

When Seed Dispersal Matters

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A profusion of fruit forms implies that seed dispersal plays a central role in plant ecology, yet the chance that an individual seed will ultimately produce a reproductive adult is low to infinitesimal. Extremely high variance in survival implies that variations in fruit production or transitions from seed to seedling will contribute little to population growth. The key issue is that variance in survival of plant life-history stages, and therefore the importance of dispersal, differs greatly among and within plant communities. In stable communities of a few species of long-lived plants, variances in seed and seedling survival are immense, so seed-to-seedling transitions have little influence on overall population dynamics. However, when seedlings in different circumstances have very different chances of survival—in ecological succession, for example, or when dispersed seeds escape density-dependent mortality near parent trees—the biased survival of dispersed seeds or seedlings in some places rather than others results in pervasive demographic impacts.

Keywords: elasticity analysis, seed dispersal, spatial demography

The profusion of fruit sizes, shapes, colors, and scents, and the variety of rewards for the agents that disperse plant seeds, imply a central role for seed dispersal in plant ecology (figure 1). However, this leaves open the ecological questions of why seed dispersal is important and how understanding it can help predict population and community change. Early studies of dispersal ecology emphasized natural history, asking which animals take such fruits as *Viola* or *Ficus*, or how the winged pods of the legumes *Platypodium* and *Tachigalia* ensure sufficient dispersal by wind. Such questions can still be iterated for tens of thousands of plant species from Cape Horn to the Arctic, but they no longer define the field. The challenge now is to understand such natural-history lore in light of the demographic processes that shape plant populations and communities.

The role of seed dispersal in plant reproduction presents curious contrasts. Despite the evident importance of their dispersal, most seeds fall near their parents. Genetic markers confirm that the vast majority of the offspring of one common European cherry species end up within 10 meters (m) of the tree that produced them, while a minority travel much further. The consequences of seed distributions are therefore important to know. For a highly fecund tree such as the tropical fig *Ficus insipida*, which may produce 5 million seeds per year and hundreds of millions in a lifetime, the likelihood that a seed distribution reflects later stages is all but nil. For the less fecund *Viola nobilis* (Myristicaceae), with 100,000 seeds in a lifetime, the chance that seed distributions reflect distributions of surviving offspring is orders of magnitude greater, but still minuscule.

Processes of survival and mortality determine plant fate in space and time. One way to overcome the challenges of

calculating the effects of dispersal on populations with immense mortality is to calculate the likelihood of transitions among life stages, from seed to seedling, seedling to juvenile, juvenile to sapling, and sapling to adult. Probabilities of transitions allow projections of subsets of populations into the future; variances in those transitions indicate which steps between life stages, under different ecological conditions, contribute most to population growth. In this article, we use a demographic context to explore ways in which varying degrees of dispersal success may or may not influence plant populations. We conclude by discussing the implications of those insights for conservation and management of plant communities.

Demographic pattern and process

Demography enumerates processes of population recruitment and mortality in populations over time. An evolving insight of spatial demography is that patterns of recruitment and mortality in space are enlightening.

Evolving a conceptual framework. Dispersal attributes, which offer insights into the ways in which plant species have

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Figure 1. Bird and bat frugivory, bird hoarding, and wind dispersal syndromes. Top left: Golf ball-sized capsule with the arillate seed of *Virola nobilis*, a toucan-dispersed nutmeg of Central America (Howe 1993). Top right: A fig (*Ficus insipida*) tenaciously held by a fruit bat (*Artibeus jamaicensis*) on Barro Colorado Island (Kalko et al. 1996). Bottom left: Marble-shaped seed of a pinyon pine (*Pinus edulis*), awaiting jays or nutcrackers, which bury seeds in forest openings in mountains of the southwestern United States (Vander Wall 1990). Photographs: Henry F. Howe. Bottom right: Winged seeds of *Platypodium elegans* (left) and *Tachigalia versicolor* (right), wind-dispersed canopy-emergent legumes of Central and South America (Augspurger and Franson 1987). Photograph: Carol K. Augspurger.

adapted the dispersal process, provide the first glimpses into understanding the advantage of seed dispersal for different kinds of plants. In the mature rain forests of Central and South America, the genus *Virola* produces fruits that appear specialized for a few large fruit-eating birds and monkeys, a plant tactic that makes use of large animals that track the ripening of especially favored foods (Howe 1993, Russo 2003). However, a limited set of bird or primate dispersal agents is not an advantage for a tree that colonizes after massive, unpredictable disturbances, such as mudslides. Because no particular animal consistently frequents such places, a generalized strategy of animal or wind dispersal is more advantageous. So, for instance, small fleshy fruits of *Trema* (Ulmaceae) are eaten by many birds of a variety of sizes and behaviors, allowing opportunistic invasion of expanses of exposed earth by thousands of *Trema* saplings when an earthquake drops an entire watershed into the sea (Garwood et al. 1979). Perhaps natural selection even differs in its effects on variation between

