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Why are some plant species missing from restorations? A diagnostic tool for temperate grassland ecosystems

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The U.N. Decade on Ecosystem Restoration aims to accelerate actions to prevent, halt, and reverse the degradation of ecosystems, and re-establish ecosystem functioning and species diversity. The practice of ecological restoration has made great progress in recent decades, as has recognition of the importance of species diversity to maintaining the long-term stability and functioning of restored ecosystems. Restorations may also focus on specific species to fulfill needed functions, such as supporting dependent wildlife or mitigating extinction risk. Yet even in the most carefully planned and managed restoration, target species may fail to germinate, establish, or persist. To support the successful reintroduction of ecologically and culturally important plant species with an emphasis on temperate grasslands, we developed a tool to diagnose common causes of missing species, focusing on four major categories of filters, or factors: genetic, biotic, abiotic, and planning & land management. Through a review of the scientific literature, we propose a series of diagnostic tests to identify potential causes of failure to restore target species, and treatments that could improve future outcomes. This practical diagnostic tool is meant to strengthen collaboration between restoration practitioners and researchers on diagnosing and treating causes of missing species in order to effectively restore them.

KEYWORDS

restoring plant diversity, germination bottleneck, establishment limitation, abiotic and biotic filters, restoration genetics, mutualism and antagonism, soil ecology and microbiome, restoration planning and land management

1 Introduction

The world is experiencing an unprecedented loss of natural ecosystems (IPBES, 2019). In response, the United Nations proclaimed 2021-2030 the Decade on Ecosystem Restoration, recognizing the key role that ecological restoration plays in reversing the worldwide degradation of ecosystems and maintaining the long-term sustainability of our planet (United Nations, 2019). The practice of ecological restoration requires a high degree of ecological knowledge that can be drawn from weaving together available practitioner experience, Traditional Ecological Knowledge, Local Ecological Knowledge, and scientific discovery (Gann et al., 2019). Spontaneous, or passive, ecological restoration allows degraded ecosystems to recover without intervention following the removal of a disturbance and can be effective in some cases (Jones et al., 2018), but is often insufficient for reestablishing the target community. For example, the restoration site may have a soil bank depleted of propagules, limiting opportunities for a diverse native plant community to regenerate (Lamb et al., 2022), or the level of fragmentation may limit seed dispersal and colonization by desirable species from nearby natural habitats (Prach and Hobbs, 2008). This is the case for the tallgrass prairie ecosystem in North America, where fragmentation is high and regeneration without human assistance is unlikely unless robust remnant populations are adjacent (Kindscher and Tieszen, 1998). In most cases, active restoration of plant diversity is required *via* the deliberate reintroduction of native species that have been lost (McDonald et al., 2016).

When restoring ecosystems, a reference community with similar environmental (e.g., climate, soil, hydrology) conditions is often used to identify the pool of species to introduce at a restoration site (Cornell and Harrison, 2014; Durbecq et al., 2020). Depending on the goals of the restoration (e.g., to restore ecosystem function), it may not be necessary to have the exact complement of species or species combinations found in the reference community. Restoration practitioners often wish to include certain species based on their conservation value or ability to support ecosystem functions such as soil stabilization or pollination. However, even when germplasm for these target species is available, is introduced into a restoration site that appears to be suitable, and diligent efforts are made, some species may not germinate, establish, or persist (Barak et al., 2017). The inability of a target species to thrive at a restoration site is typically a symptom of one or more interacting factors, including genetics of the plant materials, biotic, and abiotic conditions at the site, and planning and management activities (Figure 1), all of which can be challenging to diagnose, let alone treat (Godefroid et al., 2011).

Many species seeded into grasslands do not establish: in studies of the establishment of restored prairie species, one quarter to half of planted species were never found in subsequent surveys (Foster et al., 2007; Hillhouse and Zedler, 2011; Barak et al., 2017). Establishment is often hindered by filters such as seed dispersal, seeding density, and environmental conditions at the restoration site, or a combination of factors (Grman et al., 2015). For example, native *Viola* species in tallgrass prairies of the USA are restoration-relevant because they are the larval host of the threatened Regal Fritillary butterfly (*Speyeria idalia*; Selby, 2007). Unfortunately, populations of *Viola* have rarely been successfully reintroduced (see *Supplementary Information*) despite using locally-sourced plant material installed in sites that harbor seemingly appropriate conditions and native plant communities.

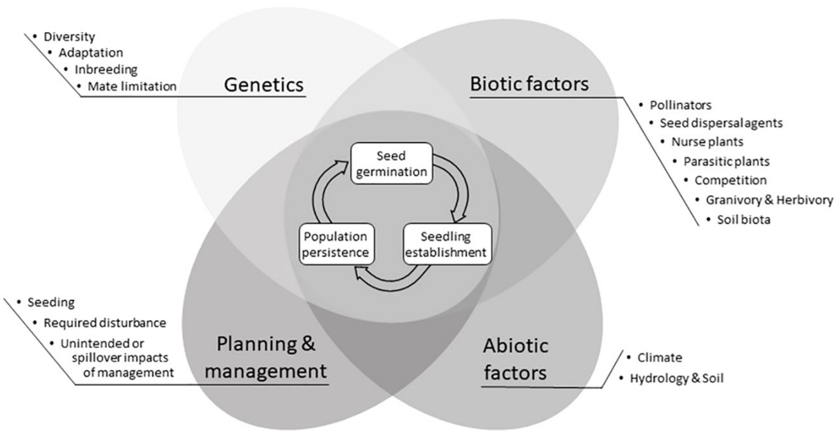

FIGURE 1
Major factors that may impede germination, establishment, or persistence of the target species at the restoration site. Each factor is grouped into four categories and has a corresponding explanation within the text on how to diagnose and treat the factor. Questions about restoration sites and target species intended to help readers focus their attention on one or more of these different sections are located in Table 1.

The plants fail to germinate, establish, or persist, hindering self-sustaining populations which in turn limits their ability to provide ecosystem services such as support for butterfly populations.

There are numerous factors acting on seed germination, seedling establishment, and population persistence which may influence the occurrence of target species at restoration sites (Figure 1). To diagnose why a species is not present at a site that appears appropriate, practitioners and researchers must work together to understand which factors act as bottlenecks, at what stage these bottlenecks occur, and to design and test measures to overcome or "treat" these bottlenecks. In this practical review, we use temperate grasslands and associated vascular plant species as a model to provide a framework for identifying and addressing bottlenecks.

To begin to diagnose the underlying factors limiting successful restoration outcomes, we suggest measures to fully identify the issues (Figure 2) beginning with a literature review of the target species. Next, it is critical to survey healthy native populations of the target species, as close to the restoration site as possible, and talk with experts who have worked with the target species. Collaboration between researchers and practitioners knowledgeable on the subject is crucial and will continue to shrink the science-practice divide (Ladouceur et al., 2022) critical to improving restoration outcomes. Practitioners should ensure baseline assumptions about the target species and the restoration site are met. We provide a tool to help determine which factors may contribute to the absence of the target species at a restoration site (Table 1), as well as diagnostic tests, and possible treatments after the discussion of each factor.

We make several assumptions with these diagnostic tools and their recommendations, including that the target species is an appropriate member of the site's reference community and species lists for restored and reference sites should be revisited and

