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Diversifying Landscapes for Wild Bees: Strategies for North American Prairie Agroecosystems

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Abstract

Purpose of Review We reviewed the common mechanisms through which intensively cropped landscapes are modified to increase wild bee abundance and diversity in North American prairie ecosystems. We categorized these efforts into three main categories: retaining parcels of land identified as important to wild bee communities, augmenting currently cropped areas to increase available resources, and restoring spaces from cropland to pollinator habitat. We discuss considerations that should be included at both the farm and "farm-neighborhood" scale, and review the literature pertaining to the costs and benefits of each strategy.

Recent Findings Wild bee conservation has been a topic of much interest in the past decade, with research generally focused at the field scale. Initial studies have focused on providing evidence that restoring, augmenting, and retaining land for wild bees shows the desired effects. Research quantifying the costs associated with each method still has significant knowledge gaps, as does understanding patterns of variability common in natural prairie ecosystems.

Summary Retaining, augmenting, and restoring habitat for wild pollinators can create "win-win" scenarios for both wild bees and land-use decision-makers, whereby increased insect abundance has the potential to increase yield. There are considerations to be taken into account at both the farm and farm-neighborhood scale, and we present a framework which can be used to demonstrate the value of non-cropped areas to land-use decision-makers. Rapidly developing technology, such as GPS yield monitoring, has the potential to dramatically increase our power to detect which areas of a field may be ideal candidates for restoration or augmentation efforts.

Keywords Bee conservation · Habitat · Augment · Retain · Restore

Introduction

Wild bee populations have suffered recent and alarming declines, and a major contributor has been habitat loss [1, 2]. The problem is particularly acute in prairie ecosystems, where intensive farming practices, such as field expansion, have reduced the availability of habitat. Wild bees often face shortages of the food and nesting resources needed to thrive [1, 3]. This has consequences for pollination ecosystem service provision to pollen-limited food crops, and in turn for crop yields, nutritional quality, and food security [4, 5, 6••]. Retaining, restoring, and augmenting habitats beneficial to pollinators within agroecosystems has the potential to mitigate pollinator declines (e.g., [7, 8]) and to export pollination services to neighboring fields through a spillover effect [8, 9].

Creating habitat for bees in agroecosystems presents the enticing possibility of "win-wins," where farmers may be motivated to engage in land conservation in part to improve pollination services for their crops [10, 11], or to obtain other soil retention, climate, or hydrological services from that uncultivated land. However, achieving this mutually beneficial outcome for bees and people will likely require land-use

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decisions at both the farm and "farm-neighborhood" scale [12]. In this review, we refer to the farm scale as parcels of land in proximity to one another and under the same management practices, while the "farm-neighborhood" scale involves multiple land-use decision-makers within a geographic region, working together for a mutually beneficial outcome. Landscape ecologists, accustomed to working with biodiversity and ecosystem services at large spatial scales such as these, are well-equipped to generate evidence to inform decision-making.

This review is intended to support landscape ecological inquiries into wild bees and the pollination services they provide, with a particular focus on North American prairie agroecosystems. Existing research tends to focus on finer spatial scales, for example, where the conditions at a study site or field rather than its landscape context are of principal interest (but see [13] for an example). Studies focusing on habitat quality are common, and much has been published on how floral resources influence the establishment of bee species [14–17]. Studies at the site-level nonetheless provide insight into the mechanisms that drive bee abundance and diversity at broader spatial scales. To provide a window into how bees are influenced by site conditions, we summarize evidence on how habitat and its interactions with bee life history are likely to influence wild bee distribution in Box 1.

Pop-out Box 1

Nesting resources, flowers and wild bee life history

Within wild bee communities, different species have different resource requirements, meaning that landscape variables have the potential to impact each species in a different way [13, 17, 18]. Wild bee abundance and diversity tend to be primarily influenced by the availability of nest sites and suitable floral resources [16, 19•, 20]. Species also differ in their life history strategies, which may determine their response to typical conditions found in prairie agroecosystems. Female bees of non-parasitic species collect pollen on which to lay their eggs. These pollen balls provide essential nutrition to developing offspring.

Nesting Resources:

Ground nesting species - Females excavating nests in soil each year represent the majority of the species, we see in NA prairie agroecosystems. Soil disturbances (e.g., tillage and seeding) may destroy nests of these species and makes areas where annual crops are sowed generally uninhabitable.

Cavity nesting species - These species require pre-existing cavities in which to create nests. Frequent land disturbance (e.g., removal of shrubs and trees) will prevent appropriate nest sites from forming. In newly restored areas, it may take time for cavity nesting sites to become available.

Twig nesting species - Like ground nesting species, twig nesting females do the work of excavation; however, these females require twigs for their nests (often limited to one or several plant species). This tends to be the least abundant group in prairie landscapes, even in undisturbed areas, likely because nesting sites may not be abundant. In restored areas, these may be the last bees to recolonize, as it takes time for the required plants to become established.

