Pollination and Restoration

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PERSPECTIVE

Pollination and Restoration

Kingsley W. Dixon

Pollination services underpin sustainability of restored ecosystems. Yet, outside of agri-environments, effective restoration of pollinator services in ecological restoration has received little attention. This deficiency in the knowledge needed to restore pollinator capability represents a major liability in restoration programs, particularly in regions where specialist invertebrate and vertebrate pollinators exist, such as global biodiversity hotspots. When compounded with the likely negative impacts of climate change on pollination services, the need to understand and manage pollinator services in restoration becomes paramount.

Robust pollination services underpin the plant reproductive continuity of a restored ecosystem and rely on an understanding of how to support pollination processes and vectors after restoration activities. In agriculture and horticulture, the economic value of pollination is well recognized, with 75% of crop species and 35% of crop value dependent on pollination by animals (*1*, *2*). The importance of pollinators in agricultural production has been highlighted by the emergence of colony collapse disorder and varroa mite infestation in honeybee hives (*3*). This has led to remediation measures that include importation of hives from countries free of these disorders to use of electric vibrators to replicate buzz pollination in tomato crops.

Conversely, reestablishment of pollination services in restored native ecosystems is not well understood, yet biotically driven pollination services, particularly animal-based pollination services, sustain reproductive potential and genetic resilience in many ecosystems. To date, little has been done in the restitution of pollinator services in ecological restoration projects (*4*, *5*). This is despite a plea 10 years ago for fauna-mediated pollination services to be "…[reintroduced] as part of critical habitat management and restoration plans" (*6*). For example, due to a lack of pollination knowledge, one of Australia's largest urban woodland restoration programs at Kings Park and Bold Park in Perth, involving $5 million and reestablishment of 1 million plants, could not consider pollinator enhancement as part of the programs.

Specialist pollinators are often the first casualties when ecosystems degrade. However, the most pervasive ecosystem impact will arise from the loss of generalist pollinators (*7*–*9*), as witnessed with colony collapse disorder and honeybees. Similar pollination consequences will occur in natural and restored natural ecosystems if generalist pollination services are disrupted.

For the global biodiversity hotspots that represent 44% of the world's vascular plant species and contain most of the specialized plant-pollinator mutualisms and interactions (*10*, *11*), restoring pollination services may be critical for ensuring restoration success. However, with 60% of global landscapes disturbed by humans and at least 70% of the land area in the 25 biodiversity hotspots cleared, future restoration capability will depend on the ability of pollinators to migrate and establish across often highly fragmented habitat matrices. In such fragmented landscapes, nonflying or restricted-range pollinators, such as terrestrial mammals, lizards, and many invertebrates, are doomed as pollinators particularly when the alienated matrix is ecologically hostile. In these cases, highly specific and obligate pollination interactions are most at risk and likely to pose the greatest challenge to conservation biologists and restoration ecologists.

Only a handful of research papers specifically investigate pollination networks and persistence in the face of climate change (*7*, *8*), yet climate change represents a major threat to pollination services. Climate-change trends predict alteration in timing of greening, flowering and senescence, and overall shortening of the growing season (*12*), factors with direct impact on pollination mutualisms. However, climate change will also lead to a decrease in precipitation and a shift in seasonality of rainfall, particularly in mediterranean regions, resulting in reduced plant vigor, delayed plant maturation, and a decline in nectar production capacity, with potentially devastating effects on nectar-dependent mutualists.

In addition, global warming may lead to partial or total asynchrony between pollinator life cycles and flowering phenologies. In the case of obligate pollination systems, this may lead to a breakdown of pollination mutualisms (*13*, *14*). Both have important implications for restoration, where species mixes may need to source nonlocal native plant species from a climate zone that matches the predicted new climate regime at the target restoration site. Such actions would necessitate the careful consideration of the invasive potential of introducing such plant species.

Ecosystems with high levels of specialized plant-pollinator interactions present substantial risks in achieving restoration success. These are heightened when the associations involve mutual dependencies between pollinator and plant leading to coextinction (*15*)—the "buy one, get one free" phenomenon. In turn, decay or shifts in pollinator assemblages servicing a plant species can lead to undesirable consequences such as lowered seed set or increased inbreeding, as seen in some plant species (*16*, *17*). In cases of one-on-one commensal relationships, as found in orchids, extinction risks for the plant partner can be substantial. This is exemplified in sexually deceptive orchid-wasp relationships in the southwest Australian biodiversity hotspot where the first recorded orchid extinction for the region may be a direct result of habitat loss, altered fire regimes (e.g., prescribed spring burning), and/or pollinator loss (*18*). Conservation and restoration of these highly specialized pollinator associations will require detailed knowledge of the ecological requirements for both plants and their pollinators.