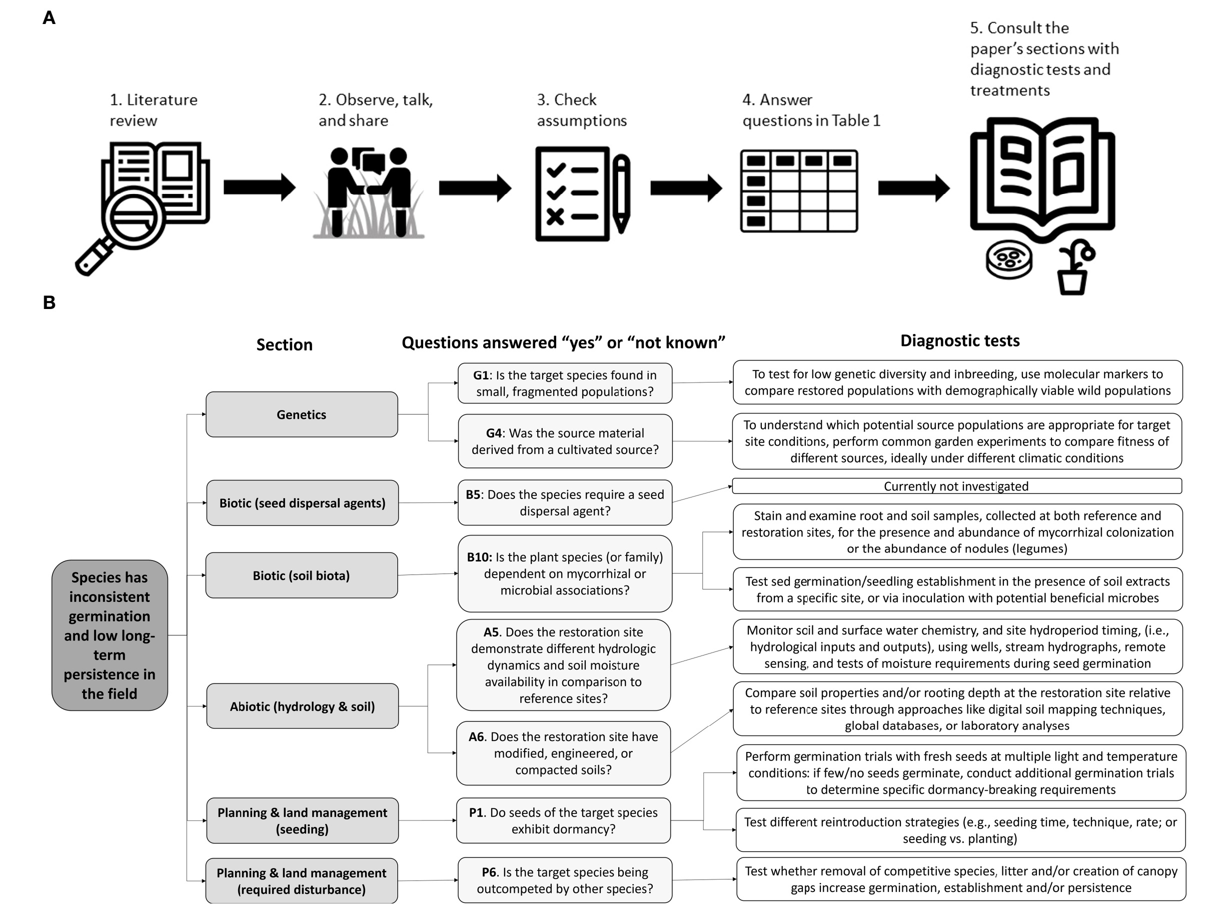

FIGURE 2
(A) Key steps of our diagnostic framework for identifying restoration bottlenecks starting with a literature review to a roadmap of potential solutions (Table 1), followed by **(B)** an example of how to use the diagnostic framework laid out in Table 1 for conservative violet species, identifying the section, specific questions answered "yes" or "don't know", and related diagnostic tests applied. See Supplementary Information for more details about this violet case study.

TABLE 1 List of questions to identify possible reasons a target species fails to persist as a viable population at a site. For each question, a "yes" answer means the factor may be affecting the presence of the target species.

Question	Section of paper	How to determine	Part of life cycle affected
Genetic Factors			
G1. Is the target species found in small, fragmented populations?	Diversity	LS/Q	G, E, P
G2. Was the source material derived from a few plants or small, isolated populations, or just a single population?	Diversity, Inbreeding	Q	G, E, P
G3. Was the source site(s) climatically, geographically, and/or ecologically differentiated from the restoration site?	Adaptation	LS, Q	G, E, P
G4. Was the source material derived from a cultivated source?	Diversity, Adaptation	Q	G, E, P
G5. Do seeds show low germination or do seedlings show low vigor?	Inbreeding, Adaptation	Obs/Q	G, E,
G6. Is the species self-incompatible?	Mate limitation	LS/Exp	P
G7. Are there only a few co-flowering conspecifics in the population?	Mate limitation, Inbreeding (see also Pollinators)		P
G8. Does the species flower, but fail to produce viable seeds?	Mate limitation (see also Pollinators)	Obs/Q	P
G9. Is the species clonal?	Mate Limitation, Diversity	LS/Obs	P
Biotic Factors			
B1. Does the species require an animal vector for pollination?	Pollinators	LS/Obs	P
B2. Is the species reliant on one/a few specialist pollinators for effective pollination?	Pollinators	LS	P
B3. Are there only a few co-flowering conspecifics in the population?	Pollinators (see also Mate limitation)	Obs	P
B4. Is the restoration site isolated from other natural areas?	Pollinators, Seed dispersal agents	Obs	P
B5. Does the species require a seed dispersal agent?	Seed dispersal agents	LS	G, P
B6. Does the species typically grow close to/under the canopy of other plants (particularly if the habitat is harsh, e.g., arid or alpine)?	Nurse plants	Obs	G, E, P
B7. Is the species parasitic/hemiparasitic?	Host plants	LS/Obs	G, E, P
B8. Are there invasive non-native or aggressive native species at the site?	Competition (see also Seeding and Required disturbance)	Obs	G, E, P
B9. Is there evidence of granivory or herbivory (e.g., oviposition holes on fruits, browsed stems)?	Granivory & Herbivory	Obs	G, E, P
B10. Is the plant species (or family) dependent on mycorrhizal or microbial associations?	Soil biota	LS/Obs/Exp	G, E, P
B11. Do the roots show evidence of nodules?	Soil biota	Obs	E, P
B12. Is there evidence of flower, root, or stem rot, or fungal colonies on the leaves?	Soil biota	Obs	G, E, P
Abiotic Factors			
A1. Have substantial climate changes been recorded for the area where the restoration site occurs?	Climate	Q/LS	G, E, P
A2. Has a shift in the phenology of plants been observed at the restoration site or adjacent areas?	Climate	Obs/Q	G, E, P
A3. Are the target species' development, establishment, and reproduction known to be affected by climate change?	Climate	Q/LS/Exp	G, E, P
A4. Has the hydrology of the restoration site been modified (e.g., dams, ditches, drainage tiles)?	Hydrology & Soil	Obs/Q/LS	G, E, P
A5. Does the restoration site demonstrate different hydrologic dynamics and soil moisture availability in comparison to reference sites?	Hydrology & Soil	Obs/Q/Exp	G, E, P
A6. Does the restoration site have modified, engineered, or compacted soils (e.g., agricultural field, building site, etc.)?	Hydrology & Soil	Obs/Q	G, E, P
A7. Does vegetation exhibit symptoms of nutrient deficiency?	Hydrology & Soil	Obs	E, P
Planning & Land Management Factors			
P1. Do seeds of the target species exhibit dormancy?	Seeding	LS/Q/Exp	G
P2. Were seeds sown in a season different from when they naturally disperse?	Seeding	Obs/Q	G
P3. If the target species was sown in a seed mix, did some species germinate or establish more poorly than others, compared to their individual seeding rate?	Seeding (see also Competition)	Obs	G, E
P4. Does the target species usually germinate and establish on bare ground?	Required disturbance	Obs/Q/Exp	G, E
P5. Does the target species need a certain amount of organic material to germinate and establish?	Required disturbance	Obs/Exp	G, E
P6. Is the target species being outcompeted by other species?	Required disturbance (see also Competition)	Obs	G, E, P

(Continued)

TABLE 1 Continued

Planning & Land Management Factors			
P7. Does the species or its community historically require disturbance such as fire or grazing? Is the restoration disturbance regime different from reference sites?	Required disturbance	LS/Q	G, E, P
P8. Has the restoration site been fertilized or occur in an area with high levels of N deposition?	Spillover (see also Hydrology & Soil)	Obs/Q	G, E, P
P9. Are on-site or nearby land uses likely to impact the species through nutrient enrichment, pollution, or herbicide/pesticide drift?	Spillover (see also Hydrology & Soil)	Obs/Q	G, E, P

For a summary of possible factors, see Figure 1. In this table, we reference the appropriate section of the paper for discussion, indicate what may be needed to determine the answer (Obs, observation; LS, literature search; Q, asking questions of stewards/seed providers; Exp, experiment), and note at what life cycle stage symptoms of this factor are likely to be seen (G, seed germination; E, seedling establishment; P, population persistence).

updated periodically to account for successional and climatic changes. Furthermore, if the target species has known taxonomic issues, the issues have been incorporated into selecting appropriate source material. Taxonomic issues include intraspecific ploidy variation (Kramer et al., 2018), cryptic diversity (Espíndola et al., 2016), or hybridization with other species (Mitchell et al., 2019). We also assume that if seeds were used for the target species restoration, they were viable. Additionally, sufficient time should have elapsed since propagules were introduced for the target species to be detected. This will vary by species and will depend on how long it takes for seeds to germinate and plants to grow large enough to be detected with established monitoring protocols. We assume that the target species can be detected by monitoring protocols in place. And lastly, we assume the restoration site is adequate in size to support a persistent population of the target species.

2 Factors that may influence the occurrence of target species at restoration sites

2.1 Genetic factors

Genetic factors are common precursors to population extinction (Frankham, 2005). If source material is genetically inappropriate, it may have low fitness at the restoration site and fail to persist after one or more generations. Early failure is often associated with inbred and/or poorly adapted source material (Leberg and Firmin, 2008). However, insufficient genetic diversity to respond and adapt to environmental pressures, or lack of appropriate mates (mate limitation), are not immediately evident and may take years to drive population extinction (Robinson et al., 2019). This can make it hard to pinpoint genetic factors as the cause of the target species not establishing at the restoration site. However, knowing the life history of the target species, as well as how source populations were selected and used in the restoration can provide important clues (Frankham et al., 2017).

2.1.1 Diversity

When collecting, producing, and using seeds or plugs for restoration, care must be taken to capture the genetic diversity present at a source site while avoiding steps that may narrow diversity reintroduced (Basey et al., 2015). Large populations, especially where plants are distributed over a wide range of microhabitats, should harbor higher genetic diversity, while small populations (especially those that are fragmented) are more likely to have lower diversity as well as greater risk of being inbred (McGlaughlin et al., 2002; Rosenberger et al., 2021; question G1, Table 1). For longer-term persistence, genetic diversity helps populations survive local disturbances and adapt to future climate changes (Lau et al., 2019). Collecting or using only a portion of diversity present in larger populations, relying on clonal propagation (Fant et al., 2008), or collecting only plants from small populations (Fant et al., 2013) may set restored populations up for future genetic issues, such as inbreeding depression and mate limitation.

Species that are clonal (question G9, Table 1), where restoration source material was derived from a few plants (question G2), and/or cultivated material (question G3) are most at-risk for genetic diversity-related failures to germinate, establish, or persist. For example, *Ammophila breviligulata* is a clonal beach grass widely used for habitat restoration. Fant et al. (2008) compared restorations in both Lake Michigan and Lake Superior (USA) to assess genetic diversity between native and restored populations after 15 years. They found that the restored populations had lower diversity than native populations, and in many cases the restored populations, which were recreated using plugs, were composed of a single commercially available cultivar. Although these monotypic populations are providing a service of sand stabilization, previous studies have shown that increasing genetic diversity of this dominant plant species may increase productivity of other co-occurring plant species (Crawford and Rudgers, 2012), and was more important than plant species diversity in increasing arthropod (Crawford and Rudgers, 2013) and fungal (Emery et al., 2010) community diversity.

