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Advantages of seed dispersal: A re-evaluation of directed dispersal

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ABSTRACT

Seed dispersal can be advantageous (1) in escape from density- or distance-dependent seed and seedling mortality, (2) by colonization of suitable sites unpredictable in space and time, and (3) by directed dispersal to particular sites with a relatively high probability of survival. Most previous research on the consequences of seed dispersal has focused on escape and colonization because adaptations ensuring directed dispersal are not expected under the paradigm of diffuse mutualism that characterizes the modern view of seed dispersal evolution. In this paper, I suggest that directed dispersal is more common than previously believed even in the absence of plant adaptations to promote it. Directed dispersal may be seen in particular among animal-dispersed plants and in arid ecosystems or successional areas, but has been overlooked due to the lack of detailed data on seed shadows generated by particular species, and the fact that the alternative advantages of dispersal are not mutually exclusive. Although directed dispersal is never thought to be the only advantage of dispersal, it may often be ecologically important if one dispersal vector has a disproportionate effect on plant recruitment. Furthermore, in human-disturbed and managed ecosystems, directed dispersal may be important in restoration. More studies detailing the consequences of different patterns of seed dispersal will be useful for conservation and management strategies.

Keywords: colonization, directed dispersal, dispersal quality, escape, nurse plants, recruitment foci, safe sites, seed dispersal, seed shadow.

INTRODUCTION

It matters who defecates what where. (Janzen, 1986: 251)

Seed dispersal has a major influence on plant fitness because it determines the locations in which seeds, and subsequently seedlings, live or die. Theoretically, plants could increase fitness if a higher proportion of seeds were dispersed to sites where offspring have a predictably high probability of survival relative to random sites, a process known as directed dispersal. To do so, a plant must have a predictable dispersal vector, either biotic or abiotic, that takes seeds disproportionately to suitable sites. Such a pattern of dispersal will probably be retained in the distribution of adult plants (Schupp and Fuentes, 1995), in

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which case a particular dispersal agent has a disproportionate effect on plant recruitment. If true, then patterns of dispersal may have a greater role in the structure and composition of plant communities than currently believed.

Directed dispersal consists of disproportionate arrival in sites especially favourable for survival (Howe and Smallwood, 1982; Howe, 1986). Although non-random movement patterns and habitat selection by animals, and variation in microhabitat suitability for plant growth, are well documented, examples of directed dispersal are thought to be rare and unusual (Howe, 1986). I suggest that directed dispersal is more common and ecologically significant than previously believed but has been overlooked for several reasons. First, the current paradigm of diffuse co-evolution between plants and their dispersers does not predict the evolution of adaptations for directed dispersal. Second, the alternative advantages of dispersal (escape, colonization, directed dispersal; see below) are not mutually exclusive and can be difficult to distinguish; the demonstration of one advantage does not preclude the others. In particular, the emphasis of research on escape obscures the occurrence of directed dispersal. Third, few studies have integrated patterns of seed distribution (seed shadows) and the consequences of such patterns for plant recruitment in a way that can detect directed dispersal. Plant recruitment is a multi-stage process that has most often been studied in a stage-specific manner (Houle, 1995; Jordano and Herrera, 1995; Schupp and Fuentes, 1995). Zoologists have tended to study the fruit removal and gut treatment stages, while botanists have focused on the seedling stages (Howe, 1993). Fourth, finding dispersed seeds, especially those dispersed by vertebrates, is difficult. Identifying parents of dispersed seeds is also difficult and so far has been limited to studies of isolated trees (Janzen *et al.*, 1976; Gladstone, 1979) or genetic studies (Gibson and Wheelwright, 1995; Hamrick and Nason, 1996). Fifth, several different names have been used for the same or closely related ideas. The term 'directed dispersal' was introduced by Howe and Smallwood (1982) at the same time the initial framework of seed dispersal theory was being critically examined (Wheelwright and Orians, 1982; Janzen, 1983b; Herrera, 1985, 1986). Thus, because directed dispersal was not expected under the diffuse mutualism view, the term was not widely adopted, and terms such as 'safe sites', 'nurse plants', 'recruitment foci', 'succession facilitation' and 'targeted dispersal' were used instead for concepts related to directed dispersal (Grubb, 1977; Harper, 1977; Stiles, 1989; Bazzaz, 1991; Vieira *et al.*, 1994).

I suggest that directed dispersal is not inconsistent with the diffuse mutualism paradigm and, although subtle, may be quite common. After defining and describing the advantages of dispersal for plants and outlining the development of the diffuse mutualism paradigm, I briefly outline three classic examples of directed dispersal. I then discuss other possible examples of directed dispersal to illustrate how widespread it may be. Finally, I suggest specific research needed to demonstrate directed dispersal.

ADVANTAGES OF DISPERSAL

Plants display many morphological features uniquely associated with differing methods of seed dispersal (Beal, 1898; Ridley, 1930; Van der Pijl, 1972). Considering the cost to the plant of producing such dispersal-related structures, it is reasonable to expect some advantage to dispersal (Thompson and Willson, 1978; Howe and Smallwood, 1982). Several explanations have been proposed: (1) escape from high mortality caused by distance- or density-dependent factors near conspecifics; (2) colonization of rare, unpredictable or

ephemeral sites, such as treefall gaps; and (3) directed dispersal to particular microhabitats especially suitable for survival (Howe and Smallwood, 1982; Howe, 1986; Willson, 1992). Because these three advantages of dispersal are not mutually exclusive, they can be assessed only if deposition sites and post-dispersal fates are known. Another possible benefit for vertebrate-dispersed seeds is enhanced germination after gut passage. The evidence for enhanced germination is mixed and depends on the plant and animal species involved (Janzen, 1983a; Chapman, 1995; Traveset and Willson, 1997). This aspect is arguably not an advantage of dispersal *per se* and will not be discussed in this paper.

