A review of the challenges and opportunities for restoring animal-mediated pollination of native plants

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Ecological restoration is increasingly implemented to reverse habitat loss and concomitant declines in biological diversity. Typically, restoration success is evaluated by measuring the abundance and/or diversity of a single taxon. However, for a restoration to be successful and persistent, critical ecosystem functions such as animal-mediated pollination must be maintained. In this review, we focus on three aspects of pollination within ecological restorations. First, we address the need to measure pollination directly in restored habitats. Proxies such as pollinator abundance and richness do not always accurately assess pollination function. Pollen supplementation experiments, pollen deposition studies, and pollen transport networks are more robust methods for assessing pollination function within restorations. Second, we highlight how local-scale management and landscape-level factors may influence pollination within restorations. Local-scale management actions such as prescribed fire and removal of non-native species can have large impacts on pollinator communities and ultimately on pollination services. In addition, landscape context including proximity and connectivity to natural habitats may be an important factor for land managers and conservation practitioners to consider to maximize restoration success. Third, as climate change is predicted to be a primary driver of future loss in biodiversity, we discuss the potential effects climate change may have on animal-mediated pollination within restorations. An increased mechanistic understanding of how climate change affects pollination and incorporation of climate change predictions will help practitioners design stable, functioning restorations into the future.

Introduction

We are experiencing unprecedented global biodiversity declines driven primarily by habitat loss and land-use change [1]. Ecological restoration has become an effective and widespread method to mitigate biodiversity decline to the extent that the United Nations General Assembly declared 2021–2030 the ‘Decade of Ecosystem Restoration’ [2,3]. Early in its development, the field of restoration ecology in terrestrial systems focused on specific species or communities, usually plants, at a particular location [4]. This single taxon approach is relatively straightforward to implement and ultimately evaluate in terms of restoration success. However, other trophic levels can have large effects on restoration outcomes, especially for plant communities [5]. Furthermore, practitioners are often interested in conserving animals and ecosystem functions in addition to plant communities. Thus, the field of restoration ecology has begun to explicitly consider multiple trophic levels [6,7].

One goal of ecological restoration is to enhance or sustain the function of animal-mediated pollination (herein pollination for brevity); a function that benefits nearly 88% of angiosperm species globally [8]. Plants in fragmented landscapes may suffer reduced pollen deposition and pollen quality [9,10] that ultimately leads to negative effects on population growth and persistence [11]. Reduction in pollination quantity and quality are particularly concerning for rare plant species or those of...
conservation concern [12,13]. Changes in pollination may extend past individual species and affect entire communities [14]. For example, plant–pollinator interactions may be important drivers of plant community assembly within a restoration [15]. Finally, the loss of pollinators may have large-scale regional effects. Biesmeijer et al. [16] found that throughout the Netherlands, declines in outcrossing, animal-pollinated plants were correlated with declines in native bee diversity.

An ecological restoration is an important tool for reestablishing, enhancing, and sustaining pollination. We focus on ecological restorations defined as ‘the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed’ [17]. We limit our review to the pollination of native plants within restorations as the persistence of native plant communities is vital to ecosystem recovery. In this review, we do not discuss the role of pollinator floral plantings for crop pollination (see [18] for a review) as the objectives (e.g. yield) and ecology (e.g. plant distribution, density, and diversity) of cropping systems differ considerably from natural systems. Programs such as Agri-Environment Schemes (EU) and the Conservation Reserve Program (U.S.A.) often entice landowners to plant a high density of forbs in order to sustain or enhance crop pollination and/or protect pollinator diversity [19,20]. These practices are targeted at pollinators or natural enemies without explicit consideration of entire ecosystems. In contrast, land managers often have multiple objectives and must consider the entire ecosystem when implementing ecological restorations. Finally, our review is global in scope; however, we recognize that geographic biases in pollination studies may limit our scope of inference [21].

Our review is organized into three sections. First, we discuss how pollination is measured within restorations. Second, we highlight how management and environmental factors at the local and landscape scale can affect ecosystem restoration and discuss how these might impact pollination function. Third, we discuss how climate change may affect pollination in a restoration context.

