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Review Article

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

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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

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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

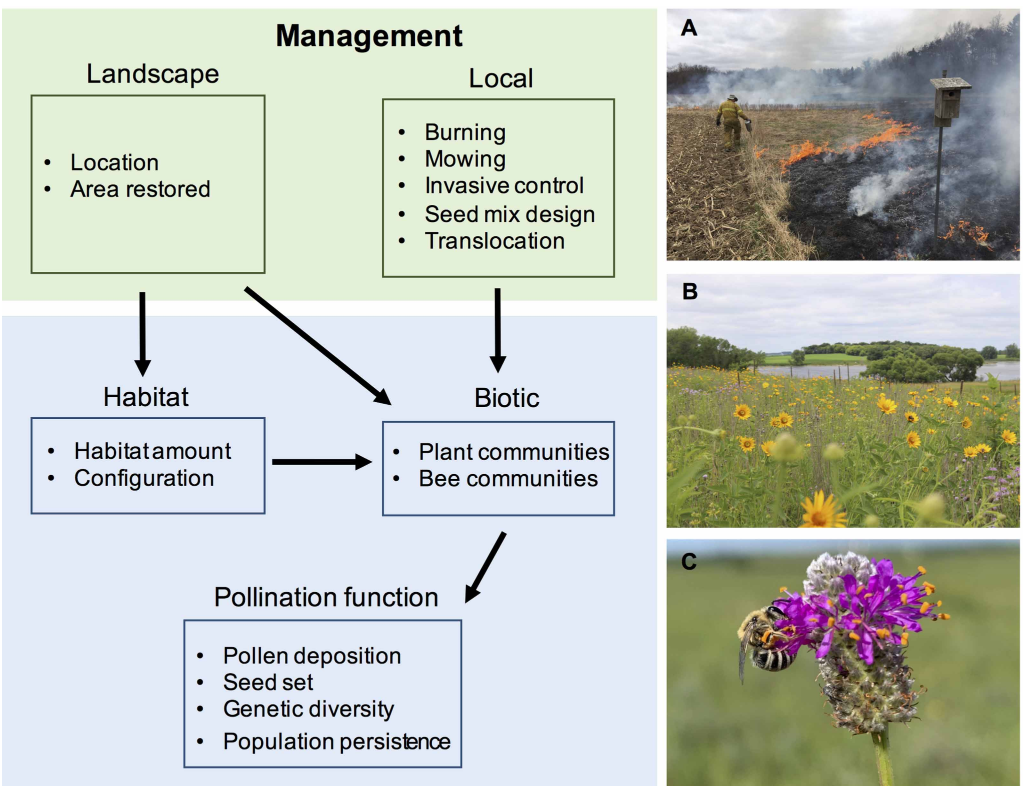

Figure 1. Conceptual framework illustrating how landscape and management practices can affect habitat and biotic communities.

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.

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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 [86–89]. 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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Author Contributions

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

Abbreviations

IPPC, Intergovernmental Panel on Climate Change.

References

1 Dobson, A., Lodge, D., Alder, J., Cumming, G.S., Keymer, J., McGlade, J. et al. (2006) Habitat loss, trophic collapse, and the decline of ecosystem services. *Ecology* **87**, 1915–1924 https://doi.org/10.1890/0012-9658(2006)87[1915:HLTCAT]2.0.CO;2
2 Miller, B.P., Sinclair, E.A., Menz, M.H.M., Elliott, C.P., Bunn, E., Commander, L.E. et al. (2017) A framework for the practical science necessary to restore sustainable, resilient, and biodiverse ecosystems. *Restor. Ecol.* **25**, 605–617 https://doi.org/10.1111/rec.12475
3 UN Environment Programme (2019). Decade on Ecosystem Restoration. https://www.decadeonrestoration.org/ Accessed Jan. 2020
4 Young, T.P. (2000) Restoration ecology and conservation biology. *Biol. Conserv.* **92**, 73–83 https://doi.org/10.1016/S0006-3207(99)00057-9
5 Montoya, D., Rogers, L. and Memmott, J. (2012) Emerging perspectives in the restoration of biodiversity-based ecosystem services. *Trends Ecol. Evol.* **27**, 666–672 https://doi.org/10.1016/j.tree.2012.07.004
6 Perring, M.P., Standish, R.J., Price, J.N., Craig, M.D., Erickson, T.E., Ruthrof, K.X. et al. (2015) Advances in restoration ecology: rising to the challenges of the coming decades. *Ecosphere* **6**, 131 https://doi.org/10.1890/ES15-00121.1
7 Suding, K., Higgs, E., Palmer, M., Callicott, J.B., Anderson, C.B., Baker, M. et al. (2015) Committing to ecological restoration: efforts around the globe need legal and policy clarification. *Science* **348**, 638–640 https://doi.org/10.1126/science.aaa4216
8 Ollerton, J., Winfree, R. and Tarrant, S. (2011) How many flowering plants are pollinated by animals? *Oikos* **120**, 321–326 https://doi.org/10.1111/j.1600-0706.2010.18644.x
9 Aguilar, R., Ashworth, L., Galetto, L. and Aizen, M.A. (2006) Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecol. Lett.* **9**, 968–980 https://doi.org/10.1111/j.1461-0248.2006.00927.x
10 Aguilar, R., Cristóbal-Pérez, E.J., Balvino-Olvera, F.J., de Jesús Aguilar-Aguilar, M., Aguirre-Acosta, N., Ashworth, L. et al. (2019) Habitat fragmentation reduces plant progeny quality: a global synthesis. *Ecol. Lett.* **22**, 1163–1173 https://doi.org/10.1111/ele.13272
11 Law, W., Salick, J. and Knight, T.M. (2010) The effects of pollen limitation on population dynamics of snow lotus (*Saussurea medusa* and *S. laniceps*, Asteraceae): threatened Tibetan medicinal plants of the eastern Himalayas. *Plant Ecol.* **210**, 343–357 https://doi.org/10.1007/s11258-010-9761-6
12 Becker, T., Voss, N. and Durka, W. (2011) Pollen limitation and inbreeding depression in an "old rare" bumblebee-pollinated grassland herb. *Plant Biol.* **13**, 857–864 https://doi.org/10.1111/j.1438-8677.2011.00452.x
13 Anderson, S.H., Kelly, D., Ladley, J.J., Molloy, S. and Terry, J. (2011) Cascading effects of bird functional extinction reduce pollination and plant density. *Science* **331**, 1068–1071 https://doi.org/10.1126/science.1199092
14 Dixon, K.W. (2009) Pollination and restoration. *Science* **325**, 571–573 https://doi.org/10.1126/science.1176295
15 Wolowski, M., Carvalheiro, L.G. and Freitas, L. (2017) Influence of plant–pollinator interactions on the assembly of plant and hummingbird communities. *J. Ecol.* **105**, 332–344 https://doi.org/10.1111/1365-2745.12684
16 Biesmeijer, J.C., Roberts, S.P.M.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T. et al. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* **313**, 351–354 https://doi.org/10.1126/science.1127863