2.1.2 Adaptation

Using appropriate source material with traits adapted to local conditions increases likelihood of germination, establishment, and persistence at the restoration site (McKay et al., 2005; Balazs et al., 2020). Mixing local sources to increase diversity can help overcome issues associated with lack of appropriate source material that closely matches the restoration site (Bucharova et al., 2019). While local wild populations are often assumed to be adapted to site conditions, this is not always the case (Bucharova et al., 2017a), especially for small populations with few individuals and low genetic diversity (Leimu and Fischer, 2008; Hereford, 2009) or given altered site conditions (Leger, 2008) and rapid climate change (Havens et al., 2015). Selecting adapted source material for a restoration could be a challenge when conditions at restoration sites differ from potential sources (Lawrence and Kaye, 2011), or if no remnant sites exist with similar habitat or climate analogues, which is exacerbated by habitat loss and degradation and climate change (Havens et al., 2015). Seed zones, where available, can guide selection of appropriately adapted germplasm (Bower et al., 2014), also considering local variation (e.g., wetlands and uplands ecotypes) and future climate conditions (Richardson and Chaney, 2018).

If the source site is climatically, geographically, and/or ecologically differentiated from the restoration site, if restoration germplasm is derived from a cultivated source, or if seedlings show low vigor, adaptation may be one of the reasons that a species is not able to germinate, establish, and/or persist at a site (questions G3, G4, and G5 on Table 1, respectively). An example is provided by the federally threatened golden paintbrush (*Castilleja levisecta*) where common garden experiments were conducted to test how each of six remaining wild populations from Washington State, USA performed at potential reintroduction sites in Oregon. Lawrence and Kaye (2011) grew these six sources at a field site targeted for reintroduction and monitored them during two growing seasons. Overall, plant community characteristics of the source site were better predictors of *C. levisecta* performance at the site than genetic diversity, population size, and geographic distance. These results were used to select source material for reintroductions, preferentially selecting populations from ecologically similar habitats, rather than just geographically close populations. Controlled crosses between populations in this common garden also revealed inbreeding depression. As a result, a regional admixture provenancing strategy (Bucharova et al., 2019) was used to develop germplasm for reintroductions, mixing four populations in a nursery setting to produce ample, genetically diverse germplasm for reintroductions. This strategy has been successful, establishing many genetically diverse and demographically viable populations (St. Clair et al., 2020).

2.1.3 Inbreeding

Inbreeding is common in nature (Keller & Waller, 2002). Small and isolated populations have higher likelihood of inbreeding than large, well-connected populations (Angeloni et al., 2011). Inbred plants can exhibit inbreeding depression, or a loss of fitness (e.g., low pollen viability, seed set, or competitive ability) relative to outbred plants, which is often more obvious under stressful field conditions (Fox and Reed, 2011). In a restoration setting, indications that inbreeding limit the ability of a target species to germinate, establish, or persist include seeds with low germination rates, seedlings with low vigor, or restored populations that have only a few co-flowering conspecifics (questions G5 and G7 on Table 1, respectively).

One example of inbreeding driving low germination rates comes from the eastern prairie fringed orchid (*Platanthera leucophaea*), where Bell et al. (2021) found significant differences in seed germination based on different hand-pollination treatments. Seedlings produced by crossing parents from different populations had the highest germination, while self-pollinating plants produced the lowest, with crosses between individuals within populations having intermediate germination. Demographic models showed that outcrossing among populations had a significant positive effect on population growth rate compared to the other two treatments, while self-pollination resulted in a negative growth rate and reduced population viability, driving populations to extinction in around 27 years.

In another example, *Cirsium pitcheri*, a federally threatened species, was reintroduced in Illinois, USA using source material from multiple small nearby populations in Wisconsin and Indiana. Both plugs and seeds were used to reintroduce the population over multiple years. While the population was initially deemed viable based on demographic monitoring, its population growth rate subsequently declined to less than 1, requiring additional inputs of new material (Halsey et al., 2017). Molecular genetics research showed significantly higher inbreeding in the source populations and the reintroduction relative to more distant but larger and more demographically-viable populations (Fant et al., 2013; Fant et al., 2014). This result may reflect the fact that few flowers are available for crosses each year. As a monocarpic perennial, *C. pitcheri* plants take several years to flower and then flower once and die, so the number of individual plants available for cross pollination in any given year is much smaller than the population size. This highlights the importance of considering not only potential diversity and inbreeding issues in the source material, but the effective population size of the reintroduction.

Sourcing exclusively from small populations can result in poor-performing plants at establishment, which could be mistaken for poor site match rather than inbreeding depression. Similarly, populations established from few maternal lines or clonal species will also lead to increased inbreeding over time, which can limit long-term persistence (Frankham, 2015).

2.1.4 Mate limitation

Low fruit and seed set can be due to a lack of suitable mates in the population (i.e., mate limitation: Young and Pickup, 2010). Initial signs of mate limitation such as scarce fruit and seed set (question Q8, Table 1) are easy to miss if seed set is not monitored (Kirchner et al., 2006). Mate limitation is more likely in in self-incompatible species (~39% of flowering plants; Igic et al., 2008; question Q6, Table 1) than self-compatible species (Levin et al., 2009; Thrall et al., 2014), as well as in species that produce different types of individual plants (e.g., dioecious species that produce female and male flowers on different plants; Molano-Flores, 2004). Additionally, clonal species, particularly those in populations with few co-flowering conspecifics, are particularly at risk of undetected mate limitation (questions Q9, Q7 respectively, Table 1) because they may look large but have very few genetically different individuals flowering at the same time (Gitzendanner et al., 2012; Van Rossum et al., 2021). Alternative causes of low seed production may include lack of pollinators (see *Biotic Factors/Pollinators*), outbreeding depression (decreased fitness because parents are too genetically different, see Frankham et al., 2011), and/or environmental stress.

An excellent example of mate-limited species comes from two self-incompatible, clonal species found in remnant habitats in Illinois, USA. In one species, seed production was only possible following genetic augmentation, i.e., the addition of plant material with different incompatibility genotypes (*Eurybia furcata;* Gavin-Smyth et al., 2021). In the other species (*Asclepias lanuginosa*, Kim et al., 2014), mate limitation was detected *via* molecular genetics and pollinator limitation was excluded as a possible reason for low seed set by comparing seed production in *A. lanuginosa* with a similar and co-occurring species (*A. viridiflora).* Both species are rare in Illinois but *A. lanuginosa* rarely produces pods, even in large populations. After comparing pollinators, genetic diversity, and seed set in both species at a number of sites, authors found that all populations of *A. viridiflora* produced pods, but not a single pod was found in *A. lanuginosa* populations, despite both species occurring at the same site and having similar numbers of individuals. Since the flowers were visited by the appropriate pollinators (*Bombus griseocollis* and *Megachile brevis*) they concluded the populations were not pollinator-limited. The lack of seed production was attributed to high clonality in *A. lanuginosa* populations (ranging from 1-11 unique individuals) resulting in a limited number of unrelated mates in the population. By contrast, in *A. viridiflora* populations, almost every plant was unique (13-43 unique individuals).

2.1.4.1 Diagnosing genetic factors

- To test for low genetic diversity and inbreeding, use molecular markers to compare restored populations with demographically viable wild populations (St. Clair et al., 2020).
- To investigate inbreeding and mate limitation, monitor seed production in restored populations and compare to large, demographically viable wild populations (Kim et al., 2014).
- To understand which potential source populations are best adapted to target site conditions, perform common garden experiments to compare fitness of different sources, ideally under different climatic conditions (Bucharova et al., 2017b) and over multiple years.
- To test for inbreeding, outbreeding, and mate limitation, conduct controlled crosses between increasingly different parents (self, within and between population) and compare seed set and offspring fitness (ideally growing in natural conditions) (Hufford et al., 2012).

2.1.4.2 Treating genetic factors

- Supplement existing populations by introducing genetically diverse germplasm, ideally from other source populations within the same ecoregion (Willi et al., 2007).
- Reintroduce populations by sourcing germplasm from large populations (>500 plants) whenever possible (Frankham et al., 2014); use seed zones or other regional sourcing tools where available (e.g., Bower et al., 2014); minimize loss or changes to genetic diversity when collecting, propagating and using germplasm (Basey et al., 2015); consider mixing source populations within a region to treat genetic issues (Bucharova et al., 2019) and minimize outbreeding depression risks (Frankham et al., 2011).
- In fire-dependent grasslands, conducting prescribed burns may increase flowering synchrony (Wagenius et al., 2020).

2.2 Biotic factors

Many biotic factors influence whether plants germinate, establish, and persist at a specific site (Ackerly, 2003). Here we consider how the presence of mutualists and antagonists may affect species restoration success.