the winged fruits of giant *Tachigalia versicolor*, a statuesque “suicide tree” that breeds once and dies, and its relative *Platypodium elegans*, which seeds for many years in the same forest (Foster 1977). *Tachigalia* has a predictable target for its seeds and seedlings under a dying parent, whereas *Platypodium* offspring must occupy new ground in distant light gaps (holes in the forest canopy). For species that colonize nearby unoccupied ground, selection may act less on precision in dispersal ability than on the capacity of parent plants to saturate their environs with offspring.

Quantitative logic. Quantitative thinking introduces different perspectives, relying less on speculation about the adaptive features of fruits and more on the consequences of numerical patterns of survival and mortality (Harper 1977). Demographic matrix projections indicate whether incremental differences in the success with which seeds or young juveniles survive affect overall population growth (Wang and Smith 2002). Estimates of survival, growth, and fecundity at different life-history stages, represented as transition probabilities (a_{ij}), may be used to project future population size and structure. An accounting of the survival of seeds, seedlings, or other stages at different distances from parent trees, or in distinct ecological circumstances of slope, light, or soil type, provides the first step in spatial demography.

The importance of variance in transitions is not as widely recognized and has only rarely been applied to the dispersal process. An important tool is elasticity analysis, which estimates the influence of different life stage transitions on population growth rate. Elasticity is calculated as

$$e_{ij} = \left(\frac{a_{ij}}{\lambda} \right) \left(\frac{\partial \lambda}{\partial a_{ij}} \right)$$

where e_{ij} quantifies the proportional change in the asymptotic population growth rate λ resulting from an infinitesimal proportional change in the matrix transition probabilities, a_{ij} . Elasticities help evaluate the relative importance of particular transitions (e.g., seed to seedling, seedling to older juvenile) for population growth. The greater the variation in a transition probability, the lower the elasticity value and the less likely that such a transition will influence population growth (Pfister 1998). For instance, conservation measures that enhance the adult survival of endangered gopher tortoises (*Gopherus agassizii*) or peregrine falcons (*Falco peregrinus*) are far

more effective than those that increase birth or fledging rates, which have much lower elasticities. Extremely low elasticities are the rule in seed-to-juvenile transitions of long-lived plants. This implies that variations in this transition, or in the seed production that precedes it, have little effect on population dynamics.

Bur sage, *Ambrosia dumosa* (Asteraceae), a long-lived and often dominant shrub of the desert Southwest of North America, illustrates both the power and the limitations of demographic thinking (Miriti et al. 1998, 2001). In Joshua Tree National Park in southern California, these shrubs grow singly or in small clumps separated by unvegetated space (figure 2). Seeds drop off plants and are blown along the ground by wind, accumulating under shrubs and other vegetation. Adult “nurse” plants facilitate seed germination and shelter young seedlings (Franco and Nobel 1989). However, as seedlings grow, they compete with each other and with the former nurse. A switch from facilitation to antagonism occurs within 5 to 10 years, contributing to high variance and low elasticity in the transition from seedling to older juvenile. On average, the seedling-to-juvenile transition contributes almost nothing to overall population growth if one counts only “nursed” seedlings and juveniles under adult shrubs. The transition from old adult (which may live dozens to hundreds of years) to dead adult does affect the population growth rate: When the number of adults that die changes, λ changes. If the number of adults dying does not change, annual variation in fecundity or seedling establishment may vary by orders of magnitude without affecting λ .

Spatial demography, or partitioning recruitment of parts of a cohort in different microhabitats or zones of risk, shows that dispersal away from adult shrubs does matter, even in this saturated community of ancient plants. *Ambrosia dumosa* seedlings that survive the first few years in the open have a better chance of survival and growth than seedlings that establish under the protection of adult nurse shrubs (Miriti et al. 2001). When partitioned by spatial association, neither the dynamics of the nurse plants nor those of the nursed influence λ much; in the course of time, the contributions of initially disadvantaged isolated individuals on λ are greater. In effect, isolation from nurse plants decreases the variance in the transition from seedling to less vulnera-



Figure 2. Colorado Desert of Joshua Tree National Park, California (top). Seed germination and seedling establishment of the dominant shrub bur sage (*Ambrosia dumosa*) are initially favored under adult “nurse” plants of the same or different species. Shown at bottom left is a swarm of *Ambrosia* and other seedlings under an adult shrub; each metal tag is attached to a loop around an individual seedling 5 to 10 centimeters (cm) tall. Some seedlings establish away from living shrubs (bottom right). In this case, a 10-cm yearling *A. dumosa* is growing among the wind-exposed roots of an adult that died decades earlier. Early nurse effects eventually create the clumped distributions of adult shrubs shown here. However, demographic projections partitioned by neighbor proximity show that neither the nurse plants nor the nursed contribute as much to population growth as the unusual isolated individuals that survive the early years and then prosper for centuries without competition from neighbors (Miriti et al. 2001). Photographs: Henry F. Howe.

ble juvenile, thereby increasing the likelihood that differences in mortality of plants at some distance from nurses will influence population growth.

