

C. J. Clark · J. R. Poulsen · E. F. Connor · V. T. Parker

Fruiting trees as dispersal foci in a semi-deciduous tropical forest

Received: 7 March 2003 / Accepted: 8 December 2003 / Published online: 27 January 2004
© Springer-Verlag 2004

Abstract Quantification of seed rain patterns is an initial step toward explaining variation in plant recruitment, and consequently, organization of forest communities. Spatially contagious patterns of seed deposition, where seeds are patchily dispersed with some sites receiving relatively high densities and others receiving low densities of seeds, may be a common phenomenon for which we have very little knowledge. For example, prior feeding events by frugivores (monkeys and birds) combined with transport and dispersal of seeds to other fruiting trees may result in the contagious deposition of non-conspecific seeds below them. Here, we examined whether fruiting trees act as dispersal foci in the semi-deciduous tropical rainforest of the Dja Reserve, Cameroon. Seed rain was sampled below the canopies of nine tree species: three typically dispersed by large, frugivorous birds, three dispersed by monkeys, and three dispersed by wind. We found no evidence that monkeys generate spatially contagious patterns of seed rain under fruiting trees at which they feed. However, we found that rates of deposition of non-conspecific seeds and species richness of seeds delivered by birds (hornbills and turacos) were significantly greater during fruiting than non-fruiting periods, and significantly greater under fruiting individuals of bird-dispersed tree species than under fruiting individuals of monkey- or wind-dispersed tree species. Additionally, during fruiting periods, the composition of non-conspecific seed rain under bird-dispersed tree species was more similar to other bird-dispersed trees than to monkey- or wind-dispersed tree species. The contagious dispersal of non-conspecific seeds to fruiting, bird-dispersed trees leads to higher seed

densities under fruiting trees than those caused by local seed production. Non-conspecific seeds deposited in high densities may experience increased seed mortality even far from parent trees if predators are generalists. Alternatively, in the absence of complete density-dependent mortality, contagious seed dispersal could result in associations among species dispersed by the same dispersal agent.

Keywords Seed rain · Seed dispersal · Contagious dispersal · Frugivory

Introduction

Spatial patterns of seed rain represent a template for the subsequent recruitment of individuals into plant communities. Therefore, identifying patterns of seed rain and determining the processes that generate these patterns are essential steps toward understanding the organization and diversity of plant communities (Nathan and Muller-Landau 2000). In the tropics, where between 62 and 93% of all plants are consumed by frugivores (Jordano 1992), patterns of vertebrate seed deposition are widely believed to have a direct impact on plant fitness, demography, and community structure.

Although seed dispersal by frugivores confers a variety of benefits on plants, perhaps the most widely cited advantage is the escape of seeds away from the vicinity of parent plants (Howe and Smallwood 1982). Janzen (1970) described the seed density distribution as a curve declining exponentially with distance from the parent tree, and hypothesized that host-specific seed and seedling predators prey upon conspecifics near the parent, thus preventing recruitment. In this way, distance and density were inversely linked, and vertebrate dispersers assumed an essential role by moving seeds away from the parent, thereby increasing the probability of seed survival with “escape” from density-dependent and distant-dependent mortality. However, the hypothetical leptokurtic curves of vertebrate-generated seed shadows may not adequately describe actual patterns of seed deposition (Schupp et al.

C. J. Clark (✉) · J. R. Poulsen
School of Natural Resources and Environment and Department
of Zoology, University of Florida,
223 Bartram Hall,
Gainesville, FL 32611–8525, USA
e-mail: cclark@zoo.ufl.edu

E. F. Connor · V. T. Parker
Department of Biology, San Francisco State University,
1600 Holloway Ave.,
San Francisco, CA 94132, USA

2002). Seed-dispersing frugivores exhibit distinct behaviors, such as defecating seeds in latrines, which may disrupt leptokurtic patterns of seed rain (Fragoso 1997). These behaviors may result in the dissemination of seeds in high seed densities at specific sites, even far from parent plants, potentially decoupling the distance-density component of the Janzen-Connell hypothesis.

The degree to which vertebrate seed dispersal creates spatially contagious patterns of seed deposition, where seeds are patchily deposited with some sites receiving relatively high densities and others receiving low densities of seeds, has not been well examined. Recent studies suggest that spatially contagious patterns of seed dispersal caused by vertebrates may be widespread (Schupp et al. 2002). For example, isolated perches in pastures, breeding display sites, latrines and primate sleeping trees may be foci for the contagious deposition of frugivore-dispersed seeds (Silva et al. 1996; Fragoso 1997; Julliot 1997; Kruijger et al. 1997; Wenny and Levey 1998; Duncan and Chapman 1999; Wenny 2000). But, in addition to these landmarks, frugivores may also disperse seeds in contagious patterns to the fruiting trees in which they regularly feed.

For tree species consumed by vertebrate frugivores, seeds may experience contagious patterns of seed deposition due to a number of frugivore behaviors. These include: (1) dropping or spitting of conspecific seeds directly under the parent plant; (2) regurgitation or defecation of conspecific seeds of the parent or a different conspecific; and (3) regurgitation and defecation of non-conspecific seeds under a focal tree. Here we are concerned with the deposition of non-conspecific seeds under a focal tree. This may be a common phenomenon. After all, tropical trees rarely fruit in temporal isolation (Chapman et al. 1999; Jordano 2000), so that seed-dispersing vertebrates consume several species of fruit in a short period of time (Blake and Loiselle 1992; Poulsen et al. 2002). But rather than being dispersed across the landscape, the combination of prior feeding visits to non-conspecific trees and the proper timing of regurgitation/defecation could result in the dispersal of non-conspecific seeds to focal trees. This additional input from non-conspecific trees may exaggerate an already clumped pattern of conspecific seeds that have fallen under the parent.

The contagious dispersal of non-conspecific seeds under a fruiting tree may have important consequences for seed survival, patterns of plant recruitment, and the spatial and genetic structure of forests. First, because spatially contagious patterns of seed deposition will result in a landscape where some sites receive high seed densities, density-dependent effects on seed survival and seedling recruitment may be enhanced. Non-conspecific seeds deposited in high densities may experience increased seed mortality even far from parent trees if predators are generalists. Second, seed dispersers may concurrently disperse more than one species of seed, resulting in suites of species dispersed to specific sites together (Loiselle 1990). Such 'taxonomic contagion' could result in the

presence of recurrent groups of tree species in spatial proximity (Tewksbury et al. 1999). Therefore, in the absence of complete density-dependent mortality, contagious seed dispersal could lead to associations among species dispersed by the same dispersal agent.

