Ecology of Seed Dispersal

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INTRODUCTION

Identification of the selective forces on plant dispersal engenders theoretical argument, empirical study, and speculation. We separate evidence, testable hypotheses, and conjecture surrounding two major questions in dispersal ecology. The first asks what ecological, and ultimately evolutionary, advantages exist in seed dispersal. Astonishingly little is known about the advantages to a parent plant that are actually conferred by investment in dispersal structures. Does dispersal enable seeds and ultimately seedlings to escape mortality near the parent? Is continual recolonization of unstable habitats the primary advantage? Must seeds find rare microhabitats suitable for reestablishment? Such issues are addressed through joint consideration of dispersal and establishment—those stages both mediated by parental provisioning and subject to the highest mortality in the life of a plant. The second broad question asks what general and explicit environmental forces influence the timing and mode of dispersal. Do climates or seasons favor one dispersal mode over another? Do differences in number, size, morphology, or nutritional quality of fruits influence frugivore choice, and consequently differential dispersal of species or individuals within species? Studies of dispersal process and mode should be intimately connected. A general objective of this paper is to explore the degree to which they are integrated and, in so doing, to catalyze their union.

We emphasize topics most in need of critical attention: the evolutionary ecology of dispersal process and mode. Excellent recent reviews consider such related topics as dispersal mechanism (131, 184), seed dormancy (1, 30), phytogeography (11, 115, 146), masting and predator satiation (105, 156), and succession (68, 69, 189).

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TERMS AND DEFINITIONS

Critical terms in this paper invite multiple interpretations. We use *adaptation* as a functional property of an organism, evolved by natural selection, which enables it to survive and ultimately reproduce. The term implies functional configuration and not accidental advantage, no matter how great such an advantage might be (see 37, 193). *Diaspore* is the unit of a plant that is actually dispersed (184). *Dispersal* is the departure of a diaspore (e.g. seed or fruit) from the parent plant. *Establishment* is the process during which a germinating seed takes root, uses up parental provisioning, and assumes independent growth as a seedling. A *fruit* is the matured gynoecium with or without other floral organs or parts of organs. Loosely, it is the ripened ovary including the embryo, seed nutrient (endosperm), and other parental tissues. An *individual* is the genetically homogeneous unit upon which selection acts: the diploid sporophyte or "genet" of Harper (72). An individual plant may be one organizational unit (e.g. shoot and root of a maple), or a clonal composite (e.g. shoots and roots of an aspen clone). A *gymnosperm seed* is the embryo embedded in the female gametophyte. An *angiosperm seed* is either the embryo embedded in endosperm, or the embryo and digested endosperm within the megasporangium, surrounded by one or more integuments (45). A *seed predator* is an animal that eats and kills a seed (100).

DISPERSAL MECHANISMS

Fruit and seed morphology often indicate the general means of dispersal (149, 184). The various modes, listed in Table 1, include adaptations as spectacular as nutritious fruits adapted to attract vertebrate or invertebrate consumers (14, 86, 95), buoyant coconuts that float hundreds or thousands of miles (149), dustlike seeds produced by the hundreds of millions on a single orchid (149), elegant wings and plumes capable of aerial transport (21, 66), and ballistic fruits that can toss seeds several meters (10, 149). One germane comment is that adaptations for dispersal have varied evolutionary origins. A qualification is that dispersal syndromes, in lieu of field evidence, can only be tentatively applied.

Fruit parts have many anatomical origins. Fleshy fruits eaten by vertebrates are thought to be ancestral in angiosperms (12, 31, 184), but the pulp has several derivations (184). The edible portion may be homologous with the seed coat, an outgrowth of the seed coat called an "aril," an outgrowth of the endocarp, or tissue derived from the ovary wall. In *Ribes,* all are involved. Convergent adaptation is no less apparent in wind-dispersed diaspores (184). In many cases, wings evolve from the seed coat or ancestral arilloids; in others they are derived from the ovary wall or calyx tube.

Table 1 Summary of major dispersal syndromes of fruits and seeds

Dispersal agent and general adaptation	Modification	Derivation	Comment
Animal			
fleshy nutrient	aril, pericarp, pulp	seed coat or floral parts	vertebrate dispersal
chemical attractant	elaiosome	seed integument	ant dispersal
clinging structures	hooks, viscous material	usually floral parts	sticks to fur or feathers
mimesis	colored seed coat	seed coat	eaten by birds
Wind			
size reduction	dustlike seeds	seeds	up to millions/plant
high surface/volume ratio	wings, plumes, balloons	seed coat or fruit	balloons uncommon
tumbleweeds	shoot breaks loose	entire shoot	seeds scattered
Water			
resistance to sinking	hairs or slime	seed coat	submerged transport
uses surface tension	small size, unwettable	seed coat	float until wetted
low specific gravity	air spaces, cork, oil	seed or fruit	floats long distances
Self dispersal			
explosive fruits	varied	fruits	secondary transport common
creeping diaspores	hydroscopic bristles	fruits	occurs with varying humidity

Conversely, dramatically different dispersal mechanisms within a family indicate effective divergent selection. In a huge family such as the Leguminosae [17,000 species (80)], seeds may be adapted for dispersal by birds, bats, rodents, water, fur or feathers, wind, ballistics, or simple gravity (60, 184). Even in a small family, such as the tropical Lecythidaceae [450 species (80)], the common theme of a large woody fruit is modified for dispersal by birds, primates, fish, water, wind, or gravity (140). Selective pressures on fruits are clearly varied and effective.

An obvious modification for dispersal may not predict the actual process, nor does the absence of an obvious mechanism preclude dispersal by inanimate or animate agents. Plumed seeds may be dispersed by either wind or water (184), while thick-husked fruits adapted for consumption by an extinct Pleistocene megafauna are scattered by rodents and wind (108). Seeds without modifications for dispersal may be regularly scattered in rainwash (19), while nuts lacking obvious adaptations for animal consumption are hoarded and effectively dispersed by birds and rodents (17, 122, 160, 161, 181, 185, 186). Syndromes are useful only as general organizing tools; their identification is no substitute for study of the dispersal process.