Why seed dispersal matters

Seed dispersal matters if dispersed seedlings (a) escape from density-dependent mortality near parents, (b) colonize open habitats, or (c) find microsites critical for establishment

(Howe and Smallwood 1982). If any of these mechanisms apply, dispersed seedlings are more likely to survive to reproductive age than undispersed seedlings. The advantage to a parent of occupying a new region or continent with its seeds are obvious, but demographic logic suggests that long-distance dispersal may not be the primary advantage to most species most of the time. Subtle but consistent differences in dispersal may bias processes of establishment and survival, conferring a potentially strong advantage to local seed dispersal. Partitioned cohorts in space are likely to show reduced variance in seed-to-seedling or seedling-to-juvenile transitions for subsets of a population, thereby indicating which parts of seed or seedling distribution influence population growth and, ultimately, community composition.

Advantages of local dispersal. Distributions of seeds in space serve as “templates” (Schupp and Fuentes 1995) for whatever population processes follow. A population’s seed template is not a faithful guide to seedling or adult distributions if mortality is density dependent or is influenced by spatially distinct light, soil, or drainage microhabitats. The seed template defines what is possible for seedling recruitment in a given place. To predict what actually happens, studies of dispersal that discover where seeds go can be integrated with spatially partitioned demographic analyses, thereby predicting population trajectories for seeds or seedlings starting in different circumstances. Elasticities then show which transitions among stages influence population growth and, therefore, which transitions yield the best predictions of future population dynamics.

One plausible advantage to seed dispersal is escape from enemies that live near the parent plant or that seek concentrations of seeds or seedlings. Janzen (1970) and Connell (1971) hypothesized that, among tropical trees, seeds or seedlings near the parent plant suffer density-dependent mortality from insects, mammals, or pathogens, while those that are carried away end up at much lower densities and therefore are more likely to survive to adulthood. Widely scattered seeds and seedlings are less likely to be destroyed or infested by enemies than those in clumps.

Dispersal of *V. nobilis* nutmeg trees on Barro Colorado Island in Panama illustrates spatially biased survival for seeds and seedlings (Howe 1993). A monkey (*Ateles geoffroyi*) and a number of small birds, such as motmots (*Baryphthengus martii*) and trogons (*Trogon massena*), eat the fruits (figure 1) and regurgitate or defecate seeds in viable condition, but these species leave most seeds under or near the parent tree. There *Conotrachelus* weevils lay eggs on seeds as they germinate; the larvae kill virtually all seeds and young seedlings. The area in which a seed might fall, or in which a weevil must search, increases as πr^2 with r distance from the trunk. Dispersal agents diffuse the seed distribution in space and thereby maximize the work of seed and seedling enemies. Larger toucans (*Ramphastos swainsonii* and *Ramphastos sulfuratus*) and turkey-sized guans (*Penelope purpurascens*) carry most seeds that they eat beyond the edge of crown, leaving at least

half more than 45 m away, where weevils are much less likely to find them (box 1, figure 3). For instance, a motmot dropping 10 seeds between 5 and 10 m from a *Virola* trunk in a morning of foraging would scatter them over 236 m², also occupied by hundreds of other *Virola* seeds or seedlings under the crown of the parent tree. A toucan dropping 10 seeds 40 to 45 m from the parent plant would scatter them over 133,610 m², more than a 500-fold difference in density. In a forest of loose aggregations of two to five individuals of this tree, most seeds in a band 40 to 45 m away from their parent would be even further from other *Virola* trees. Here seed dispersal matters, as does the identity and behavior of the animals that remove the fruits.

One might ask how cohorts of *Virola* seeds 20 m away from their parents fare compared with seeds or seedlings at much lower densities 100 or 200 m away from trees of the same species. This would distinguish success reflected in the average “recruitment distance” at the intersection of seed rain and seed survival curves from potentially greater success farther away (note that toucans and guans carry most seeds beyond the intersection of the dispersal and survival curves in figure 3). Seeds dispersed far from adult trees on a tail of a long, skewed seed distribution might in fact have the highest chance of survival (Nathan and Muller-Landau 2000). Spatially explicit demographic analysis could confirm or reject speculation, based on estimates of high seedling mortality close to *V. nobilis* trees, that the species is in decline on Barro Colorado Island (Howe 1993). Such an analysis would indicate whether enough very sparsely distributed seedlings, perhaps at 100 or 300 m from parent plants, offset density-dependent loss of seeds and seedlings from weevils.