Floral resource requirements:

Oligolectic - These species have evolved specializations to collect pollen only from a small number of plants (in rare cases a single species). Thus, the reproductive success of these species requires that their associated plants are growing close to their nests to minimize the energetic burden of foraging.

Polylectic – These are generalist species that will collect pollen and successfully rear offspring from many flower species. This is the most common strategy in prairie systems.

Life history strategy

Solitary - Females provision pollen and lay eggs without help from conspecifics. Many species forage for short periods of time—often only a few weeks each year. Reproductive success for these species is associated with appropriate and abundant floral resources synchronized with emergence dates and times at which pollen is being collected to provision offspring.

Eusocial - In the prairie climates, queens of eusocial species emerge in the spring, first laying a set of eggs which will develop and become workers. Once workers emerge, they assume foraging duties while the queen remains in the nest to continue laying eggs. These workers provision next year's queens (referred to as gynes) at the end of the season. Floral resources are required for an extended period of time to support both queen and worker development. Nest site requirements vary by species, but often pre-existing cavities are preferred.

Parasitic - This group of species does not collect any pollen of their own, but furtively enters nests of other species and take over the entire colony (e.g., in several species of *Bombus*) or lay eggs on pollen collected by the owner of the nest. The success of parasitic species is linked to the establishment of their host in any given location.

The emphasis of this review, however, is at the broader scale. In particular, we focus on approaches intended to support wild bees and pollination services through landscape diversification in prairie grassland ecosystems, i.e., strategies that can be implemented by land use decision-makers to increase the amount, configuration, and complexity of land covers necessary for bee species in crop-dominated landscapes. In particular, we focus on the prairie grasslands of North America. This region has seen more than 80% of its native grassland converted to agricultural farmland [21]. As a result of the Dominion Land Survey (Canada) and the Public Land Survey System (USA), land in this region was typically divided into 2.6 km^2 (1 sq. mi) parcels, often leading to regular field sizes. Our objectives are to (1) clarify how wild bees in prairie grassland ecosystems are affected by landscape diversification, (2) diagnose aspects of these strategies that may hinder their implementation, and (3) propose a systematic methodology that scientists can use to assess whether these strategies may be beneficial for wild bees and land use decision-makers. In each case, we highlight farm and farm-neighborhood scale considerations that may affect the success of these initiatives.

Defining Retaining, Restoring, and Augmenting Habitat for Wild Bees

The protection of wild pollinators in prairie agroecosystems will require management with pollinator conservation in mind [17, 22]. We have identified three commonly implemented and effective strategies intended to increase the diversity and complexity of land covers in prairie agroecosystems: the *retention* of existing high quality landscapes that promote wild bee biodiversity, the *restoration* of previously degraded landscapes to pre-disturbance state, and the *augmentation* of intensively cropped landscapes. In addition, we propose a research framework to assess the potential benefits of the strategies for both wild bees and land-use decision-makers (Fig. 1; Box 2).

Pop-out Box 2

Can we demonstrate the value of non-crop patches to land-use decision-makers?

One of the largest barriers to the implementation of conservation strategies is the lack of evidence that the commitments necessary by land-use decision-makers will lead to financially sound outcomes. We propose the following framework that can be used by researchers to determine whether conserving natural features or other uncultivated patches in or near fields ("non-crop patches") may be beneficial and to demonstrate the value of doing so.