ADVANTAGES TO DISPERSAL

A great deal is known about the morphological adaptations that mediate seed and fruit dispersal, but little is understood about the selective forces that produce them. Recent work emphasizes alternative advantages to local dispersal, as a means either of (a) avoiding disproportionate seed and

seedling mortality near the parent (26, 100), (b) colonizing disturbances (6), or (c), locating fixed microhabitats suitable for establishment and growth (e.g. 40). The alternatives are not exclusive, but may differ in importance from one plant population to another. The "Escape Hypothesis" (a) implies disproportionate success for seeds that escape the vicinity of the parent, as compared with those that fall nearby. The "Colonization Hypothesis" (b) assumes that habitats change; dispersal in space and time allows a parent to produce offspring capable of taking advantage of uncompetitive environments as they open. The "Directed Dispersal Hypothesis" (c) assumes that adaptations ensure that diaspores reach localized sites suitable for establishment. The ultimate null hypothesis is that adult distributions closely reflect seed distributions (see 19).

We bypass some putative advantages to dispersal. Historical interest in long-distance dispersal has diminished because long-distance dissemination is not the selective "reason" for seed or fruit vagility. Many early examples of long-distance dispersal are best explained by continental drift (146, 154) or sheer accident (64), while potentially adaptive dispersal to islands is an epiphenomenon of design for local colonization. Genetic evidence even indicates that outbreeding depression occurs in some plants (119, 141), accounting for maximal seed set at intermediate distances from parents (but see 65). Selective explanations for local dispersal are sufficient evolutionary causes, though chance long-distance dispersal will undoubtedly continue to figure importantly in biogeography (23, 123, 149). Other supposed advantages appear less important than they once did. Animals may scarify seeds in the gut, thereby enhancing germination. Without treatment by animals, some seeds fail to break dormancy (121, 130, 148) or summarily rot (95). Such cases are unusual. Most animal-dispersed seeds germinate without handling, or achieve only a slight advantage by handling (61, 84, 86, 89, 93). In most cases, scarification is incidental to an attempt to digest the seed, rather than a coevolved means of enhancing germination (e.g. 107, 126, 148).

Escape Hypothesis

Is the selective advantage to dispersal an escape from disproportionate mortality near parent plants? Most seeds fall in leptokurtic distributions in relation to the parent (120). Density-dependent mortality of seeds or seedlings near the parent might be due to insect or rodent predation (26, 32, 100), pathogen attack (2), or seedling competition (26, 72). Or "distance responsive" seed predators might search for food only in the immediate vicinity of parent plants, ignoring seeds and seedlings only a few meters away (100). The Escape Hypothesis can be falsified by showing that mortality is random with respect to density of siblings or distance from the parent;

no per-capita advantage exists because density-independent mortality reduces numbers below that at which predation, disease, and competition take their toll. It is plausible to suppose that few seeds under a parent establish and ultimately reproduce; it is fair to ask whether those 10 or 100 meters away are any better off.

The Escape Hypothesis, first proposed by Janzen (100) and Connell (26), achieved almost universal acceptance with practically no empirical support. Some data cited as supportive are irrelevant (102, 103) or negative (26, 104, 197). Some weak support did exist at the time. Noctuid moth larvae feeding on the leaves of a Costa Rican vine (*Dioclea megacarpa*) sometimes fall underneath the canopy, where they eat vine seedlings. Janzen (101) showed that seedlings under two vines were damaged more than those a few meters away. Connell (26) found that seedlings of Australian *Planchonella* spp. survived better under other trees than under conspecifics. At the time the Escape Hypothesis was posed and generally accepted, far more evidence contradicted than supported it.

Subsequent studies of temperate and tropical trees and shrubs argue for and against the Escape Hypothesis. Howe & Primack (91) found far higher densities of bird-dispersed *Casearia corymbosa* (= *nitida*) seeds under than away from two fruiting trees in a Costa Rican rainforest. Eight weeks later up to three times as many seedlings survived 10–30 m away from the crown edges as under the trees, probably due to localized rodent herbivory (84). Janzen et al (109) report mortality of *Andira inermis* seeds dropped by frugivorous bats (*Artibeus jamaicensis*) in western Costa Rica. *Cleogonus* weevils killed 60% of the seeds under parent trees, 30% under feeding roosts, and 10% of the single seeds scattered by the bats. Salmonson (150) and Clark & Clark (25) compare seed fall with seedling distributions of North American *Juniperus monosperma* and Galapagos *Bursera graveolens,* respectively. In both cases, dispersal of seeds by birds for only a few meters results in dramatic enhancement of survival to the seedling stage. Chinese elm (*Ulmus parvifolia*) seedlings directly under parents suffered 580 times the mortality from leaf beetles (*Pyrrhalta luteoloa*) as those a few meters away on suburban lawns (118). Stapanian & Smith (172) show that preferred sites used by squirrels (*Sciurus niger*) for hiding walnuts (*Juglans nigra*) from competitors correspond with sapling distributions. Scattering seeds evidently reduces predation, both by squirrels that hide the seeds and by neighbors that rob the stores. Vandermeer (182) found that isolated *Calliandra grandiflora* trees had less seed predation by lepidopteran larvae than plants in clumps, suggesting an ultimate advantage in the reproduction of dispersed offspring (182). In another study (183), *Welfia* palm seedlings under parents suffered disproportionate mortality from fronds shed by the adult trees. One piece of solid negative evidence is reported by Silander

(155), who found a distinct advantage to clumping in a Costa Rican shrub, *Cassia biflora*. Attack of pods by the two bruchid weevils *Acanthscelides obrienorum* and *Sennius* sp. increases with density, but the proportion of seeds killed is unchanged. A strong advantage in pollination to plants growing close together indicates that clumping, not dispersion, is advantageous. The general conclusion is that initial mortality from herbivores or seed predators is consistent with the escape hypothesis in most cases, but not in others.