The *Virola* example suggests other demographic tests that could clarify the forces acting on the dispersal process. The large birds that do most of the work for this tree in Panama favor individual trees that have small seeds and large ratios of edible aril to indigestible seed. The trees must balance powerful selective forces: Small seeds are more likely to be dispersed and therefore to escape almost certain death under their crowns, but large seeds, if they are dispersed, produce large seedlings that are better equipped to establish and survive in the shaded understory. A parent tree cannot maximize both dispersal and establishment by adjusting seed size alone, because a seed cannot be small and large at the same time.

The optimization criteria for dispersal of a tree species may differ in different environments (Forget and Sabatier 1997). For instance, an aril-to-seed ratio that is optimal for *Virola* in Panama might be inappropriate in Peru, where different birds could favor a different balance of pulp reward to seed ballast, or where other dispersal agents could choose fruits on the basis of other criteria. The competitive environment for seed dispersal differs in the two sites; many more primates feed on fruits of trees in the forests of the Peruvian Amazon, and more of these trees are adapted for primate dispersal than in Panama (Janson 1983). Russo (2003) found that birds in Peru, as in Panama, favor *Virola calophylla* fruits with high aril-to-seed ratios. However, these preferences matter little to the

Box 1. Comparison of chestnut-mandibled toucans with other species as dispersal agents of *Virola nobilis* away from weevil infestations under parent trees on Barro Colorado Island, Panama.

As dispersal agents of *Virola nobilis*, chestnut-mandibled toucans (*Ramphastos swainsonii*, body mass 700 grams [g]) are

- 30 times better than smaller rufous motmots (*Baryphthengus martii*, 190 g) or slaty-tailed trogons (*Trogon masseana*, 145 g): 15 times more dispersal per seed carried (toucans carry seeds farther) and twice as many seeds taken (toucans eat more seeds).
- 8 times better than spider monkeys (*Ateles geoffroyi*, up to 9 kilograms [kg]): twice the dispersal per seed carried (toucans do not leave seeds in clumps, monkeys do) and four times as many seeds taken (monkeys knock down more than they carry).
- 4 times better than keel-billed toucans (*Ramphastos sulfuratus*, 400 g): the same dispersal per seed carried, but four times as many seeds taken (keel-bills are smaller and eat fewer seeds per visit).
- 3 times better than crested guans (*Penelope purpurascens*, 1.7 kg): the same dispersal per seed carried, but three times as many seeds taken (toucans are more common).

Data are from Howe (1993).

trees, because almost all the fruits of this species are dispersed by a spider monkey, *Ateles paniscus*, which visits trees with large fruit crops. A challenging but potentially useful demographic analysis might evaluate the actual success of seeds taken by monkeys from large fruiting trees compared with those scattered by birds from all trees in the population.

Comparative studies of dispersal between close relatives indicate that the questions suggested by *Virola* are more than academic. For instance, comparing bird dispersal of the tree *Commiphora* (Burseraceae) in Madagascar and in mainland Africa, Bleher and Bohning-Gaese (2001) find that dispersal for the island species *Commiphora guillaumini* involves far fewer potential frugivores, fewer effective dispersal agents, less seed dispersal, and more spatial aggregation of juveniles around adults (and of the adults themselves) than for the continental species *Commiphora harveyi*. The island tree has larger seeds and a much smaller aril than the mainland species, indicating a strategy of reduced reliance on animals for dispersal. On Madagascar, fewer than 10% of the seeds are dispersed, and the median distance from an adult to the nearest seedling is less than a meter. It costs more seeds to make a seedling on Madagascar, and the chances are that the seedling will be under the parent plant. These contrasts sug-