1. **Can retaining or creating new non-crop patches be revenue neutral in the short term?**
   Farmers, with good reason, may believe that any land area not in production equates to lost revenue. However, poorer soil patches found within a field may not represent a profit for the farmer if crop yields on that patch fall below a threshold (i.e., because the cost of inputs to the patch such as seeds, fertilizers, fungicides, and insecticides may be greater than the value of the crop harvested from the same area). Helping farmers to calculate this threshold for their fields and identify which patches may fall below, and it could be used to incentivize land conservation as an alternative to losing money. Recent advances in GPS-based precision agriculture, such as variable-rate seeding, spraying, and yield monitoring make such calculations practicable in croplands, and permit mapping of zones within a field that may have negative profitability, and could be allowed to passively restore for conservation benefit. These technologies can also be used to map which landscape features contribute to the yield of surrounding crops and could be retained for this service.
2. **Do non-crop patches act as reservoirs for insect pest species, agricultural weeds or host crop pathogens, diseases and their vectors?** A prevailing concern among prairie farmers is that non-crop patches near fields will be reservoirs for unwanted insect pest species, weeds, and plant pathogens. Work done in this area should quantify the prevalence and transmission of pests and pathogens most important in prairie agroecosystems. Much of the work done to answer these questions has been conducted in perennial fruit cropping systems; however, these results have demonstrated that this is typically not the case [23]. Weed seed bank studies conducted adjacent to existing non-crop areas can be used to demonstrate their relative importance as sources. Equally paired fields in close proximity with different amounts of non-crop area *in situ* can be contrasted for the presence of insect pests.
3. **Is there evidence that the wild bees residing in non-crop areas are providing ecosystem services?**
   More than providing habitat for wild bees, it will also be necessary to quantify the efficacy of native bees as pollinators in prairie cropping systems. Many crops, cereals for example, will not benefit at all from animal pollination and can be excluded. Oilseed rape (or canola) is one widely important grassland crop where there is evidence of a yield benefit associated with bees and other pollinators, though evidence to date suggests that the effect size is not uniform globally [24–26]. Additional research is needed on this and other pollen-limited crops, and it could be investigated from two perspectives. One is to compare yield differences between plots when pollinators are excluded and when they are present. Alternatively, behavioral experiments could quantify pollen transfer from various bee species to different crops, after which yield differences could be calculated. Further work targeted to crop and geographic context remains important to demonstrate the value of pollination services.
4. **How far into the field from non-crop patches do these ecosystem service "halos" extend?**
   If wild bees are nesting in non-crop patches and providing pollination services to the surrounding crop, we would expect there to be pollination spillover effect, or an "ecosystem service halo" surrounding the patches where females are nesting. Native bees are central place foragers, implying that they make trips from their nest, or central place, to collect pollen, always returning to the same location. This means that each bee will have a commuting distance from their nest out to floral resources nearby. We would hypothesize that levels of pollination will decrease as we move further away from a bee's nest, which means that increased yields from pollination services will drop as we look further into the field. Work on this component has only just begun, with many studies needed to understand the size of these service halos and whether they are associated with crop yields. This has particular implications in prairie systems, where very large and regular field sizes are typical.
5. **Does this matter, here?**
   The world's prairies are distinct. Any one may be large and encompass a broad gradient in environmental conditions and therefore in crop productivity, bee species diversity, and agricultural practices. Transferring research from one grassland to another, or even at different localities within a single agroecosystem may not be convincing to local farmers. Attempts to replicate research both within and among a particular prairie agroecosystem will be essential to measure the amount of geographic variation, and provide locally appropriate evidence to decision-makers.

Retaining natural or semi-natural grassland cover that might otherwise be cultivated is perhaps the simplest solution to the problem of habitat loss, and involves identifying habitat important for wild bees and protecting it from disturbance. However, farmers may face a tradeoff, leading to challenging financial decisions when opting not to cultivate land, especially in the event where such land may be profitable for crop production [27, 28]. Knowledge of which types of land covers may be most beneficial for wild bees, as well as how much of this habitat needs to be retained may be useful for farm-level decision-making [29]. At the farm-neighborhood level, it may be important to consider sites which are connected or in proximity to other suitable habitat at a specific distance [26, 30], representing a network of habitat patches in an agricultural matrix.

Habitat restoration involves restoring areas to a pre-disturbance condition, often by manipulating the vegetation community to create suitable habitat (e.g., food, nesting, and hibernation resources). Restoration is typically a decision made at the farm-level, but may sometimes be coordinated by conservation organizations at a farm-neighborhood scale [31]. Implementation and post-restoration management strategies, as well as the habitat resources present in the farm-neighborhood, can influence the effectiveness of restoration

