

CHAPTER ELEVEN

Seed dispersal of woody plants in tropical forests: concepts, examples and future directions

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Introduction

Understanding seed dispersal is critical to understanding plant population and community dynamics (Nathan & Muller-Landau 2000), especially in tropical forests where seed rain of virtually all plant species is sparse and patchy (Hubbell *et al.* 1999; Muller-Landau *et al.* 2002). Seed rain determines potential population growth rates and spatial patterns, as well as the relative influences of post-dispersal processes such as seed predation (e.g. Wright *et al.* 2000), microhabitat requirements for establishment (e.g. Svenning 1999) and density-dependent survival (e.g. Harms *et al.* 2000). Despite its importance, we know very little about seed dispersal of tropical trees, because it has been studied in only a tiny proportion of the many tropical tree species and seed dispersers, and because the patterns that have been observed have largely eluded easy generalization.

Just as there is a greater diversity of plant species and animal species in the tropics than in other regions, there is also a greater diversity of seed-dispersal strategies and patterns. Seed dispersal by animals predominates – it is the main strategy of 70%–90% of tropical forest plant species (Willson *et al.* 1989) – and involves a tremendous diversity of animal species and behaviours. Birds, bats, arboreal and terrestrial mammals (everything from mice to elephants), ants, dung beetles, even fish can disperse seeds (Levey *et al.* 1994). Animals may consume fruit and drop, spit or defecate the seeds, carry seeds in their coats or scatter-hoard seeds for later consumption. Abiotic strategies such as wind, water and ballistic dispersal form the main mode of seed movement for the remaining 10%–30% of tropical tree species (Willson *et al.* 1989). The seeds of many species may experience both primary dispersal (movement before the seed reaches the ground) and secondary dispersal (subsequent movement) usually by different modes or different animal species (e.g. movement by ballistic dispersal and then

by ants; movement by primate frugivores and then by rodent scatter-hoarders). Thus, understanding the complete seed rain of any given plant species may require understanding seed movement by a wide range of processes, each influenced by many different factors.

In this chapter, we begin by considering the relative importance of different vectors and animal groups to seed removal and the degree of specialization in plant–frugivore interactions in tropical forests. Next, we turn to seed deposition, where we examine patterns with respect to distance from the parent plant, habitat and clumping, in turn. Most seed-dispersal research has focused on patterns of seed deposition with respect to distance from the parent and/or distance to the nearest conspecific. We argue that the scales and magnitude of clumping of seed rain, and any biases in where seeds arrive by habitat, are at least as important. For each type of pattern, we consider the selective forces involved, and provide examples of variation in observed patterns and recommendations for researchers. Throughout, we draw extensively on studies from Barro Colorado Island, Panama (BCI), one of the best-studied tropical forests in the world (Leigh *et al.* 1996), both because we know this forest best, and because the multitude of studies at this site makes more comprehensive analyses possible. In the last section, we discuss exciting new developments in technologies and analytical methods and their promise for studies of seed dispersal, as well as areas most urgently in need of further study, including conservation implications.

Seed removal

The relative importance of different vectors

Overall, the proportion of plant species that are fleshy-fruited and thus presumed to be animal-dispersed varies between 70% and 100% in tropical rain forests around the world, with the proportion of tree species consistently above 65% (Willson *et al.* 1989). As precipitation decreases and dry-season length increases, animal dispersal becomes less common and wind dispersal more common (Bullock 1995; Gentry 1982; Willson *et al.* 1989). Water dispersal is, unsurprisingly, more common on wetter sites (Gentry 1983). There appears to be no relationship between edaphic conditions and dispersal mode (Gentry 1983). Within all forests, dispersal mode varies with life form. Wind dispersal is most common in lianas (often > 50% species), less common in large trees, and very rare in the understorey of tropical forests (Bullock 1995; Gentry 1982). Studies inferring whether plants are bird- or mammal-dispersed based on congener information or fruit morphology further suggest that mammal dispersal is more common than bird dispersal among taller trees while bird dispersal is relatively more common in lower-statured trees (Gentry 1982).

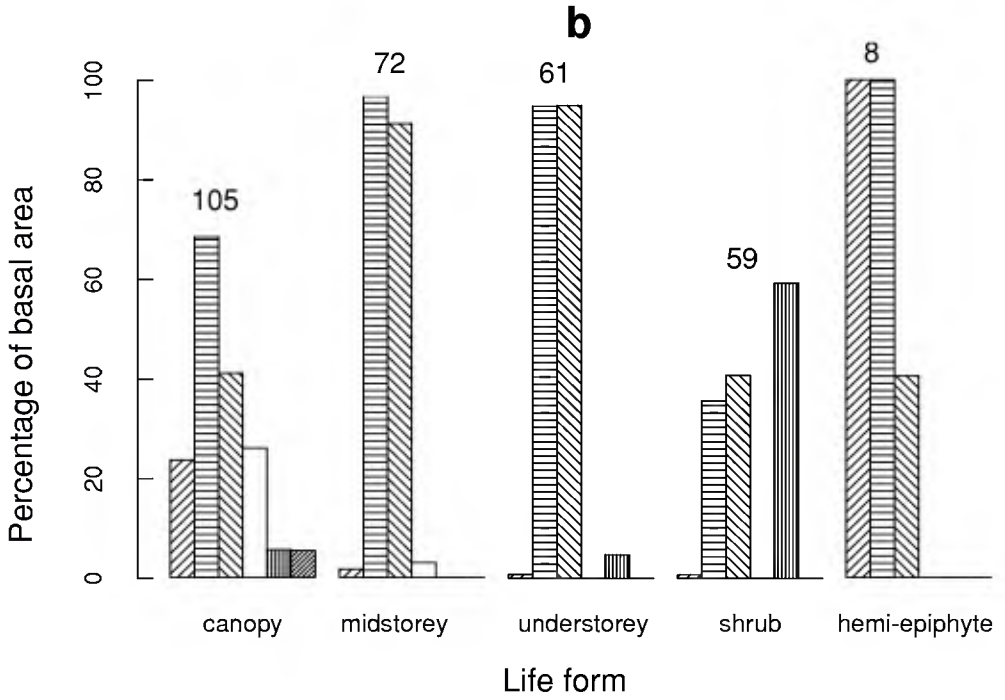
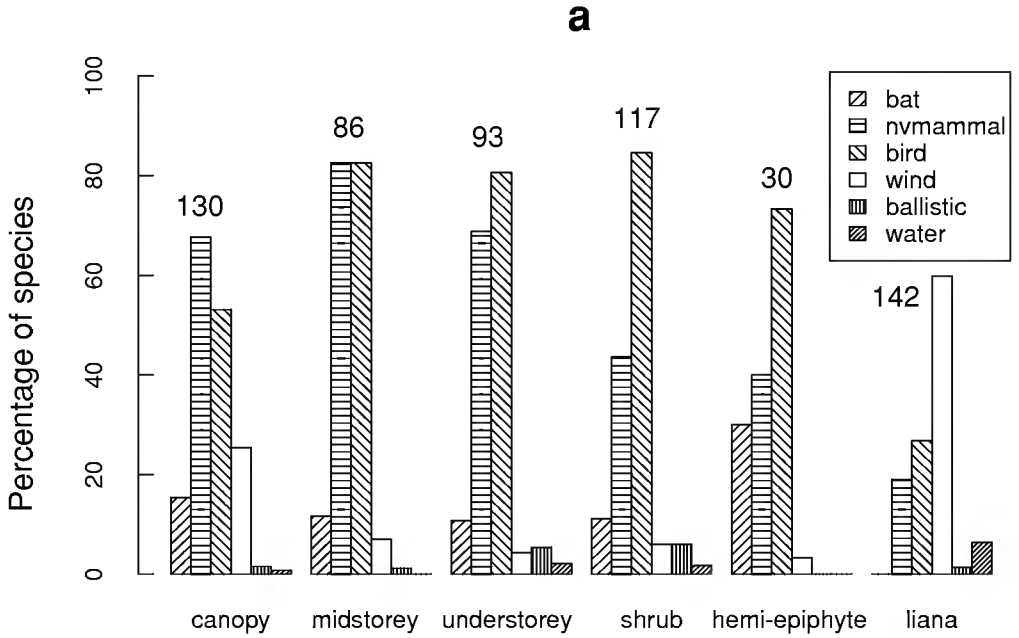
Most studies of the frequency of different dispersal syndromes among plant species in tropical forests infer dispersal syndrome from seed and fruit morphology. It is relatively straightforward to classify species as primarily wind-dispersed, ballistically dispersed, ectozoochorously dispersed (on the coats of animals) or

endozoochorously dispersed (by fruit consumption). It is more difficult to go further and infer which group of animals is the principal disperser of endozoochorous fruits. Janson (1983) proposed that fruits in a Peruvian forest could be identified as predominantly bird- or mammal-dispersed on the basis of their colour, size and degree of protection. In particular, he classified as bird-dispersed fruits that were unprotected (no husk), relatively small (< 1.4 cm in the smallest dimension) and red, black, white, blue, purple or multi-coloured. Fruits that were protected, large and coloured orange, yellow, brown or green were classified as mammal-dispersed. This is similar to classifications used by other authors (Gautier-Hion *et al.* 1985; Gentry 1982; Willson *et al.* 1989), although Gautier-Hion *et al.* (1985) find that in an African forest this division corresponds not to dispersal by birds versus mammals, but rather birds and monkeys versus ruminants, rodents and elephants.

The accuracy of the Janson classification of fruits as mainly bird- or non-volant mammal-dispersed (Janson 1983) was tested on BCI (S. J. Wright and O. Calderón, unpublished data), another neotropical forest with a relatively similar animal community (Leigh 1999; Terborgh & Wright 1994). Of 78 common, animal-dispersed, woody plant species, only 37 (47%) fit neatly into one of Janson's two categories. Of the 20 species thus classified as bird fruits, all are indeed known to be dispersed by birds, and all 17 species classed as mammal species are known to be dispersed by mammals. However, these species are also dispersed by other means (all 20 'bird' fruits are dispersed by nonvolant mammals, and 14 of 17 'mammal' fruits by birds). Of the 41 unclassified species, all are known to be dispersed by at least two of the three vertebrate groups (birds, bats and nonvolant mammals). Overall, it appears that inferences from fruit morphology do not reliably identify fruit consumers of a given plant species in this moderately diverse tropical forest (Howe 1986).

