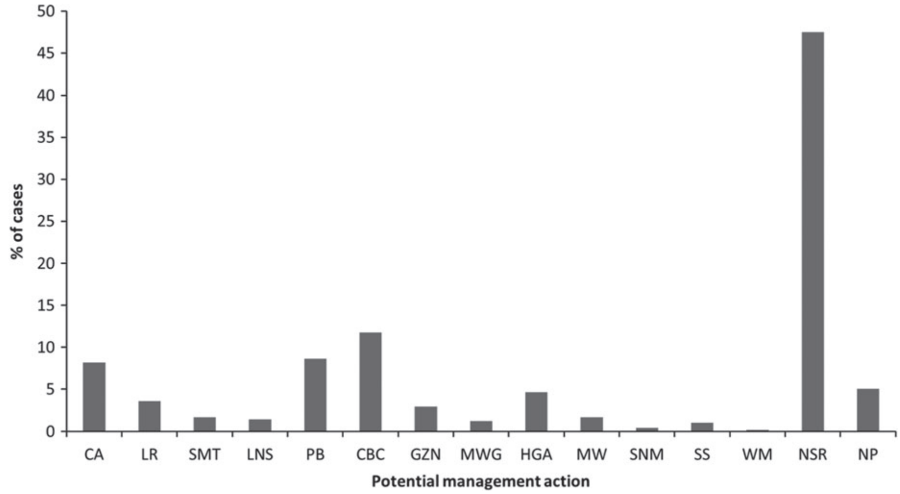

Figure 2. Percentage of cases ($n = 476$) identified from 405 studies describing potential management actions to address barriers to restoration presented by soil legacy effects of invasive alien N_2-fixing woody species included in this review. CA, carbon addition; CBC, classical biological control; GZN, grazing; MWG, mowing; HGA, herbicide or graminicide application; LNS, establish species adapted to low N levels; LR, litter removal; MW, manual weeding; NP, nurse plants; NSR, native species reintroduction; PB, prescribed burning; SMT, soil microbial treatments; SNM, soil N management; SS, soil solarization; WM, weed mats.

Table 2. Potential management actions to address barriers to restoration presented by soil legacy effects of invasive alien N_2-fixing woody species.

	Barrier to Restoration				
Management action	*Elevated soil N status*	*Secondary invaders and weedy native species*	*Reinvasion*	*Depleted native soil seed banks*	*Altered soil microbial communities*
Soil carbon addition	X				
Litter removal	X				X
Soil microbial treatments					X
Establishing species adapted to low N availability	X				
Prescribed burning	X	X	X		
Classical biological control			X		
Grazing		X	X		
Mowing		X	X		
Herbicide or graminicide application		X	X		
Manual weeding		X	X		
Soil N management		X			
Soil solarization		X	X		
Weed mats		X	X		
Native species reintroduction				X	
Nurse plants				X	

repeated volatilization (Prober et al. 2005). For example, in grasslands of the United States repeated burning reduced total N by up to 40% in the top 10 cm of the soil (Haubensak et al. 2004). There is a need to consider the effects of fire on restoration sites because the application of fire may be inappropriate for some habitat types—e.g. riparian zones (Richardson & Kluge 2008). In areas where the use of fire is inappropriate, manual techniques such as raking can be used to remove the invasive species' litter (Elgersma et al. 2011). However, such techniques are labor intensive and logistically limited to small areas.

Labile carbon sources such as sawdust and sucrose can be added or leached into the soil to immobilize soil N (Blumenthal et al. 2003**;** Prober & Thiele 2005). Briefly, the added carbon increases soil microbial biomass and activity—by serving as a substrate for heterotrophic soil microbes, which in turn increases microbial N uptake and lowers soil N availability (Baer et al. 2003). Furthermore, carbon addition in anaerobic soils can increase the activity of denitrifying bacteria and increase N loss through denitrification (Perry et al. 2010). For example, in a coastal sage scrub in the United States, addition of organic mulch resulted in a significant decrease in soil N availability (Zink & Allen 1998). Success of carbon addition depends on whether or not soil microbes are C-limited, method and duration of application, environmental conditions, habitat type, and target species (Rice et al. 2004; Prober & Thiele 2005), and its long-term effects are often difficult to predict (Török et al. 2014). Furthermore, the success of carbon addition may be hindered because it is labor intensive and expensive to apply at large scale (Perry et al. 2010).