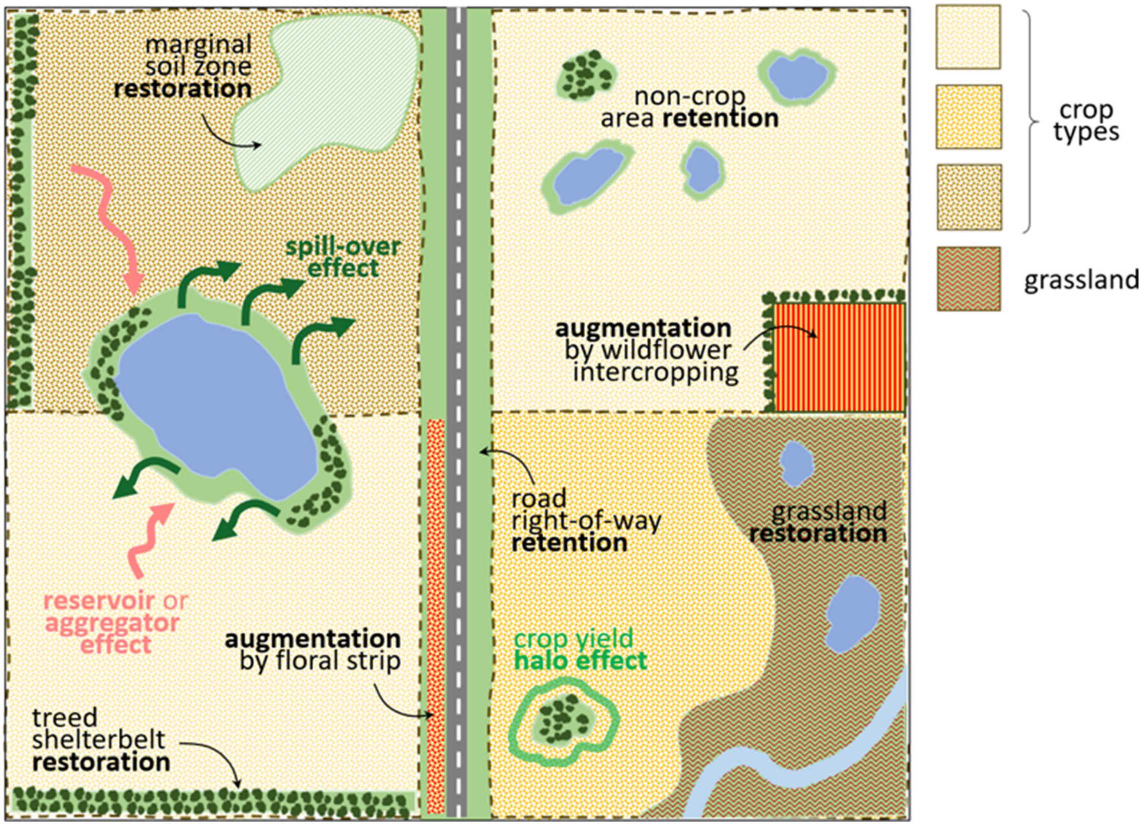

Fig. 1 Schematic of potential ways to retain, restore or augment the landscape to promote wild bees in North American prairie agroecosystems. Restoration efforts can focus on field areas of marginal soil, adding treed shelterbelts and restoring larger areas of previously cropped area to grassland. Retaining land can take the form of maintaining semi-natural areas in fields or maintaining roadside allowances. Spaces in the agricultural matrix can also be augmented with resources targeted at promoting wild bees, such as intercropping with wildflowers, or adding floral strips to different areas in the field. These actions can lead to reservoir of aggregator effects in the areas surrounding the restored areas, and may lead to increased pollination services surrounding the restored area causing a crop yield halo effect on the areas immediately adjacent. The figure depicts crop yield halo effects, reservoir effects and spillover effects on only one semi-natural feature, but these effects could occur on any semi-natural feature adjacent to or embedded in cropped land

for pollinators and the success at reinstating pollination services [32].

Related to restoration is the practice of augmenting floral abundance and diversity at targeted locations within or near fields in order to increase the nutritional resources available to wild bees [33, 34]. Wildflower augmentation can be designed to suit different cropping systems and local on-farm conditions. Generally, augmentation can be accomplished by introducing flowers to distinct patches of land within the agricultural landscape (often called the set-aside method), or by intercropping wildflowers within target crops [35]. These augmentation strategies can take the form of flower-rich buffer strips that can provide nectar and pollen resources [36], hedgerows that may enhance pollinator habitats [37], and field margin plantings and sown perennial strips that encourage establishment of native perennial plant species [38, 39]. The success of conservation efforts for wild bees in prairie habitats, like many other species, hinges on developing practices that benefit the species in question as well as incentivize land-use decision-makers to undertake and maintain conservation efforts in the longer term.

Local and Farm-Neighborhood Considerations

Farm Level Considerations

Retaining, restoring, or augmenting to maximize wildflower availability and continuity for bees will be an important consideration on farms, in order to affect the abundance and diversity of wild bees. There is a well-documented positive relationship between wild bees and the abundance and diversity of flowering plant species found at a site [7, 8, 16, 40]. Quantifying flowering plants may also be more convenient than measuring other important habitat characteristics (e.g., nesting substrates), which could account for their ubiquitous use. The wildflower species already present in a habitat as well as the seed mixes used during augmentation or restoration of a site are likely to affect the pollinator community that establishes [31, 41]. If augmentation or restoration strategies are to be implemented, choosing seeds for planting requires consideration of wildflower species that are from the local or regional species pool to avoid the introduction of weeds [41]. Furthermore, seed mixes that contain diverse plants (e.g., a mixture of legumes, forbs, and grasses) would also be beneficial for attracting functionally and taxonomically diverse pollinator communities and reducing the temporal variability of food resources [42, 43].