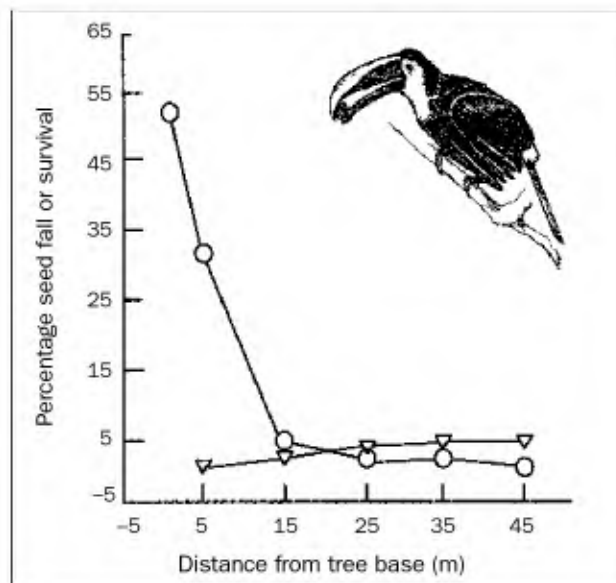


Figure 3. Immediate advantages to dispersal in rain forest on Barro Colorado Island, Panama. *Conotrachelus weevils* oviposit on germinating seeds of *Virola nobilis* under fruiting trees, and the larvae destroy the seed. Seeds carried away from fruiting trees by toucans or guans have a much better chance of survival than those dropped directly underneath the tree by monkeys or smaller birds. The curve for seed distribution (triangles) is the percentage of the total crop of a tree in blocks 10 meters (m) by 10 m; the curve for survival (circles) is the percentage of seedlings from planted seeds alive after 12 weeks. The curves cross an average of 17 m from the tree base. The mean nearest-neighbor distance of these trees in the forest is 18 m (Howe 1993).

gest that there may be adaptive advantages to broad dispersal and recruitment in mainland Africa and to lowered dispersal and perhaps greater allocation to seed defense in the island flora.

The advantage of escape from the parent plant appears to be general. Focal studies of particular tree species and their dispersal show that bird dispersal of a Spanish cherry, *Prunus mahaleb* (Rosaceae), confers an immediate advantage to local seed dispersal (Jordano and Schupp 2000). In North America, bird dispersal of black cherry (*Prunus serotina*) helps seedlings avoid rapid buildup of a pathogenic pseudo-fungus (*Pythium* spp., Kingdom Protocista) that kills seedlings under fruiting trees (Packer and Clay 2000). Community-level analyses decisively confirm the advantages of seed escape (see below); it costs several times more to produce a seedling in dense than in sparse aggregations, and many times more to produce a reproductive adult offspring near the parent plant than farther away. The question is no longer whether the advantage to escape from parents predicted by Janzen (1970) and Connell (1971) exists. The questions are, when and where is the effect important, and what is the relative importance of spatially defined components of seed or seedling

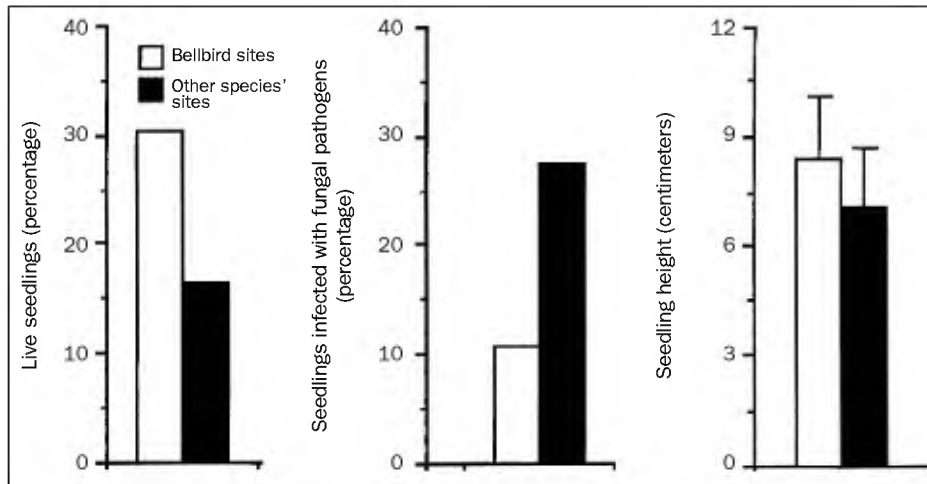


Figure 4. Seedling distributions produced by wattled bellbird foraging and courtship activities, as compared with those produced by four other common visitors to *Ocotea* plants in Costa Rican cloud forest (Wenny and Levey 1998). The error bars in the graph on the right indicate mean plus one standard deviation.

distributions in contributing to population and community structure?

Projections of plant population growth, based on the types of dispersal agents that take the seeds, may provide a window into the future in understanding how different animals bias recruitment of plants. In a dispersal study of the giant cactus *Neobuxbaumia tetezo* in Mexico, Godinez-Alvarez and colleagues (2002) find that a bat (*Leptonycteris curasoae*) is probably the most effective dispersal agent for this species. Compared with other bats, birds, and coyotes (*Canis latrans*), *Leptonycteris* eats many fruits and deposits a large number of seeds under bushes and trees that could serve as nurse plants. Matrix projections suggest higher estimates of λ with bat dispersal than with bird dispersal. Given the mismatch between initial recruitment and survival of *Ambrosia* discussed above (Miriti et al. 2001), a spatial matrix analysis could determine whether projections for seedlings emerging in clumps under bat roosts fare as well as those scattered by different animals under shrubs and cacti.