Many species adapted to low N availability can lower soil N because they produce high C:N litter, which slows N cycling, and they have lower minimum N requirements, which allow them to continue to grow and capture more limited available N (Perry et al. 2010). Therefore, establishing species adapted to low N availability in the site designated for restoration can ultimately lower soil N (Perry et al. 2010). For example, the establishment of native *Themeda australis* in temperate grassy woodlands significantly reduced soil N availability (Prober et al. 2005). Native restoration species in areas invaded by N_2-fixing woody species are often adapted to low N availability; hence, waiting for them to establish from their soil seed banks, seeding, or transplanting them (i.e. if soil seed banks are depleted) in restoration sites may be appropriate. Furthermore, use of nurse plants adapted to low N availability during native species reintroduction could potentially lower soil N. However, establishment of species adapted to low N availability may not significantly lower soil N over short time scales or when certain N levels have been reached (Perry et al. 2010). Repeated prescribed burning can favor species adapted to low N availability (Perry et al. 2010). For example, in an oak savanna in the United States, repeated prescribed burning led to a shift from oak to grass dominance and a subsequent decline in soil N levels due to low tissue N concentrations in grasses (Dijkstra et al. 2006).

Secondary Invasion and Weedy Native Species Dominance. Establishment of secondary invaders and weedy native species can be reduced through soil solarization (i.e. heating the soil surface by covering with a plastic sheet) or setting up weed mats (i.e. woven plastic mats that allow passage of water but prevent emergence of seedlings) in restoration sites. For example, weed mats set up in a coastal dune cleared of *Lupinus arboreus* reduced the establishment of secondary invaders (Pickart et al. 1998). However, the cost and logistical challenges restrict the use of soil solarization or weeds mats to small areas (Pickart et al. 1998; Richardson & Kluge 2008).

Secondary invaders and weedy native species that establish can be manually weeded, mowed, selectively grazed (Maron & Jefferies 2001; Gooden et al. 2009; Milchunas et al. 2011), or controlled through herbicide or graminicide application (Szitár et al. 2016). For example, mowing followed by biomass removal during restoration of coastal prairie grasslands reduced the abundance of secondary invaders (Maron & Jefferies 2001). If grazing or mowing are used to control secondary invaders and weedy native species, season, intensity, and duration of application need to be considered to obtain satisfactory results and avoid negative ecological consequences (Milchunas et al. 2011; Dee et al. 2016). Appropriate herbicides or graminicides should be selected and proper timing of their application, toxicity, residence times, and specificity should be carefully considered (Hobbs & Humphries 1995; Oneto et al. 2010). The technique used to apply the herbicide or graminicide would depend on the size of the restoration site—e.g. broadcast foliar treatment for large areas and drizzle technique for small areas (Oneto et al. 2010).

Invasive alien and weedy native species often prefer high N availability (D'Antonio & Meyerson 2002; Pearson et al. 2016); hence, their dominance can decline if elevated soil N is addressed with soil N management, as described above (Kulmatiski 2011). For example, reduction of N availability after the death of *L. arboreus* significantly reduced the abundance of secondary invaders (Alpert & Maron 2000).

Reinvasion. To address reinvasion by N_2-fixing, invasive alien plants, classical biological control can be set up when available to reduce seed production and seed banks over time (Buckley et al. 2004). For example, long-term classical biological control of invasive *Acacia* spp. in South Africa using nine insect species and a fungus has led to significant reductions in their seed production, seed banks, and distribution (Moran & Hoffmann 2012). However, It should be noted that biological control is not a quick-fix solution to reduce persistent seed banks (Moran & Hoffmann 2012). Furthermore, predation rate of biological control agents should be high (>90%) for classical biological control to be effective (Noble & Weiss 1989). Biological control agents often take time to establish but once established they can be efficient in reducing fecundity of invasive species by destroying their flowers, buds, or pods (Holmes & Cowling 1997; Buckley et al. 2004).

Numerous invasive species accumulate persistent soil seed banks characterized by seeds that need a heat pulse to break dormancy (Richardson & Kluge 2008). Therefore, persistent soil seed banks can be reduced by triggering mass germination through prescribed burning using low-intensity fires after clearing the invasive species (Holmes & Cowling 1997). Use of low-intensity fires is recommended because high-intensity fires tend to destroy native seeds and seedlings that may be present on restoration sites (Richardson & Kluge 2008). Furthermore, burning will kill a significant part of the invasive species' seed on the soil surface and litter (DiTomaso et al. 2006). Seedlings that germinate can be manually weeded (Fill et al. 2017), treated with herbicides (Krupek et al. 2016), and mowed or selectively grazed (Richardson & Kluge 2008) to avoid the development of a second generation of dense invasive species. Multiple treatments may be required to achieve desired effects (Mandle et al. 2011). For example, a combination of prescribed burning and herbicide application after invasive *Acacia mearnsii* control in South Africa significantly reduced its soil seed banks (Campbell et al. 1999).