Wild pollinators are sensitive to the timing of floral resource availability and the resulting composition of bloom. This underlines the importance of phenological complementarity between bees and wildflowers, their primary food resource [44], a relationship that is even more important for oligolectic species [45]. Preferentially seeding plants, in restoration or augmentation settings, that flower at certain times of the growing season or have a combination of annual, biennial, and perennial life histories can better support pollinators during more vulnerable life stages (e.g., following emergence from hibernation or at peak population times) or supplement food resources provided by adjacent flowering crops [33, 46, 47]. Furthermore, plants can be selected specifically for the purpose of optimizing ecosystem service provisioning to prairie crops; for example, Robson [48] identified tallgrass prairie flowers that share pollinator visitors with canola crops, but bloom at different times of the growing season. This study highlighted smooth blue aster (*Symphyotrichum laeve* (L.) A. & D. Löve), stiff goldenrod (*Solidago rigida* L.), wild bergamot (*Monarda fistulosa* L.), and others as ideal candidates for improving ecosystem service provision to canola crops in the northern prairies. Including these "companion plantings" adjacent to agricultural fields could potentially buffer the negative impacts of mass-flowering crops on pollinators, since abundant floral resources would be present when canola is no longer in bloom [48]. This ecosystem service driven floral augmentation method, where crops and adjacent prairie flowering plants bloom at complementary times, may also increase the likelihood that pollinators will forage outside natural or semi-natural patches to deliver pollination services to adjacent crops. However, decoupling of phenological complementarity between bees and their host plants has been associated with climate change [49], underlining the importance of planting a portfolio of wildflowers to support both pollinators throughout the season and to guarantee their spillover to the target plants of pollination.

It has been widely established that incorporating diverse flowering plants and increasing their abundance will benefit pollinators, but the relationship between nesting or hibernating resources and pollinator abundance or diversity is addressed far less often [17]. Pollinators establish nests in a variety of substrates (Box #1), both above (e.g., in pithy stems or woods) and below ground (e.g., in excavated tunnels in soil). Of the potential nesting resources, the percent bare ground is most often identified as important for predicting bee abundance and diversity in a habitat [7, 50], but a target amount of bare soil per habitat area is not known. Bare soil is expected to decrease over time as vegetation becomes denser in a habitat, in turn decreasing potential nesting sites for ground-nesting bees in grassland habitats [51, 52]. However, changing vegetation structure may also promote the establishment of above-ground nesters. In all systems, but especially in agricultural landscapes where frequent soil disturbance may be expected, a better understanding of how nesting resources influence bee population sizes and community structure remains an important area for increased research.

High levels of wild bee species richness have been demonstrated to buffer against fluctuating community composition [49] to maintain pollination services over time [4, 6••]. Temporal variation in wild bee community composition can be high, with some species being abundant during certain times of the season and rare (or absent) during others. In order to maintain high and consistent levels of pollination from wild bees, it is important to maintain high levels of species richness, not simply abundance [6••, 53•]. This underlies the importance of providing a diverse set of nesting and floral resources for wild bees, as this will increase the number of species the area can support.

Farm-Neighborhood Considerations

Suitable habitat patches for bees do not exist in isolation from the surrounding landscape; the pollinators that forage or nest in a habitat at the farm-level are influenced by resources (or lack thereof) in adjacent areas as well as by connectivity with other suitable habitats (i.e., the proximity of resource patches or presence of habitat stepping stones among those patches) [54, 55]. Proximity of surrounding habitat resources may affect the ability of pollinators to establish in a habitat following augmentation or restoration activities intended for this purpose. For example, in prairie ecosystems, the amount of additional grassland habitat in the surrounding landscape has been identified as an important predictor for the recovery of pollinator abundance and diversity to pre-degradation levels following local habitat restoration [54, 55]. Beyond just the amount of surrounding available habitat, broad scale habitat heterogeneity or the variety of available habitat types at a specified radius can also positively influence pollinator abundance and diversity for individual non-crop areas on farms [56], likely through the presence of additional feeding, nesting, and hibernating opportunities for pollinators within their flight radius. Structurally complex landscapes can also provide insurance for pollinator communities at a farm or field scale; by including suitable habitat patches in the surrounding landscape, the regional species pool can better buffer against losses caused by local disturbance events [57].

We are just beginning to understand how the scale at which ecosystem services are measured can change the interpretation of the results [6••, 58]. When pollination services in blueberry, cranberry, and watermelon systems were examined at the farm level, Winfree et al (2015) demonstrated that a small number of abundant species of wild bee were responsible for the majority of pollination services. But, when they studied the same system across multiple states, they found that it was species diversity that was most important for pollination services [6••]. While these two studies took place in the NE United States and not the prairies, they underlie an important knowledge gap for much of the ecosystem and pollinator conservation literature.

Costs and Benefits of Prescribed Methods

The costs and benefits associated with prairie landscape diversification need careful consideration, because they weigh heavily on the decision-making of landowners who are tasked with implementing these strategies. Like any approach to landscape diversification, each of the three methods described here has several important costs associated with their implementation. In general, the costs of these methods can be categorized as follows: (i) opportunity costs, which are associated with foregone spaces that could otherwise have been farmed; (ii) establishment costs, which include site preparation and establishment of vegetation; and (iii) operational costs allocated to site maintenance after initial implementation of a landscape diversification strategy. Following the discussion of costs, we highlight several options available for mitigating the associated costs and summarize the benefits.