The Escape Hypothesis was originally framed for tropical trees, but much of its best support comes from studies of herbs. Two-stage ballistic and ant-mediated dispersal suggests both escape and directed dispersal in such familiar genera as *Dicentra* (13) and *Viola* (10). Ballistic discharge slows harvest by rodents, allowing time for removal to ant nests (10). *Viola papilionacea* seeds screened from mice disappeared more slowly than those accessible to mice (35). More detailed experiments (74) with *Asarum canadense, Jeffersonia diphylla,* and *Sanguinaria canadensis* show similar effects in plants without ballistic dispersal. When ants (*Aphaenogaster rudis, Myrmica punctiventris, Formica subsericea* and others) were denied access to *Asarum* seeds, 70% of the seeds were eaten by mice (*Peromyscus leucopus*). With ants present, 24–39% were killed by mice. Mice killed 84% of *Sanguinaria* seeds denied to ants, but only 13–43% when ants were allowed access. Rodents were less interested in *Jeffersonia* seeds. These experiments show an advantage in removal of seeds by ants insofar as rodent predation is reduced, but the per-capita success of seeds taken by ants is unknown (but see 36). In these systems dispersal is local; ants bury seeds within centimeters or meters of parent plants. Similar work in American deserts shows that harvester ants (*Vermessor pergandei* and *Pogonomyrmex californicus*) carry *Datura discolor* seeds to nests, where food bodies rich in amino acids are removed and the seeds are discarded. Seeds placed in petri dishes under *Datura* plants are more likely to be eaten by rodents (*Dipodomys merriami, Perognathus baileyi,* and *Peromyscus eremicus*) than those under perennial shrubs, in the open 1–3 m from surrounding vegetation, or on *Vermessor* middens (132). The mortality due to rodent predation is distance-related, not density-dependent. Interactions between herbs, ants, and seed-eating animals are undoubtedly more widespread than previously supposed, if only because seed dispersal by ants is far more common than was once thought (8, 14, 71).

One model investigation reports effects of dispersal from the seed to first reproduction in a North American prairie community. In western Iowa a perennial herb, *Mirabilis hirsuta,* occupies newly exposed earth in badger (*Taxidea taxus*) mounds (136). Platt (137) shows density-dependent seed predation near this plant by nondisperser ants (*Formica fossaceps*) and

jumping mice (*Zapus hudsonicus*), followed by pronounced competition for water that affects seedling size and survival. A clear advantage to local (more than 40 cm) dispersal exists from the time seeds leave the parent until first reproduction. Platt uniquely links seed dispersal to eventual success in a natural community, and further distinguishes sources of mortality on seed and seedling stages. To date, this is the best support on record for the Escape Hypothesis.

Colonization Hypothesis

Might the primary advantage to dispersal be chance occupation of favorable sites that are unpredictable in time and space? The Colonization Hypothesis presumes that habitats change with time; the "goal" of a parent is to disseminate seeds so widely that some encounter a favorable situation as it occurs, or wait in the soil or understorey until a treefall, landslide, fire or other disturbance permits seedlings to establish and grow. The hypothesis is testable in a comparative sense by determining whether some diaspores are more likely to colonize new sites than others. Demographic analysis can further show that the tenure of any species in a newly opened site is short; parents fail to replace themselves in situ, relying upon the chance that diaspores find new openings for establishment. Escape from the parent is irrelevant in the sense of avoidance of density-dependent mortality, because shading by the parent itself or crowding from the advance of more competitive species obviates any possibility of extended local replacement. The Colonization Hypothesis applies to successional communities in both the classical sense of progression towards climax (189), and the more novel sense of continual flux in species abundance and distribution within mature forests (42, 69, 96).

Comparative natural history unequivocally distinguishes diaspores with obvious adaptations for dispersal from those with none (149). More generally, small seed size and a morphological design for dispersibility are associated with colonization potential, while large seed size and correspondingly reduced vagility are associated with competitive ability in saturated habitats (151, 187, 188). Plants that occupy temporary habitats, reproduce quickly, and are soon overcome by more competitive species are termed "fugitives" by Hutchinson (98); adults rarely persist in one location for more than one or a few generations. Baker (6) and Williams (194) discuss the "weedy" syndrome at length, noting that fugitive species are often short-lived, have vigorous vegetative reproduction, possess seed dormancy and intermittent germination, are capable of self-fertilization, and often have winged, plumed, or animal-dispersed seeds. Examples include many or even most roadside composites, grasses, and umbellifers. A particularly well-integrated community analysis is that of badger mounds, mentioned above.

Platt (136, 137) discusses dispersal, colonization, and persistence of two congenerics (*Physalis*) disseminated by squirrels and seven other genera (*Oenothera, Cirsium, Mirabilis, Verbena, Solidago, Asclepias, Apocynum*) dispersed by wind. The species sort along a covarying continuum of seed size and persistence. Significantly, the distances that seeds fall from these fugitive parents are far greater than those of species that later claim the mounds. Werner (187, 188) documents similar trends within the genus *Solidago* in Michigan and in the same prairie used by Platt. Within these herb communities, the assertion of a continuum from colonizing ability to persistence is well-founded.

   But a plant may be both a colonist and a persistent. Poplars (*Populus tremuloides*) and sequoias (*Sequoiadendron giganteum*) persist as clones or standing trunks for millennia, yet annually bear millions of seeds weighing less than 0.001 g each (32, 54, 153). In the same vein, seed size does not always predict colonizing ability. An examination of pollen records by Davis (41, 42) shows that twelve genera of trees have colonized the face of North America at rates averaging 100 (*Castanea*) to 400 (*Pinus*) m per year (median = 250 m/yr). Spruce (*Picea*) seeds weigh 0.002 g, while acorns (*Quercus*) are 500 to 1,500 times heavier. Yet spruces advanced during the Pleistocene interglacials at 250 m per year, oaks at 350 m. The rates are not likely to be uniform; jays and nutcrackers carry acorns and other seeds 1–20 km at a time (17, 185). But the high dispersibility of large-seeded ($\approx$ 1.0 g) trees over the last interglacial is provocative; the negative correlation of the rate of advance and seed size is weak ($r_s = -0.41$, $p > .05$). One lesson is that both large- and small-seeded trees broadcast seeds widely enough that rapid colonization of new habitat is possible. A second insight is that "persistent" forest communities are in fact ephemeral, on a time scale appropriate to trees that may live hundreds of years. Davis reports repeated invasions of "climax" communities by one "climax" species after another. Dispersal rate and climatic tolerance appear to regulate community composition more than attributes linked to the "colonizing" versus "persistent" dichotomy.