Emerging Topics in Life Sciences (2020) **4** 99–109
https://doi.org/10.1042/ETLS20190073

17 Society for Ecological Restoration International Science & Policy Working Group (2004). The SER international primer on ecological restoration. Society for Ecological Restoration International, Tucson, AZ www.ser.org
18 Garibaldi, L.A., Carvalheiro, L.G., Leonhardt, S.D., Aizen, M.A., Blaauw, B.R., Isaacs, R. et al. (2014) From research to action: enhancing crop yield through wild pollinators. *Front. Ecol. Environ.* **12**, 439–447 https://doi.org/10.1890/130330
19 Blaauw, B.R. and Isaacs, R. (2014) Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *J. Appl. Ecol.* **51**, 890–898 https://doi.org/10.1111/1365-2664.12257
20 Williams, N.M., Ward, K.L., Pope, N., Isaacs, R., Wilson, J., May, E.A. et al. (2015) Native wildflower plantings support wild bee abundance and diversity in agricultural landscapes across the United States. *Ecol. Appl.* **25**, 2119–2131 https://doi.org/10.1890/14-1748.1
21 Archer, C.R., Pirk, C.W.W., Carvalheiro, L.G. and Nicolson, S.W. (2014) Economic and ecological implications of geographic bias in pollinator ecology in the light of pollinator declines. *Oikos* **123**, 401–407 https://doi.org/10.1111/j.1600-0706.2013.00949.x
22 McAlpine, C., Catterall, C.P., Mac Nally, R., Lindenmayer, D., Reid, J.L., Holl, K.D. et al. (2016) Integrating plant- and animal-based perspectives for more effective restoration of biodiversity. *Front. Ecol. Environ.* **14**, 37–45 https://doi.org/10.1002/16-0108.1
23 Winfree, R., MacLeod, M., Harrison, T. and Cariveau, D.P. (2015) Conserving and restoring mutualisms. In *Mutualism* (Bronstein, J.L., ed.), pp. 268–286, Oxford University Press, USA
24 Meissen, J.C., Glidden, A.J., Sherrard, M.E., Elgersma, K.J. and Jackson, L.L. (2019) Seed mix design and first year management influence multifunctionality and cost-effectiveness in prairie reconstruction. *Restor. Ecol.* 1–10 https://doi.org/10.1111/rec.13013
25 Denning, K.R. and Foster, B.L. (2017) Flower visitor communities are similar on remnant and reconstructed tallgrass prairies despite forb community differences. *Restor. Ecol.* **26**, 751–759 https://doi.org/10.1111/rec.12615
26 Griffin, S.R., Bruninga-Socolar, B., Kerr, M.A., Gibbs, J. and Winfree, R. (2017) Wild bee community change over a 26-year chronosequence of restored tallgrass prairie. *Restor. Ecol.* **25**, 650–660 https://doi.org/10.1111/rec.12481
27 Tonietto, R.K., Ascher, J.S. and Larkin, D.J. (2017) Bee communities along a prairie restoration chronosequence: similar abundance and diversity, distinct composition. *Ecol. Appl.* **27**, 705–717 https://doi.org/10.1002/eap.1481
28 Denning, K.R. and Foster, B.L. (2018) Taxon-specific associations of tallgrass prairie flower visitors with site-scale forb communities and landscape composition and configuration. *Biol. Conserv.* **227**, 74–81 https://doi.org/10.1016/j.biocon.2018.08.023
29 Tonietto, R.K. and Larkin, D.J. (2018) Habitat restoration benefits wild bees: a meta-analysis. *J. Appl. Ecol.* **55**, 582–590 https://doi.org/10.1111/1365-2664.13012
30 Vázquez, D.P., Morris, W.F. and Jordano, P. (2005) Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecol. Lett.* **8**, 1088–1094 https://doi.org/10.1111/j.1461-0248.2005.00810.x
31 Pan, C.C., Qu, H., Feng, Q., De, L.L., Zhao, H.L., Li, Y.L. et al. (2017) Increased pollinator service and reduced pollen limitation in the fixed dune populations of a desert shrub. *Sci. Rep.* **7**, 16903 https://doi.org/10.1038/s41598-017-17253-w
32 Williams, N.M. (2011) Restoration of nontarget species: bee communities and pollination function in riparian forests. *Restor. Ecol.* **19**, 450–459 https://doi.org/10.1111/j.1526-100X.2010.00707.x
