Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms

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Ecological restoration of plant–pollinator interactions has received surprisingly little attention, despite animal-mediated pollination underpinning reproduction of the majority of higher plants. Here, we offer a conceptual and practical framework for the ecological restoration of pollination mutualisms. Through the use of targeted restoration plantings to attract and sustain pollinators and increased knowledge of the ecological requirements of pollinators, we propose that pollination could be successfully restored in degraded ecosystems. The challenge for pollination biologists is to integrate their findings with those of plant restoration ecologists to ensure sustainable pollination in restored ecosystems.

Pollinator loss and the need for pollination restoration

Approximately 90% of flowering plant species globally are reliant on biotic pollination for reproduction and maintaining genetic viability [1]. Because of the economic implications of reduced crop yield due to pollination failure, the purported decline of pollination services in agri-environments has received considerable scientific attention (e.g. [2–8]). Consequently, there is a growing literature on restoring pollination services within agricultural settings [9–12]. Given that crop plants represent <0.1% of angiosperm species globally [13,14], this represents a considerable bias towards restoration of pollination services in agricultural landscapes compared with restoration of pollination in non-agricultural habitats.

In human-modified landscapes, habitat degradation, loss and fragmentation can cause declines in plant and/or pollinator populations, potentially leading to pollination limitation [4,15]. Furthermore, the majority of plant populations surveyed to date experienced pollination limitation of plant sexual reproduction [16], although the magnitude of pollination limitation could be overestimated by studies that fail to take into account that not all pollination events result in fruit-set [17]. Given the importance of pollination and its sensitivity to human disturbance, it is surprising how little focus has been placed on restoration of animal-mediated pollination in natural habitats [18,19]. Based on a search of the terms 'pollinat*' and 'restoration' in ISI Web of Science, only five papers have used plant–pollinator communities as a metric for determining functional success in the restoration of natural landscapes [20–24], out of 22,137 papers devoted to pollination biology (pollinat* in ISI Web of Science). The few previous studies comparing plant–pollinator networks between restored and natural sites have highlighted lower network complexity and robustness in restored sites [21,24]. Failure to understand, manage and promote pollinators could lead to decline or collapse in ecological restoration. With ecological restoration estimated to be a trillion dollar global activity [25], establishing animal-mediated pollination will be of widespread importance for ensuring resilience in restored plant communities.

Glossary

Allee effect: reduced per capita reproductive output or demographic viability in small populations.
Asymmetric interactions: occur when a specialist interacts with a generalist, such as a specialist plant interacting with a generalist pollinator.
Bridging plants: a type of keystone plant that provides nectar and pollen resources during bottlenecks of resource availability.
Framework plants: a type of keystone plant that provides considerable nectar and/or pollen resources to a large number of pollinator species.
Generalist plant: plant species pollinated by a large number and often a broad taxonomic range of pollinator species.
Generalist pollinator: pollinator species that visit a large number and often a broad taxonomic range of plant species.
Pollination network: all the interactions between plants and pollinators within a given area or time period. Analogous to (or a type of) food web.
Specialist plant: plant species that are pollinated by one or a small number of pollinator species from a restricted taxonomic range.
Specialist pollinator: pollinator species that visit one or a small number of plant species from a restricted taxonomic range.

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Owing to the paucity of information on pollinator restoration, here we review findings from recent community and population level pollination ecology studies to assess the challenges involved in reconnecting plants and pollinators, with particular emphasis on natural area restoration. We discuss several of the key issues surrounding the development of a pollination-based restoration program: (i) structural characteristics of plant–pollinator networks; (ii) selecting plants to restore pollinators; (iii) ecological requirements of pollinators; (iv) landscape structure and facilitation of pollinator movement; and (v) variation among biogeographic regions.

Not all restoration projects have the same objective. For example, if the aim is to restore native plant reproduction, it might not be crucial that the species composition of the pollinator community differs from the target natural ecosystem. As long as all functional pollinator groups are retained and plants are consistently producing viable seed across years, then pollination could still be considered to have been functionally restored [26]. However, a far more intimate knowledge of the ecological requirements of the whole system is required if the goal is reestablishment of the original pollinator community or the restoration of both plants and pollinators.