2.2.1 Pollinators

Pollinator abundance, behavior, diversity, and identity can be strongly influenced by characteristics of the target species population, the plant community in which it grows, and the landscape matrix surrounding the site (Carrié et al., 2016). Most plant species depend on animal-mediated pollination (87%; Ollerton et al., 2011) and pollinator limitations can hinder reproductive success and population viability (Cariveau et al., 2020) (question B1, Table 1). Plant species most at risk from pollinator loss have tightly co-evolved adaptations to a single pollinator (Knight et al., 2005; question B2, Table 1). For example, *Brighamia insignis*, an endemic Hawaiian plant, is now extinct in the wild. One of the primary drivers of its decline was the extinction of its pollinator, believed to have been a hawkmoth (US Fish and Wildlife Service, 2007). Prior to the extinction of the last wild individuals, *B. insignis* plants never set seed on their own and relied on hand pollination by botanists who rappelled down the cliffs to reach the last extant population. Now found only in *ex situ* populations, reintroduction may not be possible without continued human management for pollination (Walsh et al., 2019).

Another example comes from *Platanthera praeclara*, an orchid from the Great Plains of the USA that seemed to be facing the same problem as *Brighamia:* pollen limitation due to lack of pollinators. It is pollinated by several species of hawkmoths, but visits were infrequent and seed set was quite low. However, recent pollinator surveys found a Eurasian hawkmoth, *Hyles euphorbiae*, introduced in the late 1990s to control the invasive plant leafy spurge, began visiting the orchid. It is now the most common visitor of *P. praeclara* by an order of magnitude, and has greatly increased pollinator service (Fox et al., 2013). This example demonstrates that new mutualisms can develop, giving hope for species where specialist pollinators have been lost, although we would not recommend introducing non-native organisms solely for this purpose.

Most flowering plant species, particularly in temperate regions, are pollinated by multiple species of varying efficiency (Koski et al., 2018). Any changes in the composition of the community, such as shifts in plant or pollinator phenology under climate change or asynchronous flowering of compatible mates (Luijten et al., 2000), can impact seed production (Byers, 2017). Decreases in population size can result in a smaller floral display making plants less attractive to pollinators (question B3, Table 1), with an increase in inbreeding risk (Menges, 1991) and decrease in seed set (Groom, 1998). Landscape fragmentation and site quality will also impact pollinator densities (question B4, Table 1), with greatest impact on less mobile specialist pollinator species (Dixon, 2009), leading to a higher proportion of generalist species (Xiao et al., 2016). Restoration sites that are larger, closer, and more connected with natural areas are likely to have greater pollinator abundance and diversity (Steffan-Dewenter and Tscharntke, 1999; Kremen et al., 2004; Townsend and Levey, 2005).

2.2.1.1 Diagnosing pollinator factors

- Assess floral resource levels of the site to ensure they are sufficient and span the growing season (Ebeling et al., 2008).
- Conduct pollinator observations and surveys and quantify seed set to determine abundance and diversity of pollinators, and pollination success after restoration activity (Breland et al., 2018).
- Use pollen limitation experiments to assess if pollen supplementation boosts seed set (Wagenius and Lyon, 2010).

2.2.1.2 Treating pollinator factors

- Increase population size of the target species (Bernhardt et al., 2008).
- Increase abundance and diversity of floral resources throughout the growing season (Delaney et al., 2015; Havens and Vitt, 2016).
- Provide proper resources and habitat for pollinators to nest (Winfree, 2010).
- Be aware of, and minimize, pesticide drift.
- Alternate burn areas and vary times of prescribed burns to protect fire-sensitive pollinator species (Carbone et al., 2019).
- Connect restorations to other natural areas *via* corridors to facilitate pollinator migration into the site (Townsend and Levey, 2005).
- Hand-pollinate to overcome pollen limitation (typically not sustainable for the long-term).

2.2.2 Seed dispersal agents

Most plants in temperate grasslands rely on wind, rather than animals, to disperse their seeds (Collins and Uno, 1985). For plant species that rely on both wind and animal dispersal, creating suitable conditions (e.g., corridors that connect fragmented habitat) to promote the movement of the target species could be a crucial step in promoting their establishment and persistence in restoration sites (Damschen et al., 2014; Prior et al., 2015). Seed dispersal and deposition, and species richness in restored sites have been shown to be negatively affected by fragmentation, with reduced recruitment of native species coinciding with increased fragmentation (Poschlod et al., 1998; Damschen et al., 2006; Vanden Broeck et al., 2015). Species that require animal dispersal agents or that are in fragmented populations where dispersal agents are not able to disperse seeds across fragment barriers (questions B5 and B4, respectively, Table 1) are most at-risk for seed dispersal as a limiting factor in their long-term establishment and persistence at a site. For example, some species that require ant dispersal benefit from nest mounds that create microsite conditions and patchiness favoring plant species that are generally less competitive with tall grasses in unmanaged meadows (Dean et al., 1997). Much larger dispersal agents, such as cattle and bison, may play a larger part in seed dispersal for some species than previously thought. As bison have been incorporated into North American grassland restorations, they have potential as dispersal agents through both epizoochory and endozoochory, with seed from over 70 species found in both hair and dung samples in one study (Rosas et al., 2008). Active seeding may still be needed for large-seeded species and for those for which the animal disperser is extinct, extirpated, or threatened (Pires et al., 2018).

For example, Bischoff (2002) investigated the dispersal and establishment of two species characteristic of wet grasslands, *Serratula tinctoria* and *Silaum silaus*, comparing them between a natural grassland, where both species were common, and a restored grassland, where both were still extremely rare after 10 years of extensive management. Results showed that in both species poor dispersal was the main limiting factor of their establishment in the restored grassland. Management activities did not increase dispersal distances, while grazers (cattle) did not appear to disperse seeds. While occasional water-based long-distance seed movement was not ruled out, the spatial distribution of seedlings around the parent plants suggested that wind was the main dispersal agent. These results suggest that suitable abiotic conditions at the restoration site alone cannot guarantee successful restoration of floodplain grasslands because dispersal may be the limiting factor, and therefore, an initial input of seeds may be necessary to establish new populations.

2.2.2.1 Diagnosing seed dispersal agent factors

- Identify possible seed dispersal agents of the target species and dispersal range through observations, field experiments, molecular markers, and fluorescent dyes (Levey and Sargent, 2000; Bischoff, 2002; Gelmi-Candusso et al., 2019).
- Determine whether seed handling by dispersers (e.g., ingestion, transport) affects germination, establishment and persistence by comparing germination of fresh and dispersed seeds (Steyaert et al., 2019) and/or by experimentally manipulating seed location and tracking success at the site (Calviño-Cancela, 2002).
- Use molecular markers to estimate recent patterns of seed dispersal and understand population connectivity (e.g., Vanden Broeck et al., 2015).

2.2.2.2 Treating seed dispersal agent factors

- Protect (Lindsell et al., 2015) and, when possible, reintroduce dispersers and eradicate non-native invasive species shown to displace native dispersers.
- For species requiring animal dispersal to germinate (e.g., passage through an animal gut), if the natural disperser is missing, a short-term solution is to treat seeds appropriately (e.g., acid scarification) to mimic natural dispersal (Kildisheva et al., 2020).
- Protect remnant grasslands and reduce fragmentation by increasing habitat connectivity to support species movement (Damschen et al., 2006; Damschen et al., 2014; Howe, 2016).

2.2.3 Nurse plants

Adult plants that facilitate seed germination and seedling establishment of other species are called nurse plants and play a particularly important role in environments with high abiotic stress (Padilla and Pugnaire, 2006; Gonzalez and Ghermandi, 2019) (question B6, Table 1). Aboveground, nurse plants can provide protection against herbivores (e.g., thorny plants), buffer against high irradiation and temperature, and attract pollinators; belowground, nurse plants can improve levels of soil moisture (e.g., hydraulic lift) and key nutrients (Padilla and Pugnaire, 2006; Gonzalez and Ghermandi, 2019), *via* their common mycorrhizal networks (Querejeta et al., 2009). For example, Dona and Galen (2007), studied the nurse effects of alpine willows (*Salix* spp.) on the over-winter survival of fireweed (*Chamerion angustifolium*), a circumboreally distributed herbaceous perennial, by planting established seedlings of fireweed under five different treatments (willow canopy, shade, wind block, shade plus wind block and control, i.e., open meadow vegetation with no manipulation), measuring also abiotic environmental conditions (soil moisture, light intensity, wind speed, and maximum temperature) within treatments, and by comparing results under these treatments. They found that willows promote over-winter survival of established seedling and adult fireweed.

Nurse plants may also increase germination rates in restorations, as seen in the facilitative shading effect of a leguminous shrub on the cactus *Neobuxbumia tetetzo* (Valiente-Banuet and Ezcurra, 1991). In this case, shaded microsites provided by the shrubs were found to increase germination and survival due to lower daytime temperatures and lower evaporative demand. Similarly, planting scattered N-fixing trees can accelerate forest regeneration, by ameliorating conditions beneath their canopies. The N-fixation restores soil nitrification to pre-clearing levels or those of reference forests, favoring establishment and growth of woody montane seedlings (Rhoades et al., 1998). Finally, Gonzalez and Ghermandi (2019) found that *Acaena splendens* shrubs act as nurse plants in grasslands of northwestern Patagonia, by facilitating the seedling recruitment of *Festuca pallescens*, a grass of high forage value present with a low cover in degraded grasslands. However, the authors found that the facilitation mechanism will fail in extremely stressful conditions, such as drought conditions, indicating that this restoration tool can be limited by the specific yearly climatic conditions.

2.2.3.1 Diagnosing nurse plant factors

- Assess whether the target species commonly co-occurs near particular species or plants with a certain structure at reference sites (Padilla and Pugnaire, 2006).
- Conduct field germination and seedling establishment trials with potential nurse plants to confirm if the target species requires, or benefits from, the presence of nurse plants (Padilla and Pugnaire, 2006).