Directed Dispersal Hypothesis

A somewhat different phenomenon is occupation of special habitats by species requiring unusual edaphic conditions. "Directed dispersal" has been suggested for nuts cached by birds (185), fruits eaten by birds (90, 178), and diaspores carried to rotten logs by ants (176). A convincing confirmation must include a demonstration that dispersal agents take seeds to nonrandom places that are well-suited for establishment and growth. The best example comes from the Australian saltbush, where closely related shrubs (*Sclerolaena diacantha* and *Dissocarpus bilflorus*) occupy ant mounds. Da-

vidson & Morton (39, 40) show that both ant-dispersed and nonant-dispersed congeners grow well on ant mounds, but that ant-dispersed species have demonstrably poor growth off the mounds. For these and other plants (36), ant-assisted colonization of these well-drained and ion-rich soils appears to be obligate. Handel (70) shows that ant-dispersed sedges (*Carex pedunculata*) are disproportionately common on logs inhabited by ants in North American forests (70). Greenhouse studies show this species to be less competitive in other respects than other sedges (*C. plantaginea* and *C. platphylla*), suggesting that directed dispersal is a critical part of its fugitive strategy. The probability of seedling emergence of *Viola odorata* and *V. hirta* is greater for seeds taken to ant nests than for seeds placed randomly on or slightly below the soil surface (36). For many herbs, including *Viola* and *Carex,* the chance of seedling establishment is probably enhanced when seeds are left behind by ants moving to new nest sites (9, 35, 157, 158). A vertebrate example is the dispersal of parasitic mistletoes (*Loranthus* sp.) by Asian flowerpeckers (*Dicaeum sanguinolentum*) that scrape seeds onto host bark during defecation (44). As with dispersal by ants, seeds are taken to the best possible place for establishment.

PATTERNS OF PRODUCTION AND DISPERSAL

Four levels of analysis allow an evaluation of the spatial and temporal patterns of fruit production and the ecological processes that promote or depress dispersal. The first two sections on geographical and seasonal distributions of dispersal syndromes use inductive reasoning in an effort to identify physical correlates of dispersal modes. The third section examines the evidence that plants in the same dispersal guild (e.g. wind-dispersed, bird-dispersed) compete reproductively vis à vis fruit production and dispersal. This is a more exacting analysis, because data are used to test a priori hypotheses. The last section discusses sources of variation in dispersal success within populations.

Geographical Distribution of Syndromes

A large proportion of plants in most communities are dispersed by animals. In tropical forests, at least 50% and often 75% or more of the tree species produce fleshy fruits adapted for bird or mammal consumption (Table 2). In tropical riverine forests, an unknown but clearly large proportion of fruits is dispersed by fish (62, 63). The proportion of tree species dispersed by vertebrates is likewise high in temperate communities (> 60%, Table 2), although many plants such as oaks (*Quercus*) and hickories (*Carya*) have nuts that are regularly hoarded by birds and mammals, but lack clear modification for dispersal by animals (161). Most temperate herbs are dis-

Table 2 Percent woody plants exhibiting morphological adaptations for dispersal[a]

Location	Annual precipitation (mm)	Plant form	Percent species dispersed by:					Total no. spp.	Reference
			Vertebrates (fleshy fruits)	Wind	Water	Self	Other		
Temperate Deciduous Forests:									
1) Jennings Co., Ind.	1205	trees (>1″ dbh)	25	38	0	0	38[b]	16	114[c]
		shrubs & woody vines	100	0	0	0	0	10	
2) Orange Co., Ind.	1091	trees (>1″ dbh)	24	29	0	0	48[b]	21	139[c]
		shrubs & woody vines	85	0	0	0	15[d]	13	
3) SW Ohio	1015	canopy trees	10	38	0	0	52[b]	21	18[c]
Neotropical Aseasonal Forest:									
4) Alto Yunda, Colombia	5530	trees	89	3	—	—	8[d]	133	81
Neotropical Wet Forests:									
5) La Selva, Heredia Prov., Costa Rica	4000	canopy trees	85	13	—	—	3[d]	79	55
		sub-canopy trees	98	2	—	—	—	82	
6) Rio Palenque, Ecuador	2650	canopy trees	93	4	1	2	—	145	57
		sub-canopy trees	91	5	2	2	—	96	
		lianas	63	33	1	4	—	83	

Neotropical Moist Forest:

7) Barro Colorado Is., Panama	2650	canopy trees	78	16	1	4	—	291	57[e]
		sub-canopy trees	87	5	3	5	—	131	

Neotropical Dry Forests:

8) Santa Rosa Natl. Park, Costa Rica	c. 1800	canopy trees	64	29	1	6	—	138	57
		sub-canopy trees	77	8	0	15	—	60	
		lianas	22	71	0	6	—	49	
9) Guanacaste Prov., Costa Rica	1533	trees	51	31	—	—	18[d]	104	55

Paleotropical Forests:

10) Mt. Kinabalu, Borneo	>3985	various, including herbaceous as well as woody species	35–40	25–28	—	—	32–40[d]	360	173
11) Okomu Forest Reserve, Nigeria	1991	canopy trees	~46	~46	—	—	8[d]	180[f]	110, 111
		sub-canopy trees	70–80	6–8	—	—	12–14[d]		

Note: Dashes indicate that no data were given. Zeros indicate that fewer than 0.5% of the sample exhibited the dispersal strategy.
[a] Data from Mt. Kinabalu, Borneo, includes herbaceous as well as woody species.
[b] All represent species with nuts that may be scatter-hoarded by rodents and birds. The exception is one species (*Gymnocladus dioica*), which has no apparent means of dispersal (139).
[c] Species lists were analyzed for dispersal mode using Schopmeyer (153) and Gleason (60).
[d] No apparent means of dispersal or none mentioned by the author(s).
[e] Foster's (53) seed trap data closely approximate these results.
[f] Species list includes 180 trees not listed by life form.

persed by animals. In a mesic beech-maple forest in New York, 67% of 36 herbaceous angiosperms are animal-dispersed (71). Of these, 36% are dispersed by ants. Similarly, 30% of 23 herbs in a mixed hardwood forest in West Virginia are ant-dispersed (9). The prevalence of adaptations for animal dispersal is not limited to moist continental forests. "Waif floras" of oceanic islands include a disproportionately large number of animal-dispersed species (23), and Australian heathlands contain more than 1,500 ant-dispersed species, amounting to 35% of the total (15). In fact, communities containing few adaptations for dispersal by animals are rare. Small coral islands and beach strands have a disproportionate number of water-dispersed plants (23). Old World deserts are also depauperate in animal-dispersed species. Of 1,560 plants in the Mediterranean and semi-desert regions of Israel, only 5% have adaptations for animal dispersal. Of 604 plants in a true desert in Israel, 3% are animal-dispersed (46).