33 Breland, S., Turley, N.E., Gibbs, J., Isaacs, R. and Brudvig, L.A. (2018) Restoration increases bee abundance and richness but not pollination in remnant and post-agricultural woodlands. *Ecosphere* **9**, e02435 https://doi.org/10.1002/ecs2.2435
34 Ashman, T.L., Knight, T.M., Steets, J.A., Amarasekare, P., Burd, M., Campbell, D.R. et al. (2004) Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology* **85**, 2408–2421 https://doi.org/10.1890/03-8024
35 Knight, T.M., Steets, J.A., Vamosi, J.C., Mazer, S.J., Burd, M., Campbell, D.R. et al. (2005) Pollen limitation of plant reproduction: pattern and process. *Annu. Rev. Ecol. Evol. Syst.* **36**, 467–497 https://doi.org/10.1146/annurev.ecolsys.36.102403.115320
36 Bennett, J.M., Steets, J.A., Durka, W., Vamosi, J.C., Arceo-Gómez, G., Burd, M. et al. (2018) GloPL, a global data base on pollen limitation of plant reproduction. *Sci. Data* **5**, 180249 https://doi.org/10.1038/sdata.2018.249
37 Menz, M.H.M., Phillips, R.D., Winfree, R., Kremen, C., Aizen, M.A., Johnson, S.D. et al. (2011) Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. *Trends Plant Sci.* **16**, 4–12 https://doi.org/10.1016/j.tplants.2010.09.006
38 Ritchie, A., Lane, I. and Cariveau, D.P. (2020) Pollination of a bee dependent forb in restored prairie: no evidence of pollen limitation in landscapes dominated by row crop agriculture. *Restor. Ecol* https://doi.org/10.1111/rec.13157
39 McCallum, K.P., Breed, M.F., Lowe, A.J. and Paton, D.C. (2019) Plants, position and pollination: planting arrangement and pollination limitation in a revegetated eucalypt woodland. *Ecol. Manag. Restor.* **20**, 222–230 https://doi.org/10.1111/emr.12382
40 Forup, M.L., Henson, K.S.E., Craze, P.G. and Memmott, J. (2008) The restoration of ecological interactions: plant–pollinator networks on ancient and restored heathlands. *J. Appl. Ecol.* **45**, 742–752 https://doi.org/10.1111/j.1365-2664.2007.01390.x
41 Kaiser-Bunbury, C.N., Mougal, J., Whittington, A.E., Valentin, T., Gabriel, R., Olesen, J.M. et al. (2017) Ecosystem restoration strengthens pollination network resilience and function. *Nature* **542**, 223–227 https://doi.org/10.1038/nature21071
42 Noreika, N., Bartomeus, I., Winsa, M., Bommarco, R. and Öckinger, E. (2019) Pollinator foraging flexibility mediates rapid plant–pollinator network restoration in semi-natural grasslands. *Sci. Rep.* **9**, 15473 https://doi.org/10.1038/s41598-019-51912-4
43 King, C., Ballantyne, G. and Willmer, P.G. (2013) Why flower visitation is a poor proxy for pollination: measuring single-visit pollen deposition, with implications for pollination networks and conservation. *Methods Ecol. Evol.* **4**, 811–818 https://doi.org/10.1111/2041-210X.12074
44 Ballantyne, G., Baldock, K.C.R. and Willmer, P.G. (2015) Constructing more informative plant–pollinator networks: visitation and pollen deposition networks in a heathland plant community. *Proc. R. Soc. B Biol. Sci.* **282**, 20151130 https://doi.org/10.1098/rspb.2015.1130
45 Zhao, Y., Lázaro, A., Ren, Z., Zhou, W., Li, H., Tao, Z. et al. (2019) The topological differences between visitation and pollen transport networks: a comparison in species rich communities of the Himalaya–Hengduan mountains. *Oikos* **128**, 551–562 https://doi.org/10.1111/oik.05262
46 Dobson, A.P., Bradshaw, A.D. and Baker, A.J.M. (1997) Hopes for the future: restoration ecology and conservation biology. *Science* **277**, 515–522 https://doi.org/10.1126/science.277.5325.515
47 Nemec, K.T., Allen, C.R., Helzer, C.J. and Wedin, D.A. (2013) Influence of richness and seeding density on invasion resistance in experimental tallgrass prairie restorations. *Ecol. Restor.* **31**, 168–185 https://doi.org/10.3368/er.31.2.168
48 Carvell, C., Westrich, P., Meek, W.R., Pywell, R.F. and Nowakowski, M. (2006) Assessing the value of annual and perennial forage mixtures for bumblebees by direct observation and pollen analysis. *Apidologie* **37**, 326–340 https://doi.org/10.1051/apido:2006002