Structural characteristics of plant–pollinator networks

Inherent characteristics of pollination networks can affect how they respond to ecological perturbations and ultimately impact their ease of restoration. Pollinator communities typically comprise a small number of rare, highly specialized species, many moderately specialized species and a few common, generalist species, which provide the majority of animal-mediated pollination [27,28]. There are consistent structural characteristics of pollination networks, including high levels of asymmetry (i.e. specialist plants interacting with generalist pollinators) [27,29–32] and nestedness (specialists interacting with a subset of species that generalists interact with) [31,33]. These features of pollination networks confer resilience to disturbance, because as long as the core of generalists is retained, most plants will have pollinators. The loss of a rare specialist pollinator is unlikely to result in the loss of a plant [30,34].

General topological patterns of network structure, such as asymmetry and nestedness appear to vary little temporally [35–37]. However, species composition and pair-wise relationships among species can show high temporal variation [35–38]. Similarly, the food plants used by a given pollinator species often change between seasons and years due to shifts in the composition of the flowering community. This means that species that appear to be dietary specialists in a short-term study might prove to be generalists if the study is extended over multiple years or a greater number of observations are made [35,37]. These characteristics suggest that restoration for maximal pollinator diversity is important, so that species can continue providing functional replacements for each other over time [35–38].

Although generalist pollinators visit many plant species [39], they might not be as effective at transferring pollen as pollinators specifically adapted to visiting that plant [40,41]. For example, several typically bird pollinated plants suffered reduced seed set when birds were excluded, allowing visitation only by bees (e.g. [41,42]). Furthermore, a recent study has shown that when pollen transfer is considered relative to pollinator visitation, levels of specialization in plant–pollinator networks increase [43].

Selecting plants to restore pollinators

Several studies have proposed that when restoring natural areas, plant species should be planted that attract and sustain pollinators for the duration that they require nectar and/or pollen [18,44–47]. These have been referred to as framework and bridging plants depending on how they function quantitatively and temporally to support the pollinator community [18].

'Framework' plants support pollinator communities by providing considerable nectar and/or pollen resources to numerous pollinator species and individuals [18]. Consequently, the use of framework plants might sustain a pollinator community that could also service smaller or less attractive members of the plant community [48–53]. For example, restoration research in agricultural landscapes has shown that a disproportionate number of visits by bumblebees are to a small number of plant species [9–12,54]. Identification and planting of these framework species can be used to promote effective pollinator restoration (Box 1) and potentially facilitate the reproduction of less attractive plants within the restoration palette.

A risk in the use of exceptionally nectar- or pollen-rich plants is that they might compete via pollination, rather than facilitate the pollination of less attractive plants [50,52,55]. A key challenge is that it is currently difficult to predict if plant species that share pollinators will interact competitively or facilitatively. However, there is some evidence that the directionality of these interactions can depend on relative plant abundance [50], possibly because individual pollinators can temporarily specialize on the more abundant species at the expense of rarer species [50,56]. Therefore, careful consideration needs to be given to relative abundances of the different plants when seeking to enhance pollinator visitation to targeted plant species.

'Bridging' plants provide nectar and pollen resources during otherwise resource-limited times [18,57]. The use of bridging plants is most important in communities with pollinators that require pollen or nectar all or most of the year, such as some vertebrate pollinators [58,59], and social and/or multivoltine bee species such as bumblebees (*Bombus* spp.; Figure 1). Bridging plants can be particularly important for pollinators with relatively specific food requirements. For example, the honey possum (*Tarsipes rostratus*, Tarsipedidae) only consumes the pollen and nectar of vertebrate-pollinated plants making it reliant on one or few species of food plants during some seasons [58]. The necessity for bridging plants varies between ecosystems. For example, in some environments, such as tropical forests, species of pollen-feeding or nectarivorous insects can be active throughout the year necessitating a year-round flower supply [60]. Conversely, in some environments with short growing seasons, bridging species might not be needed because flowering is intense during the growing season and insects persist during the non-growing season as eggs or larvae [61].

Box 1. Case study: restoration of pollination services in the Central Valley of California

In the Central Valley of California, land is managed intensively for row crop, vineyard and orchard production in large monoculture fields. Wild bee communities and the pollination services they provide to a variety of crops are greatly diminished in such landscapes, compared with diversified, organic plantings grown in more heterogeneous landscapes that include regions of natural habitat [6,112]. However, growers are increasingly planting native plant hedgerows along field edges to restore a range of ecological functions, including pollination services (Figure I). We used a large dataset on plant–bee interactions from farms and natural area sites in this region [113] to select plants that would support the 20 most important crop pollinators (based on [5,6,114,115]) across their flight seasons. First, we identified the plant species visited by the largest number of individuals and the species of these crop–pollinators (framework plants). Second, we compared the blooming periods of these plants against the flight seasons of the crop–pollinating bee species to identify any gaps in the provisioning of floral resources. We added plant species that both bloom during those gaps and were visited by our crop–pollinating species (bridging species). Finally, we removed plant species that were impossible to cultivate or were ''weedy'' in habit (and therefore unlikely to be accepted by grower partners), identifying substitute species whenever possible.