**Measuring pollination function**

A key knowledge gap in restoring pollination is accurately measuring pollination function. Restoring pollination necessitates the explicit consideration of both plants and animals, yet previous restoration and research efforts have typically focused on one group [22,23]. Much of the literature on pollination restoration measures floral abundance and/or diversity [24] or pollinator abundance and/or diversity [25–29]. Assessing the recovery of pollinators and plants can be a useful first proxy for determining the effects of restoration on pollination. For example, pollinator abundance is likely positively associated with floral visitation rate which is an important predictor of pollination [30,31]. Pollinator visitation rate is relatively simple to measure and can provide important insights into plant–pollinator interactions (e.g. [32]). However, variation in pollinator abundance and/or diversity does not necessarily translate to concomitant effects on pollination success in restorations [33].

Pollen limitation of seed set is common in many native plant species [34–36] and it has the potential to affect restoration success [15,37]. Pollen supplementation experiments as well as sentinel plant studies offer a robust methods for directly measuring pollen limitation [33,35]. In particular, pollen supplementation experiments can elucidate the relationship between the quantity of pollen deposited and resulting seed production is a saturating curve. Pollen supplementation experiments can, therefore, determine the degree to which pollen is limiting seed production [35]. Furthermore, while visitation and plant reproduction are often positively associated, these two factors may simply covary with resource level [35]. Pollen supplementation studies can help to quantify the relative effect of resources and pollen receipt for limiting plant reproduction. Few studies have directly tested for pollen limitation in restorations (but see [38]) [31,39].

Even if pollen receipt is limiting seed production, variation in seed production may or may not have large effects on plant population growth and persistence. Few studies have investigated whether changes in pollination lead to changes in plant population dynamics. In one study, Anderson et al. [13] found that an endemic shrub in New Zealand experienced an 84% reduction in seed production and 55% decrease in seedling recruitment due to the loss of bird pollinators. While time-consuming, these types of studies allow researchers to more accurately quantify whether variation in pollination services is driving changes in plant populations. Similar studies in restored systems will help to uncover the role of pollination in the re-establishment and persistence of plant communities.

Network analysis is a tool for assessing how restoration affects community-level pollination processes. Pollination networks benefit from restorations and this may be due, in part, to flexibility in pollinator foraging [40–44]. However, in some restored systems, networks may be simplified compared with reference systems and thus potentially susceptible to disturbance [32,40]. Most previous pollination network studies have focused on either presence/absence or interaction frequency (i.e. floral visitation rates) to infer pollination. However, these metrics may not be...
accurate measures of pollination as not all visitors contribute to pollination [43]. Incorporating measures such as single-visit pollen deposition [43,44] or collecting pollen from flower visitors [45] can reveal network patterns that differ from simply measuring visitation rates. Such studies are logistically difficult but can provide a detailed, mechanistic understanding that will help managers more successfully restore pollination.

**Environmental and management factors affecting pollination in restorations**

Successful restoration of pollination function is affected by local and landscape factors (Figure 1). We consider the local scale to be the level of the restoration site, i.e. the area that is undergoing restoration and often under direct management. We consider landscape scale to include areas beyond the site undergoing restoration. Some factors operate at multiple scales, e.g. invasive species we treat here as a local factor because in restoration much discussion of invasive species centers on site-level effects and removal. However, invasive species operate at the landscape scale as well, in that a site is more likely to be invaded if it is located near areas where the invasive species is already established.

**Local factors**

**Establishment of plant and pollinator communities**

Seed mixes of plant species are commonly used to restore diverse plant communities in ecological restoration, with the assumption that higher taxa, including pollinators, will colonize on their own [22,46]. While

![Figure 1. Conceptual framework illustrating how landscape and management practices can affect habitat and biotic communities.](image)