Though many factors will influence the capacity of pollinator guilds to become established in restored landscapes, there are continental-scale trends that provide some guidance for restoration practitioners. For example, plants in biodiversity hotspots are more likely to exhibit higher levels of pollinator specialization due to increased competition for pollinator services in species-rich plant communities (*19*), resulting in ecological restoration that may involve specialized, obligate, and potentially unrecoverable pollinator associations. In the case of Southern Hemisphere continents, nonspecialist-to-specialist vertebrate pollination occurs along a continental gradient from east to west (*20*). Thus, in southwest Australia, which has the highest recorded incidence of bird pollination, 15% of plant species are pollinated by birds that exhibit generalist foraging strategies (*21*). In contrast, some tropical South American hummingbirds exhibit a high level of coadapted dependency on particular plant species (*20*), placing these relationships at greater risk. Thus, undertaking restoration in a South American context is likely to involve more plant species where specialized vertebrate pollinator commensalisms and mutualisms need to be considered and factored in than for southern Australian ecosystem restoration.

A key component in facilitation of pollinator activity in restoration is proximity to natural landscapes that support pollinator communities (*22*).

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However, with habitat fragmentation rife in most of the world's ecosystems, ecological linkages may not adequately support pollinator migration to restored sites. Here, pollinator facilitation through intervention management may be required and involve establishment of corridors of pollinator-friendly plant species (*23*), including use of framework species (species that provide a major nectar or pollen source), bridging species (plants that provide resources over resource-limited times), and magnet species (*24*) (plants with attractive flowers associated with species with unattractive or small flowers). For example, in agri-environments, optimizing pollinator-friendly blends of plant species has provided improved forage opportunities for pollinators (*25*, *26*), and similar "plant mixes" may enhance pollinator migration, colonization, and persistence in restoration programs. Alternatively, pollinator shifts have enabled replacement of extinct pollinators by extant species. In the case of *Freycinetia aborea* from Hawaii, the extinct bird pollinator was replaced by an introduced bird (*27*), suggesting that pollinator substitution may be an effective tool in restoration where native pollinators are absent. Such action needs to be considered with extreme caution, because introduced pollination surrogates such as honeybees have been implicated in the disruption of natural plant-pollinator mutualisms (*28*). In the event that pollinators fail to arrive in restored landscapes, unproven restoration technologies, such as captive breeding and reintroduction, are a last-resort and potentially costly solution for reinstating pollination capacity.

Ultimately, restoring pollination capability in restored landscapes will rely on research that addresses key information needs based on the following: (i) Understanding pollinator dispersability as a key predicator of natural migration of pollinators into restored landscapes (Fig. 1); (ii) restoring plant species that facilitate and assist pollinator migration across landscapes (identifying plants that operate as framework, bridging, and magnet species for pollinators); and (iii) ensuring that foraging patterns of pollinators optimize plant reproductive outputs (seed quality; heterozygosity).

Pollination research and restoration ecology need to find common ground if we are to avert a global meltdown in pollination capability in natural and restored ecosystems. By including pollination ecological considerations in ecological restoration planning, local abundance of pollinators can be increased and act as source populations to reinforce pollinators in nearby natural areas with potential pollination spin-offs for adjacent agri-environments (*2*).