Escape

The escape hypothesis is expected to be an advantage for most plants and is supported by many studies that have shown density- or distance-dependent mortality near parent trees (Clark and Clark, 1984; Howe, 1986). The evidence should be disproportionate mortality negatively correlated with distance or positively correlated with density (Howe, 1986).

Colonization

The colonization model is most relevant when suitable sites for establishment are unpredictable or randomly distributed, as is thought to be the case for new treefall gaps in forests (Hartshorn, 1978; Brokaw, 1985; Van der Meer and Bongers, 1996). For species that require canopy gaps to reach reproductive maturity, the expected dispersal strategy is colonization via blanketing the understory with propagules capable of dormancy or suppressed growth until a gap forms and increased light induces germination or more rapid growth. Widespread dispersal of seeds in the area around the parent plants will maximize the number of different sites occupied and increase the chance that some sites will become suitable in the future. Colonization of sites currently favourable, such as recent disturbances, should involve dispersal to such sites in proportion to their abundance and distance from sources.

Directed dispersal

Directed dispersal can result if dispersal agents deposit seeds disproportionately in suitable locations. Thus, directed dispersal has two components: non-random arrival and survival in predictable locations (Howe and Smallwood, 1982; Howe, 1986; Schupp *et al.*, 1989). To benefit from directed dispersal, a plant must have fruits with characteristics that enable one mode of transport more than others (assuming all vectors are not equal), or must have a morphology that enables the propagules to arrive in certain habitat patches more often than expected by chance (Venable and Brown, 1993). Note, however, that the examples below show that plants need not be adapted specifically for directed dispersal as was originally theorized. Instead, I argue that directed dispersal occurs in many situations in which a plant has multiple dispersal agents, some of which provide directed dispersal while others provide colonization.

Distinguishing the alternatives

The three advantages of dispersal defined above are not mutually exclusive. Many plants are likely to benefit from more than one, if not all three advantages. Distinguishing the relative roles of each advantage for different plants should implicate which specific dispersal

agents are particularly important in different ecosystems. If seeds are dispersed to sites with random microhabitat characteristics, then the colonization hypothesis is supported. If seeds disproportionately arrive in a non-random subset of the available microhabitats *and* post-dispersal survival is predictably higher in those microhabitats than in random sites, then directed dispersal is supported. Escape is supported if dispersal decreases the probability of being killed by seed predators, herbivores or other mortality factors that act in a distance- or density-dependent fashion. In practice, however, these three hypotheses can be difficult to distinguish (Howe, 1986). Here I discuss the reasons for this difficulty and potential solutions.

Because most seeds die, research on escape has overshadowed colonization and directed dispersal. Because most dispersal does not result in seedling establishment, even by 'high-quality' dispersers, directed dispersal is likely to be subtle. Much larger sample sizes are needed to detect factors correlated with seedling survival than with seed mortality in a natural setting (e.g. Howe, 1990). In addition, many studies have not tried to distinguish the three advantages, have combined colonization and directed dispersal into colonization, or have ignored directed dispersal altogether (Herrera and Jordano, 1981; Dirzo and Domínguez, 1986; Martínez-Ramos and Alvarez-Buylla, 1986; Levey *et al.*, 1994). Furthermore, the data to evaluate directed dispersal have seldom been collected in one study. In particular, the ecological literature is dominated by stage-specific studies whose results cannot necessarily be used to distinguish among the advantages. Long-term studies that document survival through sequential stages, including dispersal, germination, seedling establishment and growth to maturity, are needed to evaluate the consequences of dispersal and thereby tease apart the hypotheses (Herrera *et al.*, 1994; Houle, 1995; Schupp and Fuentes, 1995; Clark *et al.*, 1999a).

In most cases, the distribution of dispersed seeds is highly leptokurtic, with most seeds near the parent and progressively fewer farther away (Janzen, 1970; Levin and Kerster, 1974; Willson, 1993; Herrera *et al.*, 1994; Houle, 1995; Schupp and Fuentes, 1995). The shape of the curve is best described by either negative exponential or inverse power functions (Portnoy and Willson, 1993; Willson, 1993; Laman, 1996a; but see Murray, 1988; Clark *et al.*, 1999b). Therefore, seed shadows are always non-random with respect to distance from the parent plant. Plotting the abundance of seeds over distance as a linear function, however, can obscure the great heterogeneity within the distribution (Janzen, 1983a; Stiles, 1989; Portnoy and Willson, 1993; Willson, 1993; Clark *et al.*, 1999b; Nathan *et al.*, 2000; Wenny, 2000). It is important to note that non-random dispersal associated with such heterogeneity is a necessary but not sufficient condition for directed dispersal. For directed dispersal to occur, non-random dispersal must be to suitable sites, so that the overall result is a disproportionate effect on recruitment. Many studies show heterogeneity in seedling distributions, yet these patterns could be caused by higher seed fall in some areas than others, or by higher survival in some areas, or both (Hubbell, 1980; Jordano and Herrera, 1995; Schupp and Fuentes, 1995). The important point is that directed dispersal yields a higher probability of survival to maturity, on a per-seed basis, than colonization.

A key element for distinguishing directed dispersal from colonization is determining where seeds actually land. Few studies have determined the seed shadows generated by different dispersal agents. This aspect is particularly important for plant species dispersed by many different dispersal agents. By attracting many disperser species with different behaviours and dietary requirements, the seeds are likely to be dispersed to many different sites. Such a pattern has been interpreted as support for colonization (e.g. Laman, 1996b).

However, a subset of the disperser assemblage may be responsible for dispersing most of the seeds that eventually establish. Even for plant species with a restricted set of dispersers, it has been shown that disperser species differ in the per-seed probability of establishment (Reid, 1989; Wenny and Levey, 1998).