2.2.3.2 Treating nurse plant factors

- Reintroduce nurse plant species before adding target species (Padilla and Pugnaire, 2006).
- Sow seeds and/or plant seedlings around mature nurse plants, near enough to allow root intermingling and provide benefits from hydraulic lift (Izumi et al., 2018) and mycorrhizal networks.
- Use artificial structures that provide same functions as nurse plants (Tuya et al., 2017).

2.2.4 Parasitic plants

Parasitic plants connect to the vascular tissues of the host, using specialized structures called haustoria, to obtain some or all (hemiparasitic and parasitic, respectively) of their carbon, water, and nutrient needs. Parasitic plants are often desired in restoration because they can increase soil nitrogen cycling (Bardgett et al., 2006), suppress dominant vegetation (which facilitates other species including forbs; Pennings and Callaway, 1996; Cole et al., 2019), and increase species and floral diversity (Bardgett et al., 2006; DiGiovanni et al., 2017; Těšitel et al., 2017). Yet these species are also most likely to be missing from restored grasslands (Barak et al., 2017) (question B7, Table 1). Many plant taxa of conservation concern are hemiparasites, including *Castilleja levisecta* in the Orobanchaceae, for which reintroduction is an important conservation tool; however, determining appropriate restoration strategies for parasitic or hemiparasitic species is challenging, as they may require specific host species to establish or persist (Molano-Flores et al., 2003; Lawrence and Kaye, 2011). Even generalist parasitic plants may be able to form haustoria or a connection from the roots with many different host plant species but may still show high levels of host preference (Press and Phoenix, 2005; Lawrence and Kaye, 2011). For example, Matthies (2017) grew *Melampyrum arvense* (Orobanchaceae), a hemiparasite from a German calcareous grassland with 27 potential grass, forb, and legume host species at two nutrient levels. Seeds of *M. arvense* and the host species were germinated in petri dishes in a refrigerator, then transplanted together into pots outdoors. Results showed variation in the quality of hosts, with legumes supporting the greatest parasite biomass, followed by forbs, then grasses (Matthies, 2017). Similar methods in controlled settings can help determine whether specific parasitic or hemiparasitic target species form effective parasitic relationships with different hosts.

2.2.4.1 Diagnosing parasitic plant factors

- If permitted, field-collect target species with nearby plants suspected of serving as host(s) and look for haustorial connections (Yoshida et al., 2016).
- Grow target species and suspected host species together in pots, then examine roots for haustorial connections (Ren et al., 2010).
- When more than one host plant is known for the target species, run greenhouse experiments measuring the target species' fitness with different hosts (Lawrence and Kaye, 2008).

2.2.4.2 Treating parasitic plant factors

- Ensure appropriate host plants are present at the restoration site prior to seeding or planting the target species (Lawrence and Kaye, 2008).

2.2.5 Competition

Competition occurs when one plant negatively impacts another, either indirectly such as by exploiting common resources like water (Foxx and Fort, 2019) and light, specifically in grasslands where woody encroachment limits grass species diversity (Hare et al., 2021) or by direct interference such as through allelopathy (Amarasekare, 2002; Adomako et al., 2019). It occurs both within and between species and is a key ecological process that shapes and determines plant community compositions (Vellend, 2010; Czarniecka-Wiera et al., 2019), and can limit restoration success (Mangla et al., 2011). While it is well-recognized that competition from aggressive plant species often negatively impacts species diversity in plant communities (Bennett et al., 2011) (question B8, Table 1), the magnitude of impact is not always well established. As reduction in competition can require time and labor-intensive measures, it is helpful to consider testing the degree to which competition may be affecting target species. By coupling neighbor removal with long term monitoring, the effects of competition can be quantified. For example, Maron (1997) found that bush lupine (*Lupinus arboreus*) had a 32% increase in survival of seedlings when neighboring species were removed. Lupine plants grown with competitors also had decreased root biomass.

Another study by Seahra et al. (2019) identified competition as a bottleneck to species establishment by comparing species performance when they were sown alone versus in mixtures with other species. Most of the studied target species showed greater establishment when sown alone than in mixtures. This method, sometimes referred to as mosaic planting, allows more time for species sensitive to competition to establish in patches and can thus facilitate the coexistence of dominant and subordinate species.

Additionally, changes to resource availability (e.g., nitrogen deposition; Funk and Vitousek, 2007) and interannual weather variability (e.g., precipitation; Groves and Brudvig, 2019) can alter the competitive landscape, favoring some species over others (see *Abiotic Factors*). Management activities that begin with observing declines in co-occurring species can help ameliorate some of these changes (see *Planning & Land Management Factors*).

2.2.5.1 Diagnosing competition factors

- Use monitoring data to determine if co-occurrence of some species leads to decline of others (Rinella et al., 2016).
- At the restoration site, test if and how partial or complete removal of invasive or aggressive species affects the target species (Maron, 1997).

2.2.5.2 Treating competition factors

- Plant species in monospecific patches to minimize competition with co-seeded species (Seahra et al., 2019).
- Plant subordinate species earlier than dominant species, or use seed priming (Deering and Young, 2006) so they germinate more rapidly than dominant species and are able to establish in lower-competitive environments (Young et al., 2017).
- Manipulate seed densities in mixes, with target species overrepresented and dominant species underrepresented (Dickson and Busby, 2009).
- Minimize or eliminate competition from dominant or aggressive species by either mowing, targeted scything, or complete removal (manually or with herbicide) at appropriate times to reduce biomass, energy reserves, and/or prevent seed set (Maron, 1997; Abella et al., 2020).
- Introduce appropriate parasitic or hemiparasitic plants to weaken dominant competitors (Press and Phoenix, 2005).
- Remove or replace topsoil where too many propagules of invasive/aggressive species are present (Buisson et al., 2008).
- If already heavily impacted, manage the site in row crops for 2-3 years to deplete the weed seed bank in the soil before sowing native species (Rowe, 2010).
- Seed in difficult to establish species over multiple years to overcome interannual variation in establishment success due to weather or other factors (Groves and Brudvig, 2019).

2.2.6 Granivory and herbivory

Granivory, or seed predation by wildlife or insects before or after it is dispersed, can drive species to extinction (Kurkjian et al., 2017) or keep them from establishing entirely (Vaz Ferreira et al., 2011). This is particularly true at sites where granivore densities are high due to a lack of natural predators (Hulme and Benkman, 2002). Some species have strategies like masting to compensate for losses due to seed predation, but these may only occur when conditions are suitable (Kelly and Sullivan, 1997). Some management practices can help minimize exposure of seeds to predation (e.g., sowing seeds that don't require cold stratification in the spring instead of fall to minimize predation during the winter; Linabury et al., 2019; see *Planning & Land Management Factors*). Annual or biennial plants with transient seed banks are particularly vulnerable to seed predation (Maron and Crone, 2006).

Herbivory by wildlife or insects can also significantly impact plant establishment and persistence (Bevill et al., 1999; Orrock et al., 2009). Many herbivores are generalists, although they may prefer some species over others, while specialists are tightly co-evolved with specific plant species or families (Davidson, 1993). Herbivory can produce plant communities largely composed of species (Howe et al., 2002; Barlow et al., 2013), or even ecotypes (Scherber et al., 2003), that are less palatable to herbivores present at the site. This is particularly true in systems with unnaturally high herbivore densities (Anderson et al., 2007). Evidence of granivory or herbivory, such as oviposition holes on seeds or fruits, or stems that are browsed, are clear signs that a population may be impacted by granivory or herbivory (question B9, Table 1). However, the impacts of granivory or herbivory are not always obvious.

In particular, pre-dispersal granivory from insects can be difficult to identify, come from unexpected places, and lead to unexpected outcomes. For example, several insect species have been deliberately introduced to North America (or actively promoted and distributed after arriving on their own) as biocontrol agents for non-native weedy thistle species (e.g., *Cirsium arvense*, *C. vulgare*). These insects include *Rhinocyllus conicus* and *Larinus planus* (now known as *L. carolinae*), both seed-feeding weevils, and *Cleonus pigra*, a root weevil. Unfortunately, none of these insects are host-specific and they have been found feeding on a wide array of native thistles, including the federally-listed threatened species, *Cirsium pitcheri* (Havens et al., 2012). Although no longer promoted for use by USDA, these insects are widespread in the USA, and are negatively impacting fecundity and/or survival to reproductive maturity of many native thistle populations (Louda and O'Brien, 2002; Louda et al., 2003; Rose et al., 2005). Symptoms of infestation of seed head weevils include the presence of larvae or frass in heads and few or no seeds. Small oviposition holes are visible upon close inspection. *Cleonus pigra* causes mature plants to wilt and die, typically before any seed set. At present, there are no successful treatments for the seed head weevils because they are active at the same time flowers open and require pollinator visitation for seed set (i.e., any pesticide use would also kill the pollinators).

The impacts of post-dispersal granivory can also be challenging to identify. Selective foraging by birds, rodents, and ants can influence plant population dynamics. Bird granivory of large and intermediate seed sizes in Midwest prairie experiments resulted in reduced plant densities and grass biomass, while plant species with small seeds, deemed below optimal foraging level, were unaffected (Howe and Brown, 1999). In an experiment using fluorescent dye coatings on seeds to track their fates, roughly 10 more seedlings/m^2 emerged in closed exclosures compared to controls accessible to small vertebrate granivores in tallgrass prairie restorations (Pellish et al., 2018). Exclosures of different mesh sizes were used to study the impact of different sized consumers in restoration of a native grass in California. The study concluded that voles and mice were able to reduce seedling recruitment by 30% through granivory, but they did not affect subsequent seedling height or tiller length (Orrock et al., 2009). In California rangelands, the giant kangaroo rat (*Dipodomys ingens*) reduced seedling recruitment by 7% *via* granivory and by 20% *via* soil disturbance from burrowing (Gurney et al., 2015).