The degree of spatial and taxonomic contagion in vertebrate-generated seed rain may be a function of specific characteristics of the habitat (e.g. spatial arrangement of fruiting trees), and the feeding and post-feeding behavior of the dispersal agent (e.g. movement patterns and seed passage times) (Jordano 1992; Schupp and Fuentes 1995). Our study is driven by evidence suggesting that fruiting plants may attract greater numbers of dispersers, frequently ready to regurgitate or defecate seeds, than do non-fruiting plants (Guimaraes Vieira et al. 1994; Silva et al. 1996). Thus, we hypothesize that prior feeding events by frugivores (monkeys and birds) combined with subsequent visitation to other fruiting trees results in the contagious deposition of non-conspecific seeds below them. To test the hypothesis that fruiting trees serve as dispersal foci for frugivorous birds and monkeys, we examine the density, species richness, and species composition of seeds deposited by birds and monkeys under bird-, monkey-, and wind-dispersed trees during the fruiting and non-fruiting periods for nine tree species. Wind-dispersed species serve as controls in this study.

If our hypothesis that frugivorous birds and monkeys disperse seeds in contagious patterns under fruiting trees is correct, the following five predictions should be true: (1) greater seed densities and numbers of species of non-conspecific seeds will be deposited under trees during fruiting periods than during non-fruiting periods; (2) seed density and species richness of non-conspecific bird-dispersed seeds will be higher under fruiting bird-dispersed trees than under monkey- or wind-dispersed tree species; (3) the density and species richness of non-conspecific monkey-dispersed seeds will be higher under focal fruiting monkey-dispersed trees than under bird- or wind-dispersed tree species; (4) the density and species richness of non-conspecific bird- and monkey-dispersed tree species will not be higher under fruiting wind-dispersed trees than under bird- or monkey-dispersed trees; and (5) seed dispersal by vertebrate vectors will lead to the deposition of similar suites of species of seeds under canopies of trees disseminated by common vectors.

Materials and methods

Overview of the experimental design

To test the hypothesis that the transport and deposition of seeds under frugivore-dispersed trees leads to spatial and taxonomic contagion of non-conspecific seeds, we sampled the seed rain under fruiting bird-, monkey-, and wind-dispersed trees using seed traps (described below). We then compared the rate of dispersal of seeds and species among the three classes of trees, using wind-dispersed species as a control. Trees dispersed by these three vectors account

for well over 90% of the forest composition in our study area (Letouzey 1970; M. Fogiel, unpublished data).

Study site and seed dispersal agents

Our study took place from May 1998 to May 1999 at the Bouamir Research Station in the Dja Reserve, Cameroon. The Dja Reserve, an IUCN Biosphere Reserve, encompasses an area of 526 km². Our study area is a 25 km² site located at the center of the reserve (N 3° 11'27", E 12°48'41"). The vegetation is semi-deciduous tropical rain forest and has never been logged (Letouzey 1970). The climate is characterized by two wet and two dry seasons with major and minor rainfall peaks in September and May. Average annual rainfall is approximately 1,600 mm year⁻¹ (Laclavère 1980).

The arboreal seed dispersers investigated in this study include six species of large frugivorous turacos and hornbills (Musophagidae: *Corythaeola cristata*, *Tauraco persa*, *T. macrorhynchus*, Bucerotidae: *Ceratogymna atrata*, *C. cylindricus*, *C. fistulator*) and four species of monkeys (Cercopithecidae: *C. nictitans*, *C. cephus*, *C. pogonias*, *Lophocebus albigena*). Other species of seed dispersal agents such as bats, gorillas, and chimpanzees, occur on our study site, but this study focuses strictly on the contribution of monkeys and large birds to seed dispersal. Furthermore, we focused on primary seed dispersal, not on the secondary redistribution of seed by terrestrial seed dispersal agents, such as duikers, or seed predators, such as squirrels and rats.

Tree species selection and plot characterization

Seed rain was sampled below the canopies of nine tree species. Three species were predominantly dispersed by monkeys: *Gambeya boukokoensis* (Sapotaceae), *Garcinia smeathmannii* (Clusiaceae), and *Uapaca paludosa* (Euphorbiaceae). Three species were predominantly dispersed by large birds: *Cleistopholis glauca* (Annonaceae), *Maesopsis eminii* (Rhamnaceae), and *Staudtia kamerunensis* (Myristicaceae). Three species were wind-dispersed: *Terminalia superba* (Combretaceae), *Pteleopsis hylodendron* (Combretaceae), and *Funtumia elastica* (Apocynaceae) (nomenclature follows Hutchinson et al. 1963; Letouzey 1970; Tailfer 1989). The selection of potential animal-dispersed tree species was based on feeding observations made by researchers at BRS from 1994 to 1998 and the knowledge of local Baaka guides (Whitney et al. 1998; Poulsen et al. 2002). Tree species were selected at random from a pool of all known potential tree species within each dispersal category. We selected ten adult individuals of each tree species,

totaling 90 individuals. Individual trees were selected such that they were a minimum of 60 m from the nearest conspecific tree. To verify our classification of trees, the randomly selected bird-dispersed and monkey-dispersed tree species were observed for a total of over 1,500 h to determine which animal species fed upon their fruits. Over 90% of all observed fruit removal was by the category of seed dispersal agent to which a tree species was assigned (Clark 2001).

Of the 90 study trees, 13 trees failed to fruit or aborted fruit early in the fruiting period. Therefore, only data collected from the remaining 77 trees were used in data analyses. To determine if tree characteristics other than the dispersal vector could explain patterns of dispersal, we measured the height of each tree with a clinometer and calculated the crown area using the average of ten measurements of canopy radius, assuming circularity of canopy shape (Table 1). The diameter-at-breast height (dbh) was also measured for each tree.

When a focal tree came into fruit, we estimated crop size visually by randomly choosing several branches in the tree crown, meticulously counting the number of fruits on these branches, averaging the number of fruits per branch, and multiplying that number by the total number of branches on the tree. This method is widely used to achieve the best estimate of crop size for canopy trees in tropical forests (Janzen et al. 1976; Laman 1996). Because light conditions, fruit ripeness, and observer bias can influence the detection of fruits high in the canopy, we estimated crop size by averaging estimates obtained by several different observers and rounding to the nearest thousand fruits. When possible, we checked fruit production estimates against extrapolations from the number of husks (*Staudtia kamerunensis*) or bracts (most other species) that fell into seed traps (41 of 45 visual estimates fell within 95% confidence limits of estimates based on husks and bracts).