49 Hicks, D.M., Ouvrard, P., Baldock, K.C.R., Baude, M., Goddard, M.A., Kunin, W.E. et al. (2016) Food for pollinators: quantifying the nectar and pollen resources of urban flower meadows. *PLoS One* **11**, e0158117
50 Filipiak, M. (2019) Key pollen host plants provide balanced diets for wild bee larvae: a lesson for planting flower strips and hedgerows. *J. Appl. Ecol.* **56**, 1410–1418 https://doi.org/10.1111/1365-2664.13383
51 Gresty, C.E.A., Clare, E., Devey, D.S., Cowan, R.S., Csiba, L., Malakasi, P. et al. (2018) Flower preferences and pollen transport networks for cavity-nesting solitary bees: implications for the design of agri-environment schemes. *Ecol. Evol.* **8**, 7574–7587 https://doi.org/10.1002/ece3.4234
52 Barr, S., Jonas, J.L. and Paschke, M.W. (2017) Optimizing seed mixture diversity and seeding rates for grassland restoration. *Restor. Ecol.* **25**, 396–404 https://doi.org/10.1111/rec.12445
53 Burton, C.M., Burton, P.J., Hebda, R. and Turner, N.J. (2006) Determining the optimal sowing density for a mixture of native plants used to revegetate degraded ecosystems. *Restor. Ecol.* **14**, 379–390 https://doi.org/10.1111/j.1526-100X.2006.00146.x
54 Wilkerson, M.L., Ward, K.L., Williams, N.M., Ullmann, K.S. and Young, T.P. (2014) Diminishing returns from higher density restoration seedings suggest trade-offs in pollinator seed mixes. *Restor. Ecol.* **22**, 782–789 https://doi.org/10.1111/rec.12141
55 Harmon-Threatt, A.N. and Hendrix, S.D. (2015) Prairie restorations and bees: the potential ability of seed mixes to foster native bee communities. *Basic Appl. Ecol.* **16**, 64–72 https://doi.org/10.1016/j.baae.2014.11.001
56 Thomson, J.D. (1978) Effects of stand composition on insect visitation in two-species mixtures of Hieracium. *Am. Midl. Nat.* **100**, 431–440 https://doi.org/10.2307/2424843
57 Braun, J. and Lortie, C.J. (2019) Finding the bees knees: a conceptual framework and systematic review of the mechanisms of pollinator-mediated facilitation. *Perspect. Plant Ecol. Evol. Syst.* **36**, 33–40 https://doi.org/10.1016/j.ppees.2018.12.003
58 Antonsen, H. and Olsson, P.A. (2005) Relative importance of burning, mowing and species translocation in the restoration of a former boreal hayfield: responses of plant diversity and the microbial community. *J. Appl. Ecol.* **42**, 337–347 https://doi.org/10.1111/j.1365-2664.2005.01023.x
59 Menges, E.S. (2008) Restoration demography and genetics of plants, when is a translocation successful. *Aust. J. Bot.* **56**, 187–196 https://doi.org/10.1071/BT07173
60 Seddon, P.J. (2010) From reintroduction to assisted colonization: moving along the conservation translocation spectrum. *Restor. Ecol.* **18**, 796–802 https://doi.org/10.1111/j.1526-100X.2010.00724.x
61 Vitt, P., Havens, K., Kramer, A.T., Sollenberger, D. and Yates, E. (2010) Assisted migration of plants: changes in latitudes, changes in attitudes. *Biol. Conserv.* **143**, 18–27 https://doi.org/10.1016/j.biocon.2009.08.015
62 Watson, D.M. and Watson, M.J. (2015) Wildlife restoration: mainstreaming translocations to keep common species common. *Biol. Conserv.* **191**, 830–838 https://doi.org/10.1016/j.biocon.2015.08.035
63 Morton, E.M. and Rafferty, N.E. (2017) Plant–pollinator interactions under climate change: the use of spatial and temporal transplants. *Appl. Plant Sci.* **5**, 1600133 https://doi.org/10.3732/apps.1600133
64 LaBar, T., Campbell, C., Yang, S., Albert, R. and Shea, K. (2014) Restoration of plant–pollinator interaction networks via species translocation. *Theor. Ecol.* **7**, 209–220 https://doi.org/10.1007/s12080-013-0211-7
65 Brosi, B.J. and Briggs, H.M. (2013) Single pollinator species losses reduce floral fidelity and plant reproductive function. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 13044–8 https://doi.org/10.1073/pnas.1307438110
66 Forrest, J.R.K. and James, D.T. (2011) An examination of synchrony between insect emergence and flowering in Rocky Mountain meadows. *Ecol. Monogr.* **81**, 469–491 https://doi.org/10.1890/10-1885.1
67 Roulston, T.H. and Goodell, K. (2011) The role of resources and risks in regulating wild bee populations. *Annu. Rev. Entomol.* **56**, 293–312 https://doi.org/10.1146/annurev-ento-120709-144802
68 Harmon-Threatt, A. (2020) Influence of nesting characteristics on health of wild bee communities. *Annu. Rev. Entomol.* **65**, 39–56 https://doi.org/10.1146/annurev-ento-011019-024955
69 Requier, F. and Leonhardt, S.D. (2020) Beyond flowers: including non-floral resources in bee conservation schemes. *J. Insect Conserv.* **24**, 5–16 https://doi.org/10.1007/s10841-019-00206-1
70 Potts, S.G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'eman, G. et al. (2005) Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecol. Entomol.* **30**, 78–85 https://doi.org/10.1111/j.0307-6946.2005.00662.x
71 Rowe, H.I. (2010) Tricks of the trade: techniques and opinions from 38 experts in tallgrass prairie restoration. *Restor. Ecol.* **18**, 253–262 https://doi.org/10.1111/j.1526-100X.2010.00663.x
72 Hansen, M.J. and Gibson, D.J. (2014) Use of multiple criteria in an ecological assessment of a prairie restoration chronosequence. *Appl. Veg. Sci.* **17**, 63–73 https://doi.org/10.1111/avsc.12051
73 Williams, D.W., Jackson, L.L. and Smith, D.D. (2007) Effects of frequent mowing on survival and persistence of forbs seeded into a species-poor grassland. *Restor. Ecol.* **15**, 24–33 https://doi.org/10.1111/j.1526-100X.2006.00186.x
74 Collins, S.L. and Smith, M.D. (2006) Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. *Ecology* **87**, 2058–2067 https://doi.org/10.1890/0012-9658(2006)87[2058:SIOFAG]2.0.CO;2
75 Fuhlendorf, S.D., Engle, D.M., Kerby, J. and Hamilton, R. (2009) Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. *Conserv. Biol.* **23**, 588–598 https://doi.org/10.1111/j.1523-1739.2008.01139.x
76 Winter, S.L., Allred, B.W., Hickman, K.R. and Fuhlendorf, S.D. (2015) Tallgrass prairie vegetation response to spring fires and bison grazing. *Southwest Nat.* **60**, 30–35 https://doi.org/10.1894/FMO-19.1
77 Buckles, B.J. and Harmon-Threatt, A.N. (2019) Bee diversity in tallgrass prairies affected by management and its effects on above- and below-ground resources. *J. Appl. Ecol.* **56**, 2443–2453 https://doi.org/10.1111/1365-2664.13479
78 Decker, B.L. and Harmon-Threatt, A.N. (2019) Growing or dormant season burns: the effects of burn season on bee and plant communities. *Biodivers. Conserv* **28**, 3621–3631
79 Carbone, L.M., Tavella, J., Pausas, J.G. and Aguilar, R. (2019) A global synthesis of fire effects on pollinators. *Glob. Ecol. Biogeogr.* **28**, 1487–1498 https://doi.org/10.1111/geb.12939
80 Swengel, A.B. and Swengel, S.R. (2001) Effects of prairie and barrens management on butterfly faunal composition. *Biodivers. Conserv.* **10**, 1757–1785 https://doi.org/10.1023/A:1012051510584