Opportunity, Establishment, and Operational Costs

Opportunity Costs

Farmers, in particular, understand that space not used in crop production represents lost income, and this is potentially costly in any landscape diversification method. For restoration and augmentation strategies, this is a consequence of setting aside land that could otherwise be used for crop production. Retaining land limits the expansion of production into new areas, which may be desirable both to increase the area cropped and improve efficiency of operating large machinery [59, 60]. This is particularly true in many prairie agroecosystems, where field sizes are large and regular in shape. Quantifying the potential dollar value of yields lost is challenging and will vary at the field-scale. In addition to the loss of land itself, changing the physical configuration of the field can increase the amount of time that it takes to seed, spray, and harvest a particular field (i.e., by forcing operators to turn farm equipment more frequently). It may also increase the quantity, and therefore cost, of fertilizer or crop protection products applied due to the inevitable overlap that occurs, for example, when circling a wetland or a patch of trees. For operations with large areas of land under cultivation, increasingly common in prairie grassland ecosystems due to farm consolidation [61], speed is of particular importance, because seeding, spraying, and harvesting must happen across all the fields in a small time window (Fig 2).

Establishment Costs

Leveraging inexpensive, but still compositionally diverse, seed mixes (i.e., those with a mixture of legumes, forbs, and grasses) during wildflower installation or restoration is an effective method for mitigating the cost of seed purchase, while still benefiting pollinators [42]. Additionally, cost-sharing through incentivization can be a means of relieving farmers of some percentage of cost associated with seed purchase, thus reducing the individual financial burden or risk. For example, government agencies can support farmers by providing financial subsidies and incentives, such as those currently implemented in USDA programs [62].

Additional costs such as labor and material purchases are associated with site preparation. This is a critical step that, if done correctly, has the potential to reduce upfront and recurring costs required for the establishment and long-term success of plantings in augmentation or restoration landscape diversification strategies [63]. Weed control constitutes a major challenge during site preparation for wildflower planting. Proper site preparation before planting (e.g., the removal of vegetation and suppression of weed seed banks through the use of technologies like landscaping fabrics) can encourage the establishment of wildflowers by reducing direct competition between wildflowers and weed species and further discourage the rapid return of weeds thereby reducing the burden of post-establishment weed control [64]. This ensures that additional financial investment required to remove weeds and for re-establishing wildflowers often associated with improper site preparation can be avoided in the long-term with proper site preparation.

Operational Costs

Restoration of prairie grasslands may often require additional inputs to successfully return the area to a natural state, largely because these communities are adapted to disturbance as a means of reducing competition and maintaining ecosystem structure, function, and productivity [65]. Any disturbance is expected to initially disrupt the pollinator community and cause reductions in some species [66]. However, over longer time scales disturbance can result in benefits to the plant

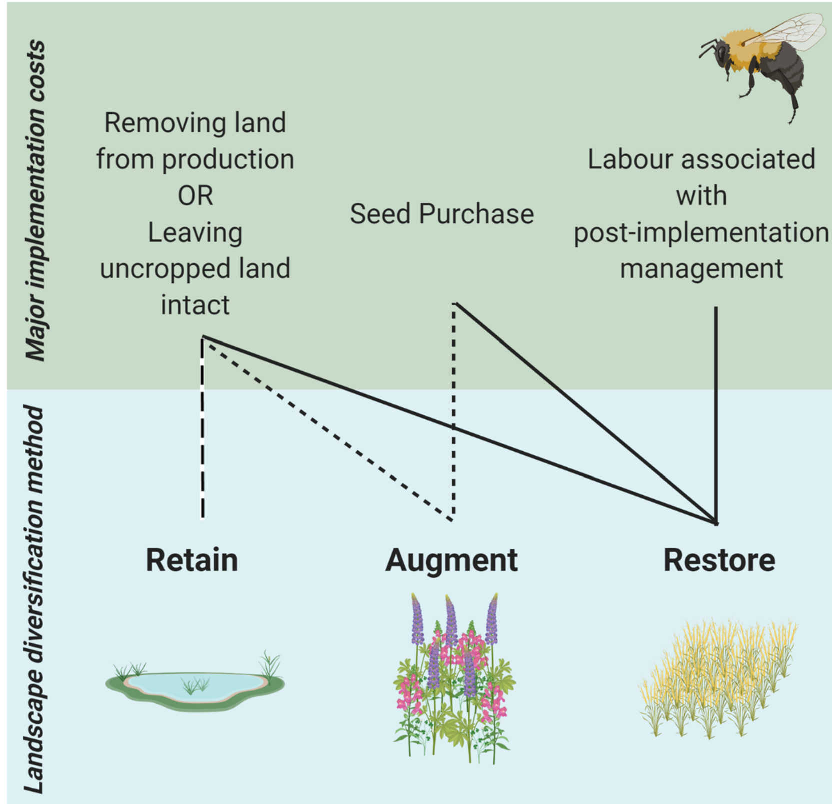

Fig. 2 Implementation costs of retaining, augmenting and restoring the prairie grassland for wild bees. Retaining previously undisturbed land incurs costs associated with potential yield losses. Augmenting the landscape incurs two categories of costs; those associated with lost yields as well as with augmentation costs such as seed purchase. Restoring a portion of the landscape incurs costs from all three categories, potential yield losses, seed purchases and the labor associated with post-implementation management