Our conservation partners (Xerces Society, Audubon Society) identified interested growers and convinced them to use this planting palette in their hedgerow restoration planting. From 2006, we began monitoring five pre-restoration sites, along with 11 control sites, matched in pre-restoration vegetation, adjacent land use and landscape context (a ''beyond Before-After-Control-Impact design'' [116]). Although we monitor the pollinator communities at these sites annually, we do not expect to see strong differences among hedgerow and control sites (which are unmanaged, often weedy, field edges) until hedgerows mature in several more years. Meanwhile, we are also studying mature hedgerows (established more than a decade ago) that contain many of the same plant species, but that were developed to promote natural enemies and pest control services rather than pollinator communities and pollination services [117]. A promising initial finding is greater bee diversity (but not abundance, which is dominated across all sites by several superabundant halictid species) on the mature hedgerows compared with controls. In addition, at hedgerow sites, both honey bees and native bee species preferred foraging on native hedgerow shrubs relative to exotic weeds co-flowering at these sites, and native plants were visited by more species and individuals than exotic plants (L. Morandin and C. Kremen unpublished data).

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Figure I. Hedgerow restoration in the Central Valley, California. The image on the left depicts the initial stages of hedgerow restoration (M. Vaughan, Xerces Society), whereas the image on the right shows a mature hedgerow, approximately 10 years following restoration (L. Morandin, University of California Berkeley).

Plant populations in restored areas need to be large enough to avoid Allee effects, (see Glossary), the commonly observed reduction in fecundity of plants in small populations [62–65]. Experiments using supplemental hand-pollinations across a range of population sizes have shown that these Allee effects are often due to pollen-limitation of seed production [66,67]. Pollen deficits can arise when pollinators are less likely to visit plants in small populations or when plants in these populations receive insufficient compatible pollen on stigmas [68]. Some plants appear to be resilient to Allee effects even though they depend on pollinators (compare with [69]); knowledge about the reproductive biology of these species might provide clues as to which plant–pollinator interactions are easier to restore.

Studies on the restoration of animal-mediated pollination should focus on both the ecological requirements of the target plant community and the associated pollinators. Once candidate framework and bridging plants have been identified, researchers should identify which of these plants supports the greatest abundance and diversity of pollinators for the given area.

Ecological requirements of pollinators

Pollinator colonization and persistence in restored natural areas requires that the ecological needs of pollinators are met either entirely within the restoration site or within foraging distance of the restoration site. Pollinators depend on several factors for the completion of their life cycle, such as the availability of food sources, nesting material and nest sites [4,70–72]. For example, solitary bees can be limited by the availability of nest sites [73,74], butterflies require both larval host plants and nectar resources as adults [75], thynnid wasps (Hymenoptera: Thynnidae; Figure 1), which are important pollinators of Australian orchids [76], require a carbohydrate source as adults (i.e. nectar, secretions from larval psyllids: Hemiptera: Psyllidae, or honeydew) [76] and scarab beetle larvae (Coleoptera: Scarabaeidae), which they parasitize [77,78]. Although measures such as providing artificial nest sites can facilitate colonization and increase bee populations [73,74], there is little known about the importance of life cycle requirements other than nectar and pollen for the successful restoration of most pollinator species.