The fruiting period of each species of tree is highly variable. Some individuals do not fruit in a particular year, and fruiting is not completely synchronous within or between species. In the Dja Reserve, there are some trees in fruit throughout the year, although there are large differences in the number of trees and species in fruit depending on the season. For example, approximately 33% of randomly placed seed traps contained fruit at every sampling period throughout an earlier 12-month study (Hardesty and Parker 2003). Therefore, we treat the 'fruiting period', both its duration and temporal distribution, as an attribute of an individual tree.

Seed trap placement and monitoring

Seed traps representing 5% of the crown area were randomly placed under the canopy of each individual tree. Traps placed under each

Table 1 Tree size and fruit production for the nine study species (mean±SE, *n* =10 for each species). Estimated crop size has been rounded to the nearest thousand seeds. [DBH : diameter-at-breast height, Clgl: *Cleistopholis glauca*, Maem: *Maesopsis eminii*, Stka: *Staudtia kamerunensis*, Uapa: *Uapaca paludosa*, Gasm: *Garcinia*

smeathmannii, Gabo: *Gambeya boukokoensis*, Pthy: *Pteleopsis hylodendron*, Fuel: *Funtumia elastica*, Tesu: *Terminalia superba*. *F*-statistic (and *P*-value) from ANOVA to test the hypotheses that tree species dispersed by different vectors differ in size or fruit production are presented at the bottom of the table]

Species	Vector	Height (m)±SE	DBH (m)±SE	Crown area (m ²)±SE	Crop size
Clgl	Bird	40.64±2.13	0.87±0.07	169.44±28.86	25,000±2,010
Maem	Bird	48.44±2.15	0.97±0.07	305.54±34.87	48,000±8,558
Stka	Bird	34.99±2.99	0.77±0.19	167.20±34.07	41,500±16,872
Uapa	Monkey	33.29±1.90	0.71±0.09	160.31±23.91	70,000±18,719
Gasm	Monkey	22.34±2.05	0.32±0.02	24.77±2.18	10,000±2,665
Gabo	Monkey	30.49±1.93	0.80±0.06	94.09±13.08	29,500±6,961
Pthy	Wind	47.79±3.55	0.96±0.08	223.64±32.94	14,000±7,850
Fuel	Wind	34.17±1.63	0.44±0.06	47.38±5.73	72,500±15,661
Tesu	Wind	40.29±2.04	1.05±0.19	240.54±32.94	51,000±11,465
Tests for differences between vectors					
	<i>F</i> _{2, 6}	3.68 (0.091)	0.925 (0.447)	1.515 (0.293)	0.110 (0.898)

tree ranged in size (range: 0.25 m²–1.25 m²) and number (range: 2–25 traps), reflecting differences among the crown areas of individual trees (range: 24.1 m²–366.3 m²). The combined sampling area under all trees totaled 779 m². Traps were constructed of durable, plastic mesh stapled to rattan frames. We elevated seed traps to a height of 1–1.5 m to discourage the removal of seeds by animals. Even so, elevation of traps did not completely eliminate seed removal. Approximately 10% of 896 experimentally marked seeds were either removed or showed signs of having been chewed by vertebrates within 10 days of placement in seed traps.

We gathered the contents of seed traps in plastic bags and returned them to the field station for processing at 10-day intervals for 12 months. Fecal clumps defecated into traps were collected intact to insure that all seeds within the clumps were counted and identified. We recorded fruit and seed number, condition (mature, immature, rotten, chewed, defecated, regurgitated), species, and dispersal mechanism for all propagules collected from seed traps. Unlike many other studies of seed dispersal, we did not rely on seed morphology or knowledge of a tree species' predominant dispersal vector to classify seeds as being dispersed by a particular vector. We looked for physical evidence that a seed had been chewed, passed or regurgitated by bird or monkey vectors. Each seed or fruit was classified into one of the following dispersal categories: bird-dispersed (the presence of white uric acid indicated defecation, whereas seeds completely clean of an aril or fruit and free of uric acid indicated regurgitation), monkey-defecated (identified by the presence of monkey scat), dispersed by unknown vertebrate vector (intact seeds or fruits that have visible teeth, claw or bill marks), preyed-upon (severely damaged or chewed seeds), and wind- or ballistically dispersed.

To determine seed origin, all trees, lianas and understory shrubs with vegetative structures hanging within 5 m of the crown of the focal tree were identified and recorded. Because we are interested in determining the extent to which birds and monkeys transport and deposit seeds away from parent canopies toward bird-, monkey-, or wind-dispersed trees, we used these data to classify each seed as being of local or immigrant origin. We defined local seeds as conspecific seeds and seeds produced by species of plants whose fruiting crowns were located within 5 m of the crown of the study tree. We selected a distance of 5 m as the cut-off distance for the classification of local seeds because seeds from trees or lianas overlapping with, or next to, our focal trees could be dispersed this distance without the assistance of a vertebrate vector. Immigrant seeds were defined as those produced by non-conspecific plants whose fruiting crowns were not located within 5 m of the crown of a study tree. Seeds produced by distant conspecific individuals could not be distinguished from seeds of the focal tree. Therefore, by considering all conspecific seeds as local seeds, we underestimate the degree of dispersal to the focal tree. However, we minimized the possibility for this kind of error by selecting study trees located at least 60 m from the nearest conspecific tree. In a separate study, we examined the seed shadows of the tree species included in this study

and determined that a very low proportion (\bar{x} =6.3%) of their seed crops are dispersed greater than 60 m from the parent plant (Clark 2001). Even so, overestimating the number of local conspecific seeds will result in conservative estimates of contagious dispersal to fruiting trees. Any observed patterns of spatial contagion in the seed rain would only be amplified had we been able to use more sensitive techniques to determine the origin of a given conspecific seed (e.g. Godoy and Jordano 2001).

Seed rain description and data analysis

To determine if fruiting trees act as dispersal foci for non-conspecific seeds, we examined differences in the rate of seed deposition (seeds m⁻² day⁻¹) and species richness (species m⁻²) of immigrant bird- and monkey-dispersed seeds deposited among trees between fruiting and non-fruiting periods. We present results for differences in the rate of seed deposition instead of the absolute number of seeds to account for the fact that each tree fruited for a different length of time. However, the analysis was also conducted using the absolute number of seeds, and the pattern of results did not differ from those presented here. To identify differences in the rate of deposition of seeds and species richness of seeds by birds and monkeys among trees dispersed by each type of vector (bird-, monkey-, and wind-dispersed trees) and between periods (fruiting and non-fruiting), we used a 3-factor ANOVA with tree species nested within dispersal type and repeated measures on the period factor. Dispersal type and period were treated as fixed factors and species and trees were treated as random factors. Response variables were log-transformed to meet the assumption of normality.