Given the diversity of plants and animals in tropical forests, there are very few sites at which we can identify the major animal fruit consumers (and generally seed dispersers) of many plant species from observations rather than inferences. In Central Panama, such information has been compiled for most plant species by S. J. Wright and O. Calderón from their own observations and numerous studies of frugivorous animals (e.g. Forget & Milleron 1991; Kalko *et al.* 1996b; Milton 1980; Poulin *et al.* 1999; Wehncke *et al.* 2003) and animal-dispersed plants (e.g. Croat 1978; Martin 1985). Furthermore, long-term studies of forest dynamics provide complementary information on the adult stature and abundances of free-standing woody plant species, allowing us to examine not only the proportion of species but also the proportion of basal area within various life-form classes that are dispersed in different ways (Condit *et al.* 1996; Hubbell & Foster 1983).

On BCI, primary dispersal of 73% of the woody plant species (encompassing 71% of the basal area of free-standing woody plants over 1 cm in diameter within the 50 ha Forest Dynamics Plot) is exclusively by animals, and of 26% (25%) is



exclusively abiotic by wind, water, and ballistic means (Fig. 11.1). Wind dispersal is very common among lianas (60% of species) and is found in a quarter of canopy trees, but is rare among smaller-statured trees and hemi-epiphytes. Explosive dispersal is generally rare, but is the strategy employed by several of the most common shrub species (especially *Hybanthus prunifolius*), and thus 60% of shrub basal area is accounted for by ballistically dispersed species. Bird dispersal is most common in midstorey trees, understorey trees and shrub species. Dispersal by bats appears to be rare, although this probably reflects a relative paucity of knowledge even at this well-studied site, where 72 species of bats (E. Kalko, personal communication), including 25 frugivorous species, are known to occur (Kalko *et al.* 1996a). Water dispersal is very rare, and is found most often among liana species, 6% of which are thought to be mainly water-dispersed. The proportion of species secondarily dispersed by ants, dung beetles and other invertebrates is not known on BCI, but is likely to be high.

An alternative way to assess the importance of different animal groups to seed removal is to calculate the amount of fruit and seed biomass consumed by each. This requires information for each species on population density, feeding rates (grams dry weight consumed per day) and the proportion of fruit in the diet. Feeding rates can be estimated from body mass using allometric relationships (Nagy 1987). To truly understand the implications for seed dispersal requires further information on seed treatment and subsequent viability – disperser quality as well as quantity (Schupp 1993). In the absence of this information, and, more generally, in the absence of information distinguishing fruit and seed consumption, the estimates that we can make include both seed dispersal and seed predation.

Although birds and nonvolant mammals are similarly likely to participate in dispersing seeds of a particular species on BCI (Fig. 11.1), nonvolant mammals

← **Figure 11.1** For each life form, the percentages of (a) all species on BCI and (b) species weighted by their basal area in the BCI 50-ha Forest Dynamics Plot whose seeds are dispersed by different groups of animals (nvmammal = nonvolant mammals) and/or different abiotic methods. Species that are dispersed in multiple ways are accordingly counted multiple times, and thus the totals in each category often exceed 100%. All animal-disperser assignments are based on actual observations. Species for which no dispersal syndrome information was available were omitted. Free-standing woody plant life forms are defined by mature height: canopy trees as > 20 m, midstorey trees as 10–20 m, understorey treelets as 4–10 m, and shrubs as 1–4 m. Note that no basal area data is available for lianas, and that the basal area data for hemi-epiphytes includes only free-standing individuals. The number of species included in each life-form category in each panel is given above the corresponding bars. Dispersal syndrome data courtesy of S. J. Wright and O. Calderon; basal area data courtesy of the Center for Tropical Forest Science, Smithsonian Institution, Washington DC.

consume many times more fruit and seed biomass than birds and bats combined (Tables 11.1, 11.2). Two-thirds of this consumption is by animals that are known to be both seed dispersers and seed predators – mostly by terrestrial mammals. Even if we exclude species that act exclusively or in part as seed predators, however, nonvolant mammals still dominate in the biomass of fruit consumed. Seed predation is much less common among birds (Willis 1990) and has rarely been recorded among bats (but see Flannery 1995; Nogueira & Peracchi 2003). Each of these groups of animals includes many species on BCI: 16 species of nonvolant mammals (Leigh 1999), 25 species of bats (Kalko *et al.* 1996a) and 79 species of birds (Willis 1990) are known to consume fruits and/or seeds. Fruit and seed biomass consumption varies tremendously within groups, with most species and families contributing relatively little (Table 11.1). One species, *Alouatta palliata* (mantled howler monkey), accounts for over half the total for nonvolant mammals that are exclusive seed dispersers, and one species of bat, *Artibeus jamaicensis* (Jamaican fruit bat), similarly accounts for over half of all fruit biomass consumed by bats. Among birds, the most important species, *Tinamus major* (great tinamou), accounts for only 11% of the fruit and seed biomass consumption.

Animal communities differ among tropical forests, and thus the relative importance of different animal groups to fruit and seed consumption, and seed dispersal, also vary. We expect that most other tropical sites, with the exception of some monodominant forests, will have frugivore assemblages as diverse as or more diverse than that of BCI. For example, a family-level analysis suggests that the frugivore community is more diverse at La Selva, an everwet site in Costa Rica (Levey *et al.* 1994). In more-diverse frugivore communities, the most important species are likely to account for a smaller share of total fruit and seed consumption than on BCI. A pantropical comparison of primarily frugivorous birds by Snow (1981) finds ecologically similar though taxonomically disparate groups of avian frugivores in each region, except that Africa has comparatively few species of both specialized avian frugivores and plants belonging to families that such birds prefer. Levey *et al.* (1994) compare frugivore communities across the tropics for selected groups of birds and mammals, and find many parallels, but also some intriguing differences among the mammals. Calculations by Leigh (1999) suggest that mammals eat several times more fruit on the ground in BCI than they do in a climatically similar tropical forest in Parque Manu in Amazonian Peru, while consumption in trees by nonvolant mammals and birds is similar. Corlett (1998) reviews fruit and seed consumption by vertebrates in the Asian tropics, and finds frugivory to be very common among both mammals and birds, while seed predation is restricted to fewer species. Overall, few quantitative data are available for comparisons of frugivore communities, beyond examinations of species lists and general dietary information, and this is an obvious avenue for further research.

Table 11.1 *The densities and estimated fruit and seed consumption of birds and mammals whose diets include a substantial proportion of seeds and fruits (>10%) on BCI, by family*

Family	Status	Frugivorous species	Frugivore density (km ⁻²)	Estimated fruit and seed consumption (kg ha ⁻¹ yr ⁻¹)
Mammals				
Cebidae (cebid monkeys)	disperser	4	104	57
Procyonidae (raccoons)	disperser	3	44	19
Phyllostomidae (leaf-nosed bats)	disperser	25	346	8.9
Didelphidae (opossums)	disperser	5	107	6.7
Cervidae (deer)	disperser	1	3	2.8–6.3
Megalonychidae (two-toed sloths)	disperser	1	50	0–2.9
Mustelidae (weasels)	disperser	1	2	0.80–1.4
Callitrichidae (marmosets and tamarins)	disperser	1	3	0.36
Dasyproctidae (agoutis)	disperser/predator	1	100	59
Agoutidae (pacas)	disperser/predator	1	40	50–56
Tayassuidae (peccaries)	disperser/predator	1	10	17–30
Echimyidae (spiny and tree rats)	disperser/predator	1	180	20
Sciuridae (squirrels)	disperser/predator	1	180	14
Tapiridae (tapirs)	disperser/predator	1	0.5	1.0–6.1
Muridae (mice)	disperser/predator	1	133	3.3–3.7
Birds				
Ramphastidae (toucans)	disperser	3	60	0.7–6.2
Tyrannidae (tyrant-flycatchers)	disperser	14	239	0.3–3.0
Cotingidae (cotingas)	disperser	6	55.3	0.17
Thraupidae (tanagers)	disperser	11	149	0.2–2.1
Trogonidae (trogons)	disperser	5	47	0.2–1.7
Cracidae (curassows, guans and chachalacas)	disperser	2	4.7	0.9
Cathartidae (American vultures)	disperser	1	4.7	0.1–1.1
Pipridae (manakins)	disperser	3	77	0.11–0.96
Motmotidae (motmots)	disperser	1	13	0.09–0.80
Muscicapidae/ Turdidae (solitaires, thrushes and allies)	disperser	5	15	0.04–0.32
Picidae (woodpeckers)	disperser	1	10	0.03–0.30

(cont.)

Table 11.1 (cont.)

Family	Status	Frugivorous species	Frugivore density	Estimated fruit and seed consumption
Icteridae (American orioles and blackbirds)	disperser	5	6	0.02–0.20
Parulidae (wood-warblers)	disperser	2	4	0.005–0.042
Vireonidae (vireos)	disperser	2	3.7	0.005–0.042
Corvidae (jays, magpies and crows)	disperser	1	0.1	0.0005–0.0042
Columbidae (Pigeons)	disperser/predator	7	68	4.2
Tinamidae (tinamous)	disperser/predator	1	13	2.8
Emberizidae (New World sparrows and Old World buntings)	disperser/predator	9	137	0.2–2.1
Fringillidae (fringilline and cardueline finches and allies)	disperser/predator	1	2	0.021
Psittacidae (parrots)	predator	4	67	5.1
Rallidae (rails, gallinules and coots)	predator	2	6.7	0.04–0.38

Families are ordered by decreasing fruit and seed consumption within each category (mammalian dispersers, mammalian dispersers and predators, etc.). Estimated fruit and seed consumption for each species was calculated as the product of animal density (per square kilometre), feeding rates per animal (kg dry mass per year), and the proportion of the diet composed of fruits and seeds. Densities and estimated fruit and seed consumption were summed over fruit- and seed-consuming species to arrive at totals for each family. Feeding rates for each species were calculated from body mass using allometric equations given in Nagy (1987). Densities, body masses and diets for nonvolant mammals from Leigh (1999), Gompper (1996) and J. Giacalone Willis (personal communication); for birds from Willis (1990); and for bats from Kalko *et al.* (1996a). The complete species list and species-level data are available from the authors upon request.

Specialization and generalization among plant–disperser interactions

Researchers have long debated whether there are strong coevolutionary relationships between plants and their animal dispersers (Howe 1993). While there is ample evidence of mutual benefits in these relationships in tropical forests, neither theory nor data support the idea of tight coevolution, such as that observed between figs and fig wasps (Wheelwright & Orrians 1982). Individual plant species are seldom adapted to dispersal by one particular frugivore species (Levey *et al.* 1994). Tight coevolutionary relationships are the exception rather than the rule.

