Plant selection for pollinator restoration in seminatural ecosystems

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Individual plant species play valuable roles in meeting restoration goals for pollinators. However, the selection of plant species for pollinator restoration is rarely informed using empirical evidence and is usually developed in agroecosystems, which experience frequent human interventions to ensure plant success as compared to seminatural ecosystems. We highlight concepts and future research needs to design planting mixes that fulfill the ecological requirements of pollinators in seminatural ecosystems. Native plants that are attractive to pollinators, increase the stability of pollination services, and provide consistent floral resources across the landscape and growing season should be prioritized in pollinator restoration projects in seminatural ecosystems. Furthermore, condensing criteria of desirable plant traits into a composite score can aid managers in selecting plant species that meet restoration goals. Developing restoration strategies for pollinators on seminatural lands is important for preserving organisms essential for biodiversity maintenance and ecosystem function.

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Informing pollinator restoration with empirical evidence is critical during this era of biodiversity decline, land-use change, and habitat loss (Dixon 2009; Cariveau *et al*. 2020). Restoration of degraded ecosystems is necessary to counteract reductions in pollinator diversity, and to recover ecosystem function and services required by society. Restoration accelerates the succession of ecosystems through applied management actions to achieve predefined targets related to community structure, function, and stability. However, it has been argued that the translation of advances in restoration science into applied land management actions has been slow, resulting in a lack of guidance for practitioners to meet these targets (Cabin *et al*. 2010). As a result, it remains unknown whether current restoration strategies for pollinators are sufficient for meeting explicit goals to improve pollinator community structure, function, and stability.

In a nutshell:

- There is an urgent and growing need to restore habitat for pollinators, but information about how to do this in seminatural ecosystems is generally lacking
- Increasing the availability of floral resources by revegetating landscapes with native flowering plants could benefit pollinators and pollinator health
- A framework is provided for determining the most effective mixes of plant species to reach defined goals for pollinator restoration
- Following restoration actions, monitoring is required to assess success, and to improve and adapt plantings for current and future climate conditions

Understanding the *functional roles* (Panel 1) of plant species in guiding pollinator community succession toward predefined endpoints is essential for achieving pollinator restoration goals (Devoto *et al*. 2012). Plants can be attractive to pollinators, contribute to interaction network structures associated with stability (eg interaction diversity, nestedness, modularity, and connectivity) (Tylianakis *et al*. 2010; Kaiser-Bunbury and Blüthgen 2015; Biella *et al*. 2017), and be the preferred resources of species of conservation concern. Plants with these traits may achieve *structural endpoints*, *functional endpoints*, and *targeted support for species of conservation concern*, which return species richness and abundance, pollination services, and populations of endangered species, respectively, to levels found in a reference system (Panel 1) (Palmer *et al*. 1997). Furthermore, pollinator diversity improves pollination services (van der Plas 2019), underscoring the importance of plant selection in strengthening positive feedbacks between plant and pollinator communities (Tylianakis *et al*. 2010). Revegetating critical habitats threatened by human activities with plants that occupy important functional roles could be necessary to counteract pollinator declines.

Seminatural ecosystems are landscapes modified by anthropogenic and natural disturbances (Panel 1). These ecosystems have higher levels of bee abundance when compared to ecosystems dominated by anthropogenic activities and contain crucial habitats for bee communities (Figure 1) (Koh *et al*. 2016; Carril *et al*. 2018). Yet restoration strategies for pollinators have primarily been developed within agroecosystems as opposed to seminatural ecosystems (Winfree 2010). Restoration techniques on farmlands – including installing

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Panel 1. Glossary of terms defined for planting mixes and pollinator restoration in seminatural ecosystems

Structural endpoint: levels of pollinator abundance and diversity are equivalent to those found in a reference system.

Functional endpoint: levels of pollination services are equivalent to those found in a reference system. Pollination services are the delivery of pollen between conspecific plant individuals to facilitate reproductive success. Improving the abundance of key service-providing species and plant reproductive success following restoration activities may be indicators of whether restoration goals have been achieved.

Targeted support for species of conservation concern: pollinator populations of an individual species are equivalent to those in a reference system. Planting mixes should include the preferred resources of species listed as "endangered" under the US Endangered Species Act or key service-providing species.