We employed cluster analysis to determine whether similar suites of species are deposited under trees dispersed by the same vector. If the composition of the seed rain of trees dispersed by the same vector is more similar than the seed rain under trees dispersed by other vectors, then trees dispersed by the same vector should be classified together. Species-by-sample matrices were used for all cluster analyses, with the total number of seeds for each seed species recorded in the columns and individual trees represented as rows. All seed species represented by fewer than five seeds over the course of the study and conspecific seeds (i.e., seeds of the tree species being sampled) were excluded from data matrices. The similarity in species composition of seed rain was examined for fruiting periods and non-fruiting periods. Data were standardized by row and column totals in order to weight seed species and trees equally. We report results from cluster analysis using Ward's grouping, which is recommended as a good general-purpose linkage method (Gauch 1982). PC-ORD was used to derive cluster analyses that were hierarchical, agglomerative, and polythetic (Sneath and Sokal 1973; Jongman et al. 1995).

Table 2 Analysis of variance on rates of deposition of both immigrant and locally produced seed from all sources (seeds m⁻² day⁻¹) under bird-dispersed, wind-dispersed and monkey-dispersed tree species during fruiting and non-fruiting periods. The vector effect refers to the dominant dispersal vector of each species of tree. The period effect refers to fruiting and non-fruiting periods; and the

tree effect refers to the individual trees. The analysis was performed on log(*n*+1) transformed data. Because tree species is a random factor, the error term for the Period effect and Period × Vector interaction was the mean square Period × Species (Vector), and the error term for the Vector effect was the mean square Species (Vector)

	Source of variation	SS (Type III)	df	MS	F	P
Within subjects effects	Period	0.1350	1	0.135	1.195	0.2782
	Period × Vector	0.0488	2	0.0244	0.216	0.8063
	Period × Species(Vector)	0.6760	6	0.1130	2.343	0.0408
	Tree × Period × Species(Vector)	3.2720	68	0.0481		
Between subjects effects	Vector	1.1940	2	0.5970	0.987	0.3780
	Species(Vector)	3.6320	6	0.6050	7.835	0.0001
	Tree × Species(Vector)	5.2540	68	0.0773		

Results

Characterization of study trees

The height, dbh, crown area, and crop size of trees dispersed by birds, monkeys, and wind did not differ significantly (ANOVA F -tests, $P > 0.05$, Table 1).

Characterization of the seed rain

A total of 159,696 seeds representing 371 species were recorded in seed traps. Total annual seed density was 204.9 seeds m^{-2} . Seeds dispersed into seed traps by vertebrate dispersers represented a fraction of the total seed rain. Vertebrate dispersal contributed 12.4% of the seed rain and comprised 254 species (68.5%). Wind and ballistic dispersal accounted for 16.3% of all seeds in the seed rain, but represented only 8.4% (31) of the seed species. All other seeds and species were either preyed upon or fell directly below a conspecific adult (Clark et al. 2001). The total rate of deposition of seeds under trees was highly variable both within and among species, and among dispersal vectors. We detected no differences in the rate of total seed deposition among trees dispersed by different vectors, between the fruiting and non-fruiting period, nor an interaction between fruiting period and vector (Table 2).

Patterns of seed rain associated with avian dispersal

Averaging across fruiting and non-fruiting periods, the rate of seed deposition by birds did not differ among tree

species that are dispersed by different vectors (Vector effect, Table 3, Fig. 1a). We also detected no differences in the rate of seed deposition by birds between the fruiting and non-fruiting period when averaging across the categories of tree dispersal vectors (Period effect, Table 3, Fig. 1a). However, the rate of seed deposition by birds to bird-dispersed tree species was significantly higher during the fruiting period than the non-fruiting period (Period by Vector effect, Table 3, Fig. 1a). The rate of seed deposition by birds under monkey- and wind-dispersed species did not differ between fruiting and non-fruiting periods (Fig. 1a). Birds deposited significantly greater numbers of species of seeds under bird-dispersed than under monkey- or wind-dispersed tree species in the fruiting period (Period by Vector effect, Table 3).

Patterns of seed rain associated with monkey-dispersal

There were no differences in the rate of seed deposition by monkeys under tree species dispersed by different vectors (Table 4, Fig. 1b). However, the rate of seed deposition by monkeys was greater during the non-fruiting period than during the fruiting period (Table 4, Fig. 1b). Unlike birds, monkeys did not disperse seeds at a higher rate to monkey-dispersed tree species during the fruiting period (no Period by Vector interaction, Table 4, Fig. 1a). ANOVA indicated that the number of species of seeds dispersed by monkeys did not differ among periods or vectors, nor was there an interaction of period and vector (Table 4).

Table 3 Analysis of variance on rates of deposition of immigrant seeds (seeds $m^{-2}day^{-1}$) and numbers of species of seeds deposited by large-frugivorous birds under bird-dispersed, wind-dispersed and monkey-dispersed tree species during fruiting and non-fruiting periods. The vector effect refers to the dominant dispersal vector of each species of focal tree. The period effect refers to fruiting and

non-fruiting periods; and the tree effect refers to the individual trees. The analysis was performed on $\log(n+1)$ transformed data. Because tree species is a random factor, the error term for the Period effect and Period \times Vector interaction was the mean square Period \times Species (Vector), and the error term for the Vector effect was the mean square Species (Vector)

Source of variation		SS (Type III)	df	MS	F	P
Bird-dispersed seeds ($m^{-2}day^{-1}$)						
Within subjects effects	Period	0.0009	1	0.0009	1.537	0.261
	Period \times Vector	0.0093	2	0.0046	8.252	0.019
	Period \times Species(Vector)	0.0034	6	0.0006	1.590	0.163
	Tree \times Period \times Species(Vector)	0.0240	68	0.0004		
Between subjects effects	Vector	0.0051	2	0.0026	2.969	0.127
	Species(Vector)	0.0052	6	0.0009	2.353	0.040
	Tree \times Species(Vector)	0.0249	68	0.0004		
Bird-deposited species (m^{-2})						
Within subjects effects	Period	0.035	1	0.035	5.069	0.0655
	Period \times Vector	0.592	2	0.296	43.300	0.0003
	Period \times Species(Vector)	0.041	6	0.007	1.565	0.171
	Tree \times Period \times Species(Vector)	0.297	68	0.004		
Between subjects effects	Vector	0.365	2	0.183	3.124	0.118
	Species(Vector)	0.352	6	0.059	4.579	0.0006
	Tree \times Species(Vector)	0.870	68	0.013		

