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The role of plant-animal mutualisms in the design and restoration of natural communities

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Introduction

The restoration of native plant communities can be approached from the perspective of many different disciplines. Scientists are interested in testing ideas about community organization and structure, and patterns of succession in manipulated systems. Landscape architects are interested in adding ecological principles into design, to extend their options and 'palette' of plants for different sites. Land managers need to develop methods to more easily sustain natural communities for many public uses. Public officials want more area for recreation and amenity. Developers are interested in buffers between construction projects and neighbouring areas.

Although the focus and interest of each group differs, the need for effective and efficient protocols for planting remains the same. Effective protocols will give us communities that will be sustainable, with minimal human intervention and management. Efficient protocols will minimize the expenditure of funds, so often from hard-pressed government sources, while maximizing the number of plants, and the area covered. In these ways the *economics* of restoration ecology cannot be separated from the other, ecological design limitations that a restorationist always must consider.

What can the restoration ecologist offer to maximize extent and complexity in a project, while keeping costs down to satisfy economic concerns? I would like to explore how a focus on the principles of plant-animal mutualisms can improve both the demographic functioning of an ecological restoration, and also the economic balance sheet that is integral to projects aimed at improving our natural areas. Can research into these mutualisms facilitate improvement in both these areas of concern?

Mutualisms in ecological theory

In many natural communities the co-occurrence of certain species is not associated with a competition for resources, or a battle for an ecological advantage, but with a benefit to both parties. Living together improves the performance of both, yielding, for example, a higher rate of population growth and the ability to spread more quickly into the habitat. Sometimes the association is an *obligate* mutualism; each species requires the other at a critical stage of the life history for survival. Sometimes the association is *facultative*, causing an enhanced performance when both are present, but persistence is still possible when one partner deserts or never finds the other. Theoretical consequences and predictions deriving from these simple concepts are under active investigation (Boucher, James, & Keeler 1982; Boucher 1985; Price 1991). Both types of mutualisms can occur in a restored community, and will affect the fate of many species.

The demographic principle that operates when two species are mutualists is a simple modification of the logistic growth equation, where the presence of one species increases the numbers of the other. In this way the two populations increase their respective sizes when co-occurring, although there are obvious constraints to ever-increasing populations (May 1981).

Attention to the requirements of mutualisms and their protocols would increase the probability of them becoming established. These positive interactions must receive comparable attention to negative plant-animal interactions, particularly herbivory, that are a regular concern of restoration biologists.

Pollination mutualisms and restoration

Ecological symmetry at the project site

The addition of a plant species to a restoration plan does not guarantee that pollinators will be attracted in numbers or types adequate to ensure abundant seed set. Seed set can be low or absent if the pollinators are not present and spread of the plants in numbers and in space may fail. Even if the precise pollinator guild is not known for all the plant species in a restoration, important groups of pollinators can usually be determined by the floral syndrome, or suite of characters, that is associated with major classes of floral visitors (Barth, 1985; Howe & Westley, 1988; Proctor, Yeo, & Lack 1996). For example, some plant species have generalized, open, radially symmetrical flower shapes, and can be successfully pollinated by

many different insects. Other plants have an intricate zygomorphic floral shape, restricting the spectrum of pollinators that is attracted to the plant and can deliver pollen.

A successful restoration must ensure that there is a match between the installed plant species and the habitat's pollination guild. The guild will develop through time, of course, and the project must focus on two problems: do the existing pollinators visiting the plants in the first few years produce seed; and what is the probability that the developing guild will be similar to the pollinators typical of the target plant community on undisturbed sites? For example, many early spring flowering herbs in temperate North America require queen bumble-bees (*Bombus* spp.), often the only large insect flying on the chilly days, for pollination. Other spring plants require visits by solitary bees (Andrenidae) for pollination. Later in the warming spring other plants have floral traits that attract migrating hummingbirds. Consequently, characteristics of the physical habitat of the restoration must be appropriate for these required mutualists, as well as for the plants. If the plants need these unusual mutualists, but they are unavailable, the species is unlikely to survive.

Several ecological factors can be identified as acting on the expression of this mutualism. For example, although bumble-bees are relatively wide-ranging and will visit many species of flowers, they have a series of behavioural requirements. Queens make new nests in existing holes in the ground, such as those made by rodents or rotting wood (Wilson 1971). Early in the spring only these nest-founding queens are flying and pollinating. New workers are produced later, and will take over the pollination role as their numbers increase. Consequently, a restoration of spring woodland plants might be pollinator-limited if isolated from land where bumble-bee colonies are not quickly founded.

Scientific attention to foraging insects searching for flowers has been concentrated on species of *Apis*, honey-bees (e.g., Waddington 1983; Seeley 1985; Gould & Gould 1988), and of *Bombus*, bumble-bees (Heinrich 1979), the most conspicuous but certainly not most typical temperate pollinators. Data on smaller bees are available, but they are much less studied (Richards 1978; Buchmann & Nabhan 1996; Proctor, Yeo, & Lack 1996). The large social bees, wide-ranging and active over most of the growing season, are not useful mutualists for all members of an installed plant community. These bees choose among available plants, and are sensitive to the requirement for a positive energy balance during their foraging flights. They will disregard smaller, less rewarding flowers with which no mutualism can be established.

The larger bees do, however, forage over quite long distances for nectar. Honey-bees have been shown to forage over 8 km from the hive (Visser & Seeley 1982), suggesting that a restored plant community could be visited by distant workers, if these plants compete favourably as energetic rewards with other stands nearer to the nest.

Similarly, bumble-bees can travel long distances (Heinrich 1979; Thomson, Maddison, & Plowright 1982). Some bumble-bees, for example, have been tracked foraging many kilometres from their nest, sequentially visiting ('trapping') nectar producers. However, these bees do not communicate nectar locations to their sisters so that plant populations close to the nest are likely to be visited by many workers. Restoration projects using spring flowers (such as *Dicentra* species), that require visits by queen bumble-bees, must be near nests for any chance of pollination. The numbers of overwintering queens is fewer than the number of new workers that are produced and forage later in the growing season. Consequently, the relative efficiency of pollination by bumble-bees will vary over a season, with more workers being present for late flowering species.