Wind-dispersed plants are relatively common in number and proportion in dry habitats, and animal-dispersed species gain importance in wet habitats. The trend is readily apparent in communities with comparable floras, such as neotropical forests (Table 2). For six such forests with samples of over 100 species of trees, there is a significant negative correlation between the percentage of wind-dispersed canopy trees and annual precipitation ($r = -0.78$, $p < 0.05$). Daubenmire (38) and Gentry (57) give similar data for sites in Costa Rica, Brazil, Venezuela, Panama, and Ecuador, but the samples of trees discussed average less than 10% of the species in those sites. Gentry (57) attributes the trend toward animal dispersal in wet habitats to increasing representation of families dispersed by vertebrates as one moves from dry to wet forests. That ecological factors can play a local role is, however, shown by Handel and his co-workers (71), who document a greater number and proportion of animal-dispersed herbs in damp than dry sites within a mesic temperate forest. Carlquist (23) suggests a trend towards animal dispersal on mesic oceanic islands, but the distance from source areas confounds interpretation. Virtually no wind-dispersed species occur on extremely isolated atolls (23).

Finally, clear differences exist in the syndromes characteristic of different life forms in a forest. Most wind-dispersed plants are canopy trees or vines; few are small trees or shrubs (Table 2). Keay (113) found that none of the five liana species producing fruit below the canopy was wind-dispersed, whereas 48% (n = 25) of those with fruits in the canopy were wind-dispersed (Fisher test, $p = 0.06$). We conclude that consistent strong winds promote wind-dispersal, while mesic conditions promote animal-dispersal, whether the level of analysis is comparison of communities (Table 2), life forms within a community (Table 2), or local differences within a life form (71, 113).

Seasonal Fruiting Patterns

All studies of tropical fruiting phenologies report seasonality, ranging from the extreme in forests with a distinct wet and dry cycle (24, 33, 34, 53, 55, 83, 99, 127, 134, 162, 198; also 51, 52, 117) to minor in forests with heavy rainfall throughout the year (81). Wind-dispersed fruits tend to be produced in the dry season in deciduous forests of western Costa Rica (55), and in seasonal wet forests of Panama (53), Guyana (24), and Brazil (99). Conversely, vertebrate-dispersed fruits tend to be produced during the wettest months of the year at those sites, as well as in relatively aseasonal forests of eastern Costa Rica (55) and Colombia (81). Some phenologies may be keyed to times optimal for germination and establishment (56). But these seasonal patterns support the interpretation that dry, windy weather favors wind dispersal, wet weather promotes animal dispersal.

The temperate winter enforces pattern on fruiting phenology; most plants flower in the spring or summer and fruit later the same year. But schedules of fruit production and depletion do suggest adaptation to dispersal opportunities. Thompson (177) notes that spring herbs are usually ant-dispersed, while late summer and autumn herbs take advantage of migrant birds. The pattern even holds for members of the same family (Liliaceae) in the same habitat. Thompson & Willson (179) and Stiles (175) discuss patterns of fruit production and depletion for woody plants in American deciduous forests. Most bird-dispersed plants ripen in late summer and early fall. Some (e.g. *Smilacina, Lindera*) are taken immediately; others (e.g. *Smilas, Euonymus*) persist through the winter and are slowly eaten by wintering birds (179). Only a few (e.g. *Prunus serotina*) ripen and disperse fruits in the summer (179). The plants apparently are keyed to the presence of birds gathering for migration or wintering in the north.

Production and Dispersal: Variation Among Species

Empirical tests of general hypotheses are leading to rapid advances in dispersal ecology. Most work concerns fruit removal by birds and bats, but recent studies of dispersal by wind and water challenge long-held assumptions about the causes and consequences of dispersal. One unique investigation even indicates competition among seeds that stick to mammal fur.

FRUGIVORY   Interest in the feeding ecology of tropical birds led to the original framework for interpreting plant competition for dispersal agents. Snow (165) provided an ecological context by suggesting that adaptive strategies of fruit production, presentation, and nutritional rewards are "designed" to attract the greatest number and variety of dispersers possible. A second germinal paper by McKey (126) suggested two alternative strate-

gies of dispersal in tropical plants that compete for dispersal agents. In the "low investment model" plants invest little in individual seeds and fruits, using large crops to attract a variety of opportunistic birds willing to use a superabundant, if nutritionally limited, source of food. In the "high investment model" plants limit fruit production to large seeds and rich pulp, and thereby limit dispersal to specialized birds willing and able to seek out a rare and bulky, but exceptionally nutritious, food resource.

Howe & Estabrook (90) extend McKey's argument to make it testable. They reason that individual tropical trees should time fruit production to take best advantage of their disperser assemblages. "Low investment trees" should produce superabundant fruits in peaked displays that attract the largest number and variety of visitors possible. Lack of competition among dispersal agents for superabundant fruits promotes diverse assemblages, dissemination of seeds to a variety of habitats, and freedom from dependence on a limited set of dispersal agents. "High investment plants" extend fruiting seasons to avoid satiating a limited set of specialists, thereby promoting predictable seed removal by efficient foragers.