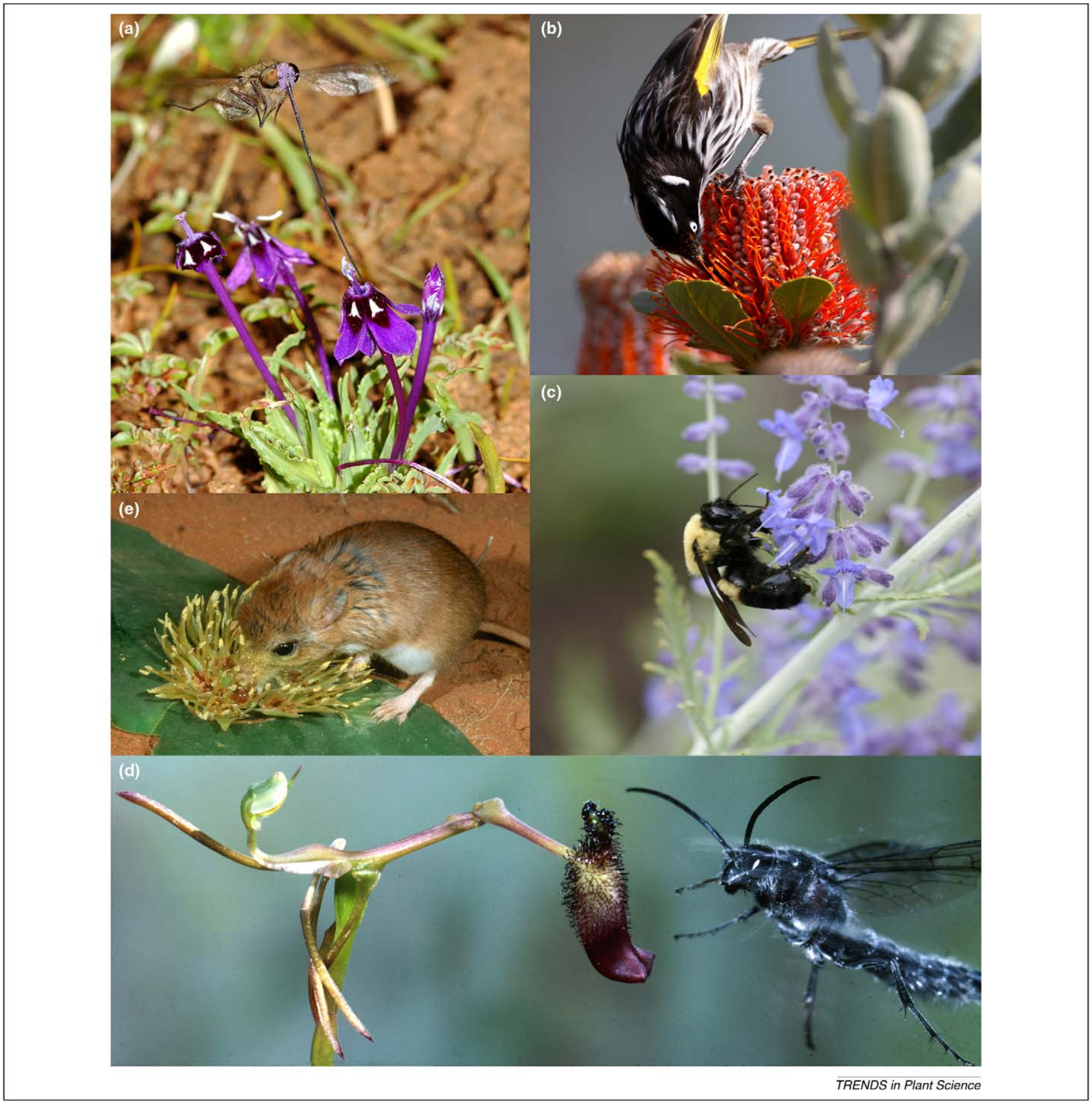

Figure 1. Examples of plants and pollinators demonstrating different levels of specialization. **(a)** Flowers of *Lapeirousia oreogena* (Iridaceae) are pollinated exclusively by an undescribed long-proboscid fly species (*Prosoeca* sp., Nemestrinidae) (South Africa). **(b)** A New Holland honeyeater (*Phylidonyris novaehollandiae*, Meliphagidae), a generalist bird pollinator, feeding on the specialist plant *Banksia coccinea* (Proteaceae), which is pollinated by vertebrates (southwestern Australia). **(c)** The generalist pollinator *Bombus* sp. (Apidae) on *Perovskia atriplicifolia* (Lamiaceae) (North America). **(d)** The sexually deceptive *Drakaea gracilis* (Orchidaceae) attracts only a single species of pollinating thynnid wasp (an undescribed species of *Thynnoides*, Thynnidae), a generalist nectarivore (southwestern Australia). **(e)** A gerbil (*Gerbillurus paeba*) feeding on flowers of *Massonia depressa* (Hyacinthaceae), a lily specialized on pollination by small, ground-dwelling mammals (South Africa). Photographs: **(a)** and **(e)** S.D. Johnson, **(b)** D. McGinn, **(c)** L. Mandle, **(d)** B. and B. Wells.