The other critical aspect necessary to assess directed dispersal is determining post-dispersal fate. It is well known that plant mortality is highest in the seed and seedling stages for most species (Darwin, 1859; Harper, 1977). Every potential recruit requires a space in which to grow, in addition to water, nutrients and light. Such spaces are rare in the environment relative to the number of seeds produced. Therefore, the probability of establishment for any seed is very low. It follows, then, that any survival benefit at early stages is likely to increase the chances of further survival (Schupp and Fuentes, 1995).

As further illustration of distinguishing the hypotheses, consider the following hypothetical situation. A tree or shrub with small-seeded fruits attracts a variety of birds that disperse 100 seeds around the parent plant in a typical leptokurtic distribution. Insects kill 74 of 75 seeds within 10 m of the plant, and rodents kill 15 of 25 seeds beyond that distance. Nine of these seeds are taken by ants, eight of which are eaten and one of which is discarded on a refuse pile. The seed not taken by ants is incorporated into the soil seed bank when an animal steps on it and pushes it into the mud, where it can remain dormant for 2 years. The other two seeds, one within 10 m of the parent plant and one in the ant refuse pile, both germinate and establish as seedlings. Because of the nutrients in the refuse pile, that seedling grows larger. In this example, note that escape, colonization and directed dispersal are all supported, but for different seeds. Of the three live offspring produced by the plant, which is most likely to reach maturity? The best choice is the largest seedling, in which case the relatively rare event of directed dispersal contributes as much or more to the plant's fitness as escape and colonization. In summary, more detailed studies on where seeds are dispersed, how they get there and what happens afterwards are necessary to distinguish the hypotheses. Few studies have attempted to examine the three advantages (Masaki *et al.*, 1994; Hoshizaki *et al.*, 1999; Wenny, 2000).

THE DIFFUSE MUTUALISM PARADIGM

The evolutionary aspects of the fruit–frugivore interaction were first discussed by Snow (1965, 1971). These ideas were later expanded into the specialist/generalist dichotomy of plant traits and dispersal quality (McKey, 1975; Howe and Estabrook, 1977). The expectation was that large-seeded, nutrient-rich fruits would attract dispersal agents that provided high-quality dispersal in terms of dispersal to sites appropriate for establishment. In contrast, small but abundant nutrient-poor fruits would attract opportunistic foragers that provided lower quality dispersal, but the sheer number of seeds dispersed would result in a few landing in appropriate sites. In other words, high-quality fruits were expected to benefit from directed dispersal, whereas low-quality fruits were expected to benefit from colonization. Both benefited from escape. The implication was that fruit–frugivore evolution could be relatively specific, involving adaptations between pairs or small sets of species, as seen in flower–pollinator evolution (Wheelwright and Orians, 1982). Over the next decade, however, the view that emerged from more detailed studies (mainly on avian foraging behaviour) was that co-evolution between plants and their dispersers was not species-specific, but instead was diffuse, involving adaptations between large groups of plants and groups of dispersers (Wheelwright and Orians, 1982; Howe, 1984; Herrera, 1985,

1986; Malmborg and Willson, 1988; Levey *et al.*, 1994). Indeed, although plant species vary tremendously in the number of potential dispersers they attract, and a few have very restricted sets of dispersal agents (Janzen and Martin, 1982; Tutin *et al.*, 1991; Chapman *et al.*, 1992; Tewksbury *et al.*, 1999), no unequivocal examples of a plant species entirely dependent on one species of disperser are known (Witmer and Cheke, 1991).

Some interpretations of the diffuse mutualism theory seem to exclude the possibility of directed dispersal. Two of the main objections to the specialist/generalist dichotomy are (1) that plants reward dispersers for removing fruits but not for dispersing them to appropriate sites and thus can do little to influence where dispersers take seeds, and (2) suitable sites for plant establishment (safe sites) are spatially and temporally unpredictable (Wheelwright and Orians, 1982; Janzen, 1983b). Studies on pollination were well ahead of those on seed dispersal (Howe, 1993) and both the specialist/generalist dichotomy and the critiques that followed were based on comparisons with pollination, as exemplified by the statement 'plants cannot direct the dispersal of seeds to a particular location with a degree of exactness comparable to pollen dispersal, though possibly they could favor animal vectors with particular foraging behaviors, habitat preferences, or probabilistic patterns of seed dispersal' (Wheelwright and Orians, 1982: 406). Based on these criticisms of the role of species-specific co-evolution in seed dispersal, some ecologists may have assumed that escape and colonization were the most probable benefits of dispersal and that directed dispersal was unlikely as an adaptive strategy. Note, however, that 'particular foraging behaviors, habitat preferences, or probabilistic patterns of seed dispersal' are exactly the conditions that result in non-random patterns of dispersal. If these patterns of dispersal are coupled with arrival to suitable sites, then directed dispersal is achieved.

CLASSIC EXAMPLES OF DIRECTED DISPERSAL

Three systems are typically given as examples of directed dispersal: mistletoe dispersal by small birds, dispersal of elaiosome-bearing seeds of herbaceous plants by ants and scatterhoarding by corvids. Although these systems are often thought of as exceptions to the general rule of diffuse co-evolution (Wheelwright and Orians, 1982; Levey *et al.*, 1994), they are actually consistent with the theory, as all three examples involve each species of plant being dispersed by more than one species of disperser, which in turn disperse several other species of plants (e.g. Restrepo, 1987). They may be more specialized than most other plant–disperser systems and perhaps illustrate one endpoint of a continuum of dispersal strategies.