Most plant species are dispersed by multiple dispersers, and most dispersers disseminate seeds from multiple plant species. The interaction may vary with site, seasonality, resource availability, nutrient reward of the plant and dietary

Table 11.2 *The estimated dry biomass of seeds and fruits consumed*

	Exclusive disperser	Both disperser and predator	Exclusive predator
Consumption in trees			
by nonvolant mammals	77.8 (13.5)	7.2 (0.5)	
by bats	8.94 (25)		
by birds	13.14 (66.5)	1.13 (4)	5.16 (7)
Consumption on ground			
by nonvolant mammals	11.83 (2.5)	168.38 (6.5)	
by birds	2.92 (5.5)	2.85 (2)	0.17 (1)

Values are in kg per ha per year on Barro Colorado Island and (in parenthesis) the number of species involved, for various categories of seed dispersers and predators (see Table 11.1 for families included; sums were taken at the species level). Species that consume substantial amounts of fruits and/or seeds on the ground as well as in trees were counted as half in each list. The complete species list and species-level data are available from the authors upon request.

requirements of the frugivore. In general, dietary requirements and fruit availability shift seasonally and regionally, with many species of large frugivorous animals tracking different fruit resources as they become available throughout the year (Blake & Loiselle 1991; Whitney & Smith 1998). The disperser assemblage of a given tree species can vary with habitat, as Howe and Vande Kerckhove (1979) found for *Casearia carymbosa* at wet- and dry-forest sites in Panama.

Despite the lack of clear specialization, there is abundant evidence that animals differ in their effectiveness as seed-dispersers (Schupp 1993), and that plants differ in the rewards they offer and the costs to animals of obtaining these rewards (Gautier-Hion *et al.* 1985). The next section discusses differences among animals in their seed deposition patterns, which affect both the quality and effectiveness of seed dispersal (Schupp 1993). Also of concern when evaluating dispersal is how the frugivore treats the fruit or seed ingested, since this determines whether the frugivore acts as a disperser or seed predator. A meta-analysis of gut treatment effects found that, on average, bats and birds had strong positive impacts on germination, while nonvolant mammals had slight positive effects (Traveset & Verdú 2002). However, such generalities mask important variation: ecologically similar species may exert very different effects on fruits, and the same animal species may have very different effects on different plant species. Small seeds pass intact through the guts of guenons (*Cercopithecus* sp.), Old World monkeys, whereas larger seeds are increasingly likely to be destroyed, and no seeds above 2 mm in diameter survive gut passage (Gautier-Hion 1984). However, large seeds may be effectively dispersed by guenons if they are carried away from the parent in cheek pouches and then spat out rather than swallowed (Rowell & Mitchell 1991). In contrast, seeds of most species pass

intact through the gut of the ecologically analogous New World capuchins (*Cebus* sp.): 31 of 35 plant species tested in Panama germinated after gut passage (Rowell & Mitchell 1991).

Differences among animals in dispersal effectiveness and food preferences should provide scope for selection on plant species for traits that attract or repel potential fruit consumers based on their dispersal effectiveness and related contributions to plant fitness. Fruit syndromes, discussed previously, certainly suggest that these differences have been important for fruit-trait evolution (Levey *et al.* 1994). Cases of directed deterrence provide even stronger evidence for such selection. The capsaicin found in the fruits of wild chiles repels mammals, which tend to be seed predators of chiles, while having no effect on birds, thus ensuring that virtually all fruit removal and subsequent seed dispersal is by birds (Tewksbury & Nabhan 2001).

Once again, we turn to the extensive history of research on BCI to assess the actual degree of specialization and generality by both animals and plants with respect to fruit consumption and seed dispersal, and to test for patterns in variation in specialization among taxa. Such comparisons among species are best done in the same forest, as the diversity of plants and animals varies among forests, and the diversity of available partners is expected to affect the diversity of interactions for most species. A valuable recent review of the diet diversity of frugivorous vertebrates in another tropical site, the Guiana Shield, is provided by Forget and Hammond (2005).

Among the 13 species of frugivorous mammals whose diets have been intensively studied on BCI, the number of plant species whose fruits or seeds are consumed varies between 8 and 166. Monkeys have particularly broad diets: *Ateles geoffroyi* (Central American spider monkey) has been observed consuming the fruit of 130 plant species over one year (C. Campbell, personal communication), *Alouatta palliata* (mantled howler monkey) 103 species (Milton 1980), and *Cebus capucinus* (white-throated capuchin monkey) 95 species in just a 4-month period (Wehncke *et al.* 2003). Other nonvolant mammals have somewhat more restricted diets: *Potos flavus* (kinkajou) has been observed feeding on 74 species (Kays 1999), *Sciurus granatensis* (red-tailed squirrel) on 58 (Glanz *et al.* 1982), *Nasua narica* (white-nosed coati) on 51 (Gompper 1994), and *Dasyprocta punctata* (Central American agouti) on 38 (Smythe *et al.* 1982). Among bats, all those studied seem to have relatively narrow diets: only 17 plant species have been recorded in observations and faecal samples of the dominant frugivorous bat *Artibeus jamaicensis* over many years of study (Handley *et al.* 1991), and only 18 and 19 species are consumed by the much smaller bats *Carollia castanea* and *C. perspicillata*, respectively (Thies 1998).

An understorey mist-netting study near BCI in Central Panama provides information on the diversity of bird diets, which seems generally to be lower than that of mammals – but this may in part reflect more-limited sampling (Poulin

et al. 1999). Of the four bird species for which more than 50 diet samples were obtained (via regurgitation or defecation), samples from *Pipra mentalis* (red-capped manakin) included fruit material from 45 plant species, *Pipra coronata* (blue-crowned manakin) 26 species, *Mionectes oleagina* (ochre-bellied flycatcher) 19 species, and *Phaethornis superciliosus* (long-tailed hermit) just three species (Poulin *et al.* 1999). (*Pipra coronata* and *Mionectes* are not found on BCI, and *Phaethornis* is not listed as a fruit consumer there by Willis 1990.)

In-depth studies of fruit removal from individual plant species on BCI paint a similarly varied picture of the number of fruit- and seed-consuming species per plant species – although overall there are fewer fruit-consuming species per plant species than fruit food-source species per animal species. Martin (1985) summarized results of avian frugivore visitation studies in seven canopy tree species in Panama and found that between 7 and 46 bird species visit and presumably consume fruit of a particular tree species, with larger-fruited species receiving fewer visitors. In the forest understorey, the diversity of animal species recorded as taking fruit of a given plant species seems to be lower than in the canopy, and the relationship between fruit size and number of avian visitors (Martin 1985) appears to break down. Two species of manakins account for 62% of all *Miconia* fruit found in diet samples of more than 2000 individuals of 103 bird species in central Panama (Poulin *et al.* 1999). Similarly, a mere six species of birds, three resident manakins and three migrant thrushes, account for 97% of all *Psychotria* fruits found in the same bird-diet samples. Focal watches of individual shrubs of *Piper dilatatum* revealed that 49% of all fruits are taken by bats – probably almost entirely by the two *Carollia* species mentioned earlier (Thies 1998).

Records of feeding observations on BCI overall show that most plant species have their fruit consumed not only by many different animal species, but by species from multiple major animal groups. Of the 431 BCI woody plant species that are biotically dispersed, 40% are thought to be dispersed almost exclusively by one of three major groups of vertebrates: birds, bats or nonvolant mammals (S. J. Wright and O. Calderón, unpublished data). A full 60% are known to be dispersed by species belonging to two or more of these groups (S. J. Wright and O. Calderón, unpublished data). If we consider basal area, we find an even higher proportion with multiple disperser groups: 93% of the basal area of species that are dispersed by vertebrates are dispersed by species belonging to two or more groups of vertebrates; the proportion for shrubs alone is 89%. The abundant species that dominate basal area are the ones whose fruit consumption is best-known; thus, we expect that a similar proportion of rare species will prove to be consumed by multiple vertebrate groups as more data accumulate.

Not only are some fruits of a species taken by some animals and other fruits by other animal species, but the same fruit and seed may itself be handled by multiple animal species. Many species on BCI – as elsewhere – experience

primary dispersal by birds, bats or arboreal mammals, and then secondary dispersal by ground-dwelling rodents or other animals, including ants and dung beetles (Feer & Forget 2002). For example, leafcutter ants disperse seeds of *Simarouba amara*, whose fruits are also consumed by birds and nonvolant mammals. The impact of ant dispersal activity is evident in the exceptionally high *Simarouba* seedling densities observed near leafcutter-refuse piles located near reproductive trees, in comparison to other sites without ant nests nearby (B. D. Hardesty, unpublished data). While ants and dung beetles move only small seeds, scatter-hoarding rodents such as agoutis are important as seed dispersers, as well as seed predators, of many particularly large-seeded plant species (Forget & Milleron 1991). In addition to their effect on seed movement, seed treatment by secondary dispersers can be important to seed survival; in particular, seed burial by agoutis, ants or dung beetles can help seeds escape subsequent predation by other insects and rodents (Wright & Duber 2001).

While all these data indicate a tremendous diversity of frugivores for any given plant species, a small proportion of these partners are responsible for a disproportionate share of fruit consumption and associated seed-dispersal services. For example, closer examination of focal tree watch data discussed earlier shows that in all cases the majority (> 50%) of visits are by just 1–3 animal species, and 90% by at most 10 species, and seed-removal rates are even more skewed (e.g. Howe 1977; Howe 1980; Russo 2003b). Indeed, if we calculate a Shannon diversity index of animal visitors instead of merely examining species richness, we find that values for visits range from 2.5 to 3.5, and values for actual seed removal range from 1 to 1.5. If we could also incorporate information on ultimate seed fate, we might well find that the diversity of animal species that provide effective seed-dispersal services is even lower.

Similarly, relative specialization of animals on particular fruits is more apparent when we examine the numbers of fruits consumed for each species, rather than simply the number of species, and when we look at somewhat broader taxonomic groups. On BCI, there are several animal species whose diet is dominated by one genus of plants: for example, 92% of the occurrences of fruit or seed material in *Carollia castanea* fecal samples were of *Piper* species (as were 58% of those of *C. perspicillata*) (Thies 1998). Dietary overlap among different animal groups is also much lower when fruit species are weighted by their proportional abundance in the diet, as exemplified by a study of overlap between hornbill and primate diets in Cameroon (Poulsen *et al.* 2002). This disparity between occurrence and quantitative importance could potentially explain the mismatch between fruit-dispersal syndromes that seem designed to attract a particular species or group of dispersers and the wider diversity of species that actually consume fruit. To evaluate these possibilities fully, we need more such quantitative data on fruit removal and consumption, and ultimate seed fate.

Neither complete specialization nor complete generalization is found among either plants or their seed dispersers in tropical forests. Instead, we find more

complicated intermediate patterns. At their most specific, plant–disperser interactions seem to involve particular genera that account for a majority – but never all – of each other’s fruit removal and diet, respectively. Sets of fruit traits that appear designed to attract birds over mammals, or mammals over birds, do not reliably predict the array of fruit consumers of a species. But it is possible that they may be better predictors of the dominant consumers, or alternatively, of those that are most effective at dispersing seeds – of the animal species whose actions are really determining plant fitness, and thus selection on plant traits. In the next section, we examine patterns of seed deposition, and how they differ in favourability among animals and other dispersal vectors.