Pollinator life histories vary in their susceptibility to disturbance. For example, above-ground nesting and social bee species have been shown to be more negatively affected by isolation from remnant native habitat than below-ground nesting and solitary bee species [72]. Furthermore, invertebrate pollinators with narrow habitat requirements, slower development, fewer generations per year and lower mobility have been shown to experience greater declines in some countries [79]. These trends might indicate that pollinator species with more complex life cycles, or life cycles that do not facilitate rapid colonization or recovery from local extinction might be more difficult to restore.

Landscape structure and facilitation of pollinator movement

Anthropogenic habitat removal and subsequent landscape fragmentation can alter pollination and pollinator communities [57,80–83]. Habitat fragmentation can result in decreased pollinator abundance and diversity in small fragments [81]. However, pollinators exhibit a broad range of responses to habitat fragmentation and ecosystem disturbance [81,84,85]. For example, some bee species are negatively affected by human disturbance [72,81], whereas others might benefit [86]. A common consequence of habitat fragmentation is reduction in plant population size [64], which can lead to a decline in levels of pollination, seed set and recruitment regardless of any effect from the pollinator community (e.g. [15,66,67,87]).

Ideally, knowledge of dispersal, subsequent colonization capability, minimum habitat area requirements and potential barriers to dispersal [82,83,88] of the focal pollinator groups would be desirable before undertaking restoration. To facilitate colonization of restored sites, consideration needs to be given to the layout of restoration plantings in relation to the ability of pollinators to use and cross the landscape matrix. In cases where pollinators forage widely and are able to traverse a variety of habitats, initial restoration of animal-mediated pollination might occur through foraging by wide-ranging generalist pollinators, such as Australian honeyeaters (Meliphagidae; [45]; Figure 1), bumblebees (Figure 1) and the honey bee *Apis mellifera* [89–92].

In cases where pollinators are able to move through a hostile matrix, remnant plants, such as individual trees can serve as stepping stones, increasing landscape and genetic connectivity (e.g. [93,94]). The creation of a stepping stone habitat could form the initial step of restoration programs to facilitate dispersal of pollinators between otherwise isolated fragments to promote diverse pollinator communities at the landscape scale.

Alternatively, pollinators with limited dispersal capability can require contiguous links of favorable habitat (corridors) to facilitate movement into restored sites. Depending on the landscape and the target organisms, corridors can refer to either strips of vegetation in an agricultural landscape, or strips of open vegetation within a forested matrix. Connection of plant populations by corridors has been shown to facilitate pollinator movement [95]. Furthermore, in agricultural and silviculture dominated landscapes, for some plants, pollen transfer has been shown to be significantly higher between populations connected by corridors than those that were not [96,97]. In some cases, pollen transfer declined with increasing distance to the source, indicating limitations to the use of corridors [98]. Furthermore, the efficacy of corridors for facilitating dispersal can vary between taxonomic groups [98]. The abundance of wild bees along linear habitat corridors in an agricultural landscape has been shown to decline with distance to remnant semi-natural habitat, whereas hoverflies showed the reverse trend [98]. However, corridors might be the only viable option when the majority of the landscape is dedicated to agriculture and large-scale revegetation is impossible.

Corridors can potentially create undesirable side effects such as facilitating the spread of invasive or edge species [99]. An alternative is to enlarge the existing habitat area to reduce the negative effects of small fragment size. This could have a more pronounced effect on increasing population sizes within a patch, compared with corridors, particularly when patches increase beyond the minimum area required for supporting viable pollinator populations [100].

The natural colonization of a restored site and the complexity of the pollinator community present can be strongly influenced by its proximity to remnant habitat [20,21,26]. For relatively immobile pollinator species, pollination restoration might require habitat remnants to be directly connected by favorable habitat patches, such as vegetated corridors. For example, foraging ranges of bees can vary from less than a hundred meters for small-bodied species to several kilometers for large-bodied species [91,92]. Where pollination restoration can be achieved by highly vagile generalist species, stepping stone plantings might be sufficient to facilitate colonization. In the presence of a hostile landscape matrix, colonization could be facilitated by direct connection via corridors. Consequently, the landscape context of a restoration site and the ecology of the fauna will both have considerable bearing on whether or not corridors or stepping stones are effective or needed in facilitating pollinator colonization.