Mistletoes

Mistletoes (about 40 genera; Viscaceae, Loranthaceae, Eremolepidaceae) are obligate stem-parasites that occur worldwide and are dispersed by passerine birds. The pulp contains sticky viscin that is difficult to separate from the seed, even during gut passage. The viscin enables the seeds to cling to a branch until germination and connection with the host xylem. Viscin also allows several seeds to stick together and to the bird, during defecation or regurgitation, and increase the chances that the string of seeds will hit a branch or be wiped directly onto the branch by the bird. In Australasia, mistletoes are dispersed by several species of flowerpeckers and mistletoebirds (Dicaeidae; Docters van Leeuwen, 1954; Reid, 1991). In forested regions of Central America and South America, they are dispersed

mainly by euphonias and other tanagers (Thraupidae) and to a lesser extent flycatchers (e.g. *Zimmerius vilissimus*, Tyrannidae; Davidar, 1983; Restrepo, 1987; Stiles and Skutch, 1989; Monteiro *et al.*, 1992; Sargent, 1995). In a Chilean desert site, mockingbirds (*Mimus thenca*; Mimidae) are the main dispersers of mistletoe (Martínez del Rio *et al.*, 1995), while in North America, waxwings and phainopeplas (Bombycillidae) are the main mistletoe dispersers (Walsberg, 1975; Larson, 1996). Seeds in fruits not eaten by birds and seeds dispersed to the ground have no chance of survival.

Studies by Reid (1989) and Sargent (1995) illustrate directed dispersal of mistletoes. Suitable establishment sites are live twigs of a certain size, depending on the species. In Australia, *Amyema quandang* mistletoes established best on 1–6 mm diameter twigs (Reid, 1989), while in Costa Rica, *Phoradendron robustissimum* established best on 10–14 mm twigs (Sargent, 1995). Larger twigs and branches have thicker bark that may preclude establishment, and smaller twigs are more likely to die than larger twigs after mistletoe infection (Sargent, 1995). Sargent (1994) showed that euphonias tended to perch on twigs of the appropriate size for establishment and, therefore, within a tree establishment was on a non-random set of the available twigs and branches. Reid (1989) similarly showed that mistletoebirds (*Dicaeum hiruninaceum*) were more likely to deposit seeds on the appropriate-sized twigs than were honeyeaters (*Acanthagenys rufogularis*). In both cases, a restricted set of dispersers is entirely responsible for successful mistletoe establishment. Non-random distribution of mistletoes among the available host plants (host preferences) has been shown in several other studies (Monteiro *et al.*, 1992; Martínez del Rio *et al.*, 1995; Larson, 1996).

Host preferences have been noted for other epiphytes (e.g. *Ficus*; Putz and Holbrook, 1989; Daniels and Lawton, 1991; Laman, 1996b; Patel, 1996), but it is unclear if they are related to the pattern of dispersal or of survival. Laman (1995, 1996b) suggested that host preferences in *Ficus* are not caused by differential dispersal but by differences in establishment requirements, as *Ficus* seeds are dispersed by many species of birds and mammals and probably achieve widespread dissemination. The dispersal ecology of most other epiphytes is unknown.

Ants

A wide variety of tropical and temperate plants produce seeds with lipid-rich arils or elaiosomes that attract ants (Beattie and Culver, 1981; Horvitz and Schemske, 1986, 1994; Ohkawara *et al.*, 1997). This ant–plant mutualism is worldwide, occurring in habitats ranging from deserts to tropical forests and involving representatives of over 80 plant families and numerous ant taxa (Beattie, 1985). Typically, ants take the seeds back to their nests and discard the seed after the nutrient-rich elaiosome has been consumed. Seeds are dispersed when placed on refuse piles or abandoned in nests (Beattie and Culver, 1982). Because the nests or refuse piles have higher concentrations of nutrients available to seedlings compared with the surrounding soil, seedling growth or establishment is often higher in such sites than in random sites (Davidson and Morton, 1981; Horvitz, 1981; Hanzawa *et al.*, 1988). Arrival to nutrient-rich sites, however, is apparently not an advantage of myrmecochory in some areas (Rice and Westoby, 1986; Bond and Stock, 1989).

In contrast to vertebrate frugivores that usually eat the reward (fruit pulp or aril) before dispersing seeds, ants typically take seeds back to their nests before eating the elaiosome (Culver and Beattie, 1978; Horvitz, 1981). In some species, removal of the elaiosome

induces germination, and thus ant-dispersal provides a predictable cue that a suitable site has been reached (Horvitz, 1981). Seeds not taken by ants are likely to be eaten by rodents and other seed predators (O'Dowd and Hay, 1980; Heithaus, 1981; but see Smith *et al.*, 1989), but many species release the seeds during the morning, when ants are active but most rodents are not (Gibson, 1993; Ohkawara *et al.*, 1997). Ants also act as secondary dispersers of seeds in bird and mammal droppings (see p. 62).

Corvids

Approximately 20 species of pines (*Pinus*; most in the subgenus *Strobus*) are dispersed by jays and nutcrackers (Corvidae; Tomback and Linhart, 1990). Most other pines are wind-dispersed, although they may benefit from secondary dispersal by scatterhoarding rodents (Vander Wall, 1992, 1993). These pines occur in western North America and across Eurasia and are distinguished from the primarily wind-dispersed species by having large seeds that lack a well-developed winged appendage for wind dispersal and cones that require seed removal by animals (Tomback and Linhart, 1990). The most specialized dispersers are the two species of nutcrackers (*Nucifraga*). Nutcrackers have a sublingual pouch (unique among birds) in which they carry up to 90 seeds (Vander Wall and Balda, 1977; Tomback, 1982). They bury seeds in the ground in shallow surface caches of 1–4 seeds. They presumably disperse seeds over considerable distances (Lanner, 1996). Each nutcracker caches thousands of seeds each year, exceeding its dietary requirements 2–5 times (Vander Wall and Balda, 1977; Tomback, 1982). Several other corvids cache pine seeds and are important dispersers, including pinyon jays (*Gymnorhinus cyanocephalus*), western scrub jays (*Aphelocoma californica*) and Steller's jay (*Cyanocitta stelleri*). These birds have highly developed spatial memory (Balda and Kamil, 1989; Kamil and Jones, 1997) but do not retrieve all caches every year (Lanner, 1996). Most seeds that are not taken by birds and fall beneath adult *Pinus monophylla* trees are harvested by rodents that are less effective dispersers than corvids because they larderhoard many seeds in burrows (Vander Wall, 1997). Most of the corvid-dispersed pine species are found in xeric habitats where burial protects seeds from desiccation (Lanner, 1996). However, both the corvids and the rodents scatterhoard some seeds in sites under bushes that provide shade and thus are beneficial for germination and establishment (Vander Wall, 1997). In addition, some of the pines are early successional species (pioneers) and the birds – nutcrackers and pinyon jays in particular – are known to make frequent caches in open areas (Lanner, 1996).