Smaller bee species from families such as Andrenidae and Halictidae are virtually unavailable from commercial sources, and natural invasion of these pollinators to the restoration site might take many years, and be difficult to guarantee. Only a few, apparently hymenopteran vagabonds or fugitive species such as *Halictus ligatus*, regularly enter newly restored areas at an early stage (Reed 1995). Since these bees probably forage over very restricted areas (Buchmann & Nabhan 1996), adding small patches of artificial habitats for some important bee pollinators may be possible, to induce these species to come into the area (Figure 7.1).

Most solitary bee species apparently have a patchy distribution across the landscape, and cannot be relied upon to appear on a restoration site until several years have passed, as a result of chance invasion from the scattered bee populations. The element of chance is high, and study of restored prairies in North America (Reed 1995) shows very different bee faunas in nearby patches (Table 7.1).

Adding a plant population to a restoration site can be considered in a similar way to recovery after a disturbance. The chance that a pollinator will reinvade a disturbance area unassisted is a function of the favourableness of the new habitat and the pollinator's dispersal behaviour, again poorly known for many species. For one highly specialized, obligate pollinator, the agaonid wasp pollinating the fig, *Ficus aurea*, population levels reached near equilibrium levels only months after a major hurricane disturbance (Bronstein & Hossaert-McKey 1995). However, too few

Table 7.1. Distribution of bee species on eight native and restored prairies in the northern United States (from Reed 1995)

On each site there were bee species found at no other site.

Distribution	Number of bee species
Total bee species found in study	298
Only found on prairie remnants	83
Only found on restored prairies	73
Found on both remnants and restored prairies	129
Found only on one site	121
Found on all eight sites	6



Figure 7.1. Creation of open, sandy soil plots can be used to speed the introduction of ground-nesting pollinators to newly restored sites, especially to areas which have highly engineered soils (Yurlina & Handel in preparation).

studies with insect pollinators and disturbance patterns have been reported to make generalizations. Some bees, such as the well-studied tropical euglossines (Dressler 1968; Janzen 1971; Williams 1982) can travel over many kilometres, but the dispersal behaviour of most small bees remains to be uncovered.

The introduction of plants known to require pollinators of low occurrence is undesirable during early stages of restoration. There will even be

cases where local extinction of the original pollinator guild precludes the mutualisms from ever being re-established. Plants without access to essential mutualists have been called the 'living dead', meaning that their future reproduction is impossible. It is pointless to insist on keeping such species in a restoration scheme, when ecological function is the goal!

The foraging behaviour of these solitary bee species is also poorly known (Eickwort & Ginsberg, 1980), though we do know that they behave quite differently from the larger, social genera. For example, *Ceratina calcarata* flies at the edges of wildflower stands, and visits fewer blossoms than a typical honey-bee which has just left its hive (Ginsberg 1984). Study of a new *Brassica campestris* population planted in different densities and arrays showed that flowers were only visited by solitary bee species, even when in dense (plants at 20 cm spacing) arrays. Indeed, it was notable that no honey bees visited these new populations of plants, even though several large hives were within 50 metres of the planting; the nectar reward of the plants was too low to be used by the honey-bees (Handel 1985).

Plant populations, community structure, and pollination

The interplay between number of available pollinators and number of nectar-rewarding plants must be addressed in determining the scale of a local restoration. When number of pollinators is relatively low compared with the number of flowers, many flowers fail to set seed. When there are too many pollinators compared with flower number, the insects cannot receive adequate rewards, and they move to other resources or their numbers decline.

For the restorationist, a large population of flowers may yield few seeds when pollinators are sparse, or if the local pollinator guild is inappropriate for the plant species that have been introduced. A small population of a plant may be ignored if the pollinators have the floral equivalent of 'greener pastures' elsewhere. For example, studies of *Viscaria vulgaris* and *Dianthus deltoides* in Europe have shown that larger populations receive significantly more visits and seed set than smaller or fragmented stands (Jennersten 1988; Jennersten & Nilsson 1993). Similarly, in Argentina, fragmented forest stands suffered decreases in pollination success (Aizen & Feinsinger 1994). Very small plant populations may have different breeding systems and genetic structures than is typical of larger populations (Falk & Holsinger 1991; Washitani 1996). In this way, lower seed set is only the most overt effect of pollinator loss. The higher seed set in large stands may be due to more visits or to more pollen being deposited at each visit; these

two components of plant reproductive success are related in a complex way.

The nature of the balance between insect and plant numbers that optimizes reproduction is poorly known, but a cautious restoration should avoid extremely large or small stands of single plant species. Certainly the members and proportions of taxa in the pollination guild will change as the number of rewarding plants increases and as the insects colonize the area (e.g., Conner & Neumier 1995). Clusters that resemble local natural population sizes and distribution patterns seem likely to be the most effective initial restoration plan. However, if a longer time period can be tolerated before the target of seed reproduction is reached, this design criterion can be relaxed, since, given time, pollinators should colonize all but the most isolated patches. This is an area where careful monitoring of reproductive success (such as proportion of flowers that set seed, or number of plants which produce any seed) at comparable restorations would provide valuable information. If time is available, preliminary plantings before the main installation may be useful to indicate whether appropriate pollinators are in the area.

To sustain any plant population, reproduction is necessary to replace the inevitable deaths. Any steps that increase natural regeneration and make a long-term replanting programme unnecessary are obviously desirable.

The microsite placement of a plant may also affect its attractiveness to pollinators. Many insects are restricted to narrow portions of larger landscapes. For example, geometrid moths prefer the cover of woods, and only forage at the edge of fields, while noctuid moths range more broadly into the open (Morse & Fritz 1983). Milkweeds (*Asclepias* spp.) in the field have different lepidopteran pollinator guilds because of this microsite preference (Morse & Fritz 1983).

In shady forests growing on formerly disturbed land, there is interest in restoring wildflowers (Kubikova 1993-4; Francis & Morton 1995). There is a sharp difference in the temperature regimes experienced by plants in sunflecks, and plants under continual shade. Although woodland herbs are able to photosynthesize and persist in shady sites, seed production is often confined to sunnier microsites. One reason is that flowers in the sunny microsites have several-fold more visits by pollinators (Figure 7.2). Installation of wildflowers in a woodland restoration must concentrate on these microsites, not follow a regular grid on the land, as in most ornamental plantings, if seed set and population spread is an immediate goal of the restoration.