Functional role: a plant species' ability to advance pollinator communities toward restoration endpoints.

Seminatural ecosystem: large landscapes modified by natural and anthropogenic processes. These landscapes contain habitats with growing conditions following disturbances and remote areas resulting in infrequent human interventions to ensure success of plant restoration projects.

Planting mix: an assemblage of plant species dispersed across seminatural ecosystems to establish vegetative cover and floral resources for pollinators.

Resource bottleneck: period during the growing season with scarce availability of nectar and pollen, which can reduce pollinator population productivity. Periods of scarce resource availability can be mitigated depending on plant species' bloom period and duration.

Framework plant: plants that have an outsized influence on the provision of floral resources to the pollinator community. Pollinator visitation rates (number of visitors per flower per time) and pollinator visitation richness (number of pollinator species per flower per time) can be used to identify plants preferred by pollinators in relation to the availability on the landscape.

Landscape simplification: planting mixes that support a similar suite of pollinators despite changing environmental contexts across a landscape.

Climate analog: the current geographic area that resembles the environmental conditions of a restoration site in the future resulting from climate change.

hedgerows and flower strips, using diversified farming methods, and preserving natural land cover in surrounding fields – increase the abundance and diversity of native plants and provide floral resources for pollinators (Burkle *et al*. 2017). Other management activities in seminatural ecosystems – like prescribed burning, thinning, and invasive species removal – can also have positive effects on pollinators (Glenny *et al*. 2022a) via increased early seral stage habitat rich in floral and nesting resources, but post-management restoration projects may favor revegetating areas with grasses, which reduce erosion and outcompete invasive species but provide few benefits to pollinators. In addition, unlike agroecosystems, restoration projects in seminatural ecosystems are frequently conducted in remote areas, which impedes human interventions to ensure plant success, and natural disturbances like wildfire or drought select against the establishment of some plant species. Restoration strategies that establish flowering plants in seminatural ecosystems may provide land managers with feasible tools to counteract pollinator declines.

Currently, land managers lack guidance for selecting plant species for pollinator restoration in seminatural areas, resulting in *planting mixes* that contain species that are not attractive to pollinators (Panel 1) (Cane and Love 2016). Variation in the abundance and composition of flowering plants across the growing season and in different habitat types may lead to *resource bottlenecks* for some pollinator species (Panel 1) (Ogilvie and Forrest 2017). Analyzing patterns of pollinator visitation to plant species and documenting the occurrence of plants across the growing season and in different habitats can help in designing planting mixes that support pollinators in seminatural ecosystems (Panel 2). We propose that planting mixes for pollinator restoration in seminatural ecosystems can be developed by defining explicit endpoints for pollinator communities, using empirical evidence to identify the most effective plant species to achieve endpoints and then evaluating the success of planting mixes and restoration projects through monitoring of pollinator communities.

Define explicit goals for pollinator restoration

Structural endpoints

Structural endpoints can be achieved by selecting plant species that increase the abundance and diversity of pollinator communities at restoration sites (Figure 1). Planting mixes that contain the most attractive plants for pollinators consistently support more pollinator species than do mixes comprising random plant species, suggesting that some plant species are more important than others for achieving structural endpoints (Harmon-Threatt and Hendrix 2015). However, plant mixes typically support common, generalist pollinators and neglect rare species that are sensitive to habitat loss (Wood *et al.* 2015). The total number of pollinator species supported by restoration actions could be increased by using plant species that attract rare pollinator species or unique pollinator assemblages and that have complementary functional roles within planting mixes (Blüthgen and Klein 2011; Devoto *et al.* 2012).

Functional endpoints

Pollinators fulfill a valuable ecological function by transporting pollen between conspecific individuals of plants to facilitate reproduction. Declining plant reproductive success may indicate reduced pollinator function due to suboptimal delivery of pollination services (ie pollen limitation), but can result from other factors like seed predation, herbivory, and drought (Iler *et al.* 2021). Selecting plant species that support key service-providing pollinator species may be important for reaching functional endpoints (Figure 1). However, measuring changes in pollinator function following restoration is rarely conducted in seminatural ecosystems because it requires time-consuming and tedious work using sentinel plant species and pollen supplementation experiments (Cariveau *et al.* 2020). Instead, managers can gain insights into changes in pollinator function by monitoring the reproductive success of plants in the community following restoration activities. Plants that support pollinator species that occupy unique pollination niches (Blüthgen and Klein 2011) and buffer the delivery of pollination services from biodiversity loss (Senapathi *et al.* 2021) may be especially important for strengthening the positive feedbacks between pollinator diversity and delivery of pollination services (Panel 2).