Corvids and squirrels also disperse oaks and beeches (Fagaceae) by scatterhoarding. Although the presumed mutual adaptations in these species are less clear than for nutcrackers and pines, it is clear that many seeds are cached in suitable sites for germination and establishment (Darley-Hill and Johnson, 1981; Sork, 1983; Johnson *et al.*, 1997). In addition, dispersal by jays has been implicated in the rapid post-Pleistocene northward spread of oaks and other species (Johnson and Webb, 1989; Wilkinson, 1997; Clark *et al.*, 1998).

POSSIBLE ADDITIONAL EXAMPLES OF DIRECTED DISPERSAL

Abundant circumstantial evidence hints that directed dispersal is more common than previously believed. In this section, I describe several possible examples of directed dispersal that should be investigated in future studies. None of these examples is unequivocal

because seed shadows generated by individual disperser species and post-dispersal seed fates are not well understood. But in all cases, one of the two requirements of directed dispersal are met: either non-random patterns of dispersal or dispersal by a particular vector to certain sites.

Dispersal by wind and birds to gaps

Canopy gaps caused by dead or fallen trees or branches are crucial recruitment sites in most forest ecosystems. Typically, 1–2% of the forest canopy is opened annually, and about 5% of the forest area is in gaps formed in the last 5 years (Runkle, 1985; Lawton and Putz, 1988; Martínez-Ramos *et al.*, 1988; Murray, 1988; but see Kneeshaw and Bergeron, 1998). Because many plant species require gaps for germination and seedling growth, seed arrival in gaps would be highly advantageous. Seeds can arrive via the seed bank (past dispersal) or via seed rain (current dispersal). The former case would be colonization, while the latter could be colonization if arrival is in proportion to the area available or directed dispersal if arrival is more often than expected by chance.

Air currents around gaps may pull in wind-dispersed seeds from the surrounding area (Schupp *et al.*, 1989). In support of this hypothesis, at least three studies have found higher seed rain of wind-dispersed species in gaps than in forest (Augspurger and Franson, 1988; Denslow and Gomez Diaz, 1990; Loiselle *et al.*, 1996). Many wind-dispersed species are shade-intolerant and require gaps for establishment, thus wind dispersal may often result in directed dispersal.

Gaps may also be foci for bird-dispersed seeds. It is well known that fruiting plants produce larger crops in gaps (Levey 1988a,b, 1990; Martínez-Ramos and Alvarez-Buylla, 1995) and that frugivorous birds are also especially active in and around gaps even though few species can be considered gap specialists (Schemske and Brokaw, 1981; Willson *et al.*, 1982; Levey, 1988b; Malmborg and Willson, 1988). Based on these studies, Schupp *et al.* (1989) hypothesized that seed rain of small-seeded, animal-dispersed species would be higher in tropical forest gap edges than gap centres. In Illinois, Hoppes (1988) did find such a pattern; seed rain was often bimodal with most seeds landing near the parents and a second smaller peak at gap edges. Overall, Hoppes (1988) estimated 50% of bird-dispersed seeds landed in gaps and gap edges, which comprised 16.8% of the study area. In a temperate rainforest in Chile, bird-dispersed seeds tended to land near gap edges, while some wind-dispersed species were most commonly found in gap centres (J.J. Armesto *et al.*, unpublished manuscript). In Japan, seed dispersal of *Cornus controversa* by birds was not disproportionate to gaps, but gap and gap-edge sites were not distinguished (Masaki *et al.*, 1994). Both Hoppes (1987) and Denslow and Gomez-Diaz (1990) noted the likely occurrence of seed dispersal from plants in one gap to another gap. The most likely plant species to benefit from directed dispersal to gaps are those that can establish, not in new gaps, but in building-phase gaps a few years old (Denslow, 1987; Brandani *et al.*, 1988).

Canopy gaps are formed when a tree or branch falls or when a tree dies standing. Locations of new gaps are thought to be randomly distributed and unpredictable (Hartshorn, 1978; Brokaw, 1985; Martínez-Ramos *et al.*, 1988; Van der Meer and Bongers, 1996). The fact that trees on gap edges are more likely to fall than trees in closed canopy forest (Young and Hubbell, 1991; Van der Meer and Bongers, 1996) suggests that gap edges are predictably more favourable locations than random understory locations for species that benefit from more light. In addition, in some forests, gaps are aggregated (Lawton and Putz,

1988; Runkle, 1990; Van der Meer and Bongers, 1996; Gale and Barfod, 1999). Thus, gap locations may not always be as unpredictable as is commonly believed. The possibility of directed dispersal to gaps or gap edges remains to be examined.

Habitual perches and roosts

Many frugivorous tropical birds have lek breeding systems in which the males have display perches where they spend most of the day during the breeding season. Such species range from manakins (Pipridae) to the much larger bellbirds, umbrellabirds and cocks-of-the-rock (Cotingidae) in Neotropical forests, and birds-of-paradise (Paradisaeidae) in New Guinea. The males of two species of manakins and two species of bellbirds spent 87–95% of the day at display perches, leaving only for brief bouts of foraging (D.W. Snow, 1962a,b; B.K. Snow, 1970, 1977). Most of the seeds dispersed by males of these species are probably deposited in the vicinity of the leks or display perches.