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https://doi.org/10.1042/ETLS20190073

81 Moranz, R.A., Fuhlendorf, S.D. and Engle, D.M. (2014) Making sense of a prairie butterfly paradox: the effects of grazing, time since fire, and sampling period on regal fritillary abundance. *Biol. Conserv.* **173**, 32–41 https://doi.org/10.1016/j.biocon.2014.03.003

82 Ne'eman, G., Dafni, A. and Potss, S.G. (2000) The effect of fire on flower visitation rate and fruit set in four core-species in east Mediterranean scrubland. *Plant Ecol.* **146**, 97–104 https://doi.org/10.1023/A:1009815318590

83 LoPresti, E.F., Van Wyk, J.I., Mola, J.M., Toll, K., Miller, T.J. and Williams, N.M. (2018) Effects of wildfire on floral display size and pollinator community reduce outcrossing rate in a plant with a mixed mating system. *Am. J. Bot.* **105**, 1154–1164 https://doi.org/10.1002/ajb2.1129

84 García, Y., Clara Castellanos, M. and Pausas, J.G. (2018) Differential pollinator response underlies plant reproductive resilience after fires. *Ann. Bot.* **122**, 961–971 https://doi.org/10.1093/aob/mcy122

85 Stout, J.C. and Tiedeken, E.J. (2017) Direct interactions between invasive plants and native pollinators: evidence, impacts and approaches. *Funct. Ecol.* **31**, 38–46 https://doi.org/10.1111/1365-2435.12751