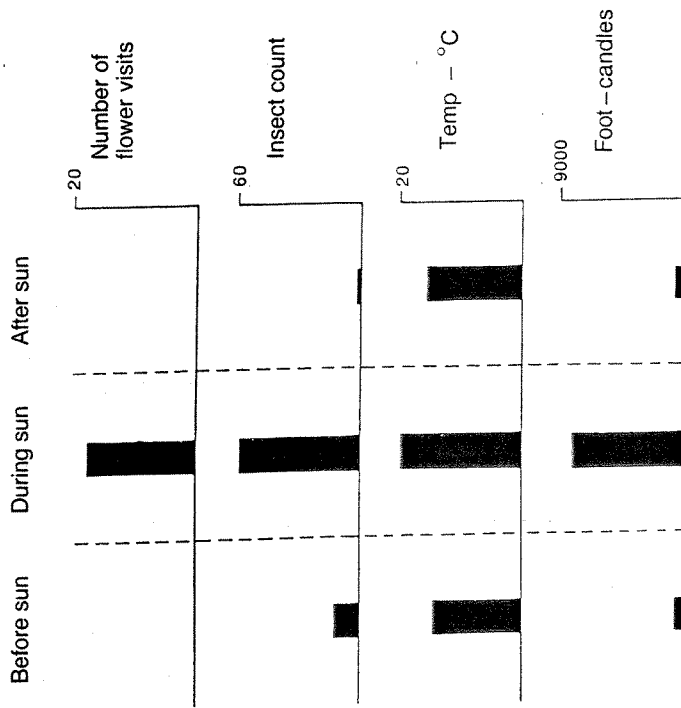


Figure 7.2. Woodland pollinators often prefer to forage in sun flecks. Beattie (1971) showed that the number of flower visits and illumination from ephemeral flecks were highly correlated. Microhabitat will strongly influence pollination success for woodland herbs.

Finally, there is a community interplay in pollination ecology that will effect the reproductive performance of the stand. Many more pollinators sample the components of the plant community than visit the most energetically rewarding species (Dafni 1992). This process may have helped drive the temporal distribution of flowering that we see in many communities (Kochmer & Handel 1986; Rathcke 1988). Potential competition for pollinators can be relieved in a restoration plan by constructing communities, as far as is possible, of sequentially flowering species. Bronstein (1995) has developed a framework for thinking about the temporal match between pollinators and their food plants, and how this relationship affects successful reproduction (Table 7.2). Flowering times can be obtained from many local floras, or be recorded in model communities that the restorationist wishes to imitate.

Table 7.2. Pollinator/plant 'landscapes' that influence the effectiveness of the mutualism, and their consequences (from Bronstein 1995)

1. Highly specialized pollinators and synchronously flowering plants. Rare, a mismatch in timing is very costly.
2. Highly specialized pollinators and asynchronously flowering plants. More common, less of a chance for failure.
3. Relatively generalist pollinators and synchronously flowering plants. Most common, especially in temperate interactions.
4. Relatively generalist pollinators and asynchronously flowering plants. Mobility of the visitors can persist, allowing continuation of the mutualism.
5. Generalist pollinators that may migrate. Visitors may be able to use geographic gradients in flowering time, allowing persistence of mutualisms across this range.

Sequential flowering may maximize seed set among plant species, and also enhance populations of generalist pollinators in the area. In situations where the local pollinator guild is poorly known, planning for sequential flowering will be a prudent course, increasing the probability that some fraction of the plant community can be visited by the local pollinators. This has a positive feedback on the next year's probability of pollination success, in a similar way that the flower species themselves can act as 'sequential mutualists', increasing the overall success to each component (Waser & Real 1979). In this way a longer-term season of flowering in the plant community, appealing to many on aesthetic grounds, can also be ecologically important.

Seed dispersal mutualisms and restoration

Seed dispersers as facilitators in restoration

Seed production has many important functions in plant communities, for example expanding existing populations, starting new ones, usually introducing new genotypes into the population, allowing perennation during stressful periods (Fenner 1992), and many of these functions are necessary components of a successful restoration. Although it would be possible to continue to add seeds to aid in the maturation of a project, taking advantage of natural dispersers to spread seed is like having a free assistant whose work schedule can span many years (Harmer & Kerr 1995). The seed-dispersers' activity and behaviour may eventually make them the primary 'landscape architects' of the site, in the sense that their actions determine which species of plants predominate on the site, and how they are distributed. How can one facilitate this activity, and what will be its impact?

Seed dispersal by animals is generally a diffuse mutualism, and there are few known examples where only one animal species is the sole agent for a plant species. In contrast, there are many cases of pollination mutualism where an animal specializes on one or several closely related plant species (Proctor, Yeo, & Lack 1996). This functional difference has been explained in several ways, focusing on the necessity of pollen to reach a very specific and small-scale location (a conspecific stigma) in the habitat, while a deposited seed has potentially much broader favourable destinations, usually away from another individual of the same species (Wheelwright and Orians 1982).

The kinds of animals that act as seed dispersers have long been studied, and offer wonderful stores of natural history, as well as windows into ecological function (e.g., Sernander 1927; Ridley 1930; Howe & Smallwood 1982; van der Pijl 1982; Fenner 1992). Some animal dispersal syndromes such as passive dispersal by adhesion to fur and feathers (Sorensen 1986) are not true mutualisms. Many others can be classified as mutualism as the diaspore includes a reward for the disperser. This often takes the form of energy-rich tissue surrounding the seed or seed cluster. Birds, bats, and other mammals, reptiles, and even fish participate in these mutualisms in various habitats, but invertebrates, especially ants, also play a major role in dispersal in some areas, including temperate woodland forests and the sterile soil shrublands of Australia and South Africa (Beattie 1985; Huxley & Cutler 1991).