Seed deposition

In the last section we examined seed removal from parent plants. Now we turn to examine what we know about where seeds are deposited. We can divide considerations of seed deposition into three general, somewhat overlapping areas: dispersal distance, habitat-specificity and clumping. All three aspects contribute to determining the quality and effectiveness of seed dispersal (*sensu* Schupp 1993), which varies among plant species and dispersal vectors. To understand the importance of each aspect, we must consider not only how it affects the probability of success of individual seeds, but also how it affects parent-plant fitness – especially since it is largely maternal genes that determine fruit morphology and other traits affecting seed dispersal (Ronce *et al.* 2001).

The most obvious impacts of seed-deposition patterns are on seed success, and these impacts have been the principal focus of many studies evaluating the advantages of particular dispersal strategies. Seed survival, establishment probability and subsequent recruitment success may be improved by dispersal to sites with better environmental conditions and lower numbers of natural enemies. Because natural enemies are thought to concentrate near conspecific adults and in areas of high conspecific density (Connell 1971; Janzen 1970), and seed success is strongly negatively density-dependent in tropical forests (Harms *et al.* 2000), much research has focused on how longer seed-dispersal distances and reduced clumping enhance seed survival (described as the ‘escape’ hypothesis by Howe & Smallwood 1982). In addition, abiotic conditions for establishment may be more favourable at sites beyond the shade of the parent crown. Disproportionate dispersal to particularly favourable types of regeneration sites, or ‘directed dispersal’ (Howe & Smallwood 1982), has thus been another focus of study (nonetheless, its importance may still be underestimated: see Wenny 2001).

More generally, however, seed dispersal away from parents will be favoured even if individual seeds actually have a lower probability of succeeding if dispersed (Levin *et al.* 2003). This is because dispersal reduces kin competition and allows for bet-hedging over environmental variation, and thus enhances reproductive success of the parent plant and its genes favouring dispersal. If all

seeds stay beneath the parent, then they compete intensively with their siblings, severely constraining the number that could possibly survive to adulthood. As a result, a genotype that has even a minute chance of successfully dispersing and succeeding in another site will always outcompete one that never disperses and merely retains the same site (Hamilton & May 1977). If the environment varies in space and time, dispersal away from parent plants and from siblings may be selected because it allows for bet-hedging over spatial and temporal uncertainty, even if it means that some individual seeds are dispersed to habitats where they have only a very low probability of success (Cohen & Levin 1991; Howe & Smallwood 1982).

Here we consider patterns of seed deposition with respect to distances from parent trees and habitat, as well as clumping that is due to other factors. In each case, we begin by drawing attention to the selective forces on these patterns, noting especially cases in which they are conflicting. We briefly summarize how these patterns are measured, and review typical examples. Finally, we make suggestions for standard methods.

Distances

Dispersal distances are the most frequently studied aspect of seed deposition. Studies have examined both the true dispersal distance from the mother tree, and the 'effective dispersal distance' – the distance of a seed from the nearest conspecific adult (Bustamente & Canals 1995). Effective dispersal distances are often easier to measure, and they too have ecological and evolutionary relevance. In general, longer true dispersal distances make it possible for the offspring of a single parent to sample a larger area, thus reducing kin competition and effecting bet-hedging over a greater number and variety of regeneration environments (although severe clumping of seed deposition can reduce or even eliminate these benefits). On the population level, longer dispersal distances generally reduce seed limitation by reducing dispersal limitation (Clark *et al.* 1998; Nathan & Muller-Landau, 2000). On population fronts, longer dispersal distances also aid the colonization of new habitats free of conspecific competitors (dispersal distances determine rates of population advance). However, if there are environmental gradients or the habitat is patchy, longer dispersal distances may also be more likely to land seeds in unfavourable environments. Longer effective dispersal distances are expected to reduce exposure to natural enemies and intraspecific competition, but they may also reduce the likelihood of encountering specialized mutualists or tapping into parental resources via mycorrhizal networks (Fitter *et al.* 1998).

Seed-dispersal distances can be measured or estimated via a number of methods. Each method has different advantages, disadvantages and biases. Comparing dispersal distances for different dispersal vectors is fraught with difficulties because different methods are more appropriate and more often used for some

vectors than others, and because each method has its own distinct inherent biases. Dispersal by scatter-hoarding rodents is typically investigated with seed mark-recapture studies, dispersal by wind with seed-traps or seedling mapping studies, and dispersal by arboreal and volant animals by following animals and predicting dispersal distances from movement rates and gut passage time. Thus, while we report dispersal distances for a range of studies, we generally restrict our comparisons to studies using similar methods.

Patterns

A rare study that used the same methods to assess primary dispersal of multiple species dispersed by multiple vectors took place on BCI. Seed shadows of 81 individual tree species were estimated from a seed-trap study (Wright *et al.* 1999) within a mapped plot (Hubbell & Foster 1983) using inverse modelling (Muller-Landau 2001). Species' mean dispersal distances ranged from 2.8 to 152 m, with considerable variation within each dispersal syndrome. The identity of the most important dispersal vector (wind, water, ballistic, small bird, large bird, bat or nonvolant mammal) did not explain variation among species in mean dispersal distances, except that ballistically dispersed species had shorter mean dispersal distances (Muller-Landau 2001).

Spatial genetic structure can be used to infer the spatial scales of gene flow, which includes pollen as well as seed movement. If pollen movement modes or distances can be controlled for, or are uncorrelated with seed dispersal modes, then comparisons of spatial genetic structure among seed dispersal modes should provide information on seed-dispersal distances. Hamrick and Loveless (1986) compare genetic diversity within and among populations of eight tree and shrub species on BCI dispersed variously by birds, by bats and ballistically. They found that the relationship between seed-dispersal mode and the distribution of genetic variation was not as significant as they had anticipated. A review combining temperate and tropical studies found that overall, gene flow rates were lowest for gravity- and explosively dispersed species, and highest for species dispersed by wind or seed ingestion by animals (Hamrick *et al.* 1995). No studies presenting genetic data on actual seed-movement patterns in the tropics are published at this time, though there are several studies currently under way (B. D. Hardesty, unpublished data; F. A. Jones, personal communication; C. Woodward, personal communication).

Biogeographic patterns can also provide some insight into dispersal distances. All other things being equal, longer dispersal distances are expected to result in larger range sizes (Chave *et al.* 2002). Gentry (1983) notes that range sizes and geographic distributions are largest for wind-dispersed species, intermediate for species with characteristics suggesting bird dispersal, and smallest for species apparently mammal-dispersed. This implies that seed dispersal by wind results in the longest dispersal distances, seed dispersal by birds intermediate, and seed

dispersal by mammals the shortest distances. Of course, dispersal syndrome may be correlated with other factors that also influence range size, such as life-history strategy or habitat specialization. Information on long-distance dispersal rates can be gleaned from an examination of floras of isolated islands, since the arrival of a species there demonstrates a capacity for long-distance dispersal. Island floras tend to have many bird-dispersed species, some wind-dispersed species and sometimes a few bat-dispersed species, but no species dispersed by terrestrial and arboreal mammals (Gentry 1983; Yockteng & Cavelier 1998). It is possible, however, that dispersal distances by arboreal and terrestrial mammals can be quite long on contiguous land, even if these animals cannot generally move seeds across long expanses of water.

For animal seed dispersers, movement rates, home-range size and gut-passage time together should predict dispersal distances, and as these vary among disperser groups, so should dispersal distances. Comparing among studies, mean dispersal distances for animal groups seem to be shortest for ground-dwelling rodents and small birds, intermediate for bats and monkeys, and longest for large canopy birds. The longest measured mean dispersal distances are reported by Holbrook and Smith (2000), who estimate that the mean seed-dispersal distances for two species of African hornbills (*Ceratogymna atrata* and *C. cylindricus*) range from 1127 to 1947 m, depending on seed size and disperser species. In a later study, they record large-scale movements of hornbills up to 290 km, suggesting this species also has the potential to occasionally provide super-long-distance dispersal (Holbrook *et al.* 2002). Thies (1998) found that mean seed dispersal distances by a neotropical fruit bat (*Carollia castanea*) on BCI were 106 m for females and 280 m for males, with a range from 15 to 1400 m and modal dispersal distances of 100–200 m. Wehncke *et al.* (2003) estimated that modal dispersal distances by white-faced monkeys (*Cebus capucinus*) on BCI were also in the 100–200 m range, with a mean dispersal distance of 216 m and a range of 20–844 m. For a small tropical tyrant flycatcher, *Mionectes oleagineus* in Costa Rica, seed-dispersal distances estimated from the mean gut-passage time and the mean movement in that time (which will generally not be equal to the mean dispersal distances) ranged from 21 to 100 m, depending on the plant species (Westcott and Graham 2000). In comparison, a seed mark-recapture study of seed dispersal by the red acouchi (*Myoprocta exilis*) in French Guiana found seeds cached at distances of 0 to 124 m from their original locations (Jansen *et al.* 2002).

Within each of these broad categories of animal disperser there is considerable variation in dispersal distances. Some of this variation seems to be related to body size, which is hardly surprising since metabolic rates, feeding rates and home ranges all scale with body size (Brown 1995). Westcott and Graham (2000) show that there is a positive, almost linear, relationship between body mass and median dispersal distance among eight tropical bird species. Kalko *et al.*

(1996b) report that home-range size scales positively with body size among fig-eating bat species on BCI, and suggest that seed-dispersal distances will be correspondingly larger for larger bats. It has also been suggested that the larger primate species provide longer-distance seed-dispersal services than smaller ones (Peres & van Roosmalen 2002). Additional research is needed to assess these patterns. Nevertheless, there are certain to be exceptions; for example, large, but less-mobile arboreal birds such as guans and turacaos may not move seeds as far as smaller avian dispersers.

The same animal species may move seeds of different plant species different distances (Westcott & Graham 2000). Gut-passage times typically increase with seed size (Holbrook & Smith 2000), and also vary among seeds of similar size (Murray 1988), possibly because of differences in fruit chemical composition. Because gut-passage times for larger-seeded species tend to be longer, we might expect a positive relationship between seed size and dispersal distances among endozoochorously dispersed species. Mean estimated dispersal distances of large-seeded species by hornbills are larger than those for small-seeded species (Holbrook & Smith 2000). To evaluate whether overall mean dispersal distances are higher for large-seeded plants, we must further consider changes in which species take fruit. Because larger-seeded fruits are typically eaten by larger animal species (Kalko *et al.* 1996b; Peres & van Roosmalen 2002), and because these larger animals should have larger home ranges, we might expect a positive relationship to hold up overall as well. Among 44 animal-dispersed species on BCI, however, there was no relationship between seed mass and mean dispersal distance (Muller-Landau 2001). Theory suggests that dispersal distances by scatter-hoarding rodents should increase with seed size for a different reason – because larger seeds offer more reward for the effort of caching (Jansen *et al.* 2002). Several studies have found such an increasing relationship between seed size and caching distance (Forget *et al.* 1998; Jansen *et al.* 2002).