A series of studies of Costa Rican and Panamanian dispersal systems generally supports the dichotomy between nutrient-rich fruits eaten by a few specialists, and minute or starchy arils utilized by a wide variety of birds and mammals (Table 3). Two Panamanian *Virola* species have virtually identical assemblages, even though *V. sebifera* has an arillate seed of 0.3 g that could be eaten by almost any frugivore on Barro Colorado Island, while the 3.79 g *V. surinamensis* diaspore is too large for most birds to swallow. In a community of 78 fruit-eating birds and mammals, an assemblage of 7 or 8 dispersal agents indicates considerable specialization. The fact that the trees share the same assemblage is intriguing because the same birds eat similar fruits of very different sizes. Plants with minute or starchy arils, such as *Guarea* and *Tetragastris,* attract more diverse assemblages but disperse smaller proportions of fruits. Plants with rich fruits are efficiently depleted by relatively small assemblages, but aril richness is not closely linked to seed size. Anomalous results include visitation of *Stemmadenia donnell-smithii* by 22 species of Costa Rican birds (125). Competition for the extremely oily *Stemmadenia* fruit should produce a limited assemblage (90). As intriguing is Greenberg's (67) discovery that two North American wood warblers (*Dendroica*) are found at Panamanian *Miconia* and *Lindackeria* trees far out of proportion to the abundance of the birds in surrounding forest. In fact, *Lindackeria* is likely to be a "warbler tree." Specialization on fruits by normally insectivorous migrants is not expected in McKey's scheme.

Phenological records of the quantity of fruits produced throughout the season neither strongly support nor contradict the hypothesis that tropical trees regulate fruit production to maximize dispersal (see 174). Toucans

Table 3 Assemblage size and relative dispersal success of neotropical trees visited by birds and mammals

| Species | Trees (N) | Frugivore spp. (N) | Percent of the crop taken | | | Source |
			Total (%)	Range per tree (%)	Mean per tree (± SE %)	
High investment						
Casearia corymbosa	17	14	91	0–98	83 ± 6	93
Virola sebifera	14	7	75	40–89	76 ± 4	87
Virola surinamensis	19	8	62	13–91	62 ± 5	95
Low investment						
Guarea glabra	12	19	"low"[a]	not calculated[a]		89
Tetragastris panamensis	19	23	28	1–38	23 ± 3	86

[a] Seed traps not used.

feeding on heavily laden *Virola sebifera* trees do regurgitate seeds in place rather than carry them away (87; also 84), but individual fruiting curves are nonetheless peaked (H. F. Howe, personal observation). Fruiting curves of *Virola surinamensis* are, as expected, significantly more flattened than those of *Tetragastris panamensis,* but both are definitely peaked (88). Dry-forest *Casearia corymbosa* phenologies may be peaked, flattened, bimodal, or simply irregular (93). Fleming (48) does show that a shrub, *Piper amalago,* has an extended fruiting period and is consistently and preferentially depleted by the Costa Rican bat *Carollia perspicillata* (also 50, 75). But most tropical shrubs appear to have extended fruiting seasons (55, 57, 81, 134; also 53, 99, 164), suggesting that alternative patterns (e.g. 3) may be infeasible in the deep shade of the forest understory (147). As yet, neither feeding assemblages nor kurtosis values for fruiting phenologies are well enough known to test predictions regarding the shapes of fruiting curves of tropical trees.

Other species may intercede in the interaction between frugivores and trees. Howe (85) added a "predator avoidance" model in which small "fearful frugivores" process fruits in the cover of surrounding underbrush, rather than expose themselves to predators in open feeding trees. The predators complicate the effect of bird visitation on fruiting phenology because bird activity is only loosely tied to fruit abundance. Peripatetic movements of small birds (67, 84, 85, 93) and bats (4, 75, 128, 129) in and around fruiting trees suggest that predator avoidance is a credible hypothesis, but the "predator avoidance" model has not been rigorously tested.

The facultative and highly seasonal nature of temperate frugivory precludes the sort of dichotomy envisioned by McKey (126), but recent studies of temperate dispersal ecology clarify the selective forces on fruiting plants.

Several authors, for instance, have emphasized that the pulp of tropical fruits averages higher in energetic and nutritive value than the pulp of temperate fruits, presumably taking advantage of a high diversity and abundance of tropical fruit specialists (90, 126, 165, 191). But Herrera (77) shows that the ratio of energetic reward of the pulp to indigestible ballast of the seed is equivalent in temperate and tropical fruits. The real difference is that many tropical fruits have large seeds (see 147) and correspondingly rich pulp, while most temperate fruits have small seeds and a smaller nutritional reward. The diaspores of large-seeded temperate trees dispersed by animals are nuts, not fleshy fruits (77, 161, 181, 185). Further, considerable variation exists in fruit quality within a temperate forest (175). Most species fruit in the late summer and early fall when birds are storing fat for migration. Shrubs fruiting at that time have energy and nutrient-rich pulp, while those with fruits persistent through the winter have starchy pulp. Presumably plants competing for dispersal agents do so partly on the basis of pulp quality, while those dispersed during times of avian food shortage need not invest as much (175). The local abundance and diversity of both fruits and birds may, however, be all-important. Winter fruits in southern Spain have high profitabilities, matching the needs of wintering birds (76). Plants may compete for birds more intensely in southern Europe than in eastern North America. The general insight from these studies is that temperate fruits are on average as "profitable" as tropical ones, and that this "profitability" may vary with the ecological conditions under which each species must disseminate its fruits.

Complementary to documentation of high reward to bulk ratios in temperate fruits is the discovery that some temperate plants are completely stripped of fruits, while others are not (79, 169, 171, 175, 179). Many studies fail to distinguish actual removal by birds from rodent predation or spontaneous fruit drop, but direct observations in extensive forests in England (169) and southern Spain (79) make it clear that temperate migrants deplete some crops (e.g. *Sambucus, Crataegus, Prunus*) under natural circumstances. "Efficient" dispersal is not solely a tropical phenomenon, nor is it necessarily closely linked to fruit quality. As important are the seasonal abundances of birds and the presence of alternative food sources (78, 169, 171).