Each animal involved in a mutualism has its own foraging and dispersal behaviour which, combined with its social structure, moulds the quality of its role as a mutualist (e.g. Pratt & Stiles 1983; Herrera 1984; Levey 1986). Distance of seed dispersal, microhabitats where seeds are most often deposited, clustering of seeds, and proportion of seeds that survive the dispersal event are all parameters that the ecologist can measure (Murray 1986; Jordano 1992). Long-distance dispersal has received much attention for its dramatic and important role in initiation of plant communities on distant islands (Carlquist 1974), but it is the mundane, more local dispersal that is of relevance to those who restore sites embedded in a matrix of terrestrial habitats.

Shape of the seed shadow

In restoring degraded landscapes, two aspects of seed dispersal will contribute to future plant community patterns. The first aspect is the removal and deposition of seeds from the plants that we introduce. This

activity increases population size and local range, and begins the slow development of an age-distribution and genetic structure in the restored population that is typical for the species. We may want to accelerate this process by installing plants that will produce seeds quickly during the restoration process. Rapid spread of progeny from installed plants can take advantage of a relatively open substrate, before ground cover clogs microsites needed for seedling emergence.

The second aspect is the transport of seeds onto the site from surrounding vegetation. This process has the potential to add new species to the community, and thus commence the demographic changes mentioned for installed plants. This process is a two-edged sword. On the one hand, species and genotypes that are typical of native communities of the area are added including those which may not be available from the nurseries used to supply the restoration. In this way the local biodiversity can increase incrementally, and ecological 'communication' between the project and its landscape matrix can begin (Handel, Robinson, & Beattie 1994). On the other hand, unwanted species may invade. Often plants of alien origin sweep through restorations, using the sites which one has reserved for native species (Drake, *et al.* 1989; di Castro, Hansen, & Debussche 1988). If the goal is to mimic native stands, these plants must be removed by management of the restoration until the threat of invasion is curbed. A constant, low-level management may be needed if the surroundings have large populations of the unwanted plants.

Some installed plants will not require mutualists for dispersal (most gymnosperms, wind-dispersed angiosperms) because they spread in response to the vagaries of wind speed and direction. Others have passively dispersed seeds (by adhesion, for example) and need sympatric animal populations for seed movement. Lack of true mutualisms does not negate the importance of plant-animal interplay for these species. The shape of seed shadows for these species has been explored in many systems, using techniques ranging from mathematical simulations to ingenious field manipulations (e.g., Bullock & Primack 1977; Greene & Johnson 1989; Okubo & Levin 1989).

For plants requiring mutualisms for dispersal, animal behaviour becomes critical in understanding the pace of the population spread. Different birds, for example, have idiosyncratic foraging and flight behaviours (Wegner & Merriam 1979; Howe and Westley 1988; Abrahamson 1989). Deposition of seed will not necessarily decline with increasing distance from the source plant, but may peak at particular locations where the birds nest or perch (Stiles 1989; Izhaki Walton, & Safreil 1991) (Figure 7.3).

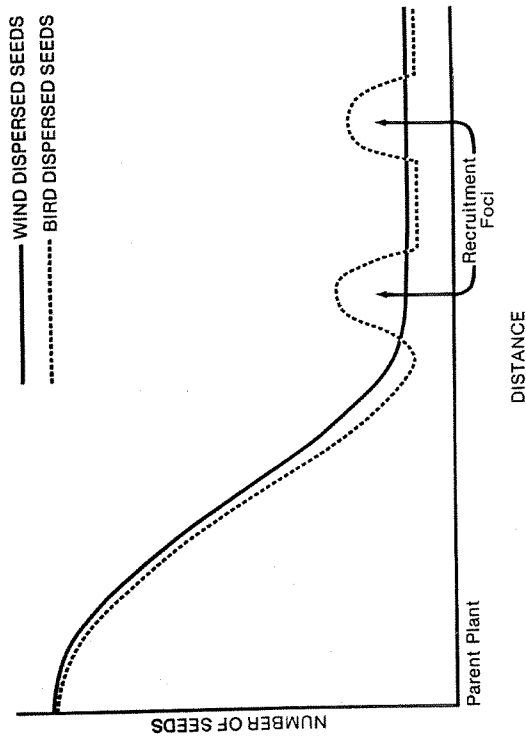


Figure 7.3. Animal dispersal behaviour influences the pattern of seed deposition from a plant source. Recruitment foci, often tree perches in open areas, can be quite different from wind-dispersed systems (from Stiles 1989).

Much seed deposition, by regurgitation or defecation, is remarkably close to the parent plant (Willson 1993). Chemicals encouraging the fast passage of seed through the gut are common in the fruits of bird-dispersed species and are of obvious advantage to the plant (Levey 1986). For example, Hoppes (1988) surveyed a variety of native temperate species, and produced data showing that most deposition was within 10–15 m of the source plant (Figure 7.4). Whether seeds travel from the edge of a site or from plants installed on the body of a site, knowledge of the seed shadow patterns allow the designer to estimate the possible location of seedlings in the next plant generation.

Once deposited on the ground, new seed becomes the object of many additional ecological forces. Seeds are often dispersed again, for example by small rodents who tear through animal droppings for seeds or find wind-dispersed seeds, and cache them elsewhere (Janzen 1983; Vander Wall 1992). This interaction may lengthen the tail of the seed shadow and cause clustering of seedlings. Many factors can then limit the number of seedlings, such as herbivory at the young stages, competition from other established plants, and attack by pathogens (Silvertown & Lovett-Doust 1993). Although the dispersal phase is critical and may be a limiting factor

on a newly restored site, dispersal is only the first ecological hurdle in the contest for a mature plant community. Other mutualists may play their part during these later stages, such as ants protecting plants against herbivores in return for the rewards of extra-floral nectaries (Abrahamson 1989; Koptur 1992). These numerous ecological strands make the whole cloth of restoration, but it is my purpose to emphasize only the interactions in the earliest stages, as this is where the most planning is required.

Factors effecting the pattern of dispersal

Given an empty site availability for restoration, what can be done to increase the probability of many seed dispersers visiting the site, and thus increase seed deposition? Again, as more is learned about the behavioural requirements of the animals, we can modify the planting regime to exploit certain preferences. One successful approach has been to increase the amount of perching space for visiting birds. Birds do not move across and rest on random locations in a habitat, but search out areas most favourable for food, shelter, and protection from their enemies (Smith 1975).