Figure 1. Restoration projects in seminatural ecosystems are conducted to achieve structural and functional endpoints and provide resources for species of conservation concern. (a) Planting mixes revegetate ecosystems to provide pollinator communities with floral resources and increase the abundance and diversity of pollinator species. Credit: S Simanonok. (b) Planting mixes that increase the abundance of key service-providing species could enhance the delivery of pollination services to ensure plant reproductive success. Credit: Montana State University/K Gorham. (c and d) Revegetating landscapes with the preferred resources for species of conservation concern, like (c) *Bombus affinis* and (d) *Bombus occidentalis*, may expand habitat and recover populations. Credits: USFWS (c) and C Delphia (d).

Targeted support for species of conservation concern

Documenting and establishing the preferred resources of endangered pollinator species could restore and expand the amount of potentially suitable habitat for pollinator species of conservation concern (Figure 1). As a result of recent and rapid population declines, multiple bee and butterfly species have received protection under the US Endangered Species Act (www.fws.gov/endangered). Notably, population declines of the rusty patched bumble bee (*Bombus affinis*) have correlated with the conversion of wildlands into agroecosystems, which drastically reduced foraging resources throughout the midwestern US (Mola *et al.* 2021). Planting lists for habitat revegetation could include plants like wild bergamot (*Monarda fistulosa*) – which is known to be visited by *B affinis*, produce nectar, and provide immune benefits for individuals – to restore bee population health (Palmer-Young *et al.* 2017). Furthermore, population declines of the western bumble bee (*Bombus occidentalis*) are also correlated with increased prevalence of the gut pathogen *Nosema bombi* (Cameron *et al.* 2016). Establishing plants with anti-parasitic properties, such as sunflowers (*Helianthus* spp), may lower levels of pathogen infection (Giacomini *et al.* 2018) among species of conservation concern, provide physiological benefits to whole pollinator communities (Vaudo *et al.* 2015), and achieve structural and functional endpoints, but this has yet to be tested in a field setting (Panel 2).

Select plants based on pollinator–flower interaction patterns

Plant attractiveness to pollinators

Determining which plant species are most attractive to pollinators and occupy functional roles associated with stability of ecosystem processes requires observations of pollinating visitors to focal plant species and identification of pollinator species by insect taxonomists. Focal plant species observations consist of using a hand net to collect all insects that visit the reproductive parts of flowers from selected plant species for a defined time period. Focal plant observations should be conducted consistently at multiple sites within different habitat types, over multiple growing seasons, to compare pollinator–flower interaction patterns evenly across plant species (Delmas *et al.* 2019). Each round of sampling should be conducted on warm, sunny, and calm days during peak pollinator activity to avoid biasing

Panel 2. Future directions and research priorities to design effective planting mixes for pollinator restoration in seminatural ecosystems

- Analyzing pollinator–flower visitation patterns to identify plants that occupy important functional roles in pollinator–flower networks.
- Are positive feedbacks between pollinator diversity and the delivery of pollination services strengthened by plants that support unique pollination niches?
- Do plants with anti-parasitic properties lower levels of pathogen infection in bees in a restoration setting?
- Can planting mixes increase pollinator population health by prioritizing plants that provide resources during critical stages and times of pollinator development?
- What plant traits are related to successful establishment and propagation to help achieve pollinator restoration goals?
- Can plant populations be strategically mixed to generate seed stock that is attractive to pollinators and adapted to future environmental conditions?
- Can a single, broadly applicable seed mix be developed and used within different habitat types? Would this result in landscape simplification following disturbances?
- How can monitoring programs provide cost-effective and reliable data on pollinator population trends following restoration?

results toward pollinators that can fly in inclement conditions (Gibson *et al.* 2011). Although focal plant species observations provide high-resolution data of potential pollinators, they can be biased toward large-bodied, easily identifiable pollinators, and are labor intensive even at small spatial and temporal scales. Labor-intensive sampling techniques are sometimes supplemented by passive sampling techniques, like pan trapping, but severe taxonomic biases with passive methods reinforce the need for focal plant species observations to acquire reliable data (Portman *et al.* 2020). In addition, the diversity of pollinators requires trained taxonomists for species identification. Managers implementing pollinator restoration projects across seminatural ecosystems should anticipate costs associated with laborious sampling techniques and trained taxonomists to evaluate the importance of focal plants for achieving restoration goals.