Among wind-dispersed species, mechanistic models predict that dispersal distance will decrease with increasing seed size, because heavier seeds tend to fall more quickly (Augspurger 1986). Estimated mean dispersal distances did indeed decrease with seed mass among 16 wind-dispersed species on BCI (Muller-Landau 2001).

Rare, long-distance seed dispersal events may be particularly important for plant populations (Cain *et al.* 2000). The magnitude and frequency of long-distance dispersal events will not necessarily vary in parallel with mean or typical dispersal distances among species (Muller-Landau *et al.* 2003). For example, while bats usually have fast food processing and/or gut-passage times and correspondingly short to moderate dispersal distances, Shilton *et al.* (1999) find that some small seeds are ingested and may remain in the gut of the Old World fruit bat *Cynopterus sphinx* for more than 12 hours, resulting in potential dispersal distances of kilometres or even tens or hundreds of kilometres. Unfortunately,

such rare, long-distance dispersal events are particularly difficult to measure (Nathan *et al.* 2003), although inferences using genetic techniques make their study much more feasible (Cain *et al.* 2000).

Recommendations

Comparisons of distributions of dispersal distances among studies are complicated not only by differences in methodology but also by the fact that dispersal distance distributions vary in their shapes and that different statistics on these distributions are reported by different authors. Because of the variation in shapes, a distribution with a higher mean dispersal distance may not also have a higher median, much less a higher number of seeds going beyond 100 m, a longer 90th percentile distance, etc. No single statistic can adequately summarize any distribution, and for this reason we encourage authors to report multiple statistics. In particular, we recommend reporting the mean as well as the 10th, 25th, 50th (median), 75th and 90th percentiles of the distribution. Minimum and maximum dispersal distances are also interesting, but are particularly sensitive to sample size (which should, of course, also be reported). Many papers present histograms of observed or estimated dispersal distances, which provide valuable information on the entire distance distribution. Future syntheses and comparisons would be greatly aided if authors also report the entire distribution of dispersal distances in electronic appendices.

Habitat-specific deposition

In addition to variation with distance from tree, seed-deposition rates may also vary with habitat (Nathan & Muller-Landau 2000), for example between gaps and understorey sites (Schupp *et al.* 1989). Our definition of a habitat worthy of consideration is one that makes a difference for the recruitment of the plant species under consideration – whether positive or negative – for reasons beyond simply the distance from parent trees (treated in the previous section) or the density of seeds deposited (treated in the next section, on clumping). Disproportionate deposition of seeds to particularly favourable sites for recruitment via directed dispersal (Howe 1986; Howe & Smallwood 1982) is one example of habitat-specific deposition. The other possibility, of course, is that seeds are disproportionately deposited in sites that are less favourable for recruitment – a possibility that has rarely been considered in the literature. Directed dispersal has the obvious selective advantage that it increases the odds of success of individual seeds. Countering this advantage are the kin-selection and bet-hedging benefits of spreading seeds over a larger area, including less-favourable sites, as long as there is some probability of successful recruitment at these sites. Thus, even were it possible, dispersal exclusively to the best regeneration habitat may not be the optimal strategy, although higher-than-average seed deposition in these areas should always be favoured over random deposition with respect to habitat.

Patterns

Disproportionate dispersal to gaps is undoubtedly the most frequently studied type of habitat-specific deposition (Schupp *et al.* 1989; Wenny 2001; Wenny & Levey 1998). Gaps are a favourable recruitment environment for many species (Brokaw & Busing 2000), and are the only environment in which regeneration can occur for some species (Dalling & Hubbell 2002). The most spectacular cases of directed dispersal to gaps involve birds that display or lek in gaps (e.g. Wenny & Levey 1998). Several studies have also suggested that wind-dispersed seeds may arrive in gaps at higher densities than in adjacent forests due to small-scale turbulence, but evidence remains equivocal (e.g. Augspurger & Franson 1988; Dalling *et al.* 2002). Much less noted is the opposite pattern – disproportionate dispersal to understorey sites. Such habitat-specific deposition is likely to be common for seeds dispersed by arboreal animals that rarely or never come to the ground. If the species thus dispersed regenerate better in the understorey, then this too would qualify as directed dispersal; for most species, however, it is likely to constitute the opposite.

Numerous studies have also documented patterns of tropical forest seed deposition (Duncan & Chapman 2002) and subsequent recruitment (Alrich & Hamrick 1998; Sezen *et al.* 2005) in pastures and fields near forests. Such fields and pastures offer a very different regeneration environment from forests, one that is considerably more hostile to most tropical forest plant species (Holl *et al.* 2000). Seed deposition by arboreal and terrestrial species typically drops off sharply at forest edges, while seed deposition by wind declines slowly with distance beyond the forest boundary, and seed deposition by birds and bats decreases but continues in a patchy fashion (e.g. Gorchoff *et al.* 1993). Some bird and bat species move over and into open areas, where they deposit seeds mostly, but not exclusively, beneath isolated trees or other emergent structures (Duncan & Chapman 2002; Slocum & Horvitz 2000). Because abiotic conditions for seedling regeneration are better under isolated trees (Toh *et al.* 1999), relatively high seed deposition in these areas can also be considered directed dispersal.

Recommendations

Few studies have examined, or at least reported, disproportionate dispersal to any habitats other than gaps, fields or abandoned pastures. This is surprising, because there are numerous other habitat divisions upon which many tropical forest plants are specialized (e.g. Clark *et al.* 1995; Svenning 1999), and because many animal species show uneven patterns of habitat use (e.g. McShea *et al.* 2001). We believe that biases in seed-deposition with respect to habitats other than gaps are likely to be widespread, and deserve greater attention. More studies should examine whether seed-deposition rates vary with habitats distinguished by their topography, soils and/or water availability. In addition, habitats may also differ in abiotic ways as a result of animal activity. For example, trails used frequently by animals, including humans, may present a difficult

regeneration microhabitat in which seedling densities are lower than in surrounding areas (Voysey *et al.* 1999). Such microhabitat differences deserve further attention.

The habitats and microhabitats worth studying will depend on the plant species involved and the factors that affect its regeneration success. When detailed information on such factors is lacking (as it usually is), we recommend tests for biases with respect to multiple classes of habitat, distinguished not only by understorey light availability but also by topography, soils and water availability, when possible. Better methods of recording locations of seed deposition (e.g. use of the global positioning system, GPS), of combining this information with available data on landscape characteristics (e.g. from satellite images) and of analysing the resulting associations or lack thereof (via geographic information systems, GIS) will greatly facilitate such studies. It is important that even negative results be reported. Finally, such studies will be greatly enriched if they are paired with parallel investigations of seed- and seedling-recruitment success in different habitats.

Clumping

While seed-dispersal distances have received much more theoretical and empirical attention, the degree and scale of clumping of seed deposition are important for seed success and parental fitness for most of the same reasons. When seed rain is highly clumped, seeds experience higher density-dependent mortality, reducing seed success (Harms *et al.* 2000, but see Fragoso 1997). Further, clumping increases kin competition and allows the offspring of a tree to sample fewer sites, thus limiting bet-hedging over spatiotemporal variation. Clumping increases seed limitation of populations because fewer sites are reached by seeds, an effect Schupp *et al.* (2002) refer to as dissemination limitation. Like short dispersal distances, clumping reduces interspecific competition, slows competitive exclusion and can potentially help to maintain nonequilibrium diversity (Chave *et al.* 2002; Hurtt & Pacala 1995).

Clumping of seed rain can occur at multiple spatial scales (area over which seeds are distributed), temporal scales (time over which seeds are deposited) and intensities (numbers of seeds deposited). An example from BCI illustrates how clumping at small spatial scales is evident over multiple temporal scales in the seed rain of two tree species, one animal- and one wind-dispersed. Looking only at traps that are more than 15 m from a conspecific adult, an examination of all weekly seedfall records over 15 years shows that most records have very few seeds, while some have very high seedfall – evidence of clumping of seed rain among traps (Fig. 11.2). If we look by year, some traps continue to have much higher seedfall than others, because high-seedfall weeks are nonrandomly distributed among traps. Similarly, the 15-year record continues to show clumping of seed rain, with high concentrations in a few traps – evidence of even longer-timescale

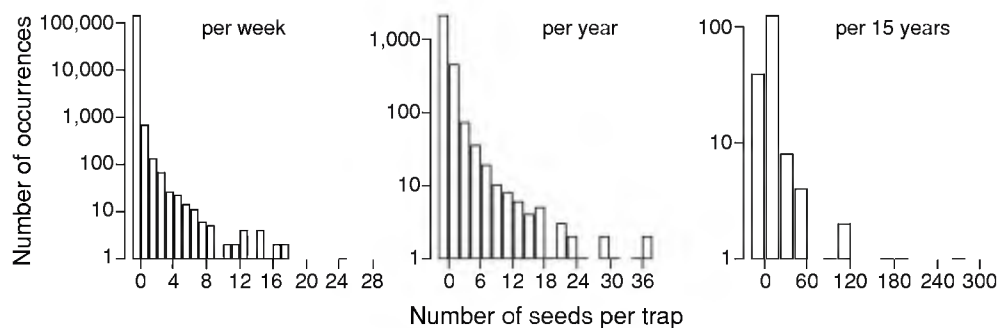
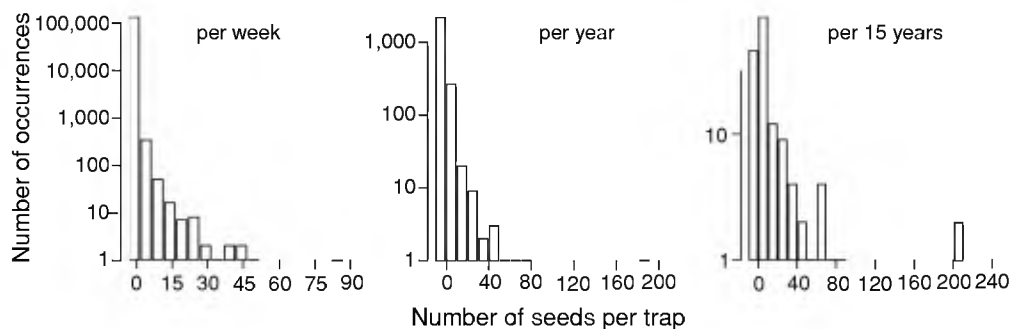
a. *Tabebuia rosea*b. *Dendropanax arboreus*

Figure 11.2 Number of occurrences of different numbers of seeds of (a) the wind-dispersed tree *Tabebuia rosea* and (b) the animal-dispersed tree *Dendropanax arboreus* falling into traps in a given week, year, or 15 years on Barro Colorado Island, Panama. This includes only those traps more than 15 m from conspecific adults. A horizontal mark along the horizontal axis represents a single trap characterized by that combination of seed number and time interval. Each seed-trap is 0.5 m². Seed-trap data courtesy of S. J. Wright, O. Calderón, and the Environmental Science Program of the Smithsonian Institution.

spatial autocorrelation in seed rain (Fig. 11.2). Some of the nonrandomness of the distribution of seeds among traps is due to differences in distances to, number of, and fecundity of nearby reproductive adults. However, the magnitude of clumping exceeds what would be expected from distance-dependence alone (H. C. Muller-Landau *et al.*, unpublished analyses), and it is not associated with any identified differences in regeneration habitat (Dalling *et al.* 2002). It appears that this clumping is the result of other processes that result in clustered deposition of seeds, and repeated deposition of seeds in some sites over others.