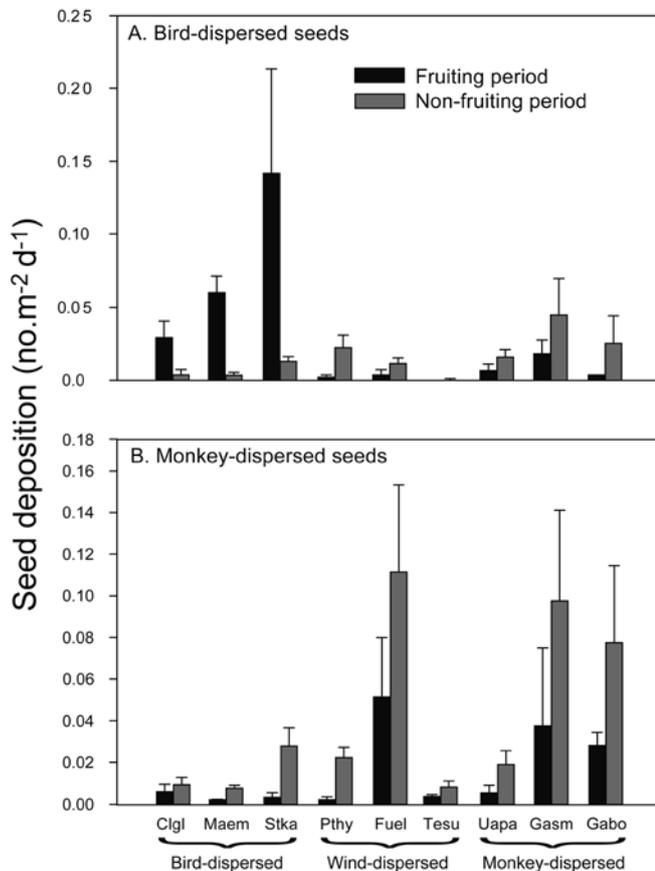


Fig. 1 Mean rate of deposition and standard error of immigrant seeds deposited by **A** birds and **B** monkeys under canopies of bird-, monkey- and wind-dispersed tree species during fruiting and non-fruiting periods. **A** The seeds dispersed to wind- and monkey-dispersed trees by birds represent incidental seed rain, seeds dispersed by birds in flight or at rest, but not while feeding at the tree. Similarly, **B** seeds dispersed to wind- and bird-dispersed trees by monkeys represent incidental seed rain, deposited by monkeys while resting or moving but not while feeding at the tree. (Clgl: *Cleistopholis glauca*, Maem: *Maesopsis eminii*, Stka: *Staudtia kamerunensis*, Uapa: *Uapaca paludosa*, Gasm: *Garcinia smeathmannii*, Gabo: *Gambeya boukokoensis*, Pthy: *Pteleopsis hylodendron*, Fuel: *Funtumia elastica*, Tesu: *Terminalia superba*)

Seed rain composition associated with frugivore dispersal

The species composition of non-specific seed rain was more similar among bird-dispersed tree species during fruiting periods than among monkey- or wind-dispersed tree species (Fig. 2a). Tree species dispersed by birds clustered as a group, but tree species dispersed by monkeys and wind did not cluster with other species disseminated by the same dispersal vectors. During non-fruiting periods, no pattern of clustering among tree species dispersed by birds was identified, and we observed little similarity in the species composition of seeds beneath tree species sharing dispersal vectors (Fig. 2b).

Discussion

Fruiting trees as dispersal foci

Our data indicate that in the Dja Reserve birds deposit seeds in spatially contagious patterns beneath fruiting trees, but monkeys do not. The rate of deposition of seeds and the species richness of seeds delivered by birds were significantly greater under fruiting individuals of bird-dispersed tree species than under fruiting individuals of monkey- or wind-dispersed tree species. Also, during fruiting periods, tree species dispersed by birds were more similar to each other in the species composition of seeds falling below their canopies than they were to monkey- or wind-dispersed tree species. In contrast, we find little evidence that monkeys generate contagious patterns of seed rain under fruiting bird-, wind-, or monkey-dispersed tree species. Although the rate of seed deposition by monkeys was greater during the non-fruiting period, monkeys did not deposit seeds at a greater rate under monkey-dispersed trees. In addition, the number of monkey-dispersed species of seed did not differ between monkey-dispersed tree species and bird- or wind-dispersed species.

Contagious patterns of seed rain under canopies of fruiting bird-dispersed trees are likely related to the observation that most seed defecation and regurgitation by birds occurs when they are perched or immediately after they take wing (McDonnell and Stiles 1983; Charles-Dominique 1986). Therefore, seeds deposited by birds accumulate under fruiting trees frequented by birds throughout the day. Additionally, birds consume the fruits of several plant species in relatively short time periods and may defecate several species of seeds simultaneously after very short gut passage times of 51–230 min on average (Herrera 1984; Loiselle 1996; Holbrook and Smith 2000). Therefore, the combination of prior feeding by birds to accumulate non-conspecific seeds, together with the proper timing of defecation and regurgitation, leads to the high densities of non-conspecific seed rain under fruiting, bird-dispersed trees.

The lack of contagious dispersal of seeds by monkeys to monkey-dispersed trees may be explained by their flexible diets, diffuse foraging patterns, and slow seed passage times (Clark et al. 2001; Poulsen et al. 2002). In contrast to frugivorous birds that fly directly between fruiting trees, monkeys in the Dja Reserve generally forage as they move, seemingly sampling the forest. Monkeys may revisit a fruiting tree over periods of days or weeks (Olupot et al. 1997), but rarely follow routine pathways. Combined with the relatively slow seed passage times by monkeys (1,320 min on average) monkey feeding and movement patterns lead to diffuse patterns of seed deposition (Poulsen et al. 2001; Clark 2001).