Identify framework plant species

Plant species that are attractive to pollinators may help achieve structural endpoints for restoration. A plant species visited by many pollinator individuals and/or many pollinator species may have an outsized influence providing resources to the pollinator community (ie "*framework plant*") (Panel 1; Figure 2) (Dixon 2009; Menz *et al.* 2011). Importantly, the visitation rate and species richness of pollinators to a focal plant species are often positively correlated with the floral abundance of that plant species in the community (Lázaro *et al.* 2009). Furthermore, pollinator visitation to a focal plant species can increase or decrease depending on the presence and abundance of co-occurring plant species (Lázaro *et al.* 2009). To help disentangle the effects of plant community context on pollinator visitation to focal plant species, the floral display of all focal and co-occurring plant species should be recorded during every focal species observation. Focal plants that are utilized at higher rates relative to their availability can be used to revegetate landscapes with floral resources that are preferred by pollinators.

Functional roles of plant species in pollinator–flower networks

Knowledge of community-wide patterns of pollinator–flower interactions can be useful for identifying plant species that contribute to interaction network structures associated with the stability of ecosystem processes (Figure 2). Pollinator–flower networks (maps of the interactions and frequency of interactions between individual pollinator and flowering plant species in a community) can provide information about the properties of ecosystems, like community stability (Tylianakis *et al.* 2010), which are rarely evaluated as an outcome of restoration activities. Pollinator–flower networks typically have high levels of asymmetry (specialist plants interacting with generalist pollinators, and vice versa) and nestedness (specialists interacting with a nested subset of more generalist species), which are thought to confer stability to ecosystem processes by supporting redundancy in interactions and functional roles (Tylianakis *et al.* 2010). To construct realistic pollinator–flower interaction networks and conduct accurate analyses of plant functional roles, focal plant species observations must be conducted throughout the growing season, over multiple years, and across different habitat types. Results can identify plants that are highly connected (high interaction diversity) and occupy nested roles within networks to restore robust network topologies following community reassembly (Figure 2) (Kaiser-Bunbury and Blüthgen 2015; Biella *et al.* 2017).

Avoid resource bottlenecks across the growing season

Revegetation projects frequently lack plant species that bloom during critical times in the growing season, resulting in potential resource bottlenecks for pollinators in restoration areas (Havens and Vitt 2016). Vegetation communities that lack floral resources during periods of the growing season can reduce bee population productivity (Mola *et al.* 2021) and may exclude some pollinator species from habitats (Ogilvie and Forrest 2017). To avoid potential resource bottlenecks and provide consistent floral resources throughout the growing season, the suites of plant species used in restoration projects should be composed of plants that bloom at different times during the growing season and have long bloom durations (time between first and last date of flowering) (Figure 2) (Dixon 2009; Menz *et al.* 2011). Revegetation projects may prioritize plants with long bloom durations at the beginning or end of the growing season to extend the total number of days pollinators can collect resources during nest initiation or before entering diapause. Providing consistent floral resources for pollinators during critical stages of development may be important to ensure population productivity and stability (Panel 2).