Soil solarization and weed mats could be viable alternatives to prescribed burning in sites where use of fire is inappropriate. For example, soil solarization treatments substantially reduced the number of buried seeds of *A. saligna*, *A. murrayana*, and *A. sclerosperma* in Israel (Cohen et al. 2008). Weed mats set up in a coastal dune in the United States reduced reinvasion of *L. arboreus* (Pickart et al. 1998). However, the use of soil solarization and weed mats is logistically and financially limited to small areas (Pickart et al. 1998; Richardson & Kluge 2008).

Depleted Native Soil Seed Banks. Native species reintroduction through seed, vegetative propagules, transfer of seed containing plant material, or native topsoil translocation is a viable option to manage depleted native soil seed banks (Holmes & Cowling 1997; Baasch et al. 2012; Ferreira & Vieira 2017). For example, seeding with native species during restoration of coastal sandplain grassland in the United States increased native species diversity (Neill et al. 2015). There is need for careful planning and clearly defined restoration goals before conducting native species reintroduction (Honnay et al. 2002; Szitár et al. 2016). For example, some restoration programs might focus on rehabilitation of functional groups or clusters of focal species, whereas others might focus on particular endangered species (Palmer et al. 1997). Practicing restoration ecologists should consider the native species to be reintroduced, donor sites to be used, timing, order, and methods of reintroduction, seed mixtures, and seeding rates for each species.

To the extent possible, timing, order, and methods of reintroduction should be informed by ecological community theory, based on known patterns of community structure (Zedler 2000). This might involve, for example, mimicking natural successional processes by introducing early-successional or mid-successional species first, to help create suitable conditions for later-successional species introduced later (Lithgow et al. 2013). Alternatively, it could involve introducing rare species first to make sure they are not excluded by more common, rapidly establishing species (Palmer et al. 1997). Seed mixtures should be site specific and carefully selected, but diverse seed mixtures are often preferred because they offer insurance that some species will establish (Kiehl et al. 2010). Seeding rates are difficult to gauge, being species and site specific. Therefore, if available, practicing restoration ecologists should select seeding rates according to reference sites (Holmes & Richardson 1999).

Seeds should be harvested from nearby areas to match the genetic composition of native species that occupied the restoration site before invasion (Schaefer 2011). Furthermore, seeds should be harvested from multiple source populations to increase genetic variability (Ödman et al. 2012). Consideration should be made on the seed ecology of the native species to be reintroduced so that seeds of best quality are collected at the right time and stored appropriately to maintain their viability (Holmes & Richardson 1999). To improve germination, pre-treatment of native species' seeds that require certain conditions to break dormancy should be conducted before sowing (Neill et al. 2015). Seeds should be sown using an appropriate method (e.g. mechanical broadcast seeding) at a time that coincides with ideal conditions for germination and survival (Carrick & Krüger 2007). Care should be taken to cover the seeds with substrate to reduce seed predation and prevent them from blowing away (Pausas et al. 2004).

If available, seed containing plant material (e.g. hay and litter) can be harvested from multiple native sites, transferred, and spread on the site designated for restoration as a seed source (Kiehl et al. 2006). Some species such as late successional and endangered species can be transplanted to the site designated for restoration after being grown in pots to improve their chances of establishment (Manchester et al. 1999). If native topsoil becomes available due the native site being destroyed, it can be collected (depth of 10 cm), transferred and thinly spread on the site designated for restoration as a seed source (Rokich et al. 2000). The topsoil should not be stockpiled, but spread as soon as possible to maintain viability of seeds in the soil (Rokich et al. 2000). Disturbance during topsoil translocation may be enough to break seed dormancy, but the soil can also be treated with smoke water solution to break the dormancy of some seeds (Rokich et al. 2002). However, not all seeds will germinate (Klimeš et al. 2010). Furthermore, topsoil translocation can damage species that reproduce through vegetative means (Craig & Buckley 2013).