Addition of perches in an open field has been shown to highly increase the number of seeds deposited on that site (McDonnell & Stiles 1983; McClanahan & Wolfe 1993). When perches are present, apparently they act as lures to focus bird movement onto the site. Where no tall structures are present, few seeds are deposited since those sections of the field are avoided by birds. The threshold height of an attracting structure may be relatively short, only 2 m (McDonnell 1986), similar to the height of many woody plants which are introduced during restorations. Similarly, in natural settings Kollmann & Pirl (1995) found that most seed rain was in mature shrub, not into adjacent grasslands. McDonnell's studies showed that simple structures – they need not even be living plants – could act as efficient attractors. The seeds found in these studies were mostly brought in from surrounding areas. Use of early successional woody plants that have large displays of fruit might maximize the quality of the plant lure for birds, and subsequently increase the number of seed introduced to the site. But even modest fruit displays can lure birds into open areas to feed (Davidar & Morton 1986).

Actual plants have been used in experimental work to show the speed with which new plantings can attract birds carrying seeds of new species into a restoration area (McClanahan & Wolfe 1993; Robinson & Handel 1993). In the latter study, 20 new species were added to a woodland restoration. After only 1 year following their introduction, over 1000

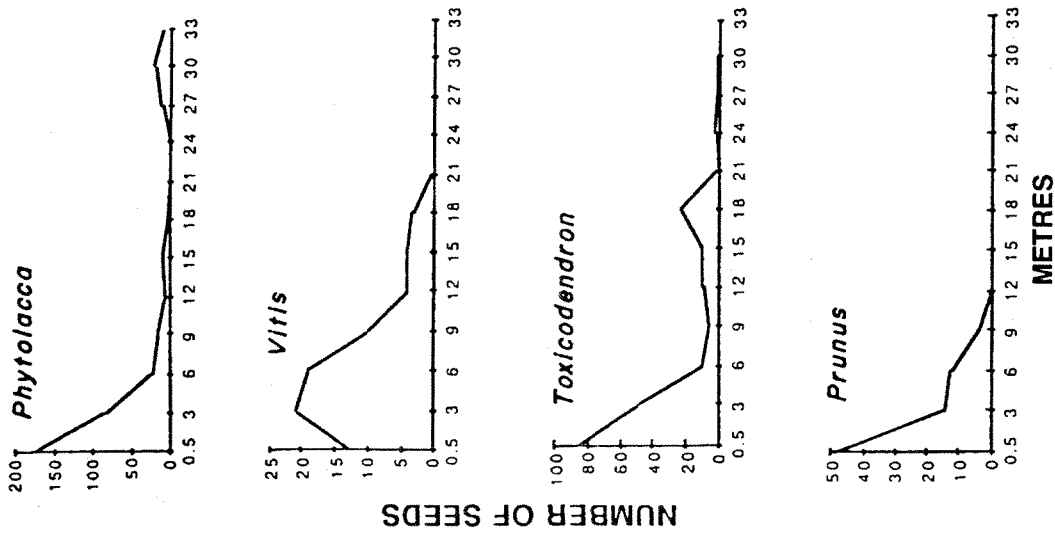


Figure 7.4. Although birds can carry seeds long distances (e.g. Ridley 1930), many seed shadows by frugivores foraging on fleshy-fruited species are quite close to the source plant (from Hoppes 1988).

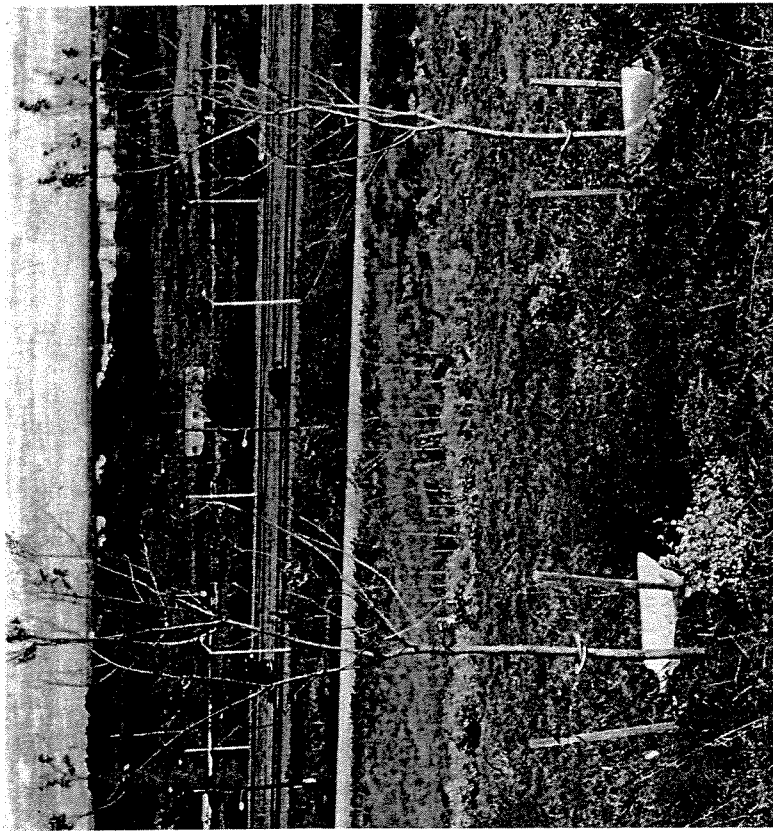


Figure 7.5. Traps placed beneath perching sites (patches of hackberry, *Celtis occidentalis*, in a woodland restoration on an urban hillside), can be used to estimate the speed, quantity, and diversity of seeds brought into a site by frugivores (Mattei & Handel in preparation).

seedlings were found, of which 95% came from surrounding areas. In this particular restoration, only 20% of the installed plants were reproductive. One could predict that, if the fruit display were greater, the number of attracted birds would have been significantly greater.