The full impacts of herbivory can also be challenging to see without a control that excludes the herbivore. For example, the use of deer exclosures in degraded riparian corridors led the density of saplings of woody riparian plant species to be ten times higher in exclosures than in control areas where dark tailed deer could freely browse (Opperman and Merenlender, 2000). Deer exclosures in restored wet meadows improved species richness and diversity significantly (Fraser and Madson, 2008). While the threshold at which herbivore densities will negatively impact a specific target species likely varies depending on the species, site, and year, Urbanek et al. (2012) found that deer densities greater than 21 deer/km^2 negatively impacted species diversity in Midwestern USA savanna and forest restorations.

2.2.6.1 Diagnosing granivory/herbivory factors

- Assess extent of seed predation either experimentally (Calviño-Cancela, 2002) or visually (e.g., examine fruits for damage/oviposition holes).
- Conduct granivore/herbivore exclosure experiments (Orrock et al., 2009).
- Test different reintroduction strategies (seeding *vs.* planting; Godefroid et al., 2011).
- Estimate granivore/herbivore densities at the restoration site and compare with those found in sites where persistent populations of the target species occur (Pender et al., 2013).
- Track seeds with fluorescent dye to determine their fate (Pellish et al., 2018).

2.2.6.2 Treating granivory/herbivory factors

- For some species, fences, cages, or netting can be used to exclude herbivores to protect plants (Bevill et al., 1999; Orrock et al., 2009), but this can be expensive and time-consuming, and does not address the causes of high herbivore or granivore densities.
- If the issue is at the seed stage (granivory), reintroduce the species *via* plugs instead of seeding (Wallin et al., 2009), or overseed to compensate for predation (Orrock et al., 2009; Longland and Ostoja, 2013).
- Seed or plant the target species near thorny plants to protect plants from mammalian herbivory (see *Biotic Factors/Nurse Plants*).
- Coat seeds to deter granivory (Taylor et al., 2020).
- Investigate approaches to decrease mammalian densities range such as removing favorable herbivore habitat (e.g., cutting tall grass that mammals prefer) to hunting/trapping or increasing predator habitat (Wasson et al., 2021).
- Approaches to decrease insect densities range from pesticide application to biocontrol introduction, but these pose challenges and present risks that need to be

carefully considered (see *Planning & Land Management factors/Unintended or spillover impacts of management*) (McLaughlin and Dearden, 2019).

2.2.7 Soil biota

Plant interactions with soil microbes (e.g., rhizobia, mycorrhizal fungi) comprise one of the major mechanisms contributing to plant diversity (Moeslund et al., 2017). Legumes form symbioses with nitrogen-fixing bacteria called rhizobia in their root nodules (Hirsch et al., 2001) (question B11, Table 1), while around 80% of all plant species, and 92% of all plant families, are believed to form associations with mycorrhizal fungi (Wang and Qiu, 2006) (question B10, Table 1). Mycorrhizal symbioses typically increase acquisition of nutrients like nitrogen and phosphorus, otherwise inaccessible to plant roots, and this promotes seedling establishment and enhances the competitive ability of subordinate plant species relative to dominant taxa (Van Der Heijden et al., 1998). Fungal and bacterial inoculations of the soil or even seeds can promote germination and plant establishment and can prove to be a useful management tool (Pedrini et al., 2020).

In tallgrass prairie species, numerous studies have shown that mycorrhizal inoculation improves plant establishment relative to non-inoculated plants. For example, inoculated plants showed greater plant height, root length, and biomass production (Ghimire et al., 2009) as well as increased survival rates in the first year of restoration *vs.* non-inoculated plants (Maltz and Treseder, 2015; Koziol et al., 2018). Such increases may be correlated with higher levels of mycorrhizal root colonization (e.g., Smith et al., 1998) and the development of mycorrhizal networks (Middleton et al., 2015). However, inoculation does not always enhance productivity in a target native grass species (Paluch et al., 2013) and root colonization may not correspond to improved plant establishment, especially in sites with existing mycorrhizal communities (White et al., 2008).

Similarly, other beneficial soil microbes may be introduced to enhance plant growth. In a study by Chaín et al. (2020), a superabsorbent polymer was used to deliver two strains of the bacteria *Pseudomonas* to greenhouse-grown *Eucalyptus* species. Plants inoculated with *Pseudomonas* showed greater growth (e.g., larger leaves, stems, water use efficiency) under drought than plants grown without the bacterial inoculants.

Conversely, accumulation of species-specific pathogens or microbial communities within the rhizosphere may lead to a species' decline and/or replacement (Reynolds et al., 2003). Evidence that this may be contributing to the inability of a species to establish or persist at a site include flower, root, or stem rot, or fungal colonies on leaves (question B12, Table 1). Restoration actions also affect soil microbial communities (Dickens et al., 2015). For example, feedbacks between soil nutrients and early successional plant species (Kardol and Wardle, 2010) may create bacterial- or pathogen-enriched environments that are less favorable to seed germination and seedling establishment of target species (Kulmatiski et al., 2008).

2.2.7.1 Diagnosing soil biota factors

- Stain and examine root and soil samples, collected at both reference and restoration sites, for the presence and abundance of mycorrhizal colonization or the abundance of nodules (legumes) (Vierheilig et al., 1998).
- Test seed germination and seedling establishment in the presence of soil extracts from a specific site, or *via* inoculation with potential beneficial microbes (see Ghimire et al., 2009 for methodology).
- Analyze the abundance of bacteria relative to fungi in soil samples, comparing reference and restoration sites (Robertson et al., 1999).
- Assess mycorrhizal or microbial infectivity and efficacy using a bioassay (Djuuna et al., 2009).

2.2.7.2 Treating soil biota factors

- Inoculate soil restoration site with whole soil from a remnant site through the application of fresh topsoil, soil cores, or monoliths (Bulot et al., 2017).
- Introduce locally adapted mycorrhizal fungi or microbial-inoculated plants (Middleton et al., 2015), and include consortia of mycorrhizal or microbial species as inoculum rather than a single species (Koziol et al., 2018).
- Introduce native leguminous (Fabaceae; Rhoades et al., 1998) and actinorhizal plants (Betulaceae) to enhance communities of N2-fixing microbes (Paschke, 1997).
- Coat or pellet seeds with encapsulated microbes to facilitate the inoculation of seedlings (Rocha et al., 2019).
- Where appropriate, introduce biological crusts using cultivated or natural materials (Doherty et al., 2020).

2.3 Abiotic factors

In addition to biotic constraints, the establishment of target species is largely affected by resource requirements and physiological tolerances to abiotic conditions, including climate, soil, and hydrology (Fløjgaard et al., 2020). Here, we outline approaches available to diagnose and treat issues with these abiotic factors at the restoration site.

2.3.1 Climate

Climate is a significant factor controlling the distribution and abundance of species and altered temperature and precipitation patterns have a profound impact on species' range expansion (e.g., Brusca et al., 2013; Guittar et al., 2020) and contraction (Leopold and Hess, 2019). As reported in the Intergovernmental Panel on Climate Change's Sixth Assessment Report, including the Regional Synthesis Interactive Atlas (Gutiérrez et al., 2021), not all regions of the world are changing at the same pace for different factors like temperature and precipitation (question A1, Table 1). This intra- and inter-annual variation in temperature and precipitation can cause shifts in seasonality, hydrology, snow cover dynamics, soil temperature and moisture, and fire regimes that may affect when, where and whether different plant species and sources will be able to germinate, survive, establish, reproduce, and persist as adults as well as seeds and buds (Ooi, 2012; Ott et al., 2017). Rapidly changing climates and extreme climate conditions, expected to increase in frequency (Easterling et al., 2017), may shift current species (e.g., C3 *vs.* C4) geographic ranges and phenology (Knapp et al., 2020), and clonal growth (Sluis, 2020; Bam et al., 2022), making restoration efforts more important but also more challenging (Havens et al., 2015). This also means that reference plant communities may rapidly change, creating a need to periodically update reference communities for any given restoration site (Shackelford et al., 2022).

Other concerns related to climate change include impacts on plant germination as well as long-term survival, and mutualisms with species plants depend on for reproduction and dispersal. For example, climate impacts litter accumulation and decomposition rates (Fekete et al., 2016), potentially altering microclimate conditions at a site, which can affect seed germination and seedling emergence and establishment (Loydi et al., 2013). And over the long-term, remnant or restored plant populations may be threatened with extinction if climatic changes exceed their climatic niches, adaptive capabilities, and migration paces, especially in fragmented landscapes (Aitken et al., 2007). Finally, antagonistic (e.g., herbivores and their food plants) as well as mutualistic (e.g., pollination) relationships between plants and insects or vertebrates they interact with may be impacted if the species involved do not have similar phenological responses to climate change (Renner and Zohner, 2018; question A2, Table 1).

Understanding how extreme weather events or more variable climatic conditions impact the relative performance of native species, especially at early life history stages, could offer insight into their potential success under future climate change scenarios. The predicted increase in intra-annual precipitation variability in North American grasslands will produce larger individual precipitation events with longer intervening dry periods (Easterling et al., 2017). Such changes will generate more temporally dynamic soil moisture regimes creating more stressful conditions for native plants. While a recent experimental approach did not find any impacts of precipitation frequency on the clonal growth in *Pascopyrum smithii*, a common C3 grass species in North American grasslands (Bam et al., 2022), much more work is needed to understand how changing climates will impact germination, establishment, and persistence of different species (question A3, Table 1).