86 Russo, L., Vaudo, A.D., Fisher, C.J., Grozinger, C.M. and Shea, K. (2019) Bee community preference for an invasive thistle associated with higher pollen protein content. *Oecologia* **190**, 901–912 https://doi.org/10.1007/s00442-019-04462-5

87 Brown, B.J. and Mitchell, R.J. (2001) Competition for pollination: effects of pollen of an invasive plant on seed set of a native congener. *Oecologia* **129**, 43–49 https://doi.org/10.1007/s004420100700

88 Bartomeus, I., Vilà, M. and Santamaría, L. (2008) Contrasting effects of invasive plants in plant–pollinator networks. *Oecologia* **155**, 761–770 https://doi.org/10.1007/s00442-007-0946-1

89 Goodell, K. and Parker, I.M. (2017) Invasion of a dominant floral resource: effects on the floral community and pollination of native plants. *Ecology* **98**, 57–69 https://doi.org/10.1002/ecy.1639

90 Iler, A.M. and Goodell, K. (2014) Relative floral density of an invasive plant affects pollinator foraging behaviour on a native plant. *J. Pollinat. Ecol.* **13**, 174–183 https://doi.org/0.26786/1920-7603%282014%2915

91 Masters, J.A. and Emery, S.M. (2015) The showy invasive plant *Ranunculus ficaria* facilitates pollinator activity, pollen deposition, but not always seed production for two native spring ephemeral plants. *Biol. Invasions* **17**, 2329–2337 https://doi.org/10.1007/s10530-015-0878-3

92 Hanula, J.L. and Horn, S. (2011) Removing an invasive shrub (Chinese privet) increases native bee diversity and abundance in riparian forests of the southeastern United States. *Insect Conserv. Divers.* **4**, 275–283 https://doi.org/10.1111/j.1752-4598.2011.00131.x

93 Fiedler, A.K., Landis, D.A. and Arduser, M. (2012) Rapid shift in pollinator communities following invasive species removal. *Restor. Ecol.* **20**, 593–602 https://doi.org/10.1111/j.1526-100X.2011.00820.x

94 Hanna, C., Foote, D. and Kremen, C. (2013) Invasive species management restores a plant–pollinator mutualism in Hawaii. *J. Appl. Ecol.* **50**, 147–155 https://doi.org/10.1111/1365-2664.12027

95 Baskett, C.A., Emery, S.M. and Rudgers, J.A. (2011) Pollinator visits to threatened species are restored following invasive plant removal. *Int. J. Plant Sci.* **172**, 411–422 https://doi.org/10.1086/658182

96 Lomov, B., Keith, D.A. and Hochuli, D.F. (2010) Pollination and plant reproductive success in restored urban landscapes dominated by a pervasive exotic pollinator. *Landsc. Urban Plan.* **96**, 232–239 https://doi.org/10.1016/j.landurbplan.2010.03.009

97 Harkreader, I. and Ross, N.J. (2018) Nonnative honeybee functions as pollinator for rare, native lily (*Lilium michiganense*, Liliaceae) in fragmented tallgrass prairie. *J. Torrey Bot. Soc.* **145**, 195–201 https://doi.org/10.3159/TORREY-D-15-00025

98 Nabors, A.J., Cen, H.J., Hung, K.L.J., Kohn, J.R. and Holway, D.A. (2018) The effect of removing numerically dominant, non-native honey bees on seed set of a native plant. *Oecologia* **186**, 281–289 https://doi.org/10.1007/s00442-017-4009-y

99 Alger, S.A., Burnham, P.A., Boncristiani, H.F. and Brody, A.K. (2019) RNA virus spillover from managed honeybees (*Apis mellifera*) to wild bumblebees (Bombus spp.) *PLoS One* **14**, e0217822

100 Hung, K.-L.J., Kingston, J.M., Lee, A., Holway, D.A. and Kohn, J.R. (2019) Non-native honey bees disproportionately dominate the most abundant floral resources in a biodiversity hotspot. *Proc. R. Soc. B Biol. Sci.* **286**, 20182901 https://doi.org/10.1098/rspb.2018.2901

101 Valido, A., Rodríguez-Rodríguez, M.C. and Jordano, P. (2019) Honeybees disrupt the structure and functionality of plant–pollinator networks. *Sci. Rep.* **9**, 4711 https://doi.org/10.1038/s41598-019-41271-5

102 Grman, E., Bassett, T., Zirbel, C.R. and Brudvig, L.A. (2015) Dispersal and establishment filters influence the assembly of restored prairie plant communities. *Restor. Ecol.* **23**, 892–899 https://doi.org/10.1111/rec.12271

103 Zirbel, C.R., Grman, E., Bassett, T. and Brudvig, L.A. (2019) Landscape context explains ecosystem multifunctionality in restored grasslands better than plant diversity. *Ecology* **100**, e02634 https://doi.org/10.1002/ecy.2634

104 Hadley, A.S. and Betts, M.G. (2012) The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. *Biol. Rev.* **87**, 526–544 https://doi.org/10.1111/j.1469-185X.2011.00205.x