Management at the landscape level impacts both habitat and biotic factors, while management at the local scale primarily affects biotic factors. Changes in plant and pollinator communities can ultimately lead to changes in pollination function. Photo (A) shows an example of management efforts through managed burn (local effect), photo (B) is a restored prairie in Western, Minnesota (U.S.A.), and photo C is a native bee visiting Dalea purpurea (Fabaceae). Photo credits: (A) Sean Griffin, (B) Christina Herron-Sweet, (C) Gabriella Pardee.
practitioners often prioritize creating high diversity plant, floral display size (e.g. number of inflorescences within and/or across species) is a better predictor of native bee abundance and richness than seeded plant diversity [47]. Restoring high plant diversity may not be required to reinstate diverse pollinators if highly diverse plant mixes do not produce the significantly greater quantity or quality of floral resources compared with less diverse mixes [24]. Plants vary in their attractiveness to pollinators due to variation in floral morphology and rewards [48,49]. Furthermore, particular plant species may provide crucial nutritional needs for developing larvae [50]. Therefore, practitioners must carefully select which plant species to include in seed mixes. Of 15 standard plant species used in seed mixes, only one was found in pollen samples from common solitary bee species [51], thus suggesting that some plant species commonly used in restoration do not support much of the native bee community. Practitioners must design seed mixes that prioritize not just plant species diversity but also a range of floral morphologies and span an entire season to support the local pollinator community.

Seed mixes vary not just in diversity but also in the density, or rate, at which seeds are planted. Due to competition among plants for limited resources, the seeding rate plays a strong role in the establishment and persistence of the plant community [47,52]. Where the desired outcome is inflorescence production for pollinator provisioning, high seeding rates see diminishing returns compared with intermediate seeding rates due to the trade-off between cost and density-dependent mortality [53,54]. In some restored ecosystems, a few dominant plant species may be attractive to many pollinator species [54,55]. Including dominant plants may be essential for the restoration of the pollinator community and restoration of ecosystem pollination function [24,55]. Dominant plants may facilitate the persistence and pollination of rare plant species by supporting a robust, diverse pollinator community (magnet effect [37,40,56–57]). Future research should explicitly measure the effects of varying density and the role of dominant plant species on floral resource production, the pollinator community, and ultimately, pollination function.

Translocation of plants has long been used in restoration [58–61]. Translocation of animal pollinators has been proposed as a method to restore pollinator communities and pollination function [62–63]. Such efforts would target common species that likely provide much of the pollination function in the ecosystem, and theoretical models suggest that reintroducing species that visit and pollinate many plant species may restore plant–pollinator community networks [64]. However, translocating pollinator species may alter plant–pollinator interactions and pollinator foraging behavior, with possible repercussions for pollination function [65]. Translocating pollinator species may not fully restore pollination function if the phenology of the introduced species does not match up with the phenology of local plant species [66]. Furthermore, translocation would increase the cost of restoration and its ability to restore pollination function remains untested in empirical systems [63].

Finally, pollinators require more than just floral resources to establish and persist in restored communities. For example, pollinators require appropriate substrates for nesting and non-floral resources for food and/or immune function [67–69] and nesting resources can influence the structure of native bee communities [70]. Yet, ecosystem restoration does not routinely include the provisioning of these non-floral resources [69]. We know of no studies that have evaluated how these factors may limit pollinator populations and subsequently pollination within restorations. This is an important avenue for future research.

Management of restoration for pollination

One challenge facing restoration practitioners is designing management to mimic historic ecosystem processes to benefit both plant and pollinator communities, thus supporting pollination function. In tallgrass prairie, for example, mowing, prescribed fire, and grazing by cattle or bison are commonly used to simulate historic disturbances [71]. The disturbance is important for maintaining plant diversity and heterogeneous communities over time in these systems [72]. Mowing is frequently used as a proxy for grazing regimes and generally increases plant community richness and inflorescence production, although in grass-rich restorations, grasses may benefit more from mowing than forb species [24,73]. Prescribed fire and grazing are used to create a mosaic of areas of varying plant composition and vegetation structure because plant functional groups vary in their response to these ecosystem disturbances [74–76]. Prescribed burns increase wild bee abundance and richness though grazing generally has the opposite effect [77,78], suggesting that maintaining a spatial and temporal mosaic of management is recommended for the bee as well as plant communities in this system.