If perch or lek areas are also suitable establishment sites, then these species may provide directed dispersal. For example, three-wattled bellbirds (*Procnias tricarunculata*) in Costa Rica typically display on tall exposed perches such as dead branches or dead trees (Snow, 1977). In a study on seed dispersal of the canopy tree *Ocotea endresiana* (Lauraceae), 52% of the seeds dispersed by bellbirds landed in gaps (under display perches), compared with only 3% of the seeds dispersed by four other species. Overall, including seeds whose dispersal agent was unknown, 12% of the seeds landed in gaps, much greater than the 5.3% expected based on the area of the forest in gaps < 5 years old (Wenny and Levey, 1998). Seedlings in gaps had almost twice the chance of surviving 1 year compared to seedlings in closed canopy forest. Other species of bellbirds and cotingas display similar behaviour in perching on exposed limbs or in trees with sparse foliage (Snow, 1982) and, considering the wide variety of fruits they eat, bellbirds are likely to provide directed dispersal for other species as well.

Other bird species with habitual perches display in the forest understory. Guianan cock-of-the-rock (*Rupicola rupicola*) and white-throated manakin (*Corapipo gutturalis*) select lek areas in specific light environments in the forest understory so as to maximize conspicuousness during displays (Endler and Thery, 1996). Some species of manakins even maintain their leks by removing leaves that obstruct the view at lek height (Snow, 1976). The importance for plant growth of differences as small as 1–2% in light availability has been demonstrated for some shade-tolerant seedlings (Howe, 1990); it is possible that some of the species dispersed by lekking species benefit from higher light levels around leks. In leks of *Rupicola*, 77% of the plants present as seedlings and saplings were probably dispersed by *Rupicola*, while only 11.5% of the species in a forest understory site were shared with the lek (Théry and Larpin, 1993). Thus, the *Rupicola* leks can have a major impact on the vegetation structure and may contribute to clumped and patchy distributions of fruiting plants. In contrast, manakins that disperse seeds of shade-intolerant Melastomataceae, but display in the understory, contribute heavily to the soil seed bank but apparently not to the vegetation around the lek (Krijger *et al*., 1997).

Some primates use sleeping roosts repeatedly (Chapman, 1989b). Six plant species dispersed by howler monkeys (*Alouatta seniculus*) in French Guiana were more common as seedlings in the vicinity of sleeping roosts than on control sites (Julliot, 1996, 1997). This difference could be a result of higher seed input (Julliot, 1997) or differential survival of seedlings under roosts. A clearer example is of gorillas (*Gorilla gorilla*) in Gabon (Tutin

et al., 1991; Voysey *et al.*, 1999). Gorillas are highly frugivorous and defecate many seeds, particularly at nest sites, which tend to be located in open areas of the forest (Voysey *et al.*, 1999). Nest sites are used for a few days at most and, for a few plant species examined in detail, seedling survival was higher at nest sites than at other sites in the forest (Tutin *et al.*, 1991; Voysey *et al.*, 1999).

Rhinoceros (*Rhinoceros unicornis*) in Nepal and tapirs (*Tapirus terrestris*) in Brazil have habitual latrine sites (Dinerstein and Wemmer, 1988; Dinerstein, 1991; Fragoso, 1997). Rhinoceros latrines in floodplain grasslands provide crucial recruitment sites for the shade-intolerant tree *Trewia* that dominates the riverine forest. Seeds in dung piles are not secondarily dispersed by rodents but may be scattered by repeated use of latrines and occasional floods (Dinerstein, 1991). The seedlings may face interspecific competition but also have nutrient-rich sites. Seeds in tapir latrines are scatterhoarded by rodents (Fragoso, 1997; see pp. 62–63).

Nurse plants

In a variety of arid ecosystems, shrubs and trees provide the critical recruitment sites for many plants and are referred to as 'nurse plants'. In contrast to treefall gaps in forests, the spaces between plants in arid lands are hostile to seedlings; water and heat stress rather than light availability are often the factors limiting plant growth (Valiente-Banuet *et al.*, 1991; Fulbright *et al.*, 1995; Callaway *et al.*, 1996; Nabhan, 1997; Tewksbury *et al.*, 1999). Soil under nurse plants, especially nitrogen-fixing species, is sometimes higher in nutrients than the surrounding soil (Barnes and Archer, 1996), but nutrient availability is not necessarily the main limiting factor (Franco-Pizaña *et al.*, 1996). Whereas the lack of perches in recent gaps or abandoned pastures may limit seed rain of animal-dispersed seeds in some areas, nurse plants in arid and semi-arid ecosystems are often the only perches available and thus provide both high seed input in a non-random pattern and a favourable microclimate for bird-dispersed species. Several studies have shown birds leaving fruiting plants in non-random directions and higher seedling emergence under certain post-foraging perches than others (Herrera and Jordano 1981; Tester *et al.*, 1987; Izhaki *et al.*, 1991; Chavez-Ramirez and Slack, 1994). Some studies have reported that seed predation under shrubs is lower than in the open (Callaway, 1992), but others have suggested the opposite (Owens *et al.*, 1995). Dispersal by birds to nurse plants in arid and semi-arid ecosystems presents a strong case for directed dispersal, but virtually all studies have focused on seedling growth and interspecific plant associations without documenting patterns of dispersal. The best example is of chilies (*Capsicum annum*) dispersed by birds in Arizona (Tewksbury *et al.*, 1999). Most chili plants were found under other fleshy fruited species, especially two species of *Celtis*. Not only were *Celtis* trees used preferentially as perches by the main dispersers, but survival of transplanted chilies tended to be higher under *Celtis* than under other nurse plants (Tewksbury *et al.*, 1999; J.J. Tewksbury, unpublished data).