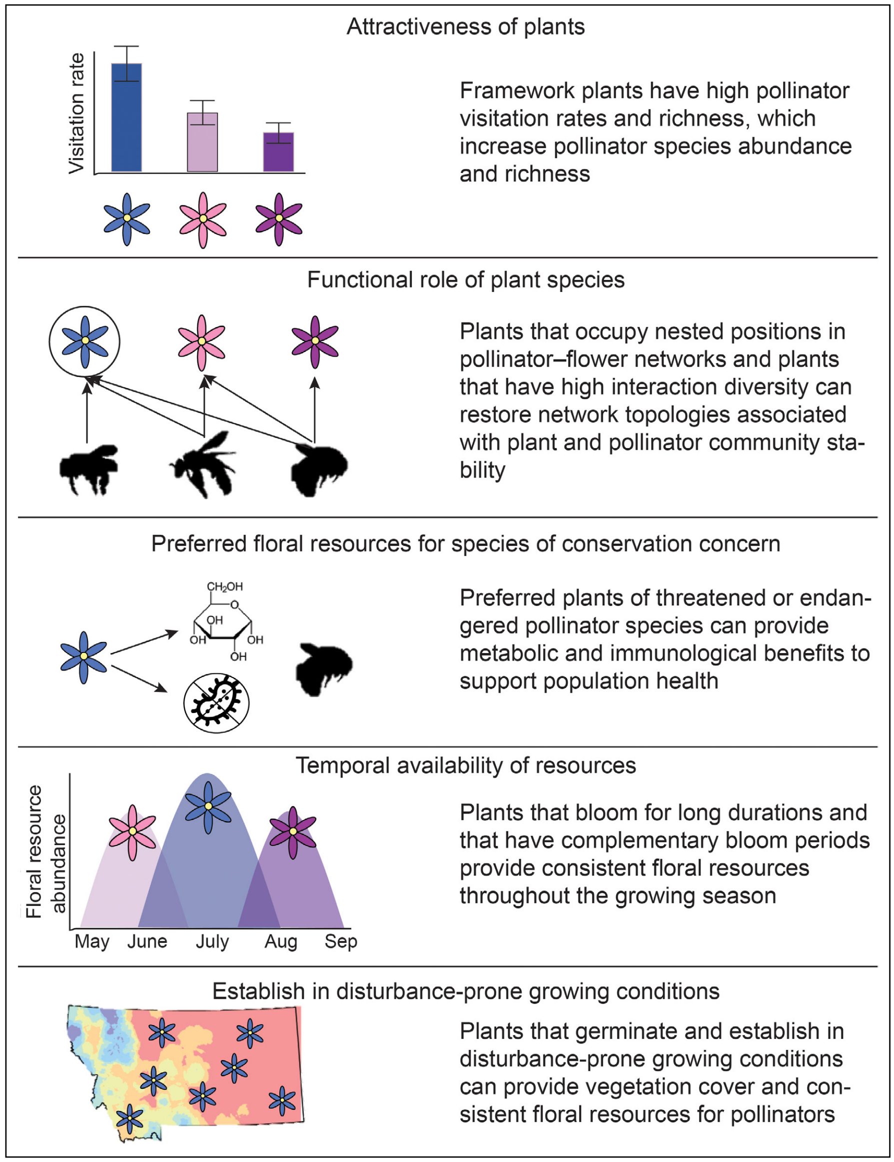


Figure 2. Integrating information from pollinator–flower interaction patterns and occurrence across the landscape may help in the selection of plant species to design planting mixes for pollinator restoration. Plants that are attractive to pollinators, occupy important functional roles within pollinator–flower networks, serve as the preferred floral resources for species of conservation concern, fill resource bottlenecks during the growing season, and provide consistent floral resources for pollinators across the landscape should be prioritized in planting mixes to restore pollinator habitat in seminatural ecosystems.

Increase the availability of plant materials adapted to seminatural ecosystems

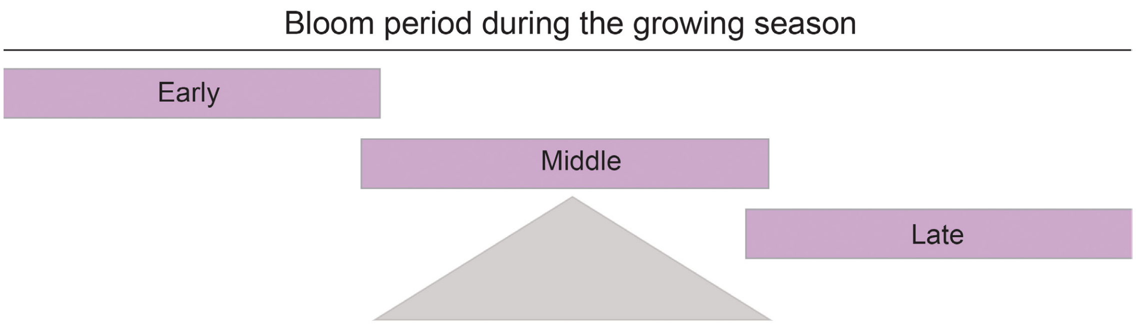
Selecting plants adapted to post-disturbance growing conditions