Nurse plants can be planted before or together with the native species to be reintroduced to create safe sites with favorable microclimates for germination and survival of the reintroduced native species (Padilla & Pugnaire 2006). Nurse plants can shade the reintroduced native species, reduce solar radiation and soil temperatures, protect from herbivore damage, and/or improve the water status of the target seedlings by reducing evaporation (Aerts et al. 2007). For example, use of shrubs as nurse plants enhanced growth of native conifers during reforestation in Spain by improving seedling water status, and therefore reducing seedling mortality by drought. (Castro et al. 2002). Species that can be used as nurse plants should have a facilitative effect on the native restoration species (Gómez-Ruiz et al. 2013). It is advisable to use short-lived species as nurse plants, so that they exist for a limited period and eventually give way to the native restoration species (Gómez-Aparicio 2009). Also, nurse plants planted at too high densities may compete with and exclude target species (Paz Esquivias et al. 2015).

Altered Soil Microbial Communities. Practicing restoration ecologists should consider determining the extent of changes to microbial communities in the site designated for restoration (e.g. using the analysis of phospholipid fatty acids method to compare microbial communities to reference sites; Frostegård et al. 2011), to inform the selection of appropriate management actions to aid recovery of microbial communities. Soil microbial treatments can be utilized to aid the recovery of microbial communities (Richter & Stutz 2002). For example, application of fungicides, bactericides, and microbial and fungal inoculants had a positive impact on the recovery of soil microbial communities and various native plant species in an experimental study in the United Studies (Perkins & Hatfield 2016). However, the success of efforts to restore soil microbial communities has been inconsistent, context-dependent, and logistically limited to small areas (Perkins & Hatfield 2016). Restoration of native species in the site designated for restoration could promote arbuscular mycorrhizal fungi proliferation and diversity (Tanner & Gange 2013). Removal of invasive species' litter in the site designated for restoration (through prescribed burning or manually) could be an easier way to rectify altered soil microbial communities (Elgersma et al. 2011). However, changes to microbial communities after litter removal are often minimal and unpredictable (Elgersma et al. 2011).