Captive breeding and reintroduction programs might be effective in cases where pollinators have been extirpated and natural colonization processes are unlikely through lack of source populations or low dispersal [18], particularly for restoring habitat patches that are isolated from sources of recruits. However, there could be many challenges associated with restoring certain pollinators that have highly specific ecological requirements. To our knowledge, there are no published studies of reintroduction or captive breeding of native pollinators primarily for reinstating pollination in natural or restored areas.

Variation among biogeographic regions

The optimal techniques for facilitating pollination in restored environments could differ markedly between habitats and biogeographic regions. For example, there are significant geographical differences in levels of specialization and diversity of plant–pollinator interactions [101,102]. Among the comparatively well-studied floras, the Cape Region stands out as a region characterized by remarkably high levels of both plant and pollinator specialization [103]. This suggests that pollinators and pollination, if lost from this region, would be comparatively difficult to restore. Furthermore, pollinator functional groups (*sensu* [102]) might show varying levels of morphological and ecological specialization between regions depending on the evolutionary and ecological histories of the plants and pollinators involved [104,105]. Areas where there is high functional diversity are likely to require an increased diversity of targeted plantings to assist in the restoration of these more complex pollinator communities.

Plants and pollinators from landscapes of different ecological and evolutionary history are likely to have varying reproductive and dispersal behaviors and resilience to habitat fragmentation [106,107]. For example, the old, geologically diverse but stable landscapes of the Cape Floristic Region and the Southwest Australian Floristic Region have facilitated the evolution of diverse heathland floras characterized by a high incidence of naturally frag-

Box 2. Incorporating the difficulty of restoring plant species into plant selection

Owing to differences in the ease of restoring plant species, the most attractive plant species will not necessarily be the most efficient for achieving rapid restoration of pollinators. Difficulty of restoring each plant species might be caused by factors such as limitation of propagule sources, difficulty of establishment (susceptibility to disease, lack of vigor) and poor long-term establishment. We use examples from another system that has been well-researched in terms of restoration practices, the biodiverse *Banksia* woodland of the Southwest Australian Floristic Region, to illustrate how the characteristics of the species in each of these boxes can be used to guide the restoration process (Figure I). Although Panel 1 contains few plant species, these are the highest priority for restoration due to ease of restoration and the large number of pollinator species that they support. For example, the canopy forming *Eucalyptus marginata* (Myrtaceae) can attract over 80 species of nectar- and pollen-feeding insects at a single site [119]. Panel 2 contains plant species with a higher level of pollination specialization. Therefore, in restoration, plant species in this category should be chosen for minimal overlap with the generalists from Panel 1 to maximize pollinator diversity. For example, in the Southwest Australian Floristic Region (SWAFR), the kangaroo paw species, *Anigozanthos humilis* (Haemodoraceae) is readily restored and is visited by several honeyeater species [120], birds that are specialized on a subset of the plant community [47]. Panel 3 contains plant species that are difficult to restore but, if restoration is successful, will attract a wide range of pollinators. This option could be pursued if the species attracted a suite of pollinators not already accounted for in Panel 1 species. In the SWAFR example, *Philotheca spicata* (Rutaceae) is difficult to restore (Alcoa World Alumina, personal communication) but attracts a range of understory Hymenoptera. Panel 4 represents species that should only be targeted for restoration if they are plants of special conservation concern, such as rare or threatened species. For example, many orchids have specialized mycorrhizal and pollinator relationships making restoration challenging [76,121]. However, because of their popularity and high degree of threat, orchid conservation is a relatively high priority in the conservation community.