Plant species adapted to growing conditions resulting from disturbances may be required to improve rates of establishment in restoration contexts. For example, wildfires can consume soil organic matter, vaporize available nitrogen, and kill overstory trees. Aerial broadcast seeding also has little control over seeding depths and locations, resulting in highly variable rates of establishment for perennial forbs in seminatural ecosystems (Carter and Blair 2012). Rates of establishment in post-disturbance revegetation projects and the frequency of occurrence of plant species at a landscape scale can be used to select plant species that establish vegetative cover and provide consistent floral resources across seminatural ecosystems (Figure 2). Future work may identify plants with seeds that disperse over long distances and have high longevity in soil seed banks to establish persistent plant populations following restoration in seminatural ecosystems (Panel 2).

Locally sourced native plants have adaptations to establish large populations with genetic variation to persist through dynamic environmental conditions in seminatural ecosystems, like drought, wildfire, and anthropogenic activities (Isaacs *et al.* 2009). Locally sourced plant populations have suites of floral traits that preserve evolutionary relationships with pollinators and can sustain the reproductive success of plants in some specialized systems (Sun *et al.* 2014). However, for large-scale restoration projects encompassing entire pollinator communities, plant materials sourced from local populations can have lower pollinator visitation rates and can bloom for shorter durations as compared with plants sourced from other locations (Bucharova *et al.* 2022). To achieve defined restoration endpoints, restoration projects may use plant materials sourced from populations that are the most attractive to pollinators (Panel 2).

Farming wildflower seeds

Farming wildflower seeds may be critical to meet the growing demand for native plant materials in restoration projects in seminatural ecosystems. Nurseries established through



Forb and shrub species	Bloom period	Visitation rate	Visitation richness	SCC	Bloom duration	Frequency of occurrence	Composite score
Rosa woodsii	Middle	8	9	7	3	5	32
Lupinus sericeus	Middle	3	3	8	9	8	31
Symphoricarpos albus	Middle	9	1	7	6	7	30
Achillea millefolium	Middle	1	8	4	7	9	29
Phacelia hastata	Middle	5	6	9	5	3	28
Penstemon spp	Middle	4	5	3	8	4	24
Hedysarum boreale	Middle	7	7	3	2	1	20
Eriogonum umbellatum	Middle	2	4	3	4	6	19
Spiraea betulifolia	Middle	6	2	5	1	2	16

Figure 3. Within each bloom period (pink rectangles), a scorecard that integrates information across desirable plant traits can help in identifying the most effective plants for pollinator restoration. In this example, adapted from a study assessing the pollinator value of plants available to the US Forest Service for restoration in Montana (Glenny *et al.* 2022b), plant species were ranked depending on the observed pollinator visitation rate, visitation richness, value to species of conservation concern (SCC), bloom duration, and frequency of occurrence across the landscape; rankings were then totaled into a composite to select the best overall plants for pollinators (green composite score).

federal programs – like the US Department of Agriculture Forest Service's Native Plants Material Policy, the US Bureau of Land Management's Native Seed and Plant Material Development Process, or the UK's Native Seed Hub – collect, cultivate, and distribute native plant materials for restoration and other uses at commercial scales. However, farming native plant seeds is slow and labor intensive, and can result in inadvertent artificial selection of maladaptive floral traits. Managers often rely on seeds from commercial sources to revegetate large landscapes quickly, reduce soil erosion, and suppress invasive species establishment. For small-scale and intentionally planned projects, strategically mixing genetic diversity from plant populations that are the most attractive to pollinators into seed stock could provide land managers with native plants optimized for pollinator restoration (Panel 2) (Bucharova *et al.* 2019).