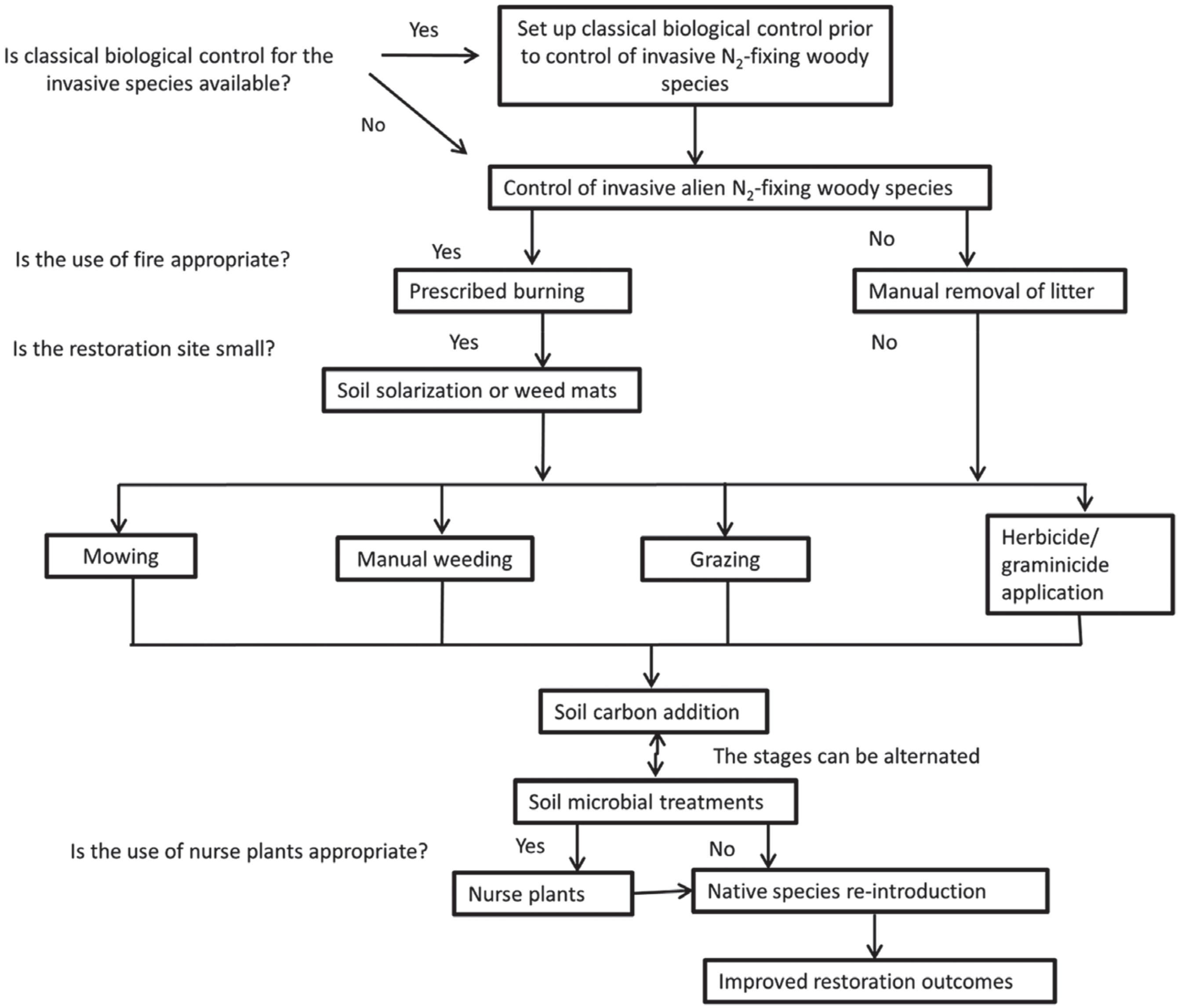

Figure 3. How to combine potential management actions to address barriers to restoration presented by soil legacy effects of invasive alien N_2-fixing woody species into an integrated management effort to improve restoration outcomes.

The Way Forward

Soil legacy effects can present several barriers to restoration after clearing invasive N_2-fixing woody species (Fig. 1). The unique N_2-fixing ability of these invasive species contributes directly to elevated N status, secondary invasion and weedy native species dominance, and altered soil microbial communities. Only a few studies in our review provided evidence that elevated N status, depleted native soil seed banks, and altered soil microbial communities are common barriers to restoration, but this does not necessarily indicate that these barriers to restoration are unimportant. Instead, we believe that the low number of reported cases for some barriers to restoration is a result of these barriers to restoration not being investigated during restoration programs. An investigation of these barriers, however, is crucial to gain a better understanding of the mechanisms of barriers to restoration following invasive species control and of what actions are most needed to improve restoration outcomes.

Management of barriers to restoration is often necessary to improve restoration outcomes and a wide array of potential approaches is available (Fig. 2). We concede that management actions included in this review cannot be uniformly applied in every site designated for restoration because their selection is often context-dependent (e.g. habitat type, site conditions, and scale). However, we believe that the low numbers of reported cases for many of the management approaches is a result of practicing restoration ecologists not applying them even when necessary and appropriate for managing barriers to restoration.

There is a need for restoration ecologists to investigate all potential barriers to restoration during restoration programs. Furthermore, given that they are appropriate in their context, we encourage restoration ecologists to apply the management actions included in this review. Also, we encourage the publication of results (even if they are negative) obtained when investigating all potential barriers to restoration and applying management actions included in this review.

Management actions were often applied individually. However, individual application of potential management actions is often ineffective because it does not address all of the factors giving rise to the target barrier to restoration, does not address all barriers to restoration present in the site designated for restoration, and/or has unintended consequences. We believe that restoration outcomes can be improved by combining potential management actions into an integrated management effort (Fig. 3).

Practicing restoration ecologists need to determine the type and extent of barriers to restoration that exist in the restoration site to inform the selection of management actions. If biological control organisms are available, classical biological control can be set up to reduce seed production and seed banks over time. If burning is appropriate, prescribed burning can be used to manage the litter. If burning is inappropriate, litter can be manually removed. Soil solarization or weed mats can be set up to reduce the establishment of secondary invaders, weedy native species, and/or a second generation of the target invader. Regardless of whether burning is applied, a combination of mowing, manual weeding, herbicides, or grazing can then be used to manage the resulting vegetation. Soil carbon addition and microbial treatments can be applied and then native species can be reintroduced, with or without the aid of nurse plants. Different combinations of approaches will be effective in different contexts (Fig. 3). For example, a combination of prescribed burning, herbicide application, and native restoration species seeding improved restoration outcomes during restoration of prairies and oak savannas in the United Studies (Stanley et al. 2011). There is need for further research on the efficacy of different integrated combinations of management approaches to address barriers to restoration presented by soil legacy effects of alien N_2-fixing woody species.

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LITERATURE CITED

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Supporting Information

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

Appendix S1. List of studies included in the review.
Appendix S2. Barriers to restoration presented by soil legacy effects of invasive alien N_2-fixing woody species.
Appendix S3. Available management actions for the barriers to restoration presented by soil legacy effects of invasive alien N_2-fixing woody species.

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