Perches in successional landscapes

Numerous studies have documented high rates of seed dispersal by animals to perches in pastures, oldfields or other human-disturbed landscapes (Debussche *et al.*, 1982; Willson and Crome, 1989; Guevara and Laborde, 1993; McClanahan and Wolfe, 1993; Robinson and Handel, 1993; Da Silva *et al.*, 1996; Ne'eman and Izhaki, 1996; Holl, 1998; Toh *et al.*, 1999). Such sites are referred to as recruitment foci (McDonnell, 1986; Myster and Pickett,

1992) or succession facilitators (Vieira *et al.*, 1994). In these situations, the dispersal pattern is clearly non-random, as seed rain beneath perches is often one or two orders of magnitude greater than in open areas (Robinson and Handel, 1993; Nepstad *et al.*, 1996; Ferguson and Drake, 1999).

Although the pattern of seed rain is similar to that for nurse plants in arid ecosystems, the suitability of such sites for growth and survival is less clear. In active pastures, where grazing animals would eat or trample seedlings in the open, dispersal beneath shrubs, fencerows or by rocks may represent the best recruitment sites within the pasture (Livingston, 1972; Herrera, 1984). In areas without grazing, seedlings of woody species may face frequent fires or competition from thick grass cover (Cochrane *et al.*, 1999; Duncan and Duncan, 2000). Once woody species are established above the existing matrix, however, recruitment of additional vertebrate-dispersed species is likely to increase (Hatton, 1989; Li and Wilson, 1998; Toh *et al.*, 1999).

This situation raises the possibility that directed dispersal may become more common in managed or highly disturbed landscapes, where the distribution of safe sites is more predictable. Safe sites in managed landscapes may be more common than in undisturbed areas, especially if they are provided by a highly invasive species (De Pietri, 1992; Vieira *et al.*, 1994) or planted shrubs or trees (Robinson and Handel, 1993; Debussche and Isenmann, 1994; Toh *et al.*, 1999). If true, this also suggests that plants may not be adapted for directed dispersal but can take advantage of it in some situations. It may be that, in successional landscapes, the species most likely to benefit from directed dispersal are the smaller-fruited 'generalist' plants that attract many dispersers rather than the larger fruits with a more restricted disperser assemblage (Da Silva *et al.*, 1996). It follows, then, that the advantages of directed dispersal in successional landscapes would diminish for the generalist plants as succession approaches the climax stage (see also Debussche and Isenmann, 1994).

Secondary dispersal by ants, rodents and dung beetles

Recent studies in tropical forests indicate that dispersal by vertebrates is often only the first of two stages of dispersal. Seeds in frugivore defecations are removed by ants (Roberts and Heithaus, 1986; Kaspari, 1993; Levey and Byrne, 1993) and rodents (Fragoso, 1997). In both cases, the secondary dispersers act mainly as seed predators, but the beneficial treatment of the seeds they do disperse may lead to a large influence on plant recruitment.

Ants are ubiquitous in Neotropical forest understory environments and rapidly remove small seeds from bird and mammal feces (Levey and Byrne, 1993; Pizo and Oliveira, 1999). Ants take seeds to their nests and most seeds are eventually eaten. Among some twig-dwelling ants, about 6% of the seeds are discarded on refuse piles, but perhaps more importantly, nest twigs and the seeds within them are abandoned on average every 3 months (Levey and Byrne, 1993). Seedlings had higher survival on experimental refuse piles under light levels typical of small gaps. Thus, ants remove seeds from a high-density pattern in a frugivore defecation where interspecific competition may be intense (Howe, 1989; Loiselle, 1990) and place a few in low-density, high-nutrient sites favourable for seedling growth. Some plant species have been noted in association with rotting logs (Thompson, 1980; Lawton and Putz, 1988; Lack, 1991); perhaps ants are the mechanism of seed arrival at such nurse logs.

Tapirs in Amazonian Brazil disperse palm seeds (*Maximiliana maripa*) to latrine sites that are used repeatedly (Fragoso, 1997). Most seeds not dispersed by tapirs are killed by insects.

The most remarkable aspect of this system is that agoutis (*Dasyprocta* sp.) were shown to remove seeds from tapir latrines and bury them in shallow surface caches. The density of seedlings and saplings less than 5 years old was significantly higher around latrine sites than around either parent trees or non-palm control trees. Fragoso (1997) suggested that this pattern of dispersal was responsible for the clumped distribution of the palms observed over large areas of the forest. Clumped distributions of trees dispersed by agoutis have been noted in other studies (Peres and Baider, 1997), although clumped distributions are common among tropical trees regardless of dispersal type (Condit *et al*., 2000).

Scatterhoarding by rodents can be either primary or secondary dispersal, depending on the plant species, although the benefits of scatterhoarding to seeds are similar in both cases; in addition to escape from some insect and mammalian seed predators, burial may prevent desiccation and facilitate germination and establishment (Hallwachs, 1986; Smythe, 1989; Forget, 1990; Vander Wall, 1990). Scatterhoarding of *Aesculus turbinata* seeds by rodents in Japan was beneficial in expanding the seed shadow but not for arrival at currently favourable sites (Hoshizaki *et al.*, 1999). In contrast, pine seeds cached by small rodents after wind dispersal in western North America were taken to sites more suitable for establishment than seeds dispersed by wind alone (Vander Wall, 1993). Scatterhoarding by rodents occurs worldwide and is understudied despite its probable importance in plant dynamics (Price and Jenkins, 1986; Brewer and Rejmánek, 1999).

Another example of secondary dispersal is removal of mammalian dung, and the seeds it may contain, by dung beetles (Estrada and Coates-Estrada, 1991; Estrada *et al.*, 1993; Shepherd and Chapman, 1998). In this case, the dung beetles have no interest in the seeds and may even discard larger seeds (Andresen, 1999). The beetles bury small balls of dung several centimetres deep. The females oviposit on the dung; the larvae consume most of the dung ball and leave the seeds behind. Estrada and Coates-Estrada (1991) found that 80% of the plant species dispersed by howler monkeys (*Alouatta palliata*) benefited from secondary dispersal by dung beetles. They suggested that burial by beetles allows escape from rodent seed predators, but the probable benefits of burial in nutrient-rich dung have not been examined. Many species of dung beetles are involved in secondary dispersal; they differ in the amount of dung taken, how far it is taken and how deep it is buried (Estrada *et al.*, 1993; Andresen, 1999).