105 Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G. et al. (2013) Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss - a meta-analysis. *Ecol. Lett.* **16**, 912–920 https://doi.org/10.1111/ele.12128

106 Öckinger, E., Winsa, M., Roberts, S.P.M. and Bommarco, R. (2018) Mobility and resource use influence the occurrence of pollinating insects in restored seminatural grassland fragments. *Restor. Ecol.* **26**, 873–881 https://doi.org/10.1111/rec.12646

107 Kormann, U., Scherber, C., Tscharntke, T., Klein, N., Larbig, M., Valente, J.J. et al. (2016) Corridors restore animal-mediated pollination in fragmented tropical forest landscapes. *Proc. R. Soc. B Biol. Sci.* **283**, 20152347 https://doi.org/10.1098/rspb.2015.2347

108 Hadley, A.S., Frey, S.J.K., Robinson, W.D., Kress, W.J. and Betts, M.G. (2014) Tropical forest fragmentation limits pollination of a keystone understory herb. *Ecology* **95**, 2202–2212 https://doi.org/10.1890/13-0929.1

109 Hansen, J., Sato, M., Ruedy, R., Lo, K., Lea, D.W. and Medina-elizade, M. (2006) Global temperature change. *Proc. Natl. Acad. Sci. U.S.A.* **103**, 14288–14293 https://doi.org/10.1073/pnas.0606291103

110 Urban, M.C. (2015) Climate change. Accelerating extinction risk from climate change. *Science* **348**, 571–573 https://doi.org/10.1126/science.aaa4984

111 Boukal, D.S., Bideault, A., Carreira, B.M. and Sentis, A. (2019) Species interactions under climate change: connecting kinetic effects of temperature on individuals to community dynamics. *Curr. Opin. Insect Sci.* **35**, 88–95 https://doi.org/10.1016/j.cois.2019.06.014