Other studies report that monkeys defecate the majority of passed seeds under the trees in which they sleep (Julliot 1997). Thus, analogous to perches, nest cavities, and fruiting trees for birds, sleeping trees may act as dispersal foci for monkey-dispersed seeds. In the Dja Reserve,

Table 4 Analysis of variance on rates of deposition of immigrant seeds (seeds $\text{m}^{-2}\text{day}^{-1}$) and numbers of species of seeds deposited by monkeys under bird-dispersed, wind-dispersed and monkey-dispersed tree species during fruiting and non-fruiting periods. The vector effect refers to the dominant dispersal vector of each species of tree. The period effect refers to fruiting and non-fruiting periods;

and the tree effect refers to the individual trees. The analysis was performed on $\log(n+1)$ transformed data. Because tree species is a random effects factor, the error term for the Period effect and Period \times Vector interaction was the mean square Period \times Species (Vector), and the error term for the Vector effect was the mean square Species (Vector)

Source of variation		SS (Type III)	df	MS	F	P
Monkey-dispersed seeds ($\text{m}^{-2}\text{day}^{-1}$)						
Within subjects effects	Period	0.0043	1	0.0043	12.874	0.012
	Period \times Vector	0.0008	2	0.0004	1.211	0.362
	Period \times Species(Vector)	0.0020	6	0.0003	1.467	0.203
	Tree \times Period \times Species(Vector)	0.0155	68	0.0002		
Between subjects effects	Vector	0.0049	2	0.0025	1.044	0.408
	Species(Vector)	0.0142	6	0.0024	4.201	0.001
	Tree \times Species(Vector)	0.0383	68	0.0006		
Monkey-deposited species (m^{-2})						
Within subjects effects	Period	0.006	1	0.006	0.900	0.621
	Period \times Vector	0.063	2	0.032	4.418	0.066
	Period \times Species (Vector)	0.043	6	0.007	2.0699	0.068
	Tree \times Period \times Species(Vector)	0.235	68	0.003		
Between subjects effects	Vector	0.081	2	0.040	1.266	0.348
	Species(Vector)	0.192	6	0.032	2.364	0.039
	Tree \times Species(Vector)	0.920	68	0.014		

however, contagious patterns of defecation are unlikely because monkey groups often sleep spread among a few large trees. They rarely sleep in the same tree more than once (Poulsen, unpublished data), decreasing the probability of repeatedly passing high densities of seed under a single tree.

Howe (1989) proposed that frugivorous birds are more effective dispersers than monkeys because they scatter seeds singly rather than in clumps of several seeds. Seeds dispersed in multi-seeded clumps are thought to be more susceptible to density-dependent mortality (Janzen 1970; Augspurger 1984; Clark and Clark 1984; Condit et al. 1992; but see Forget 1993; Forget and Sabatier 1997; Fragoso 1997; Fragoso and Huffman 2000). However, information on both the number of seeds deposited per defecation and on the timing and location of defecations is necessary to understand patterns of seed deposition generated by a particular group of dispersal vectors. For example, although birds may disperse seeds singly, the high concentration of seeds they deposit at dispersal foci, such as fruiting trees and nest cavities, may result in contagious dispersal. Monkeys, on the other hand, may defecate clumps of 1–6 seeds (Lambert 1999; Poulsen et al. 2001), but in the Dja Reserve, these defecations are apparently less directed, or more diffusely, disseminated throughout the forest. Thus, contagious seed dispersal exists at various spatial scales, from small-scale clumped defecations of monkeys to the large-scale patches of high seed densities deposited by large birds under fruiting trees described in this study. Reconsideration of the spatial scales at which we develop and examine dispersal theory may offer critical insights into dispersal processes.

Implications

We demonstrate that in the Dja Reserve large birds create spatially contagious patterns of seed deposition by dispersing seeds under fruiting trees. In contrast, monkeys disperse a different suite of seeds diffusely throughout the forest. These distinct patterns of primary dispersal initiate subsequent dynamics that potentially lead to tree recruitment. Seeds deposited by large birds are dispersed toward fruiting trees at high rates, thereby reducing the density of bird-dispersed seeds in the remainder of the forest. Thus, bird-dispersed plants are potentially more dispersal limited than monkey-dispersed species (Schupp et al. 2002).

Dispersal patterns of bird-dispersed species suggest two alternative scenarios for recruitment. First, contagious dispersal could exaggerate patterns of density-dependent seed predation by generalist seed predators and/or seedling competition resulting in high seed and seedling mortality. Several studies demonstrate that high seed density increases the chance of seed mortality, even far from parent plants (Augspurger and Kelly 1984; Janzen 1986; Augspurger and Kitajima 1992). If contagious dispersal reinforces density-dependent seed mortality, then contagious dispersal of bird-dispersed trees should lead to a repulsed pattern of distribution of bird-dispersed trees. Alternatively, if predators are host-specific, satiated or absent altogether, contagious dispersal could lead to higher survival of non-conspecific bird-dispersed seeds under bird-dispersed trees, given competition and secondary dispersal are not enhanced. In this case, contagious dispersal of seeds by birds should lead to an aggregated distribution of bird-dispersed species in the forest. But while we demonstrate that birds contagiously disperse