OTHER CASES   Investigations of dispersal by water, wind, and external adhesion to animals lack the theoretical development characteristic of the study of frugivory, but nonetheless distinguish alternatives. Reciprocal plantings show that the size of water-dispersed mangrove propagules accounts for zonation of five species along the coast of Panama; microhabitat

adaptation by seedlings cannot account for adult distributions (142–144). A question of general significance is whether weight or aerodynamic properties determine the maximum dispersal of wind-dispersed diaspores (see 21, 66, 131). Field tests show that peculiarities of morphology are more influential than weight in prairie grasses (145) and forbs (138). Experimental tests of persistence of seeds that stick to animal fur show that three Costa Rican herbs have dramatically different dispersal distances in different habitats (20). The rationales for these studies differ, but all show a progressive step from description to hypothesis-testing.

Production and Dispersal: Variation Within Species

Variation exists in both the absolute and relative dispersal of fruits eaten by vertebrates. The number of seeds removed from a tree is directly related to its crop size in six tropical and temperate species (84, 87, 89, 93, 95, 170); large plants clearly disseminate more seeds than small ones. As important, some individuals disperse a higher proportion of seeds than others (Table 3). If consistent throughout the lives of the plants, such differences could result in dramatic differences in reproduction. The question facing the evolutionary ecologist is whether variations in relative success are inherent to the plants or imposed by environmental circumstance.

Both quantity and quality of fruits are influenced by genetic differences (e.g. 135) and are consequently subject to natural selection. Howe & Estabrook (90) argue that different patterns of fruit production should make best use of feeding assemblages, whether "limited" or "diverse." Intraspecific comparisons should show that assemblage size is independent of crop size in "high investment" trees, and that a higher fraction of fruits is taken from crops of intermediate size than from small crops that are difficult to locate or from large crops that satiate the assemblage. On the other hand, assemblage size as well as relative success should increase with fruit availability in "low investment" trees that depend on a wide array of opportunists. Alternatively, fruit quality may vary among individuals (94). As has been suggested in interspecific comparisons (126, 165), selection might act upon individual differences in the nutritional composition of the pulp, or the ratio of edible pulp to inedible seed. Adaptive modulation of crop size would imply a trade-off between crop size and longevity (90), while adaptive regulation of fruit and seed characters could indicate a trade-off between dispersibility and seedling vigor.

Assemblage characteristics generally conform to the "high investment" and "low investment" frameworks, but evidence that crop size influences relative dispersal success is equivocal or negative (cf 7, 59). The number of species eating the oily fruits of *Virola surinamensis* and *V. sebifera* is both

small (Table 3) and unaffected by crop size (87, 95). The richness of the assemblage increases with crop size at *Casearia corymbosa,* which also has an oily aril, but the rare additions eat a negligible number of fruits (93). Assemblage richness increases with the number of fruits available at *Guarea glabra* (89) and *Tetragastris panamensis* (86), indicating that "low investment" fruits are acceptable to a wide range of fruit-eating animals. But influences of assemblage diversity on dispersal are not clear, aside from the general observation that rich fruits are depleted more consistently than others (Table 3). There is no correlation between the fraction of fruits taken and crop size at either of two *Virola* species [(95); H. F. Howe, personal observation).] Higher proportions of fruits are taken from *Casearia* trees of intermediate fecundity (93), but birds leave the trees to avoid raptors, not because fruit availability controls their actions (85). "Low investment" trees likewise fail to show the expected disproportionate increase in dispersal with crop size. At *Guarea,* no significant relationship exists (89). At *Tetragastris,* there is a weak tendency for trees of intermediate size to disperse a higher proportion of seeds than others (86). An initial enhancement of fruit removal with increasing crop size is reversed by heavy parrot predation at two very large trees. In the cases surveyed so far, intraspecific variation in crop size accounts for little, if any, variation in relative dispersal success.

Fruits from different species of trees vary dramatically in energetic and nutritional quality (163, 175, 191), but few studies address the possibility that fruit quality varies within species. Howe & Vande Kerckhove (94, 95) show substantial differences in the total and proportional representation of lipid, protein, and soluble carbohydrate of arils from different *Virola surinamensis* trees, but none is correlated with the proportion of fruits taken by dispersal agents. Arils from different trees also differ in weight and energetic content, but neither is associated with dispersal success. The startling result is that the ratio of edible aril to inedible seed weight varies from 0.32 to 0.60 ($\bar{x} = 0.48 \pm 0.03$ SE) among trees, accounting for 52% of the variation in the percentage of fruits taken during a "normal" year (see Table 3). Toucans and other frugivorous birds evidently optimize the ratio of food to bulk, perhaps using seed weight as the proximate cue (94). The aril/seed ratio accounted for a significant but lesser proportion of the variation in dispersal success during a "bumper" year when the proximity of neighbors played a more important role (124). The variances in seed weight within and between trees are both sufficient to influence seedling vigor, but the variation between trees is three times that within trees (92). Selection may alternately favor plants with dispersible fruits when frugivores are common, and those with competitive seedlings when fruit-eating animals are rare. In such a scheme, most individuals within the population represent a trade-off in dispersibility and seedling vigor, the relevance of

which can only be detected in individuals on the extremes of the reward/ bulk continuum.

Other evidence suggests that aril/seed ratios figure importantly in dispersal ecology. Herrera found that high aril/seed ratios are characteristic of *Smilax aspera* populations in regions of southern Spain where they must compete with several other species of fruiting plants, as compared with areas where few competitors co-occur (76). Differences were due to variations in seed number per fruit; where several common competitors co-exist, *Smilax* usually has one seed per fruit. Where few co-occur, there may be as many as three per fruit. The challenge in this system will be distinguishing effects of intraspecific from interspecific competition. Individuals should compete within a population for whatever dispersal agents are available, whether or not other plant species are common (90). The critical factor may be the preferences and abundances of dispersal agents rather than the presence or absence of competing plants of other species. A second challenge will be exclusion of regional selection on seed size and number independent of dispersal (5; see 192). At this point, however, Herrera's argument that competition for a limited disperser resource modulates aril/seed ratios is the most convincing on record.

CONCLUSIONS

Recent approaches to seed dispersal contribute both an awareness of the consequences of spatial relations and a commitment to distinguishing alternative hypotheses. At the same time, changing views of the role of dispersal in species regeneration or replacement shape evolving concepts of the community.