112 Parmesan, C. and Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42 https://doi.org/10.1038/nature01286

113 Rafferty, N.E. and Ives, A.R. (2011) Effects of experimental shifts in flowering phenology on plant–pollinator interactions. *Ecol. Lett.* **14**, 69–74 https://doi.org/10.1111/j.1461-0248.2010.01557.x
114 CaraDonna, P.J., Iler, A.M. and Inouye, D.W. (2014) Shifts in flowering phenology reshape a subalpine plant community. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 4916–4921 https://doi.org/10.1073/pnas.1323073111
115 Rafferty, N.E. and Ives, A.R. (2012) Pollinator effectiveness varies with experimental shifts in flowering time. *Ecology* **93**, 803–814 https://doi.org/10.1890/11-0967.1
116 Olliff-Yang, R.L. and Mesler, M.R. (2018) The potential for phenological mismatch between a perennial herb and its ground-nesting bee pollinator. *AoB Plants* **10**, ply040 https://doi.org/10.1093/aobpla/ply040
117 Kudo, G. and Cooper, E.J. (2019) When spring ephemerals fail to meet pollinators: mechanism of phenological mismatch and its impact on plant reproduction. *Proc. R. Soc. B Biol. Sci.* **286**, 20190573 https://doi.org/10.1098/rspb.2019.0573
118 Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.L. and Totland, Ø. (2009) How does climate warming affect plant–pollinator interactions? *Ecol. Lett.* **12**, 184–195 https://doi.org/10.1111/j.1461-0248.2008.01269.x
119 Renner, S.S. and Zohner, C.M. (2018) Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annu. Rev. Ecol. Evol. Syst.* **49**, 165–182 https://doi.org/10.1146/annurev-ecolsys-110617-062535
120 Bartomeus, I., Ascher, J.S., Wagner, D., Danforth, B.N., Colla, S., Kornbluth, S. et al. (2011) Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 20645–9 https://doi.org/10.1073/pnas.1115559108
121 Wolkovich, E.M., Jonathan Davies, T., Schaefer, H., Cleland, E.E., Cook, B.I., Travers, S.E. et al. (2013) Temperature-dependent shifts in phenology contribute to the success of exotic species with climate change. *Am. J. Bot.* **100**, 1407–1421 https://doi.org/10.3732/ajb.1200478
122 Zettlemoyer, M.A., Schultheis, E.H. and Lau, J.A. (2019) Phenology in a warming world: differences between native and non-native plant species. *Ecol. Lett.* **22**, 1253–1263
123 Willis, C.G., Ruhfel, B.R., Primack, R.B., Miller-Rushing, A.J., Losos, J.B. and Davis, C.C. (2010) Favorable climate change response explains non-native species' success in Thoreau's Woods. *PLoS One* **5**, e8878 https://doi.org/10.1371/journal.pone.0008878
124 Haeuser, E., Dawson, W. and van Kleunen, M. (2019) Introduced garden plants are strong competitors of native and alien residents under simulated climate change. *J. Ecol.* **107**, 1328–1342 https://doi.org/10.1111/1365-2745.13101
125 Giejsztowt, J., Classen, A.T. and Deslippe, J.R. (2019) Climate change and invasion may synergistically affect native plant reproduction. *Ecology* **101**, e02913
126 Silva, D.P., Groom, S.V.C., da Silva, C.R.B., Stevens, M.I. and Schwarz, M.P. (2017) Potential pollination maintenance by an exotic allodapine bee under climate change scenarios in the Indo-Pacific region. *J. Appl. Entomol.* **141**, 122–132 https://doi.org/10.1111/jen.12337
127 Stavert, J.R., Pattemore, D.E., Gaskett, A.C., Beggs, J.R. and Bartomeus, I. (2017) Exotic species enhance response diversity to land-use change but modify functional composition. *Proc. R. Soc. B Biol. Sci.* **284**, 20170788 https://doi.org/10.1098/rspb.2017.0788
128 Scaven, V.L. and Rafferty, N.E. (2013) Physiological effects of climate warming on flowering plants and insect pollinators and potential consequences for their interactions. *Curr. Zool.* **59**, 418–426 https://doi.org/10.1093/czoolo/59.3.418
129 Pardee, G.L., Inouye, D.W. and Irwin, R.E. (2018) Direct and indirect effects of episodic frost on plant growth and reproduction in subalpine wildflowers. *Glob. Chang. Biol.* **24**, 848–857 https://doi.org/10.1111/gcb.13865
130 Takkis, K., Tscheulin, T. and Petanidou, T. (2018) Differential effects of climate warming on the nectar secretion of early-and late-flowering Mediterranean plants. *Front. Plant Sci.* **9**, 1–13 https://doi.org/10.3389/fpls.2018.00874
131 Hoiss, B., Krauss, J. and Steffan-Dewenter, I. (2015) Interactive effects of elevation, species richness and extreme climatic events on plant–pollinator networks. *Glob. Chang. Biol.* **21**, 4086–4097 https://doi.org/10.1111/gcb.12968
132 Burdine, J.D. and McCluney, K.E. (2019) Differential sensitivity of bees to urbanization-driven changes in body temperature and water content. *Sci. Rep.* **9**, 1–10 https://doi.org/10.1038/s41598-018-38338-0
133 Nicholson, C.C. and Egan, P.A. (2020) Natural hazard threats to pollinators and pollination. *Glob. Chang. Biol.* **26**, 380–391 https://doi.org/10.1111/gcb.14840
134 Oliver, T.H. and Morecroft, M.D. (2014) Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. *Wiley Interdiscip. Rev. Clim. Chang.* **5**, 317–335 https://doi.org/10.1002/wcc.271
135 Newbold, T., Adams, G.L., Albaladejo Robles, G., Boakes, E.H., Braga Ferreira, G., Chapman, A.S.A. et al. (2019) Climate and land-use change homogenise terrestrial biodiversity, with consequences for ecosystem functioning and human well-being. *Emerg. Top. Life Sci.* **3**, 207–219 https://doi.org/10.1042/ETLS20180135
136 Travis, J.M.J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D. et al. (2013) Dispersal and species' responses to climate change. *Oikos* **122**, 1532–1540 https://doi.org/10.1111/j.1600-0706.2013.00399.x
137 Carroll, C., Parks, S.A., Dobrowski, S.Z. and Roberts, D.R. (2018) Climatic, topographic, and anthropogenic factors determine connectivity between current and future climate analogs in North America. *Glob. Chang. Biol.* **24**, 5318–5331 https://doi.org/10.1111/gcb.14373
138 García, F.C., Bestiona, E., Warfielda, R. and Yvon-Durochera, G. (2018) Changes in temperature alter the relationship between biodiversity and ecosystem functioning. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 10989–10994 https://doi.org/10.1073/pnas.1805518115
139 Groves, C.R., Game, E.T., Anderson, M.G., Cross, M., Enquist, C., Ferdaña, Z. et al. (2012) Incorporating climate change into systematic conservation planning. *Biodivers. Conserv.* **21**, 1651–1671 https://doi.org/10.1007/s10531-012-0269-3
140 Lau, J.A., Magnoli, S.M., Zirbel, C.R. and Brudvig, L.A. (2019) The limits to adaptation in restored ecosystems and how management can help overcome them. *Ann. Missouri Bot. Gard.* **104**, 441–454 https://doi.org/10.3417/2019430
141 Prober, S.M., Byrne, M., McLean, E.H., Steane, D.A., Potts, B.M., Vaillancourt, R.E. et al. (2015) Climate-adjusted provenancing: a strategy for climate-resilient ecological restoration. *Front. Ecol. Evol.* **3**, 1–5 https://doi.org/10.3389/fevo.2015.00065
142 Townsend, P.A. and Levey, D.J. (2005) An experimental test of whether habitat corridors affect pollen transfer. *Ecology* **86**, 466–475 https://doi.org/10.1890/03-0607
143 Cranmer, L., McCollin, D. and Ollerton, J. (2012) Landscape structure influences pollinator movements and directly affects plant reproductive success. *Oikos* **121**, 562–568 https://doi.org/10.1111/j.1600-0706.2011.19704.x
144 Ponisio, L.C., de Valpine, P., M'Gonigle, L.K. and Kremen, C. (2019) Proximity of restored hedgerows interacts with local floral diversity and species' traits to shape long-term pollinator metacommunity dynamics. *Ecol. Lett.* **22**, 1048–1060 https://doi.org/10.1111/ele.13257