Seed dispersal has other advantages. Seeds can colonize not only distant sites from which a given species is absent but also vacant sites in the local ecological succession. Once thought to be primarily a means of colonizing distant places, seed dispersal may also be locally important if some species' inability to get to a region or habitat affects community composition (Clark et al. 1998, Terborgh et al. 2002). The advantages of local colonization are real. Open ground is occupied by small-seeded, fast-growing species, followed by successive invasions of larger-seeded trees that are slower to arrive but are capable of establishing under a dense secondary forest canopy. In demographic terms, seed-to-seedling and seedling-to-juvenile elasticities change with the advancing front. For instance, Parker (2000) finds that the seed-to-seedling transition explains almost all population growth at the front of advancing populations of the invasive shrub *Cytisus scoparius*

in California, while adult death explains population change behind the front.

Directed dispersal occurs when an animal preferentially carries seeds directly to situations that are critical for seedling establishment. Examples include bird dispersal of parasitic mistletoes to appropriate host trees (Davidar 1983), ant dispersal of seeds that establish better in and around ant nests than elsewhere (Beattie 1985), and jay or nutcracker dispersal of pine and oak seeds to forest edges or openings (Vander Wall 1990). Seeds can also be dispersed to forest light gaps by male birds frequenting habitual display sites. For example, bellbirds (*Prociias tricarunculata*) carry the seeds of a montane tree (*Ocotea endresiana*,

Lauraceae) to clearings where males display to females (Wenny and Levey 1998). Other birds take *Ocotea* fruits but do not consistently deliver them to suitable habitats (figure 4). Elaiosomes (seed appendages, typically rich in fat, that attract ants or other animals) and the sticky seeds of mistletoes are adaptations for directed dispersal, but many plants without these adaptations, including oaks, bird pines, and *Ocotea*, opportunistically use birds to disseminate seeds to a suitable environment.

Synergy of escape and colonization. Colonization and escape may be synergistic. Temperate hickory (*Carya tomentosa*) seedlings in abandoned fields have both light and freedom from the rodents, rabbits, and deer that prefer not to forage in the open (Myster and McCarthy 1989). Synergisms are obvious when large areas are denuded by agriculture and abandoned or are exposed by fire, earthquake, or rain-induced landslides. At first, the colonization advantage is pronounced, as the land is populated by rapidly growing bird-, bat-, and wind-dispersed pioneers (Finegan 1996, Guariguata et al. 1997). In extensive regrowing pastures in Brazil, a few small-seeded pioneer species (e.g., *Cecropia*, *Solanum*, *Trema*, and *Vismia* spp.) may produce low-diversity landscapes for 30 to 70 years (Uhl et al. 1988). Dispersal limitation slows the successional process for larger-seeded species from deep forest into large openings. In disturbances of a few hectares (ha) or less, however, dispersal of larger-seeded trees from nearby forests does occur (figure 5). Spatial demography may show that seedlings that establish under the canopy of pioneer trees fare better than members of cohorts in the forest itself.

Synergy of escape and diversity. Escape from density-dependent mortality near parents may also help maintain forest diversity. Janzen (1970) argued that density-dependent seed and seedling mortality is severe enough to leave openings for other species if seed predators are species-specific. It follows

that seeds escaping from parent trees are safer if they land under a tree of another species rather than one of their own. Much as a pattern of seed distribution is a template for what may follow for a particular population, a community of seeds or seedlings is a community template of possibilities for the future (Howe and Miriti 2000). The community of established plants that actually develops is the result of an array of density-dependent and density-independent processes that influence later juvenile distributions in different ways. Spatial demography is one way to tease apart these effects.

As dense patches of sibling seeds or seedlings under parents are decimated by insects or pathogens, one community-level result is the release of seedlings of different species, an effect that turns out to be general. In rain forest, density-dependent mortality may occur in all stages of growth. Harms and colleagues (2000) recorded the densities of almost 400,000 seeds of 53 species that fell into 200 fruit traps over 4 years in the Panamanian rain forest, and compared the distributions of species in each trap with samples from more than 13,000 seedlings growing nearby. Not only were abundances of emerging seedlings inversely correlated with the number of seeds that fell into traps, the species abundance distributions of seedlings were more even, and therefore more diverse, than those of seeds in the traps. Peters (2003) further shows that density-dependent mortality occurs in sapling and adult stages in the vast majority of species that are not acutely rare in both Panamanian and Malayan rain forests; rain-forest trees survive better when neighbors are of other species. The effect of neighbor identity might be expected to be reflected in lower elasticities for seedling-to-sapling and sapling-to-adult transitions in common trees when the trees are close to neighbors of their own species than when they are close to other species. Peters (2003) shows that the escape advantage, and the enhancement of diversity through release of less common species when local dominance is suppressed, extends well beyond seed and seedling transitions. The escape advantage may be magnified in diverse forests, where it actually helps maintain tree diversity.