community, including higher forb cover and species richness [52, 65], which benefits pollinators. Historically, natural disturbance in the prairies was generated by fires, drought, or wildlife grazing, though today these are often mimicked manually through prescribed burns, mowing, or livestock grazing. Consequently, restoring a site with the goal of reinstating a functioning prairie ecosystem requires perpetual post-restoration management to mimic natural disturbance regimes, and thus potentially increasing labor costs.

Ecosystem Service and Disservice Costs

A common concern of farmers is that non-crop areas may create habitat for pest species, agricultural weeds, crop diseases, and their vectors [23, 67]. However, evidence that these disservices are increased by proximity to non-crop areas appears to be variable. For example, in some studies, prairie restoration decreased weed invasion [64, 68]. Retained, restored, and augmented areas may provide habitat for some pest species, while also providing refuge for other arthropods such as carabid beetles and spiders [69, 70]. These beneficial organisms may predate on any new pest species promoted by these areas. More research on the trophic interactions within non-crop areas is needed to better estimate the risks of pest attraction. For disease transmission to agricultural crops, it may be that some management is required to minimize the establishment of plants which could vector disease to the surrounding crops. However, in general, studies generally support the idea that despite potential for disservice, we should expect a net gain in ecosystem services associated with non-crop areas [8, 24, 26], though there will undoubtedly be considerable geographic variability in this response.

Individual habitats could result in the net export of pollination services to neighboring crops or aggregate pollinators away from cropped areas, which may influence their importance at broad scales [71]. For example, Kohler et al. [72] identified that the presence of flower-rich patches amidst crop agriculture caused decreases in hover fly abundance over 125 m from the habitat edge, with no further declines observed beyond this distance. A possible explanation is that the higher quality habitat patch aggregated pollinators away from the surrounding area, thus reducing pollination services to adjacent crops. However, several studies that also examined pollinator populations at increasing distances from natural habitat patches into crop fields have indicated that these patches act as population sources [8, 9], resulting in increases to the quality and quantity of surrounding crops [24, 43, 73, 74]. These contradicting aggregation and spillover effects from pollinators to natural habitat underline the importance of understanding the relative roles of amount, proximity, and quality of non-crop areas to the outcome of ecosystem service provision to different crops. It is also difficult, and potentially misleading to make landscape level inferences from patch scale studies [75]. Here, a landscape-scale view will have much to offer, for example, to understand how the spatial organization of non-crop areas with patches requiring pollination service influences outcomes [30, 76, 77]. Regional understanding of the conditions that lead non-crop areas to complement crops, rather than offer competition for pollinators, will be crucial. Pseudo-experimental studies that select sites a priori in order to control for patch configuration within the landscape [78], or designed to measure the independent contributions of patch size, patch configuration, and habitat loss will help scientists to guide landowners which areas may be best to consider restoring [79, 80••].

Mitigation of Costs and Additional Benefits of Increasing Suitable Wild Bee Habitat

Removing Land from Production

If the option is available, retaining existing uncultivated areas is the most direct way to reduce costs, since no additional land will need to be cleared. When restoration or augmentation are preferred, then parts of fields that are marginally productive for crops and have been consistently low yielding (e.g., due to soil or moisture conditions) may come at a small cost or even some benefit [81]. Ceasing to cultivate these areas has the potential for reducing input costs (e.g., pesticides and fertilizer) on patches that do not generate an adequate return on investment. By using marginal areas within existing fields to develop pollinator habitat, the cost may be further offset by an anticipated increase in pollination and other ecosystem services—including pest control—to remaining neighboring crops [9, 82].

Uncropped land within prairie agroecosystems for pollinator habitat can not only increase species richness and abundance, but can also benefit landowners through increased pollination services to neighboring crops. For example, Morandin and Winston [24] identified that uncultivated land surrounding canola fields in the northern Canadian prairies was positively correlated with in-field bee abundance, which in turn was correlated with increased seed set. Improvements in crop yields through the addition of non-crop patches provide a connection between conservation and agricultural productivity, and generates an economic incentive for landowners to invest in habitat restoration.