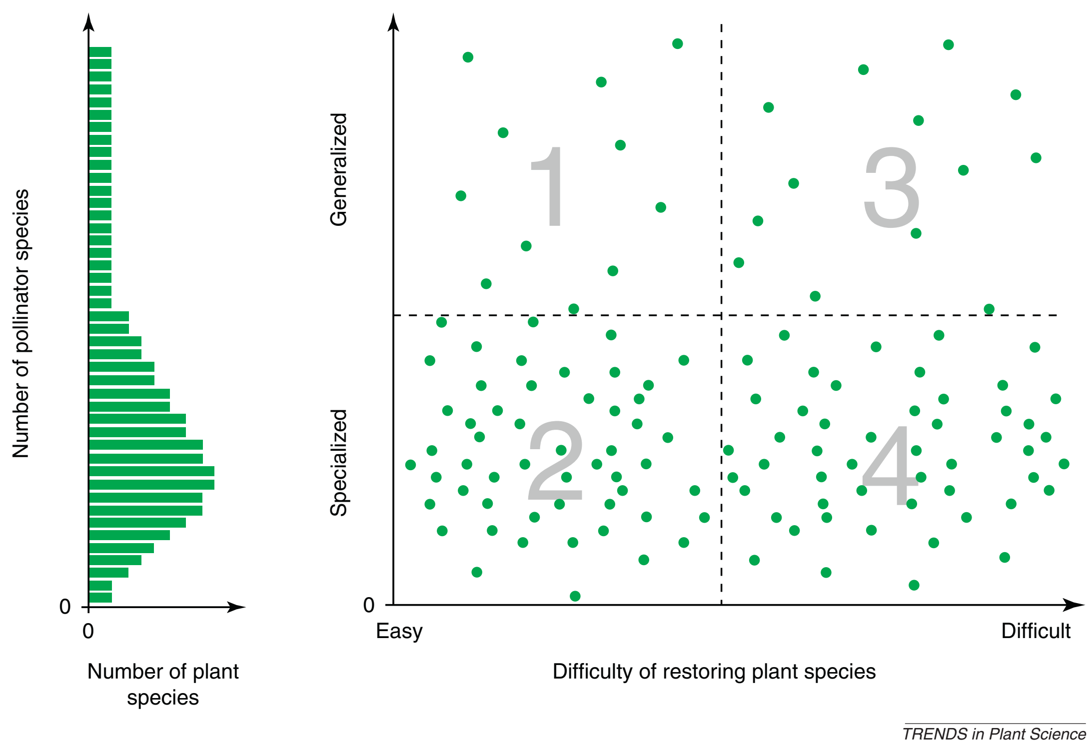

Figure I. A framework for the choice of plant species in restoration, based on specialization of pollination system versus ease of restoration. The scatterplot depicts a hypothetical plant community, with each point representing a single plant species. The difficulty of restoring each plant species has been plotted against the number of species of visiting pollinators. Panels 1 and 3 depict generalist plants that receive visits from many pollinator species, and Panels 2 and 4 depict plants with more specialized pollination (fewer visitor species). The relative proportions of plant species that have specialized versus generalized pollination systems (based on the number of visitors) has been based on an actual plant–pollinator network [118], as shown in the histogram on the left, which shows the number of plant species in the community exhibiting each level of specialization (expressed as the number of species of visiting pollinator).

mented plant populations [107,108]. We predict that in these landscapes, small-bodied generalist pollinator species might be able to access a range of species within a small area and have naturally small foraging ranges. Similarly, more specialized small-bodied species might have restricted dispersal so that they remain in the relatively small, disjunct patches of suitable habitat. At the other extreme, species from environments with episodic and patchy flowering, such as deserts, might contain species with large foraging ranges. Although these remain predictions, it highlights the caution required when extrapolating restoration practices between environments or biogeographic regions.

Concluding remarks: future research directions

Restoration of pollination systems provides an example where management at the local scale could potentially have profound effects on the diversity of pollination interactions at the landscape scale [109]. Future research should resolve patterns of dispersal by pollinators and how this process can be facilitated through planting flora that attract and sustain a variety of pollinator species, with the ultimate aim of colonization and persistence in restoration sites. The stage of restoration in which specific framework and bridging species are planted will need to be determined based on plant phenology and pollinator requirements. Recent evidence suggests that when pollen transfer is taken into account in plant–pollinator visitation webs, levels of specialization increase [43], highlighting the need for research on the ability of different pollinators to transfer pollen effectively to target plant species.

Further research is required to determine the extent of the impacts of invasive pollinators on the success of pollinator restoration projects, through competition and transmission of diseases [110]. Given that invasive pollinators are known to be a problem on multiple continents [111], such research would have broad implications. By designing restoration plantings to favor native pollinators, restoration sites could represent an opportunity to create pollinator communities free from invasive pollinators.

To maximize the efficiency of the restoration process, practitioners should, when choosing plant species for restoration of pollination networks, consider not only the pollinator species attracted but the ease of restoring the plant species (Box 2). Likewise, choosing the pollinators to target for restoration should involve both consideration of the efficacy of the pollinator and how readily they can be attracted to the site. As such, the final challenge for pollination biologists is to integrate their findings with the work of plant restoration ecologists to achieve the highest degree of ecosystem function.

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