Patterns

Seed dispersal by animals is particularly likely to result in clumping, which varies depending on the dispersing animal and its behaviour (Schupp 1993;

Schupp *et al.* 2002). Clumping of seed dispersal by wind is much less pronounced. When seed shadows that varied only with distance from source trees were fitted to seed-rain data for animal and wind-dispersed species on BCI, animal-dispersed species showed much higher variances around the best-fit expected values than did wind-dispersed species (H. C. Muller-Landau *et al.*, unpublished analyses; Dalling *et al.* 2002). However, wind-dispersed species still deviated considerably from the expectation if all seeds were independently dispersed and their deposition depended only on distance from source trees – suggesting that seed deposition by wind is also significantly clumped.

At the shortest temporal scales (seconds to minutes), clumping among animal-dispersed species typically reflects simultaneous or near-simultaneous deposition of multiple seeds by a single animal or a group of animals. For example, individual defecations of white-faced monkeys (*Cebus capucinus*) on BCI almost always contain multiple seeds of the same species of plant (Wehncke *et al.* 2003). Depending on the plant species, the mean number of seeds per dropping varies from 4.3 (*Cordia bicolor*) to 1430 (*Cecropia insignis*). These seeds are all generally deposited within several metres of each other. For social animals, larger-scale clumping (tens of metres) may also be generated by defecation at around the same time (within half an hour) by multiple members of a group, spread out over the crown of one tree or a few neighbouring trees (Christina Campbell, personal communication).

At longer temporal scales, it is the repeated use of particular trails or sites that induce most clumping in seed deposition by animals. On scales of hours to days, clumping on short spatial scales (one to a few metres) can result from the repeated use of the same feeding roosts by bats, who return there to process fruits and drop or defecate multiple seeds beneath the roost (Fleming & Heithaus 1981). Over the course of one fruiting season of a given plant species, additional clumping can accumulate at medium spatial scales (tens of metres) because of continued or repeated use of nest sites by birds (Kinnaird 1998), sleep or nest trees by primates (Voysey *et al.* 1999), latrines by tapirs (Fragoso 1997) and display sites by birds (Krijger *et al.* 1997). Indeed, some of these sites may be used repeatedly for multiple years, inducing clumping over yet longer timescales. J. M. Fragoso (personal communication) has observed some tapir latrine sites used consistently for 12 years, and Théry and Larpin (1993) suggest that the same leks may be used by bird species for multiple generations. Unfortunately, few studies are long enough to document such patterns.

Different animal species and groups vary in the clumping of their seed deposition depending on their food-handling, gut physiology, social system and other traits. Howe (1989) suggested that animal species could be classified as either scatter or clump dispersers, based on their seed-deposition behaviour. We argue that it is important to characterize clumping more precisely, because it can occur at many different scales, with potentially very different implications. In

general, the consensus is that the ranking of primary disperser groups, from most clumped to most scattered, is primates to terrestrial mammals to bats to birds. Of course, the degree of clumping varies further among species within groups, and among individuals and over time within species (e.g. Thies 1998; Wenny 2000).

Consideration of clumping highlights the importance of secondary dispersers such as rodents, ants and dung beetles. Secondary dispersers rarely move seeds as far as primary dispersers and their movements will mostly be at random with respect to seed-bearing trees; therefore they can often be ignored when dispersal-distance distributions are calculated. However, secondary dispersers often substantially change the clumping of seed distributions by their activities. Scatter-hoarding rodents generally reduce seed-clumping, as they remove individual seeds from tapir latrines (Fragoso 1997), bat feeding roosts and other sites of concentrated seed deposition and then most often cache seeds individually (Forget & Milleron 1991). Dung beetles also generally move one or a few seeds at a time from the clumps found in defecations of primates and other mammals, and thus spread those originally concentrated seeds over a greater area through their activities (Andresen 2001). On the other hand, central-place foragers such as ants may increase clumping of seed deposition by collecting seeds from a wide area and depositing most of them within the relatively smaller area of the nest or its refuse piles (Passos & Oliveira 2002).

Clumping of seed deposition by wind has received very little attention. One obvious source of variation in seed deposition beyond that due to distance from source trees is wind direction. For example, Augspurger (1984) noted that seed shadows of wind-dispersed trees on BCI were displaced to the south of fruiting trees, reflecting the prevailing northerly wind direction during the dry season when these species released their seeds. Yet while this process certainly increases variance in seed densities, it does not result in the same intensity or short spatial scales of clumping evident among animal-dispersed species. Two other processes, affecting primary and secondary dispersal by wind, respectively, have the potential to produce such more obvious clumping. Variation in canopy geometry and topography may entrain winds and generate turbulence that results in seeds disproportionately dropping in some areas rather than others. Variation in ground cover (e.g. mud vs. dry leaf litter) may affect whether wind-dispersed seeds stick where they first land, or are potentially picked up and redispersed by subsequent gusts. These possibilities deserve further investigation. Overall, however, seed deposition by wind is likely to result in relatively little clumping, particularly in comparison with vertebrate-dispersed plant species.

Recommendations

Better quantification of the intensity and scale of clumping of seed deposition is needed if we are to improve our understanding of this phenomenon and

its implications. Studies of animal seed dispersers would ideally take data on all the information necessary to recreate the patterns of clumping produced. The required information would vary depending on the species. For a social primate, for instance, we would want data on the number of conspecific seeds per defecation, the spatial area covered by defecations of individual animals, the likelihood that multiple group members defecate at the same time, the area over which individuals in a group are typically distributed, the proportion of defecations that are under sleep trees, the average area into which defecations occur beneath a sleep tree, the number of sleep trees used during the fruiting period of a plant species, etc. (Russo 2003a). Knowledge of the natural history of an animal species will be invaluable in determining what sort of data will be useful.

When seed-deposition data are collected from seed traps or censuses rather than by following animals, the appropriate scales of data collection may be more difficult to determine. Ideally, all seeds would be mapped, so that spatial patterns at all scales could be detected, and censuses would be nearly continuous, so that patterns at all temporal scales could also be assessed. More often, data consist of counts of seeds in seed traps or sample plots of a fixed size with a fixed census interval, and data can only be analysed at a few spatial and temporal scales (e.g. Fig. 11.2). In this case, the best that can be done is to try to choose spatial and temporal scales that are most biologically relevant, given what is known about the plants and their dispersers (the scales at which clumping is likely to occur, and the scales at which it is likely to matter). Additionally, using a nested (or even fractally nested) spatial or temporal sampling design may make it possible to analyse processes at multiple spatial or temporal scales (Hardesty & Parker 2003), even if the fundamental sampling unit has a fixed size. Just as for dispersal distances, no single statistic can capture the clumping of seed deposition. Again, we recommend authors report multiple statistics, for multiple spatial and temporal scales. In particular, for studies that involve monitoring seed densities in traps or plots of fixed dimensions and fixed duration, we recommend reporting the proportion with seeds, the mean, variance and skewness of seed densities, and the 10th, 25th, 50th, 75th and 90th percentiles of the numbers of seeds per trap (or sample) among traps (samples) having seeds. Finally, we encourage authors to make as much of their original data as possible available in electronic appendices or other formats, so that the results of their studies can continue to enlighten us beyond the lifetimes of individual research projects or even investigators.

Future directions

Here we highlight both the most promising new techniques and the most pressing needs for research into the dispersal of tropical forest seed. Recent advances in technology and analytical methods have great potential for enhancing our

understanding of seed dispersal. Particularly promising are new developments in genetic techniques (Ouborg *et al.* 1999), methods for collecting and analysing spatially explicit data (Hunsaker *et al.* 2001), and modelling abilities and tools (Turchin 1998). More research is also urgently needed on applied issues relating to disruption of plant–disperser interactions, and on understudied taxonomic and functional groups.

Genetic methods

In the past, most studies using genetic methods have focused on overall spatial patterns of genetic variation, gene flow, and relatedness (e.g. Nason *et al.* 1998). When gene flow is mainly by seed dispersal, dispersal distances can be inferred from genetic relatedness. For example, Kinlan and Gaines (2003) estimate dispersal distances from genetic isolation-by-distance slopes for numerous marine species in order to compare dispersal among taxonomic and trophic groups. Spatial variation in plants reflects both seed and pollen movement. Because pollen movement tends to occur over longer distances and thus dominate large-scale patterns of genetic variation, most studies of genetic variation in plants have focused on gene flow via pollen (e.g. Dick *et al.* 2003). In plants, we can also estimate historical dispersion patterns by combining information on nuclear markers with uniparentally inherited chloroplast or mitochondrial markers (Ouborg *et al.* 1999).

Molecular techniques make it possible not only to determine overall relatedness but positively to identify parents for any given seed or seedling (Ouborg *et al.* 1999). Matching highly variable multilocus genotypes (using microsatellites) from known maternal individuals to embryo tissue of seeds permits unambiguous identification of the mother tree, and thereby direct estimates of seed movement (Godoy & Jordano 2001). With highly variable microsatellite markers, direct multilocus genotype-matching or likelihood techniques both can be used to assign mother trees to established offspring. In contrast, allozymes generally show more limited variability among individuals – especially at local spatial scales. Thus, allozyme data often require use of more loci to achieve high parental-exclusion probabilities, and most studies allow only probabilistic linkage of offspring to parents using likelihood techniques (Schnabel *et al.* 1998). Allozymes have the advantage that they are inexpensive and much less time-consuming to develop than costly microsatellite markers, although the latter are rapidly becoming more accessible. For any method selected for parentage assignment, the number of potential parents in the study population as well as the number and evenness of alleles or loci in the population play a substantial role in determining exclusion probabilities. Numerous freeware genetic analysis programs (e.g. CERVUS, Marshall *et al.* 1998) are now available to aid in parentage analysis to measure seed-dispersal distances, evaluate relative reproductive success of parents in a population, and calculate differences in gene movement

and hence the relative contribution to spatial genetic structure of both pollen and seed movement. A number of recent reviews evaluate DNA-based techniques (Campbell *et al.* 2003; Ouborg *et al.* 1999) and compare methods of kinship and pedigree analysis (Jones & Arden 2003).