Spatial pattern of plants across the landscape may also affect bird activity. This is being tested in a large experiment where seven woody species have been installed in four size patches: 7, 21, 42, and 70 plants, representing 1, 3, 6, and 10 individuals of each species. Patch diameter range from 3 to 12 m. Seeds can be transported into the patches from birds living in surrounding forest remnants, mostly on one side of the experimental area. During the first growing season, seed deposition was recorded from traps placed in each patch (Figure 7.5). The amount of seed deposited

Table 7.3. Deposition of seeds beneath clusters of woody plants planted in an open field

Data are averages of 5 replicates of each patch size, from seeds collected August–November, 1994 (Mattei & Handel in preparation).

Patch size (number of plants)	Seeds/patch	Seeds/trap
7	3203	641
21	1996	200
42	4921	328
70	4137	165

was very high, and many new species were found. Although the largest patches received more seed in total the average seed number per trap was highest in the smallest patch (Table 7.3). Apparently small patches still attract many frugivores, and flocks of birds will congregate even on patches of only 7 plants. These data suggest that initial plant dispersion can be high (many small patches), and still facilitate this mutualism. The resultant seed shadows may then fill the whole area more quickly, though more data are needed before detailed recommendations can be made.

These field studies illustrate a concept of using nucleating centres to initiate the successional process on barren restoration sites. Yarranton & Morrison (1974) discussed a similar concept termed 'nucleation', as a model for plant migration into open sites. The general pattern seen is that the initial plantings can attract mutualist dispersers quite rapidly, adding biodiversity and numbers to the site.

Secondary phases of restoration may be necessary, as not all mutualists will visit a sunny, open site. Ant foragers, important for many woodland species, would come into the habitat only later, when soil conditions had developed a structure more amenable for the ant nests. Planting herbs that need ants as dispersers (myrmecochores) must be considered as something which comes later in an effective restoration. When shady conditions have developed, the initial mutualist links will themselves be modified. Many of the frugivorous birds prefer openings and disturbed microhabitats at the edges of woodlands to hunt for fruit (Thompson and Willson 1978; Moore & Willson 1982). The tempo and pattern of mutualist service will change through time, and create the mosaic and complexity that is typical of mature, self-sustaining stands.

A new mutualism

The enticing of mutualists to a site, their activity in developing the stand, and the interplay between the restoration site and the surrounding landscape conditions, all complement each other. This process, once initiated, becomes a low-cost economic engine of ecological change, allowing the land managers to concentrate more of their efforts on routine maintenance and protective measures, instead of on endless, additional plantings. The mutualists, when present, take over much of the fundamental job of species introduction and population expansion.

Ecologists have a valuable role to play working with land development and management experts in identifying areas where ecological impacts of development can be minimized, delineating areas of habitat that must be protected, and determining how much buffer zone is needed between human activities and natural resources that must be sustained. An understanding of the advantages of mutualists in the development of new natural areas, can be important in making restoration economically viable. The ecologists can identify the processes that facilitate community structure and change, and ecological economists, applying these findings, can exploit ecological processes into cost-effective management.

Conclusions

Population growth and community development in a restored habitat requires a variety of plant mutualists. For plant reproduction, pollinator guild composition and pollinator numbers must be adequate for the number and types of flowers introduced during the first stages of the project. Successful pollination will depend on the rates of invasion of the pollinators to the site. Protocols for restoration must include provisions for attracting pollinators, as well as for the habitat requirements of the plant community itself. Plant species that require specialized pollinator species may suffer the greatest limitation of seed set during early stages of the restoration process.

Similarly, increase in local biodiversity and population spread will depend on attracting seed dispersers to the site. Frugivores must have adequate food and resting microsites in the restoration area, which can be manipulated by structural components of the design. Experiments on plant restorations show that bird frugivore movements can be shaped by perches placed in the new habitat, and that birds have non-random movements across the site. Many new plant species can be introduced, over a short

period of time, by attracting seed dispersers. The number of seeds introduced to the site can be orders of magnitude more than seeds produced on site by the new plants themselves. In these ways, attention to the critical role of mutualists can increase the speed and success of a restoration, at no additional cost to the land manager.

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References

- Abrahamson, W. G., ed. (1989). *Plant-Animal Interactions*. New York: McGraw-Hill.
- Aizen, M. A., & Feinsinger, P. (1994). Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology*, 75, 330-51.
- Barth, F. G. (1985). *Insects and Plants: the Biology of a Partnership*. Princeton University Press.
- Beattie, A. J. (1971). Itinerant pollinators in a forest. *Madroño*, 21, 120-4.
- Beattie, A. J. (1985). *The Evolutionary Ecology of Ant-plant Mutualisms*. Cambridge University Press.
- Boucher, D. H., ed. (1985). *The Biology of Mutualism: Ecology and Evolution*. New York: Oxford University Press.
- Boucher, D. H., James, S., & Keeler, K. H. (1982). The ecology of mutualism. *Annual Review of Ecology and Systematics*, 13, 15-47.
- Bronstein, J. L. (1995). The plant-pollinator landscape. In *Mosaic Landscapes and Ecological Processes*, eds. L. Hansson, L. Fahrig, & G. Merriam, pp. 256-88. London: Chapman & Hall.
- Bronstein, J. L. & Hossaert-McKey, M. (1995). Hurricane Andrew and a Florida fig pollination mutualism, resilience of an obligate interaction. *Biotropica*, 27, 373-81.
- Buchmann, S. L. & Nabhan, G. P. (1996). *The Forgotten Pollinators*. Washington, DC: Island Press.
- Bullock, S. H. & Primack, R. B. (1977). Comparative experimental study of seed dispersal on animals. *Ecology*, 58, 681-6.
- Carlquist, S. (1974). *Island Biogeography*. New York: Columbia University Press.
- Conner, J. K. & Neumier, R. (1995). Effects of black mustard population size on the taxonomic composition of pollinators. *Oecologia*, 104, 218-25.