2.3.1.1 Diagnosing climate factors

- Examine historical long-term relative to current and projected climate data trends using the Intergovernmental Panel on Climate Change's Interactive Atlas (https://interactive-atlas.ipcc.ch/).
- Track changes in plant phenology (e.g., using Budburst (www.budburst.org) or USA National Phenology Network (www.usanpn.org/usa-national-phenology-network).
- Conduct germination and establishment experiments to understand micro-climatic requirements, e.g., litter modification experiments (Loydi et al., 2013); light; bare soil, etc.
- Conduct field and/or laboratory experiments to simulate different climate scenarios (Knapp et al., 2020; Bam et al., 2022).
- Conduct common garden experiments to evaluate species-specific climatic tolerance limits (Leopold and Hess, 2019).

2.3.1.2 Treating climate factors

- Take into consideration climate predictions and extremes in restoration designs (e.g., using Climate–Smart with Seed Tool to select seed mixes to match with current and future projected key climatic variables in the USA.; e.g., Finch et al., 2019; https://climaterestorationtool.org/csrt/).
- Improve microclimatic conditions by managing the vegetation surrounding the reintroduction plots, e.g., manage litter cover and depth (Loydi et al., 2013).

- To manage climatic challenges at a site, ensure germplasm is genetically diverse and adapted to climate conditions at the site (see *Genetic factors*).

2.3.2 Hydrology and soil

Target species' germination, establishment, and persistence can be impacted by site hydrology (e.g., erosion dynamics, currents, and flooding; Kettenring and Tarsa, 2020), with even small changes in hydrology influencing the plant community (Silvertown et al., 2015). Hydrology of restoration and remnant sites can be significantly impacted by engineering approaches like damming, ditch construction, and drain tile installation (Kelly et al., 2017) (questions A4 and A5, Table 1). This can make it challenging to understand variation in hydrologic dynamics and soil moisture availability between restoration and reference sites, but restoration of site hydrology may be critical prior to attempting to reintroduce target species or communities (Kettenring and Tarsa, 2020), but climate change is making this increasingly challenging (Cuthbert et al., 2019).

Similarly, shifts in soil nutrients, pH, conductivity, organic matter, contaminants, compaction, and structure can directly or indirectly (e.g., *via* microbial communities) impact seed germination and plant survival (Bach et al., 2010; Turley et al., 2020; question A6, Table 1). Nutrient-rich soils generally support fast-growing, early successional species, and inhibit slower-growing ones (de Vries et al., 2012). A loss of soil structural stability (e.g., *via* plowing of agricultural fields) may lead to compaction, especially in clay-rich soils (Rosenzweig et al., 2016), thereby decreasing soil porosity, water infiltration, and the ability of roots to forage for water and nutrients (Correa et al., 2019). In soils contaminated from metals, salt, or pollutants, reductions in root growth coupled with metal accumulation limits water and nutrient uptake, leading to dramatic declines in plant growth and gross macronutrient deficiencies (Rahman et al., 2018) (question A7, Table 1). Target species with low tolerances to these conditions may show negligible recruitment (Moeslund et al., 2017).

In natural sedge meadows, the highly organic soils act as a sponge, retaining water and drawing water upward from deeper sources by capillary action. These meadows also drain slowly owing to the low hydraulic conductivity of peat. Together, the capillarity and low hydraulic conductivity keep soils in sedge meadows largely saturated throughout the year. Conversely, restored wetlands contain soils with lower organic content and higher hydraulic conductivity. Many restored sites also lack the vegetative cover that would drive litter inputs. As a result, soils in created sedge meadows are exposed to direct sunlight (higher temperatures) and greater wind speeds and are often dry and cracked at the surface, even if saturated at depth. For example, the failure of *Carex* spp. to germinate in restored wetlands was attributed to low soil moisture levels (Van Der Valk et al., 1999). The authors tested the effect of five different soil moisture levels on germination in *Carex stipata* and *C. stricta*, and the effect of soil organic amendments on the growth of *C. stricta* seedlings. The results showed that amending the soil with organic matter improved seed germination and seedling establishment in *Carex* spp. by improving the water holding capacity of the soil and its fertility. Organic amendments may thus be useful in acidic soils or those sites where the topsoil has been removed.

In extreme situations, topsoil removal (or turf cutting) has been recognized as a measure to restore oligotrophic conditions by reducing organic matter and nutrient levels. This approach has been applied in heathlands where atmospheric N and S deposition has resulted in soil acidification and low base saturation. Van Den Berg et al. (2003) conducted field experiments that examined the impact of turf cutting to different depths on the germination of *Arnica montana*. In some of the experimental plots, lime was an additional treatment. The authors also conducted laboratory experiments to test the effect of Al and humic acids on the germination of the target species. They found that herbaceous plants of species-rich heathlands and grasslands, like *A. montana*, are vulnerable to the soil conditions created by turf cutting. The addition of lime and/or humic acids resulted in higher germination and improved plant establishment because the amendments increased soil base saturation and pH and reduced the levels of phytotoxic metals, such as Al.

2.3.2.1 Diagnosing hydrology and soil factors

- Compare soil properties and/or rooting depth at the restoration site relative to reference sites through approaches like digital soil mapping techniques (Goldman et al., 2020), global databases (e.g., Web Soil Survey), or laboratory analyses (e.g., bulk density, moisture, pH, aggregation, nutrients, organic matter, microbial abundance; Robertson et al., 1999).
- Monitor soil and surface water chemistry, and site hydroperiod timing, (i.e., hydrological inputs and outputs), using wells, stream hydrographs, remote sensing (drones, MODIS), and tests of moisture requirements during seed germination (Chasmer et al., 2020).

2.3.2.2 Treating hydrology and soil factors

- Restore site hydrology, e.g., remove drain tiles and plug drainage ditches (Kettenring and Tarsa, 2020); amend nutrients and organic matter (Van Der Valk et al., 1999).

- Create dams or micro-catchments to reduce run-off, erosion, and nutrient loss without inverting the upper soil profile, as tillage would do (Pueyo et al., 2009).
- Use high-quality carbon substrates to stimulate N (and P) immobilization in the microbial biomass and decrease soil N (or P) fertility (Sollenberger et al., 2016).
- Introduce natural disturbance regimes, e.g., fire, to induce functional shifts in plant community diversity and rhizosphere microbes by altering the quality and quantity of root-derived substrates entering the soil (Forest et al., 2005).
- Improve aeration and infiltration (e.g., alleviate soil compaction; reintroduce native burrowing invertebrate (Colloff et al., 2010) and vertebrates (Platt et al., 2016).
- Use soil amendments to improve plant growth including N or P fertilizer to ameliorate plant nutrient deficiencies in metal-contaminated soils and calcium amendment (liming) in acidic soils (Rahman et al., 2018).
- Remediate metal-contaminated soils using metal-tolerant plants (Wei et al., 2021) or nutrient beads with immobilized metal-tolerant mycorrhizal fungi (Egerton-Warburton, 2015) or bacteria (Sharma et al., 2018).

2.4 Planning and land management factors

From decisions about planting methods and seeding rates to ongoing management, adequate planning, preparation, and management are vital to support germination, establishment, and persistence of restored plant populations and communities.

2.4.1 Seeding

While the seeds of some species germinate immediately after exposure to ideal temperature and moisture conditions, others have specific seed dormancy requirements that dictate the conditions under which they will germinate (question P1, Table 1). A limited understanding of dormancy and germination behavior can hamper restoration efforts. For some species, seed dormancy and dormancy break are complex and can take months or even years to occur, however, there may be pre-treatments that can be applied prior to planting to encourage germination (Baskin and Baskin, 2014; Kildisheva et al., 2020). When determining timing of seeding, managers should consider information about seed dormancy and natural cycles of dispersal at restoration sites (question P2, Table 1). Optimizing dormancy break in restoration-relevant species can improve restoration outcomes by promoting recruitment and reducing post-emergence seedling mortality. For example, sowing seeds at an inappropriate time could cause seeds and germinants to be attacked by pathogens, or be damaged or killed by environmental conditions like wet-dry or freeze-thaw cycles (James et al., 2012).

For species introduced as part of a seed mix containing multiple species, seed mix composition can influence the probability that a given species will establish (question P3, Table 1). For example, in prairie seed mixes if the ratio of grasses to forbs is too high, it can impede the establishment of individual forb species (Dickson and Busby, 2009; Grman et al., 2015). Some species may benefit from repeated seeding (Sluis et al., 2018) and/or a higher seeding rate (Grman et al., 2015; Shackelford et al., 2021). For species that are difficult to establish from seed, planting plugs is often recommended (Gallagher and Wagenius, 2016), but some species are more likely to establish and persist at a site when planted from seeds (St. Clair et al., 2020; Anderson and Minor, 2021). Successful establishment of seeded or planted species is likely to be influenced by management and the level of disturbance at a site (see below).

2.4.1.1 Diagnosing seeding factors

- Track seed germination and early establishment (Kulpa and Leger, 2013).
- Perform germination trials with fresh seeds at multiple light and temperature conditions: if few/no seeds germinate, conduct additional germination trials to determine specific dormancy-breaking requirements (Kildisheva et al., 2020).
- Poor germination may be a sign that seeds are not viable, due to a range of possible factors, including environmental conditions at the collection site, genetic factors in the source population(s), and/or seed collection and storage conditions. Seed viability can be assessed using a range of methods (Riebkes et al., 2015).
- Test different reintroduction strategies (e.g., seeding timing, technique, rate; Shaw et al., 2020; or seeding *vs.* planting; Godefroid et al., 2011).
- Investigate seed longevity in the field and the ability to form a soil seed bank (Bakker et al., 1996).