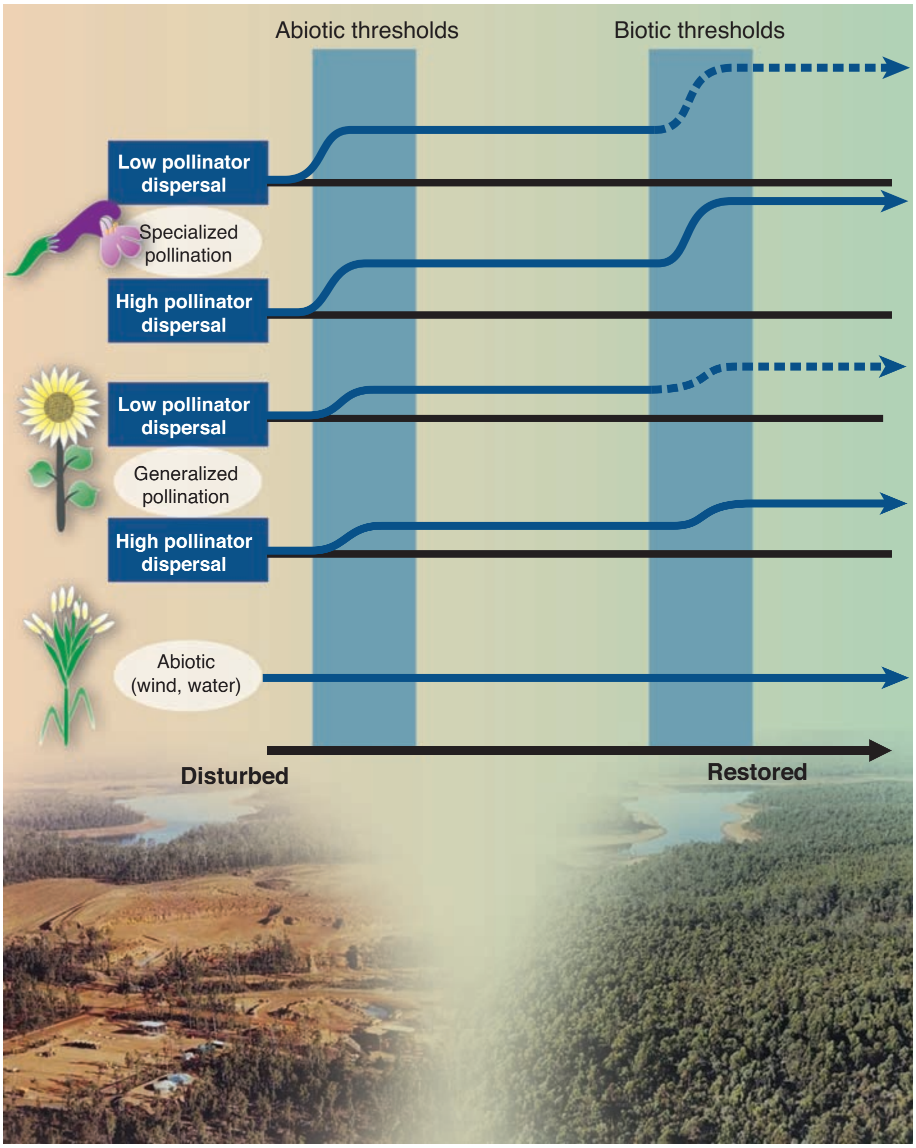

Fig. 1. Generalized models for restoration trajectories of pollination services where degree of pollinator specialization by plants when linked to natural dispersability of pollinators influences the capacity and complexity to achieve pollinator reinstatement. Achieving restoration outcomes will depend on establishing abiotic (soil, hydrology, topography) and biotic (living organisms necessary to maintain an ecosystem) thresholds, with level of technical difficulty represented by the relative height of each lift—the greater the lift, the greater the technical difficulty to achieve the outcome. Dashed lines indicate a very high degree of technological intervention or difficulty (captive breeding, translocation) to restore natural pollinators. (Photos) Postmining ecological restoration in the biodiversity hotspot of Western Australia, showing a bauxite extraction pit in jarrah forest (left) and restoration of the same area (right). [Photos: Alcoa World Alumina]

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PERSPECTIVE

Soil Microbial Communities and Restoration Ecology: Facilitators or Followers?

Jim Harris

Microorganisms have critical roles in the functioning of soil in nutrient cycling, structural formation, and plant interactions, both positive and negative. These roles are important in reestablishing function and biodiversity in ecosystem restoration. Measurement of the community indicates the status of the system in relation to restoration targets and the effectiveness of management interventions, and manipulation of the community shows promise in the enhancement of the rate of recovery of degraded systems.