The ability to identify mother trees of seeds or seedlings genetically makes it possible to 'view' seed dispersal events in a whole new way. For example, genetic studies have shown that the conspecific seeds concentrated under fruiting trees of *Prunus mahaleb* are not, as often presumed, all the offspring of that tree; instead, a significant fraction have other mothers and apparently were deposited there by animal dispersers that move from one fruiting tree to another (Jordano & Godoy 2002). Molecular markers allow us to understand better the types of clumping created by animal seed dispersers in particular. We can determine whether clumped individuals are full siblings, half sibs, or unrelated, and thus, the likelihood that they were dispersed together or by an animal making repeated visits to a perching site after ingestion. These different kinds of clumping of animal-generated seed shadows will all be reflected in population genetic structuring, which will subsequently influence gene movement and recruitment patterns (Jordano & Godoy 2002). Using genetic markers, we can measure dispersal distances at both the seed and seedling stages, and use comparisons of the two to determine whether seeds that were dispersed to different sites (e.g. farther from the parent) have different probabilities of successful recruitment. These and related genetic analyses may have important implications for the evolutionary consequences of dispersal and may also provide insights to the ecological and genetic basis of local differentiation in rainforest tree populations.

Spatial measurements and analyses

Because dispersal is inherently a spatial process, advances in collecting and analysing spatial data are particularly exciting. Small, lightweight handheld global positioning systems (GPS) that work within the forest make mapping of trees, seeds, disperser movements and seed-deposition events much easier and faster. Our ability to track movements of animals via attached transmitters has also improved greatly in recent years. Technological advances in automated radiotelemetry systems (Briner *et al.* 2003) hold great promise for constant, fine-scale tracking of frugivore movement patterns of multiple individuals and species, arboreal and terrestrial, without the labour-intensive fieldwork required for obtaining locations using handheld telemetry. Increasing miniaturization of transmitters makes it possible to track ever smaller animals (Bradshaw & Bradshaw 2002) – and even seeds (Sone & Kohno 1996) – for ever-longer periods. Furthermore, new transmitters make it possible to track not only location but also additional information such as the amount of activity (Kenward 2001), physiological data such as intestinal movements (Meile & Zittel 2002), or even sound

recordings (Roland Kays, unpublished data). Finally, GPS and satellite tracking permit very large-scale monitoring of movements (Weimerskirch *et al.* 2002).

Advances in remote sensing also enhance our ability to collect spatial data on terrain, vegetation and other habitat variables that may affect seed and disperser movements. Excellent satellite images of many types are now available (Foody 2003), sometimes at little or no cost. These images can be used to classify habitats and thus inform analyses of animal movement (McShea *et al.* 2001) and potential seed rain with respect to habitat. Inexpensive ultralight aeroplanes also bring an older remote-sensing technology – aerial photographs – within easier reach. High-resolution aerial photographs can be used to delineate crowns and potentially identify trees to functional groups (Trichon 2001) or even species in some cases (S. Bohlman, personal communication). Particularly for tree species whose fruits are apparent in the upper canopy, it may also be possible to estimate fruit production of individual trees from overflights or aerial photographs.

All these spatial data can be analysed more easily and in ever greater detail using Geographic Information Systems (Hunsaker *et al.* 2001). Numerous methods and software tools have been developed specifically to analyse the home ranges and movement patterns of animals (Kenward 2001; Worton 1987). Such analyses can incorporate information on habitat features and investigate preferential use of different habitats by animals (McShea *et al.* 2001), thus improving analyses of the potential for habitat-specificity and large-scale clumping of seed deposition. Further, these more precise data on animal-movement patterns can allow better construction and tests of mechanistic models of animal behaviour. Moorcroft *et al.* (1999) use a mechanistic model of animal behaviour to predict home ranges of wolves in Yellowstone. Such models offer the promise of greater generality than phenomenological descriptions alone can provide.

Modelling

Both mechanistic and phenomenological models have proved useful to the study of seed dispersal (Nathan & Muller-Landau, 2000). Phenomenological models are fitted to data on, for example, densities of seeds at different distances from an isolated tree. Their main utility is to serve as a concise description of those data (e.g. the distances from the tree may be said to follow a roughly exponential distribution with a mean of 8 m) and as a basis for interpolating and extrapolating from those data (Ribbens *et al.* 1994). Mechanistic models, in contrast, are parameterized based on independent data – for example, models of dispersal distances may be based on data on disperser movements and gut-passage times for seed dispersal by animals (Murray 1988), or on wind speed, tree height and diaspore terminal velocity for seed dispersal by wind (Nathan *et al.* 2002a). Such models allow us to predict patterns from processes, and to understand better how variation or changes in processes could alter the resulting patterns.

In the past, models have been used mainly to describe or predict the distribution of dispersal distances. But models can be, should be and increasingly are used to describe and predict other patterns as well, including clumping of seeds at different scales, differential seed deposition by habitat (LePage *et al.* 2000) and the overall distribution of seeds over the whole landscape (Dalling *et al.* 2002). Both mechanistic and phenomenological models of increasing complexity and realism are easier than ever to construct and implement, and can serve as tools to help us better describe, investigate and understand seed dispersal in tropical forests.

The simplest mechanistic models of dispersal by animals predict seed-dispersal distances from data on how much time elapses between an animal taking a fruit and depositing seeds and data on how far an animal moves in that time (Murray 1988; Wehncke *et al.* 2003). For endozoochorous dispersal, this involves measuring gut-passage time and animal movement while foraging. Because seed deposition by animals may be highly clumped or diffuse depending on the disperser, and may vary with habitat, such models are generally insufficient to predict patterns of seed rain over a landscape. The next step is to incorporate information that produces clumping at different scales, including number of seeds per defecation, animals per group, proportion of seeds deposited under sleep trees, number of sleep trees, etc., as well as data on the actual spatial distribution of fruiting trees. Russo (2003a) has done exactly this in a study of dispersal of *Virola calophylla* seeds by *Ateles paniscus* (spider monkeys) in Manu, Peru. In the future, such models might also include information on how seed production and seed removal vary among trees and/or patch sites, and may reflect increasingly sophisticated models of fine-scale animal-movement patterns. To fully predict seed rain of any given animal-dispersed plant species would, of course, require constructing such mechanistic models for multiple species of seed-dispersing animals, and incorporating information on the proportion of seeds removed by each.

Recently, there have been tremendous advances in mechanistic models of seed dispersal by wind (Nathan *et al.* 2002b; Tackenberg 2003). These new models incorporate spatiotemporal variation in windspeed and thus can reproduce seed uplifting by turbulent updrafts – a necessary and sufficient condition for long-distance seed dispersal by wind (Nathan *et al.* 2002b). In contrast, early pioneering work by Augspurger (1986) simply used the height of seed release and seed terminal velocity to predict how far seeds might go at different windspeeds if vertical windspeed was zero. Thus far, the new models have been applied only in temperate forests (Nathan *et al.* 2002b) and grasslands (Tackenberg 2003). However, the same principles apply everywhere, and given sufficiently precise data on windspeed, similar models can be constructed for seed dispersal by wind in tropical forests. Recent theoretical work has also improved our understanding of how differently shaped wind-dispersed diaspores move through the air

(Minami & Azuma 2003). This is a necessary precursor for understanding seed dispersal by wind in tropical forests, where diaspores vary tremendously in their size and shape (Augspurger 1986), and thus in their behaviour in different wind environments (Minami & Azuma 2003).

We know of no mechanistic models of seed dispersal by water, and this seems an obvious frontier for future research. Hydrochory is particularly important in flooded forests in the Amazon and in mangroves the world over. Hydrological models of water movement in various river systems (e.g. Coe *et al.* 2002) and oceanographic models of currents are already available, as are increasingly good remote-sensing data on water levels and flooding extent (Campos *et al.* 2001). In combination with information on fruit flotation characteristics (e.g. Williamson & Costa 2000) and the phenology of fruit production, hydrologic and oceanographic models should allow for prediction of seed movement via water dispersal. Indeed, oceanographic models have already been incorporated into mechanistic models of larval fish dispersal (Cowen *et al.* 2000). The increasing availability of data on climate (especially precipitation), topography and soils also aids construction of hydrological models, where none are yet available. Given the long distances that seeds may disperse in rivers, along floodplains and in oceans, studies of genetic relatedness may be the best way to test and validate models of seed dispersal by water. In these systems, seed movement is likely to be over longer distances than pollen movement, making large-scale genetic structure an accurate reflection of seed movement. Extensive data on the genetic structure of mangroves are already available, and have been used to test hypotheses concerning historical distributions and gene flow (Dodd & Rafii 2002; Duke *et al.* 2002).

Like mechanistic models, phenomenological models have focused mainly on the distribution of seed-dispersal distances. Early models relied on data collected around isolated trees, but techniques now exist for fitting dispersal-distance distributions from seed or seedling data collected in areas of overlapping seed shadows of multiple trees (Clark *et al.* 1998; Ribbens *et al.* 1994). Collection of more seed data at multiple spatial scales should allow fits not only of dispersal distances but also of the clumping and patchiness of seed deposition. Given additional information on the microhabitat of all the areas where seed data were collected, models could also incorporate habitat-specific deposition, much as in LePage *et al.* (2000). They examined the combined effects of seed-dispersal distances and habitat on seedling recruitment. As with all modelling efforts, additional parameters can be reliably fitted only given sufficient data, and fitting of more parameters will generally require more data.

Mechanistic models of seed-dispersal processes could be used to constrain phenomenological models, reducing the number of parameters that need to be fitted and narrowing their confidence intervals. For example, mechanistic models of seed dispersal by wind might reveal that in general, seed shadows of

wind-dispersed trees have a characteristic functional form. In this case, new data on seed distributions of a wind-dispersed tree (in an area where windspeeds or other information necessary for constructing a mechanistic model are lacking) might be fitted with a phenomenological model having this form. Similarly, data on seed production of individual trees might be used in inverse modelling of seed shadows, thus allowing for higher confidence in dispersal distances and other purely fitted parameters.

Understudied areas

A review of the tropical forest seed-dispersal literature shows that some woody plant groups are relatively well studied (although not necessarily yet well understood), while others have been studied very little, if at all.