2.4.1.2 Treating seeding factors

- Sow dormant seeds at the time of natural dispersal to increase chances of seed and seedling survival, or break the dormancy of seeds prior to sowing, adjusting timing of sowing to the ideal time for emergence (Shaw et al., 2020; Kildisheva et al., 2020).

- Adjust the seeding rate (or seed multiple times) if the target species does not establish well from the first seeding (Grman et al., 2015) or develop a persistent soil seed bank (Sluis et al., 2018).
- Mow, or apply similar management measures, to ensure seedlings have enough light for growth (see section 'Required disturbance').
- Identify topographic microsites (mounds, pits, flats) or use amendments (e.g., hay, mulch) to create microsites that enhance seed germination and establishment (Naeth et al., 2018).
- For species that have proven difficult to establish from seed, introduce as plugs (Gallagher and Wagenius, 2016).
- Coat seeds to help regulate dormancy and promote germination at the appropriate time (James et al., 2012).

2.4.2 Required disturbance

Landscape-level disturbance management, for example fire and grazing, is often necessary for the germination and persistence of many plant species in restored grasslands (Grman et al., 2015; Alstad et al., 2018; Török et al., 2021; questions P4, P5, and P6, Table 1). These disturbances may be natural and/or historically managed by indigenous people (Kimmerer and Lake, 2001). On a habitat level, disturbance may be required to maintain a particular grassland type (e.g., preventing woody encroachment and grassland conversion; Leach and Givnish, 1996) and be important in promoting establishment and persistence of individual target species. In general, habitats that are disturbance-managed, such as through fire, mowing, or grazing, often support species establishment and persistence because the applied management can decrease plant competition and litter; allow seeds to have better soil contact; reduce predation from pests; and increase heterogeneity in light, as well as nutrient and water availability (Vickery, 2002; Overbeck et al., 2003; Loydi et al., 2013; Alstad et al., 2018; Meissen et al., 2020).

Prescribed fire, mowing, and grazing have all been important in supporting establishment of target species in restored grasslands. Fire suppression has been a driver of the loss of many important prairie species, and prescribed fire can aid in their germination, establishment, and persistence (Leach and Givnish, 1996; Alstad et al., 2016). In grassland habitats where historical disturbance regimes include fire, but prescribed fire isn't feasible, mowing or targeted weeding may be acceptable management substitutes (Macdougall and Turkington, 2007). Finally, some species may require multiple types of disturbance management, such as some native forb species in serpentine grasslands that emerged and persisted only following both burning and grazing (Hernández et al., 2021). It is important to note that management can only support the germination, emergence, and establishment of species that are on site (i.e., as resident plants, in the soil seedbank, or seeded into the site as described above).

In the tallgrass prairie, fire represents both a natural disturbance and a site preparation tool (Alstad et al., 2018). Alstad et al. (2018) tested the impacts of prescribed burning on germination on the seeds of eight prairie species in a field experiment. Despite very low emergence percentages overall, all species had higher germination and emergence when seeded into burned plots, as compared to unburned plots. Some species did not emerge at all in unburned plots, but emerged in burned plots, including *Amorpha canescens*, *Dalea candida*, and *D. purpurea*. Their hypothesis was that fire reduced the amount of litter in the system and allowed better soil contact for seeded species. In another tallgrass prairie study, frequent mowing facilitated establishment of forb species into a grass-dominated restoration: multiple species of forbs persisted through flowering stages in mowed plots, while they did not establish at all in non-mowed control plots (Williams et al., 2007).

2.4.2.1 Diagnosing required disturbance factors

- Test whether removal of competitive species, litter and/or creation of canopy gaps increase germination, establishment and/or persistence.
- If the target species or community has been historically managed through disturbance (e.g., fire, grazing), conduct an experiment testing the disturbance and compare germination, establishment, and persistence of the target species in both sites where the disturbance has been reintroduced and control (unmanaged) sites.

2.4.2.2 Treating required disturbance factors

- When indicated and possible, restore necessary disturbance regimes to support the target species, but be aware that co-occurring species may be negatively impacted (Palmer et al., 2017). Timing disturbances accordingly may help mitigate impacts on other species (Knapp et al., 2009).
- If a natural or managed disturbance is not possible at a landscape-level, simulate the effect of a disturbance at smaller scales (e.g., remove litter cover manually, clip vegetation) to increase heterogeneity in conditions (Overbeck et al., 2003; Loydi et al., 2013).

2.4.3 Unintended or spillover impacts of management

Management activities conducted at the restoration site to manage other species can have unintended or spillover impacts on the target species. For example, herbicides applied to manage aggressive or invasive species can damage other species or allow for secondary invasions (Bennion et al., 2020) (question P8, Table 1). In addition, while periodic management like prescribed fire is important for promoting germination of some species, decreasing the abundance of dominant species, and preventing woody encroachment, it can negatively impact other species, both plants and animals. For example, *Lupinus oreganus* is the larval host of the endangered butterfly, *Icaricia icarioides fenderi* in Willamette Valley prairie habitats (USA). Invasive grasses are taller than the lupine, and therefore interfere with the relationship between the plant and butterfly. Grass-specific herbicide has been tested to reduce the height of grasses so they are lower than the lupine. While the herbicide did reduce grass height, and improve access by pollinators, as well as increase seed production in the lupine, it also had unintended impacts on the lupine, including suppression of its growth, and introduction of several secondary invaders (particularly forbs) that arrived after the grass was reduced. The authors conclude that grass-specific herbicide is not the ideal tool to use in the restoration of *L. oreganus/Icaricia icarioides fenderi* habitat due to the secondary impacts (Bennion et al., 2020; Schultz and Ferguson, 2020). Herbicide has an important role in restoration, but it is important to consider the costs, benefits, and possible spillover impacts when deciding on an herbicide plan.

2.4.3.1 Diagnosing unintended or spillover impacts of management factors

- Carefully monitor germination, establishment, and persistence of the target species if herbicides or fertilizers are used on, or adjacent to, the restoration site (McManamen et al., 2018).
- Estimate the net benefit of restoration management practice: weigh the potential benefits of the management application (e.g., herbicides, pesticides) with the unintended consequences (Bennion et al., 2020).

2.4.3.2 Treating unintended or spillover impacts of management factors

- See *Abiotic factors* section.
- Avoid herbicide application in areas near developing seeds/seedlings (McManamen et al., 2018) or modify herbicide application interval (Crone et al., 2009).
- Isolate spatially or temporally fire-sensitive species from fire management (Knapp et al., 2009).

3 Discussion

Challenges in plant species germination, establishment, and persistence are critical problems preventing restorations from achieving the goals of the U.N. Decade on Ecosystem Restoration to re-establish species diversity. In this paper, we highlight key factors affecting why plant species may be missing and offer considerations to identify and treat these factors (ranging from genetic to biotic, abiotic, and planning & land management challenges). We hope this document will be useful to both practitioners and researchers as they work together to improve long-term restoration outcomes and support species diversity. We recognize that many of these diagnoses and treatments require access to equipment, funding, and staff that may not be readily available at many land management agencies and organizations. Partnering with universities and other scientific organizations can be a way to both accomplish the needed research and help build bridges between our communities. Additionally, while a wide range of resources are available to help identify and treat these factors, much more work is needed. Continued knowledge and data-sharing that supports synthesis to advance restoration science will be critical to continued progress in meeting these goals (Ladouceur et al., 2022).

In addition to the factors detailed above, it is important to note that a site's history and time since restoration will also impact its capacity to meet species or diversity targets. Long-term studies from around the world illustrate that it can take decades for restored grassland communities to approach the diversity of a reference natural community and will depend on the intensity and kind of disturbance the site experienced prior to and following restoration (Kindscher and Tieszen, 1998; Fagan et al., 2008). Climate change, habitat loss and fragmentation, and pollution will increasingly influence plant population dynamics, with possible alteration, disruption, and shifts in species composition and range (Guittar et al., 2020), making it important to periodically revisit reference species lists to adjust expectations (Shackelford et al., 2022). And particularly in heavily-impacted, novel environments like urban and former industrial sites that do not have reference systems, restoration that supports biodiversity will require a new conceptual framework (Klaus and Kiehl, 2021).

Monitoring restoration sites is important for informing management actions, but this is resource-intensive and provide the most valuable data when they are conducted periodically over the long-term. This is because floristic surveys conducted at an early stage of restoration may be poor predictors of long-term restoration outcomes related to species composition, as some seeds may take several seasons to germinate and emerge, or only appear at a later successional stage. To limit the costs associated with long-term monitoring, project managers can leverage open-source datasets to update regional species lists. Such datasets include permanent monitoring programs (e.g., US National Ecological Observatory Network), community science approaches (e.g., Chicago Botanic Garden's Plants of Concern), and their regional or global aggregation (e.g., Global Biodiversity Information Facility, iNaturalist). Novel approaches relying on open-source remote sensing datasets (e.g., Sentinel) or the custom acquisition of aerial images *via* low-cost drones (Anderson and Gaston, 2013), could help managers identify when field surveys are warranted to identify missing species.

Finally, building and sustaining respectful and reciprocal relationships among researchers and restoration practitioners will be critical to this work, supporting evidence-based practice (Suding, 2011). Additionally, while this tool was developed through the lens of western science, we acknowledge the importance of Indigenous knowledge and the leadership of Indigenous communities in stewarding natural areas (Dickson-Hoyle et al., 2022). While time and resource constraints might limit the feasibility of certain diagnostic tests and treatments highlighted here, we hope these relationships and the use of this tool will lead to improved restoration outcomes, one species at a time.

Author contributions

AK conceived the idea; MD, KaH, and AK developed and structured the idea; MD, AK, and KaH led the writing of the manuscript and produced figures and tables; All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

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