Soil microbes ranging from free-living bacteria to single fungi covering several square kilometers are a vastly diverse group in terms of taxonomy, structure, and function. We know the biology of few species directly because most soil microbes are currently impossible to cultivate (less than 1% grow readily on agar plates), and we instead rely on indirect means of analyses, principally biochemical markers, and measurements of the whole, or selected parts, of the communities' metabolic activities. Does the soil microbial community merely reflect what is happening in the rest of the ecosystem, or could it be a key player in facilitating restoration objectives? We do know that microorganisms are essential to soil function, particularly in organic matter decomposition and nutrient cycling, and therefore in regulating plant productivity and community dynamics (*1*, *2*) and in soil structural generation (*3*). Hence, their study could be an essential part of any program aimed at the restoration of an ecosystem. However, soil microbes have only recently become a focus for restoration ecology, and research on the interactions between microorganisms and plants in both undisturbed and degraded ecosystems has begun to yield interesting results (*4*).

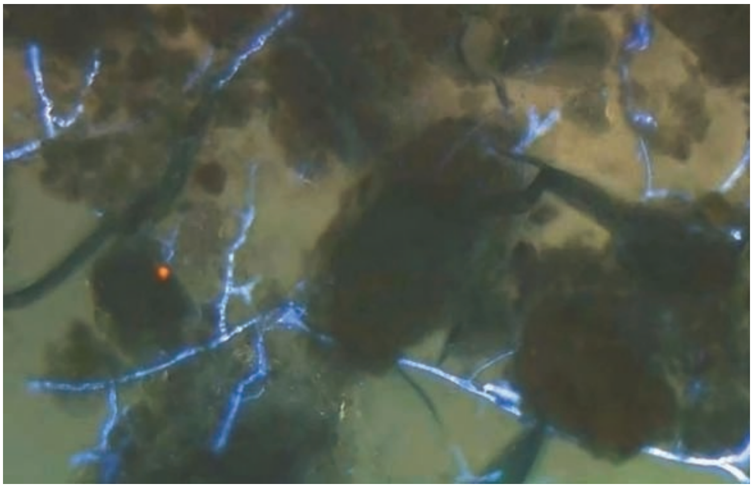

Fig. 1. Fungal hyphae ramify through soil, enmeshing and binding soil particles tighter so as to stabilize structure, accelerate decomposition, and affect plant diversity. [Image courtesy of K. Ritz, National Soil Resources Institute, Cranfield University]

Recently, microbes have been investigated in two ways in relation to restoration: first to indicate the state of the ecosystem in reference to "target" sites or conditions, and second as a system component to be manipulated so as to enhance the speed with which the system can be moved along to the desired state by overcoming "biotic barriers," either the absence of desirable components (such as mutualists) or the presence of undesirables (such as invasive plants) (*5*). We can distinguish between studies carried out on restoration sites to elucidate mechanisms and those on "natural" sites, which have implications for restoration practice. Sometimes the division between the two is not clear cut; how might we classify an investigation in which the site of interest is field-abandoned for many years and now being "restored" to species-rich grassland? Restoration purists may regard this as reversing the wrong way down a successional gradient, away from a climax endpoint of mature forest in temperate ecosystems (of, for example, northern Europe), but the restoration of species-rich grassland is a common target for many conservation bodies.

There has been a long history of using analysis of the soil microbial community to indicate the condition of soil-based ecosystems. Work in this area provides clear evidence that as intensive use of sites is deliberately decreased in order to achieve a more natural state, there is an increase in the ratio of fungal to bacterial biomass (*6*) as more-complex organic material enters the soil matrix in these systems and physical perturbations decrease. The ratio increases further with scrub and forest development, which is consistent with the observation of a shift of resource and energy flows from root to fungal "energy channels" (*7*) as systems move from early to later successional stages. This work suggests that the microbial community "follows" and is dependent on what is going on in the above-ground community and can indicate the impact of restoration-management practices (*8*).

More difficult to assess is the role the microbial community plays in facilitating the establishment of plant communities at various successional stages and the possibilities for manipulation of the soil microbial community to "enhance" the rate at which a mature, stable ecosystem is established. In recent years, there has been an increasing focus on restoring ecosystem function, with associated flows of ecosystem goods and services, rather than "putting things back the way they were"—particularly in regard to shifting of species ranges caused by climate change and local extinction of key species. We are attempting to hit a moving target in this rapidly changing biophysical environment: Species assemblages that would have been found at a particular geographical location in the past may be impossible to reestablish under a changed climatic regime

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