The goal of using prescribed fire in restoration management is generally to mimic the effects of natural wildfire, but we lack a body of literature assessing the effects of fire on pollination function. A recent global meta-analysis across fire-prone ecosystems showed no effect of prescribed fire on pollinators, but did describe a positive effect of wildfire on pollinator abundance and species richness, especially Hymenoptera [79].
Lepidoptera in particular decrease in abundance and richness following wildfire [79] and prescribed burns [80,81]. Only a few studies explicitly address pollination function in response to wildfire [82–84]. Species and trait composition of bees visiting focal plant species is altered postfire, leading to reduced outcrossing rates in focal plant species [82,83]. However, in a specialized pollination system after a fire, the fruit set of the focal plant was maintained following the loss of the specialist beetle pollinator by a functionally similar beetle [84].

Managing invasive species is vital in restoring pollination function. Invasive plant species present novel rewards for pollinators, often resulting in competition for pollinators with native plant species [85,86]. This results in the disruption of pollinator visitation patterns, altered community level plant–pollinator networks, and reduced reproductive success of native plants [86–91]. Disruption of pollinator visitation does not necessarily lead to negative reproductive outcomes for plants, however [89–91], suggesting that the negative impacts of invasive plants on pollination function are context-specific. Studies show that the removal of invasive plant species can successfully restore native bee communities and pollination of native plants [92–94]. Removal of invasive plants can be particularly important for restoring pollination of rare or declining species due to reduced competition for pollinators [95]. Invasive pollinators, particularly *Apis mellifera*, can provide valuable pollination services to native plants [96–98]; and in some contexts, they will not disrupt the native pollinator community [99]. However, recent research cautions that they may spread the disease to wild bee species, disrupt plant–pollinator networks, or compete with wild bee species for floral resources [99–101]. Therefore, non-native species should only be viewed as a temporary solution in restoration contexts.

**Landscape factors**

The landscape surrounding a restoration can have large effects on community structure and ecosystem function within a restoration [102,103]. Landscape effects are often conceptually separated into two components, habitat amount and configuration, and each may have distinct effects on pollination (reviewed in [104]). Individual restoration sites are embedded within a matrix that encompasses a variety of land cover types. As the amount of land cover containing suitable habitat for pollinators increases, the abundance and diversity of pollinators foraging and subsequently pollination within a restoration should also increase. Farms and fragmented habitats with increasing amounts of surrounding land cover in agriculture have lower pollinator abundance and richness, although this pattern seems to be consistent mainly in areas of extreme habitat loss [104]. In Europe, agri-environment-based pollinator plantings are most effective at increasing relative abundance and richness of pollinators in landscapes were between 1% and 20% of the surrounding landcover was still in semi-natural habitat [105]. Ritchie et al. [38] did not find a relationship between the increasing area of agriculture surrounding a restoration and overall bee abundance and pollen limitation of an annual forb, suggesting that restorations can have positive effects on pollination regardless of placement within the landscape.

Landscape configuration such as proximity to natural habitat and patch size can also affect pollination within restorations [104]. Higher connectivity is predicted to have a positive influence on pollinator abundance, richness, and pollination within a restoration. This is likely due to increases in colonization and pollinator movement [104]. However, these effects can vary across taxa and restoration contexts. In Sweden, connectivity increased solitary bee abundance but had no effect on bumblebee abundance and a negative effect on hoverfly abundance [106]. In a tropical rainforest in Costa Rica, restorations with corridors had dramatically higher pollinator abundance and pollination compared with restorations without corridors [107]. One of the major challenges of examining landscape configuration is that these metrics are often confounded with habitat amount [104]. Hadley et al. [108] found that compared with habitat amount, patch size had a greater influence on the pollination of a tropical hummingbird-pollinated plant. This demonstrates that configuration can have impacts on pollination independent of the amount of habitat.