Testability

Conceptual and methodological difficulties hamper attempts to tease apart advantages to dispersal processes and modes. The Escape, Colonization, and Directed Dispersal Hypotheses are in principle difficult to distinguish because they are not exclusive. Demonstration of density-dependent seedling mortality under parent trees supports the Escape Hypothesis, but does not necessarily exclude the possibility that seedlings need light gaps for growth. Similarly, directed dispersal to ant mounds may work in conjunction with escape from rodent predation. Even demonstration of density-independent seed and seedling mortality cannot exclude a local advantage to dispersal, if seeds must colonize disturbances for seedling growth and establishment. The real challenge, in most systems, is to determine the relative importance of each advantage, not the exclusive advantage of one.

Existing methods help address the challenge. Quantitative demographies unequivocally show disproportionate mortality in seed and seedling stages (see 29, 72, 152; also 168, 180). When applied to spatial distributions, such methods become tools for determining the influences of dispersal on parental fitness (137). Further documentation of sources of mortality gives some insight into the selective forces acting on plant reproduction. Dispersal studies document density-dependent predation on seeds and seedlings (e.g. 25, 91, 109, 150; but see 19), but mapping studies implicate competition among saplings more than a legacy of insect depredation (96). It is quite possible that seed predators fail to affect plant distributions because they rarely push density below that at which competition ultimately limits occupation of space (72). As important, few investigations exclude the possibility of edaphic specialization (143). Conditions required for establishment or growth may offset an apparent early advantage to escape from parents, thereby reversing confirmatory evidence for the Escape Hypothesis and blurring the distinction between broadcast colonization and directed dispersal. Work has begun (e.g. 25, 36, 39, 136–138, 142–144, 150, 187), but enormous potential still exists for clarifying dispersal by relating factors affecting growth and survival to distributions of seeds, seedlings, and later stages.

As integration of demography and dispersal processes proceeds, the study of dispersal mode is emerging from anecdote. Some surveys of fruiting phenologies are replicated (33, 53, 83, 162) and are complemented by studies of seed germination (56), disperser abundance (82, 196; see 112), and disperser impact (67, 82, 89, 116). Complementation allows a more detailed inductive evaluation of the timing of fruit production than is possible when phenology is considered in isolation. The most rapid advances come from explicit tests of theoretical frameworks, such as the "high" and "low investment" dichotomy for tropical fruits dispersed by birds (90, 126). In a few short years, direct tests have clarified the roles of assemblage characteristics, fruit quantity and quality, and neighborhood effects in fruit dispersal (84–95, 124), while challenges to the tropical framework have demonstrated efficient dispersal in many temperate systems (79, 159, 169, 171, 175, 179). Even the widely cited assertion that tropical fruits are inherently more nutritious than temperate fruits is in question (77). Integration of description, demography, and a dialectical method is leading to an explosion of interest and understanding in an important facet of plant population biology.

Community Implications

Processes and modes of dispersal figure in our views of succession (see 189), biogeography (23, 123, 149), competitive exclusion (123, 136, 188, 194),

tropical species diversity (26, 100), disturbance ecology (27, 73, 96, 195), and plant and animal coevolution (31, 90, 126, 161, 165). Of particular current interest are the implications of material reviewed here for our notions of "community integrity" and coevolution.

Dispersal hypotheses reflect historical biases in community ecology. The distinction between colonizing "r-selected" and persistent "K-selected" species has its roots in classical phytogeography (23, 149), and has had a critical influence on views of niche-partitioning and island biogeography during the past 20 years (123). Now the utility of the r-K dichotomy is in question (see 192), as evidenced by the surprising vagility of large-seeded species (42, 181, 185, 186) and the observation that seed size varies with climate (5). Yet the theory figures prominently in current models of forest disturbance and regeneration (96, 97, 189). The Escape Hypothesis was proposed to account for the hyperdispersion of trees thought to promote high tropical species diversity (26, 100). It is now clear that tropical trees are not hyperdispersed (96; also 49) and that recorded levels of seed predation cannot account for high species diversity (97). Yet the Escape Hypothesis is a demonstrably viable alternative in dispersal ecology. Escape may be the primary advantage in dispersal for some shade tolerant forest trees and is likely an important secondary benefit for others. One current view is that species do not coexist in long, predictable relationships: Colonization of disturbances and random local extinctions continually alter species abundances and interactions (27, 96; also 41). The observation that many or most forest trees (43, 73, 195), like herbs (6, 187, 188), recruit best in local disturbances is consistent with the general notion of nonequilibrial assemblages, and promises a prominent role for the Colonization Hypothesis.

Do plants and their dispersal agents coevolve? A general lack of specificity in seed dispersal is consistent with the notion that coevolution reflects adaptation to arrays of similar organisms rather than to particular species (78, 86, 87, 190). Interactions between herbs and ants are general: Most ground-foraging ants take seeds, and different plant species rely on the same guild of seed vectors (9, 10, 14, 35). Some tropical fruits are eaten by a few birds, but even most limited assemblages include species with quite different taxonomic affinities (87, 93, 94). Other fruits are eaten by dozens of birds and mammals differing in size by up to two orders of magnitude (86, 125). Apparent specialization may reflect differences in the relative abundance of dispersal agents (86), or facultative local specialization (84, 93). Adaptations are often asymmetrical. Jays and nutcrackers have well-developed morphological (16) and behavioral (186) adaptations for carrying and storing seeds and nuts that have few modifications for dispersal. Perhaps most telling, many plants of the Old World Tropics evolved before their present dispersal agents existed (166). Coevolution, where it occurs, reflects long-

term interactions between taxonomic categories far wider than the species or genus (47, 87). Dynamic associations simply preclude consistent, long-term coevolutionary relationships between dispersal agents and particular food plants.

In sum, dispersal ecology has contributed to several paradigms in community ecology. At present, ubiquitous importance of colonization of local disturbances and the loose nature of relationships between plants and dispersal agents contribute to the view that communities exist in continual flux. The only caveat is that studies of dispersal, applied to this and other paradigms, must be done in a discriminating fashion. Somewhere, there may be a bird that eats only one fruit.

ACKNOWLEDGMENTS

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