Genetic promise. Genetic variation is not random in seed and seedling cohorts. Microsatellites are hypervariable, noncoding regions of chromosomes, with several or many alleles at a locus, that behave like Mendelian genes without selection (Dow and Ashley 1996). Godoy and Jordano (2001) use microsatellites to measure dispersal distance and mosaics of



Figure 5. Seed dispersal and secondary succession. Seed rain into abandoned pastures in tropical Mexico includes both rapidly growing pioneers, such as *Cecropia peltata*, and a variety of seeds from later-successional trees in gallery forests along streams or nearby rain forests. Pioneer trees dominate the overgrown pastures, while fruit traps like these show that seeds of forest interior species are unlikely to arrive at sites more than a few meters from a forest edge (Martinez-Garza and Gonzalez-Montagut 1999). Dispersal limitation may allow pioneer dominance for 30 to 70 years. Photograph: Cristina Martinez-Garza.

seedling dispositions for the well-studied European cherry *P. mahaleb*, which is dispersed by birds and mammals. Microsatellite techniques are still new to the field of spatial demographics, but the results for *P. mahaleb* indicate both how spatially contingent survival might be influenced by non-random arrangements of genotypes in a population and how genetic issues add a dimension to dispersal and its consequences.

Microsatellites confirm that most *P. mahaleb* seeds go no farther than 10 m from parent trees, and most seedlings around a fruiting tree share at least one parent. More surprising is the finding that deposition sites at some distance from fruiting trees have offspring of only one or a few parents, while those under fruiting trees, though dominated by full or half siblings, include a number of other parentages as well. A substantial minority (more than 17%) of seedlings come from outside the study area, having no parents within the stand. A demographic question that should be addressed is whether these outsiders have a better or worse chance of growth and survival than closely related members of the cohort. Hypervariable markers will alter the questions that can be asked of dispersal processes. For instance, does chance

immigration of plants from outside a stand contribute genes that have unusual fitness in a new site?

When studying seed dispersal matters

The apparent paradox of the profuse adaptations for seed dispersal and the inconsequential prospects of any given seed lies in the confounding of averaged with partitioned demographic effects. In homogeneous habitats occupied by a few species of long-lived plants (with fewer than 1% of adults dying per year), as in the desert shrub *A. dumosa*, overall population growth is negligible (λ close to 1). Spatially defined demographics exist, but the benefits of isolation are subtle (Miriti et al. 2001). At the other extreme of ecological succession in open or highly heterogeneous habitats, partitioned demographic projections will clearly show differences in λ between cohorts of dispersed and undispersed seeds (Parker 2000). Between the extremes of totally closed and open habitats lies most of nature, where a thoughtful application of this distinction can be enlightening.

Habitat restoration. Ecological restoration reestablishes ecological patterns and processes where they have been destroyed by humans, bypassing the slow stages of natural succession. Intensive agriculture and long-term grazing not only destroy complex and species-rich aboveground communities, they also destroy seed banks that might permit revegetation. A realistic goal of directed succession is to reestablish processes that accelerate the development of community complexity. Demographic projections, using estimates parameterized from field or garden studies, may offer a much better chance of predicting success of key species than the usual trial-and-error approach.

Reforestation of large areas disturbed by humans is often dispersal limited; most forest species are very slow to arrive. Dispersal may be encouraged within a matrix of disturbed and remnant communities. Janzen (1988) argues that effective ecological restoration creates habitat buffers around ecological remnants and connects these habitats with corridors and stepping-stone patches, thereby increasing the movements of pollinators and dispersal agents on which plants depend (Tewksbury et al. 2002). In the tropics, a dispersal pattern that promotes reforestation may be established by encouraging seed dissemination where many species are strongly dispersal limited. Managers might place perches in fields to attract birds and their loads of seeds (Miriti 1998, Holl 1999) or plant cover of short-lived trees to encourage shade-tolerant tree seedlings and suppress competition from grasses (Hooper et al. 2002). The goal of these methods is to overcome dispersal limitation by promoting seed arrival (through birds) and plant survival (though tree cover), thereby accelerating the growth of buffers and corridors and increasing their effectiveness. In these cases, demography could be a tool, but not a critical one.