Seed dispersal of lianas appears never to have been examined – virtually the only work is on their general dispersal syndromes and as information on consumption of liana fruits when diets of animal frugivores are studied. This parallels the general understudy of lianas – a situation which should be remedied since they are a major component of tropical forests (Schnitzer & Bongers 2002) and seem to be increasing in abundance with global change (Phillips *et al.* 2002; Wright *et al.* in press). The lack of work on seed dispersal by lianas may be due in part to the difficulty of precisely mapping the spread of individual lianas in the canopy, and thus the locations of fruits, by observers on the ground (S. Schnitzer, personal communication). Lianas can be distinguished on aerial photographs with a resolution of 1:6000 (S. Bohlman, personal communication), and this sort of remote sensing may aid future studies of seed dispersal by lianas.

Seed dispersal by wind, water and explosion are understudied relative to their prevalence among species and basal area in tropical forests. In our literature searches of seed-dispersal studies on BCI in particular and in tropical forests in general, approximately 6% concerned seed dispersal by wind. In contrast, between 10% and 25% of trees and over 50% of lianas in tropical forests are dispersed primarily by wind (Bullock 1995; Gentry 1982). Water dispersal and ballistic dispersal, while considerably less common in tropical forests, are even rarer in the literature. Water dispersal is an important component of Amazonian floodplain forests, and ballistic dispersal appears to be a successful strategy for a number of dominant shrub species. Both deserve additional attention.

Studies of seed dispersal by animals are much more numerous, but among these, attention has focused on some animal groups more than others. Naturally enough for diurnal animals such as ourselves, we have investigated diurnal dispersers and dispersal activities much more than nocturnal ones. Bats – although they generally comprise more than half the mammalian fruit-consuming species in tropical forests – have been studied at only a few sites (BCI being a notable example: see Kalko *et al.* 1996a). Other nocturnal frugivores such as kinkajous and olingos have received hardly any attention (but see Kays 1999). Terrestrial

herbivores such as deer, peccaries and tapirs, which are known to consume fruits and seeds, have also rarely been studied in the context of seed dispersal (but see Fragoso 1997) – in general, we do not even know whether they serve primarily as seed predators or seed dispersers. Overall, monkeys, large birds and the large caviomorph rodents have received much more study than bats, small birds, ants and dung beetles.

Conservation implications

Severe disruptions of plant–disperser interactions are widespread in tropical forests, and their ultimate consequences for seed dispersal and plant communities remain unknown. Hunting and forest fragmentation are changing animal abundances in many if not most forests (Laurance & Bierregaard 1997; Redford & Robinson 1987). Population declines or even local extirpation are particularly likely for certain taxonomic and functional groups: among important seed dispersers, large birds and primates are at particularly high risk (Redford & Robinson 1987). Because for many plant species these animals are the most important, or perhaps only, dispersers observed in intact tropical forests, ecologists have long speculated that their loss could catastrophically reduce seed dispersal and recruitment in affected plant species (e.g. Bond 1994; Corlett 1998). This argument alone is not persuasive, however, because it is possible that fruits will be consumed and seeds successfully dispersed by the remaining taxa, which are likely to experience compensatory increases in abundance (Wright 2003). Indeed, Hawthorne and Parren (2000) find that even though forest elephants are known to disperse seeds of many species in the rain forests of Upper Guinea, an examination of forest inventory data suggests as few as two plant species have historically depended exclusively on elephants for seed dispersal and germination-promoting seed scarification, and even those can regenerate occasionally without elephants.

Only a few studies have compared seed-dispersal processes in areas of perturbed and intact animal communities, although the number of such studies is increasing. Pizo (1997) found that the number of bird species taking fruits of the neotropical tree *Cabralea canjerana* decreased from 35 in contiguous forest to 14 in a 250-ha fragment. The species identities of the most important fruit consumers changed, with associated changes in seed-deposition behaviour including an increase in fruit dropped beneath crowns in the fragmented forest (Pizo 1997). In a study in central Panama, Wright *et al.* (2000) found that the proportion of seeds of two palm species left under conspecific crowns increased from 15% at protected sites to greater than 90% at highly hunted sites (Wright *et al.* 2000), while seed-dispersal distances decreased (Wright & Duber 2001). Cordeiro and Howe (2003) present compelling evidence of significantly reduced seedling recruitment for an endemic bird-dispersed tropical tree in Tanzania in fragmented versus intact forest. This study, at a large spatial scale and using

forest fragments over 70 years old, provides an excellent example of the effect of vertebrate dispersers on local forest diversity. Two other studies in Gabon and Tanzania have demonstrated decreased seedling recruitment in fragmented forests (Chapman & Onderdonk 1998; Cordeiro & Howe 2001), but these studies cannot rule out the possibility that changes in seed predation rather than seed dispersal are responsible.

Evidence of the longer-term impact of changes in disperser communities can be gleaned from studies of areas that lost dispersers in the last few centuries or millennia. McConkey and Drake (2002) examine seed dispersal on the Polynesian island of Tonga, where the largest avian seed dispersers became extinct following human colonization approximately 3000 years ago. They conclude that even those species whose fruits have the usual features associated with consumption and dispersal by birds and whose seeds are too large to be dispersed by the extant avian fauna are currently being consumed by bats, whose diet appears to be more varied on these islands than on the mainland (McConkey & Drake 2002). Corlett (2002) reports that in Singapore, where the animal species that would usually disperse seeds of large-fruited plants are absent, large-fruited animal-dispersed species as well as large-fruited wind-dispersed species are absent from secondary forests. Again, however, it is possible that this is due not to changes in seed dispersal but to changes in seed predation and/or the seedling recruitment environment; experiments are needed to resolve this question. An examination of the palaeological evidence might also reveal whether the extinction of Pleistocene megafauna precipitated further extinctions of plants for which they may have served as obligate dispersers (Howe 1985; Janzen & Martin 1982).

Overall, it appears that changes in animal communities following hunting and forest fragmentation will have significant qualitative effects on seed dispersal for some plant species. The identities of fruit consumers are likely to change, and with them seed-dispersal distances and deposition patterns. Whether these changes will result in population declines or disappearance of any plant species remains an open question. At present, it appears that no extinctions, local or otherwise, of tropical forest tree species can unambiguously be attributed to loss of seed dispersers. More studies are urgently needed to assess how seed dispersal changes in disturbed forests, and how altered dispersal affects plant populations and communities.

Knowledge of seed dispersal would also be useful in enhancing seed input to degraded lands that are open for restoration and reforestation. While wind-dispersed seeds of tropical forest plants typically disperse beyond forest edges as well as, or better than, they do within forests, animal-mediated seed rain generally decreases quickly beyond the forest boundary (e.g. Ingle 2003). Studies have shown that seed rain is much greater beneath emergent structures such as isolated trees and snags (Duncan & Chapman 2002; Slocum & Horvitz 2000), because birds and bats are more likely to visit there (da Silva *et al.* 1996). Seedling

densities and diversities also tend to be higher in these areas (Toh *et al.* 1999). This suggests that planting trees or adding artificial perches or other structures could enhance tree seed input and thus forest regeneration in degraded tropical areas, just as they do in some temperate systems (McClanahan & Wolfe 1993). However, an experiment in which artificial perches were added to abandoned pasture found no difference in recruitment beneath them relative to nearby open areas (Holl *et al.* 2000). It appears that microclimate differences beneath isolated trees are at least as important for tree regeneration as seed input (Toh *et al.* 1999). As a result, establishment of some sort of preliminary woody cover, via plantations or other means, may be necessary to enhance both seed rain and seedling establishment of tropical forest species on degraded lands, and thereby jumpstart succession (Holl *et al.* 2000; Wunderle 1997).

Conclusions

The plants and animals involved in the biotic interactions that result in seed dispersal have very different selective forces acting upon them. Plants seek to have their seeds well-distributed and deposited intact in favourable environments at the lowest cost in animal rewards or deterrents, while animals seek nutritional rewards at their lowest cost in energy expenditure and risk. There is often a parallel disparity between the plant and animal foci of different dispersal studies (Howe 1993). Animal ecologists are most often interested in who is taking what and from where, and such studies may not report the results – from the plant perspective – of the fruit removal, ingestion and subsequent deposition. Plant ecologists often overlook the relative importance of who is moving the seeds in favour of where seeds are surviving. Ideally, studies should integrate both perspectives, investigating both ultimate seed fate and the processes that produce that fate. Happily, increasing numbers of investigators are bridging this gap (e.g. Balcomb & Chapman 2003), and the resulting studies, by contributing to our understanding of both seed-dispersal processes and their consequences, will ultimately provide the best basis for generalization.

To grasp the larger picture of seed dispersal requires integration – not only of different methods, but also of results over multiple studies. Such integration is greatly facilitated by the Internet, and by the many databases that are increasingly available there. For example, digital images of herbarium specimens and electronic florulas make it easier to assess many traits for many plant species, from any place on the globe that has Internet access. Electronic archives of old and new journal issues make it easier to do meta-analyses of previous studies, although there are still important gaps, as few tropical natural history journals are thus available. However, the true potential of the web is just beginning to be realized in ecology. In molecular biology, it is now expected that investigators deposit essentially all their data in publicly available databases at the time of journal publication. A similar effort in ecology could revolutionize our ability

to make comparisons among sites and species, assess the generality of patterns, test our models and generally improve our understanding. While the deposition of data in electronic appendices to journals is a start, it would be far more useful if data were deposited in topic-specific archives, such as those provided by the Interaction Web Database at the National Center for Ecological Analysis and Synthesis (NCEAS) (<http://www.nceas.ucsb.edu/interactionweb/>), in a standardized format that made comparisons easier. Increasing use of such databases offers great promise for advances in our ability to integrate results across studies.

Fundamentally, we need not only better studies and better tools for bringing together their results but also simply more studies, and especially more geographically comparative or at least easily comparable studies. We know animal assemblages (as well as plant communities) vary among tropical forests, especially between neotropical and palaeotropical forests (Cristoffer & Peres 2003). We do not know how these differences affect seed dispersal and thereby plant regeneration. Long-term studies replicated at multiple sites across the tropics would be the ideal means to document the spatial and temporal variability of seed-deposition patterns and their consequences among tropical forests. Even without explicit coordination or replication, convergence on standard methods and analyses will make subsequent comparisons and integration more feasible.

Essentially every generalization or rule that has been or could be advanced regarding tropical forest seed dispersal has exceptions. Syndromes of fruit traits do not necessarily predict the identity of fruit consumers and seed dispersers; many plant–disperser pairs are neither very specialized nor very generalized; etc. This is hardly surprising, given the tremendous diversity of tropical plants and animals. Such outcomes should be seen not as failures that indicate that generalization is impossible and each plant–disperser system must be studied anew, but as partial successes and opportunities to fine-tune our understanding and better represent reality.

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