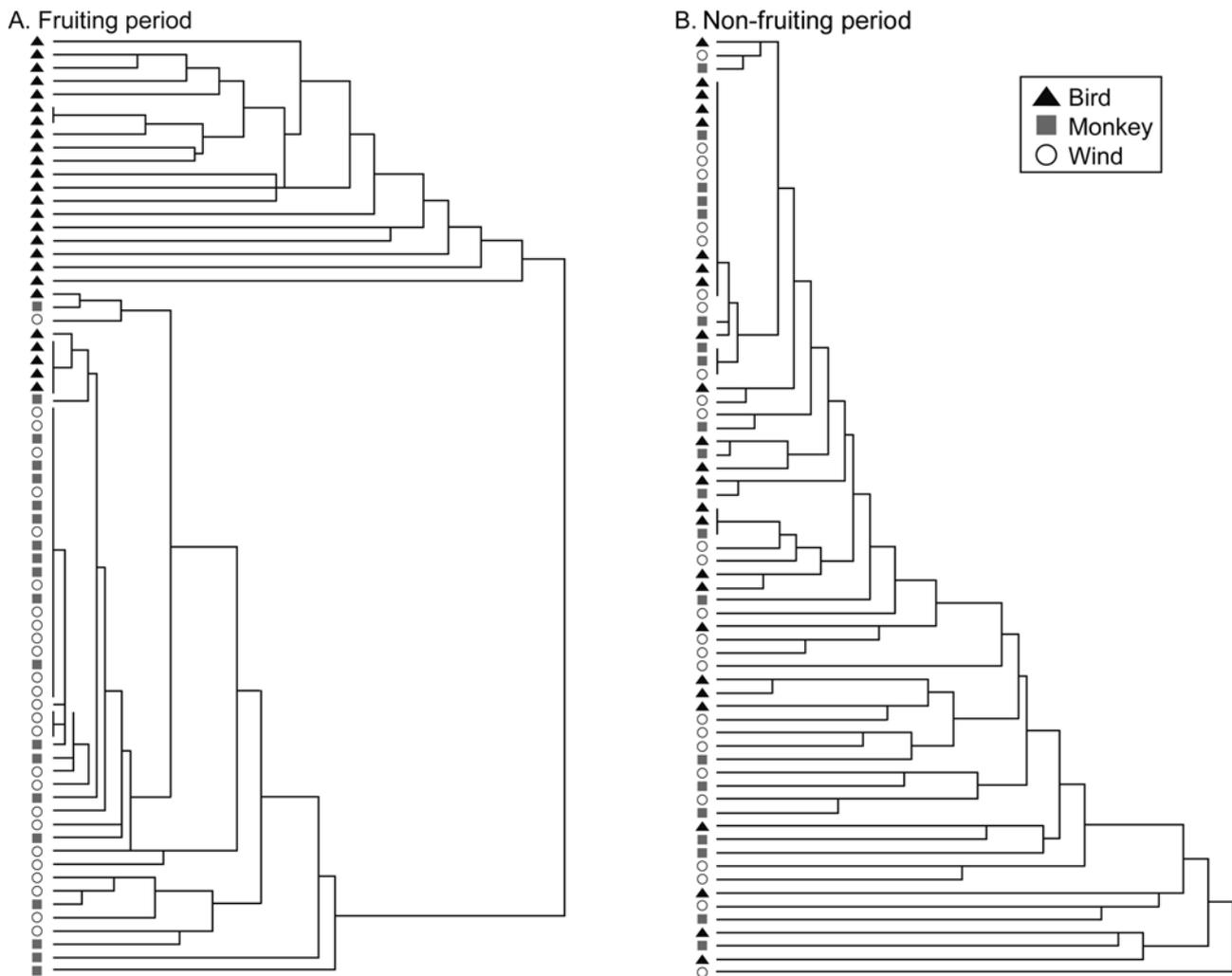


Fig. 2A, B Results of cluster analyses using Ward's average clustering methods to group 77 trees based on species composition of seed recorded from seed traps. All conspecific seeds and species of seed with less than five records were excluded from this cluster.

Triangle bird-dispersed tree species; *square* monkey-dispersed tree species; *circle* wind-dispersed tree species. **A** Data represent only the fruiting period of the individual trees. **B** Data represent only the non-fruiting period of the individual trees

seeds to fruiting bird-dispersed trees, such dispersal only results in a 5–15% increase in the rate of seed deposition. The density of seeds to which predators respond is unknown, and a 5–15% increase may or may not have an effect on the probability of seed survival and establishment.

Our results also demonstrate that bird-dispersed species of seed are likely to be deposited together in relatively predictable suites of species under the fruiting trees at which birds feed. Though immigrant seeds have been effectively removed from the competitive environment of their parent trees, they are deposited against a background of high seed density at a non-conspecific tree. As discussed above, high seed densities, regardless of species or seed source, could increase the risk of seed or seedling mortality if seed predators are generalists, essentially negating the competitive advantage of being dispersed away from its own parent canopy. On the other hand, suites of species could recruit together forming predictable clumps of bird-dispersed species in the forest. We are

aware of no studies that have examined the interactions among seed species that are co-dispersed and the effects of the background seed densities on seed fate and seedling recruitment.

Large birds and monkeys create distinct spatial patterns of seeds they disperse. The fate of dispersed seed depends on a combination of post-dispersal factors, including overall seed density, competitive ability of seedlings, and the relative attractiveness of seeds and seedlings to predators and herbivores. The degree to which the distribution patterns of co-dispersed tree species are clumped is also determined by a combination of these factors. We emphasize the need for empirical studies specifically designed to address the consequences of spatially contagious and diffuse dispersal patterns for community dynamics.

Acknowledgements We are grateful to the Ministry of Environment and Forests, Republic of Cameroon, for permission to work in the Dja Reserve. Financial and logistical support were provided by ECOFAC Cameroon, the NYZS/Wildlife Conservation Society, the EPA STAR Fellowship #U-915665-01-0, the Center for Tropical Research at San Francisco State University and the NIH Office of Research on Minority Health grant # 5 P20 RR11805. For dedicated field assistance we are indebted to D. Amiezeh, S. Hansen, S. Joe, P. Krushelnycky, K. Lucas, J. Mann, B. Martinez, C. Nishida, R. Sama, A. Scie, C. Stickler and S. Wahaj. Comments from K. Holder, D. Levey, W. Rendell, E. Schupp, H. Slabbekoorn, T. Smith, and two anonymous reviewers greatly improved this manuscript. We wish to acknowledge the additional support and contributions of B. Curran and J-P. Vautherin.