A complementary approach is to actively establish a diverse matrix to encourage processes of dispersal by and for diverse assemblages of animals and plants (Martinez-Garza and Howe 2003). Properties of the matrix between habitat

patches determine both recruitment in ecological remnants and migration of remnant plants into the matrix. One way to accelerate succession in tropical situations is to plant late-successional trees capable of handling the rigors of open pasture, but to choose species whose fruits will attract large-bodied mammals and birds (Wunderle 1997). Small-seeded pioneers that are less dispersal limited will occupy such habitat anyway (Ingle 2002). By creating food patches attractive to dispersal agents, animal-borne seeds of many species enrich community templates and ultimately change forest composition. Tucker and Murphy (1997) provide an example in their study of reforestation in northern Australia. Trees bearing fleshy fruits planted among pioneers draw a variety of birds and mammals that appear to accelerate the succession of complex forest structure. A restoration scheme grounded in demographic thinking would revegetate agricultural land with late-successional species that have low variance in seedling-to-juvenile transitions, thereby permitting predictable recruitment of species that provide resources for fruit-eating, seed-dispersing animals. Projections of populations in subsets of communities parameterized by different planting circumstances may permit predictions of successful and unsuccessful species decades before forests mature.

Loss of dispersal agents. Unreliable seed dispersal has consequences for plants. In the tropics, hunting for “bush meat” eliminates monkeys, tapirs, toucans, agoutis, peccaries, deer, and guans, which disseminate seeds or eat seedlings on the forest floor (Redford 1992). Less directly, large fruit-eating animals are the first to disappear from small habitat fragments when continuous forests are subdivided into smaller patches (Laurance and Bierregaard 1997). How will these “silent forests,” devoid of herbivores and dispersal agents, change?

Subsistence hunting in the American tropics exterminates animals ranging from 1-kilogram (kg) agoutis (*Dasyprocta punctata*) to hefty 300-kg tapirs (*Tapirus bairdii*). The most obvious result is what Dirzo and Miranda (1991) call the “defaunation syndrome.” In Mexico, where the phenomenon was first noticed, extinction of browsing mammals causes a huge increase in the number of seedlings on the forest floor and a sharp decrease in their diversity. With no thinning of dominant plants by mammals, these aggressive species take over. In forests where defaunation threatens, demographic projections of the same species in hunted and unhunted areas may predict quite different forest communities 20 or 30 years into the future.

Forest fragmentation occurs when continuous forests are divided into smaller patches of varying sizes and degrees of isolation; intervening water or cropland is a barrier for forest plants and animals. Because the number of species is related to habitat area, one expects habitat fragments to lose species randomly as area declines. Where plants depend on dispersal agents, consequences of habitat fragmentation are anything but random. In the East Usambara Mountains of Tanzania, fragments have been isolated from forest by tea

plantations for 60 to 80 years (Cordeiro and Howe 2001). Primates and large fruit-eating birds disappear quickly from isolated forest fragments. Seedlings and juveniles of 31 animal-dispersed tree species are three times more common in continuous forest and large forest fragments (more than 30 ha) than in small fragments (less than 10 ha), whereas the recruitment of eight wind- and gravity-dispersed trees of the forest interior is unaffected. Recruitment of 10 endemic, animal-dispersed tree species is 40 times lower in small fragments than in larger patches. A study of one endemic tree dispersed by birds, *Leptonychia usambarensis* (Sterculiaceae), finds that the understory birds that commonly eat its fruits in continuous rain forest are rare or absent in small forest fragments (Cordeiro and Howe 2003). Moreover, fewer seeds are taken, more seedlings accumulate under parents, and fewer seedlings or juveniles occur away from parents in small fragments than in rain forest. Overall, seedling and juvenile recruitment near parents in small fragments is about half that in extensive forest. One might expect that an elasticity analysis would show lower elasticities for the seedling-to-juvenile transition in forest fragments, perhaps accounting for local attrition of this species from small habitat patches. In this tropical forest, dispersal matters. As in the defaunation example, projections of the same species in continuous forest and in forest fragments might help a manager gauge the consequences of loss of dispersal agents or other factors that affect tree recruitment.

Conclusions

At what distance, or in what local circumstances, do variances in survival decline, thereby indicating where seed dispersal is predictably effective? Spatial demography shows that average variations in seed and seedling transitions do not reflect the overall population dynamics of a species. Where long-lived adults saturate species-poor communities, the advantages of dispersal are subtle: Dispersal of the vast majority of seeds is demographically inconsequential in any given generation, although even these subtle impacts may matter over large enough scales of time and space. In successional populations, or among long-lived trees in diverse forests, dispersal can save seeds and seedlings from intense competition or from foci of pathogen or insect infestation under parents or others of the same species. Here the impact of slightly biased survival of dispersed versus undispersed seeds is pervasive. A challenge will be to discover how spatially contingent consequences of seed dispersal influence the fortunes of species in areas where human activities have reset successional clocks, hunted out dispersal agents, or fragmented once continuous habitats. In such circumstances, spatially contingent demography may be used to show where seed dispersal and seedling recruitment matter most in the past, in the present, and in the projected future.

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