**Future impact of climate change on pollination in restorations**

The Earth is warming at unprecedented rates [109] and climate change is predicted dramatically increase species extinction [110] and affect species interactions [111]. Climate change can disrupt restoration efforts, which can ultimately affect the pollination of native plants. Here, we briefly touch on three examples of how pollination within restorations can become altered due to climate change. First, the blooming period of many plant species used in seed mix designs will likely shift in response to the earlier onset of spring [112–114]. As a result, we could see decreased reproductive success due to a phenological mismatch in which the blooming
period of plant species no longer coincides with the foraging period of its respective pollinator species [115–117]. This often occurs when pollinators either respond to different abiotic cues, or to the same cues but at different rates [118,119]. However, Bartomeus et al. [120] found evidence that plants and their pollinators are maintaining phenological synchrony despite both organisms shifting their phenologies under climate change. Secondly, despite efforts to control invasive species, extended growing seasons under climate change can create vacant niches that non-native plant species can exploit [121,122]. Once established, non-native plants could outcompete native plants for pollinators as they can often better adapt to changes in abiotic conditions [123–125]. There is also evidence that non-native pollinators might also better adapt to climate change than native pollinators, which has allowed them to expand their ranges [126]. However, some studies have suggested that invasive pollinators may add response diversity to pollinator assemblages, thus maintaining pollination function under climate change [126,127]. Finally, restorations may experience harsh weather events under climate change, such as false springs, droughts, heat waves, or heavy precipitation. Plants may respond to these events through smaller flower size or reduced flower production and pollen and nectar rewards [128–130], making them less attractive to pollinators. Furthermore, pollinators could respond to harsh weather events through reduced foraging behavior, thus limiting opportunities for pollination [131–133].

Climate change and land-use change will likely interact to have synergistic effects on biodiversity loss [134,135]. For example, restorations set within hostile landscapes could hinder an organism’s ability to either adapt to changing climatic conditions or disperse into more hospitable environments [136,137]. Thus, the homogenization of plant and pollinator communities could occur if a reduced set of species will be able to withstand climatic extremes, thereby decreasing pollination function [135,138].

Fortunately, there are several steps that conservationists can take when planning restorations to mitigate the negative effects of climate change on biodiversity and ecosystem functioning. First, future region-specific IPCC climate predictions should be taken into account when designing a restoration [139]. This will allow land managers to plant species that can withstand local changes in weather patterns. For example, species that are drought tolerant could be included in seed mix designs for areas that are predicted to undergo periods of drought under climate change to maintain plant communities. Second, creating seed mixes from genetically diverse seed sources can allow for rapid adaptation to novel growing conditions [140,141]. Finally, increasing restoration efforts and installing restorations that are highly interconnected will allow organisms to disperse into more favorable environments to maintain populations, genetic diversity, and ultimately pollination in a warming world [142–144].

Summary

- Habitat loss is the leading cause of biodiversity declines worldwide. Ecological restoration is increasingly used to minimize or even reverse biodiversity loss. It is important to consider ecosystem functions such as animal-mediated pollination within restorations. However, there are relatively few studies of pollination of native plants within ecological restorations.

- Accurate measurement of pollination is necessary to determine long-term plant reproductive success within restorations. The vast majority of studies use proxies such as pollinator abundance and visitation rate to infer pollination in restorations. However, these proxies do not directly measure pollination. Pollen supplementation experiments, pollen deposition studies, and pollen transport networks offer a more robust method for assessing pollination within restorations.

- Local factors such as plant community composition and management actions such as prescribed fire and removal of non-native species can have large impacts on plant communities, pollinator communities, pollinator foraging, and ultimately pollination. Understanding how these factors affect pollination will help land managers create and manage for high functioning restorations.
- Ecological restorations are embedded in a landscape matrix that can be hostile to plants and pollinators. Landscape components such as the total amount of natural habitat or habitat configuration can influence pollination. Determining how these components affect pollination will help practitioners design restorations and prioritize where on the landscape to create new habitat.

- Climate change is rapidly becoming one of the largest drivers of biodiversity loss. This will almost certainly have large impacts on pollination in restorations. Understanding how climate change affects pollination will help practitioners ensure resilient, functioning restorations well into the future.

Competing Interests
The authors declare that there are no competing interests associated with the manuscript.

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All three authors developed the ideas, contributed to writing and revising, and checked the final version.

Abbreviations
IPPC, Intergovernmental Panel on Climate Change.

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