References

- Augsburger CK (1984) Seedling survival of tropical tree species: interactions of dispersal distance, light gaps and pathogens. *Ecology* 65:1705–1712
- Augsburger CK, Kelly CK (1984) Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia* 61:211–217
- Augsburger CK, Kitajima K (1992) Experimental studies of seedling recruitment from contrasting seed distributions. *Ecology* 73:1270–1284
- Blake JG, Loiselle BA (1992) Fruits in the diets of Neotropical migrant birds in Costa Rica. *Biotropica* 24:200–210
- Chapman CA, Wrangham RW, Chapman LJ, Kinnard DK, Zanne AE (1999) Fruit and flower phenology of two sites in Kibale National Park, Uganda. *J Trop Ecol* 15:189–211
- Charles-Dominique P (1986) Inter-relations between frugivorous vertebrates and pioneer plants: *Cecropia*, birds and bats in French Guyana. In: Estrada A, Fleming TH (eds) *Frugivores and seed dispersal*. Junk, Dordrecht, The Netherlands, pp 119–135
- Clark CJ (2001) Frugivore influence on patterns of seed rain, seed shadows and forest structure. Thesis. San Francisco State University, San Francisco, Calif., USA
- Clark CJ, Poulsen JR, Parker VT (2001) The role of arboreal seed dispersal groups on the seed rain of a lowland tropical forest. *Biotropica* 33:606–620
- Clark DA, Clark DB (1984) Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *Am Nat* 124:769–788
- Condit R, Hubbell SP, Foster FB (1992) Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. *Am Nat* 140:261–286
- Duncan RS, Chapman CA (1999) Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecol Appl* 9:998–1008
- Forget P-M (1993) Post-dispersal predation and scatterhoarding of *Dipteryx panamensis* (Papilionaceae) seeds by rodents in Panama. *Oecologia* 94:255–261
- Forget P-M, Sabatier D (1997) Dynamics of the seedling shadow of a frugivore-dispersed tree species in French Guiana. *J Trop Ecol* 13:767–773
- Fragoso JMV (1997) Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. *J Ecol* 85:519–529
- Fragoso JMV, Huffman JM (2000) Seed-dispersal and seedling recruitment patterns by the last Neotropical megafaunal element in Amazonia, the tapir. *J Trop Ecol* 16:369–385
- Gauch HG (1982) *Multivariate analysis in community ecology*. Cambridge University Press, Cambridge, UK
- Godoy JA, Jordano P (2001) Seed dispersal by animals: exact identification of source trees with endocarp DNA microsatellites. *Mol Ecol* 10:2275–2283
- Guimaraes Vieira IC, Uhl C, Nepstad D (1994) The role of the shrub *Cordia multispicata* Cham. as a ‘succession facilitator’ in an abandoned pasture, Paragominas, Amazonia. *Vegetatio* 115:91–99
- Hardesty BD, Parker VT (2003) Seed rain of a central African tropical forest. *Plant Ecol* 164:49–64
- Herrera CM (1984) A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. *Ecol Monogr* 54:1–23
- Holbrook K, Smith TB (2000) Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. *Oecologia* 125:249–257
- Howe HF (1989) Scatter- and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia* 79:417–426
- Howe HF, Smallwood J (1982) Ecology of seed dispersal. *Annu Rev Ecol Syst* 13:201–228
- Hutchinson HM, Dalziel D, Hepper FN (1963) *Flora of West Tropical Africa*, 2nd edn. Crown Agents, Millbank, London
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528
- Janzen DH (1986) Mice, big mammals, and seeds: it matters who defecates what where. In: Estrada A, Fleming TH (eds) *Frugivores and seed dispersal*. Junk, Dordrecht, The Netherlands, pp 251–271
- Janzen DH, Miller GA, Hackforth-Jones J, Pond CM, Hooper K, Janos DP (1976) Two Costa Rican bat-generated seed shadows of *Andira inermis* (Leguminosae). *Ecology* 57:1068–1075
- Jongman RHG, ter Braak CJF, van Tongeren OFR (1995) *Data analysis in community and landscape ecology*. Cambridge University Press, Cambridge
- Jordano P (1992) Fruits and frugivory. In: Fenner M (ed) *Seeds: the ecology of regeneration in plant communities*. Commonwealth Agricultural Bureau International, Wallingford, UK, pp 105–156
- Jordano P (2000) Fruits and frugivory. In: Fenner M (ed) *Seeds: the ecology and regeneration of plant communities*. CAB International, Oxon, UK, pp 125–166
- Julliot C (1997) Impact of seed dispersal of red howler monkeys *Alouatta seniculus* on the seedling population in the understory of tropical rain forest. *J Ecol* 85:431–440
- Kruijger DL, Opdam M, Théry M, Bongers F (1997) Courtship behavior of manakins and seed bank composition in a French Guianan rain forest. *J Trop Ecol* 13:631–636
- Laclavère G (1980) *Atlas of the United Republic of Cameroon*. Editions Jeune Afrique, Paris, France
- Laman TG (1996) *Ficus* seed shadows in a Bornean rain forest. *Oecologia* 107:347–355
- Lambert JE (1999) Seed handling in Chimpanzees (*Pan troglodytes*) and Redtail monkeys (*Cercopithecus ascanius*): implications for understanding Hominoid and Cercopithecine fruit-processing strategies and seed dispersal. *Am J Phys Anthropol* 109:365–386
- Letouzey R (1970) *Manuel de botanique forestière*. CTFT, Nogent sur Marne, France
- Loiselle BA (1990) Seeds in droppings of tropical fruit-eating birds —importance of considering seed composition. *Oecologia* 82:494–500
- Loiselle B (1996) Spatial and temporal variation of seed rain in a tropical lowland wet forest. *Biotropica* 28:82–95
- McDonnell MJ, Stiles EW (1983) The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* 56:109–116
- Nathan R, Muller-Landau HC (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol Evol* 15: 278–285
- Olupot W, Chapman CA, Waser PM, Isabirye-Basuta G (1997) Mangabey (*Cercocebus albigena*) ranging patterns in relation to fruit availability and the risk of parasite infection in Kibale National Park, Uganda. *Am J Primatol* 43:65–78

- Poulsen JR, Clark CJ, Smith TB (2001) Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. *J Trop Ecol* 17:787–808
- Poulsen JR, Clark CJ, Connor EF, Smith TB (2002) Differential resource use by primates and hornbills: implications for seed dispersal. *Ecology* 83:228–240
- Schupp EW, Fuentes M (1995) Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* 2:267–275
- Schupp EW, Milleron T, Russo SE (2002) Dissemination limitation and the origin and maintenance of species rich tropical forests. In: Levey DJ, Silva WR, Galetti M (eds) *Seed dispersal and frugivory: ecology, evolution and conservation*. CABI, Wallingford, Oxfordshire, UK
- Silva JMC, Uhl C, Murray G (1996) Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. *Conserv Biol* 10:491–503
- Sneath PHA, Sokal RR (1973) *Numerical taxonomy*. Freeman, San Francisco
- Tailfer Y (1989) *La forêt dense d’Afrique centrale. Identification pratique des principaux arbres*. CTA, Paris
- Tewksbury JJ, Nabhan GP, Norman D, Suzan H, Tuxill J, Donoman J (1999) In situ conservation of wild chilies and their biotic associates. *Conserv Biol* 13:98–107
- Wenny DG (2000) Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecol Monogr* 70:331–351
- Wenny DG, Levey DJ (1998) Directed seed dispersal by bellbirds in a tropical cloud forest. *Proc Natl Acad Sci USA* 95:6204–6207
- Whitney KD, Fogiel MF, Lamperti AM, Holbrook KM, Stauffer DJ, Hardesty BD, Parker VT, Smith TB (1998) Seed dispersal by *Ceratogymna* hornbills in the Dja Reserve, Cameroon. *J Trop Ecol* 14:351–371