Integrate information to select plant species

Integrating results from pollinator–flower interaction patterns and occurrence across the landscape, along with considering the cost of plant materials, may help in designing cost-effective planting mixes to meet multiple restoration goals in seminatural ecosystems. Revegetating landscapes with the fewest number of plant species that support the maximum number of pollinator species and pollination services may be important to implement cost-effective restoration projects (Williams and Lonsdorf 2018). Furthermore, studies from the Intermountain West in the US (Glenny *et al.* 2022b) and the Pampas of Argentina (Malena *et al.* 2021) ranked plants using criteria related to the attractiveness of each plant species for pollinators, the ability of a plant species to proliferate in the environment, and the cultural importance of a plant species, ultimately creating a composite score for managers to select the most important plants and design a single seed mix for restoring pollinator communities and ecosystem health (Figure 3). However, if each criterion is weighted equally and information that is gathered across multiple habitat types are integrated, then the resulting planting mix may not establish within a specific habitat type or meet a defined restoration goal. Land managers may consider first choosing plant species suited for a habitat type and then integrating information on pollinator visitation to select plant species that meet explicit goals for pollinator restoration.

Variation in plant and pollinator communities throughout the growing season and across biogeographic gradients may require distinct planting mixes to support pollinator communities at local and landscape scales. Interactions between pollinators and a focal plant can be lost or gained depending on the composition of co-occurring plants and plasticity in foraging behaviors of pollinator individuals (Poisot *et al*. 2015), suggesting that the role of some plant species is context-dependent. Consequently, individual plant mixes may be required to support local pollinator communities that differ between restoration sites. Variation in planting mixes may establish complementary floral communities, which can buffer pollinator populations from landscape-level resource scarcity (Ponisio *et al*. 2016). In addition, almost nothing is known about the influence of patch size for pollinator restoration. Locally small restoration patches may provide refuges of floral resources across the landscape, while expansive restoration projects that use the same seed mix for revegetation may homogenize plant communities, resulting in *landscape simplification* (Panels 1 and 2).

Evaluate the success of planting mixes

Although rarely conducted, monitoring of pollinator populations is essential for determining the degree to which restoration endpoints are met (Woodard *et al*. 2020). As a result of naturally high inter- and intra-annual variability of pollinator species abundance and diversity, pollinator monitoring requires a large number of sites, high frequency of sampling efforts, and long periods of time (up to 10 years) for reliable detection of population changes, which can become prohibitively expensive (Breeze *et al*. 2021). Monitoring programs could detect changes in pollinator communities while reducing costs by comparing the results of surveys following restoration to historical collections and previously well-sampled areas (Panel 2) (Bartomeus *et al*. 2019).

Anticipate climate change for pollinator restoration

Given global climate change, prioritizing plant species that maintain consistent functional roles in pollinator restoration and improving adaptations within seed stock may be required to preserve pollination services into the future. Climate change is anticipated to alter plant species phenology, spatial distribution, and floral traits, leading to the reorganization of plant–pollinator interactions at a community level. To identify plants that maintain consistent roles for pollinator restoration under future climate conditions, pollinator visitation could be observed to focal plant species within *climate analogs* (Panel 1). Moreover, local adaptations within plant populations are anticipated to lag the pace of climate change. Strategically mixing genetic material from plant populations sourced from climate analogs into seed stock could select for plant materials that are resilient to climate change and increase preparedness among land managers for future climate scenarios (Panel 2) (Bucharova *et al*. 2019).

Conclusion

Plant material selection is critical for designing restoration strategies that achieve structural and functional endpoints for pollinators in seminatural ecosystems. Plant species that are native, attractive to pollinators, and support network structures associated with community stability are the most ideal for use in restoration projects. Furthermore, plant species that commonly occur across the landscape, and that bloom for long durations and during resource bottlenecks, are important for providing consistent floral resources for pollinators. Integrating multiple criteria about the importance of plants for pollinators is essential for creating assemblages of plants that are effective for pollinator restoration. Collaboration between restoration ecologists and land managers can ensure the development of tools that can be easily implemented to meet the habitat requirements of pollinators in complex environments. Restoration strategies for pollinators in seminatural ecosystems can counteract pollinator declines resulting from climate change, anthropogenic activities, and altered disturbance regimes.

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Data Availability Statement

No data were collected for this study.

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