- Dafni, A. (1992). *Pollination Ecology: A Practical Approach*. Oxford University Press.
- Davidar, P. & Morton, E. S. (1986). The relationship between fruit crop sizes and fruit removal rates by birds. *Ecology*, 67, 262-5.
- di Castro, F., Hansen, A. J. & Debussche, M., eds. (1988). *Biological Invasions in Europe and the Mediterranean Basin*. Dordrecht: Kluwer Academic Publishers.
- Drake, J. A., Mooney, H. A., di Castro, F., Groves, R. H., Kruger, F. J., Rejmanek, M. & Williamson, M., eds. (1989). *Biological Invasions: A Global Perspective*. Chichester: John Wiley & Sons.
- Dressler, R. L. (1968). Pollination by euglossine bees. *Evolution*, 22, 202-10.
- Eickwort, G. C. & Ginsberg, H. S. (1980). Foraging and mating behavior of Apoidea. *Annual Review of Entomology*, 25, 421-6.
- Falk, D. A. & Holsinger, K. E., eds. (1991). *Genetics and Conservation of Rare Plants*. New York: Oxford University Press.
- Fenner, M., ed. (1992). *Seeds: The Ecology of Regeneration in Plant Communities*. Wallingford: C-A-B International.
- Francis, J. L. & Morton, A. J. (1995). Restoring the woodland field layer in young plantations and new woodlands. In *Restoration Ecology in Europe*, eds. K. M. Urbanska & K. Grodzinska, pp. 1-13. Zurich: Geobotanical Institute, SFTI.
- Ginsberg, H. S. (1984). Foraging behavior of the bees *Halictus ligatus* (Hymenoptera: Halictidae) and *Ceratina calcarata* (Hymenoptera: Anthophoridae): foraging speed on early-summer composite flowers. *Journal of the New York Entomology Society*, 92, 162-8.
- Gould, J. L. & Gould, C. G. (1988). *The Honey Bee*. New York: Scientific American Library.
- Greene, D. F. & Johnson, E. A. (1989). A model of wind dispersal of winged or plumed seeds. *Ecology*, 70, 339-47.
- Greene, D. F. & Johnson, E. A. (1996). Wind dispersal of seeds from a forest into a clearing. *Ecology*, 77, 595-609.
- Handel, S. N. (1985). Pollen flow and the creation of local genotypic variation. In *Structure and Functioning of Plant Populations. 2. Phenotypic and Genotypic Variation in Plant Populations*, eds. J. Haeck & J. W. Woldendorp, pp. 251-66. Amsterdam: North-Holland Publishing.
- Handel, S. N., Robinson, G. R. & Beattie, A. J. (1994). Biodiversity resources for restoration ecology. *Restoration Ecology*, 2, 230-41.
- Harmer, R. & Kerr, G. (1995). Creating woodlands: to plant trees or not? In *The Ecology of Woodland Creation*, ed. R. Ferris-Kaan, pp. 113-28. Chichester: John Wiley and Sons.
- Heinrich, B. (1979). *Bumblebee Economics*. Cambridge, Massachusetts: Harvard University Press.
- Herrera, C. M. (1984). A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. *Ecological Monographs*, 54, 1-23.
- Hoppes, W. G. (1988). Seedfall pattern of several species of bird-dispersed plants in an Illinois woodland. *Ecology*, 69, 320-9.
- Howe, H. F. & Westley, L. C. (1988). *Ecological Relationships of Plants and Animals*. New York: Oxford University Press.
- Howe, H. F. & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, 13, 201-28.

- Huxley, C. R. & Cutler, D. F., eds. (1991). *Ant-plant Interactions*. Oxford University Press.
- Izhaki, I., Walton, P. B. & Safreil, U. F. (1991). Seed shadows generated by frugivorous birds in an eastern Mediterranean scrub. *Journal of Ecology*, 79, 575-90.
- Janzen, D. H. (1971). Euglossine bees as long-distance pollinators of tropical plants. *Science*, 171, 203-5.
- Janzen, D. H. (1983). Dispersal of seeds by vertebrate guts. In *Coevolution*, eds. D. J. Futuyma & M. Slatkin, pp. 232-62. Sunderland, Massachusetts: Sinauer Associates.
- Jennersten, O. (1988). Pollination in *Dianthus deltoides* (Caryophyllaceae), effects of habitat fragmentation on visitation and seed set. *Conservation Biology*, 2, 359-66.
- Jennersten, O. & Nilsson, S. G. (1993). Insect flower visitation frequency and seed production in relation to patch size of *Viscaria vulgaris* (Caryophyllaceae). *Oikos*, 68, 283-92.
- Jordano, P. (1992). Fruits and frugivory. In *Seeds: The Ecology of Regeneration in Plant Communities*, ed. M. Fenner, pp. 105-56. Wallingford: C-A-B International.
- Kochmer, J. P. & Handel, S. N. (1986). Constraints and competition in the evolution of flowering phenology. *Ecological Monographs*, 56, 303-25.
- Kollmann, J. & Pirl, M. (1995). Spatial patterns of seed rain of fleshy-fruited plants in a scrubland-grassland transition. *Acta Oecologia*, 16, 313-29.
- Koptur, S. (1992). Extrafloral nectary-mediated interactions between insects and plants. In *Insect-Plant Interactions*, ed. E. Bernays, vol. IV, pp. 81-129. Boca Raton: CRC Press.
- Kubikova, J. (1993-1994). Oak-pine afforestation of agricultural land: an attempt to enrich its understory diversity. *Novitates Botanicae Charles University, Prague*, 8, 63-73.
- Levey, D. J. (1986). Methods of seed processing by birds and seed deposition patterns. In *Frugivores and seed dispersal*, eds. A. Estrada & T. H. Fleming, pp. 147-58. Dordrecht: Dr W. Junk.
- May, R. M., ed. (1981). *Theoretical Ecology, Principles and Applications*. 2nd edn. Oxford: Blackwell Scientific Publications.
- McClanahan, T. R. & Wolfe, R. W. (1993). Accelerating forest succession in a fragmented landscape: the role of birds and perches. *Conservation Biology*, 7, 279-88.
- McDonnell, M. J. (1986). Old field vegetation height and the dispersal pattern of bird-disseminated woody plants. *Bulletin of the Torrey Botanical Club*, 113, 6-11.
- McDonnell, M. J. & Stiles, E. W. (1983). The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia*, 56, 109-16.
- Moore, L. A. & Willson, M. F. (1982). The effect of microhabitat, spatial distribution, and display size on dispersal of *Lindera benzoin* by avian frugivores. *Canadian Journal of Botany*, 60, 557-60.
- Morse, D. H. & Fritz, R. S. (1983). Contributions of diurnal and nocturnal insects to the pollination of common milkweed (*Asclepias syriaca* L.) in a pollen limited system. *Oecologia*, 60, 190-7.
- Murray, D. R., ed. (1986). *Seed dispersal*. Sydney: Academic Press.