CONCLUSIONS: GOING THE DISTANCE AND BEYOND

The examples given above illustrate the potential for directed dispersal in a wide variety of systems and suggest its importance in understanding plant–animal interactions, in restoration ecology and in conservation. A test of the directed dispersal hypothesis is within reach, but the lack of detailed data on patterns of dispersal generated by particular vectors, integrated with post-dispersal seed and seedling fate, limits our understanding of the role of directed dispersal in plant recruitment. In addition, seed rain into different patches at the community level is still poorly understood. Surprisingly, the models of Schupp *et al.* (1989) have not been adequately tested. Testing their predictions of seed rain patterns into gaps, gap edges and forest understory should be fairly straightforward and should identify certain plant species and their dispersers suitable for more detailed study that will yield insight into plant community dynamics.

Tests of the escape hypothesis have shown that some mortality agents respond to distance and/or density whereas others do not (Howe *et al.*, 1985; Merg, 1994). What is required

are studies that go beyond the distance and density factors and examine the characteristics of sites in which seeds actually land and the subsequent fate of those seeds. Even more important is the need for studies that examine the sequential stages of recruitment, from dispersal through establishment (e.g. Herrera *et al.*, 1994). Studies that ignore the possibility of secondary dispersal are likely to lead to misleading conclusions about the importance of dispersal patterns (Levey and Byrne, 1993; Chambers and MacMahon, 1994). Thus, it would be useful to examine the influence of areas of high seed rain, such as habitual perches, leks, primate sleeping roosts, large-mammal latrines, gap edges and nurse plants, on plant distributions and community composition. Are dense concentrations of seeds away from the parent plants foci for (1) recruitment for seedlings, (2) seed predation or (3) secondary dispersal? In addition to perches in successional landscapes, recruitment foci may also be present within forested areas. Emergent trees, standing dead trees, or perhaps trees with abundant fruit crops (e.g. *Ficus*) may attract vertebrate seed-dispersers and have higher seed rain than beneath trees nearby (Smith, 1975; Coates-Estrada and Estrada, 1986; Masaki *et al.*, 1994). In a preliminary study, Fleming (1988) found no difference in the diversity or density of vertebrate-dispersed plants around five *Ficus* spp. trees and five wind-dispersed *Calycophyllum candidissimum* trees, but the scale (1600 m^2 plots), small sample size and the different sizes of the trees are confounding factors.

Venable and Brown (1993) suggested that deposition in dung, which acts as a fertilizer, is a component of directed dispersal. High rates of post-dispersal seed removal from defecations cast doubt on this idea as a general rule (Janzen, 1986; Chapman, 1989a; Levey and Byrne, 1993; Fragoso, 1997; Pizo and Oliveira, 1999), although dung composition can influence germination and seedling growth of vertebrate-dispersed seeds (Traveset *et al.*, in press). Nevertheless, Dinerstein and Wemmer (1988; Dinerstein, 1991) showed that the distribution of *Trewia nudiflora* in riparian forests in Nepal is almost entirely attributable to dispersal by rhinoceros and suggested that rhinoceros dung piles provide nutrients necessary for the seedlings. Similarly, mesquite (*Prosopis glandulosa*) seedling survival was higher with than without cow dung, implicating cattle in the spread of mesquite into grasslands of southwestern North America (Brown and Archer, 1987). The importance of dung for seeds buried by dung beetles has not been examined and should be amenable to experimentation.

One of the difficulties in evaluating directed dispersal is that suitable locations for establishment (i.e. 'safe sites') are often difficult to specify or are poorly known for most species (Grubb, 1977; Fowler, 1988). In addition, safe sites for seeds may not be the same as those for seedlings or adults (Smith, 1984; Lamont *et al.*, 1993; Schupp, 1995), leading some researchers to believe that safe sites become more specific over time (Oswald and Neuenschwander, 1993). For tropical forest species, the hypothesized partitioning of gaps among seedlings in terms of gap age and position within the gap (Denslow, 1987; Brandani *et al.*, 1988) suggests that recruitment conditions could be defined. If so, the next step would be to examine seed arrival to such sites (e.g. Schupp *et al.*, 1989).

Another theme illustrated by the examples above is that directed dispersal may often be a fortuitous outcome of disperser behaviour rather than an adaptive strategy by plants. Thus, where disperser behaviour can be predicted, dispersal can be manipulated to increase the probability of directed dispersal. Regeneration of degraded land is often limited by low seed rain (Aide and Cavelier, 1994; Duncan and Chapman, 1999). Accordingly, manipulation

of dispersal to increase seed arrival at sites conducive to seedling survival has the potential to play a major part in restoration ecology (De Pietri, 1992; Robinson and Handel, 1993; Wunderle, 1997; Holl, 1998; Toh *et al.*, 1999).

The implication of directed dispersal is a disproportionate effect on plant recruitment. Therefore, the loss of a disperser species providing directed dispersal may result in a marked decrease in fitness for that plant species. The corollary of this idea is that, in depauperate communities that have lost dispersers providing colonization, plant species benefiting from directed dispersal will become more common (and vice versa). Similarly, directed dispersal may play a role in facilitating encroachment of invasive plant species (Stiles, 1982; Meyer and Florence, 1996; Malo and Suarez, 1997; Richardson *et al.*, 2000).

Abundant evidence hints at directed dispersal in both natural and disturbed ecosystems. Examining movement and dispersal patterns of individual disperser species, in combination with seed and seedling survival in different patch types into which seeds are dispersed, should yield insight into the role of plant–animal interactions in ecosystem function. When data are available to test the directed dispersal hypothesis, some of the examples above may not be supported. Demonstrating directed dispersal, however, is not the most important goal. By conducting the necessary studies, we will learn a great deal about the importance of dispersal patterns in community dynamics.

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