Post-Restoration Management

Prescribed burns, mowing, or livestock grazing are all used for mimicking natural disturbance in prairie ecosystems, where the latter two options, in particular, may reduce costs and offer potential benefits from post-restoration management [31, 83]. Grazing and mowing of restored sites have been found to be effective methods for maintaining high vegetation diversity throughout the spring and summer, in turn benefitting prairie pollinator communities [42, 43, 46, 84]. Studies assessing the comparative benefits of employing grazing or mowing have not reached a consensus on which is preferred for the purpose of pollinator habitat restoration. It is possible that grazing can better maintain floral diversity over time by increasing the temporal persistence of both forb and legume species in a restored habitat [42], though other studies have found no difference between management strategies over shorter time scales [43]. Generally, some form of spatially and temporally heterogeneous disturbance is beneficial for maintaining a functioning prairie ecosystem [65, 85], and either mowing or grazing is preferred over no post-restoration management. Furthermore, utilization of restored areas for livestock grazing or mowing can generate additional benefits to landowners by providing feed; for example, cattle could graze these areas during interspersed growing seasons or alternatively these areas could be partially hayed to produce winter feed.

Additional Benefits

The primary incentive for the retention, restoration, or augmentation of land is improvement to ecosystem service provisioning. We have highlighted the benefits of increased pollination services to neighboring crops in prairie grassland agroecosystems, but it is important to note that reinstating natural or pre-agricultural ecosystem function may take time, if it is even possible, and determining an exact return on investment is difficult. Firstly, the benefits of increased pollination or other ecosystem services may be generated at different time scales. For example, Purvis et al. [52] showed that bumblebee diversity in restored grassland-wetland complexes resembled the undisturbed sites after 1-4 years, while the non-bumblebee species took 5-10 years to return to pre-restoration levels. The floral communities approached, but never reached, a diversity similar to the reference sites [52]. This suggests there is likely to be a lag for the return on the investment of removing land from production, and this may vary between pollinator guilds. Providing landowners with regionally specific estimates of this lag for ecosystem service improvement may also be important to improve uptake. Secondly, there are several ecosystem services that are valued by landowners, in addition to pollination, that can be derived from restoring natural habitats within agroecosystems. Natural habitats can reduce soil erosion from fields, improve the quality of surrounding streams and water bodies through reduced sedimentation, increase phosphorus retention in soil, and reduce the establishment of agricultural weeds [34, 64, 86]. Retaining or restoring non-crop patches within fields for their carbon storage potential (e.g., in trees, or in the deep root systems of perennial grasses), or to reduce the footprint of soil disturbance and its associated greenhouse gas production by soil organisms [87], may also become important decision points as climate change mitigation increasingly becomes an incentive for farmers. Natural habitats, therefore, are at the nexus of many additional ecosystem service-derived cost savings for landowners.

Conclusions

The retention, restoration, and augmentation of non-crop patches within prairie grassland agroecosystems can generate several benefits to landowners. These methods of creating or enhancing natural habitat provide several avenues of landscape diversification for the benefit of pollinators and landowners alike. It is most beneficial for the distribution of these habitats to be planned at both local and landscape scales, but the implementation of these methods is flexible and can be modified to suit different initial conditions, the desired outcome, and the budget.

Farm-level enhancements are likely more practical for individual landowners to implement and can result in direct benefits to species richness and abundance to levels comparable to native prairie grassland sites [7, 55]. Farm-neighborhood enhancements, although requiring the cooperation of the agricultural community, can benefit local wild bee populations by increasing habitat heterogeneity and maintaining a regional species pool that can buffer local disturbance [54, 55]. There is considerable evidence that maintaining the welfare of local bees can translate directly into economic reward by increasing pollinator richness and abundance within a habitat [7, 42, 50], which can lead to an spillover of pollinators into neighboring fields [9, 88] and subsequently benefit crop production through increased ecosystem service provision [43, 73, 74]. These natural habitats are also the locus of other ecosystem services; restored, retained, and augmented agricultural landscapes see such benefits as reduced soil erosion, improved quality of surrounding streams, more effective pest control, and increased phosphorus retention in the soil [34, 64, 86].

Continued efforts to quantify the economic implications of non-crop patch retention or enhancement, however, are necessary. Emerging precision agricultural technologies, such as real-time GPS-linked yield monitors in combine harvesters, can be used to "zone" a given field into areas based on their yield. This data stream can be used to understand which areas of a given field represent a net loss of profit to the farmer (e.g., by requiring a high level of inputs and/or producing lower yields). Identifying low-profit zones, in this way, is an ideal starting point to set aside land for pollinator enhancement. The wide use of these technologies on North American prairies makes this an excellent place to focus this research. This presents an enticing "win-win" scenario for decision-makers in which land conservation efforts are implemented in prairie agroecosystems to the benefit of both pollinators and farmers.

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Declarations

Conflict of Interest Jess Vickruck, Emily Purvis, Richard Kwafo, Holly Kerstiens, and Paul Galpern declare no conflict of interest associated with this work.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

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• Of importance
•• Of major importance

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