- Okubo, A. & Levin, S. A. (1989). A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology*, 70, 329-38.
- Pratt, T. K. & Stiles, E. W. (1983). How long fruit-eating birds stay in the plants where they feed, implications for seed dispersal. *American Naturalist*, 122, 789-805.
- Price, P. W., ed. (1991). *Plant-animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*. New York: John Wiley.
- Proctor, M., Yeo, P., & Lack, A. (1996). *The Natural History of Pollination*. Portland, Oregon: Timber Press.
- Rathcke, B. (1988). Flowering phenologies in a shrub community: competition and constraints. *Journal of Ecology*, 76, 975-94.
- Reed, C. C. (1995). Insects surveyed on flowers in native and reconstructed prairies (Minnesota). *Restoration and Management Notes*, 13, 210-13.
- Richards, A. J., ed. (1978). *The Pollination of Flowers by Insects*. London: Academic Press.
- Ridley, H. N. (1930). *The Dispersal of Plants Throughout the World*. Ashford, Kent: Reeve.
- Robinson, G. R. & Handel, S. N. (1993). Forest restoration on a closed landfill: rapid addition of new species by bird dispersal. *Conservation Biology*, 7, 271-8.
- Seeley, T. (1985). *Honey Bee Ecology*. Princeton University Press.
- Sernander, R. (1927). Zur Morphologie und Biologie der Diasporen. Nova Acta Regiae Societatis scientiarum Upsaliensis, vol. extraordinary edition, 1927, pp. 1-104.
- Silvertown, J. & Lovett-Doust, J. (1993). *Introduction to Plant Population Biology*, 3rd edn. London: Blackwell Scientific Publications.
- Smith, A. J. (1975). Invasion and ecesis of bird-disseminated woody plants in a temperate forest ser. *Ecology*, 56, 19-34.
- Sorensen, A. E. (1986). Seed dispersal by adhesion. *Annual Review of Ecology and Systematics*, 17, 443-64.
- Stiles, E. W. (1989). Fruits, seeds, and dispersal agents. In *Plant-animal Interactions*, ed. W. G. Abrahamson, pp. 87-122. New York: McGraw-Hill.
- Thompson, J. N. & M. F. Willson, (1978). Disturbance and the dispersal of fleshy fruits. *Science*, 200, 1161-3.
- Thomson, J. D., Maddison, W. P., & Plowright, R. C. (1982). Behavior of bumble bee pollinators of *Aralia hispida* Vent. (Araliaceae). *Oecologia*, 54, 326-36.
- van der Pijl, L. (1982). *Principles of Dispersal in Higher Plants*. 3rd edn. New York: Springer-Verlag.
- Van der Wall, S. B. (1992). The role of animals in dispersing a "wind-dispersed" pine. *Ecology*, 73, 614-21.
- Visser, P. K. & Seeley, T. D. (1982). Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology*, 63, 1790-801.
- Waddington, K. D. (1983). Foraging behavior of pollinators. In *Pollination Biology*, ed. L. Real, pp. 213-39. Orlando: Academic Press.
- Waser, N. M. & Real, L. A. (1979). Effective mutualism between sequentially flowering plant species. *Nature*, 281, 670-2.
- Washitani, I. (1996). Predicted genetic consequences of strong fertility selection due to pollinator loss in an isolated population of *Primula sieboldii*. *Conservation Biology*, 10, 59-64.

- Wegner, J. F. & Merriam, G. (1979). Movement by birds and small mammals between a wood and adjoining farmland habitats. *Journal of Applied Ecology*, 16, 349–58.
- Wheelwright, N. T. & Orians, G. H. (1982). Seed dispersal by animals, contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *American Naturalist*, 119, 402–13.
- Williams, N. H. (1982). The biology of orchids and euglossine bees. In *Orchid Biology: Reviews and Perspectives, II*, ed. J. Arditti, pp. 120–71. Ithaca, New York: Cornell University Press.
- Willson, M. F. (1993). Dispersal mode, seed shadows, and colonization patterns. *Vegetatio*, 107/108, 261–80.
- Wilson, E. O. (1971). *The Insect Societies*. Cambridge, MA: Harvard University Press.
- Yarranton, G. A. & Morrison, R. G. (1974). Spatial dynamics of a primary succession: nucleation. *Journal of Ecology*, 62, 417–28.

8

The development of criteria for ecological restoration

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Introduction

It is more than 30 years since attempts were first made to repair the damaged landscapes left as the heavy industry, which had dominated the economies of Europe, began its long decline. Much of this restoration was in the hands of civil engineers and landscape architects, and relied to a considerable extent on agricultural techniques. However, a few pioneering ecologists seized the opportunities which the restoration of this land offered to apply their science to a pressing and challenging problem. Previously the attention of ecologists had been focused on describing the composition, structure, and functioning of what we call natural or semi-natural communities. Communities in which there has been a strong human influence have largely been ignored by ecologists; yet, as Bradshaw (1987) has pointed out, ecological processes still operate in such communities, and the restoration or reconstruction of vegetation to a state comparable with that occurring naturally presents almost the ultimate challenge to ecologists in the application of their science.

The restoration of derelict or degraded land has depended largely upon one area of ecology—that concerned with the identification, description and provision of the habitat for species. By understanding the requirements for nutrition, growth, and reproduction (the autecology) of particular species, considerable success has been achieved in restoration schemes. This approach continues the traditions of plant ecology which, unlike animal ecology, where the emphasis has been on the dynamics of populations and communities, saw the occurrence of species very much in terms of their habitat and, in particular, of their physical and chemical requirements. The success of this approach depended on a sufficient understanding of the habitat requirements of the various species of plant. The damaged or degraded land was altered using agricultural techniques to